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THE EXPLOITATION OF
NATURAL ANIMAL POPULATIONS

THE BRITISH ECOLOGICAL SOCIETY

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THE EXPLOITATION OF NATURAL ANIMAL POPULATIONS

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PREFACE

For the theme of the Second Symposium of the British Ecological Society, the Programme Planning Committee decided upon some aspect of animal population ecology. 'The exploitation of natural animal populations' was finally chosen as a subject likely to bring together those interested in a wide variety of animals and both theorists and practical ecologists.

In all, 130 ecologists, from ten countries, attended, and these included not only those concerned with exploited animals but also a number interested in other fields of population ecology such as economic entomology. The discussions benefited greatly as a result.

Through the kindness of the Council of the Durham Colleges in the University of Durham, the meeting was held in Durham and the formal sessions took place in the Applebey Lecture Theatre. Most of the participants were accommodated in St Mary's College and Grey College, where much informal discussion took place. On the evening of 28th March a series of films relevant to the theme of the meeting were shown, but proceedings really began on the following morning when Professor Cragg, in his dual capacity as host and President welcomed the participants and introduced the Symposium.

Invited papers were read during the three days that followed. These have been printed here in the order in which they were delivered, and in substantially the same form, although the printed versions are naturally rather longer and contain more supporting detail than could be presented verbally. All the papers were followed by discussions, and there were also three sessions devoted to discussion alone: together these occupied about half the time of the Symposium. The records of the discussions are based on notes made at the time and later edited and somewhat shortened, and all these have been approved by the contributors before publication.

In any Symposium of this kind many people assist in one way or another, and the Society, the organizers, and the editors are grateful for all the help they have received. The Council and members of staff of the Durham Colleges, and in particular Professor Cragg, contributed greatly to the enjoyment of the meeting by their hospitality and efficient share in the organization. We received invaluable co-operation and help from people consulted in the planning stage, and from the contributors, including those who opened

discussions. We are also grateful to the sponsoring organizations who made it possible for several speakers and participants to attend the Symposium.

· E. D. LE CREN

M. W. HOLDGATE

INTRODUCTION

Although most human communities have now passed from a purely hunting economy to a pastoral and agricultural one, the capture of wild or semi-wild animals is still an important activity. Fish provide a substantial part of the protein eaten by many peoples, and predominate in the diet of some, and molluscs, birds, land mammals, whales and seals all contribute their quota. It is common knowledge that many of these important natural resources have been grossly over-exploited in the past, and that the manner in which they are now harvested often leaves much to be desired. Ultimately the rational management and development of wild populations may lead to much fuller human control and near-domestication, but for the foreseeable future we are likely to continue to rely on wild animals for some of our food and raw materials.

In addition, the capture of certain wild animals or fish has a recreational value, and this kind of sport has assumed a considerable political and economic importance in the more highly developed countries. It is not surprising therefore that there has been considerable economic and popular support for the study of exploited animals. Applied biologists, whether working on game animals or on species which are important sources of food and raw materials, like fish, whales, seals and certain sea birds, have been responsible for much of the research and many of the advances in population ecology. In this they have been aided by economic entomologists concerned with agricultural pests and disease vectors. To the contributions of these ecologists must be added those made by mathematicians and theorists and those resulting from the study of experimental populations in the laboratory. All these approaches have been concerned in one way or another with the dynamics of animal populations.

Although the exploitation of a particular species or group of animals involves many specific and practical problems, all such exploitations are intimately bound up with fundamental population ecology. This interaction between the specific and the general can be seen in the papers in the first three parts of the Symposium that deal with particular animals such as herrings, cockles, grouse, partridge, duck or whales. Some of the population factors involved seem to be peculiar to the type of animal: others are of wider relevance, and an attempt is made, especially in the discussions, to discover and define these fundamental points of similarity and difference.

The different approaches that have been adopted by the workers on different groups, the different population parameters they try to measure, and the different terminology they use, all tend to impede the fruitful comparison of results obtained for various kinds of animals. These difficulties of comparison will be apparent to any reader, and are themselves considered in the discussions. For example, it is not easy to observe marine fish in their natural habitat and sea fisheries deal with a bulk product largely assessed by weight. It is not surprising that fishery biologists have tended to concentrate their approach on the mass population dynamics of fish and their food. Conversely it is easier to observe the behaviour of individual birds or land mammals than to count them and obtain statistics on mortality rates and the like, so ornithologists and mammalogists have tended to build up their information from individual field observations rather than the statistical analysis of large samples. Insect ecologists find both approaches beset by difficulties and have to contend with special problems of their own: for example the absence of overlap in the generations of many insect species, which makes their numbers tend to fluctuate rather violently. Environments and populations alike differ in their stability, and the extent and consequences of these differences are argued about in several of the discussions.

Comparative population dynamics also suffers from a lack of the necessary data, and some of this deficiency has arisen because biologists have not always known what the essential parameters are. A detailed, comparative analysis of population parameters within one group is one approach which may lead to a clearer recognition of what data are vital, and hence to a simplification of practical problems of observation. Holt attempts such an analysis for fish.

A resilience to artificial population changes seems to be a prerequisite if a species is to be exploited successfully. Although some resilience may be a characteristic of all species, not all have been able to contribute a substantial yield to man and yet show no long-term decline in abundance. The reactions of populations to exploitation can, however, be used as evidence as to whether or not all populations possess natural regulatory mechanisms, and should throw light on how such mechanisms operate. Nikol'skiĭ reviews the features of fish populations which can be considered as adaptive and compensatory, and several other papers contribute evidence on population regulation. The relative importance of factors intrinsic to the population and extrinsic environmental factors in the control of populations is still a moot point, as is apparent from the discussions.

Progress in the understanding of population dynamics in relation to exploitation has been much assisted by the use of mathematical models. As is discussed on p. 379, some form of model is essential for almost any advance,

but the true mathematical model may produce, by mathematical argument, deductions and implications unlikely to have been discovered by other means. Such deductions can then be tested against reality, or used to make practical recommendations and forecasts. The latter has been accomplished successfully for fish populations, and some of the main approaches to the design and use of such models are discussed by Gulland, and in a more general way by Watt.

Another approach to understanding through simplification is by the use of laboratory populations. Here environmental complexity can be reduced to a minimum, and the combination of model and experiment used to test theory as, for example, Slobodkin uses experiments with *Daphnia* and *Hydra* to investigate the efficiency of exploitation.

The ultimate aim for rational human use of a population must be to obtain an efficient maximum (and economic) long-term yield. The simpler fishery models are concerned only with the efficient utilization of the fished stock, but more sophisticated and comprehensive considerations must include the whole population in all life stages and eventually the whole biota. Long-term trends and the factors controlling the numbers of young fish are described by Beverton, while Le Cren discusses the efficiency of the reproductive and recruit-rearing processes.

In most population investigations there comes a time when consideration has to be extended beyond intra-specific factors to inter-specific relationships and to the environment. Little is known about the balance of closely related species and how it may be affected by the exploitation of one or more of them, but Lindström and Nilsson contribute a paper on the probable competitive interactions of whitefish species in the same lake. In some situations man finds himself competing with predators for the same prey species: such a situation would arise if African plains game were cropped as a major protein source in the manner foreshadowed in Pearsall's paper. Such a conflict can produce practical complications when the predators are themselves of aesthetic or commercial value to man. The grey seal is considered by some naturalists to be worthy of protection, but Rae regards it as a serious predator on valuable fish. Lockie attempts an assessment of the relative importance of man and the grey seal as predators of salmon, and Shearer illustrates one way out of such conflicts by describing some practical measures to protect salmon nets from seals. The discussion following these papers seems to indicate that more real information on the population parameters of both seals and fish is needed before judgement can be given.

One might think that nature conservation would invariably involve protection against exploitation for the species or community that is being preserved, but in practice some degree of cropping is often essential,

especially where natural population controls have been artificially removed. Pearsall considers that the rational management and exploitation of wild animals is potentially the most efficient form of land use in the African plains, where present agricultural and pastoral practises tend to destroy environmental fertility.

The economic and practical importance of wild animals provides abundant justification for the study of their populations by ecologists, but there are also other reasons. The large scale on which exploited animals are taken provides the biologist with abundant samples for study, and when some record has been kept of the catches, invaluable statistical information about secular changes in abundance may be available. An ecologist studying other organisms, who has to collect his own samples every week for fifty years may well feel envious! Furthermore, observation alone of a relatively stable population will not usually lead to an understanding of its regulatory mechanism: some kind of disturbing influence is needed. Climatic trends or year to year variations may be useful, but artificially induced disturbances can be much more revealing. Exploitation by man is such a disturbance and can often constitute an experiment in population dynamics. (Paradoxically, it was the *cessation* of fishing in the North Sea during the two world wars that revealed many of the effects of exploitation on fish populations.)

The exploitation of animals thus provides ecologists with financial support to work on a wide range of animal species, abundant material to study, and experiments to observe. The following pages may be offered as a sample of what population ecologists have made of these opportunities, and how far they have progressed towards an understanding of the scientific basis of the response of natural animal populations to exploitation.

THE POPULATION DYNAMICS OF DIFFERENT KINDS
OF EXPLOITED ANIMALS

PROBLEMS CONCERNING THE POPULATION DYNAMICS OF THE ATLANTIC HERRING (*CLUPEA HARENGUS* L.) WITH SPECIAL REFERENCE TO THE NORTH SEA

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INTRODUCTION

For centuries the fisheries for herring (*Clupea harengus* L.) have contributed a major share of the total fish harvest in European waters. In the years 1950-5, the annual herring yield for all European countries averaged about two million metric tons, which was approximately one-third of the yield of about six million tons of all species. The events in these fisheries are, therefore, of major importance to the herring industries and the economies of the major fishing nations of Europe, including the United Kingdom.

The regions from which these harvests are taken in the north-east Atlantic range from the north coast of Iceland and the Barents Sea in the north to the English Channel in the south, and from the west coast of Iceland in the west to the Baltic in the east. However, two areas are of outstanding importance; the west coast of Norway and the North Sea. The first of these is the centre of the Norwegian winter fishery, between January and April, which reached peak yields of over a million metric tons in the years 1950-5; the second is the centre of a great international fishery, pursued throughout the year by the herring fleets of Germany, Holland, the United Kingdom, Sweden, Denmark, Belgium, France, Poland and the U.S.S.R., which together produced about three-quarters of a million metric tons annually in the years 1950-5.

The results of long-term biological investigations of the herring exploited in these regions have established that these two major fisheries are based on different herring 'tribes'. The Norwegian fishery exploits the oceanic 'Atlanto-Scandian', spring spawning 'tribe' which has its spawning grounds on the coastal banks along the Norwegian west coast, and its main adult feeding grounds in the deep, oceanic region between Norway and Iceland. The North Sea fishery, on the other hand, is centred principally on a summer-autumn spawning 'tribe' which has its spawning grounds on banks in the

northern, central and southern regions of the North Sea, and whose distribution is bounded by the continental slope in the north and east. Only in the 'fringe' region of the northern North Sea has any substantial overlap in the distributions of these tribes been detected in the forty to fifty years of intensive herring research in this area. Therefore, for fishery assessment purposes, the 'Atlanto-Scandian' tribe can be discounted as a substantial source of supply for the North Sea herring fishery, and as a factor governing the fluctuating yields from it, and vice versa, at least during the present century. The approximate boundaries between the two tribes and the region of overlap between them are shown in Fig. 1.

Throughout their long histories, these two fisheries have been characterized by marked long- and short-term fluctuations and trends in landings. The most striking of these have been the 'herring periods' of the Norwegian (and Swedish west coast) fishery; they have taken the form of alternate periods of high and low yield, which can be traced in the Norwegian and Swedish statistical records, back to at least the sixteenth century. The most recent 'low' in the Norwegian fishery occurred towards the end of the nineteenth century, when, between 1860 and 1875, the annual landings fell from about one million hectolitres to 200 hectolitres. An equally large and rapid rise took place early in the twentieth century, and by 1913 the annual yield had risen again to over a million hectolitres.

Marked fluctuations are also reflected in the early and later catch records of the North Sea, and neighbouring herring fisheries. In some notable instances (e.g. Firth of Forth; western English Channel) these have been of sufficient magnitude, and the period of low yield sufficiently sustained to cause the complete collapse of a traditional fishery, while in others they have resulted in sharp changes in the 'success' of the fisheries.

This 'property' of the European herring fisheries had a marked and lasting influence on the attitude of early and later herring scientists to the relative importance of natural and man-made factors in governing the yield from them. Man-made influences (i.e. fishing) tended to be regarded as of relatively small importance. This attitude persisted during the period of decline of many of the important demersal fisheries, and the rapid growth of quantitative studies of the dynamics of the exploited demersal stocks in the inter-war and early post-war years. Throughout this period the European herring stocks were generally regarded as underfished, but subject to wide natural fluctuations in abundance, distribution and habits. As a consequence, the kind of scientific data collected on the herring fisheries remained largely qualitative in nature.

Since the second world war, however, disturbing events in some components of the North Sea fishery have caused an urgent reappraisal to be

made of this long standing viewpoint and attention to be paid to the population dynamics of the exploited herring stocks. In this period major changes have taken place in the nature and size of the herring fisheries in the North

FIG. 1.—Approximate boundaries and area of overlap between North Sea and Atlanto-Scandian herring tribes.

Sea; the British component of this fishery at East Anglia has declined alarmingly; changes have taken place in the abundance and composition of the exploited stock, and changes have been detected in certain of the bio-

logical features of the stocks. In this paper, these events are described, and the problems involved in interpreting them are discussed.

CHANGES IN THE NORTH SEA HERRING FISHERY SINCE 1900

The post-war changes in the North Sea fishery are best viewed as part of a longer term development, the main features of which are illustrated in Figs. 2 and 3.

FIG. 2.—Yields by countries and total yields from the North Sea herring fisheries 1903–56.

At the beginning of the twentieth century, almost the whole of the North Sea herring landings were taken by two countries, the United Kingdom and the Netherlands, with the United Kingdom taking about three-quarters of the total. In both countries the method of capture was almost exclusively by drift net, and the fishery was centred in two main localities: (1) in the

FIG. 3.—The distribution of herring fishing by drift net and trawl in the North Sea in the periods prior to 1914, in the inter-war years and since 1945.

north-western North Sea between the Scottish east coast and the Shetlands, where the fishery took place between May and September on feeding, maturing fish; and (2) off the East Anglian coast and southwards to the entrance to the English Channel. This latter fishery took place principally in October and November on mature fish on passage to their spawning grounds off the Belgian and French coasts.

In the period up to 1914, the total landings from these fisheries grew, especially at East Anglia, to reach about 700,000 metric tons in 1913.*

The drift net fisheries again grew rapidly after the war time respite between 1914-18, and in the early post-war years the British fishery once more provided the greater part of the total North Sea catch, but at a lower level than pre-war. However, in the later inter-war years, important developments in the North Sea herring fisheries took place, which changed the picture radically. The most striking of these was the growth of the German fishery. This grew from average annual landings of less than 50,000 tons up to 1925 to over 250,000 tons in 1937. In this period the British landings dropped substantially, and in 1937 were approximately the same as the German landings.

Unlike the British fisheries, which persisted with the drift net, fished from relatively small, low-powered vessels, the German fishery was prosecuted principally by trawl, fished from relatively large, high-powered craft. Its growth also resulted in an extension of the areas fished; the 'Fladen' ground in the northern North Sea and the Dogger Bank region became important North Sea herring fishing areas (Fig. 3). In this period, both the traditional British drift net fisheries and the German trawl fishery were based almost exclusively on adult (two year old and older), good quality herring, for human consumption.

As shown in Fig. 2, the total landings of herring by all countries fluctuated widely, but in the inter-war years they grew to about the same level in the late 1930's as in the immediate pre-war period. In both of these periods, however, the published landing statistics are underestimates of the total catch, due to substantial dumping of unsold catches in years of high production in the British fishery. Although statistics of this discarded portion of the catch are unavailable, verbal reports from Scottish port authorities place the portion as high as 10-15 per cent of the Scottish catch in some of the years of high yields.

Herring fishing in the North Sea was again drastically reduced during the second world war, but it grew rapidly again after 1945. The subsequent years were marked by:

* The North Sea 'tribe' was also fished in this period in the Bohuslan fishery off the west coast of Sweden. These landings are not included in Fig. 2.

- (1) A rapid redevelopment of the German trawl fishery for adult herring to reach landings of over 300,000 tons in 1955.
- (2) A striking decline in landings from the British drift net fisheries to less than 100,000 tons in 1955.
- (3) The expansion of trawl fisheries for adult herring based on other European countries besides Germany, notably from Sweden, the Netherlands, Belgium, France and, more recently, Poland.
- (4) A further extension of the regions fished in both the northern and southern North Sea. In particular, an intensive trawl fishery for herring developed after 1952 on the Southern Bight spawning grounds off the Belgian and French coasts (Fig. 3).
- (5) An overall rise in total landings from these 'adult' fisheries to over 700,000 tons in the period 1952-5, which was rather more than the highest recorded landings in the earlier periods. In this period, however, the discarded portion of the catch was very small, so it is likely that the peak annual catches of adult herring in this period were about the same as in the earlier periods.

In addition to these developments, an intensive fishery for adolescent 'pre-recruit' herring (fish mostly less than two years of age), for industrial purposes, developed after 1950 from Denmark and Germany on the 'nursery ground' (Bløden) to the south and east of the Dogger Bank (Figs. 2 and 3). The landings from this fishery rose from about 5,000 tons in 1950 to over 100,000 tons in 1955* or to approximately one-seventh of the total North Sea 'adult' herring catch.

It is evident, therefore, that in the years since 1920 extensive changes have taken place in the nature of the North Sea herring fisheries. The trawl has superseded the drift net as the principal method of capture; the fisheries have extended their range in time and space; the herring have become exploited from a younger age, and the contributions to the total catch, by the participating countries, has changed substantially. It is in the light of these complex fishery events that the decline in the British drift net fisheries must be viewed.

DECLINE OF THE BRITISH DRIFT NET FISHERIES

Throughout this period of change the British fisheries in the north-western North Sea in summer and off the East Anglian coast in autumn remained traditional drift net fisheries for good quality herring for human consumption (the trawl fisheries for herring from the Humber and Scottish ports had ceased completely by 1952). As shown in Fig. 2, their combined landings dropped from an average level of about 450,000 tons in the years up to 1914,

* These figures are not included in the 'total' North Sea landings in Fig. 2. Those refer only to the 'adult' herring fisheries.

to about 260,000 tons in the inter-war years, and to less than 150,000 tons in the post-war years up to 1957.

In Fig. 4 are given the landings and crude effort statistics of these two fisheries respectively since 1924, the first year for which these effort data are available. The units of effort used are the number of arrivals at port, which

FIG. 4.—Statistics of yield (in crans) and fishing effort (number of landings) for the British drift net fisheries in the north-western North Sea and Southern Bight (East Anglia) respectively (1922–57).

for these fisheries provide a rough measure of the total number of shots made (recent, more detailed effort statistics for the Scottish fishery show that on average, 'arrivals' underestimate 'shots' by about 3 per cent).

These data show that the catch trend in the total British fishery was followed in both regions; further, they demonstrate that the main trends in catch were due principally to a steady fall in the size of the drift net fleets in the two areas and in the effort exerted by them. This was due largely to economic factors, particularly the loss of export markets for cured herring and the diversion of part of the Scottish dual-purpose fleet to Danish-seining for demersal species. However, a more detailed inspection of the statistics of these fisheries, and of the composition of the catches, shows that other important changes have taken place since the second world war, especially at East Anglia. The main ingredients of these changes are described below.

THE EAST ANGLIAN FISHERY

This fishery, and those of other countries (principally the Netherlands and Germany), in this region, is centred in October and November, on 'mature' herring (principally maturity stages IV and V), on passage to their spawning grounds off the Belgian and French coasts. Long-term studies of this fishery, undertaken principally at the Fisheries Laboratory, Lowestoft, have shown that the age composition of the exploited shoals differs between October and November. In October, the grounds are occupied chiefly by the youngest 'recruit' age-groups (three- and four-year-olds), while in November, these are replaced by the older 'adult' age-groups, mainly between five and ten years of age (Hodgson, 1934, 1957; Cushing & Burd, 1957). These two components are further exploited as spawning and spent fish off the Belgian and French coasts in the period November-January by the trawl fisheries of continental countries (principally Germany, France, the Netherlands, Belgium) which have developed since the war. After spawning they move northwards from the Southern Bight and spend the spring and summer feeding period in the regions to the north of the Dogger Bank (Cushing, 1955). They move southwards once more as adults in late summer and arrive on the East Anglian grounds towards the end of October. The 'recruit' component of the stock invades the East Anglian area in early October from the north and east.

The post-war changes in the size and composition of the catches in the East Anglian fishery have been investigated in detail at the Fisheries Laboratory, Lowestoft, and the results are reported by Hodgson (1956, 1957), Cushing & Burd (1957) and Cushing (1958, 1959); therefore only a summary of them is given here.

In addition to the decline in the total catch and effort already mentioned, the following important changes have taken place:

(1) Since 1949 there has been a marked drop in the catch per unit of effort, especially in November. Whereas the October catches have fluctuated widely,

FIG. 5.—Changes in catch per unit effort in the British north-western North Sea and East Anglian fisheries respectively. North-western North Sea data expressed as crans per landing; East Anglian as thousands of fish per landing.

but have shown no downward trend, at least up to 1955, the November figures reveal a steady decline since 1949. This is shown in Fig. 5, from data contained in Cushing *et al.* (1959).

(2) At the same time there was a marked change in the size and age composition of the catch. This consisted of:

(a) A change in the relative abundance of three- and four-year-old fish in the catch. Whereas in pre-war years and post-war up to 1951, four-year-olds were, on average, about twice as abundant as three-year-olds of the same year-class, after 1951 the three-year-olds become the most abundant age-group and the ratio of numbers was reversed.

(b) A reduction in the abundance of the age-groups older than four. This was very marked after 1952, and in 1955-7 the average abundance of these age-groups was only about a quarter of the pre-1952 level. These changes are illustrated in Fig. 6.

(3) Corresponding with the decrease in abundance of the older age-groups after 1951 there was an increase in the apparent total mortality rate amongst the fully recruited age-groups. These data are shown in Fig. 7.

(4) Associated changes were also detected in the mean lengths of the exploited age-groups. These are shown in Fig. 8, which shows a greater mean length for age post-war than pre-war and a further marked increase after 1949.

It is evident, therefore, that the overall change was a complex one, embracing the pattern of recruitment to the fishery and the abundance and loss rate of the fully recruited age-groups.

These phenomena are not confined to the British East Anglian fishery; they have also been detected in the drift net and trawl fisheries of other countries in the southern North Sea (Ancellin, 1955; Krefft, Schubert & Sahrhage, 1955; Zijlstra, 1957).

During this period of major decline and change in the East Anglian fishery, the total landings of herring from the Southern Bight increased. This was due to the rapid growth of trawling on the spawning grounds after 1951. It increased from between 150,000-180,000 tons in the period 1946-50, to about 250,000 tons in 1953 (Cushing & Burd, 1957, p. 20).

THE NORTH-WESTERN NORTH SEA FISHERY

The British drift net fishery in the north-western North Sea between May and early September is centred in two main regions: (1) in the outer reaches of, and eastwards from, the Moray Firth, and off the Scottish east coast (the Buchan fishery); (2) to the east of the Shetlands (the Shetland fishery). Of these, the Buchan fishery is now the largest, and has produced over 80 per cent of the total Scottish post-war herring catch in the north-western North Sea. Drift net and trawl fisheries of other European countries are also conducted in this region, the most important being the German, Swedish, Dutch, Belgian and Polish trawl fisheries on the 'Fladen' and 'Gut' grounds, and the Dutch and German lugger fisheries (Fig. 3).

The herring concentrations on which these fisheries are based are composed during the period May-July of feeding, maturing herring, which later spawn either on grounds off the Scottish east coast in August-September, on the Dogger Bank in September-October, or in the Southern Bight in Novem-

FIG. 6.—Percentage age compositions and abundance indices of three, four and older age groups in the East Anglian and Buchan pre-spawning fisheries respectively (1930-8 and 1947-57). East Anglian data taken from Cushing, 1959.

ber–December. Small concentrations of Atlanto-Scandian herring, mostly of age-groups three to five also contribute to the fished stock in the northerly regions to the east of the Shetlands. This fishing region therefore constitutes a

FIG. 7.—Estimated total mortality rates of year-classes fished in the East Anglian and Buchan pre-spawning fisheries in the periods 1933–8; 1947–57. East Anglian values estimated from Table 1 in Cushing, 1959. (Zero values represent negative estimates).

major feeding ground for the main body of herring which subsequently spawn in different parts of the North Sea.

The 'adult' components of these concentrations invade the north-western North Sea from the east and south in May, and remain in this region as

FIG. 8.—Mean lengths of three-, four- and five-year-old herring in the East Anglian and Buchan fisheries respectively, 1932-8; 1947-59. East Anglian values taken from Burd, 1958.

feeding, maturing fish until the onset of spawning in August and September. Then a movement takes place southwards to the spawning grounds; a proportion of the stock spawns off the Scottish east coast in August and September, while others move southwards to spawning grounds on the Dogger Bank and Southern Bight. After spawning, these herring move to the deeper, northern regions, where they remain prior to re-invading the north-western North Sea in the following spring.

The 'recruit' components appear on the Buchan fishing grounds in April and May. They subsequently spread over these grounds in June and July, but do not usually appear in abundance on the Shetland fishing grounds in that year. Although the nursery areas from which the 'recruit' component is derived are not fully known, it is probable that part of it originates from the major nursery area to the south and east of the Dogger Bank and part from the juvenile concentrations off the Scottish east coast.

It is evident from the above that the Scottish fishery can be subdivided into three components, which differ with respect to the composition and biological state of the herring concentrations which they exploit. These are: (1) The Buchan 'pre-spawning' fishery, which takes place between May and July, and is centred on the feeding, pre-spawning concentrations of 'recruit' and 'adult' herring.

(2) The Buchan 'spawning' fishery, which is pursued in August and early September on the banks off the Scottish east coast, and exploits the concentrations of early spawning herring, derived from the pre-spawning concentrations.

(3) The Shetland fishery, which, like the Buchan pre-spawning fishery, exploits the feeding, pre-spawning concentrations. Unlike the Buchan fishery, however, it is usually centred on concentrations of the 'adult' component.

The post-war changes in these fisheries have been described by Parrish & Craig (1957). They may be summarized as follows:

(1) The catch per unit of effort of the Buchan pre-spawning and spawning fisheries and the Shetland fishery did not decrease after 1950, as at East Anglia. In the Buchan fishery in fact it increased after 1951, while in the Shetland fishery it decreased sharply from a high immediate post-war level, but increased once more after 1954. These data are shown in Fig. 5.

(2) However, striking changes took place in the composition of the Buchan 'pre-spawning' fishery catches, resembling those observed at East Anglia (Fig. 6). There was: (i) a reversal of the three-year-old to four-year-old ratio after 1951, which corresponded in time with the change in ratio at East Anglia; (ii) a reduction in the catch per unit effort of the age-groups older than four after 1952. Between 1947 (the first post-war year for which age

data are available) and 1952, this fluctuated widely, being higher in 1952 and 1953 than in the preceding years, but between 1952 and 1957 it fell sharply to reach in 1957 a level less than a quarter of the 1947-52, and pre-war average; (iii) corresponding with this decrease, the apparent total mortality rate increased sharply after 1952, and remained at a relatively high level in subsequent years (Fig. 7); (iv) increases in mean length of the age-groups took place after 1949, similar to those observed at East Anglia. These were particularly large among the four- and five-year-olds (Fig. 8).

Therefore, although in this component of the north-western North Sea fishery, the period after 1950 was not characterized by declining unit catches as at East Anglia, similar changes took place in their composition.

In the Buchan 'spawning' and Shetland fisheries, these changes were less marked, but in both of them the unit catches of the older age-groups fell off after 1954, and the apparent total mortality rate increased.

Data from other countries fishing in the northern North Sea are less complete than those for the British fishery, but statistics and age compositions are presented for the German trawl fishery on the Fladen ground by Krefft, Schubert & Sarhage (1955) and Schubert (1957), and for the Belgian trawl fishery in the northern and central regions by Gilis (1957). Statistical data for the Dutch lugger and trawl fisheries in the north-western North Sea are also presented by Zijlstra (1959). As with the Buchan fishery, the data for these fisheries show no striking decrease in catch per unit effort in the period since 1950, but they exhibit the same general change in the composition of the catch, especially after 1954. The general phenomena are not, therefore, confined to the area exploited by the Buchan fishery, and are common to the major north-western North Sea fisheries.

INTERPRETATION OF CHANGES

The results presented above show that since the war, similar changes have taken place in the composition of the catches taken in the southern and northern North Sea fisheries and they can be identified as (a) a change in recruitment; (b) a decline in abundance and an increase in apparent total mortality rate amongst the fully recruited age-groups. These phenomena have together resulted in a marked decrease in the age and size composition of the exploited stock in both areas and a greater dependence of the fisheries on the recruit age-groups. These changes are therefore of great practical importance, and the principal question arising is whether they are the result mainly of man-made or natural influences.

In the remaining sections of this paper, the problems arising in answering this question are discussed in the light of available data for the northern and

southern North Sea herring fisheries and stocks. For convenience the two components of the change are discussed separately.

THE RECRUITMENT CHANGE

As shown in Fig. 6 the recruitment change in both regions resulted from an increase in the abundance of three-year-old herring in the catches rather than a decrease in abundance of fours. This increase was most marked in the north-western North Sea, where it more than compensated for the decrease in abundance of the older age-groups, and so gave rise to the relatively high unit catches after 1951. The abundance of four-year-olds, following this increase, remained at about the same level as before, in both regions.

It is appropriate to examine first whether this change was the result principally of man-made influences as postulated for the southern North Sea by Hodgson (1956, 1957), or whether it constitutes a natural change in the pattern of recruitment.

Hodgson attributes the reduction in the three- to four-year-old survival rate to the fishing mortality generated by the industrial fishery in the south-eastern North Sea, which grew rapidly from about 5,000 tons in 1950 to over 100,000 tons in 1955. He postulates that the faster growing component of each year class, which recruits the fisheries at three years of age are outside the area exploited by the industrial fishery, which is based, principally on the slower growing members, recruiting at four.

It is difficult however to reconcile this hypothesis with the available statistical and biological data. The following items are of particular relevance.

(1) Danish investigations show that the industrial fishery is centred principally on two-year-old herring (II Group) (Bertelsen & Popp Madsen, 1953-7; Cushing, 1959) which mostly leave this region at the end of their second year of life. In recent years, between 70-80 per cent of the exploited pre-recruit stock has been of this age.

(2) The biological characteristics of these pre-recruits are similar to those recruiting the adult fisheries at three years of age. Danish scientists (Popp Madsen, personal communication) have established a relation between the relative abundance of the smallest members of successive year-classes as two-year-old pre-recruits on the nursery grounds and as three-year-old recruits in the southern North Sea fisheries.

(3) The results of international tagging experiments on these pre-recruits, organized by the International Council for the Exploration of the Sea in 1957 and 1958 gave estimates of fishing mortality, generated by the industrial fishery, of approximately 14 per cent and 15 per cent respectively. Estimates of the loss rate using other methods (Cushing, 1959) are of the same order of

magnitude. This loss rate is much too small to account for the 'loss' of four-year-olds from adult stocks (Cushing, 1959).

Thus the evidence suggests that the recruitment change in both regions was not a direct consequence of the industrial fishery, but was the result of a natural change (Cushing & Burd, 1957; Cushing, 1959; Parrish & Craig, 1957). The main features of the mechanism of the change are considered to be as follows:

(1) The movement of herring from the nursery areas to deeper water is a function of size, which also governs the time of onset of first maturity. (The existence of a general biological relation between growth and first maturity in fish is discussed by Beverton & Holt (1959).)

(2) Since the war, and especially since 1949, the growth rate of the adolescent herring has increased, apparently as a result of an increase in the abundance of food (Cushing & Burd, 1957; Burd, 1958). In consequence, a greater proportion of each year-class has reached the 'critical' size for migration and maturation in their third year of life, than before, and moved from the nursery area to the 'adult' fishing grounds at this age. Cushing & Burd (1957) show that after 1951, over 90 per cent of each year-class recruiting the East Anglian fishery did so at three years of age. Data from the Buchan fishery provide a similar figure.

This hypothesis does not deny any effect of the industrial fishery on recruitment to the adult fisheries, but allocates it principally to the fish recruiting at three years of age. The results of the international tagging experiment provides estimates of this effect as a reduction in total recruitment of about 15 per cent. The data available at present do not provide any clear indication of its allocation between recruits to the northern and southern North Sea fisheries respectively.

THE MAGNITUDE OF RECRUITMENT

This mechanism accounts for the main facts of the change in recruitment pattern in both the northern and southern North Sea, which tends to support the view that the adults fished in both of these regions originate mainly from the same, or closely neighbouring nursery grounds, subject to similar environmental conditions and changes. However, while the change in the general pattern of recruitment has been the same in the two regions, there have been important differences in total recruitment between them, especially in recent years. In particular, the total abundance of three-year-olds, recruiting the north-western North Sea fisheries (Buchan) increased after 1951 relatively more than in the Southern Bight (East Anglia). Estimates of the relative abundance of each year-class at an age immediately prior to recruiting

at age three, before and after the recruitment change, can be made for each region from the data of the abundance of the three-, four- and five-year-olds in successive years in the fisheries, and from values of the natural and fishing mortality rates operating in these years (Cushing & Burd, 1957). Such estimates for the year-classes 1927 to 1934, and 1947 to 1953, recruiting the East Anglian (Cushing, 1959) and Buchan fisheries respectively, are given in Fig. 9. These show that the recruitment change was followed by a marked increase in estimated year-class strength in the north-western North Sea while in the south, it did not rise above the earlier level. At present the explanation of this difference in total recruitment is not clear. Of particular importance is the problem of the biological identity of the recruits to these two regions. Are they members of distinct stocks of herring or do the spawning products from all North Sea spawning concentrations form a common 'pool' of pre-recruits, the time and direction of movement of which is governed by external factors (e.g. growth rate, rate of maturation, hydrographical features, food supply)?

As stated earlier, the available information points to the vicinity of the Dogger Bank, as the nursery ground from which the bulk of the recruits to the northern and southern North Sea fisheries are derived, but it is not yet clear to what extent, and at what stage in their growth histories these components become segregated.

In view of the importance and complexity of this problem, steps have been taken recently, under the auspices of the International Council for the Exploration of the Sea, to organize a conjoint international study of the distribution, abundance and biological characters of the adolescent and adult herring concentrations in all parts of the North Sea. Amongst the questions, for which it is hoped an answer will be provided by this investigation, are the following:

- (1) Does the south-eastern North Sea nursery ground constitute the principal source of recruits to the northern and southern North Sea fisheries, or are the two regions recruited from separate nursery areas?
- (2) Can the pre-recruits of the northern spawning groups be distinguished from those to the south during their nursery ground phase?
- (3) At what time and by what route do the recruits leave the nursery grounds for the northern and southern North Sea respectively?
- (4) What are the growth characteristics of the adolescent fish, and are these related to the magnitude of recruitment to the north and south?

The answers to these questions have an important practical as well as biological significance. Studies on the Southern Bight spawning grounds have provided evidence of a marked decrease in larval production in recent years (Bridger, 1959), which is associated with the reduction in adult stock

abundance in this region. If these spawning products alone form the recruits to the Southern Bight fisheries, the dangers of reduced recruitment to this region are enhanced. If, on the other hand, the spawning products from each of the major North Sea spawning grounds constitute potential recruits to either the northern or southern North Sea fisheries, depending on their growth rate during adolescent life, these dangers are lessened.

FIG. 9.—Estimates of relative strengths of year-classes at three years of age, recruiting the East Anglian and Buchan fisheries respectively in pre-war and post-war years. East Anglian data taken from Cushing, 1959.

THE DECLINE IN ABUNDANCE OF THE FULLY RECRUITED AGE-GROUPS

This component of the recent changes in the northern and southern North Sea was due to a decrease in abundance of the older age-groups and also an increase in the total mortality rate between them (Figs. 6 and 7). The latter observation indicates that the decline in abundance was not simply a direct consequence of the recruitment change (due to additional fishing mortality experienced by each year-class between ages three and four) or to changes in relative recruitment. It shows that other influences gave rise to an increase in the loss rate amongst the fully recruited age-groups. The identification of the causes of this loss rate are therefore crucial to the interpretation of the fishery changes.

The total mortality rate is composed of two components, fishing mortality, which is generated by the fishery, and hence constitutes the chief man-made influence, and natural mortality, which is the loss due to natural agencies (defined here in its broadest sense to include loss due to emigration and changes in availability and accessibility). Natural deaths (or other losses due to natural causes) in the sea cannot be measured directly, nor, usually, can the agencies causing them be identified and measured. So, in investigating the causes of the total mortality rate change, it is necessary to examine the extent to which it is due to its fishing mortality component, through changes in the fishing intensity. This method of assessment has been used in numerous fishery investigations in recent years; its theoretical basis is described by Beverton & Holt (1957).

For the application of this method, unbiased estimates of total apparent mortality rate and accurate measures of effective fishing intensity are required. The provision of both of these for the North Sea herring present major difficulties, especially the measurement of fishing effort (fishing intensity is the fishing effort per unit area).

THE MEASUREMENT OF FISHING EFFORT

The main, current difficulties in obtaining accurate measures of fishing effort for the North Sea herring fisheries stem from two principal sources*:

- (1) The complexity of the fisheries in composition, distribution, fishing power and 'efficiency'.
- (2) Variations in, or uncertainty concerning the distribution, availability and accessibility of the stocks fished in different parts of the North Sea.

The fisheries in the northern and southern North Sea are exploited by two main gears, trawl and drift net. In the main these are separated in space and

* The lack of published effort statistics for some countries is also a current difficulty, but it can be overcome by the estimation of 'equivalent effort units' for these countries, using catch data.

time, and in some regions exploit different age and length components of the fished stocks. This is particularly marked in the northern North Sea, where the drift-net fisheries (principally British, Dutch and German) are centred in the north-western area in the months May to July and the trawl fisheries (principally German, Swedish, Polish and Dutch) take place later in the year, on the Fladen and Gut grounds. Similarly, in the southern North Sea, the drift net fisheries operate principally off the East Anglian coast, while the trawl fisheries are centred on the spawning grounds off the Belgian and French coasts (see Fig. 3). Also, throughout the inter-war and post-war periods, the relative sizes of the trawl and drift net fisheries have changed substantially (Fig. 2), and the areas fished have been extended; further, the size and engine power of the trawling fleets have increased, and the introduction of fish detection methods (e.g. echo-sounders) has probably led to an increase in the 'efficiency' of the fishing units (Cushing, 1959). It is clear therefore that the total effective effort exerted each year on the fully recruited age-groups must take into account the differences in fishing power and 'selectivity'* between the trawler and drifter fleets and the changes in fishing power and efficiency of each.

For all except the selectivity problem, these difficulties can be handled in two ways:

- (1) By choosing one fishery and method of capture for which detailed catch and effort statistics are available, and estimating total effort in 'equivalent units' by raising its effort by the ratio of its catch to the total catch (Gulland, 1955). The chosen fishery should be a major component of the total fishery, and one in which changes in fishing power and/or efficiency during the period in question are known.
- (2) By determining the relative fishing powers, efficiencies and selectivities of the fishing units in all components of the total fishery, and combining the corrected effort units.

The first of these methods has been used by Cushing (1959) in compiling the total effort for the fisheries in the southern North Sea. He used the statistics of the East Anglian drift net and German trawl fisheries as standard and estimated total effort in terms of British drifter shots and German trawlers fishing days respectively. An 'efficiency' index was used to adjust for estimated changes in the efficiency of the drifter fleet in recent years.

These two sets of effort data follow approximately the same course during the post-war period. Effort increased to a peak in the years 1951-4 and thereafter decreased, at least up to 1958.

These estimates take account of the major changes in the fishing power

* 'selectivity' is used here in its widest sense, and includes selection of stock strata (size-groups, age-groups, etc.), as well as the 'inherent' selectivity of the gear (e.g. mesh selection).

and efficiency of the fishing fleets, but they assume that (a) exploitation of the Southern Bight spawners is confined to the southern North Sea and Dogger fisheries; (b) there are no major differences in 'selectivity' between the fishing fleets.

It is known from the results of tagging experiments (Hoglund, 1955; Wood *et al.*, 1955) that some fish present in the northern North Sea in the summer are subsequently fished later in the year in the southern North Sea fisheries. However, it is not possible, from biological data available at present, to identify them and determine their distribution and abundance in this region or their proportion in the northern North Sea catch. Also, information on the time and spatial distribution of age-groups in the southern North Sea indicates that age selection differences exist both in time and between the fishing fleets exploiting the southern North Sea stock.

These observations illustrate the current difficulties and uncertainties associated with the measurement of the effort exerted on the Southern Bight spawning stock.

Similar problems arise in effort measurement for the northern North Sea fisheries. Of particular importance in this area is the marked age stratification of the exploited stock over the fishing grounds, especially over the north-western North Sea drift net grounds (Parrish & Craig, 1957; Parrish *et al.*, 1953-9). This raises difficulties in the allocation of effort to the age-groups for which the estimated mortalities refer.

However, a first assessment of the effort exerted in this region from the published statistics of the principal fisheries suggests that, as in the Southern Bight, the total effort increased between 1946 and 1951-4, due to the growth of the trawl fisheries, and thereafter decreased to some extent.

THE RELATION BETWEEN MORTALITY AND EFFORT

When the estimated total mortality rates for both regions (Fig. 8) are viewed in the light of these effort changes, it is evident that

- (1) They did not increase markedly during the period of increasing effort in the period up to 1953. In the Buchan area they were mostly low up to 1952 (negative values were obtained between 1949-50 and 1951-2), but they were consistently high in later years.
- (2) In both areas, but especially in the north-western North Sea, they fluctuated widely from year to year.

On a superficial inspection of the mortality and effort data, it is not possible to assign clearly the major changes in total mortality rate to its fishing mortality components, generated by the fishery. This difficulty is at the root of the current dilemma in the interpretation of the mortality changes, and in estimating the magnitudes of the fishing and natural mortality rates. The

problem is currently the subject of intensive investigation, involving a more sophisticated analysis of the effective effort exerted by the fisheries in the northern and southern North Sea. Steps are being taken through the International Council for the Exploration of the Sea to improve and extend the statistics of fishing effort and to examine further the distribution, ecology and identity of the herring exploited in the northern and southern North Sea.

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DISCUSSION

J. B. CRAGG: Is any country carrying out standard trawling operations which will give unbiased control data?

B. B. PARRISH: No. At present the sampling of the herring stocks in the North Sea is conducted principally by each country from its commercial fisheries. Also, there is the problem of varying accessibility of herring to different gears, which makes sampling by a standard gear in all areas and seasons very difficult. However, steps have been taken recently to undertake conjoint international herring surveys for specific purposes, and such a conjoint trawling survey is at present in progress in the North Sea to study the distribution and abundance of the pre-recruits of the North Sea herring stocks.

D. H. CHITTY: What data are the mortality estimates which you have shown us based on?

B. B. PARRISH: For both the East Anglian and the north-western North Sea data, the mortality rates are estimated from the abundance indices of successive year-classes between ages four and seven. In the slide I have shown the average annual mortality rate between ages five and seven and the corresponding values between ages four and five.

K. R. ASHBY: Can any of the changes in the herring stocks which you have described be attributed to increased pollution of the North Sea since the war?

B. B. PARRISH: There is certainly no evidence to suggest that this can have played any substantial part in the recent changes in the herring stock.

E. D. LE CREN: Is there any substantial competition for food between the pre-recruit and older age-groups, which might have contributed to the decline in abundance of the older fish?

B. B. PARRISH: The main food items of the pre-recruit and adult herring is the same, namely *Calanus*, but the competition between them is likely to be very small because of the spatial separation of the pre-recruit and adult components of the stocks.

E. D. LE CREN: It has been shown for some freshwater fish species that growth rate and natural survival rate are inversely proportional. Is there any evidence that this is so for the herring?

B. B. PARRISH: There is unfortunately no direct evidence of it, but this sort of mechanism is clearly of special significance to the observed changes in the stock composition. The changes in mean size for age since 1950 have been very striking, especially in the northern North Sea, and the substance

of the 'natural factors' hypothesis is that the natural mortality rate has increased following the growth change.

G. V. NIKOL'SKIĭ: Is there any evidence of the influence of gill-net selectivity on the 'quality' of the stock? For example, one would expect that the thickest of the smaller fish and thinnest of the large fish would be caught. This might have important long-term effects on the genetical composition of the stock.

B. B. PARRISH: There is unfortunately no detailed information either on the selection of 'quality' characteristics of the fish, nor I feel do we know enough of the determinants of 'quality' to assess this type of selectivity effect. It is an important problem which warrants close examination, but I do not envisage an easy or early solution.

A. MILNE: In recent years large fleets of Russian fishing vessels have concentrated off the Shetlands in spring. Have their activities contributed to the recent changes in the herring stocks in the North Sea?

B. B. PARRISH: The Russian fishery in the spring has in fact taken a relatively small part of the total annual herring catch from the North Sea. Furthermore, in the spring, fishery in this region is centred largely on members of the Atlanto-Scandian herring tribe and not the main North Sea stock. However, the Russian data are included in the assessment of total North Sea catch and fishing effort.

B. N. K. DAVIS: Are the continental trawl fisheries and the British drift net fisheries exploiting the same herring stock?

B. B. PARRISH: This is an important point which I have not been able to deal with in the time at my disposal. The problem of stock identity of the North Sea herring is still the subject of intensive investigation in Europe. Current evidence indicates that the trawl and drift net fisheries in the southern North Sea together exploit immediate pre-spawning and spawning members of a 'Downs' herring group, spawning off the Belgian and French coasts, while the fisheries in the northern North Sea are centred on the earlier maturity stages of this group and members of a 'Bank' group, spawning in the north-western North Sea and on the Dogger Bank.

PARAMETERS OF MARINE INVERTEBRATE POPULATIONS

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INTRODUCTION

In Britain the marine invertebrates which are exploited commercially are found among the Crustacea (lobsters, crabs, shrimps, prawns and Norway lobsters), and Mollusca (oysters, mussels, cockles, scallops, clams, whelks and winkles). They include animals with a wide range of habits — free-swimming forms (shrimps, prawns), mobile bottom-living animals (lobsters, crabs, Norway lobsters, whelks and winkles) and sedentary molluscs (oysters, mussels, cockles, scallops and clams). Exploited mussels, cockles, clams and Portuguese oysters are normally intertidal in distribution while the remaining species are exploited below low-water mark.

In Europe, only the sedentary molluscs; oysters, mussels, and to a lesser extent cockles, are cultivated. Otherwise, marine invertebrates are fished from wild, natural populations. Population studies in each kind of fishery are directed towards the same end, namely that of rational exploitation and achievement of the best long-term yield. So far, the general principles of population dynamics established for fish (Beverton & Holt, 1957) have been found to be applicable, but there are with shellfish some special problems, and certain advantages when examining exposed sedentary populations.

SAMPLING THE POPULATION

It is characteristic of most shellfish that their movements are very limited, varying from nil for the sedentary molluscs to a few miles at most for crabs and lobsters. Even the migrations of shrimps and prawns seem unlikely to prove very extensive. Any variations from one locality to another in the animate or inanimate environment which determine the growth or survival of individuals have only a local effect and are not spread widely through subsequent mixing of individuals over a wide area. For example, the growth rate and mortality rate of cockles vary in different parts of a single extensive cockle bed, and for lobsters these parameters may differ greatly within a few miles, due to local environmental factors and the proximity of a fishing port. Therefore, great care has to be taken in sampling the population either

to average out these variations or, more usefully, to obtain reliable information on the variations over the area under investigation.

Intertidal sedentary populations may be sampled by methods similar to those used in terrestrial ecology of plants. These populations have the advantage that every individual is directly accessible and stationary, so that the size of area sampled need depend only on the time available. Samples are taken by removing areas of known size from the shore, and counting and measuring their contents. Sampling stations may be arranged conveniently in the form of transects, and subsequent observations can be made at the same sampling positions. These methods have been used successfully for assessing changes in cockle densities (Fig. 1) and the distribution of mussel

FIG. 1.—Diagrammatic representation of the results of a survey of cockle resources. Llanrhidian Sands, South Wales, May 1959.

and clam resources on the shore. Sublittoral sedentary molluscs (oysters, scallops) may be sampled by dredging, which is the commercial method of exploitation. The efficiency of the gear may be calculated (Shelbourne, 1957) and the accuracy of samples checked by diving (Baird & Gibson, 1956) and by grab sampling (Mistakidis, 1951). Diving may also be used for sampling. Sampling by a dredge, as with a trawl, involves selection depending on ring size or mesh. Mason (1957) found that commercial dredges select scallops of three to four years and older. Baird & Gibson (1956) concluded that tooth

spacing is another selective agent of the scallop dredge. The smallest sizes of oysters may be either attached to large shells or 'singled', so that selection of attached small oysters may be made by the dredge. Trawling for Norway lobsters usually results in a higher proportion of males, possibly due to a difference in the burrowing behaviour of the two sexes (Poulsen, 1946).

Special sampling problems arise where direct mechanical sampling by trawl, dredge, grab, etc. is not effective because of the rocky nature of the bottom, or because of the burrowing habits or the low density of the species, e.g. lobsters, whelks, crabs. Here, catching by baited traps is the commercial method of capture and is also used as the method of scientific sampling. The reliability of sampling the population by baited traps depends on all sections of the population being equally attracted by the bait and equally readily retained by the trap. Baited traps must therefore be used with an understanding of the biases which may occur.

In obtaining data on abundance of a species from catch per unit effort, especially from commercial catches, the catches may be influenced by:

- (1) The different attractiveness of baits used.
- (2) The influence of the presence in the trap both of the desired species, and of other animals attracted by the bait. Table I gives examples of (1) and (2). Salted skate and dead shore crabs used together as bait for catching whelks were more effective than when either was used separately (A, D, E, F). The figures suggest that the attractiveness of the two baits to whelks is similar,

TABLE I. *Catches of whelks and shore crabs in pots containing different bait*

Experiment	Location	Number of pot-days	Bait	Average catch per pot		Crab population
				Whelks	Shore crabs	
A	Whitstable	78	2 shore crabs	23	1	Average
		96	Salted skate	10	4	
		92	Crabs and fish	33	2	
B	Whitstable	10	2 shore crabs	28	1	Many.
		12	Salted skate	2	10	
C	Whitstable	10	2 shore crabs	24	1	Few.
		12	Salted skate	18	1	
D	Mouth of River Crouch	20	2 shore crabs	21	0	Few
		24	Salted skate	22	1	
		20	Crabs and fish	32	1	
E	Inside River Crouch	4	2 shore crabs	67	1	Many.
		5	Crabs and fish	138	2	
F	Inside River Crouch	5	Salted skate	50	10	Many
		4	Crabs and fish	151	3	

but on areas with a high natural population of shore crabs, these enter the pots and deter the entry of whelks (B, F). In addition, dead crab bait seems to have a deterrent effect on the entry of crabs.

(3) Competition between the bait and natural food available, which will vary from place to place and year to year.

(4) Seasonal effects on the feeding behaviour of the species, e.g. laboratory experiments have shown that the feeding of whelks is at a minimum during the summer, but greatest in spring, and this was reflected in commercial catches (Fig. 2). Similarly, lobsters feed most actively in the summer and catches are then at their maximum.

FIG. 2.—Landings of whelks by commercial boats at Whitstable, 1957–9.

(5) Competition from the pots of other fishermen — here the direction of tidal flow related to the position of bait and prey is important.

(6) The design of the pots, e.g. some lobster pots retain lobsters more efficiently than others.

(7) The frequency with which the traps are emptied, and the frequency with which the bait is renewed. Whelk pots left down for more than one day at

Whitstable, had only slight increases in the catches on subsequent days — due possibly to reduced attractiveness of the bait, and to fishing out the area over which the scent of the bait was effective.

(8) Gear saturation by exploited and/or competing species. Whelk pots are frequently filled by whelks, shore crabs, starfish and hermit crabs. In (7) and (8) there is a problem similar to that described by Kennedy (1951) for pelagic fish caught in gill nets.

When sampling for the size and sex composition of the stock biases may be introduced due to the differential behaviour of sections of the stock at different times of the year:

(1) During moulting lobsters and crabs do not feed and therefore that part of the stock which is moulting at any time is under-represented in the catch.

(2) While carrying eggs the female crab is rarely caught in traps.

(3) Traps with different-sized entrances catch and retain the largest and smallest crabs with different efficiencies.

While it is probable that most of these sources of error can be avoided or measured it would appear that much more work is required on problems of sampling by traps. On the other hand, the behaviour patterns giving rise to these effects may be studied by the planned use of traps and the analysis of systematic trap data.

GROWTH AND AGE AT FIRST MATURITY

(1) METHODS

The determination of growth rates among the molluscs is fairly straightforward. The easiest to study are cockles (Orton, 1926) and scallops (Mason, 1957), which usually have well-defined 'annual' rings, representing the cessation of growth during each winter. It is wise to follow a single population over several years, in order to ensure that the true growth pattern is not confused by the presence of interference rings which sometimes occur as a result of environmental changes. The ease with which the previous growth history of these species can be determined from the rings may prove useful for providing data at present difficult to obtain in fish, due to errors in 'back calculation' interpretation of scale and otolith measurements for age/length determinations. A great advantage in examining sedentary molluscs is that the mean size and abundance of each of the pre-recruit year groups can be determined. With molluscs other than cockles and scallops age determination is more difficult, but growth increments can be estimated from marking experiments and size frequency data. Whelks have been tagged by painting the spire, and by scrubbing the periostracal layer from the area round the shell lip. Subsequent new growth was determined by the presence of the

periostracum (Hancock & Urquhart, 1959). Oysters are frequently transplanted to fresh plots and their age is often known from their previous history. Growth increments may also be determined from individuals marked with paint.

The Crustacea present greater difficulties. Here growth can occur only by shedding the rigid exoskeleton, or 'moulting'. This is followed by an immediate swelling of the newly emerged soft-shelled form, after which the shell hardens once again. Growth estimates, therefore, involve a knowledge not only of the moult increment, but also of the frequency of moulting. The loss of all hard structures during moulting has made it impossible to determine the age of individual Crustacea. The usual tags attached by wire to a cheliped are of course lost with the exoskeleton during moulting. Holes punched through the telson of a lobster are, however, found to be identifiable after moulting, so that by using a code system for punching holes in one or more flaps of the tail fans of different sizes of lobsters, growth increments can be obtained (Wilder, 1953). This method is not suitable for marking crabs, but tags attached along the line of separation of the carapace of the edible crab have been found to survive the moult (Mistakidis, 1959). It has been shown experimentally (Williamson, 1904) that crabs may moult several times during each of the first few years of life, reducing to about once a year in later years, but a satisfactory method of determining the moult frequency under natural conditions has yet to be found. Shrimps and prawns are too small for the attachment of tags, and they are handled in such vast numbers that marked individuals would be too easily overlooked. The size frequency of populations of pink shrimps (Mistakidis, 1957) and prawns (Cole, 1958; Forster, 1959) have however been analysed, and age/length determinations made.

(2) RESULTS

Growth is usually confined to definite seasons. In cockles (Fig. 6), oysters (Walne, 1958), scallops (Mason, 1957) and mussels (Baird, personal communication), there is usually little or no shell growth during the winter months. In whelks, the growth rate is reduced during the summer. In commercial molluscs the period of rapid growth is restricted to the first few years of life, and is followed by a slowing down in the growth rate in subsequent years (Fig. 3). The slower growth rate follows the onset of first maturity. This has been found to occur after the deposition of the second growth ring in scallops (Mason, 1957), and may commence even before that in cockles. Fig. 3 shows the differences which may arise when calculating the growth rate of cockles. The measurement of growth rings on seven-year-old cockles gave a slower growth rate than that obtained by measuring

the average total length of the different year-groups of cockles. This may have been due in part to poor early growth seasons for the seven-year-old cockles. However, the inset figures show the effect of fishing on cockles during their second winter, when only a proportion of the year-group had reached minimum size. This suggests that selection by sieving could have produced the apparent difference in growth rate.

A method used to estimate the size at first maturity of whelks was to divide the males according to penis size. This was usually either small and narrow or very large, with few intermediate sizes (Fig. 4). The shell length at which the change-over from small to large penis occurred corresponded

FIG. 3.—Growth of cockles. Growth curve obtained by measuring the lengths of growth rings on cockles of seven years of age from Llanrhidian Sands, April 1958. Points marked (O) show mean sizes of cockles of each year group collected from the same area. (2) shows the length distribution of 2-ring cockles (B) and the position of their first rings (A), before and after (blocked in) fishing. (3) Growth curves from cockles shown in (2).

with that of female whelks at the time of first depositing spawn in the laboratory, and this was concluded to be the shell length at maturity. Above this size the growth increments reduced rapidly. As in related gastropods like the dog whelk (Moore, 1936) and the American whelk tingle (Hancock, 1959), the slowing of the growth rate following the onset of maturity was accompanied by the continual deposition of layers of shell, resulting in thickening of the shell lip (Fig. 5). The female of the American tingle has a faster growth rate than the male, though this has not been found to be true of the whelk. Among mature lobsters, males grow faster than females.

FIG. 4.—Penis lengths of whelks from Whitstable, October 1956.

FIG. 5.—Length distribution of whelks from Whitstable, October 1956.

A wide range of physical conditions influences the growth of shellfish (Cole, 1956; Coulthard, 1929; Fox & Coe, 1943), though the separate effects of environmental conditions may be difficult to evaluate (Kristensen, 1957). However, since these species, particularly the sedentary forms, are unable to escape their environments, it is possible to investigate the range of factors influencing growth without the complications of migration. Seasonal changes in temperature affect feeding habits or availability of food and are reflected in the seasonal growth pattern. Oysters cease feeding during the

FIG. 6.—Shell lengths and cooked meat volumes of cockles from Llanrhidian Sands, using cockles settled in 1955–8. Each value of meat volume was an average of usually fifty individuals.

winter (Savage, 1925), and the rate of feeding of scallops is lowest when the sea temperature is at a minimum (Mason, 1957). The meat volume of cockles is much reduced during the winter (Fig. 6). Ciliary currents are however maintained at low temperatures in mussels (Dodgson, 1928) and oysters (Cole, 1954), while cockles have been shown to continue shell deposition during the winter, though shell length remains constant (Kristensen, 1957).

In filter feeding animals the period of immersion is obviously important,

and in mussels (Baird & Drinnan, 1957) and cockles there is a positive correlation between rate of growth and the period of immersion. The problem of density dependent effects on the growth of sedentary molluscs requires careful investigation in view of the variable growth rates which may occur as a result of other factors. Under favourable conditions, very high densities may occur, leading to competition for food and space. Kristensen (1957) concluded that the growth rate of second-year cockles of 2,000 per square metre density was reduced by competition. On Llanrhidian Sands, the substratum was found to be physically saturated by 3,000 second-year cockles per square metre, with reduction in growth rate occurring at densities less than this.

Owing to the difficulties in determining the moult increment and moult frequency of Crustacea in the field, annual growth rates are not at all fully understood. Most work has been done on the lobster, and in general terms the moult frequency decreases until at maturity the moult occurs approximately annually in males and approximately every second year in females. For the mature female, a year without carrying eggs alternates with one during which eggs are carried, with moulting occurring shortly after the eggs are shed, each second year. Just prior to maturity, the moult increments of both sexes of lobsters are similar, but after maturity the moult increment of the female decreases, so that with the reduced moult frequency the annual growth becomes considerably less than half that of the males. Fig. 7 summarizes the information at present available on the moult increment of lobsters and shows a marked similarity between the areas studied. The lack of information on moult frequency from area to area means that it is still not known whether moult frequency or moult increment is the more important in causing differences in annual growth rate between different areas.

A feature of bivalve molluscs is that the whole volume is not always an accurate indicator of the volume of meat within. This assumes importance when predicting yields from a shellfish fishery. Cockles, for example, have the best 'condition', i.e. ratio of meat volume to internal volume of the shell, in midsummer (Fig. 6). The condition falls markedly from about August onwards, and does not begin to improve again until April. Spawning begins in late April to May, but by this time the rapid assimilation of food materials soon hides any change in the meat volume, which increases rapidly. A hundredweight sack of cockles has been found to contain 50 per cent more meat in July than in February. The condition of shellfish from different areas may be quite different. This fact has been made use of during oyster cultivation, in which oysters are transplanted first to areas known to encourage rapid shell growth, and then to beds which give good growth of meat.

FIG. 7.—The percentage increase in length on moulting of male and female European and American lobsters of 55–110 mm carapace length (6.5–12 in. total length). Data from (a) south-east Scotland (Thomas, 1958); (b) North Wales (Simpson, 1957); (c) Pointe du Chêne, Canada (Templeman, 1948); (d) Grand Manan, Bay of Fundy, Canada (Wilder, 1953); (e) Lismore, Nova Scotia (Wilder, 1953).

RECRUITMENT

Egg production in commercial shellfish may be extremely high (Table II) and in all except the whelk the larvae have a pelagic phase.

Variation in the strengths of year classes is very pronounced among shellfish, and in cockles, oysters, and clams appears to take the form of a series of poor year classes, with good settlement and survival occurring only at intervals of several years. Waugh (1957) found that the spatfall of oysters in the Rivers Roach and Crouch was only moderate in 1950, and light in subsequent years until 1957, when there was a good settlement (Fig. 8). On Llanrhidian Sands there was an abundant settlement of cockles in 1951, after which annual recruitment was only slight until 1958, when settlement was

TABLE II. *Fecundity of shellfish*

Species	Number of eggs	Size of adult	Reference
Oyster	84,400–1,730,200	41–95 mm shell length	Cole, 1941.
Mussel	100,000–2,000,000	14–42 mm „ „	Matveeva, 1948.
Cockle	5,600–52,000	19–38 mm „ „	Kristensen, 1957.
Whelk	88,540–248,556	49–73 mm „ „	Hancock (in press).
	(504)–(2,264)*		
Lobster	6,000–35,000	3–5 in. carapace length	Herrick, 1911.
Crab	460,000–3,000,000	5 $\frac{3}{4}$ –7 $\frac{11}{16}$ in. carapace width	Williamson, 1900.
Prawn	1,500–4,300	6.2–10.5 cm total length	Forster, 1951.
Shrimp	200–3,000	7–17 mm carapace length	Mistakidis, 1957.

* Brackets contain numbers of juvenile whelks emerging.

good. Kristensen (1957) reported that 1947 was an extremely favourable breeding year for cockles and many other species, but spatfall in the Dutch Waddensea in following years was so poor that this remained the dominant year class until 1953. This pattern of frequent poor year classes may be related to the many factors which must be favourable for the survival of estuarine pelagic larvae if a good year class is to result. The native oyster in Britain is a viviparous hermaphrodite living towards the northern limit of its distribution, and it has been found that in cool summers in which the water temperature scarcely reached 20° C few larvae are liberated. As with most small pelagic larvae, food can be of critical importance and Waugh (1957) has found that survival of oyster larvae is related to the abundance of suitable flagellates. Oysters require a suitable substrate for settlement, and

FIG. 8.—Numbers of oyster spat which settled on ten complete oyster shells on Purleigh Shore oyster ground, River Crouch, 1948–59 (from data supplied by G. D. Waugh).

there can be intense competition for this by barnacles and other animals. There is evidence (Cole & Knight-Jones, 1949) that oyster larvae are gregarious and settle most readily where older oysters are already present. Together with these two latter requirements for settlement, the movement of the water in estuaries at the times the larvae are planktonic may be extremely important for survival. Spring tides and strong winds from particular quarters could remove all the larvae from an estuary, so that few remained where adult oysters and suitable substrates are present. Young oysters may also suffer severe mortalities soon after settlement. Waugh (1957) found a 50 per cent mortality among oyster spat during the fourteen days following settlement, and even greater mortalities have been recorded (Knight-Jones, 1952). In 1953 on one oyster laying, 73 per cent of spat which had reached fingernail size were dead by the December after settlement. Fifty-eight per cent of the spat had been eaten by the American whelk tingle (Hancock, 1954). Cockles, too, have a high mortality during their first year

of life (Fig. 10). Heavy settlement of young oysters frequently occurs well up in estuaries, where low salinity and low temperatures often cause excessive mortalities.

In his methods of cultivating oysters, man tries to improve survival by providing suitable surfaces for larval settlement in the form of cockle and mussel shell, and he removes the young oysters from the vulnerable upstream settlement grounds to safer growing grounds in deeper water and away from winter freshwater run-off. More recently (Walne, 1959) experimental work on artificial rearing of oysters is aimed at eliminating the problem of 'seed' supply.

There are, however, cases among molluscs where recruitment is remarkably regular. On the rocky outcrops off Morecambe, Lancashire, the recruitment of mussels is so regular and abundant that few mussels reach more than about three years old before they are smothered with the regular settlement and growth of the young ones. Occasionally, phenomenally heavy spatfalls of mussels have occurred (Savage, 1956), when young mussels covered the beds and smothered and killed practically the whole of the adult stock. When this occurred in the Conway estuary in 1922 and 1940 a highly productive fishery ceased until the young mussels had grown large enough to be fished.

With all populations which have pelagic larvae, the larvae from an exploited or unexploited area may provide recruits to a distant fishery, so that the exploitation of one area may affect recruitment to another.

Recruitment to crustacean fisheries is also subject to considerable fluctuations. Poor densities in the pink shrimp fishery in 1949 were correlated with the severe winter of 1947 (Mistakidis, 1957). The early stages of crabs and lobsters are rarely encountered, but fluctuations in brood strength are evident from the uneven recruitment to marketable stocks (Mistakidis, personal communication), though with lobsters the variability in recruitment is probably masked by the overlapping of year classes, since the stocks do not reach commercial size until after about the fifth year of life.

Of commercial shellfish, the whelk is the only species which has no planktonic stage in the larval life history, the whole of which is passed through in fixed chitinous capsules, from which the young emerge. In this way many of the hazards of the developmental stages are avoided. Adverse physical factors may still be an important cause of mortality — for example, ground swell caused by high winds is said to cast the spawn ashore — but there is less likelihood of catastrophic mortalities than amongst species with free-swimming larvae. The abundance of the parent stock might here be used with more confidence as an indicator of brood production, but the relationship between recruitment and size of stock has not as yet been studied.

FISHING MORTALITY

If a reliable estimate of the stock has been obtained by direct survey or by marking experiments, the fishing mortality can be calculated from it, using figures for landings from the fishery. This involves the collection of accurate catch statistics, which unfortunately are not always available for shellfish, due to the difficulty of collection. Fishing mortality may also be assessed from marking experiments, which have so far been used for crabs, lobsters (Thomas, 1955a) and whelks. A knowledge of factors which normally complicate the interpretation of data from marking experiments is necessary. Shedding of marks may be of prime importance in Crustacea, but migrations are less of a problem with shellfish than with fish. Reinforcement of the unmarked part of the population may, however, occur from areas which are unsuitable for exploitation. This should be considered when planning the distribution of marked individuals in tagging experiments. With sedentary populations a separate estimate of natural mortality can be made, and related to the total density to give the fishing mortality.

The problems of sampling have been mentioned, and these are important when calculating catch per unit of effort from commercial landings. Selective fishing mortality of certain size groups occurs in the action of dredges, trawls or traps, and also in the sieves used for riddling cockles (Fig. 3). In some cases a minimum landing size is enforced by law. This may involve restrictions on the size of the mesh of the gear used (shrimps, prawns), or on the size of the shellfish (all others) which may be taken.

Certain fisheries take place only in restricted seasons, which may vary in extent in different areas along the coast. This may be the result of national legislation (e.g. close season for native oysters), locally administered byelaws (e.g. close season for mussels in South Wales Sea Fisheries District) or merely the voluntary pursuance of an alternative fishery. An example of this is the whelk fishery of Grimsby, which is confined to the winter months, while lobster fishing is more lucrative during the summer. In all fisheries with baited pots the effective effort is greatly reduced by bad weather (Fig. 2).

A direct result of the limited amount of mixing which occurs in shellfish populations is the selective fishing of the fastest growing individuals, particularly when there is a minimum size regulation. For example, each summer on heavily exploited cockle beds the fishermen await the growing to size of cockles. The areas of fastest growth are fished first, followed by the slower growing areas, but there will be repeated visits to the areas of fastest growth as cockles reach market size. Since a higher proportion of cockles reach market size in the faster growing areas, the fishing mortality is consequently greater there. All over the beds, the fastest growing cockles are fished off

first (Fig. 3), while the remainder may not reach market size until after the winter period of about six months, during which there is no growth. Although there is, with sedentary populations, the possibility of very efficient removal down to a very low density this, in fact, rarely happens, except in certain areas where cultivated oysters and mussels may be relaid in high densities, all of one age or size, which are subsequently harvested efficiently. With cockles, patches of high density are fished down to an uneconomic level and the fisherman then moves on to another good patch. Areas between are subsequently fished, but not systematically. Oysters are dredged until catches become uneconomic, but because of the inefficiency of the method many oysters will remain, as will the lobsters, crabs and whelks left behind after catches in pots have dropped below a certain level. Individuals remaining do not normally collect up together or shoal as do fish, so that they will not be fished again until their numbers have been increased by recruitment and growth. This means that shellfish stocks can seldom be completely fished out, and this becomes important if it is considered that a certain level of spawning individuals is required to ensure proper recruitment to the fishery. A knowledge of the contributions made to the larval population by other stocks is necessary before this can be decided.

It has already been stated that on reaching maturity the growth of female lobsters becomes less than half that of the males. Thomas (1955*b*) has shown that this results in the sex ratio altering strikingly with the size of the lobsters and that the curve relating sex ratio to size will also change with the degree of exploitation of the stock. This is demonstrated in Fig. 9. Thomas suggests

FIG. 9.—Theoretical sex-ratios among lobsters of different sizes when subjected to 30 per cent and 70 per cent total annual mortalities (from Thomas, 1955*b*, Table I).

that a study of the sex ratios in certain length groups of Crustacea may afford a means of approximate estimation of the mortality rate.

NATURAL MORTALITY

Natural mortality is computed as the difference between total mortality and fishing mortality, and cannot be measured directly in exploited populations. In unexploited populations, some of the causes of mortality will not be represented in the estimate, namely the damage to the stock by fishing gear, the effects on mortality of overcrowding, and possible changes in predation rates on undisturbed or concentrated stocks. Exposed sedentary populations have the particular value that natural mortality can be estimated directly, and some of the causes of error in assessing natural mortality in unexploited populations can be estimated. Experiments to this end are in progress on the Llanrhidian Sands cockle beds. Areas of 10 metres square have been fenced off and fishing prohibited within them. Regular sampling within these areas has allowed the calculation of natural mortality rates in varying conditions of exposure and density (Fig. 10). The effects of fishing methods may be examined by marking off an area, estimating its population by sampling and then subjecting it to fishing. The effect of raking and sieving cockles, and the fate of cockles passing through the sieve can then be determined, after a period of tidal coverage, by relating the yield from the area to the original density and the number remaining.

Unlike mobile species, which are either unlikely to be subjected to extreme conditions or are able to move away from them, sedentary inshore populations have only a very limited power of evading adverse environmental conditions. A combination of unfavourable circumstances frequently results in heavy or catastrophic mortalities. This is specially true of intertidal populations which are subjected to the greater extremes of physical conditions found in the terrestrial environment. Flourishing beds of exposed shellfish are frequently found decimated by frost or unusual heat, storms, winds and strong currents (Wright, 1927). Sublittoral populations are not immune from extreme conditions. The severe winters of 1939-40 and 1947 were responsible for great mortalities amongst oyster populations on the east coast (Cole, 1940; Knight-Jones, 1952). Extremes of salinity are dangerous, particularly when combined with extremes of temperature. As mentioned previously, a feature of oyster fisheries is that nursery grounds are frequently at the heads of estuaries, where a combination of low salinities and low temperatures causes heavy winter losses (Waugh, 1957). This obviously influences management of the fishery, and young oysters are collected before winter and relaid in areas more favourable for survival.

The system of management of certain cockle beds is influenced by a knowledge of consistent mortalities, such as those due to excessive turbulence caused by high winds from a certain direction. Mortalities among shellfish due to physical conditions are generally greatest in the winter.

Seasonal mortalities may also be related to the behaviour or migrations of predators. The American tingle feeds on oysters only when the temperature exceeds 9°C (Hancock, 1959). The oystercatcher concentrates its

FIG. 10.—Mortalities of cockles on Llanrhidian Sands 1958–60. Sample area 21–26 was not fished till August 1959 when light fishing commenced followed by heavy fishing beginning in November. Sample area 1–10 was protected from fishing in August 1959. Sample area 11–20 was heavily fished from November 1959.

attention on cockle and mussel beds during the winter (Drinnan, 1957, 1958). Starfish and fish have a seasonal feeding behaviour on young molluscs. Crabs and lobsters are probably particularly vulnerable whilst in the soft-shelled stage.

The natural mortality rate varies with age. In oysters and cockles there is a heavy natural mortality during the first year after settlement (Fig. 10). Apart

from the greater vulnerability of young to physical conditions, selective feeding of predators may have its effect. This may result from actual preference, e.g. of the American tingle for young oysters, or the physical inability of certain predators like starfish to eat bivalves larger than a certain size. For example, Thorson (1955) found that young lamellibranchs were able to survive in areas containing vast numbers of predatory brittle-stars. This was because the brittle-stars did not feed during their breeding period, during which the lamellibranchs were able to grow too large to be ingested.

The causes and extent of mortality can often be estimated from the shells of dead molluscs which remain on the bottom. The numbers of live and dead oysters in a dredge may be compared, provided the time interval since death of the shell or 'clock' is known. Some predators leave characteristic marks, such as the holes drilled by the American tingle in oysters (Hancock, 1954), or the edges of oyster shells broken by the attacks of starfish (Hancock, 1955), or shells of cockles opened by oystercatchers (Drinnan, 1957). The dead shells of oysters may contain signs of disease, like shell disease or boring worm, which may have contributed to their death. The shells of dead whelks often become inhabited by hermit crabs, which are also caught in baited pots with whelks. Many hermit crabs with painted shells were recaptured in a whelk marking experiment, and with some knowledge of the habits of the hermit crabs, their numbers might be used as a guide to post-marking and subsequent natural mortality.

SUMMARY

The important parameters required for making yield estimates in exploited invertebrate populations have been discussed. Certain features appear to be characteristic of shellfish populations and of the methods used for estimating these parameters. These are briefly:

- (1) The ease of sampling of exposed sedentary populations, which allows separate estimates to be made of total density, magnitude of recruitment, fishing mortality and natural mortality.
- (2) Special problems associated with the use of baited traps.
- (3) Growth estimates are made easy in a number of molluscs by the presence of clear growth rings, but are extremely complicated in Crustacea as a result of growth by moulting.
- (4) Recruitment is very irregular among many molluscs, and mortalities may be catastrophic at all stages of the life history.
- (5) Yield assessments require consideration of seasonal changes within the exoskeleton.

LIST OF SPECIES MENTIONED IN TEXT

Native oyster . . .	<i>Ostrea edulis</i> L.
Portuguese oyster . . .	<i>Gryphaea angulata</i> Lamarck.
Cockle . . .	<i>Cardium edule</i> L.
Mussel . . .	<i>Mytilus edulis</i> L.
Scallop . . .	<i>Pecten maximus</i> (L.).
Clam . . .	<i>Mya arenaria</i> L.
Whelk . . .	<i>Buccinum undatum</i> L.
Winkle . . .	<i>Littorina littorea</i> (L.)
Lobster — European . . .	<i>Homarus vulgaris</i> Milne-Edwards.
American . . .	<i>Homarus americanus</i> Milne-Edwards.
Edible crab . . .	<i>Cancer pagurus</i> L.
Norway lobster . . .	<i>Nephrops norvegicus</i> L.
Pink shrimp . . .	<i>Pandalus montagui</i> Leach.
Prawn . . .	<i>Palaemon serratus</i> (Pennant).
Hermit crab . . .	<i>Eupagurus bernhardus</i> (L.).
Common shore crab . . .	<i>Carcinus maenas</i> (L.).
American whelk tingle . . .	<i>Urosalpinx cinerea</i> (Say).
Dog whelk . . .	<i>Nucella lapillus</i> (L.).
Common starfish . . .	<i>Asterias rubens</i> L.
Brittle-star . . .	<i>Ophiura</i> and <i>Amphiura</i> spp.
American slipper limpet . . .	<i>Crepidula fornicata</i> (L.).
Boring worm . . .	<i>Polydora ciliata</i> (Johnson) and <i>P. hoplura</i> . Claparède.
Shell disease . . .	Unidentified fungus.
Oystercatcher . . .	<i>Haematopus ostralegus</i> .

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DISCUSSION

T. B. REYNOLDSON: Have you any data on the relation between cockle growth rates and the presence of parasites, such as trematodes?

D. A. HANCOCK: No. The level of infection seems to be fairly general, but the labour involved in studying its relation to growth would be prohibitive in large samples.

J. B. CRAGG: With high densities this parasitism does seem relevant.

D. A. HANCOCK: I agree that very high densities may be prone to rapid spread of disease. Normally there is a very rapid and more or less exponential falling off in numbers of cockles per square metre as growth proceeds. When the site is full of animals there must be either reduced growth or greater mortality or both.

E. D. LE CREN: Is plankton density a relevant factor?

D. A. HANCOCK: I know of no critical work on the food of cockles but flagellates are likely to be important. Competitive effects seem to occur, and it seems that growth rates fall off at high densities, well before the substratum is full.

A. MACFADYEN: Oystercatchers (*Haematopus ostralegus*) are said to take only two-ring cockles — does this mean that they do no damage?

D. A. HANCOCK: No. The average density of two-ring cockles in one sample area fell from over 1,000 per square metre to 77.0 per square metre, i.e. over 90 per cent in one square during one year. The mortality of brood cockles was only 50 per cent and of cockles older than two-rings less than this. Thus a high selective mortality occurs at two years and is thought to be due to oystercatchers. The relationship of these high mortalities to the total population is being calculated.

J. B. CRAGG: Are there any sample areas outside the range of the oystercatcher?

D. A. HANCOCK: No. We are attempting to assess and predict natural mortalities in order to increase yield of this particular area (Llanrhidian Sands), and the oystercatcher is just one factor we are studying with an open mind.

D. CHITTY: Are good spat years uniform round the coast?

D. A. HANCOCK: There are some 'bumper years' in which everywhere has good brood settlement. Others are much more local — from river to river and site to site.

M. E. SOLOMON: After a 'bumper year' does a population peak carry through to the adult stage or does it get flattened out?

D. A. HANCOCK: After a good settlement year of cockles the physical saturation of the settlement area may lead to reduced settlement in subsequent years, even if these are potentially good. But causes of irregular recruitment are more fundamental than this. These year peaks remain evident for a number of years.

N. WALOFF: Are the 'good settlement years' due to high fecundity?

D. A. HANCOCK: In oysters good conditions of temperature and food supply seem to be the keynote. My colleague, Mr G. D. Waugh, has shown that the temperature must reach a certain level for the liberation of larvae and must remain above 18°C for a period for larvae to develop. Also food supply (flagellates) is important if early larvae live to reach settlement stage.

E. D. LE CREN: With the selection of cockles as they reach marketable size, is there any evidence to show that the size limit has led to the evolution of slower growing strain?

D. A. HANCOCK: It is important to discover where recruitment is coming from — it may come from unexploited stocks nearby. Certain parts of cockle beds are not exploited because stocks are slow growing for environmental reasons. These grow well if transplanted and much egg production may come from these.

THE APPLICATION OF COMPARATIVE POPULATION STUDIES TO FISHERIES BIOLOGY — AN EXPLORATION

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INTRODUCTION

As nations have intensified their fishing activities during the past few decades, so the attention of marine biologists concerned with the improvement of fisheries has become focused on the need to predict catches and particularly the effects on catches of changes in the fishing activity, with a view to proposing steps — which may include legislation — to ensure that increasing input will continue to give sufficiently increasing returns. Thus, while many biologists continue studies intended to result in higher efficiency of fishing operations — for example observing the behaviour of fish in relation to natural environmental factors and to fishing gear — others have considered the relations between catches, population sizes and fishing activities. In doing this they have pursued three lines of investigation. In the first line the dynamics of entire eco-systems are considered, with particular reference to the flow of energy and materials from one trophic level to another, so that the yield of animals and plants directly useful to man is seen as a function of the quality, quantity and disposition of inorganic materials and of incident energy. If the dynamic relations between the significant elements of a particular eco-system are understood and their rates of action measured, it may theoretically be possible to predict at least the order of magnitude of actual and potential yields to be obtained by certain types and patterns of fishing operations, the changes in these yields which might be expected to result from certain kinds of intervention in the system, as by transplantations, artificial mixing or fertilization, and so on. Studies of this kind are extremely complex and their results cannot yet be regarded as having practical application, at least in sea fisheries.

In the second line of investigation the population growth pattern of a fish stock or of a group of stocks is considered, growth increment, and hence capacity to yield, being regarded primarily as a function of the size (in numbers or weight) of the stock. It has been assumed that population growth

may be represented by a sigmoid curve, which might be either the logistic or a derivative of it, or any empirical curve. Schaefer (1959) has shown, how, with such assumptions and with a set of observations covering a suitable range of stock sizes, it may be possible to determine the parameters of such curves from measures of catch, indices of stock size (as by catch per unit effort) and a measure of the coefficient of assumed proportionality between fishing effort and the ratio of catch to stock size, such as might be obtained from tagging experiments.

The third line of approach is by constructing mathematical models of particular fish stocks, in which rates of reproduction, individual growth, and death are represented by functions based primarily on an analysis of the size and age structure of the population, and containing a series of parameters for all of which there exist methods of estimation. An advantage of this method is that it offers the possibility of predicting the effects on catches of changes not only in the amount of fishing, but also in the kind of fishing, and particularly in the selectivity of fishing operations in terms of the sizes and ages of fish accepted or rejected by the fishery. In practice predictions are required of the effects on catches of changes in size selection resulting from changes in the characteristics of the fishing gear (such as mesh or hook sizes), and in the pattern of operations (such as concentration of fishing at grounds on which the fish gathered there tend to be smaller or larger than the average size in the population). Predictions may also be needed of the effects of changes in the seasonal and spatial distribution of fishing operations.

Such predictions are facilitated by the use of analytical models, and a requirement for the employment of all such models has been the availability of data for the age composition of the stock. This presents difficulties in many areas, especially — but not by any means only — in tropical waters, where the ages of fish cannot reliably be determined from rings on hard structures such as scales, otoliths, opercular bones, fin-rays or vertebral centra. Other methods of inferring age-composition, for example from polymodal length frequency curves or from the seasonal progression of modal sizes, are also not universally applicable; the former can, even in the most favourable circumstances, be used to distinguish only the few youngest age-groups in the population, and the latter method may not be successful when spawning or recruitment to the stock is spread over a very long season. Even when age can be determined, it is usually a procedure so demanding of the time of scientists and technicians that there is a general interest in finding means of avoiding it, or at least reducing it as much as possible. This general problem and the contribution to its solution that might come from comparative population studies will be considered here. It should be said, however, that there appears to be plenty of scope for practical com-

parative ecological work also in the other lines of approach — the studies of the properties of eco-systems, and of population growth patterns.

A YIELD EQUATION AND ITS TRANSFORMATIONS

Under steady state conditions the annual catch in weight (Y) of fish from a stock to which there is an annual number of recruits (R) is given by the integral, over the fishable life-span, of the product of an instantaneous fishing mortality coefficient (F), an expression giving the number of fish surviving to age t as a function of R and of a coefficient of total mortality ($Z = F + M$), and an expression for the body weight (w) of a fish in terms of its age.

An expression for body growth which has been rather frequently used in recent years is that of von Bertalanffy (1957), in which weight is taken as proportional to the cube of the length and

$$\frac{dl}{dt} = E - Kl$$

from which

$$l_t = L_{\infty}\{1 - e^{-K(t-t_0)}\}$$

and

$$w_t = W_{\infty}\{1 - e^{-K(t-t_0)}\}^3$$

where

$L_{\infty} = E/K =$ upper asymptote of length

$W_{\infty} =$ upper asymptote of weight

$K =$ parameter expressing the relative rate of approach to L_{∞}

$t_0 =$ scale constant; the theoretical age at which l_t and $W_t = 0$

This gives a curve for length at age without an inflexion; the corresponding curve for weight at age has an inflexion at 0.29 of the asymptotic weight. Parker & Larkin (1959) have recently questioned the suitability of such an equation for representing the growth of some fish, and have suggested a 'parabolic' function which gives an inflected weight at age curve but does not have a finite upper asymptote. It is significant that these authors fitted their curve to data for the growth of young fish, and although there does not in fish appear to be a size or age at which growth ceases entirely, nevertheless in only a few species is a substantial rate of increase in size maintained throughout life. Even in these cases there is sometimes doubt concerning the reliability of age-determination in the larger specimens, which distorts the growth curves, and in fish with average life-spans artificially shortened by the pressure of fishing or other predation it may be difficult to identify an upper asymptote, though one may exist. There is a further difficulty

concerning the use of equations with unlimited growth, which is that if they are incorporated into yield equations without provision for an arbitrary upper limit to the fishable life-span, their extrapolation beyond the limits of the original data can lead to quite anomalous predictions. It seems for the moment generally more satisfactory, therefore, to use equations which lead to finite upper asymptotes of fish-size, provided of course that they represent the observations reasonably well. It is worth noting, in this connection, that predictions of changes in catch resulting from changes in the intensity or selectivity of fishing of the order of magnitude normally considered in practice, do not appear to depend at all critically on the precision with which the growth function used fits the observations of size at age. For many purposes it is permissible even to approximate growth by treating weight as linear with, or even proportional to, age over the middle range of sizes. On the other hand computations are commonly performed by numerical means using the original observations, instead of smoothing them by fitting a growth equation. This latter practice, while serving the purpose of empirically obtaining predictions for particular stocks and situations, seems to eliminate the possibilities of predicting density-related changes in parameter values or of comparing different stocks and situations in order to deepen understanding of the population processes and simplify methods of analysis.

Richards (1959) has generalized the von Bertalanffy growth function in such a way as to include von Bertalanffy's own extension of the simple equation, and that by Ricker (1958). Richards shows that if in general

$$\frac{dw}{dt} = \eta w^m - Kw \quad (\text{where } \eta, m, \text{ and } K \text{ are constants})$$

then

$$w^{(1-m)} = W_{\infty}^{(1-m)} - be^{-kt}$$

where

$$W_{\infty}^{(1-m)} = \eta/K$$

$$b = \eta/K - w_0^{(1-m)} \text{ and}$$

$$k = (1 - m)K$$

If the size at the inflexion is denoted by w_i then

$$w_i/W_{\infty} = m^{1/(1-m)}$$

and the relative growth rate at this point is

$$\frac{dw}{wdt} = k/m$$

An entire family of growth curves can thus be represented in terms of the three parameters, K , m , and W_∞ (or L_∞) and the scale factor b . For values of m ranging from 0.5 to 3 or more (m is 0.67 in the simple von Bertalanffy, unity in the Gompertz, and 2 in the autocatalytic equations) the growth curves are very similar over much of their range, and comparison of the values of K — which again express relative rate of approach to the asymptote — is possible if m is kept constant for any particular set of comparisons.

In the following discussion it is proposed therefore to retain the simple von Bertalanffy equation, with the knowledge that any conclusions we may reach would hardly be altered if one of the other equations in this general family had been applied to the growth data. We may then write an equation for the steady-state annual catch of fish, by weight (Y) as:

$$Y = FRW_\infty e^{-M(t_c - t_r)} \sum_{n=0}^3 \frac{U_n e^{-nK(t_c - t_0)}}{Z + nK} [1 - e^{-(Z+nK)(t_L - t_c)}]$$

where

$U_n = +1, -3, +3, -1$ for $n = 0, 1, 2, 3$ respectively.

t_r = age at which fish are recruited.

t_c = age at which fish are liable to be retained by the fishing gear in use.

t_L = age after which fish do not appear in the catch, either because very few reach higher ages, or because they move from the fishing area, or because they have reached a size at which they are no longer taken or retained by the fishing gear.

R = annual number of recruits.

F , M and Z are instantaneous coefficients of fishing, natural and total mortality ($Z = F + M$).

In using this equation account is taken of changes in the amount of fishing by varying F (and hence Z) and of changes in the selectivity of fishing by varying t_c and sometimes t_L . Holt (1958*b*) has shown that the greatest steady catch is theoretically obtained by catching all fish when they reach a size

$$w_c = W_\infty \left(\frac{3}{3 + M'} \right)^3$$

though an infinitely high fishing intensity might be needed to do this in practice.

The catch under these conditions is given by

$$Y_{\max} = RW_\infty \left(\frac{L_\infty}{L_\infty - l_r} + \frac{M'}{M' + 3} \right)^{M'} \left(\frac{3}{M' + 3} \right)^3$$

where $M' = M/K$

and l_c and l_r = length of fish at ages t_c and t_r respectively.

Beverton & Holt (1957) and Parrish (1957) examined the effect on long-term catch predictions of variations in values of growth and mortality parameters, and particularly of K . It should be noted that W_∞ and R appear as factors of proportionality, and therefore do not have any effect on the shapes of curves relating Y to F and to t_c , nor therefore on catch predictions which would normally be made in relative terms as fractions or multiples of observed levels of past catches.

The number of parameters in the yield equation can thus be reduced by one or two (W_∞ , R) if predictions are to be made in relative terms and if it can be assumed that W_∞ and R will not change with changes in the intensity or selectivity of fishing and hence in stock size and density. This may not be a reasonable assumption to make in general, but perhaps can be made in particular circumstances. The number of parameters can again be reduced by one by writing the coefficients of mortality always as numerators of ratios the denominator of which is K , i.e. putting as before

$$M' = M/K$$

$$\text{and } F' = F/K$$

$$\text{and } Z' = Z/K$$

This arrangement makes it practicable, as Holt (1957*a*) found, to prepare tabulations of the yield equation and thus avoid much laborious computation. Tanaka (1958) has indeed published such tables, for Z' values from 0 to 15.0 and $K(t_c - t_0)$ from 0 to 6.0. In his tables t_L is in effect put to infinity, but catches for $t_L \neq \infty$ can be obtained by subtracting one tabulated value from another. Jones (1957) showed that the same yield equation can be expressed in terms of incomplete beta-functions, which are of course already tabulated, so that the computation of further tables may not now be necessary. The fact that the yield can be expressed in terms of the ratios F' and M' has an important implication even in cases where age determination is possible but difficult. Thus one kind of error in age determination results in fish aged t being nearly always assigned an age $t + x$ where x is an unknown constant integer, often +1 or -1. Both K and the mortality rates will, in this case be correctly estimated from age compositions. If, however, there is also involved an error such that true age t is given as yt because the time interval between annuli is not sure, then there will occur the same error in estimates of the mortality coefficients and of K ; their ratios will nevertheless be correctly estimated, provided that the method of estimation does not involve the use of addition data, such as tag returns, for which the true time-scale

applies (see Gulland (1959) for discussion of this problem in connection with *Sebastes* investigations in the North Atlantic).

Holt (1957a) also showed that a simple substitution can be made in order to express the catch in terms only of the ratios of mortality to growth rates and of the sizes of fish at recruitment, at first liability to capture by the gear and at the end of their fishable life-span, all relative to the asymptotic sizes L_∞ , W_∞ .

Thus we find

$$Y = W_\infty R \sum_{n=0}^3 \frac{F' U_n}{Z + n} \left(1 - \frac{l_r}{L_\infty}\right)^{-M'} \left(1 - \frac{l_c}{L_\infty}\right)^{M'+n} \left[1 - \left(\frac{L_\infty - l_L}{L_\infty - l_c}\right)^{Z'+n}\right]$$

For particular types of catch prediction other simplifying substitutions are possible. Thus in a note on the assessment of proposals for mesh regulation, Holt (1958a) showed that the expected long-term benefit to be obtained by increasing the age at first liability to capture from ${}_1t_c$ to ${}_2t_c$ is, in terms of the pre-regulation catches, given by

$$Y^* = {}_2Y e^{F({}_2t_c - {}_1t_c)}$$

where Y = original average total catch weight, of which a part ${}_1Y$ consists of fish younger than age ${}_2t_c$ and ${}_2Y$ consists of fish older than that,

Y^* = the expected post-regulation catch,

and F = fishing mortality coefficient for recruited fish between the ages ${}_2t_c$ and ${}_1t_c$.

Making the substitution for age in terms of fish length, as before, we find

$$Y^* = \left(\frac{L_\infty - {}_2l_c}{L_\infty - {}_1l_c}\right)^{F'} {}_2Y$$

where ${}_2l_c$ and ${}_1l_c$ are the lengths of fish at ages ${}_2t_c$ and ${}_1t_c$ respectively.

Recently a practical improvement has been made to this method (see Gulland, 1961).

THE REQUIREMENTS FOR PARAMETER ESTIMATION

The various rearrangements of a yield equation demonstrated in the section above show that it may not always be necessary to estimate separately all the parameters of reproduction, growth and mortality; or at least that some reasonable attempt at catch prediction might be made before this is possible. They also demonstrate that in such situations it is not possible to lay down a single schedule of data or of estimates which must be obtained for purposes of fish stock assessment and yield predictions.

The methods of estimating growth parameters when the ages of fish in

samples can be determined are well known; methods of estimating mortality coefficients in similar circumstances were reviewed by Beverton & Holt (1956) and there is not, I think anything fundamentally new to add to that review, though there has since that date been some refinement of certain methods [see particularly documents of the International Commission for the Northwest Atlantic Fisheries by Paloheimo and by Taylor, and also Paloheimo (1958) and Bishop (1959)].

When age determination is difficult or impossible, attention is turned to the possible use of length frequency distributions of catches. These distributions, or 'catch curves', are, when averaged for all seasons and over several years, typically peaked curves. The ascending left-hand limb of such a curve, represents recruitment into the exploited stock by growth of fish to a size at which they are retained by the gear, or by movement of young fish of catchable size into the fishing area. The descending right-hand limb may be interpreted in several ways, depending principally on the fishable life-span of the fish, and the type of gear used to catch them. Some gears, particularly gill nets and possibly hooks, do not retain large (or small) fish so well as they retain middle-sized fish (these terms are of course relative, and must be understood in relation to the sizes of mesh or hook in use). A first step is therefore to determine the relative probabilities of retention as a function of fish length, giving a 'gear selection curve', ordinates of which may be divided into the corresponding ordinates of the 'catch curve' to estimate the length composition of the fish population accessible to the fishing gear. A general method of determining the selection curve in such cases from comparative fishing experiments is now available (see Holt, 1957*b*; Olsen, 1959).

The descent of the right-hand limb of the 'accessible population curve' may be due, if several year classes or broods of fish are present in the population, to the decline in numbers of fish present with increasing age. If there is only one or a very few broods present the descent will merely represent the variability of size among fish of the same age, but there is usually a good chance of recognizing this situation from the seasonal changes in size-distribution, from which indeed the growth rate might be estimated.

When the slope of the right-hand limb of the accessible population curve is an expression primarily of decrease in number of fish with age, the decrease may be ascribed to mortality or to a net emigration from the fished area, or both. For the assessment of that fishery, however, the processes of death or migration are equivalent; they both result in fish becoming inaccessible to the fishery and may be regarded as 'mortality'. Only when emigrating fish may thus become accessible to a fishery elsewhere is it essential to distinguish these processes for assessment purposes.

Just as the rate of descent of the right-hand limb of an age distribution provides estimates of total mortality coefficient, so the right-hand limb of the size distribution, corrected as described above for gear selectivity, can provide estimates of the ratio of growth rate to mortality.

In the simplest case we may regard size as roughly linearly related to age; this is true, for example, of the weight of fish in the region of the curve of growth in weight near its inflexion. In this case plotting logarithms of relative frequencies against weight gives a straight line, the slope of which is equal to $-Z/x$ where x is weight increment per unit time. If two size distributions are available relating to two periods in the history of the fishery between which there was a known difference in fishing intensity it is possible to calculate two values, Z_1/x and Z_2/x and from these, if it is assumed that M and x are constant, values of F_1/x , F_2/x and M/x . A yield equation which incorporates a growth function in which size increases linearly with age is readily shown to contain the mortality and growth parameters only in these ratios, and thus it may be solved by the use of data for size distribution alone. This is essentially the method used by Gulland (1956) to assess a *Merluccius merluccius* fishery.

Unfortunately it is not satisfactory to assume a linear growth function in the absence of any clues as to the range of sizes of fish represented in catches in relation to the whole growth curve. A better assumption is that growth can be represented by a three-parameter equation of the von Bertalanffy form. One of these parameters (t_0) is essentially a scale adjustment. Beverton & Holt (1956) showed that in this case

$$Z' = (L_\infty - \bar{l})/(\bar{l} - l')$$

where $\bar{l}$ is the mean length of all fish greater than some arbitrary length l' , provided that the decrease in frequency at size for fish bigger than l' can be ascribed to mortality (or emigration). It is convenient to choose $l' = l_r$. Thus the problem of assessment in the absence of knowledge of age composition is, in favourable circumstances, reduced to the estimation of L_∞ so that measures of average size may be used as before to estimate Z_1/K , Z_2/K and hence F_1/K , F_2/K and M/K . In the rest of this paper I shall explore briefly some possible methods of doing this.

MARKING EXPERIMENTS

A general method of estimating L_∞ and K which may be applied to size increments observed between marking and recapture, has recently been described by Gulland & Holt (1959). The procedure is to plot length increments per unit time x against the average of the initial length and the length

at recapture, which results in a straight line cutting the x axis at $x = L_\infty$ and having slope

$$-K \frac{1}{b} \tanh b \simeq -K \text{ for small } b$$

where $b = Ka/2$ and a = time interval.

It should be noted that it is equally applicable to the determination of crustacean growth parameters from tagging experiments even when only the increment at moulting and not the moulting frequency, is known.

Now several experiments have shown that the presence of tags may affect the growth of fish, usually adversely. It seems however that a common effect is to restrict feeding, and in this case it may be that L_∞ will be altered rather than K . A review of existing data would probably clarify this point, but unfortunately data for tagging experiments are rarely published in sufficient detail for a full study of this kind. Further light could also be thrown on the problem by a comparative analysis of data for growth of fish in aquaria and ponds. It seems from preliminary analyses that although L_∞ may for a particular species vary over a very wide range, estimates of K are obtained which do not differ very greatly from those given by the natural curves of growth in wild populations.

MAXIMUM SIZES OF FISH IN CATCHES

A possible approach to the estimation of asymptotic size might be the examination of mean sizes of the largest fish in a series of samples. Certainly one can obtain some idea of the order of magnitude of L_∞ , but further than that it is difficult to go because the sizes of the largest fish depend not only on the sample size, but also of course on the mortality rate (see Holt, 1957c). It may be, however, that for certain purposes it would suffice to have minimum estimates of L_∞ . A comparative study of samples from stocks for which the growth parameters are known would be useful to give some idea of the value of such crude estimates of L_∞ .

SIZE AT MATURITY

It is commonly stated in the literature that many fish become mature at a size which is some rather constant proportion of their final length (see discussion by Svardson (1943)). The proportion usually quoted is about two-thirds, and, if the weight of a fish is proportional to the cube of its length, this corresponds with the inflexion point of the curve of growth in weight. This observation suggests a study of sizes at maturity, which may be measured by several methods in fish for which age determination is difficult — with a view to their use as estimators of L_∞ .

Several partial compilations of the ratio of mean or median length at maturity to the asymptotic length (l_m/L_∞) have recently been published (Beverton & Holt, 1959 and also Holt, 1959*a* and *b*). From these it is clear that the variation is considerable — from about 0.3 to more than 0.9. Allowing for the fact that some of this variation is referable to errors in estimating L_∞ , and that some more can be ascribed to lack of precision in both definitions and measurement of maturity size, it seems nevertheless that only the order of magnitude of L_∞ could be estimated from this ratio. This could, however, be better than nothing.

Some of the variability of the ratio l_m/L_∞ can be ascribed to differences in growth rate, up to the onset of maturity. This growth rate is defined by both K and L_∞ , but plotting l_m/L_∞ values from the compilation cited above against corresponding values of L_∞ shows no indication of a relation. On the other hand there appears to be some correlation between l_m/L_∞ and K , such that fish which grow rather rapidly towards their asymptotic size (high K values) mature at a size which is larger relative to that asymptote than that of fish which approach the asymptotic size relatively more gradually (low K values). This is true in spite of an apparent inverse relation between K and L_∞ (see later), and is illustrated in Fig. 1 in which the transformation $-\log_e (1 - l_m/L_\infty)$ is plotted against K . (See Tables I and II.) This transformation was chosen because it can, like K , take values from 0 to ∞ , it is theoretically equal to $[K(t_m - t_0)]$, and gives, when plotted against K , no obvious departure from linearity.

The relation of maturity to size or age of fish has been considered by very many authors. Most recently Alm (1959) has reviewed the literature,

TABLE I. *Frequency distribution of $-\log \left(1 - \frac{l_m}{L_\infty}\right)$ [from data of Beverton & Holt (1959)]*

$-\log \left(1 - \frac{l_m}{L_\infty}\right)$	Frequency
0-0.20	0
0.21-0.40	2
0.41-0.60	12
0.61-0.80	12
0.81-1.00	7
1.01-1.20	8
1.21-1.40	8
1.41-1.60	5
1.61-1.80	3
1.81-2.00	0
2.01-2.20	2
2.21-2.40	3
2.41-2.60	0

Mean of 62 values = 1.02 (corresponding with $l_m/L_\infty = 0.64$).

TABLE II.—*Values of growth and maturity parameters for some fish*

Species	K	L_{∞} (cm)	l_m/L_{∞}	Sources.
<i>Tilapia esculenta</i>	0.32	34	0.67	Garrod (1959).
<i>Upeneus moluccensis</i>	0.38	16	0.67	Gottlieb (1959).
<i>Polydactylus indicus</i>	0.15	150	0.57	Mohamed (1955).
<i>Mugil parsia</i>	0.19	40	0.25	Sarojini (1957).
<i>Clupea pallasii</i>	0.39	35	0.83	Japan (1955).
<i>Gadus minutus</i> ♂	0.43	20	0.56	} Menon (1950).
♀	0.43	23	0.56	
<i>Melanogrammus aeglefinus</i>	0.16	75	0.59	Thompson (1939).
<i>Limanda yokohamae</i> ♂	1.05	24	0.90	} Hatanaka &
♀	0.63	29	0.81	
<i>Citharichthys sordidus</i> ♀	0.34	28	0.68	Iwahashi (1953). Arora (1951).

especially in relation to his own experiments with salmonoids, but he did not, to my mind, sufficiently distinguish the different aspects of what is generally referred to as 'growth rate', and recognize that at least two parameters are required to describe normal growth increments and curves. Not only have conclusions as to whether size or age is the chief determinant of maturity often been conflicting for this reason, but there has been considerable discussion of whether the onset of maturity causes changes — usually decreases — in growth rate. This question arises from the observed coincidence between the inflexion in the weight-age curve and the size at maturity (not, of course reflected in the length-age curve). Because maturity frequently occurs at well over half the final length, and often at more than three-quarters of it, it can appear that the growth pattern thereafter is changed whereas the growth curves may in reality be quite smooth and continuous.

Only for a few fish are published data sufficient for analysis of the relation between growth history and maturity in individuals of the same stock, though l_m can often be estimated from the width of the first spawning ring on scales, etc., and the preceding growth deduced from the annual ring widths. Very commonly however it is reported that faster growing fish mature at an earlier age than slower growing ones, though they may be absolutely smaller at maturity than the later maturing fish (see e.g. Parker & Larkin, 1959, for *Salmo* and *Oncorhynchus* species). Garrod (1959) showed that those *Tilapia esculenta* in Lake Victoria which mature when relatively small have higher K and lower L_{∞} than those which matured at a relatively larger size. There is in his data some evidence that the ratio l_m/L_{∞} increases with increasing K . It may be worth noting that in cases such as this, where the values of K may be in doubt because it is not known whether scale-rings are annual or represent periods less or more than a year, then a relation such as that shown in Fig. 1 might suggest which of two or more differing values of K is more likely to be the correct one.

More light would be thrown on this problem by a study, in a single

FIG. 1.—Values of the growth parameter, K , plotted against a transformation of the ratio of length at maturity to asymptotic length.

Closed circles: Data from Beverton & Holt (1959) for many different fish species.

Open circles: From Holt (1959b) for mackerels.

Crosses: From Holt (1959a) for sardines and related species.

Triangles: Various other fish species, see Table II.

cohort, of the relations between l_m , L_∞ and K for individual fish, back-calculated from scales or other hard structures. At the same time it may be necessary to examine the mortality rates in subclasses of that cohort in which are grouped fish with the same growth patterns, it being remembered that the mean age of maturity is affected by the value of total mortality in the age range over which maturation occurs; and that neither the natural nor the fishing mortality rates of late maturing fish are necessarily the same as those of the early maturing ones.

It will now be apparent that if K were known a rather better estimate could be made of L_∞ from measurements of l_m . The required knowledge of K might come from tagging or rearing experiments. In practice care would have to be exercised because it seems that K may vary with environmental conditions, and particularly with temperature. Thus, Taylor (1958, 1959) has shown that K increases with increasing temperature in cod (*Gadus morhua*)

and in the Pacific razor clam (*Siliqua patula*). Holt (1959c, 1960) has argued that this might be expected to be a general phenomenon, knowledge about which would help in the prediction of growth rate in one area and for one species from knowledge of the growth in another area, at a different temperature, of the same or of a related species. Comparative study could give measures of the temperature coefficient of K by use of which K values determined experimentally might be used to estimate K in the wild population.

There are, however, several complications to this line of argument, some of which will be mentioned here. Firstly, at least within populations of the same species, K and L_∞ are inversely correlated. Thus Taylor (1959) plotted K against $E = KL_\infty$ in several populations of a number of fish species, and obtained linear regressions. K and E are not, however, proportional; they have, as von Bertalanffy himself argued on theoretical grounds, different temperature coefficients, so that for example a certain change in K is not associated with so great a proportionate change in E , and thus L_∞ decreases as K increases. Some, but probably not all, of the correlation between K and E , may be spurious. This is so because in the common method of determining K and L_∞ , the parameters of the linear relation between values of l_t and l_{t+1} are estimated graphically and a small chance rotation of this line about its mid-point will simultaneously result in lower K and higher L_∞ estimates, and vice versa. Further, because E is estimated as the product of K and L_∞ chance variations in K will be reflected in both 'correlated' variables. It should be mentioned that the apparent correlation between K and l_m/L_∞ could, theoretically, be spurious, for similar reasons. Lastly, extrapolation of a theoretical linear relation between E and K gives finite E for $K = 0$ and hence infinitely high L_∞ , and it would seem to be a more suitable procedure to find the linear regressions of $\log K$ on $\log L_\infty$, and hence find the parameters u and v in an equation of the form

$$L_\infty^u = Ke^{-v}$$

Such an equation could not be applied to unrelated species with an assumption that u and v were constant. It is worth noting, however, that the differences in growth rate between the sexes of a particular species seem to be of the same kind as the differences between growth patterns of the same species in different areas. Thus where, as in most fish, the growth patterns of males and females are different, the difference is usually such that the growth of males can be described by higher K and lower L_∞ than for females.

The correlation of K with l_m/L_∞ might be useful in choosing the most likely value for K when two or more possible values are suggested by different interpretations of the rings on hard structure.

THE RELATION BETWEEN GROWTH AND NATURAL MORTALITY RATES

Beverton & Holt (1959) have examined the relation between values of K and of M in wild fish populations for which sufficient published data were available, and suggested as a result of their study, that within a particular taxonomic group M and K were positively correlated, so that the ratio $M' = M/K$ is less variable than either M or K , and might even be considered to have a characteristic value for each group. This seems to offer the possibility of using only taxonomic criteria to set limits to the possible values of M' for making stock assessments in the absence of other data, and even of making simultaneous assessments for a number of populations of fish of the same group inhabiting a certain area. This would alleviate one of the serious difficulties of applying analytical stock assessment methods in tropical waters in which not only may it be difficult to determine age, but in which there are a very large number of species, often very similar, caught simultaneously by the same gear.

It is very commonly reported that most big fish in catches are females. This can be a result of the growth of females to greater asymptotic sizes, but where the *older* fish in catches are also females, it means of course that the mortality rate of males is higher than that of females. Beverton & Holt (1959) suggested that this is true particularly where there are sexual differences in growth rate. It may be noted that even though both values of K and of M or Z may be higher in males than in females, the ratios M' or Z' may be nearly the same in the two sexes, which need not therefore be treated separately in making assessments, it being sufficient to use a value of L_∞ or W_∞ which is an appropriately weighted mean of the differing values for the two sexes.

It is tempting to ascribe the relative constancy of the M/K ratio to the similarity, or even the identity, of physiological processes which determine the rates of natural mortality and growth. This explanation does not, however, appear to be satisfactory for situations in which mortality is largely due to predation. The existence of a mechanism relating maturity size with K would, however, ensure that in a population subjected to a high extrinsically determined natural mortality, and containing individuals with a genetically determined range of K values, the fish with high K values, which mature earlier, would have a selective advantage over those with low K values, so that an adequate number would reach maturity in each generation to ensure its survival. Such 'fast growing' individuals would have a much slighter advantage if M were low, and their advantage might be offset by other

factors. The evolutionary consequences of such mechanisms might be worth further examination.

CONCLUSION

I hope I have said enough to illustrate my reasons for believing that comparative studies of fish populations would be expected, even at this rather early stage in our knowledge of the dynamics of exploited animal populations, to give some practically useful results. Several kinds of comparison are possible and would be interesting. They include comparisons between species, considering systematic position; comparison between different stocks of the same species; comparison between sexes; comparison between different year classes or spawning classes of the same stock; comparison between individuals in a particular stock having recognizably differing rates of growth and maturity (as observed by back-calculating life-history from scales, etc.).

Gross comparisons, as of total stock size in relation to systematic position (e.g. Clupeoids seem to have larger populations than do Perciforms) might be useful, but 'dissection' of the population is likely to be more fruitful and less misleading, in the same way as internal anatomy is more useful than general external form in comparing individual organisms. However, to relate the mortality, maturity and growth parameters eventually to population size it will be necessary to make comparisons, not attempted here, between these parameters and the specific fecundity and recruitment rates. Thus, in a recent review of literature, Woodhead (1960) has drawn attention not only to complex relations between feeding level, growth rate, and age and size at maturity, but also to the fact that the number of eggs laid per spawning (and also sometimes, the annual fecundity, through changes in the frequency of spawning) are not simply proportional to the body size, but depend on the previous rate of growth.

Difficulties in making population comparisons arise from: absence of standardization in presenting results of, for example, maturity determination; and the problem of drawing up a set of parameters all of which have been, or can be, estimated for many populations, taking account of environmental differences. Other difficulties, very important in practice, arise out of the need to use published data. These may be difficult to find in a scattered literature and their use for purposes not intended by the authors may be dangerous, especially when their true meaning in their original context is misunderstood because that context was not fully defined. These difficulties should not, however, deter fisheries biologists from attempting to formulate hypotheses which unite into a single whole the considerable volume of accumulated data pertaining to fish populations.

SUMMARY

The annual catch of fish from a stock is given by the integral, over the fishable life-span, of the product of an instantaneous fishing mortality coefficient, a function giving the number of fish remaining at a certain time from an initial number of recruits in terms of coefficients of mortality, and a function defining the body weight of fish at each age.

If the ages of fish in a sample can be determined, then the coefficients of mortality may be estimated from the age compositions of catches, and the growth parameters from the curve of fish size at age. The growth parameters can also be estimated from, for example, data of marking experiments, without knowledge of absolute age. The process of marking affects, however, the growth rate of fish, but it seems to affect L_{∞} rather than K . This would be expected if marking primarily interfered with the feeding of the fish.

The simple equation for yield can be put in a form in which the mortality coefficients appear only as numerators of fractions in which the denominator is a growth parameter. Tables of the incomplete Beta-function can be used to evaluate yield. The equation can be expressed to give yield in terms of the growth parameter and of the relative lengths of fish at first liability to capture and at the end of the fished life-span.

Comparative studies indicate that the growth parameter K increases with increase in water temperature, but that the natural mortality may vary in the same direction. Intraspecific (sexual) and interspecific relations between these parameters seem generally to be of a similar kind. Not only is their ratio relatively invariable, but it may have a characteristic limited range of values for groups of fishes up to the Order level. The ratio may be estimated from size compositions of catches if the asymptotic length can be determined. Statements in literature to the effect that sexual maturity occurs at a size about two-thirds of the final length (= one-third of asymptotic weight) suggested comparative study of the relations between maturity size and age and growth rate, because determination of the mean or median size of maturity does not require age-determination. This study revealed that the ratio of size at maturity to asymptotic size does indeed vary over a restricted range, but it is correlated with K . The implications of this relation are considered with regard to the use of maturity studies in stock assessment.

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DISCUSSION

J. G. SKELLAM: In your equation (p. 57) you use F/K in a manner which suggests that F is constant, yet elsewhere treat it as a function of t . Was F assumed as a constant for simplicity, or was it determined from studies of catches in relation to mesh size and the integral evaluated numerically?

S. J. HOLT: No integrals were actually evaluated; they were written out only to demonstrate the parameters. F and M were assumed constant for the purpose of brief exposition. The assumptions depend on the type of prediction to be made, particularly whether of an effect of change in selectivity or of fishing intensity. The equation is equally relevant to the crustacean growth problems discussed by Hancock. If one carries out a tagging experiment and can obtain the increment at moulting, and from the same data the inter-moult survival rate, it may not be necessary to know the frequency of moulting.

A. C. SIMPSON: This approach may be of great value in population studies in Crustacea where the shedding of the cuticle at each moult renders age determination impossible. Our data on the relation between moult increment and total length, if extrapolated to the base line, do give a value close to the largest known lobster size, i.e. to L_{∞} .

S. J. HOLT: This might give a reasonable estimate of L_{∞} , if not of K , and thus without knowledge of maturity size could permit use of length frequency data for assessment purposes.

B. B. PARRISH: K might be obtained from aquarium studies on starved fish for which changes in weight will be a function of K .

S. J. HOLT: Some data for starved fish which were actually shrinking in an aquarium gave a K value more or less like that in wild populations. K seems not to vary much with feeding or habitat (except temperature) — L_{∞} however, varies greatly.

L. B. SLOBODKIN: The constancy of M/K ratios seem to suggest that predation is unimportant, and that the non-fishing mortality is basically a physiological product.

S. J. HOLT: I think it is better to look at the question from an evolutionary viewpoint. For survival of the population sufficient fish must reach maturity. Even if M had been determined by predation, K might be adjusted by natural selection so as to allow enough fish to reach the breeding state.

L. B. SLOBODKIN: It would seem to imply that the rough level of predation is the same around the world wherever the species is found, if K is a species constant.

S. J. HOLT: But K does vary within a species — it is temperature dependent. There is some evidence of the physiological determination of mortality from comparative studies of the two sexes, in a few species. Where both sexes have the same growth rates, there is normally no difference in mortality. Normally, however, the K of males exceeds that of females, and in such cases M of males also seems to be higher. This allows both sexes to be considered together, provided that the sex ratio is not altered by selective fishing.

F. T. K. PENTELOW: Does the diagram you have shown imply that unmarked fish live longer?

S. J. HOLT: No. Marked fish grow more slowly. There is sometimes evidence of differential mortality, but I have omitted it from this discussion.

E. B. WORTHINGTON: The aim of this approach would seem to be to give practical advice by extrapolation to parts of the world where data are lacking. Has this in fact been done?

S. J. HOLT: No. The present position is one of intensive study of the available data, to derive ideas about the steps which must next be taken. Full details about well-studied species are essential. Only a little information is available for tropical species. One can already see the utility of the method, however, in helping to resolve uncertainties in the available data. For example, the *Tilapia* species of the African lakes show scale rings which might result from either annual or biennial spawning. If they are treated as annual, a value of K is obtainable which may be a multiple or factor of the true value: the graphs in fact suggest that the rings are six-monthly.

E. B. WORTHINGTON: Clearly also this approach should allow information about the species to be deduced from the habitat data. Growth rates and breeding size vary very widely: thus in *Tilapia* there is great variation with habitat, and extrapolation from one habitat to another without adequate data can give misleading results.

ROE-DEER CENSUS AND POPULATION ANALYSIS BY MEANS OF MODIFIED MARKING RELEASE TECHNIQUE*

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INTRODUCTION

As in most European countries, the roe-deer (*Capreolus capreolus* (L.)) is a widely distributed and popular animal in Denmark although it causes considerable damage to forestry. Fairly reliable official bag records show that about 25,000 roe-deer are killed each year in Denmark by more than 100,000 licensed sportsmen: the animal is a much-coveted bag and the heads are very popular trophies. Deer management and shooting policy are founded on a large number of currently accepted rules which, unfortunately, often seem to be erroneous or of limited value since they are based on an insufficient knowledge of roe-deer biology.

Roe-deer density reaches its maximum in mixed woodland consisting of broad-leaved trees (especially beech) and conifers, and small plantings surrounded by arable land seem to be the preferred habitat. The largest bags are obtained in districts which also show the highest agricultural yield.

The Kalø estate was made an experimental game farm in 1949. Forested land makes up about one-third of the 1,000 ha, divided almost equally between two highly productive woods, Ringelmosen (164 ha) and Hestehaven (176 ha) (Fig. 1). The roe-deer population is large — about 70 deer per 100 ha of forest — a situation which sportsmen, especially from abroad, find it difficult to believe.

INITIAL CENSUS OF DEER

As has already been described (Andersen, 1953), in the autumn of 1950 we made an estimate, to the best of our ability, of the roe-deer population inhabiting the two forests, and concluded that seventy deer were present. During the subsequent three months we managed to kill the entire herd which proved to number 213. Without experience of such a campaign it is

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FIG. 1.—Map of the Danish Game Research Farm, Kalø. The position of the two woods 'Hestehaven' and 'Ringelmoseskoven' is shown with the surrounding arable land. Black rectangles in Ringelmoseskoven indicate location of traps.

impossible to form any idea of the ability of roe-deer to escape detection. The complete failure of our prior attempt at estimating herd size is most striking, especially since this initial estimate was made by the forestry and game personnel at Kalø, who had known the two woods for years and who had spent part of every day there. The result was greeted with widespread incredulity, and I believe that many people considered that our initial counting methods were faulty. However, confirmatory results were obtained when the owners of three or four other Danish estates decided to kill all

their roe-deer and to replace them by others introduced from districts with stocks of superior quality. In all cases, despite the fact that our figures were available as a guide, the number of animals actually killed far exceeded the most optimistic estimate.

It is noteworthy that population estimates in hare (*Lepus europeus*) and red deer (*Cervus elaphus*), made in the same subjective way, tend to be equally far from the mark. The human senses cannot replace more objective methods, even when direct observation is supplemented by the study of abundant snow tracks; we are therefore forced to conclude that simple observations in the field will, invariably, lead to erroneous results when they serve as a basis for population estimates of mammals — though perhaps to a smaller extent when large and conspicuous animals living on open ground are being counted.

In 1951 twenty-four roe-deer were introduced into the then empty woods, and the herd was found to increase in size quite explosively. In 1955 we were under the impression that the herd had reached its former size. Although the entire herd could, theoretically, be descendants of the twenty-four deer introduced, it is perhaps more reasonable to assume that a certain measure of immigration had taken place.

CENSUS BY MARKING AND RECAPTURE

Since our work is primarily experimental we felt the temptation to analyse in greater detail the size and composition of the fine roe-deer herd which filled the woods to carrying capacity. After careful consideration, we decided to do this by using a marking technique, rather than by shooting all the deer again.

Methods

Although the principles used in capture-marking-recapture methods are simple, the technique proved not quite so simple when applied to roe-deer in practice. I shall here describe the method which we finally arrived at and use now.

The trap consists of a fenced enclosure 2×20 m with a gate at one end; the gate can be closed by pulling a long wire. It is placed in a thicket in one of the spruce plantings in which all our fences are situated.

The trapping commences about Christmas; oat sheaves are placed in all traps and the baiting is repeated two or three times a week throughout the trapping period. The deer soon come to the enclosures for food, and during an initial period they are allowed to enter and leave freely.

The trapping proper starts in January, usually when snow covers the

ground. A party of three men go round by car and pull the gate wires which all end at a drive, and the deer which have come to the bait are trapped. Trapping has been carried out at all hours but best results are obtained by closing the gates shortly after dark, which is the time when the deer usually come out of the woods to feed in the fields. A total of 14 traps are used, all placed in one wood, Ringelmosen. Two parties of trappers each attend to seven traps.

Among the deer trapped two age classes are distinguished: fawns born during the preceding summer, and old animals. The fawns still possess their milk teeth and have a tripartite third premolar in contrast to the bipartite persistent tooth of animals more than one year old. In order to see the third premolar the mouth must be forced open, and an electric torch and a dentist's mirror must be manipulated skilfully.

A recurrent problem is the method used for marking the deer so that they are recognizable individually at a considerable distance, and remain distinguishable for several years. After a series of studies on captive deer, we have developed a leather collar studded with plastic buttons of different colours and bearing a copper plate giving a serial number and our address. As a special precaution the deer trapped also receive a metal ear-tag from which we can get all the information needed in the — rare — cases when the collar has been lost.

We have often been asked if the collar is likely to hamper the deer or even expose them to danger. The answer must be that during the years we have used the method we have not noticed any sign of inconvenience to the more than 200 deer which have been marked: they behave and reproduce normally and seem not to differ in any way from unmarked individuals.

Trapping takes place in January and February and the trapped animals are released immediately after marking. Many enter the traps again, sometimes on the next day, in which case the collars are read and the animals released.

During the subsequent months, March, April, and possibly May, one man has the job of combing the woods and their immediate surroundings with binoculars, and noting all the individuals observed. This work also has its problems, since all doubtful records must be excluded. Recording is not equally easy at all times: light colours for example show up better during dusk hours or in dense woodland. If the observer sees a group of, say, five deer together he must be able to 'read' all five; if that is not possible they should all be disregarded.

For the observer's use a number of observation posts have been made at strategic points; in addition he stalks the deer creating the least possible amount of disturbance; he takes special precautions to cover the entire woodland and to vary the time of his visit to different parts of the wood;

and generally utilizes his experience as a professional hunter to the utmost.

Several small incidents have occurred which help to explain our failure in estimating the herd size through direct observation, a good example being the occasion when four animals were seen grazing in one particular place every day for a period, without it being realized at first that they had all acquired different collars.

This method of 'recapturing' marked animals is somewhat unusual, and each individual is usually 'recaptured' several times; so that in total the 'sample' is often a good deal larger than the population.

Results

Our first trapping took place in 1956, but many difficulties were encountered and much had to be altered. Unfortunately, no trapping was done in 1957, and I shall, therefore, concentrate on the results of 1958, our best trapping year.

Trapping took place from 3rd January to 20th February and fourteen traps were used on twenty occasions; frequent snowfall helped us much. During the trapping period the number of recaptures increased steadily — much to the annoyance of the trappers who considered it a sport to get as many new individuals as possible — and much was learned about the home range of individuals. Recapture was most common in the same or a neighbouring trap; bearing in mind that the traps are only 2–300 metres apart it must be concluded that roe-deer are fairly stationary, perhaps more so than one would expect.

During the trapping period eighty-nine captures were made:
thirty-eight fawns (43 per cent of the captures),
fifty-one adults.

The figure of 43 per cent fawns is interesting since it coincides with that found in 1950 when the entire herd was killed. But while during the *kill* the fawns seemed exposed to the same risk as the adults the *trapping* showed them to be exposed to greater risk than adults, a feature which is well reflected in the following figures:

The first 25 captures included 15 fawns, i.e. 60 per cent

„	„	50	„	„	28	„	„	56	„
„	„	75	„	„	34	„	„	45	„
All		89	„	„	38	„	„	43	„

Although the figures are small the tendency seems clear; and the percentage of fawns must be considered high. It can be added here that the sex ratio was 1.3 females to one male (including fawns), i.e. exactly the same as in the herd killed in 1950. Considering only individuals more than one year old

the sex ratio was seventy-six females to forty-six males in 1950, i.e. 1.7 : 1 and thirty-four females to seventeen males in 1958, i.e. 2 : 1; and these differences are not considered significant.

The trapping results in 1956 support the assumption that fawns are more easily trapped than adults; a total of thirty-eight deer were trapped among which were 53 per cent fawns; the corresponding data from 1959 were: sixty-eight deer trapped and 54 per cent fawns.

On the basis of the 1950 population analysis and the good trapping data from 1958 I had foreseen that in the end we would arrive at a percentage of fawns of about 40; a hypothetical diagram showing fawn percentage as a function of duration of trapping period had already been constructed, the percentage starting at about 60 and declining, first slowly and when about half the population had been trapped more rapidly, to stop at about 40 per cent. I even thought myself able to provide a detailed explanation but this year's results, coming in while this paper was being written, have shown that such an action would be unwise. Up till now (2nd February 1960) we have trapped seventy-five deer; displayed as before, the data look as follows:

The first 25 captures included 8 fawns, i.e. 32 per cent

„	„	50	„	„	18	„	36	„
All		75	„	„	30	„	40	„

It is reassuring that the final percentage seems to be stable, but I have given up the idea of drawing a curve to show how one arrives at this figure. My conclusions may be summarized by stating that it is necessary to capture a very large proportion of the population in order to get representative data. Our preliminary results are only mentioned here because they show how easily one is led to make erroneous conclusions. In 1950, during the kill, we had a similar experience: the sex ratio changed with time, and not until 75 per cent of the population had been killed was stability attained.

I shall now return to the marking procedure used in 1958. All fawns (born during the summer of 1957) received a blue collar, all older ones a green-red, i.e. a collar with green and red buttons alternating. Among the older individuals were some which had been captured in 1956 and received the collar used for fawns at that time (white); their collar was replaced by another one but the white colour was retained. Not all deer captured were released, a few died and some were removed to enclosures to be used for other experiments. The individuals actually released were seventy-four in number: nine white (12 per cent), thirty-two blue (43 per cent), thirty-three green-red (45 per cent), i.e. forty-two white + green-red (57 per cent).

During the subsequent period (19th March to 1st May) the observer made 462 observations distributed as follows:

Without collar 122, blue 154 (45 per cent of those marked), white + green-red 186 (55 per cent of those marked), (total marked 340).

Thus old and young individuals were observed in almost the same ratio as the corresponding marks were present in the herd.

On applying the Lincoln Index ($p = an/r$, where a = number released; n = number observed; and r = number of marked among those observed, the three figures being 74, 462, and 340 respectively) one arrives at $p = 100.6$ with a standard deviation of $2.8 (\sqrt{a^2 n (n - r)/r^3})$, a result which points to a spring population of $100 \pm 7 (2.5 \times s)$.

More complicated methods of calculation, like that of Bailey (1952) give exactly the same result ($p = 100.5$; $s = 2.8$). When the population estimate is based on observations made during the first month after the trapping (i.e. two-thirds of the observation period) the same estimate is obtained although the standard deviation increases.

Thus there is reason for believing that the spring population consisted of approximately 100 deer. In order to compare with the 1950 data it is necessary to add fifteen deer (removed from the herd during trapping) and six (killed during the autumn); according to this the autumn population must have been about 120 deer in this wood which in 1950 was found to hold 117 deer. We are of opinion that the close agreement indicates that this population is near the carrying capacity of the wood.

Proceeding in the same way we have made another estimate based on the thirty-three deer captured, marked and released in 1956; the calculations led to a population estimate of 100–120 deer.

What about emigration and immigration during the trapping and observation periods? We have reason to believe that during autumn and winter migrations take place to a very limited extent: the marked deer are easy to spot, all forest owners and sportsmen in the neighbourhood know of our experiments and inform us whenever they see anything relevant, furthermore we pay a reward of approximately 25/- to sportsmen who hand in a collar. Emigration has only been noticed during the summer, at which time it is considerable. This aspect of our experiments (partly based on the marking of newly-born fawns during the summer) will not be discussed further here.

Returning now to the population estimate from 1958 I would like to say that there is a limit to the number of colour combinations that can be used during a sequence of years. It may therefore be of some interest to mention how a single category of individuals, such as fawns, can be used every year — there are several reasons for marking the fawns differently from other age-classes.

In 1958 we released thirty-two 'blue' fawns, constituting about one-third of all deer present in the wood. By focusing attention on those thirty-two

and the 154 observations made of them and considering all other deer unmarked (and $n = 462$) a population estimate of ninety-six is arrived at (as opposed to 100 when the entire material is used); although the standard deviation goes up to 6 the estimate is only slightly inferior to the one mentioned earlier.

In 1959 the weather was not favourable for trapping, since it was mild and practically without snow; nevertheless we succeeded in trapping sixty-eight deer (thirty-seven fawns and thirty-one older individuals). It has already been mentioned that in all probability the percentage of fawns was too high. Four individuals were removed from the population and only sixty-four were released, among them were thirty-six fawns (born 1958) which received an orange collar. All older animals received the usual red-green collar, and this means that the number of red-green deer is, by now, unknown. The same applies to the blue deer of the previous year, and both these classes may have emigrated to some extent during the previous summer, the actual amount of emigration being unknown since we cannot be certain to receive report of all emigrants.

A total of 650 observations are available from 1959:

Without collar 183 (28 per cent), blue (born 1957) 133 (20 per cent), orange (born 1958) 155 (24 per cent), red-green 136 (21 per cent), white (born 1955) 44 (7 per cent).

It is not yet possible to set up a life table or to consider the age classes individually, primarily because a considerable number of deer were killed selectively in 1955. In general one should not expose the population to shooting as long as experiments of this kind are being conducted; the removal of a few individuals on the other hand is probably inconsequential as long as the annual emigration is of the order of one year's production. In 1955 we made the mistake of shooting eighteen deer during the autumn, a few months prior to the trapping. Under the Danish Game Act there are two open seasons for roe-deer; bucks may be killed from 15th May to 15th July and bucks and does from 1st October to 31st December. I have long been of opinion that the shooting of bucks during early summer was unlikely to affect the autumn population, but to lead primarily to decreased summer emigration. However, I am now inclined to believe that, after all, summer shooting may affect the autumn population.

Calculations based on the data from 1959 can only be made by considering the orange deer as opposed to all others. The result indicates a winter-spring population of about 150 deer, the standard deviation being rather high ($s = 10$). This would imply that the 1959 population is a good deal larger than found for previous years and that the population is not of constant size as we have believed up till now.

We have several indications that the population may well have been larger in 1959; a relatively larger number of roe-deer were seen; 650 observations are a good deal above the usual number; the observer, who is a firm disbeliever in statistics, has expressed the same idea in his own way: he handed in this year's notebooks with the remark: 'I call it a lie if your calculations say 100 deer once again'.

The trapping technique, which we find fairly easy now, provides valuable material; on the other hand one must realize that upward of 75 per cent of the population must be trapped in order to give a reliable estimate of the percentage of fawns, and hence it follows that the value of analyses carried out on an essentially unknown percentage of captures or animals killed should not be taken at face value. This also applies to other species of deer; it is necessary to have at least a rough idea of the proportion trapped.

As regards the method of making a large number of observations subsequent to trapping and marking, it seems to provide promising results although here again it must be emphasized that a large body of data must be obtained. The use of fawns only gives slightly inferior estimates. During this winter we have tried to get some additional information by placing a spot of white paint on the flanks of some of the older animals. We hoped the paint would stay until the shedding period in May but have been disappointed, instead, during the last half of this year's trapping period we are replacing some of the red-green collars by others; which will complicate the observer's job this spring.

My window faces towards the wood, and I see deer every day; I am often in the wood; the Head gamekeeper lives in the southern part of the wood, and he is working in the wood every day — and still we find it astounding that it should harbour 100 deer or more. A few days ago I talked to the gamekeeper and asked him to forget all about the kill in 1950; what would his answer be if I postulated that the wood held twenty-five deer? He admitted quite willingly that it would be much easier for him to believe in twenty-five than in 100 not to speak of even higher numbers.

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DISCUSSION

I. A. McLAREN: In your paper you implied that you were dealing with an equilibrium population of around 170. Yet there is a very high production of young. How are the numbers maintained? Is there winter starvation?

J. ANDERSEN: Obviously a number similar to the excess of production must disappear each year. They leave the estate: hunters in the neighbourhood, who return our marking collars, probably take a good deal of the balance. In past years since 1954 we have not ourselves shot deer on the estate, but this year we killed eighty as an experiment.

I. A. McLAREN: Have you any idea what would happen if you fenced the estate?

J. ANDERSEN: The estate is fenced, but public roads cross the perimeter and the animals certainly use these as routes to pass in and out. On a nearby enclosed estate which had been completely fenced for fifty years the total stock (161) was destroyed in 1954 as it was a poor one. The number of fawns was low. Only 0.9 fawns were present per doe as opposed to 1.8 at Kalø.

E. B. WORTHINGTON: Is predation a factor of any significance?

J. ANDERSEN: No. Foxes may take new-born fawns but on the whole the influence of predation must be very slight.

T. B. REYNOLDSO: Is there any evidence that the deer on the enclosed estate you mentioned were affected by starvation?

J. ANDERSEN: There was perhaps some slight indication, because dead animals were picked up each winter, but no definite evidence. There was however one interesting result of a study made on the ovaries of the deer from that enclosed estate. In Kalø does have on average 2.0 corpora lutea per ovary: on this estate the figure was 1.6. This suggests that the population-limiting effect was being felt in the enclosed wood even at the very beginning of the reproductive cycle. An age difference was also perhaps involved. The mean age was 2.0 in Kalø as compared to 3 years in the enclosed area.

D. HANCOCK: Do adults and fawns take different food? Could your difference in proportions of fawns and adults trapped from year to year be due to a variation in the relative amounts of young and adult food — thus affecting the readiness with which they came to your bait. Would not this also affect relative mortalities?

J. ANDERSEN: The fawns often suckle their dams until Christmas time. There is no real evidence of what other food they take, or of any diet differences between foraging fawns and adults.

J. A. EYGENRAAM: In Holland roe-deer are increasing rapidly. What do you consider to be the cause of their increase in Denmark?

J. ANDERSEN: Afforestation, chiefly with spruce, is going on over a large area in Denmark, which is one factor aiding the increase. Farming is also becoming more intensive, and deer, like hares and pheasants increase according to rises in farming productivity.

M. SOLOMON: You mentioned that your herd was destroyed in 1950 and has since increased from a small foundation stock to about 200. How does the population growth rate calculated from this result compare with that calculated from your rate of annual production determined by trapping?

J. ANDERSEN: In the recolonization period we know that an influx of deer took place from outside the estate. We released collar-marked deer, but within a few days unmarked ones were observed. Hence we cannot be sure of the starting population.

R. J. ELLIOTT: On a 300-acre estate known to me recolonization seems to have been proceeding as the population was being culled. Thirty-six deer were shot in 1958 and 1959 but there has been no apparent reduction in the population. In many instances when particular deer had been shot it was known that they were replaced within two or three weeks.

M. W. HOLDGATE: Could there have been any immigration during the period of shooting in 1950, thus enlarging your total stock figure?

J. ANDERSEN: Roe-deer movements normally occur in the spring and summer: our shooting was done in the autumn when they normally remain in one place. So I do not think that this was a factor.

EXPLOITED BIRD POPULATIONS

POPULATION DYNAMICS AND THE EXPLOITATION OF DUCKS AND GEESE

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The family Anatidae, comprising about 145 species, is of world-wide distribution, but statistical information is limited almost entirely to species living in the Arctic and temperate regions of Europe and North America. The family is by taxonomic standards a homogeneous one in which current opinion favours the recognition of relatively few genera, and the geographical limits of the sample restrict attention to the occupants of a small range of habitats. Thus a comparative study of present knowledge of the dynamics of different species might be expected to reveal similarities rather than differences. In the first section of this paper I assemble information about the fecundity and survival to maturity of twenty populations of fourteen species. A second section is devoted to estimates of the mean adult survival rate of populations of twenty-three species. The third section discusses specific studies of the relation between the kill by man and losses from other causes against this comparative background.

THE PRODUCTION OF YOUNG BIRDS AND THEIR SURVIVAL TO MATURITY

In comparing specific characteristics of fertility and survival it is desirable to restrict attention to populations which are in a steady state. So few long and intensive studies of wildfowl populations have been made that it is impracticable to set up very rigorous criteria for selection. The results used here have been obtained from studies during at least three years of entire specific or subspecific populations or of breeding groups in clearly-defined areas, and are limited to breeding populations which varied very little in size, or if they fluctuated more widely showed no upward or downward trend.

The most economical method I could find of presenting the information is the series of histograms in Fig. 1, which record average annual production by a hypothetical group of 100 mature females from each population. The average number of eggs actually laid is substantially less than the number expected on the hypothesis that the output is equal to (mean clutch size $\times$ 100)

because a proportion of the mature females fail to lay. There are five genera represented in Fig. 1: two 'grey' and two 'snow' geese, all in *Anser*; three 'black' geese, *Branta*; the common shelduck, *Tadorna tadorna*; four 'dabbling ducks', *Anas*; and four pochards, *Aythya*. The sequence of the species is that in the classification by Scott (1957).

FIG. 1.—The average production of eggs by some wildfowl populations and the survival of offspring to breeding age. The theoretical egg production of 100 mature females is shown by the vertical bar. The average actual output is indicated by the total length of each column. Losses between laying and fledging are shown by diagonal shading; losses of eggs to the right, of young before flying to the left. Where there is doubt about the relative size of losses before and after hatching the two patterns of shading are combined to show losses between laying and fledging. The unshaded area shows losses between fledging and maturity and the black area is proportional to the number of young surviving to maturity.

The histograms suggest that the fecundity of very closely related species is similar and that there are much greater differences between genera (and tribes). Geese (*Anser*, *Branta*) lay few eggs. Not only are their clutches small, but they are usually unable to produce more than one clutch a year and a

significant proportion of mature birds fail to lay. In the case of Arctic nesting species (such as *Branta bernicla* and *Anser caerulescens*) years in which very few females breed successfully occur frequently. These non-breeding years seem usually to be due to a delayed thaw in the spring causing nesting sites to be unavailable or to severe weather in the early nesting phase of the breeding cycle inhibiting laying or destroying eggs. In species breeding further south (*B. canadensis*) catastrophes such as losses of nests due to flooding may affect particular colonies, but non-breeding years rarely, if ever, occur and failure to breed is usually a result of unsuccessful competition for nest sites or other limiting social behaviour. So far as is known at present losses of eggs during incubation and of young between hatching and fledging are relatively small in northern-breeding geese. In Canada geese egg losses may be substantial but gosling deaths are few. Geese do not become mature until at least two years old (*A. brachyrhynchus* and *A. albifrons* not until three) so that full-grown young birds are 'at risk' for at least twenty months before possible entry to the breeding population. Yet in *Anser* pre-breeding losses are relatively few. Though geese in their first winter suffer substantially heavier losses than do older birds, the first year mortality rates of the Arctic breeding species are well below those found in ducks. There is some evidence that in *A. brachyrhynchus* and *A. c. caerulescens* individuals in their second year of life survive better than mature geese. The examples of *B. canadensis* cited here appear to be affected by very heavy juvenile mortality: in the *moffitti* population this 'mortality' may well have included substantial emigration.

The shelduck has a goose-like low mortality-rate after hatching, and delayed sexual maturity (at three or four years) but loses eggs on a duck-like scale.

The dabbling ducks are prolific, supplementing their first clutches by re-nesting attempts when necessary, which they can do by virtue of nesting in temperate regions and beginning nesting activity early in the spring. They suffer massive losses of eggs before hatching or of ducklings before fledging, though steady populations apparently do not withstand large losses in both these stages. They mature in the summer following their birth, so that the pre-breeding period is short, but nevertheless juvenile losses are usually heavier than in geese, as are those of mature birds.

The diving ducks of *Aythya* seem to resemble *Anas*, with the possible distinction that losses before fledging seem to be inflicted more on ducklings than on eggs. The pochards, though not Arctic species, nest late in the summer and do not re-nest so freely as *Anas*, but their output of eggs seems to be as high. This is apparently because, despite the lower frequency of re-nesting, the proportion of complete breeding failures or non-breeding among mature females is low. The situation is rather obscure, because

populations of *Aythya* typically show greater fluctuation than those of *Anas*, while in some of them (*A. fuligula*, *A. marila*), and possibly in most, females may not mature until two years old. The large duckling losses seem to be associated with the abandonment of broods by their mothers long before the young birds can fly. In the dabbling ducks, mothers remain with their broods until they are flying strongly and duckling losses are largely confined to the first few days after hatching. Losses of young *Aythya* are less easy to measure, because the (motherless) broods tend to aggregate, but seem to continue at a substantial level throughout the pre-flight period.

ADULT SURVIVAL

The black portions of Fig. 1, showing recruits to the (steady) breeding population, suggest that there are generic resemblances in adult losses. It is rather easier to obtain information about adult survival than about the production and survival of eggs and young. Table I shows values of the mean annual survival of adults of twenty-three species in ten genera of seven tribes. The examples are confined to populations not showing marked trends. It has not been possible to use 'adult' here in a wholly consistent way. In most cases the survival rate shown applies to birds at least one year old, rather than to birds known to be sexually mature. Differences in survival between pre-breeders more than a year old and older birds are slight, normally much less than the fluctuations in adult survival between one year and another.

This extended sample strengthens the inference that closely related species have similar adult mortality rates ($d = 1 - s$, where s is survival) and that differences between genera may be substantial. On the view that the death-rate balances the birth-rate, rather than the other way about, this is equivalent to support for the hypothesis that the effective fertility (as defined by Capildeo & Haldane, 1954) of closely related species is similar.

Another inference from the general observation that geese are bigger than ducks is that large wildfowl survive better, and produce fewer offspring, than small ones. Using average weight as a crude but simple measure of size, the Spearman rank coefficient between body weight and adult survival for the twenty-six species in the sample is $+0.579$, $P \ll 0.01$.

Males survive appreciably better than females in some species, especially among the diving ducks, in which there seem usually to be an excess of males in the adult population, despite the parity of the sexes at hatching.

EXPLOITATION

The statistics so far presented, though inadequate for constructing a detailed working model of any specific population, provide a 'natural history'

TABLE I.—*Estimates of the mean annual survival rates of adult wildfowl*

Only one estimate is given for each form (species or subspecies): where several independent estimates were available a mean value has been used. Standard deviations are given wherever the method of estimation permits their calculation. All estimates are based on recoveries of marked birds, except those marked *, derived from censuses and age-ratios.

Form	Adult survival-rate	Regional population
Tribe Anserini		
<i>Anser brachyrhynchus</i> . . .	0.74 ± 0.02 .	Iceland.
<i>A. a. albifrons</i> . . .	0.72 ± 0.11 .	W. Siberia.
<i>A. a. flavirostris</i> . . .	0.66 ± 0.04 .	Greenland.
<i>A. a. anser</i> . . .	0.77 ± 0.02 .	Iceland.
<i>A. c. caeruleus</i> * . . .	0.63 .	Entire.
<i>A. c. atlanticus</i> * . . .	0.67 .	"
<i>Branta c. canadensis</i> . . .	0.78 ± 0.03 .	England.
<i>B. c. moffitti</i> * . . .	0.82 .	Washington.
<i>B. b. bernicla</i> * . . .	0.86 .	British-wintering.
<i>B. b. hrota</i> . . .	0.83 ± 0.08 .	Spitzbergen.
<i>B. b. orientalis</i> . . .	0.85 ± 0.05 .	Alaska.
Tribe Tadornini		
<i>Tadorna tadorna</i> . . .	0.80 ± 0.05 .	German-ringed.
Tribe Anatini		
<i>Anas a. acuta</i> . . .	0.52 ± 0.01 .	Russia.
<i>A. crecca crecca</i> . . .	0.49 ± 0.03 .	British-wintering.
<i>A. crecca carolinensis</i> . . .	0.52 ± 0.02 .	Utah.
<i>A. p. platyrhynchos</i> . . .	0.52 ± 0.02 .	NW. Europe.
<i>A. rubripes</i> . . .	0.50 ± 0.02 .	Illinois-marked.
<i>A. penelope</i> . . .	0.53 ± 0.04 .	NW. Europe.
<i>A. d. discors</i> . . .	0.55 ± 0.04 .	Manitoba.
<i>A. clypeata</i> . . .	0.56 ± 0.06 .	Britain.
Tribe Somateriini		
<i>Somateria m. mollissima</i> . . .	0.61 .	NW. Europe, Greenland.
Tribe Aythyini		
<i>Aythya vallisneria</i> . . .	0.59 .	Central Canada.
<i>A. americana</i> . . .	0.51 ± 0.04 .	Utah.
<i>A. fuligula</i> . . .	0.54 ± 0.07 .	NW. Europe.
<i>A. m. marila</i> . . .	0.48 ± 0.06 .	Iceland.
Tribe Cairinini		
<i>Aix sponsa</i> . . .	0.64 .	Ohio.
Tribe Mergini		
<i>Melanitta n. nigra</i> . . .	0.77 ± 0.04 .	Iceland.
<i>Clangula hyemalis</i> . . .	0.72 ± 0.04 .	"
<i>Mergus m. merganser</i> . . .	0.60 ± 0.07 .	British-wintering.

background for the study of exploitation, which in Europe and North America consists almost entirely of the shooting of full-grown ducks and geese for sport. (It is of interest to note that public opinion, and legislation, in most countries is hardening against the commercial use of wildfowl, so far as this amounts to offering the killed birds for sale.) The motives of sports-

men are more complex than those of commercial exploiters, but initially it seems best to assume that their principal requirements are to have available the largest possible number of full-grown individuals each season and to be allowed to kill as many of them as they can without detriment to their chances in future years.

Very few wildfowl populations in Arctic and temperate regions of the north are sedentary and many of them perform lengthy annual migrations. Thus sportsmen shooting in the autumn and winter have, in general, no direct means of influencing recruitment to the populations they are pursuing. Moreover, these populations are often heterogeneous assemblies of birds from many different breeding places. For a large safe kill shooting men should favour those species rearing relatively large numbers of young and particularly those in which a high rate of loss in the first year after fledging is still consistent with the maintenance of the breeding population. But this view will only be appropriate if losses from causes other than shooting are small in these species, or if shooting losses can be substituted for natural ones.

The mallard *Anas platyrhynchos* has been marked on a large scale in many countries so that much information on the survival of different sub-populations is available. From a survey (unpublished) of this material I conclude that the species is not capable of sustaining itself when adult losses exceed about 55 per cent, although some authors (e.g. Hickey, 1952; Lauckhart, 1956) do not concede this. Self-maintaining populations of this species show close similarities in their rates of recruitment and loss, despite great differences in the shooting pressure to which they are subjected.

The relation between the kill by man and other mortality is not easily investigated but in recent years the problems have received much attention in North America and results are beginning to be announced. The most impressive studies so far are those of the U.S. Bureau of Sport Fisheries and Wildlife on the canvasback *Aythya vallisneria* (Stewart, Geis & Evans, 1958; Geis, 1959; Atwood, 1959). This is a valued game species subjected to heavy shooting pressure, which accounts for more than a half of the deaths of all canvasbacks of flying age. In North America shooting pressure is subject to legislative control through the imposition of bag limits and seasons of varying lengths and the Bureau studies have taken advantage of this situation to demonstrate not only that shooting regulations have been effective in influencing the size of the kill but also that the size of the kill has influenced the size of the breeding population. This work is notable for dealing with the entire wide-ranging specific population of the order of half a million birds.

The canvasback is an example of a species with a high turnover which shows large changes in abundance from year to year, apparently due mainly

to variations in breeding success. The mallard and the green-winged teal *Anas crecca* have a similarly large turnover, but show less striking numerical fluctuations because their breeding success is more consistent. (No convenient summary of the varied data on success could be devised for inclusion here.) A study of the survival of marked teal (Boyd, 1957a) in Europe suggested that about three-fifths of male and one-half of female losses are due to shooting, mostly in winter, and that the kill directly affected annual survival rates. But it also indicated that heavy winter losses due to shooting are offset by reduced losses in subsequent months (including a higher proportion of 'natural deaths' than occur in winter), with the implication that non-shooting mortality should not be regarded as constant and independent of the kill, as some investigators have taken it to be.

No studies of non-shooting mortality among full-grown geese have yet been published but it appears that in several species the kill must constitute a much higher proportion of the total deaths than in these ducks. Some of the geese wintering in Britain which have similar adult mortality rates (see Table I) show interesting differences in the annual distribution of shooting losses. In the pinkfoot *Anser brachyrhynchus* the kill is largely confined to the period October to February, with peaks in October and January. In the Icelandic greylag *A. anser* losses are spread more nearly uniformly through the period September to April. In the Siberian-breeding whitefront *A. albifrons albifrons* the kill in April to June seems to be as great as that in autumn and winter, while in the Greenland-breeding *A. albifrons flavirostris* most losses occur in May, July, and November to February. Despite these differences in distribution the end results appear to be similar.

Geese, with their low reproductive capacity and delayed maturity, present problems to the prudent exploiter which are particularly acute in cases like that of the brent *Branta bernicla* in which recruitment is highly erratic. In geese, and in other large aquatic birds, as Austin (1957) has pointed out, 'maintenance of the adult population seems of greater importance to the survival of the species than the success of any particular year's crop of young'. If brent are to maintain themselves it would seem to be highly desirable to regulate shooting pressure on a seasonal basis so that in years of poor breeding success the kill is kept small. Greylags or Canada geese on the other hand do not greatly need frequent adjustments of the permissible take.

CONCLUSION

Understanding of the dynamics of wildfowl populations is so imperfect that students can as yet contribute little to population research on a broader scale, but the comparative treatment of closely-related forms which is possible in the Anatidae should prove of value.

ACKNOWLEDGEMENTS

Though most of the sums are my own and I have drawn perhaps too heavily on unpublished material in the files of the Wildfowl Trust, a review of this kind is largely dependent on the work of others. The list of references is, I hope, complete enough to record my indebtedness to published work. I am particularly grateful to Dr Daniel L. Leedy, Chief, Branch of Wildfowl Research and to Dr John Lynch and Dr Allen G. Smith, all of the Bureau of Sport Fisheries and Wildlife, U.S. Fish and Wildlife Service, for permission to make use of unpublished information.

APPENDIX: SOURCES OF DATA AND NOTES ON CALCULATIONS

1. *Species Included in Fig. 1*

- Anser brachyrhynchus* Baillon. Boyd (1956).
A. a. albifrons (Scopoli). Boyd (1957b).
A. c. caerulescens (L.). Data mostly from unpublished material of U.S. Fish and Wildlife Service, supplemented from Cooch (1958), recalculated.
A. c. atlanticus Kennard. Lemieux (1959).
Branta canadensis interior Todd. Hanson & Smith (1950), recalculated.
B. c. moffitti Aldrich. Hanson & Browning (1959), recalculated.
B. bernicla orientalis Tougarinov. Hansen & Nelson (1957), recalculated.
Tadorna tadorna (L.). Taylor (1959), with survival calculations by the author from records by Goethe (1957) and British ringing results.
Anas p. platyrhynchos L. Dutch data calculated from Eygenraam (1957) and published ringing recoveries. British data from Boyd & King (1960) and unpublished material. North American data after Hickey (1952).
A. rubripes Brewster. Wright (1954), Bellrose & Chase (1950).
A. d. discors L. Iowa data from Bennett (1938); Prairie Provinces, recalculated from unpublished material of Allen G. Smith, U.S. Fish and Wildlife Service, with survival calculations from unpublished recoveries collected by Dr M. Arellano at Delta Waterfowl Research Station, Manitoba.
Aythya vallisneria (Wilson). Geis (1959).
A. americana (Eyton). Low (1945) and Hickey (1952).
A. collaris (Donovan). Mendall (1958), recalculated.
A. fuligula (L.). Unpublished material on British birds.
A. m. marila (L.). Calculated from published recoveries of Iceland-ringed birds and Russian material (Y. A. Isakov in Dementiev & Gladkov, 1952).

2. *Additional Species in Table I*

Anser anser. Boyd (1957c) and unpublished.

A. albifrons flavirostris Dalgety & Scott. Boyd (1958).

Branta c. canadensis (L.). Unpublished English data.

B. b. bernicla (L.) and *B. b. hrota* (O. F. Müller). Boyd (1959).

Anas a. acuta L. Tamantseva & Shevareva (1957), recalculated.

A. c. crecca L. Boyd (1956).

A. crecca carolinensis Gmelin. From published recoveries.

A. penelope L. From unpublished British and published Icelandic recoveries.

A. clypeata L. From unpublished British data.

Somateria m. mollissima (L.) Published Swedish and Dutch, and unpublished British, recoveries.

Aythya ferina (L.). From unpublished British data.

Aix sponsa (L.) Stewart (1957).

Melanitta n. nigra (L.). From published Icelandic recoveries.

Clangula hyemalis (L.). From published Swedish, Icelandic and Russian recoveries.

Mergus m. merganser (L.). From published Swedish and British recoveries.

Information on adult weights taken from Kortright (1943), Elder (1955) and unpublished material.

Original calculations of survival from recoveries followed the maximum-likelihood method of Haldane (1955).

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DISCUSSION

H. KLOMP: How were the mortalities between hatching and fledging determined?

H. BOYD: The method varied with the species. For mallard, for example, a direct census method was used. The most publicized method in the literature is to follow the changes in brood size, but this is complicated by a tendency of broods to aggregate in some species. In many cases it is only possible to measure the output of eggs, and the ultimate output of young, but not the progress of mortality in the intermediate stages.

H. KLOMP: Many of the species you have discussed breed in the very far north, where data must be hard to gather. How many actual counts have been done for such species?

H. BOYD: Some of these Arctic breeders have been studied fairly well. The snow geese of northern Canada have been studied extensively, and

work on 'island' colonies has yielded data from which the rate of loss after hatching and before fledging can be assessed.

A. WATSON: Do the figures take into account total loss of broods through the death of females?

H. BOYD: Yes.

J. G. SKELLAM: Are the estimates of the numbers reaching maturity, based on the progeny of a hundred breeding females, and the other estimates of adult survival rate independent? Do they agree, when taken together, and show a steady state for the population?

H. BOYD: Yes.

J. C. COULSON: You have made a distinction between clutch sizes in ducks and geese. Is this hard and fast separation really valid? Surely sea-ducks, like eider and scoters, are intermediate? The eider clutch size averages about five in my experience — which is near to the goose range.

H. BOYD: The clutch size in eider is very variable. But I think they accord fairly well with my figure on the whole and normally fall within the duck range.

FLUCTUATIONS IN A RED GROUSE (*LAGOPUS SCOTICUS* (LATHAM)) POPULATION, 1956-9

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INTRODUCTION

During the last two decades fewer red grouse have been shot in Scotland than previously, and the primary object of the present research was to discover possible reasons for the grouse shortage. The work was inaugurated by the Scottish Landowners' Federation, in co-operation with the Nature Conservancy and Aberdeen University, on study areas in Glen Esk, Angus. Numbers of grouse have declined less on this estate than in some other places and the study provides a basis for comparisons elsewhere. It is envisaged as a long-term study and the present paper is a preliminary statement of data acquired so far. Discussion is minimal since each year has been different and subsequent work may well cause us to revise our present ideas.

The research is primarily a population study and the basic techniques are counting and marking. Methods and the sample obtained by trapping are therefore described in some detail. Particular attention is paid to the results obtained in autumn and winter, when the population is exploited by man. Breeding success will be considered in another paper later but some data are already available in mimeographed reports circulated annually (Jenkins, 1957, 1958*a*, 1958*b*, 1959, 1960, 1961).

GROUSE BEHAVIOUR

Red grouse in Scotland live on heather, *Calluna vulgaris* (L.), at all seasons (Committee of Inquiry on Grouse Disease, 1911), though they will readily take other items such as grass seeds and berries. They also visit stubbles in the early autumn where they glean the scattered grain.

Family parties begin to break up in mid-July and thereafter well-grown chicks may be found alone on the moor. These are usually cocks and the first song-flights ("becking") are seen at this time. More and more cocks start singing during August and September, mostly in the mornings and sometimes on fine evenings. This behaviour continues through the winter and

subsequent spring. When one cock hears another it will respond by singing and may make a song-flight in the direction of the other bird. Sometimes two cocks come close in this way; they will then threaten and occasionally fight. We regard this as territorial behaviour.

Hen grouse stay in parties and do not, as a rule, show territorial behaviour during the autumn. These flocks vary in composition and size (from two or three to twenty-five or more) from day to day, and individual hens often wander considerable distances, the furthest autumn recovery being $22\frac{1}{2}$ km (14 miles) away. On bright mornings, when cocks are singing loudly, hens may associate with them so that they appear to be paired. Such pair associations are usually temporary and a cock has been seen in company with two different hens on the same morning as well as with a succession of different hens on different days. Despite the movements of individual hens and of some cocks (presumably those that fail to secure territories), grouse numbers may stay constant throughout the autumn and early winter.

Some hen grouse start singing in October or November but few sexual chases have been seen at this time. Much of the display at this season is between birds mated previously that often stay on their old territory. There is usually little sexual activity between cocks and hens in the autumn.

During the winter grouse behaviour depends on the severity of the weather. When it is mild, as in 1956-7, the autumn pattern may continue during December and January. Territorial display is usually confined to bright, sunny mornings, or to mild days following a colder spell, and territory-owners may join together at other times. In exposed places or during snow the birds eventually gather into packs, more readily at higher altitudes. Hens pack first and in fine snowy weather cocks may show vigorous territorial display. If the snow continues, all the birds on a moor will join into packs hundreds strong. These readily break into smaller parties which are continually on the move from ridge to ridge, to black ground swept clean of snow by the wind. Such grouse are very wild and we have often seen packs moving up to one mile; when disturbed by an eagle (*Aquila chrysaetos* (L.)), they may fly high and over ridges out of sight. They soon return, however, and we have found no evidence of emigration from our study areas owing to winter storms in 1956-9.

Sexual activity starts quite suddenly with the return of fine weather, usually in February below 300 m (1,000 ft) but later at higher altitudes where the snow lies longer. Singing, threat, fighting, courtship display and chases are all at their maxima at these times.

The first eggs are laid in April or May and the peak hatch is in early June. The largest clutches are sometimes as many as twelve or thirteen eggs, more usually seven or eight. Only the hen incubates. In 1957, the only year when

the stock was healthy and had good breeding success, both parents stayed with broods until these broke up in July or August and vigorous distraction display by one or both sexes was the rule on the principal study area. It has been rare there since. In 1957 adults and young behaved as discrete family parties and stayed on their home territories. In 1958 and 1959 broods commonly disbanded and mixed; often there was only one adult with a brood of chicks. Sometimes they moved to water and in August 1959 a number of birds moved from the lower ground to hills where there were berries.

STUDY AREA

This paper is concerned with one study area of 1,135 acres (418 hectares) of open moorland in Glen Esk, mostly at 200–270 m (700–900 ft) above sea-level. It is apparently typical of many low grouse moors in north-east Scotland and is surrounded by hills where we have other study areas. The size of the area was decided arbitrarily so that it includes all the main physiological features of this particular locality. These are: two small farms with some arable and inbye land; dry, peaty slopes; wet, rather boggy areas; some moraine hillocks; streams; a wood; several gritty access tracks; and patches of various types of moor vegetation (*Molinia*, *Festuca* and *Deschampsia* grasslands; *Juncus* and *Scirpus* bogs; *Arctostaphylos*, *Erica*, *Vaccinium* slopes, etc.). The heather is regularly burned with small fires of up to about 20 acres. Nine tenths of the heather is less than 30 cm (twelve inches) high.

Initially the area worked was 325 hectares (830 acres) of flat or gently sloping moorland that was particularly suitable for counting grouse, but this was extended to 418 hectares in December 1956 to include a hill rising to about 360 m (1,200 ft). The purposes of the extension were to include some hilly terrain different from the flattish remainder, to surround all the stubbles where grouse are caught for marking, and to incorporate some large patches of berried plants (*Vaccinium myrtillus* L. and *V. vitis-idaea* L.) in the study area.

WEATHER

Summer weather does not seem to influence the fate of young grouse to any great extent and brood sizes have been similar in wet and dry summers (Jenkins, 1960). As a rule winter snowfall does not worry grouse since it is usually accompanied by wind that drifts patches of hill-top clear of snow, but the winter weather may be important in other respects since it can have a lasting effect on food supply.

Prolonged low temperature and low humidity in the absence of snow have been associated with widespread spoiling of heather which then goes brown in colour. An apparently reasonable explanation is that the plants become

desiccated owing to high evaporation and transpiration and minimum or nil water uptake from the frozen soil. Heather was spoiled in Glen Esk in anti-cyclonic weather both in April 1958 and, more severely, in February 1959 when much heather less than about five years old was killed and some older plants growing in dry places were severely damaged. This effect was local and seems to be prevented by a covering of snow. Similar damage to young plants occurred on some shallow soils in the drought of summer 1959, but this was insufficiently widespread to be important to grouse.

The first winter of the study, 1956-7, was mild without extremes of frost or snow and the subsequent spring and summer were wet and rather cool. It was the most successful grouse season so far. In 1957-8 there was a prolonged cold spell in the late winter, with deep snow on the hills till April and severe frost at low altitudes. The summer was essentially similar to 1957, with periods of both rain and sun when the chicks were small. 1958-9 was a season of extremes — the winter was open, with little snow in Glen Esk but prolonged black frosts for weeks in the late winter, freezing the ground over 2 ft deep, while the summer that followed was one of the warmest and driest this century.

METHODS

(1) COUNTING

We use trained dogs to find both live and dead grouse. Without dogs it would often be difficult to count the birds. We do this by walking backwards and forwards across the study area at right angles to the direction of the wind. The dogs run about within 50-70 m on either side, finding and flushing the grouse. We walk the transects in different directions according to the wind at the time, so that the wind carries the flushed birds out of the area altogether or on to ground already covered. Grouse usually return within about 10-30 mins., when flushed, and our transects are never more than half a mile long so that we can see most of the ground all the time and return on the next transect before the birds come back again. The method is an attempt to count all the grouse that are present, and is suitable because the terrain is very open, the highest vegetation being shorter than 0.5 m.

The size of a piece of ground to be counted on any one occasion depends to some extent on the topography and on the urgency of the occasion (we might count more if a storm was forecast). We find that it takes about 45-60 mins. to count grouse satisfactorily on 40 hectares (100 acres) and we rarely cover more than 120-160 hectares at a time. We have divided our study area into parts and the method is standardized in that we always count at least one whole part (50-110 hectares) at once on roughly the same transects. These are not straight lines; we zig-zag to give the best chance of

finding corpses. Detailed results given in the progress reports suggest that although there is sometimes movement from one part of the area to another, upwards of 40 hectares (100 acres) is a reasonable minimum unit for counting.

Three hundred acres is the standard size for our other study areas but we do not count on these in deep snow, when grouse are moving widely. Nearly all counts are done between 10.00 and 14.00 hours, since it is mostly during the afternoons that grouse desert their territories, and counting by this method would then be less reliable; exceptionally counts are done later when a blizzard is imminent. We do not count grouse in winds stronger than force 4 (Beaufort scale) since the birds then tend to become very wild and to flush far away from us. Rain makes counting impossible.

Grouse may sometimes be counted twice if they fly in front of an observer, particularly if they are flushed at a distance. There is also a chance that some birds are missed. Figures obtained for counts are therefore often presented as a range consisting of a 'minimum', i.e. birds which flew away behind the observer and are known to have been seen only once, and a 'maximum', i.e. the minimum plus those birds which flew in front and which may possibly have been counted twice. It is usually possible to see where birds land and if known individuals are flushed a second time they are not counted again.

It is important that the area to be counted is not too large because one might then be unable to see where birds landed that flew far away; with a relatively small area it does not matter where such birds land because the place will be outside the ground to be counted. The maximum includes only birds that were not seen to land, but which from their behaviour seemed likely to land on the area yet to be counted. Few birds fly in front when there is a moderate breeze blowing, but some counts have to be done in calm weather. For convenience in dealing with figures (as in Fig. 1), we use the mid-point between the maximum and the minimum. We also count all the dead birds we find, marking them with a stick and recording the probable immediate cause of death (Jenkins, 1958a, p. 57 *et seq.*).

We have checked the accuracy of count totals by recounting with the same or a different observer and also by counting from a Land-Rover (Table I). Counting from the Land-Rover is not much use except in dry places, because of ditches and bogs which prevent one covering the whole of a piece of ground (but it is useful for checking the identities of marked birds). We do a check-count whenever time allows and as routine whenever a count total shows a large change from a previous figure or there is too large a discrepancy, more than about 15 per cent, between the maximum and minimum figures. Counts are also repeated when it seems that the grouse may have been disturbed during a count, perhaps by a shepherd or predator; an advantage of working gently sloping ground is that one can see whether

TABLE I. *Counts repeated within a day or two to check the reliability of the counting method*

A. Counts repeated on foot					B. Comparison of a count done on foot with another done from a motor-car			
Dates	Area*	Acres	1st count	2nd count	Dates	Area*	Total (on foot)	Total (from motor)
1957					1958			
22nd and 29th March	IIA	120	38	36	8th and 11th Jan.	V	22	19
21st and 23rd Nov.	IV	130	51	63	4th and 6th Feb.	V	20	21
27th and 28th Nov.	III	280	132	134	20th and 23rd Feb.	V	17	22
8th and 9th Dec.	IIIB	140	85-90	81-96	20th, 21st and 22nd Oct.	V	9	11 and 11
14th and 15th Dec.	VI	240	89	97				
1958								
21st and 22nd Feb.	High A	300	193	210	20th and 21st Oct.	VIA	45	42
21st and 22nd Nov.	IIIB	110	19	22	11th and 12th Nov.	V	9	17
5th and 6th Dec.	Corndavon	230	141-143	151-160	11th and 12th Nov.	VIA	47-52	31
6th and 7th Dec.	III	280	83-105	76-88	23rd Nov.	V	9	9
Ditto	IIIB	110	22-23	22-23	23rd Nov.	VIA	26	26
					23rd and 26th Dec.	V	10	10 and 13
1959					1959			
1st and 3rd Feb.	I	160	36-43	36-40	3rd Feb.	V	10	8
2nd and 4th Feb.	II	260	41-47	40-47	4th Feb.	V	9	9
10th and 12th March	V and VIA (50+80)	130	44-47	34	4th Feb.	VIA	22	23
29th Mar. and 2nd Ap.	IV	130	37-44	36	6th Feb.	V	10	11
19th and 21st Oct.	IV	130	20-21	21-23	6th and 7th Feb.	IIIB (part)	13-16	15
26th and 29th Oct.	IIIA	170	35-45	35-37	26th and 29th Nov.	V	21	19
26th and 31st Oct.	High B	300	95	92-104				
					1960			
					12th Jan.	V, VIA (part)	18	17
					27th Jan.	V	9-10	11

* All these counts were on the Low Glen Esk study area unless specified (viz. High and Corndavon).

grouse are disturbed or not. Marked individuals are often useful in counts and the fact that we flush them where expected gives us confidence that the counting technique is reliable.

It would be difficult to check the counting method by a capture-recapture technique because it is not easy to catch a sufficient sample and because the constituents of the populations apparently change frequently. The similarity of repeated count totals suggests that we always count a similar high proportion of the birds present. We believe that the mean value is often within 5 per cent of the actual number present and claim a general accuracy of plus or minus 10 per cent. We are satisfied that the technique is in any case sufficiently accurate to show whether grouse numbers stay constant or whether there are large changes. It may not show changes in numbers of

TABLE II. *Figures obtained on counts, November 1956–February 1960*

	First season 1956			Second season 1957			Third season 1958			Fourth season 1959	
Acres . .	830	1,135	.	1,135	.		1,135	.		1,135	
September . .	—	—	.	538	.		—	.		112-121	184-188
October . .	—	—	.	570	.		418-450	.		178-199	
November . .	409	(531)	.	583-610	.		378-430	.		207-215	
December . .	362	(471)	.	507	.		380-422	.		219-253	
				442-492	.		389-435	.		226-257	
				461-521	.		375-405	.		224-232	
				485-507	.		377-408	.			
	1957			1958			1959			1960	
January . .	367	461	.	456-501	.		No counts	.		211-228	
				467-521	.		because of	.		218-224	
							snow	.		199-216	
February . .	274	364	.	420-483	.		197-242	.		—	
							202-223	.		—	
							204-230	.		—	
March . .	274	379	.	361-417	.		191-222	.		—	
							217-234	.		—	
April . .	—	—	.	351-394	.		—	.		—	
May . .	—	—	.	—	.		281	.		—	
Un-											
	Old	Young	Total	Old	Young	Total	Old	Young	known	Total	
August . .	333	658	991	410	361	771	205	89	71	365	—
Numbers shot .			476			134				56	—
(approx.)											

Notes

1. 1958 was a late spring and an April count was possible. The May total for 1959 was derived from many visits during late April and early May.

2. Young birds were well-grown in August 1959 and it was often impossible to distinguish them from old ones during the August count. The young to old ratio was 0.4 : 1 among the known birds. Therefore the totals are estimated as 110 : 255 (the only reason birds were not distinguished was that they flew off too far away from the observer).

3. The figures for 1,135 acres for November and December 1956 are estimates based on the empirical data from 830 acres (i.e. the figures for 830 acres multiplied by the mean ratio for the January, February and March counts on 830 and 1,135 acres).

less than, say, 10–20 per cent, but many alterations in population density appear to be of the order of one-third or more (Table II) and are demonstrated by this method of counting.

In interpreting count figures it is necessary to compare data from the different constituent parts with each other and with the total. An example is given (Table III), taken from the third progress report (Jenkins, 1958a). Fourteen counts were done between September and April 1957–8 and they show that grouse numbers fell from 500–600 in the autumn to 370–390 in the spring.

TABLE III. *Some count figures between September 1957 and April 1958*

		Count No.													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Part II	. 260 acres	(193	190)	(157	151)	(135	—	150	129	131	123	125)	(115	118	111)
Part III	. 280 acres	(170	131	175	174)	(132	134	109	132	124	135	141)	(122)	(112	93)
Total	. 1,135 acres	(538	570	—	595)	(507	—	466	491	493	475	490)	(451)	(388	372)
		Dates of counts													
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
Part II	. 21st	8th	30th	16th	26th	—	8th	19th	29th	11th	31st	22nd	3rd	9th	
	Sep.	Oct.	Oct.	Nov.	Nov.		Dec.	Dec.	Dec.	Jan.	Jan.	Feb.	Mar.	Mar.	
Part III	. 20th	12th	23rd	15th	27th	28th	7th	19th	29th	10th	30th	21st	2nd	8th	
	Sep.	Oct.	Oct.	Nov.	Nov.	Nov.	Dec.	Dec.	Dec.	Jan.	Jan.	Feb.	Mar.	Mar.	

Note.—The figures are bracketed according to a possible interpretation of the data (see text).

The data also suggest that the decline may have occurred in stages and show that the count totals for parts of the study area change in a generally similar manner. (Hence we are the more confident that the counting method is reliable.) For example it is clear that on Part II the first two counts were similar at about 190; the next two show a reduction to about 150; the next five or six a further fall to 125–135; while finally numbers fell to 110–120. Similarly on Part III there was a first set of counts averaging about 170; then a fall to about 135 maintained through six counts; and finally a progressive reduction to 93. These instances could be repeated but they are summarized in the total for 418 hectares (1,135 acres), of which II and III are a portion. Clearly there were in succession three or perhaps four different levels of numbers during the winter.

Some counts were exceptions from the general trends. The figures for II were fairly consistent except for count 7. On this particular occasion the second half of the count was spoiled by the appearance of a hen harrier (*Circus cyaneus* (L.)). It was not practicable to repeat the whole count and only the second half was done again. This figure was then added to that for

the first half, and the result suggests that we should really have repeated the whole count. On III the first two runs of figures were broken by counts of 131 and 109 respectively. In both cases there was an explanation — the 131 total was obtained by a student ill-acquainted with the ground and unaccustomed to handling dogs and the figure was probable slightly inaccurate. On the 109 count eight birds rose just outside the study area and were discounted and another flock flew at extreme range. This group was noted as 'at least 20, not more than 30' and was counted as twenty birds. Had the extra 18 grouse been added to the 109 total, there would have been seven similar totals in a row, from 27th November 1957 to 30th January 1958. The method, however, does not depend on the detailed accuracy of single counts and the fact that this one count registered 109 is immaterial. Clearly the population changed between count 4 and count 5 and then remained more or less constant until after count 11. This is the sort of conclusion in which we are interested and for which we claim our method of counting to be valid.

Between August and April we do counts fortnightly if the weather allows. Each count over the whole study area usually takes one observer about five days or two people about three days. Counting is impossible in summer-time when grouse are nesting, because the disturbance would be too great. We then visit different parts of the area daily and, by summing the results of our observations, build a mosaic picture of the population. Sometimes a count has been possible before shooting starts but the figures for 12th August 1957 and 1958 are derived from several visits on different days. Through extensive ringing of young birds we are confident that movement of family parties was negligible in these years, but difficulties have arisen with non-breeding adults, particularly in 1958. Such birds apparently move into and through the study area during the summer and may cause some errors in our population estimates, particularly with regard to young-to-old ratios (Jenkins, 1957, 1958*b*, 1960). Breeding success is not considered here but we think our study area, and the numbers of breeding grouse involved, are sufficiently large to make such inaccuracies small and unimportant.

(2) MARKING

In addition to ringing young grouse, we catch full-grown birds on the study area stubbles in the autumn, mostly in October and November, in funnel-entrance traps made of wire netting and baited with oat stooks. The grouse are ringed and individually marked with coloured plastic tabs (Blank & Ash, 1956). These tabs are 11.4 cm ($4\frac{1}{2}$ in.) long by 2.5 cm (1 in.) wide and lie on the birds' backs, secured by soft leather thongs looped round the base of the wings. Apparently they cause no discomfort or disability and the

birds ignore them. We use a different coloured tab for each sex and age-group (bird of the year or older) and identify individuals by a letter and number written on the tab. These figures can be seen clearly through binocular or telescope up to about 100 m.

We know of only five tabs (about 1 per cent) that have come off the bird through the leather rotting and we think that this occurs rather seldom. When the leather rots, it breaks first on one side and the tab may hang lopsided for weeks or months before it comes off altogether and we are thus forewarned of the loss of the tab. We know of three instances where the plastic snapped through and in these cases the remnant could be seen; careful examination of many grouse in the tabbing area suggests that this rarely happens and is not an important factor influencing our conclusions. One bird managed to get its head back under the transverse thong so that the tab hung down its belly. All these events occurred after the tabs had been on the grouse a year or longer and most of the events in which we are interested occur within a few months of the birds being tabbed. We are therefore satisfied that errors of technique are not influencing the data obtained.

Grouse can only be tabbed when they are full-grown, and we have not yet devised a satisfactory means for catching them except on stubbles. The period in which both red grouse and black grouse (*Lyrurus tetrix* (L.)) will visit stubbles is rather limited, varying from about five or six weeks to more than three months in different years. We do not know if these annual differences are correlated with the behaviour of the grouse or with the supply of other sources of food or with the palatability of the waste oats on the stubble, or with something else, perhaps the weather.

The sample obtained by trapping was probably typical of the grouse in the immediate vicinity of the stubble fields though not all these birds were necessarily resident there during the previous summer. Some may have been transient visitors. When we counted the moor it was always clear that grouse were either on the heather or on the stubbles (i.e. they were living on the study area and were not visitors to the stubbles from a distance). The birds entering the traps were therefore part of the adjacent population, which sometimes did not change in numbers during the trapping period; they were not additional to the surrounding grouse stock. Each year tabbed birds were numerous within about a quarter-mile of the stubbles and scarce further away; we think that this was the usual distance that grouse moved to the tabbing field.

The sample trapped sometimes included many more first-winter (young) hens than other age-sex groups (Table IV), though in the one year, 1959, when we could trap in September we caught twelve young cocks that month compared with only two young hens. These differences probably

TABLE IV. *Numbers of each age-sex group of grouse caught and tabbed each autumn 1956-9*

	1st-winter cocks	1st-winter hens	Older cocks	Older hens	Total
1956 . .	30	34	21	25	110
1957 . .	68	119	10	8	205
1958 . .	32	109	5	20	166
1959 . .	19	11	7	10	47

reflect differences in behaviour. We suppose that young cocks move about during late July to September, selecting their territories, while young hens stay together on the family range till October or later. Birds in each class come to the stubbles in turn as they start wandering from their summer quarters.

Each year the older (second year or older) grouse were mostly resident but many first-winter birds disappeared. The date of trapping made little difference to whether the young birds concerned disappeared or not (Table V). This suggests that the birds trapped were not a biased sample (i.e. they were not particularly liable to move in comparison with the remainder of the population). There was no tendency for one lot of grouse to come to the traps and then go away, and for another lot of birds to come and stay; they tended to disappear evenly throughout the autumn, and this was probably typical of other unmarked individuals in the population. Fewer young cocks disappeared than young hens (Table V) and more young cocks were retrapped than young hens every autumn. All the tabbed birds recovered more than two miles from the study area have been hens marked in their first winter and it seems that in the trapping time (October to December) first-winter hens are more liable to move than other age-sex groups.

Many more tabbed grouse disappeared from the study area each winter than could be found dead then or later (Table VI), and presumably most of the missing grouse left the area. Distant recoveries confirm this; 528 grouse have been tabbed altogether and of 164 recoveries, 24 per cent (thirty-nine birds) were found more than one mile away. Perhaps readiness to come to the stubbles and dispersal were consequences of the same behaviour pattern. The furthest recoveries so far, both hens moving in their first winter, were 22.4 km (14) and 32 km (20 miles) away in September 1958 and April 1959.

The numbers of tabbed birds are checked two or three times a week on small areas where we are doing behaviour studies. This is impossible for the whole study area which is checked in detail four times a year, on about 31st December, 1st April, and at the beginning and end of shooting, as minimum routine and additionally as time permits. The checks are done mostly from a car; they are not confined to the study area but we also look over ground an extra quarter to half-mile round about.

TABLE V. *Losses of young birds in the first month after trapping*

	Month first trapped			Total
	October	November	December	
A.—1st-winter cocks—				
1956:				
Total tabbed . . .	16	12	2	30
Number disappeared .	10	2	1	13
Percentage disappeared .	62	17	50	43
1957:				
Total tabbed . . .	48	17	3	68
Number disappeared .	12	4	1	17
Percentage disappeared .	25	23	33	25
1958:				
Total tabbed . . .	12	15	5	32
Number disappeared .	5	3	—	8
Percentage disappeared .	42	20	—	25
1959:				
Total tabbed . . .	18	1	—	19
Number disappeared .	6	—	—	6
Percentage disappeared .	33	—	—	32
B.—1st-winter hens—				
1956:				
Total tabbed . . .	19	13	2	34
Number disappeared .	12	5	1	18
Percentage disappeared .	63	38	50	53
1957:				
Total tabbed . . .	53	49	17	119
Number disappeared .	41	38	13	92
Percentage disappeared .	77	77	76	77
1958:				
Total tabbed . . .	30	60	19	109
Number disappeared .	25	38	4	67
Percentage disappeared .	83	63	21	61
1959:				
Total tabbed . . .	8	2	—	10
Number disappeared .	5	2	—	7
Percentage disappeared .	62	100	—	70

TABLE VI. *Changes in numbers of tabbed grouse and casualties recorded*

	1956-7	1957-8	1958-9	1959-60
Numbers of tabbed grouse on the study area				
Total during autumn . . .	110	205	166	47
Total recorded 31st December . .	70	93	82	23
Total recorded 1st April . . .	56	68	41	—
Total disappeared during winter . .	54	137	125	—
Number found dead during winter . .	9	14	13	—

(3) FINDING DEAD BIRDS

We look for dead grouse during counts and they are reported to us by keepers and shepherds who patrol the ground. Much of the area is a lambing moor and is walked several times daily by shepherds in the spring when we also examine the moor thoroughly while searching for nests. It is at this

season that a number of long-dead corpses are found but it is encouraging that the number of carcasses overlooked earlier have been few in relation to those found soon after the grouse died (Table VII).

The cause of death can be ascribed to one of three classes in the field. These are (i) predation; (ii) accident; (iii) 'others'. Grouse killed by predators usually lose some feathers and are often partially eaten (but here post-mortem changes and scavengers can cause confusion). In the case of accidents the grouse is found with some injury below an overhead wire or by a fence, or entangled in wire or caught in a snare or gin. Occasionally birds are struck by motor vehicles or poached. The cause of death of birds which have not died through violence is classified under 'others'. This includes disease.

We do not know what proportion we find of the total number of grouse that die on the study area (but see Jenkins (1961). Most of the heather is short, nine-tenths being less than 30 cm (12 in.) high. The dogs point at freshly dead grouse and we can often see these at a distance. Predation usually results in some feathers lying on the heather and these detached feathers, glinting white, can be seen from 100 m or more away.

Possibly we find a higher proportion of predation deaths than of birds that died from 'other' causes but it is clear (from the relatively small number of corpses we find long after death) that most of the deaths in the latter category occur in the spring and summer. Such carcasses are often concentrated along streams and in other green places. It is noteworthy that we find dead birds in some months and not in others, and that we have found most dead birds in each category at similar seasons in different years. Our findings probably indicate the proportions dying in different seasons, if not the exact numbers dying, and they suggest that relatively few grouse die from 'other' causes in the autumn and winter, the seasons which we are concerned in this paper.

RESULTS

The count figures (Table II) suggest that losses from the population occurred in two or three distinct stages each autumn and winter. For convenience these stages may be classified as (i) between the August count and the last count in December (the autumn decrease), and (ii) between January and March or April (late winter decrease). Comparable figures for percentage change were as follows:

	Autumn	Late winter
1956-7	—	24
1957-8	50	24
1958-9	49	43
1959-60	37	—

In 1957 the total autumn decrease was similar to that caused by shooting (48 per cent), but in the two subsequent shooting seasons only 17 per cent and 15 per cent respectively of the birds available were shot (cf. Table II). Hence there was no clear relation between the bag and the total losses at this season, and the close agreement in 1957 may well have been due to chance. This is in fact suggested by the data; counts between September and November 1957 showed that the population increased at the end of shooting and fell again later (Fig. 1), probably owing to some process quite unconnected with shooting.

FIG. 1.—Changes in numbers of grouse on the study area (1,135 acres) from November 1956 to January 1960. Note. The first three points, A–B, are based on empirical data from 830 acres — see Table II.

In 1958 and 1959, when the losses through shooting were considerably less than the total decrease in numbers, the autumn declines apparently occurred all in one stage in August or September. The decreases coincided with the shooting season (when we do no counts), but were not necessarily attributable to exploitation. In 1959 some of the losses were probably due to movements, and the very low count figure for September was associated with an exodus to a temporary food supply provided by berries on some of the hills. Some grouse apparently returned later (Fig. 1).

A period of relative stability of population density during each mid-winter period followed this late summer or autumn decrease, and later there was a further fall in numbers of 24–43 per cent in February or March. Then numbers stayed level again through the spring. In the first two seasons (1956–7 and 1957–8) the mid-winter and spring populations were each similar, but the levels were different in 1958–9 and subsequently. None the

less the different stages were quite distinct each year. Apparently the annual decreases in numbers conformed to a definite pattern.

Periods of stability at mid-winter occurred each year but were particularly noticeable in the last three seasons. In these cases five, six or seven count totals were similar. It is instructive to compare known losses from the population with the count figures during this period. Comparable figures for tabulation are available each year for December (Table VIII). These show clearly that the population did not decrease to the extent expected with regard to known losses.

TABLE VIII. *Early winter losses of tabbed birds compared with numbers found dead and changes shown by counting*

Year	Number tabbed before 30th Nov.			Total found dead Nov.-Dec.	Count figures for whole population			
	Total tabbed	Number on 31st Dec.			Nov. total	Dec. total	Decrease between Nov. and Dec.	
		% lost	No.				%	
1956-7	101	63	38	11	531	471	60	11
1957-8	183	88	53	49	507	496	11	2
1958-9	132	56	58	43	412	392	20	5
1959-60	47	23	51	10	241	228	13	5

Details for the different years are as follows. In 1956 numbers fell between November and December, so this year is not considered. Between 25th November 1957 and 31st January 1958 (counts 5 and 11 in Table III), when counting suggested numbers were stable, seventy-two grouse were found freshly dead and at least seventeen tabbed birds disappeared. Losses of this order should have been detected by counting if they were not made good by immigrants. Between the end of September and 31st December 1958, about eighty tabbed grouse disappeared from the study area (Table VI), presumably through movement out as few were found dead, and over sixty other grouse were found freshly dead (Table VII). In this case at least 140 grouse disappeared from a population in which the density stayed steady.

In 1959 between September and the end of the year forty-nine birds disappeared, including twenty-five known casualties and twenty-four tabbed birds, even though no fewer than seven consecutive counts showed that the total numbers did not change correspondingly. Thus in the three years for which we have detailed information (1957-8, 1958-9, 1959-60), a minimum of 18 per cent, 32 per cent, and 26 per cent of the grouse are known to have died or disappeared at times when repeated total counts were similar. How-

ever 38–58 per cent of the tabbed birds were lost each December (Table VIII), and so the total number of individuals missing from the population may have been much greater. Clearly many more grouse were lost, presumably through emigration as well as death, than would appear from the counts alone.

The constancy of the population density at these times was evidently a result of an active process regulated by the grouse themselves. This maintained total numbers steady despite alteration of the individual membership of the population. Despite the apparent stability of the population, individual grouse must have constantly moved into and through the area from outside, replacing the casualties and emigrants.

A similar process may have operated during the late winter when count totals each year were again similar and also during the summer-time. In both 1958 and 1959 old birds that died during the breeding season were apparently replaced. In 1958 there were seventy-eight known casualties (mostly unmarked) on the study area between April and July (Table VII). Thus with a population of 370 in spring, the calculated adult population would be about 290 in August. In fact the estimate was about 410. Similarly in 1959 sixty-one deaths were recorded between April and July; yet the respective figures for spring and August populations of old birds were 225 and 255 (Table II). The differences between 370 and 410, and between 225 and 255, are slight (plus 11 per cent and plus 13 per cent), but possibly the spring level was actively maintained throughout the breeding season. Further observations are needed.

DISCUSSION

This is a preliminary account of our findings and it might be premature to form any definite conclusions. Nevertheless it appears as though the grouse population density on our study area has to a certain extent been regulated by the grouse themselves. External factors, such as predators and disease, are certainly important but apparently this population has been to some extent self-regulatory. We do not know how the mechanism works nor why the grouse themselves permit their population density to stabilize at different levels. Possibly there are annual behaviour differences, maybe correlated with changes in resources.

Observations suggest that numbers change when different types of territorial behaviour begin. During the summer there is little aggression and numbers build up to a maximum through breeding. Then in August and September the cocks take up territories and some aggressive display is seen. This coincides with the first fall in numbers. During the autumn, temporary pair associations are observed and one function of these may be

to adjust the number of hens to the number of cocks and so regulate population density.

Sexual activity starts with the first mild weather in February or March. The late winter periods of decrease have also occurred at this time and perhaps they are associated with a second change in behaviour when both sexes become more aggressive. The decrease may also be associated, as perhaps in 1959, with a change in food supply or other resources. However the process works, it is clear that the population levels observed are not due to chance, nor primarily to mortality, but that numbers are regulated by some active process operating through the behaviour of the grouse themselves.

Perhaps the August populations have not been fully exploited by man, but the amount of shooting depends chiefly on the enjoyment gained from a certain expenditure of cash and energy. There is little consideration of economics. In 1957 the study area grouse were probably exploited ideally since the population was reduced to a level similar to that one might suppose it would have fallen to anyway. Efficiency in exploiting a grouse population must depend on knowing what the subsequent levels are likely to be. This will depend on an accurate knowledge of the numbers of birds present and their history and on local conditions. Whether the population is declining or expanding may be important considerations and the condition of neighbouring moors may be involved also. A great deal of further research is necessary before the prediction of December population levels becomes a likely possibility.

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SUMMARY

1. A long-term programme of research into the population dynamics of red grouse is being organized in north-east Scotland. This paper is a preliminary report on the methods used and the results obtained in the first three years. The work described is an intensive study of the birds on 418 hectares (1,135 acres) of moorland at 210–270 m (700–900 ft) elevation in Glen Esk, Angus, with particular reference to changes in numbers during autumn and winter.

2. Total counts, using dogs to scent and flush grouse as the observer walks standard areas, show that grouse have declined in numbers from the beginning of the study in 1956 to a low level in early 1960. Decreases have occurred each winter through well-marked stages of loss (37–50 per cent and 24–43 per cent), separated by periods of one to three months during which numbers have stayed level.
3. Marking of individuals and discovery of corpses have shown that during these periods of stable numbers there have been changes in the individual membership of the populations, those that died or emigrated having been replaced by incomers from elsewhere. Thus the population density has presumably been maintained level by some active process regulated through the behaviour of the grouse themselves.
4. Efficient exploitation depends on prediction of the levels at which the grouse will stabilize their numbers at the end of the shooting season.

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DISCUSSION

I. A. McLAREN: Was there any evident difference in the amount of winter cover available for grouse between 1958 and 1960 that might account for the difference in population?

D. JENKINS: There was no evident difference as far as we could assess it.

E. DUFFEY: How do the food resources of recently burnt heather compare with those provided by old — say eight year old — stands? Could the pattern of burning cause variations in population level?

D. JENKINS: The information available shows that young heather is more nutritious than old — at least to sheep. But I doubt if there is enough year-to-year change to explain the very marked population changes. Certainly this factor is unlikely to operate in September, which is the time of the most sudden population decline.

T. H. BLANK: Would you elaborate on your statement that 'more birds are available than are present on the area'.

D. JENKINS: We have found that numbers remain constant week after week within our counting error of 10–15 per cent, although there is a known

mortality and exodus. Presumably therefore there is a surplus of birds flying in from other habitats and replacing those dying on our area.

T. H. BLANK: There must be a compensating increase in populations elsewhere at times when your populations show sharp declines.

D. JENKINS: Not necessarily; birds leaving one area may find another place that is temporarily understocked and in this case they will settle and the numbers in the second place will increase. But if the emigrating birds fail to find an understocked area, they may scatter among the marginal, more or less uninhabitable, places interspersed between the optimum habitats. Here they will eke out a living through constantly paying short visits to the optimum habitats, seeking a territory vacated by a previous resident. The mortality-rate in the marginal areas is probably very high, and the surplus birds may rapidly be lost through disease, starvation, predation and so on.

G. C. VARLEY: A consideration of the possible movements of birds leads me to wonder if Jenkins and Watson may have chosen a really favourable habitat for grouse for their census: an area selected preferentially by them. At the end of the season birds would be expected to scatter, to be displaced from such an area, returning from less favourable surrounding areas later to make up gaps left by mortality in the study area. Thus the autumn fall in the study area would be balanced by a rise in the adjoining unfavourable habitats.

D. JENKINS: The study area which I described is only one of a series which extends upward to the upper altitudinal limit of grouse in the district. A pattern of population changes similar to that on the lower ground is observed under these higher conditions. This suggests that all habitable areas are therefore in a sense 'saturated'. Even a sample area 50 miles away, where grouse are at different levels of population density, shows a comparable pattern of changes, as if a large area of eastern Scotland was similarly affected by a bird which everywhere over-reproduces itself, and is usually under-exploited.

G. C. VARLEY: But surely the stability of population in the study area can only arise because of immigrants coming in from outside. The source areas for these birds must not have stable populations. Where do these immigrants come from?

D. JENKINS: I think there are two possible sources. First, there is often a surplus of birds from areas like ours spreading in autumn and late winter, trying to colonize new areas and many of these may find suitable niches elsewhere. Secondly some surplus birds that fail to find optimum niches may be present much of the year as non-breeders in marginal habitats, from which they pass as transients through high-density areas. They would then be

available as colonists for optimal places. Most birds in marginal habitats probably die very quickly and these populations must be very unstable. Dying birds are certainly sometimes seen, even in the breeding season, in unlikely places like farmyards, grasslands and other areas which are not normal grouse habitats. Perhaps 10 per cent of the total population may sometimes be made up of these surplus dying birds. If the population is rising, presumably such birds are likely to become established. At other times when they try to inhabit marginal habitats where they do not breed, they are likely to die, perhaps through starvation or predation.

I. A. McLAREN: Surely you may have a long-term trend, like that between 1956 and 1960 and yet have the habitat in some sense saturated throughout?

D. JENKINS: Yes. I think this is a correct interpretation.

M. E. SOLOMON: If you are right about the existence of a large number of wandering grouse, presumably this means that the density of grouse on the ground may be regulated by some pattern of territorial behaviour?

D. JENKINS: Yes. I believe that territorial behaviour may be of real significance. Cock grouse are first territorial in August/September, at a time when the first big fall in population density occurs. At this stage there is an initial high density of birds not behaving in a mutually antagonistic manner. The males then take territory and are pugilistic, whereas the females still flock. However the cocks are only territorial in the mornings and may feed in flocks later in the day. This pattern persists through the autumn. At the end of the winter the females also become territorial and become sexually responsive. This change corresponds with the second drop in population. In the early winter the females adjust their numbers to the males, going around in pairs though not constant ones: numerically the population is paired but the individual alliances change. Thus in the autumn males alone are territorial and the females fit in wherever they happen to be, while in the spring both are territorial and so bring about a stricter population limitation and the second fall in numbers.

A. WATSON: In the spring, also, the birds are more consistently territorial — in the afternoon as well as the morning: the whole behaviour is intensified.

G. SURTEES: We seem to have had two examples today of migration into and out of a sample area leading to a stable population — in both grouse and roe-deer. In an exploited area we must postulate either an entry of animals or an exit. If entry, the population will be maintained with stable numbers, but if the habitats throughout the range of the species are unequal

this may be gained only by the abstraction of individuals from the less favourable habitats and their ultimate underpopulation.

R. M. LAWS: An analogy is possible here with the Elephant Seals (*Mirounga leonina*) on South Georgia. Here adult males are harvested from the beaches. As bulls are removed there is a compensating influx of others to take their place, these coming from the fourth of the large subdivisions of the island, which was formerly a sanctuary and has the largest population.

A. LUXMOORE: Was the level of grouse stock at which the area was saturated controlled by the amount of available food, or some similar condition capable of controlled management?

D. JENKINS: This is not known at present.

FLUCTUATIONS IN A PARTRIDGE POPULATION

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The data presented in this paper have been collected from a 3,600 acre (1,454 hectare) area in West Hampshire. A brief description of the area and methods used in data collecting have been given elsewhere (Blank & Ash, 1955). Censuses have been carried out in March, September and December; while a sample count of from one-third to one-half of the March population has been made in August. In addition, more than half of the partridge nests have been found each year, and this nesting data, together with the information obtained from the examination of birds shot in October, provides the basis of the material concerning a partridge population. It should be pointed out that this partridge population is a mixed one consisting mainly of the Partridge (*Perdix perdix*), but also containing a small proportion of Red-legged Partridges (*Alectoris rufa*). The latter average approximately 5 per cent of the breeding population, but have varied from 2.8 per cent to 7.6 per cent. Data concerning the two species have been obtained separately, except for the September and December censuses (when the method of counting makes it difficult to distinguish between the two species), but since the differences between the species and the proportion of Red-legged Partridges are both small, the data for the two species has been pooled (unless otherwise stated). The exploitation of this population has consisted mainly of controlled shooting in the autumn so that an adequate breeding stock will be present the following spring, together with a system of nest protection intended to ensure a relatively high nesting success. By these means an autumn surplus which can be shot has been created. Habitat improvement, supplementary feeding and the release of hand-reared partridges have been attempted on such a small scale that it is unlikely that they have had any appreciable effect on the population figures.

Autumn populations have shown well-marked fluctuations over the eleven-year period, with peaks in 1949, 1952 and 1957 and lows in 1954 and 1959. If the autumn population is compared (Fig. 1) with the breeding density of the previous spring, it will be seen that high autumn populations have resulted from both low (1949) and high (1952, 1957) breeding densities. Low

autumn populations have also followed both high and low breeding densities (cf. 1954 and 1959), and this emphasizes the point that the autumn population is a product of the breeding stock and its success in producing and rearing young birds. The number of pairs in the breeding stock is determined by four main factors:

1. The autumn population in the previous year.
2. The number of birds shot.
3. The number of birds that disappear between September and March.
4. The sex ratio of the population prior to pair formation.

FIG. 1.—March and September stocks, 1949–59.

When the autumn population has been censused, the shootable surplus has been determined each year on the assumption that approximately 40 per cent of the unshot birds will disappear between September and March, and that approximately 600 pairs (or a pair to 6 acres) is the maximum density likely to be achieved in this type of country. Unfortunately, it has often proved impossible to shoot the theoretically correct crop of partridges (due to unfavourable weather conditions or field crop distribution) so that shooting has not always been the accurate density dependent form of predation on the partridge population that it was intended to be (Table I, Fig. 2). However, the number shot has varied from 10 per cent in low years to 35 per cent in years of relatively high recruitment and adequate breeding stocks, and has resulted in December (post-shooting) populations of from 1,357 (1959) to 1,917 (1953). (1958 has been excluded since, for experimental reasons, the population was deliberately reduced to a low level in December.)

In addition to the known stock reduction due to shooting, the partridge population is considerably reduced between September and March (when

TABLE I. *September, December and March census, number shot and early and late winter loss, 1949-59*

Year	Sept. census	Shot	Early winter loss	Dec. census	Late winter loss	March census
1949-50	3,256	1,034	469	1,753	989	764
1950-1	2,783	756	613	1,414	634	780
1951-2	2,384	578	400	1,406	429	977
1952-3	3,172	1,077	504	1,591	444	1,147
1953-4	2,373	349	107	1,917	621	1,296
1954-5	1,787	179	14	1,622	581	1,041
1955-6	2,082	298	275	1,509	556	953
1956-7	2,107	386	25	1,696	537	1,159
1957-8	3,643	1,287	662	1,694	439	1,255
1958-9	1,987	620	241	1,126	398	728
1959-60	1,811	383	71	1,357	—	—

pair formation is completed) by loss from a variety of causes. Chronologically this loss may be divided into two parts — the early winter loss (between September and December), and late winter loss (between December and March). While certain types of loss (deaths due to accident, predation, disease) are common to both periods, losses due to shooting are the biggest single factor in the early period, and in the latter period loss due to local movement accompanying pair-formation is the major contributory factor.

Early winter loss has been highest in the four years (1949, 1950, 1952, 1957) which have experienced the heaviest shooting pressure and lowest (in 1953, 1954, 1956) when shooting pressure was relatively light. Since the heavier

FIG. 2.—The effect of shooting on December and March population (data in Table I).

shooting depends upon high autumn populations (high young/old ratio) it may be argued that the high early winter loss is not necessarily connected with shooting. However, in 1958 when the autumn population was low (resulting from a low rate of chick-survival) shooting pressure was deliberately increased out of proportion to the September population. The result was that in spite of the relatively low autumn stock (with a low young/old ratio) the rate of loss (17.6 per cent) was much higher than in years with similar autumn populations but much reduced shooting pressure (average 1953, 1954, 1956 = 3.3 per cent). Observation of marked coveys on an unshot area confirms that loss during this period is relatively small, although some local movement occurs. This movement is really an extension of the daily range of the coveys, and is initiated by the ploughing up of the autumn stubbles. Coveys generally extend their daily range so as to include a favourite feeding ground (i.e. on unploughed or undersown stubble). Since a large area is censused, it is unlikely that chance crop-distribution has seriously affected the validity of the censuses, but some part of the early winter loss may be due to the redistribution of feeding grounds after the autumn ploughing is completed. Early winter loss has averaged 11.1 per cent, while the range is from 0 per cent to 30 per cent of the September population.

Partridge shooting on the area censused has always ended in November. The count which has enabled us to distinguish between the early and late winter losses takes place in mid-December — just before the earliest date that pair-formation is likely to occur. From late December until early February the rate of pairing increases, and by the end of February all the coveys have broken up. Over this period, losses from accidents etc. occur, but towards the end of this period there is some evidence of slightly increased losses to predators. This loss is apparent even on the covey range, and may well be more marked in birds which emigrate. By late March a considerable reduction in partridge numbers has occurred, and observation of marked birds has shown that the major part of this reduction results from the movement of some juveniles away from the winter ranges of the parent coveys. Over the observed range in December population (1,126 to 1,917), late winter loss has been a fairly constant proportion, although modified to some extent by the crop distribution. A high proportion of arable to grass tends to reduce breeding pair density and to increase the rate of late winter loss. The relation is not necessarily an exact one, however, since the pattern of the crop distribution is also of some importance. Large areas of contiguous ploughed ground usually produce low pair densities, while ploughed land interspersed with grass or undersown stubbles, encourages relatively high breeding densities. In 1949 and 1950 the total acreage of ploughed land during the winter months was high and late winter loss well above the average.

Subsequent increases in the acreage under grass were accompanied by reductions in late winter loss.

Another factor which may modify the late winter loss figure is the sex ratio of the birds in coveys prior to pair formation. While methods for determining the sex ratios of partridge populations will be discussed elsewhere, the young/old ratios in August, the sex ratio shown by the shot birds, and the September and December censuses form the basis for these figures. In addition to the sex ratio of shot birds, in most years further evidence has been obtained from the examination of live birds netted in September and October. Each year there has been an excess of cock partridges. Among juveniles the excess is usually very small (except in the years 1953 and 1955 when the cock/hen ratio of juveniles was 156/100 and 135/100 respectively), and excluding 1953 and 1955 has averaged 103 cocks to 100 hens. Adults show a very marked preponderance of cocks, and the sex ratio from 1949-59 has averaged 157 cocks to 100 hens. Obviously, the overall sex ratio depends on the young/old ratio of the December population, and this has shown considerable variation in the different years. The proportion of the late winter loss which may be attributed to unbalanced sex ratios has averaged (1949-59) 27.6 per cent, and varied from 1 per cent in 1949-50 to 58 per cent in 1953-4. Some of these surplus cocks do remain on the estate, and there is a direct correlation between the calculated surplus cocks (December) and the observed single cocks in March (Table II). In addition to the surplus cocks which leave the estate, it has been calculated that each year between 150 and 250 hens disappear from mid-December to mid-March. From observation of marked birds, it is known that this loss is partly due to

TABLE II. *Calculated sex ratios in December stock (post-shooting) and sex ratios observed in March (following year)*

Year	December		December sex ratio	Observed sex ratio in March (following)
	♂	♀		
1949-50	889	880	101/100	106/100
1950-1	776	638	122/100	111/100
1951-2	758	648	117/100	109/100
1952-3	833	758	111/100	104/100
1953-4	1,161	756	154/100	113/100
1954-5*	910	712	128/100	129/100
1955-6	834	625	134/100	118/100
1956-7	946	750	126/100	109/100
1957-8	901	793	113/100	106/100
1958-9	636	490	130/100	118/100
1959-60	769	588	130/100	—

(Calculated sex ratios in December are based on the September and December censuses, the sex-ratio of shot birds and the August young/old ratio.)

* In this year adult cocks exceeded adult plus juvenile hens.

the death of both adults and juveniles, but the main factor is the movement of young hens (paired) beyond the estate boundary. Loss from this cause is most marked in those coveys whose winter ranges were in the peripheral region of the estate, and has shown relatively little annual variation.

While some variations in breeding density have occurred, the policy of exploitation has deliberately maintained the breeding stock at a relatively high level, and after an initial period of increase annual variations have largely depended on crop distribution during the late winter and spring.

Variations in the rate of summer gain (as measured by the September/March census or by the young/old samples in August) have been very large and are mainly responsible for the fluctuations of the September population densities. If these populations are expressed as percentage gains over the March populations, then the range is from 494 per cent in 1949 to only 38 per cent in 1954. In terms of young/old ratios in August the variation has been from 4.17 to 0.55 young per old bird, and the causes of these very marked differences will now be considered. The possible causes of these variations may be arbitrarily divided into those which are effective prior to the eggs hatching, and those which are mainly effective in the post-hatching period.

In countries with a more rigorous winter climate and with a relatively short period between the melting of the winter snows and the commencement of laying, Siivonen (1956) has claimed that the weather during this period of gonad development has a marked effect upon the subsequent production rates of game birds. The effects of weather at this time are said to be apparent in variations in clutch-size and hatchability, as well as in the survival rates of the subsequent broods. In England, where prolonged snow covering at this time is rare, weather conditions in early spring do not appear to be critical, and the minor variations in clutch-size and hatchability show no correlation with the chick survival rates that follow. Indeed the partridge usually lays a second clutch if the first is unsuccessful. Repeat clutches are smaller than first clutches (Middleton (1936), Lack (1947), Blank & Ash (in press)), and the average clutch-size in any one year would depend largely on the number of repeat nests included in the sample. On the area studied, where every effort is made to protect nests, nesting success has shown considerable variation from year to year, and has had much more effect on the chick production rate than variations in either clutch-size or hatchability (Table III). And yet from 1949-59 the chick production rate has averaged 9.89 chicks per pair with a range of only ± 2.20 . (If 1953 and 1958 are excluded, the range is from +0.73 to -0.87.) Nor do these relatively minor variations necessarily show any correlation with the subsequent number of young birds per pair when six weeks old.

Survival of young birds is measured in two ways. A series of sample counts of adult and young birds in early August provides figures from which an annual young/old ratio is obtained. While this ratio may be affected by loss of adult birds between March and August, the ratios should have comparative value since this loss has been fairly constant (15 per cent (± 4 per cent) of March population). Summer gain may also be assessed by expressing the September census minus the March census as a percentage of the March population. This figure allows for any adult loss between March and September, but since September censuses have not been carried out on any other estates, comparable figures are not available for different parts of the country. If no loss of adults occurred between March and September, and if no juvenile disappeared between mid-August and mid-September, then percentage gain and young per 100 adults should be the same figure.

Whether we consider the young/old ratio in early August or 'percentage gain' figures taken a month later, the annual variations from the eleven-year average (1949-59 young/adult pair ratio = $3.83 + 4.51 - 2.73$) are very marked. And since there appears to be little or no connection between any of the variable factors in the pre-hatching period with the subsequent young/old ratios, correlation with variable environmental factors effective during the post-hatching period must be looked for. Of the many factors which might exert control over chick survival rates, weather is perhaps the most obvious. Unfortunately, we cannot measure weather as a whole — only the many different aspects such as sunshine, rainfall, etc. can be separately recorded, and no single index representing weather conditions can be obtained. Further difficulties arise from the fact that many weather measurements are discontinuous (often only minimum and maximum daily readings), and that birds experience actual weather conditions and not the monthly average. It is quite possible that conditions of temperature and rainfall that are lethal to young birds may be masked if only monthly averages are available. Thus in 1953 a three-day period of light continuous rain combined with relatively low day temperatures, appeared to decimate brood-size, although the average rainfall for the month was normal. The date of onset of adverse weather in relation to the peak hatching period is also of importance. This period has varied from the 10th to the 19th June, and bad weather occurring before these dates is less effective in reducing brood size. However, in spite of these qualifications, there is a close correlation between the recruitment rate (as measured by the young/old ratio) and the weather (average rainfall, sunshine, etc.) during June and July. The highest rates have occurred when these months have been most dry and sunny, and the lowest recruitment has occurred when June and July have been wet and relatively sunless (Table IV, Fig. 3). Further evidence of the effect of weather during

TABLE III. Data for comparing effect of pre- and post-hatching factors on brood size at six weeks

Year	A Average clutch 1st nests	B Known successful nests	C Average clutch in successful nests	D % Hatchability	E Chicks/Successful pair	F % Nesting success	G Chicks/Pair	H Young/Old pair (six weeks)
1949	15.19	105	14.75	93.93	13.85	73.25	10.15	8.34
1950	15.01	178	14.65	94.33	13.82	72.36	10.00	4.64
1951	14.89	178	14.24	93.29	13.29	79.82	10.61	3.34
1952	14.85	181	14.63	90.20	13.20	81.90	10.81	4.96
1953	15.50	214	15.17	94.76	14.37	83.92	12.06	2.82
1954	15.00	157	14.42	93.37	13.46	69.16	9.31	1.10
1955	14.93	118	13.38	88.55	11.85	76.13	9.02	2.68
1956	15.99	149	14.81	90.71	13.43	69.63	9.35	3.28
1957	15.52	215	15.05	92.09	13.86	76.62	10.62	4.70
1958	15.27	161	15.08	90.90	13.71	67.23	9.22	1.72
1959	15.19	60	14.68	91.64	13.45	57.14	7.68	4.00
Arithmetic Mean:	15.21	157	14.62	92.16	13.48	73.38	9.89	3.83
+	0.78	58	0.55	2.60	0.89	10.54	2.17	4.51
Range	—	—	—	—	—	—	—	—
	0.32	97	1.24	3.61	1.63	16.24	2.21	2.73

Note:

A = Eggs laid in completed 1st *Perdix* nests/number of nests.B = Successful *Perdix* and *Alectoris*.C = Average number of eggs incubated in *Perdix* and *Alectoris* nests.D = Average number of eggs (*Perdix* and *Alectoris*) hatched $\times 100$ /average number of eggs incubated in successful nests.E = Total chicks hatched/ number of successful nests (*Perdix* and *Alectoris*).F = Successful nests $\times 100$ /successful nests + failures with no repeat nests (*Perdix* and *Alectoris*).G = E $\times$ F.H = 2 $\times$ August young/old ratio (*Perdix* and *Alectoris*).

TABLE IV. *Average daily hours of sunshine, number of 'wet' days and average rainfall ('wet' days) and young/old ratios, 1949-59*

Year	Average daily sunshine June and July (hrs)	Wet* days June and July	Average rain per wet days June and July (mm)	Y/O ratio
1949	9.04	8	4.5	4.17
1950	7.62	27	4.9	2.32
1951	7.65	17	2.5	1.92
1952	6.67	17	2.7	2.48
1953	6.20	35	3.5	1.41
1954	4.89	32	4.6	0.55
1955	7.22	14	6.8	1.34
1956	5.54	25	3.6	1.64
1957	7.67	28	5.0	2.35
1958	5.70	30	4.2	0.86
1959	8.06	21	2.6	2.00

* Wet = 0.2 mm or more.

the critical months of June and July may be obtained by comparing survival rates on similar areas that have experienced different weather conditions. In 1949 in the south of England the weather during June and July was dry and

FIG. 3.—Production rate and June-July weather.

(The width of the columns represents average rainfall per wet day—see Table IV).

very sunny, while in Norfolk conditions were less favourable. In 1954 the June and July weather in both Norfolk and Hampshire was wet and sunless, while in 1959 the weather was more sunny in Norfolk than in Hampshire (particularly during June). Table V shows how these weather conditions have affected the recruitment rates on two comparable estates in Hampshire and Norfolk. The failure of the chicks to survive may be due to the direct effect of low temperatures and wet herbage, resulting in 'chilling' (as has been shown to occur in Capercailzie in Sweden (Höglund, 1955)), or to starvation resulting from a lack of, or the low availability of, the necessary

TABLE V. *The effect of weather on recruitment rates*

Estate	Year	Average daily sunshine June and July (hrs)	Wet* days	Amount of rain (mm)	Y/O ratio
A	1949	9.04	9	39	4.17
B	1949	7.39	21	70	2.70
A	1954	4.89	33	147	0.55
B	1954	4.64	26	67	1.10
A	1959	8.06	21	54	2.00
B	1959	8.58	22	52	3.60

A and B are comparable estates in Hampshire and Norfolk respectively.

* Wet days = days on which 0.2 mm or more of rain fell in June and July.

insect food. While the partridge chick appears to be most vulnerable to bad weather during the first three weeks of life (i.e. when it is mainly insect feeding and still down-covered), due to the normal spread of the hatching period the weather is of critical importance during most of June and July.

Changes in the relative acreages of grass-ley and corn-land have also affected partridge survival rates in the different years. While the grass-leys are necessary to maintain maximum pair density in March, they are also the cause of heavy chick loss during June when the grass crop is being harvested. Not only are large numbers of chicks killed by the hay-making activities, but those that survive are left in an uncongenial habitat (cut grass field) at a very vulnerable period of their lives. The effect of varying crop distribution is most clearly seen when, in a period of a few years, a predominantly corn-producing area is grassed down. Under these conditions, even if the weather is favourable, survival rates are relatively low. When the weather, too, is adverse, then very few young can survive. In 1958 when weather conditions in June and July were relatively unfavourable, young/old ratios of 1.9/1.0 were recorded on a predominantly corn-producing beat (corn to grass = 312/100), while on a beat where the corn/grass acreage was 84/100, survival rates were only 0.3/1.0. From 1949 the acreage under

TABLE VI. *The relation between crop distribution, breeding density and recruitment rates, 1949-59*

Year	Corn/100 acres ley-grass	Acres per pair (March)	Young/old ratio (August)
1949	208	13.9	4.17
1950	185	9.9	2.32
1951	223	9.9	1.92
1952	169	7.8	2.48
1953	160	6.5	1.41
1954	127	6.0	0.55
1955	145	8.0	1.34
1956	140	8.3	1.64
1957	167	6.5	2.35
1958	142	6.0	0.86
1959	153	10.9	2.00

grass-leys increased, reaching its greatest extent in 1954. After that date the ley-grass area has fluctuated irregularly around a slightly lower mean (Table VI, Fig. 4).

A third factor which may affect the rate of chick survival is the incidence of diseases of various kinds. While young partridges reared in captivity may suffer from several different diseases, in wild birds known deaths from these causes are relatively rare. After severe weather, several chicks may be col-

FIG. 4.—Crops grown, breeding density and recruitment rate, 1949-59.

lected that have died as a result of 'chilling', but only a small proportion of the chicks found are sufficiently fresh to allow the cause of death to be ascertained. Lack of evidence of death from disease does not necessarily mean that this has not occurred, although the very few known cases of deaths of young birds from Coccidiosis or 'Blackhead' suggest that their effect on survival rates is negligible. The gapeworm (*Syngamus trachea*) has, however, increased very markedly over the period 1949-59, and its incidence, although unknown in chicks, has been fairly well charted in adults and juveniles. There is some evidence that the heavy rate of chick loss is not necessarily affected by this disease, but its incidence among partridge chicks is unknown. There was no evidence of this disease in 1949, and a gradual spread from a single focus of infection appears to have begun in 1951. Four years later the degree of infection in juveniles shot in October was 45 per cent, and although the area originally infected showed the highest incidence of this disease, the survival rate in this area was at least as high as on the areas least affected. By the end of 1958 all parts of the 4,000-acre (1,600 hectare) area showed some degree of infection, while the highest incidence was still found in the area of the original outbreak. In 1959, probably due to the unusually dry summer, the incidence of *Syngamus* decreased, although it was still present over the whole area.

A comparison of the breeding pair density in March with the subsequent young/old ratios in August on the summer-gain figures obtained from the September censuses, shows that there appears to be a well-marked inverse ratio. Low breeding densities have been followed by high recruitment rates (1949) and high densities by low recruitment rates (1954). If breeding densities and young/old ratios were the only available data, the correlation might appear to be significant. But when we consider the sequence of weather during the breeding season, as well as the changes in crop distribution, the partly fortuitous nature of the correlation becomes apparent. It is perhaps unnecessary to repeat that a crop distribution that is favourable to a high breeding density, often prevents the occurrence of a high production rate due to the extent of the grass-leys. Variation in the average number of chicks hatched per pair (depending on clutch-size, hatchability and nesting success) is relatively small, and shows no correlation with the breeding density. Although nesting success appears to be unaffected by breeding density, chick survival may be affected, since a larger proportion of pairs may nest in unfavourable situations where the chances of rearing a brood of chicks successfully are very small. However, it has proved impossible to measure this tendency on any quantitative basis.

No satisfactory method of measuring the amount of chick loss due to predation has been discovered, but it is unlikely that large annual variations

have occurred on an area where predators are partially controlled. Nest loss due to predation has averaged 14.6 per cent of all nests found, and has shown considerable variation from 7.2 per cent in 1953 to 23.2 per cent in 1956. It might be argued that high nest loss through predation would be followed by a high chick loss, but by no means all the nest predators are chick predators too. Trapping results have also shown considerable variation in the number of predators caught, but it has been impossible to determine whether the predator catch is in fact proportionate to the predator population.

SUMMARY

Data are presented concerning a partridge population on a 4,000-acre area in West Hampshire.

Variations in breeding density have been less marked than the variations which have occurred in the autumn population. Breeding density variations have been reduced by controlled shooting (density dependent predation), and emphasized by changes in crop distribution. Age (except indirectly through sex-ratios) has had little effect on breeding pair density.

Autumn populations have shown marked fluctuations, and are primarily dependent on the weather during June and July. In most years the weather produces a relatively low survival rate. High survival rates occur only when the weather in June and July is dry and sunny, and where the crop distribution is suitable. Crop distributions that encourage a high breeding density are often inimical to chick survival.

The effects of disease, predation and the density of the breeding population itself, although not accurately known, are considered to have had only minor effects on the fluctuations recorded in September.

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DISCUSSION

G. C. VARLEY: The graphical representation you used in an attempt to identify the main causes of variation is similar to one I have used for insects.

The trouble with your particular method is that it may suggest that the biggest mortality factor is necessarily the bigger cause of variation. A logarithmic method of plotting, as Haldane first pointed out, is more reliable for this kind of analysis.

M. GRAHAM: You said that the early diet of partridges depended on insects, and this in turn will depend on temperature. Might not this one factor be worth isolating for detailed study, and give the key to the whole situation?

T. H. BLANK: We have no measure of the availability of insect food for partridges.

G. M. DUNNET: You have indicated a change in population between September and March and March and September in terms of numbers. Does this change proceed in a gradual manner or in a step-like system like that in grouse, as illustrated by Jenkins and Watson?

T. H. BLANK: Probably the curve is not stepped. Between September and December the change is steady, apart from the effect of shooting. Between December and March there are two effects, firstly a steady component of mortality and secondly a stepped factor due to the break-up of the coveys and the pairing of the birds — and a consequent movement off the estate. This is a short phase, lasting about three weeks, and so introduces a step into the curve.

H. KLOMP: You have shown a correlation between the survival of young and the nature of the farm crops. Has this correlation been treated statistically? If this could be done it should be possible to assess the importance of this one factor out of your complex of variables.

T. H. BLANK: I think too many uncertainties are involved for this treatment of the data, though I agree that it should be done.

J. G. SKELLAM: An estimated correlation coefficient based on only eleven pairs of values is not often found to be significantly different from zero except when its value is rather high. In this particular case (where one of the variables enters into consideration after its selection from among other possible climatic variables), there is little to be gained by carrying out a formal significance test. I would say that the authors are right in presenting the basic information as they have done, thereby revealing a strong suggestion of an interesting relationship.

(*Note by Dr Skellam*): This discussion went on among various interested people later. It became apparent:

1. It is not correct to carry out a formal test *a posteriori*, rejecting all

variables (e.g. rainfall) which appear poorly correlated, and picking on those which are.

2. That if the hypothesis (about sunshine) had been framed *a priori*, the estimated correlation coefficient is sufficiently high to be just significant.

A. WATSON: In your abstract you state that predation on the young birds may be a factor. What evidence is there for this?

T. H. BLANK: There is very little real evidence. Of course it is known that predation destroys some nests, and also we have records of the numbers of predators trapped on the estate. But the latter do not give a satisfactory indication of predator abundance, and no direct work on the predation of chicks once they have left the nest is possible. There is no evidence that predation is a serious factor in the mortality of these chicks, and in the study area the population of predators is certainly too well controlled for its year-to-year variation to account for the observed variation in the total partridge population.

E. D. LE CREN: What do you suppose would be the result if there was no density-dependent shooting?

T. H. BLANK: Unfortunately we have not been able to make a test experiment on this point. But we did once shoot very heavily on a low autumn population, leaving between 1,300 and 1,400 birds after shooting. Winter mortality accounted for a normal percentage afterwards, so that a low spring breeding stock followed. Thus in our experience breeding stock is related to the amount left after autumn exploitation; within certain limits the more birds there are left, the more breeding pairs we should expect.

D. JENKINS: I once carried out population work on partridges in Hampshire for four years and reached rather different conclusions. My results suggested that an important factor governing the number of pairs on the area was the crop distribution in February. There was a constant breeding population of partridges each spring, irrespective of the numbers of birds left at the end of the shooting season, but associated with a constant pattern of winter crops. In some cases the level of the spring partridge stock was reached through the emigration of birds that were apparently surplus in the late winter, but in one case a stock that was small at Christmas was increased by birds immigrating to the study area in the late winter. Blank and Ash's first graph suggests that in their study area the variation in the number of breeding pairs is relatively minor in scale and that it too may be related to cropping changes. It suggests that if there were no shooting there would still be little variation in the breeding stock. Clearly if major mortality causes are removed, such as those which might limit a stock through nest predation, the population would be expected to rise to a ceiling but not exceed it. At Fordingbridge

I believe that a policy of very intensive keeping has protected the game which has consequently risen to its ceiling and thereafter shown only minor and incidental variation. Blank & Ash's results showing small variations in spring numbers may merely reflect variations in the partridges' environment.

T. H. BLANK: Certainly some variation in the breeding density is attributable to crop changes, as I said and showed in my slides.

D. H. CHITTY: There seems to me to be a great difficulty because of the large exodus of birds from the study area to unknown regions, and the replacement of losses from elsewhere. Are you sure that the study area is not an atypical one as a sample?

T. H. BLANK: Fordingbridge is certainly not atypical of the area in which it lies, except in being very well kept. It is this good keeping, as compared with the adjoining ground, that has led to our very high partridge density.

EXPLOITED MARINE MAMMAL POPULATIONS

SOME EFFECTS OF WHALING ON THE SOUTHERN STOCKS OF BALEEN WHALES

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Modern whaling is mainly based on the value of whale oil and for profit depends on large catches. It dates from 1904 when Antarctic rorquals (*Balaenopteridae*) were first exploited at South Georgia. Up to 1913 the industry was based on the humpback whale, *Megaptera novaeangliae* (Borowski), which was quickly depleted in the South Atlantic sector. The blue whale, *Balaenoptera musculus* (L.), then supported the industry and with the development of pelagic whaling in the late 1920's the area of the whaling grounds expanded to become almost circumpolar. Antarctic pelagic whaling now accounts for three-quarters of the world catch of baleen whales.

The decline of the blue whale in the southern hemisphere began about 1931 and increasing numbers of fin whales, *Balaenoptera physalus* (L.), appeared in the catches. This is currently the most important species and constitutes some four-fifths of both the world catch and antarctic catch of baleen whales.

This paper is therefore concerned mainly with the fin whale and with antarctic pelagic whaling during the last three decades.

In this time there have been two main periods of intensive pelagic whaling divided by the war years 1939-45, when the catches fell to a very low level. For convenience I shall refer to the two main whaling periods as the pre-war and post-war seasons.

SAMPLING PROBLEMS

There are certain basic difficulties which are not met in other groups of exploited animals, namely, the very wide geographical distribution, the large size of the animals and the prohibitive cost of an adequate research programme. These and other problems affect the interpretation and elucidation of changes in the composition of whale populations and I think it necessary to summarize and discuss them here.

(a) *Sampling the catch*

Some twenty factory ships with their attendant catchers operate in the area of ocean between the Antarctic Convergence and the ice-edge which is some 8-9 million square miles in extent during the whaling season (Mackintosh & Brown, 1956). Whaling is a skilled occupation and searching for whales plays an important part. It is not possible to collect a sample of intact whales, as with small animals, nor to examine the catch at the end of the voyage as fisheries biologists often can, for whales are large and are rapidly dismembered and processed after being hauled aboard the factory ship. Sampling opportunities are therefore limited and material for age determination must be collected during the operations on deck.

Much effort has gone into finding methods of age determination and three complementary methods are available, based on corpora albicantia in the ovaries (Laws, 1958), ridges on baleen plates (Ruud, 1945), and laminations in the ear plug (Purves, 1955). Owing to the great size variation and the fact that growth, though initially very rapid, slows down or ceases at a relatively early age, length measurements have been useful for population studies only in a very general way.

(b) *Varying restrictions on whaling activities*

Prior to the 1932-3 season antarctic pelagic whaling was unrestricted though whaling from land stations was regulated. Various voluntary agreements, national laws and regulations relating to whaling were introduced, notably by Norway and the U.K., but with the development of pelagic whaling only international measures were adequate for its control. A number of international agreements were concluded, namely the Convention of 1931, the agreements of 1937 and 1938 and the International Whaling Convention of 1946 which is at present in force. I propose briefly to summarize the more important restrictions affecting the catches of blue and fin whales:

- (1) The taking of lactating females and suckling calves is prohibited.
- (2) Minimum length regulations mean that the younger animals in the stocks are absent or under-represented in the catches. The minimum length for blue whales was in the earlier seasons 65 ft, increasing to 70 ft in 1937-8. For fin whales it was increased from 55 to 60 ft in 1951-2 and reduced to 57 ft in 1954-5 (Fig. 4).
- (3) There have been successive changes in the opening date of the pelagic whaling season, from 20th October in 1932-3 to 7th January in the five seasons up to 1958-9. The opening date for blue whales was postponed to 16th January in 1953-4, to 21st January in 1954-5 and to 1st February in 1955-6. This was designed to afford more protection to the blue whale.

The end of the whaling season in post-war years has been dependent on the attainment of the catch quota, and in recent years owing to the increasing intensity of the whaling operations the length of the whaling season has been only sixty-nine days for fin whales and forty-four days for blue whales. In 1932-3 the duration of the season was 177 days.

(4) In an industry like whaling protection is best achieved by restricting the catch to an annual quota. With the exception of the earlier voluntary agreements no overall quota was fixed until the 1946 Convention adopted a figure of 16,000 blue whale units which first came into operation in the 1947-8 season. This unit is based on oil yield; one blue whale is considered equal to two fin, two and a half humpbacks or six sei whales (*Balaenoptera borealis* Lesson). The quota has subsequently varied between 16,000 and 14,500 B.W.U. (Fig. 1) composed of these four species.

(5) By the 1937 agreement a sanctuary area was declared in the Pacific Sector from 70° W to 160° W. Virtually no whaling occurred in this extensive region until the 1955-6 season when it was opened to whaling in an attempt to reduce the pressure on the stocks of whales in other sectors. Pelagic whaling is forbidden in the southern hemisphere north of 40° S latitude.

The other provisions of these agreements do not concern us here.

(c) *Geographical segregation*

For obvious reasons research on the southern stocks of fin and blue whales has been virtually confined to the populations present on the antarctic whaling grounds in the summer months.

We may safely assume that there is a negligible interchange between the stocks in the northern and southern hemispheres. It has long been known that there is also a segregation of the antarctic stocks of baleen whales into more or less separate geographical groups. The results of whale marking show that the distribution is not random and that many fin whales return after their migrations year after year to the place of marking (Mackintosh, 1942; Brown, 1954). Hjort, Lie & Ruud (1932) divided the antarctic whaling grounds into five areas (I-V) based on the distribution of catches, mainly of blue whales, by Norwegian factory ships. In subsequent papers they confirmed the value of this division. Mackintosh (1942) examined the distribution of blue, fin and humpback whales and suggested the extension of area I; he also proposed a new area VI to include the rest of the Pacific sector. This terminology is in general use by whale biologists and by the Bureau of International Whaling Statistics, but it was based largely on the distribution of the catches of blue whales, which in pre-war years was the most important species. Since 1945 the fin whale has been the most important species and the post-war distribution of the catches suggests that the whaling areas I-VI

are not entirely valid for this species. In particular the boundary between areas II and III would appear to be without meaning in relation to the fin whale stocks.

This view is confirmed by a study of the length distribution of the catches. It is not yet complete but it is apparent that there is a size segregation according to longitude, and there appear to be four main groups roughly corresponding to the South Atlantic, South Indian, West Pacific and East Pacific Oceans. The size distribution is fairly closely correlated with the distribution of catches.

The significance of this geographical segregation in relation to population studies will be obvious and further work is planned and in progress. The results may necessitate a reappraisal of our data, but I do not think this will affect the conclusions drawn in this paper because I have been careful to choose examples and to make comparisons in such a way as to discount the effect of this segregation. However, because the size segregation may reflect a segregation by age (though not necessarily), I feel that it would be unwise to attempt to determine with precision such parameters as mortality or survival rates. Fortunately most of the points I wish to make are not affected by this.

(d) *Segregation in time*

In their long migrations between the breeding and feeding areas, the various species of baleen whales migrate at different times. Blue and humpback whales appear on the feeding grounds before fin whales, and sei whales arrive much later.

Within a species there is a similar segregation. In the fin whale the older whales appear on the feeding grounds first, and the immature whales last (Wheeler, 1934; Mackintosh, 1942). The period when samples are taken therefore has an important influence on the age composition of the sample. For example if separate survival curves are constructed for samples taken in November, December, January, February and March, the slope is found to be steeper with the progression of the season.

This changing age composition month by month does not permit absolute mortality rates to be calculated and it is only possible to compare changes in the shape of survival curves in a relative way. We must make the best use of our inadequate material.

THE CATCH PER UNIT EFFORT

Hjort, Lie & Ruud (1933) appear to have first introduced the concept of the catch per boat per day as a measure of abundance, using the expression

'catcher's day's work', which may be abbreviated to C.D.W. They discuss its advantages and drawbacks as a unit of effort and use it to compare catches in different areas. The main disadvantage is that catcher efficiency has been steadily increasing, so the C.D.W. is not a constant unit of effort (Fig. 1),

FIG. 1.—Total antarctic catches of baleen whales; changes in catch quotas; percentage fin whales (of fin and blue); fin whales per C.D.W.; and number of catchers and their average tonnage and power.

nor has it been possible as yet to correct for the variations. The average gross tonnage and power (I.H.P.) of the whale catchers have increased by 165 and 216 per cent respectively between 1930–31 and 1958–9. There are other unmeasurable improvements, in navigational aids and the introduction of asdic and helicopters. Diesel engines increase the range and endurance of catchers and lessen their dependence on the factory ship. Other factors such as competition between catchers, improvements in factory machinery, gear saturation (days when more whales are caught than the factory can handle and catching operations are limited to a few hours), and changes in the

catching season, must all influence the catch per C.D.W. but are difficult to allow for. In spite of this the C.D.W., while far from ideal, is the most acceptable measure of effort, and if the catch per C.D.W. is stable or decreasing, while at the same time the average catcher efficiency is increasing, it is safe to conclude that the stocks are decreasing. This has long been the case as regards the blue whale, even when allowance is made for the later season, and can now be shown to apply to the fin whale also. The data presented in this discussion have been supplied by the Bureau of International Whaling Statistics.

It has been the practice in some quarters to think of the catch per unit effort mainly in terms of B.W.U. per C.D.W. While this is convenient from the point of view of the whaling industry, since a stable or increasing value in terms of B.W.U. means a stable or increasing value in terms of oil production, there is little to recommend it to biologists. In post-war years wide variations in species composition of the catch have been associated with only slight changes in the catch of B.W.U./C.D.W. (Fig. 2).

In an industry based on searching, which concurrently takes several species in varying proportions, changes in the catch per unit effort of one species are influenced by the amount of effort being expended on searching for and catching other species. For practical purposes the catches of humpback and sei whales have been small (Fig. 1), and sperm whale catches during the baleen whaling season have also been small; they may safely be ignored in the present discussion. This leaves two species, the blue whale and the fin whale, individuals of the former being in general twice as valuable to the industry as the latter.

Fig. 1 shows how closely the average catch of fin whales per C.D.W. is related to the percentage of fin whales in the total catch of fin and blue whales, and to the size of the catch of fin whales. In post-war years with a fixed quota of B.W.U. the increased size of the catch of fin whales is necessarily complementary to the reduced catch of blue whales.

In Fig. 2 the annual values of fin whales per C.D.W. are plotted against blue whales per C.D.W., and pre-war and post-war seasons are distinguished. It shows that, in pre-war years, as the number of blue whales per C.D.W. declined there was a rise in the number of fin whales per C.D.W., the relationship being more or less linear. In all these pre-war seasons the catch of blue whales was more valuable than the catch of fin whales. In other words fin whales never constituted two-thirds or more of the catch of blue and fin whales combined (Fig. 1). In post-war years the emphasis shifted to fin whales, because of the depletion of the blue whale stocks, and in only one post-war season (1946-7) was the fin whale component less than two-thirds of the combined catch of these two species. The slope of the linear

relation between the catches of fin and blue whales per C.D.W. is also different for pre- and post-war seasons (Fig. 2).

The whaling grounds for blue and fin whales differ, to some extent as regards longitude, but more generally so in respect of latitude. The blue whale is usually found nearer to the pack-ice, to the south of the whaling grounds. For periods when the catch of blue whales is more valuable (that is, as long as blue whales constitute more than one-third of the combined catch of blue and fin whales) it is to be expected that the whaling fleet will

FIG. 2.—Relation between the catches of blue whales and fin whales per C.D.W.

choose to operate in waters where blue whales are most abundant. Conversely, when blue whales become less important the fleet will largely orientate itself for the catching of fin whales, though blue whales will continue to be caught as well.

In Fig. 2 I have also drawn in oblique lines showing constant values of B.W.U. per C.D.W. for differing values of fin whales and blue whales per C.D.W. It can be seen that the number of B.W.U. per C.D.W. declined in pre-war seasons from about 1.4 to 1.0 and has shown a slight increase in post-war seasons. (The values of B.W.U. per C.D.W. are only slightly higher if humpback and sei whales are also included.)

In view of this changing composition of the catch, and of the progressive increase in catching efficiency, it has not been possible to arrive at any estimate of the absolute increase or decrease in the number of each species of whale caught per constant unit of effort, and so to make a quantitative estimate of the changes in the stocks. I do not think there can be any doubt that the blue whale stocks have suffered very heavy depletion, but the position is less clear with regard to the fin whale.

Turning again to Fig. 1, let us compare the catches of fin whales per C.D.W. from 1950 onwards, with the catcher efficiency. The effect of competition between catchers has been fairly uniform over this period because agreements between the whaling companies have kept the number of catchers at a fairly constant level. The number of fin whales per C.D.W. increased up to 1955-6 and then fell in the subsequent three seasons although the average catcher efficiency continued to improve (I.H.P. increase nearly 23 per cent).

It should be noted that with the opening of the former sanctuary in the Pacific sector, new stocks were exploited and the 'centre of gravity' of whaling in the older areas also shifted. In the 1955-6 season 26.7 per cent of the total pelagic catch of fin whales was taken in these new areas; in 1956-7 their contribution was 41.0 per cent and in 1957-8 it was 23.7 per cent. In 1958-9 it dropped to 8.2 per cent. The catch of fin whales per C.D.W. in this area (I and VI combined) was 1.99 in 1955-6, the highest ever recorded in any area, and subsequently declined greatly. Blue whales were not abundant there.

For three seasons then, the opening of the sanctuary, as was intended, relieved the pressure on the other stocks of whales. The rise in the value of fin whales per C.D.W. in 1955-6 was probably partly a result of this, and the stabilization and decline of the figures for fin whales per C.D.W. should otherwise have become apparent earlier. The later opening date for the catching of blue whales probably also contributed to this. I have also calculated the values for 'sexually mature' fin whales per C.D.W. (that is females above 64 ft and males above 62 ft in length) and have plotted them in Fig. 1. These show a more marked decline, beginning after 1953-4, suggesting a differential decrease in the numbers of older animals. I will return to this point later.

The values for fin whales per C.D.W. considered separately for the various whaling areas I-VI show a similar relative stability or decline, most marked in the newly exploited stocks in areas I and VI which have always been considered to be numerically small compared with other areas. The data for area III show a rapid increase in fin whales per C.D.W. up to 1.54 in 1952-3 and subsequently a slight but noticeable increase up to 1.72 in

1958-9. It seems clear that the fin whale stocks in area III are in the best condition relative to the other areas, and may possibly be holding their own at the present rate of exploitation.

FIG. 3.—Comparison of fin whales per C.D.W. for January and for the full season with the intensity of catching.

It might still be objected that the influence of catches of other species, though small, has been responsible for the stabilization or decline in the fin whale values. Is it possible to eliminate the effect of the catches of other species? This uncertainty can be removed if we compare the January values for fin whales per C.D.W. from the 1955-6 season onwards. In these years only two blue or humpback whales were taken annually in January and negligible numbers of sei whales (average 1955-6 to 1957-8 only forty-seven, or some 0.4 per cent of the fin whale catches). Relatively small numbers of sperm whales were taken; they do not amount to more than 6.8 per cent of the fin whale catches. In Fig. 3 the values of fin whales per C.D.W. for January are compared with those for the total catches and with relative catcher efficiency. In this four-year period although the average catcher horse-power has increased by nearly 23 per cent the trend of the January values of fin whales per C.D.W. is stable or decreasing. Competition between catchers was less in the three later seasons. At the same time the percentage of 'immature' whales in the catch (based on body lengths) has increased by some 5 per cent (Fig. 4).

In spite of the many complicating factors two inescapable conclusions

may be drawn from these results; first, that the southern stocks of blue whales have been decreasing for many years and are now at a very low level; secondly that the southern stocks of fin whales are now decreasing and have probably been progressively decreasing for several years at the very least. In

FIG. 4.—Changes in the mean lengths and estimated percentage immature in antarctic pelagic catches of blue and fin whales.

the rest of this paper it is taken for granted that the stocks of fin and blue whales are not increasing.

CHANGES IN THE COMPOSITION OF THE CATCHES

Detailed information on the catches of whales is given in the annual publications of the Bureau of International Whaling Statistics. This enables variations in the composition of the catches to be followed year by year.

The more important changes in the species ratio have been discussed, and there have been no significant changes in the sex ratio, which is about unity. This suggests that the differential effect of the minimum length regulation on male and female, expected because of the sexual disparity in size, is balanced by the protection afforded to lactating females.

There have been conspicuous changes in the size and age composition.

(a) *Mean lengths*

The mean length of the catches is dependent on growth rate and age composition, and on the minimum lengths at which whales may be taken.

In Fig. 4 the yearly mean lengths of the catches of fin and blue whales from 1931-2 to 1958-9 are plotted. In both species there was a rapid decrease in pre-war years and a more gradual decrease in post-war years. Interpretation of these figures is a little complicated because of changes in the minimum lengths above which whales were allowed to be taken. An increase in the permissible minimum length should be associated with a potential increase in the mean length of the catch. This appears to be the explanation of the rise in the mean length of the blue whale catch in 1937-8 when the minimum length was raised from 65 ft to 70 ft. It also accounts for the abrupt rise in the mean length of the fin whale catch of 1951-2 when the minimum length was raised from 55 ft to 60 ft for this species.

Two other factors which affect the interpretation of these length statistics should be mentioned. There can be little doubt that the very high mean lengths of the blue whale catches in the early pre-war years were the result of selection by the gunners. Survival curves of blue whales for this period (based on corpora albicantia counts) confirm that catches were biased towards older and larger animals, though this bias later disappeared. In the fin whale there has probably been less selection of this kind. With the increased competition of post-war years active size selection by the gunners can be ruled out, but another possible type of selection must be mentioned. This is the result of the later opening date of the whaling season which means that the catches will contain a larger proportion of younger and therefore smaller animals (see above). Nevertheless the later season is not in itself sufficient to account for the observed decline in the mean lengths of the catches. The timing of the season was similar in 1949-50 and 1950-1 and in 1951-2 and 1952-3, yet each of these pairs of mean lengths for blue whales show a decline. Between 1952-3 and 1953-4 the opening date for blue whales was postponed by two weeks and the closing date was almost unchanged, yet the mean length of the blue whale catch rose by half a foot. For fin whales the season has been virtually unchanged since 1952-3, but the mean length of the catches has decreased by over $1\frac{1}{2}$ ft.

This progressive decline in the mean lengths of the catches of both species suggests that there has been a real change in the size and age composition of the stocks.

(b) *Percentage sexually immature*

In Fig. 4 the percentage of immature animals in the catches is presented. This is calculated each year by the Bureau of International Whaling Statistics on the assumption (based on earlier biological studies) that on average male and female blue whales respectively 73 ft or less and 76 ft or less, are immature. For fin whales the corresponding lengths are 62 ft and 64 ft. This should in fact give slightly low values for the percentage immature, because the mean lengths at maturity are actually slightly higher than those used in the calculations. The resulting figures show an inverse picture to that given by the mean lengths (since they are based on length statistics), and suggest that the percentage of immature animals in the catches increased in pre-war seasons, then fell slightly during the war years, and again increased in post-war seasons. The proportion of immature blue whales estimated in this way, rose from about 25 per cent in 1945-6 to nearly 40 per cent in 1952-3; for several years it remained fairly stable but in 1958-9 there was a marked decrease in the immature component of the catch. The significance of this recent decline is difficult to assess, though the stabilization and fall in the proportion of immatures suggests declining recruitment. In the fin whale the proportion of immatures has increased fairly steadily from about 14 per cent in 1945-6 to 30 per cent in 1958-9. Changes in the minimum length regulations have affected these values as in the case of mean lengths.

In Fig. 5 I have plotted the percentage of immature female fin whales in

FIG. 5.—Changes in the composition of the antarctic pelagic catches of female fin whales.

the post-war catches (derived from the length statistics) for comparison with some data bearing on this question which Professor Ruud has kindly allowed me to publish. Some of this material is presented in the paper by Hylen, Jonsgård, Pike & Ruud (1955) who discuss its validity and give reasons for believing that the material for the first two seasons is unrepresentative of the catches. The figures for the proportion of sexually immature females in the Norwegian samples are based on inspection of the ovaries, the presence of one or more corpora lutea or corpora albicantia indicating maturity. As expected, these figures are slightly higher than those published in the International Whaling Statistics (see above). They show a similar trend, increasing by about 10 per cent from 1947-8 to 1954-5, and confirm that the proportion of immature and therefore younger animals in the catch has increased.

(c) *Age composition*

In Fig. 5 are plotted some data on the age composition of the catches, also provided by Professor Ruud. These show that the proportion of the younger age groups in the catches has increased markedly, the criterion of age being the pattern of ridges on the baleen plates (Ruud, 1945). The proportion of females in baleen groups 0-III has increased from about 25 per cent in 1947-8 to about 45 per cent in 1954-5 (smoothed curve). These data from samples of the catches made by Norwegian expeditions confirm the general conclusions drawn from the length statistics of the total pelagic catches, as to the increasing representation of younger animals in the catches. The baleen plate data show that the shift towards younger age-groups in the catch is greater than is implied by the length statistics or the proportion of immatures.

It has been suggested that an increasing number of younger animals in the catches could well be an indication of increased recruitment and even of *increasing stocks*. Evidence for the view that the stocks of blue and fin whales are decreasing has been presented above, and in whales, which bear a single young each pregnancy, recruitment is within narrow limits related to the size of the adult female component of the stock. If this is progressively decreasing (as in the blue whale) then recruitment can hardly be increasing.

The changes in the composition of the fin whale catches, presented and discussed above, suggest that the average age at sexual maturity has decreased, for there has been a greater increase in the proportion of the catch which is composed of the youngest age groups than in the percentage of immature females.

I intend to present some other evidence for precocious sexual maturity in the fin whale, and for an increase in the reproduction rate of mature females linked with and presumably caused by the increased rate of exploitation.

Then I will attempt to show that in spite of this reaction the recruitment is insufficient to maintain the stocks at the present rate of exploitation.

RESPONSES TO EXPLOITATION

(a) *Pregnancy rate*

The most immediately apparent response to exploitation is an increase in the pregnancy rate. Mackintosh (1942, p. 233), referring to blue and fin whales, remarked that 'the percentage of adult females which are pregnant has been increasing in a remarkable degree year by year, as if the actual rate of breeding were becoming faster'. He suggested that this was conceivably a reaction to whaling. Additional material from post-war seasons supports this suggestion.

FIG. 6.—Variations in the relative fertility of blue whales (all areas) and fin whales (white, area II; black, areas III and IV).

In order to make use of the material collected by non-biologists the presence of one or more corpora lutea in the ovaries is taken to indicate a pregnancy. In fact, this gives an estimate of the number of pregnant females in the catch which is too high by about 8–10 per cent. The reason for this is that in the female fin whale (and probably in the blue whale) a feature of the annual cycle is a post-lactation oestrus. This means that a proportion of non-pregnant, non-lactating females in antarctic waters have a corpus luteum of ovulation in the ovaries (Laws, 1959*a* and in press). Pregnancy can be confirmed only by a search of the uterus for an embryo. Another point, which I should emphasize is that the term 'percentage pregnant' refers to the catch of adult females, and applies to the total population only in a relative way. This is due to the fact that a large proportion of lactating adult females delay the southward migration into antarctic waters (Laws, in press); because of this and also because of the prohibition on the taking of lactating females, this group is under-represented in the catches. The term 'percentage pregnant' as used here applies therefore to the proportion of non-lactating

adult females which are pregnant. Because only adult females are considered the figures are independent of changes in the age at puberty.

Another factor influencing the apparent 'percentage pregnant' is the mortality rate. Non-pregnant mature females taken in antarctic waters are on average about a year older than pregnant females, because most females become pregnant at the first ovulation at puberty and do not join the non-pregnant group until a year later. The succeeding cycles also average about two years. Thus, even if lactating females were fully represented in the samples and the actual pregnancy rate for individual females was 50 per cent (that is, one pregnancy every two years), the apparent 'percentage pregnant' of the population as a whole, associated with a total mortality rate of, say, 20 per cent should be 55.5 per cent. (For every fifty pregnant females there should be only forty non-pregnant, because ten die in the intervening year.)

However, even if these factors are allowed for, the relative changes in the 'percentage pregnant' are considerable and probably represent a real change in fertility. In the fin whale this might be caused by increased fertility at post-partum or post-lactation oestrus cycles and by reduced prenatal mortality. In the blue whale post-partum conceptions are rare. I have also examined the incidence of pregnancy in various age groups and it would appear that the youngest mature females have a slightly lower fertility rate, that fertility is maximal at about 15-25 years of age, after which it appears to fall slightly (Laws, in press). If the age composition of the population has changed then this would affect the 'percentage pregnant', but only to a very slight extent. This effect, if appreciable, is in any case likely to result in a lowering of the 'percentage pregnant'.

With these reservations in mind the variations from year to year in the 'percentage pregnant' may be briefly described. In Fig. 6 I have plotted the values for blue whales, combining samples from all areas because individual areas show a similar pattern. This indicates an apparent increase in fertility in pre-war years, levelling off at about 80 per cent pregnant. The great reduction in the intensity of whaling during the war years is apparently correlated with a fall in the percentage pregnant to the original low level of the early 1930's. Then, in post-war years, there was a similar increase in fertility up to the 1950-1 season, though it seems that the maximum fertility is lower than in pre-war years. Here again sampling difficulties are probably responsible, because pregnant females are more abundant in catches in the early part of the season (Mackintosh, 1942), and the later season for blue whales should result in a potentially lower 'percentage pregnant'. Unfortunately, with the decline in the catches of blue whales in post-war years, samples after 1954-5 have been too small to use.

The data for the fin whale follow a similar pattern and I have plotted the

values for area II and areas III and IV separately. (Areas III and IV have a similar history of exploitation, beginning long after area II.) There is not much material relating to pre-war years but the 'percentage pregnant' in area II catches was about 80 per cent just at the beginning of the war years and had fallen to a very low value in the first post-war season. There are, however, reasons for supposing that this value is too low, and that the sample was less representative of the stock than in other seasons. By 1950-1 or earlier the 'percentage pregnant' had reached the upper limit of about 80 per cent. Similarly in areas III and IV, in the earlier post-war seasons the 'percentage pregnant' was relatively low and in later seasons stabilized at about 80 per cent. The apparent drop in the percentage pregnant in area II in 1958-9 is disturbing, but it is too early to assess its full significance. If this trend should continue then it implies a fall in fertility which may be a consequence of the continued reduction in the stock.

In area I (part of the former sanctuary) the 'percentage pregnant' in the first season's catch was estimated as 68.5. However, marking returns show that there may be a significant interchange between areas I and II (Brown, 1954), and this value is probably to be considered as a compound of the area II value of 80 per cent and a lower value obtaining for an indigenous area I stock. In the two subsequent seasons the values were 73.0 per cent and 71.3 per cent. The fertility rate in area I had not reached the level of other areas up to the 1957-8 season. Unfortunately no later data are available.

I have calculated, on the basis of a detailed analysis of the reproductive cycle that a figure of 80 per cent pregnant is equivalent to a real annual fertility rate of about 60 per cent (Laws, in press). This appears to be the upper limit for the fin whale.

(b) *Earlier sexual maturity*

The data presented in Fig. 5 suggest that one response to exploitation is a reduction of the age at which breeding begins. The baleen plate method is the only one which can be used to show this because the ear-plug method was not available until 1955-6, by which time, as I shall show, this response was complete and the average age at sexual maturity had been stable for some years. For an obvious reason the ovary method is inapplicable.

Hylen *et al.* (1955, fig. 1) illustrated the percentage age composition of fin whale catches, and differentiated between sexually immature and mature animals. In both sexes there is seen to be an increase in the proportion of mature animals in baleen groups II, III and IV from 1945-56 to 1952-3. Professor Ruud has provided additional material, classified in this way, for post-war seasons up to and including 1955-6. I am indebted to him for permission to publish it.

In Fig. 7 the yearly percentages of mature females in different age groups are presented in graphical form. In baleen group V all females are mature, and in group IV, if we discount the 1945-6 season (see above), the percentage of mature animals has been fairly steady at about 90 per cent during this period. In group III, however, there has been a marked increase from 30 per cent of mature females at the beginning of the period rising to a peak at nearly 80 per cent in 1952-3 and then falling slightly to about 60 per cent in 1955-6. Baleen group II shows a small increase in the proportion of immatures, stabilizing at about 10 per cent from 1952-3 onwards. By comparison it would seem that the apparent decline in the mature component of age group III from 1952-3 onwards is not real. Probably stability was

FIG. 7.—Changes in the percentage of sexually mature female fin whales in different baleen age groups.

reached in this group also in 1952-3 at 50-60 per cent mature. These trends in the samples can best be accounted for in terms of a lowering of the age of puberty. Converted to the average ages at puberty this shows a progressive advance of about half a baleen group up to 1952-3, after which it appears to have remained stable.

(c) Accelerated growth

The evidence for a steepening of the growth curve is mainly circumstantial, because our material is not sufficient to show significant differences in length at age values from year to year.

It is suggestive that although the average age at puberty has decreased, there is close agreement between the observed and estimated values for the percentage of immatures (Fig. 5). If puberty occurs at an earlier age, but is not associated with increased growth then the average length at puberty will

be less. The proportion of females estimated from their length to be sexually immature, should therefore increase relatively to the observed proportion of sexually immature females. The (smoothed) curves showing the proportion sexually immature estimated by the length criterion and by inspection do not show the expected divergence, and this is suggestive, but not conclusive, evidence for an increase in the growth rate.

In fish increased growth is often associated with earlier maturity and in seals also accelerated growth appears to be associated with sexual precocity (Laws, 1959*b*).

If earlier puberty in whales is, as seems likely, secondary to an increase in growth rate, it is possibly a result of lessened competition for food. There will in any case be an interval of several years before its influence on the reproductive rate is effective. Fig. 7 shows that the resumption of whaling on a large scale in 1946-7 and 1947-8 did not have an appreciable effect on the age at puberty until at least 1949-50.

CHANGES IN THE SHAPE OF SURVIVAL CURVES

Owing to wear at the tip the baleen plate method of age determination can only be used for the early age-groups. We can get a better idea of the distribution of the older age-groups in the population if we study the ear plugs or ovaries. The ear plug is better because it applies to all age-groups, though there is still some uncertainty about the interpretation of the laminations. As regards adult female fin whales the results obtained by ear plugs and ovaries are practically identical, assuming two ear-plug laminations per year (Purves & Mountford, 1959) and 1.43 corpora per year (Laws, 1959*a* and in press). For present purposes the ear-plug method has the disadvantage that the first samples date only from the 1955-6 season, and I propose to draw upon the ovary data for examples.

For reasons which have been given at the beginning of this paper it is not advisable to regard the survival curves as precise life table material. The examples given have been selected from similar areas and are restricted to the same season (January, February and the first half of March). My intention is merely to show that the age composition has changed and that, even allowing for the increase in the reproductive rate, recruitment is insufficient to maintain the stock at the present level of exploitation.

First, a few words on the method of constructing these curves. In converting the ovarian corpora counts to survival data, the age composition of the samples of adult females is examined and survival (or mortality) is inferred by a dynamic method (Laws, in press). All females in each sample have survived to accumulate one corpus luteum or corpus albicans in the ovaries;

the number in the sample with only one corpus in the ovaries is subtracted from the total to give the number surviving to accumulate two corpora, and so on. It is in effect a form of smoothing. These data are then plotted on a logarithmic scale and converted to age data by interpolation, assuming that on average 1.43 corpora accumulate per year. For the later samples

FIG. 8.—'Survival curves' for female fin whales, area II.

the average age at puberty is taken to be five years from ear-plug data (Laws, in press), and for the pre-war sample puberty is assumed to be half a year later. The part of the survival curve relating to adult females therefore begins at five and a half or six years.

There is no reliable material for immatures but the number of female calves has been estimated from the total number of adult females. The conception rate is taken to be 60 per cent; a foetal sex ratio, referring to mid-pregnancy, of 48 per cent females (Laws, in press) is assumed to apply at birth and total foetal mortality is estimated at 20 per cent. This mortality estimate is the only assumption not based on firm evidence, but is probably realistic and in any case variations in this parameter have a relatively small effect on the estimates of recruitment. The recruitment is then plotted and the whole curve adjusted so that it represents the survival of a cohort of 1,000.

This method gives hypothetical survival curves, and for the reasons I have given they are probably biased and not applicable to the stock as a whole,

but they are comparable with each other. Subject to these qualifications and reservations let us now compare them.

For area II comparison of the 1939-41 and 1955-7 curves shows that the section of the survival curve referring to the older age-groups has steepened, and there are now far fewer females older than 15-20 years (Fig. 8). The maximum age in samples of similar size is now about 28 years (sample size 302) compared with about 42 years in the earlier period (sample size 336). Another feature of these curves is that in recent years the slope in the early mature groups is less steep than formerly. If the stock were not subject to a greatly increased fishing mortality in the early years this might perhaps be

FIG. 9.—'Survival curves' for female fin whales, area I.

attributed to reduced natural mortality, but it will be remembered that the early age groups (e.g. baleen groups 0-III) now comprise about 45 per cent or more of the total catch compared with less than 25 per cent in the earlier period (Fig. 5). Also the total catches are now much higher (Fig. 1) so the discrepancy is even greater. This relative change in the first section of the survival curves must therefore be a result of reduced recruitment.

The steepening of the later part of the survival curve is not entirely due to the effect of an increased rate of mortality working through the age groups. If mortality were uniform with respect to age over most age groups, as the 1939-41 curve implies, it would take over thirty years for this effect to work through the population. Yet the period between the samples is only sixteen

years. It therefore appears that there has been selective fishing mortality with respect to age.

The survival curves for two successive seasons in area I (Fig. 9) strongly support this view. In the space of one year the curve has steepened very markedly and this can only be explained by selective mortality of older whales. Both of these samples were collected by biologists working on the same factory ship, with the same catchers and men, working in the same relatively small area. Moreover, Japanese biologists in area VI (also formerly a sanctuary like area I) got almost identical results in these seasons (International Whaling Commission, Ninth Report, 1958, p. 21).

I believe that the explanation of this effect lies in the relative segregation of different age-groups, the oldest animals arriving on the feeding grounds first and the youngest last, as mentioned at the beginning of this paper. With a limited whaling season the older whales are therefore vulnerable for a longer period than the younger animals. The magnitude of this effect in area I is probably related to intensive fishing on a relatively small, geographically concentrated stock. The value for fin whales per C.D.W. fell from the very high figure of 2.40 in 1955-6 to 1.61 in 1956-7, and to the low value of 1.13 in 1957-8. In 1958-9 there was no whaling in this area, possibly because it had become unremunerative.

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SUMMARY

- (1) This paper is mainly concerned with the fin whale and with antarctic pelagic whaling over the last three decades.
- (2) For a number of reasons really adequate sampling of the stocks has not been achieved, but the samples available can be used to demonstrate the more important effects of exploitation.
- (3) The catcher's day's work is the most acceptable measure of effort. In terms of whales per C.D.W. the southern stocks of both blue and fin whales are decreasing.
- (4) Decreasing mean lengths and the rising percentage of young animals in the catches of blue and fin whales are interpreted as signs of declining stocks.

- (5) Recruitment is within narrow limits related to the size of the adult female component of the population.
- (6) The pregnancy rate of mature females has increased in response to exploitation and the age at maturity is now earlier, possibly in association with an increase in the growth rate.
- (7) In spite of the increased reproductive rate survival curves indicate that at the present rate of exploitation recruitment is insufficient to maintain the stocks.

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POPULATION STUDIES ON
THE MINKE WHALE
BALAENOPTERA ACUTO-ROSTRATA LACÉPÈDE

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INTRODUCTION

Whaling for minke or the little piked whale and other small species from small fishing vessels commenced off the Norwegian coast in the 1920's and, just before the late war, operations had spread all along the Norwegian coast. Since the war, operations have expanded, westwards to Scotland, Shetland and the Faroes and northwards to Bear Island, Spitzbergen and the Barents Sea.

Since 1938, the number of boats participating in this new industry has been regulated by licence, and at present about 200 licences are issued each year. No limitation of size or number of whales taken is enforced, and such methods of regulation are out of the question for practical reasons.

Meat for human consumption is the primary product; for economic reasons meat for animal food, and blubber, are of secondary importance. Due to difficulties of marketing in the summer, a close season of three weeks in July has been in force since 1950. Since 1955 whaling in Arctic waters north of 70° N lat. has also been forbidden after 30th June. In all other waters, the total length of the whaling season (the close season in July included) must not exceed six months, a measure introduced from 1952 by international agreement. At present the season lasts from 15th March to 15th September.

All licensed whalers have to report their catches on special forms issued for this purpose. For each individual the following data are required: Species, length in English feet, sex, position and date. For pregnant females also length, sex and size of foetus. From 1938 to 1958 completed forms for 53,786 minke whales have been received. Seven hundred and ninety-six forms are incomplete and disregarded in the following discussion. Our material includes, therefore, 52,990 specimens, of which 26,995 or 50.9 per cent are males.

During their migration in Norwegian waters, the minke whales travel more or less segregated according to size and sex. In early spring, the stocks in Norwegian coastal waters are dominated by pregnant females. Mature males are less frequently met with on their northward migration, because they evidently migrate in open waters further off the coast. The recently weaned calves are mostly found in the summer in the waters between Møre (Fig. 1, III) and Vesterålen (Fig. 1, VI) with a concentration in the Lofoten area (Fig. 1, V), and a few seem to migrate further north. In the Arctic,

FIG. 1.—Minke whaling. Statistical areas adopted.

therefore, here including the statistical areas VII, VIII and IX, we find stocks mostly of bigger animals; a high proportion of them are sexually mature, and all mature females are pregnant.

We have not been able to work out a dependable or useful method for age determination of minke whales. Our studies in the population dynamics of this species are based on statistical information revealed by the whalers' reports, and biological research upon the stocks in question (Jonsgård, 1951; 1955).

CHANGES IN THE CATCH PER UNIT OF EFFORT

Fig. 2 shows the total numbers of minke whales taken in the years 1938–59, subdivided to show the catches in Lofoten, Arctic and in all other areas. The

Fig. 2.—Minke whaling. Right-hand columns (solid black) — average catch per boat. Left-hand columns—number of whales taken, subdivided into catches in Lofoten (diagonal shading), Arctic (dots) and all other areas (white).

average catch per boat is also shown. From the figure it appears that up to the end of the last war most of the whales were taken in the Lofoten area; from 1938 to 1945, 55.6 per cent of all minke whales were caught there. During the period from 1946 to 1959, however, the expanded activities in the Arctic areas brought the relative importance of the Lofoten area down to about 29 per cent of the total, although the actual catch in Lofoten showed no decline until recently. A rise in the catch per boat also took place, from about five whales per boat during the first few seasons to about eighteen whales per boat in recent years.

Judging by the figure, the stock of minke whales seems to be in perfectly sound condition. However, besides the expansion of the industry to new and

more profitable whaling fields, the whale catchers have been considerably improved, both as regards size and equipment. Furthermore, the whalers co-operate to a much greater extent than they did before. The increased catches in recent years can thus be explained. During the season 1959, however, the total catch decreased considerably, especially in the Lofoten area, where the catch was 524 whales only. We have to look back to the 1940 season, ruined by hostilities, to find a poorer result in this area.

CHANGES IN THE NUMBER OF CALVES IN THE CATCHES

Since young animals are not protected by size limits and calves are taken indiscriminately, our material allows a closer study of calves. Our growth studies have shown that at least all animals which are up to 17 ft in length are calves in the O-group.

Fig. 3 shows the total number taken of calves in size groups 15 ft and less, 16 ft and less, and 17 ft and less in the Lofoten area and in all other areas. Despite the increasing number of whales caught during the period from 1938 to 1958 smaller calves have become more and more scarce in the catches since and including the season 1949. During the seasons 1941-8 the average catch per season was about 300 animals 15 ft and less in length, as compared to about 100 such animals today.

As mentioned before, the total number of whales taken annually in the Lofoten area has shown no decrease during the period from 1941 to 1958, but the number of animals 15 ft or less in length decreased from about 200 animals per season during the period 1941-8, to about 50 in recent years.

This decrease in the number of smaller calves may be explained by the following alternatives:

1. *The bulk of the calves may be born earlier than previously*

Such a result would be expected if a selective catch of pregnant females exploits the late breeders more heavily than the early breeders. We believe that the effect, if any, of the regulations enforced in recent years is to the contrary, because the closure of the Arctic waters to whaling after 30th June will tend to protect the late immigrants more than those arriving early.

2. *The growth rate of calves has increased*

It has been observed for several species of mammals that improved conditions of nutrition have resulted in an increasing rate of growth. Such an effect may be expected, therefore, if the stock of minke whales has been much reduced. On the other hand, the diet of the minke whale is very comprehensive, and

FIG. 3.—Minke whaling. Number of calves, subdivided into: shaded — caught in Lofoten, white — caught in all other areas.

it is hard to believe that there has been such a serious shortage of food during the past years that improved conditions should have any effect.

3. *The intensity of whaling may have shifted to a later time of the year*

If this was the case, the calves would be older when caught, and they would consequently have grown in size. No seasonal shift in the intensity of whaling has taken place, however, except that due to whaling regulations. The close

season in July, will delay the taking of some calves up to three weeks. Comparing the sizes of calves caught before the 1st July, before and after the introduction of the close season in 1950, it looks as if the closure to some degree may have influenced the taking of smaller calves, but the close season alone cannot explain the total decrease in the taking of the smallest calves.

4. *The smaller calves have been exploited more severely than the bigger ones*

This may be the case, because recently weaned calves usually seek the whale catcher and they are, therefore, more easily caught. Since almost all the calves are born between November and March with the bulk of births in January, the smallest calves would be relatively scarce in the whaling season. If, therefore, the number of calves decreases considerably, the total catch of calves cannot be kept at the same level unless all sizes of calves are caught more indiscriminately than before.

There is a good correspondence between increased catch of pregnant females and decreased number of smaller calves in the catches.

CHANGES IN THE RELATIVE NUMBERS OF SEXUALLY IMMATURE AND MATURE ANIMALS IN THE CATCHES

From biological evidence we may assume that as an average, males over 22 ft and females over 24 ft in length are sexually mature. Our material has been divided into immature and mature animals accordingly.

FIG. 4.—Percentage of mature minke whales in the catches.

Fig. 4 shows the percentage of mature minke whales in the catches in each of the seasons 1938–58. From 1938 to 1944, this percentage decreased from 42·8 to 18·3, increased again to 42·9 in 1949, decreased to 27·7 in 1950, increased to 38·9 in 1952, and decreased finally to 30·8 in 1953. From then on, there has been a continuous and even increase, and in 1958 the percentage of mature animals reached 43·2, which is the maximum for the twenty-one years covered by our statistics.

The decrease from 1938 to 1944 coincide with the period in which the Lofoten area was the most important whaling field. It would, consequently, be reasonable to expect that the percentage of mature animals in the catches from Lofoten would have a decisive influence on the percentage in the total catches.

The percentage of mature animals in the Lofoten catches decreased by 9·9 per cent from 1938 to 1944, and this decrease can be attributed to a relative increase in the number of whales caught in this area in the summer months, when calves are most abundant. Simultaneously, there was an increased intensity of whaling in this area, which was partly local, but to a great extent due to increased participation of whalers from other coastal areas. As a consequence of this last shift, the relative importance of the Lofoten catches increased from 38·3 per cent of the total in 1938 to 65·2 per cent in 1944. An increase in relative importance of this magnitude must in turn reduce the percentage of mature animals in the total catches.

As previously mentioned, the catches in Arctic waters increased considerably after the war, and since large-sized animals are more abundant there than in Norwegian coastal waters, the percentage of mature animals in the total catches increased accordingly. The variations observed in the percentage of mature animals in the period from 1944 to 1953, are, therefore mainly due to variations in the Arctic contributions to the total catches.

The continuous and even increase from 1953 to 1958 in the percentage of mature animals in the total catches, corresponds to a similar increase in the Arctic catches, from 49·0 per cent in 1953 to 61·8 per cent in 1958. A trend to increasing percentages of mature animals is also apparent in the catches from the Lofoten area in this same period. In all other areas considered together, a definite increase in the percentage of mature animals is observed, namely from 18·4 per cent in 1953 to 43·6 in 1958. For this part of the catches, some of the increase may be attributed to greater catches taken off Scotland, Shetland and the Faroes, where many big whales are met with. Summarizing these observations, it must be concluded, however, that a general increase in the percentage of mature animals has occurred since 1953 within the whole catch.

During all seasons of which we have statistics, the minke whales have been

exploited selectively to a great extent, since the percentage of sexually mature animals in the catches has always been very much less than what it must be in the normal stock at large. Females apparently attain maturity and become pregnant for the first time at an age of two years, and they give birth to one calf every year from the third onwards. The sex ratio is approximately 50 : 50. Thus the number of calves born any one year is equal to 50 per cent of the mature stock, animals in their first mature year excluded. *An accumulated stock* will consist, therefore, of approximately 60 per cent sexually mature animals, and this result will be only slightly influenced by mortality.

In the catches taken over a period of twenty-one years, from 1938 to 1958, the percentage of mature animals has varied between 18·3 and 43·2, the average for all seasons being 35·0 per cent, about 25 per cent below the approximate figure calculated for the normal stable stock. Thus, immature animals have been exposed to a much higher rate of exploitation than have the mature ones.

The net result must be a reduction in the total stock and a corresponding decrease in the abundance of whales in the whaling fields. The chances for a continuation of the highly selective catch will be reduced correspondingly if the total catch is to remain the same.

The significance of an increase in the relative number of mature animals in the catches is, therefore, in this case that the stocks of whales have been reduced appreciably.

SUMMARY

In Norway the catching of minke whales started about thirty-five years ago. Since 1938 a licence has been required for minke whaling, and since then statistical information has been collected which includes position and date, as well as numbers, sex and size of all animals caught.

Investigations of the minke whale in post-war years have given relatively good information as regards its biology in general. We are not, however, able to determine individual age in this species.

A characteristic feature relating to the catch of minke whale is that all animals met with are being hunted. No limitation by minimum length exists.

The catch per unit of effort has shown no sign of depletion up to 1958, but in 1959 there was a marked decline.

In spite of the fact that the total catch has increased, the number of smaller calves taken has decreased since 1949. We assume that this is due to failing recruitment, but other possibilities are also discussed.

The composition of the catches has shown great changes with regard to the percentage of mature animals during the period 1938-58. It can be demonstrated that the changes occurring during the period 1938-53 are due

to changes in the seasonal catches and to the geographical distribution of the catching activity. Since 1953, however, there has been a regular and marked increase in the percentage of mature animals in the catches, from 30·8 in 1953 to 43·2 per cent in 1958, which most probably must be explained by failing recruitment. Based upon known biological data for the minke whale, it can be calculated that in an accumulated stock there will be about 60 per cent sexually mature animals. During the period 1938-58, however, the corresponding figure in the catches has been about 35·0 per cent. Season after season during a span of more than twenty years, therefore, the sexually immature animals have been more heavily taxed than the matures.

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POPULATION DYNAMICS AND EXPLOITATION OF SEALS IN THE EASTERN CANADIAN ARCTIC

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Five species of seals are found in the eastern Canadian Arctic. Of these, the Harp Seal (*Pagophilus groenlandicus*) is an abundant summer migrant, but is not often killed by the Eskimos of most regions. The Hooded Seal (*Cystophora cristata*) is a rare migrant to the north-east Arctic; the Harbour or Common Seal (*Phoca vitulina*) is a rare and local resident throughout the more southerly Arctic. Only the two remaining species are common and of economic importance at present. The ubiquitous Ringed Seal (*Phoca hispida*), which is generally less than 5 ft long, forms or once formed the basis of the economy of almost all coastal Eskimos. The Bearded Seal (*Erignathus barbatus*) is a considerably larger species, up to about 8 ft long; it is far less common, but is much prized for its meat and for its hide, which is used in making boots, skin lines, and other Eskimo products.

A brief account of the pertinent aspects of the life histories of these two species will be given first as a necessary background to the bionomical considerations which will follow. Two papers by the author (McLaren, 1958a, 1958b) support and elaborate the biological conclusions offered here. The geographical names referred to in the text may be found on Fig. 1.

OUTLINE OF THE LIFE HISTORIES OF RINGED AND BEARDED SEALS

Accurate methods of age determination have laid the basis of our understanding of the life histories and bionomics of these seals. The ringed seal may be aged by means of dentinal annuli in the teeth (Laws, 1953) and the bearded seal by bands on the claws (Plekhanov, 1933). Both tooth and claw patterns depend on annual metabolic interruptions caused by fasting, the moult, and other coincident drains on the animal. Unfortunately, due to wear at the tip, the claws cease to be useful a few years after maturity.

The feeding of these seals has been studied in detail. The ringed seal takes

FIG. 1.—The eastern Canadian Arctic, showing localities mentioned in the text.

planktonic, nektonic or benthonic food and varies its diet considerably, generally turning from inshore feeding on the epibenthic *Mysis*, prawns, or polar cod (*Boreogadus*), to strictly macroplanktonic feeding in deeper, offshore waters. Food may be chosen from many points on the food web and from at least two trophic levels, and it is consequently unlikely to limit the distribution and abundance of this species. Indeed, the seal is scarce where its food is apparently abundant and is common in regions of low productivity.

The bearded seal, on the other hand, feeds almost entirely on large burrowing or sedentary bottom invertebrates (these species are not taken by the ringed seal) and is not found in deep water. It also differs from the ringed seal in being generally incapable of keeping open holes in the thick, land-fast ice in the winter. It seems most abundant in the Arctic where reasonably shallow banks are free of fast ice in winter, and equilibrium populations may be determined by the availability of food, although the nature of this dependence is not yet understood.

Both species show a decline in feeding activity in the spring, which is the moulting and basking season. The blubber of an average ringed seal drops from a winter peak of about 40 per cent of the animal's weight to a summer low of about 23 per cent. This blubber loss results in decreased buoyancy and a much greater proportion of seals killed in the water by rifle fire in early summer sink and are lost.

Our understanding of reproduction in these species is enhanced by reliable age determinations. Previous estimates of the age of newly-matured seals have usually given too low a figure, and this of course introduces a dangerous error into determinations of the rational exploitation level. In the ringed seal there are about 46·5 females to 53·5 males. The males of both species usually mature when seven years old. The females generally mature (first ovulation) in their sixth or seventh year, but in the ringed seal, for which we have much more information, they do not always become pregnant from the first ovulation. In south-west Baffin Island about 10 per cent of ringed seals produce a pup when six years old, about 50 per cent when seven, and about 75 per cent when eight. Almost 100 per cent of older females are fecund, the proportion of successful pregnancies probably decreasing slowly with age so that an average pregnancy rate of 90-95 per cent is established. We have little information about the post-reproductive period, but this is believed to begin in the late twenties or early thirties; very few females reach these ages. It should be pointed out here that population control of the ringed seal is believed to act at least partly through reproduction, so that the age-specific birth rates given above cannot be universally applied.

Both ringed and bearded seals have delayed implantation of the blastocyst, which has given rise to false assumptions about the breeding seasons. The males of both species are in full rut in the spring, from just before until shortly after the females give birth to the pups. The female ringed seal ovulates at this time and is impregnated while still nursing her pup. Those bearded seals which have given birth apparently fail to ovulate until after the rut of the males is over, and thus a two-year cycle of pup production is established.

The bearded seal lives in the open water the year round and breeds on the

pack ice, but the adult female ringed seal needs land-fast ice, covered with a good depth of snow, for the construction of a birth lair. These lairs may be hollowed out in the overlying snow, particularly in drifts over rough ice or along tide cracks, or the female may take advantage of a natural 'tent' of ice in the pressure ridges near shore. The pup is protected and fed here until weaning, which may not occur until the ice breaks up. Irregular coasts with skerries and inlets, which retain large amounts of stable, long lasting, fast ice, thus provide most suitable conditions for long and uninterrupted suckling of the pups.

In winter, the ringed seals taken in the open water at the edge of the fast ice are exclusively immature in most regions; seals killed in the peripheral ice of complex coasts or in the fast ice of adjacent simple coasts are mostly younger adults; those taken at the heads of bays, or well within island-filled regions, and in general in thick, heavily snow-covered ice, are mostly older adults. Increase of experience with age and possibly competition for more suitable pupping sites may serve to explain this distribution of adults.

The influence of ice conditions is also reflected in the higher proportion of small pups and the common occurrence of starvelings, the result of premature separation from their mothers, among seals of simple coasts. The offspring of younger, less experienced mothers dwelling on less stable, less snow-covered ice seem generally to be weaned earlier. When it was found that the seals of simple coasts of south-west Baffin Island were shorter on average (by perhaps 10 per cent as adults) than seals of the same age from nearby more complex coasts, it was presumed that the size of full-grown seals was related directly to their size at weaning. Certainly the food available along these coasts does not differ (if anything, the open coast is more productive) and it is unlikely that populations only 200 miles apart will be different genetically. A similar explanation is offered to account for size differences throughout the ringed seal's wider range. Adult seals from high-Arctic localities may average 15 per cent longer than adults from south-west Baffin Island, while those from southern Hudson Bay may be 8-10 per cent shorter. The longer suckling period permitted in the more northerly localities results in larger, more vigorous pups. These grow into larger adults, which in their turn may produce large pups. Within limits, then, the effect may be self-sustaining.

Adult bearded and ringed seals have no significant predators. The polar bear is rare and local and the killer whale all but absent from the eastern Canadian Arctic. Ringed seal pups may suffer quite heavy mortality by foxes (*Alopex*), and even be killed by gulls and ravens when in exposed situations. Only a few seals have been found suffering from apparently debilitating disease or parasites. The potential longevity of the ringed seal is

very great, one male at least 43 years old having been taken. Tooth wear is possibly the most significant natural cause of death of the adults before physiological maximum longevity. The teeth of very old seals are often badly decayed, and this may accelerate their death because they can no longer keep open holes in the ice. Immature seals, on the other hand, have to suffer the rigours of the unstable pack ice in winter; it is believed that many must meet accidental death by being crushed or trapped without access to the air.

It is apparent from the above qualitative considerations of their life histories that populations of these seals are particularly amenable to quantitative analysis. A very preliminary analysis of this kind has in fact been published as a guide to the economics of seals in the Eastern Canadian Arctic (McLaren, 1958c) and its essential points will be summarized here. This paper was not intended for wide distribution, and the study is still considered to be in a preliminary stage. A more up-to-date elaboration of some of the techniques and formulae for the assessment of numbers and availabilities of ringed seals will be published elsewhere (McLaren, in press), since detailed methodology need not concern those interested in population ecology itself.

THE NUMBERS OF SEALS

A knowledge of population size is of course almost always of great importance in the rational exploitation of animals. The direct approach, by counting or marking, is generally necessary, but the student who is fortunate enough to find simple environmental determinants of equilibrium populations may be rescued from the demands of extensive or continuous counting.

A method of census from shipboard has been developed by the author, which allows for the variables of ship-speed, limits of visibility, and the times spent by seals under water and on the surface. More information is needed on the last two variables before the results can be considered more than relative.

The importance of fast ice to the ringed seal has been emphasized above, and it can be shown to offer a deductive basis for the estimation of populations. In an under-utilized population of ringed seals pup production appears to be limited by the amount and quality of fast ice available for the reproducing females. Possibly there is a limited number of sites suitable for the construction of birth lairs and reproduction is unsuccessful elsewhere. Alternatively, each seal may require a territory of fixed size so that there is an upper limit to the number inhabiting a given area of fast ice. It is in fact unlikely that any one such abrupt mode of limitation, analogous to that applying to hole-nesting species (such as the bee, *Megachile*, discussed by

Andrewartha & Birch, 1954), applies to the seal. There is, however, ample evidence for several mechanisms which will combine to force an upper size limit and a stable age structure on ringed seal populations. As has been pointed out, surplus females may be forced to occupy less suitable ice, where their pups may be precociously abandoned or even killed by unstable conditions, and where exposure to predators may be greater. There is also evidence that the pregnancy rate of adult females may be directly governed by the availability of suitable ice. In areas of Baffin Island and Foxe Basin, where there is much suitable ice and quite high hunting pressure, only one adult female (pregnant at the end of March) has been taken in the total sample of 128 specimens from the open water outside the fast ice in late winter and spring. As might be expected, almost all the adult females were successfully engaged in reproduction within the fast ice, or at least were in a position to be impregnated by the adult males which were also under that ice. In contrast to this, near Churchill, on the open coasts of south-west Hudson Bay, where there is little suitable ice and little hunting, only two specimens are available from the open water in late winter; this would ordinarily be too small a sample to tell us anything, but both seals were adult females, and neither was pregnant! There is no doubt that both sorts of limitation on the success of reproduction are density-dependent, or compensatory, and will serve to produce populations of equivalent size and age structure in regions with equivalent amounts and qualities of fast ice. If territoriality *per se* is a factor at all, it may apply more to the occupation of fast ice by adult males, which often show severe bite-wounds in the breeding season. It has been implied that ringed seals are not limited by food supplies and indeed it is believed that the control of populations through recruitment may preclude the action of compensatory mortality on any age-group, except of course the pups. However, there is good evidence of greater dispersal from regions of high reproductive potential, and such emigration may be density-dependent.

In order to calculate the size of seal populations, we may first assume that equal areas of fast ice of the same type will contain the same number of animals. Secondly we must discover how many seals occur in unit areas of different kinds of fast ice. The quality of fast ice doubtless depends on many geographical and climatic factors, but coastal complexity is especially important. An analysis which seems to give reasonable results at present involves estimating the relative proportions of three arbitrarily-defined categories of ice — that within one mile of shore and surrounded by further ice, that within one mile of land but exposed to open water on its seaward edge, and that more than one mile from land. A few counts of seals lying on the fast ice during the spring basking season suggest that these classes of ice contain total populations of about thirty-five, ten, and five seals (or about

seven, two, and one birth lairs) respectively per square mile of ice. The estimates may have more relative than absolute validity, for they assume that the *entire* population may be counted on the fast ice at the height of the basking season. The extent of fast ice has been measured from maps, and population estimates made for different sections of coast-lines. A total population of close to a million is suggested by these means for the eastern Canadian Arctic south of Lancaster Sound and north of Cape Chidley and James Bay.

It has been suggested that populations of under-utilized bearded seals may be limited by the accessibility of shallow, ice-free feeding banks in winter. Unfortunately, suitable hydrographic charts are very few, and we cannot even begin to develop a key to the numbers of bearded seals comparable to that developed for the ringed seal. The only way to derive a first approximation of numbers at present is to compare the relative abundance of this species and the ringed seal in shipboard censuses (actually through means of the 'index of availability' outlined below) and extrapolate to coast-lines which are generally similar in shallowness and ice cover.

SUSTAINABLE YIELD OF SEALS

If the seals of a region are to support Eskimo needs indefinitely, then the mortality imposed by hunting and natural causes must not exceed the recruitment into the population.

On the Hudson Strait coast of Baffin Island, from which we have the largest collections, the catch statistics suggest that seal numbers have remained steady in recent years. Local or seasonal shortages or increased catches may safely be attributed to local changes in hunting pressure, weather or economic factors. But we have no *a priori* reason for presuming that the population is being kept in balance by hunting mortality, for it has been shown that under-exploited populations will have their equilibrium maintained by ice conditions. Future work on populations experiencing various levels of hunting mortality is planned to assess its effect on pupping success, pregnancy rates, emigration, and natural mortality.

If we assume that the equilibrium population of southern Baffin Island is in fact experiencing maximum possible hunting mortality, the result should be to give us a very safe estimate of the sustainable yield from an analysis of the available mortality and reproductive rates.

Where X_j is the number of seals in age-group j at the beginning of the seal year, where S_j is the annual survival rate of the age-group j , where B_j is the birth rate of the age-group j , and where there is no reproduction by the first or last (Z^{th}) age-groups, and no emigration or immigration, then in an equilibrium population:

$$X_0 = B_1 S_0 X_0 + B_2 S_1 X_1 + \dots + B_Z S_{Z-1} X_{Z-1} \quad (1)$$

Also, where t_j is the total annual mortality rate, m_j is the annual rate of hunting mortality, and n_j is the annual rate of natural mortality of the age-group j , then:

$$1 - S_j = t_j = m_j + n_j - m_j n_j \quad (2)$$

Where a population is sampled at random, the age composition of the catch may be used to determine the age-specific rates of total mortality (t_j). Unfortunately, samples from south-west Baffin Island, while extensive, are by no means random. There is considerable under-representation of the first-year seals, which are largely born in inaccessible areas. Immature seals probably become harder to catch and tend to spend the winter under the fast ice as they get older. Adult seals become increasingly under-represented in the catch due to local hunting and to their progressive withdrawal to the more suitable breeding grounds. However, selected catch curves or certain sections of the overall catch curve may be used to give rates of total mortality for some age-groups. For example, after the age of 15, year-groups of seals are probably equally accessible and equally easily caught, and samples of them may be compared to give mortality rates from year to year. Likewise older immature seals and young adults are probably adequately represented in summer-killed samples.

The estimates of hunting mortality in each age-group depend on the combination of local and seasonal age-samples with local and seasonal catch statistics. The derived age structure of the total annual kill (including loss by sinking), which averages around 7,000 seals along the Hudson Strait coast of Baffin Island, is thought to be sufficiently accurate.

Thus we now have the means of constructing hypothetical balanced populations which will have annual yields of 7,000 seals. This can be done by setting up an initial cohort (X_0) and changing its size to satisfy equation (1), while making various assumptions about natural mortality in the first year and the proportionate effects of decreasing catchability and natural mortality as these affect the empirical catch curve of the immature seals, but always staying within the limits imposed by known hunting mortalities, the reliable total mortality rates of some age classes, and the reproductive rates. In operation the method involves tedious and inelegant iteration and successive approximation, but the results are valuable in indicating that suitable populations can only vary in size between rather narrow limits, in which the annual kill is between about 7 per cent and 10 per cent of the total population at the beginning of the seal-year. The lower limit may be taken as quite safe, and since the population estimate of a region is based on censuses performed later in the seal-year, we may consider that a sustainable kill of at least 8 per cent will be obtainable from ringed seal populations with the

same age-specific rates of hunting mortality as seals in southern Baffin Island. Fig. 2 depicts the characteristics of such a balanced population.

The original assumption that the population of southern Baffin Island was indeed being subjected to maximum possible hunting should now be

FIG. 2.—The age structure (above) of an equilibrium population of ringed seals in southern Baffin Island from which 7,000 seals (about 7 per cent of the population at the beginning of the seal-year) are removed annually. Smoothed curves (below) are drawn through the annual rates underlying this equilibrium, although in calculation the annual mortality rates were applied to the nearest per cent.

re-examined. This would imply that all suitable 'sites' in the fast ice were being used by pupping females, that age-specific birth rates were maximal, and that no emigration from the overall area was occurring. Nothing quantitative can be said about the last of these at present, but the existence of

high pregnancy rates (over 90 per cent) in the older adults and the short lag (averaging less than a year) between first ovulation and first pregnancy in newly matured females of that region both suggest that reproductive rates are being maintained at a very high level. The sustainable annual kill of 7,000 seals would represent 7–10 per cent of a total population of 70,000–100,000, while an independent population estimate based on fast ice distribution gives a closely comparable figure of 99,800 seals. Lastly, we may cite information that the harp seal, which has much the same age of first reproduction, reproductive rates, and longevity as the ringed seal, is thought from records of the effects of over-exploitation in the White Sea to have about the same permissible catch of 8 per cent (Surkov, 1957; see also Sergeant, 1959).

While we have been dealing with the numbers of seals, yield is often best dealt with in terms of biomass. In the first place there are considerable geographical differences in the size of ringed seals (dealt with earlier). Furthermore, with the increased mortality imposed by hunting there will be an inevitable reduction in the average age, and hence size, of the seals. But there is another curious property of these populations which must be considered. If the age and size of the female seals have an effect in themselves on the size of pups produced, then, through the mechanisms discussed earlier, the *age-specific* size of seals may decrease with utilization. This is unlike the common response of fish populations, where initial exploitation, at least, often results in increased size of the fish. While at present we have empirical figures on the average sizes of seals which may be combined with the theoretically based maximum sustainable yields, more refined, dynamical considerations of biomass yield must await further study.

The bearded seal has unfortunately offered neither a completely suitable method of age determination nor a sufficiently large series of specimens for an analysis of sustainable yield. The female produces a pup only once every *two* years, and this is a severe limitation. However, the collections available do suggest that the species has a smaller mortality rate, for the ratio of immature to adult seals is somewhat less than in the ringed seal. A maximum sustainable yield of 5 per cent is suggested as a safe first approximation.

AVAILABILITY OF SEALS

Considerable discussion has been devoted to the subject of sustainable yields, which may be of more general interest to the student of population equilibrium. However, the fact is that few regions in the Canadian north, to judge from the catch statistics, are being over-hunted. Indeed, the economic problem of most areas is not the sustainable yield of seals, but their availability

to the hunter. It is obvious that the problem is an exceedingly complex one, involving elements of geography, weather, technology, sociology, psychology, and numerous other variables as well as the population dynamics of seals. Nevertheless, it is believed that the basic features of availability can be quantitatively defined at present.

The Eskimo of many regions commonly hunts from boats in the open-water season. The ringed seal is essentially a coastal species, and does not disperse very far offshore. If we can presume that its tendency to move offshore is the same on all coasts, and that its distribution is random, then a very simple index of availability may be derived by dividing the theoretical, ice-based population size of any region by the area of water within ten miles of the coast, which is believed to be a reasonable estimate of the limit of offshore dispersal. It should be noted that whereas the population estimates depend on the accuracy and generality of local censuses on the ice, the index of availability depends on relative values, and is otherwise essentially deductive. Furthermore, the index is not directly proportional to population size and tends to reduce the relative differences between regions which are suggested by the population estimates. For example, the Belcher Islands, which cover about ninety miles from north to south, have theoretically about twice as many seals as the nearby 190 miles of coast of Hudson Bay between Portland Promontory and Richmond Gulf, but the summer availability indices of these two regions prove to be about the same. It is actually this index which is properly compared with the results from ship-board censuses, and such comparisons agree quite well.

Other seasons and circumstances can be treated in like fashion. The availability of immature seals in the open water in winter should follow the summer index fairly closely. Because equivalent fast ice in different regions is expected to support equivalent populations, the Eskimo who hunts in winter at the breathing holes of seals is presumed to have comparable success throughout the ringed seal's range. Likewise the hunter who stalks seals during their short season on the spring ice should experience everywhere the same progression and peak of seal availability, although the date will vary essentially with latitude. Indeed, in areas of seal scarcity, the only really productive season for the Eskimo may be the spring.

The relative abundance of the bearded seal and the ringed seal as observed in shipboard censuses permits us to derive empirical indices of abundance for the former species. It is this index which is in turn the basis for the number of bearded seals attributed to a coast-line, as implied earlier. The index is simply multiplied by the number of square miles within ten miles of shore, although it is realized that more attention should be paid to the prevalence of suitably shallow water on different coasts.

Indices of availability are of course abstractions and must be made more meaningful by being converted to catches per unit of effort. This has been done with the aid of observations on almost 100 hunting trips carried out in favourable conditions, mostly from boats in summer. The results of such trips have been found to agree quite well with the indices of availability, and the resulting combination can claim with some reliability to give the actual expectations of a day's hunting trip.

While there are many minor conditions, apart from the obvious ones of local or extensive over-utilization, which may render the theoretically predicted catches per unit of effort valid only over large areas and long periods, there are two major modifications which affect the expectations of the hunter. The figures on catch per unit of effort are in fact based on kill, not catch for there is an important loss of seals by sinking, which may be as high as 60 per cent in full sea water immediately after the ice breaks up. Sinking loss varies seasonally, latitudinally, and with salinity, and a graph giving the best present predictions of the loss is given elsewhere (McLaren, *in press*). The other important factor is the wind, which has adverse effects at all seasons, and when it is greater than a few knots makes hunting from boats unprofitable in all but the most sheltered waters. The influence of the wind should be readily predictable from the weather records. The importance of the wind and surface salinity should not be under-estimated; their combined effect may make some regions places of hunger in the midst of plenty.

INTEGRATED ECONOMIC ANALYSIS

From what has been said thus far, how can we best compare the economies of different regions where seals are almost the only subsistence resources for the Eskimos, and what does our analysis have to say about the administration of such resources? While several products (meat, blubber, skins) have been dealt with, general conditions in terms of production of meat are most illuminating.

Considering first the maximum sustainable yield of meat, our best estimate at present can be formulated as follows. The average weight of seals in a population can be calculated from the age-specific lengths and from log-length to log-weight relationships (which gives a slight under-estimate due to the proportionately greater influence of longer seals). About 30 per cent of each species is considered to be edible as human food. Then, in a delimited region where N_r and N_b are the stocks respectively of ringed and bearded seals, where Y_r and Y_b are their respective levels of sustainable yield (ignoring sinking loss), and W_r and W_b are the expected average weights of the catch (geographically variable only in the ringed seal), we may predict the potential

TABLE I. Preliminary analysis of seal production on four Canadian Arctic coasts. *The limits of the regions considered are defined roughly by the trading regions of their posts*

	Trading post	Approx. Eskimo population	Ice-based ringed seal population N_r	Sustainable yield $Y_r = 0.08N_r$	Average weight W_r (lb)	Annual potential yield of meat $(N_r Y_r W_r)$ (lb)	Bearded seal population N_b	Sustainable yield $Y_b = 0.05 N_b$	Average weight W_b (lb)	Annual potential yield of meat $(N_b Y_b W_b)$ (lb)	Summer availability indices $\left. \begin{matrix} I_r & I_b \end{matrix} \right\}$	Potential pounds of meat per Eskimo per year (lb)	Suitability for hunting $I_r W_r + 0.5 (I_b W_b)$	
	Cape Dorset	425	68,900	5,510	86	142,200	4,800	240	465	33,500	18.2	1.0	413	1,798
	Pond Inlet	250	66,300	5,300	118	187,600	2,700	136	465	19,000	12.3	0.5	826	1,568
	Belcher Islands	190	49,900	3,990	62	74,200	13,050	653	465	91,200	9.6	2.5	871	1,176
	Wakeham Bay	170	20,400	1,630	69	33,700	3,740	187	465	26,100	8.2	1.5	352	915

of a region in terms of meat production as:

$$0.30 (N_r \cdot Y_r \cdot W_r) + 0.30 (N_b \cdot Y_b \cdot W_b) \quad (3)$$

The results of this analysis for four localities are given in Table I, and suggest, for example, that Pond Inlet and the Belcher Islands may be considerably under-settled from the point of view of available resources and that Wakeham Bay cannot depend on seals as its sole resource (considering that the subsistence economy of Cape Dorset appears today fairly sound).

Another view of the same economies might be gained from the analysis of the availability of seals. A complete statement would integrate over a year the day-by-day expectations of suitable hunting weather, the probability when relevant that a seal will float, and the expectations of meat from a given day's hunting trip, always presuming that the most productive form of hunting will be pursued on a given date. This comprehensive treatment is not yet possible. For reasons given earlier the abundance of the ringed seal in the open-water season is a fair indication of its year-round availability, and the bearded seal is hunted practically only in the summer. Thus we may simplify the presentation here by offering an abstraction based on summer conditions. We may include the parameter of weight (above). Then, where I_r and I_b are the availability indices of ringed and bearded seals, the suitability of an area for hunting might be roughly:

$$I_r \cdot W_r + 0.5 (I_b \cdot W_b) \quad (4)$$

Since the bearded seal is only hunted in summer, we have reduced its influence to half, somewhat arbitrarily at best.

The results set out on Table I might be clarified by reducing the figure from Cape Dorset to unity and comparing the rest. Then:

Cape Dorset	. 1.00
Pond Inlet	. 0.87
Belcher Islands	. 0.75
Wakeham Bay	. 0.51

This means that, for example, the native of Wakeham Bay is about twice as hard put to make a living from seals as is the native from Cape Dorset — which is certainly a good approximation of the actual situation. A complete analysis would bring in the important effects of wind and salinity; data are too few at present, but it is certain that these effects will lower the figure for the Belcher Islands and raise the figure for Pond Inlet relative to Cape Dorset and Wakeham Bay.

Any solution of the problems of such subsistence economies will be in the very general form common to all such systems. The limits of exploitation

at present imposed by availability of seals must be replaced by limits imposed by sustainable yields; this is a problem for technology. Such an increase of yield must be considered in relation to the outlay of economic effort and to the rest of the economy, and this is a problem for the economist. While economical and technological improvements are not his concern, the population ecologist cannot close without the cautionary remark that a resultant over-production of people is a far more immediate danger in the Arctic than its wide-open spaces suggest.

SUMMARY

(1) The ringed and bearded seals are important in the subsistence economies of Eskimos. Study of them has benefited from absolute methods of age determination.

(2) Equilibrium populations of ringed seals are not determined trophically or through compensatory mortality but through reproduction, by the amount and quality of land-fast ice available for the construction of birth lairs in the snow.

(3) Local censuses of ringed seals can be combined with measurements of ice areas from maps to give theoretical estimates of the size of under-exploited populations.

(4) More information is needed on the limits of response of pupping success and even pregnancy rates, but balanced tables based on known and estimated mortality and birth rates in south-west Baffin Island suggest safe maximum sustainable yields of 7-10 per cent of ringed seal populations. Biomass yields are more complex, but can be estimated.

(5) Bearded seals may be limited trophically by the availability of ice-free feeding banks in winter, but no deductive population estimates can yet be made. The analysis of numbers and yields of this species is based on its numbers relative to the ringed seal in summer, from shipboard censuses.

(6) Availability indices of seals can be calculated from their theoretical numbers and the areas of water or ice in which the populations are dispersed. These may be converted empirically to catches per unit of effort, giving the expectations of a day's hunt in any region. The probabilities of suitable weather and the loss of seals by sinking are major calculable modifications.

(7) A preliminary economic analysis of a region can thus be formulated firstly in terms of maximum sustainable yield of meat or other product per native inhabitant, and secondly in terms of availability, to reflect the economic effort presently required of the Eskimos.

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DISCUSSION

G. SURTEES: Is there any evidence that there is a significant difference in the percentage of mature but unfertilized females in unexploited and exploited whale populations? Is there any change in sex ratio?

R. M. LAWS: We are unable to study unexploited populations. Our data do show, however, that at lower levels of exploitation some parameters are different. These data — which are not very extensive — do not suggest any increase in the percentage of unfertilized mature females following exploitation, but rather the reverse.

J. B. CRAGG: Might not this situation arise in elephant seals, owing to the heavy and selective exploitation of bulls?

R. M. LAWS: It can certainly happen above a certain level of exploitation. But it has not yet done so in fin whales, where the population units are small and keep together as groups. In polygynous species, like the sperm whale, rising exploitation may well affect the reproductive rate of mature females.

A. JONSGÅRD: In monogamous species the critical condition will be whether a male and female are able to meet.

T. B. REYNOLDSON: The increasing efficiency of catching will probably affect the population in many ways. Does hunting seem to be causing genetic and behavioural changes?

R. M. LAWS: Asdic certainly induces changed behaviour, and marking returns suggest that exploitation as a whole has modified the pattern of dispersal of whales. However the data are not really adequate. Generally speaking, whales migrate over a fairly constant path and return each year to the same part of the Antarctic. One marked animal has however been found to move through 180 degrees of longitude, and others through quite large arcs.

J. G. SKELLAM: It will be difficult to relate the catch size to fishing effort owing to the continually varying methods of hunting. However, new methods must overlap with old ones in time. Has any attempt been made to calibrate one method or one type of equipment in terms of another which it is supplanting?

R. M. LAWS: The possibility of doing this has been looked into, but

with little success owing to the number of factors involved. There are changes in factory-ship processing techniques as well as in catchers. Recently the land-based station at Grytviken in South Georgia changed over from using six old and one modern catcher to seven modern catchers, but even here the effect was not clear-cut owing to other variables.

W. L. N. TICKELL: The ratio of propeller to engine speed in some catchers has been found to be critical, as certain ratios cause vibrations which scare whales. Similarly when asdic was first used it was found to scare whales and gunners refused to use it: later, faster diesel-powered catchers returned to asdic as they could outspeed the whales and so hunt them down.

G. C. VARLEY: Isn't it this sort of thing that is measured by the catch size?

W. L. N. TICKELL: No, the personal preference of the gunners has been the limiting factor — they would not use the asdic until its success was assured.

N. WALOFF: You said that 600,000 tons of oil was taken — what does this mean in terms of whales?

R. M. LAWS: This figure is equivalent to about 43,000 blue whales. Current production is in fact about 500,000 tons, and fin whales make up 83 per cent of the catch. The whole industry is closely dependant upon economic factors. Oil is the traditional product, and its price has risen from £12 per ton to £150 per ton between 1912 and 1950. During this period the rising price balanced the rising costs: latterly the price has stabilized and even fallen slightly, and it will certainly affect future exploitation. At present the protein in some two million tons of meat is not utilized, the meat merely being processed to extract about 500 tons of oil. This is wasteful and with a rising output of vegetable oils the better use of the meat may become more important.

W. EDMONDSON: Has any attempt been made to attract whales by various sounds?

W. L. N. TICKELL: So far as I am aware the only known sounds affecting whales act as deterrents.

R. M. LAWS: One company did try playing krill noises to whales, without success!

C. W. HULME: The International Whaling Commission has been investigating more humane methods of killing whales than the present explosive harpoon. The General Electric Company and a whaling company have been experimenting with an electric system which shows promise.

R. M. LAWS: One British Company has spent about £125,000 on this technique, but there are still problems to overcome.

C. W. HULME: The chief problem has been the development of a conductor which can be incorporated in a nylon fore-runner and withstand the tension and enormous stretching which this is subjected to. This has now been solved, more or less.

A. JONSGÅRD: Norwegian gunners dislike the electric method because it has been liable to errors.

C. W. HULME: Superstition (electrophobia) and prejudice also are involved in their objections.

J. B. CRAGG: I think there is no doubt that the electric system as at present constituted is more difficult to use, at least under Antarctic conditions.

M. E. SOLOMON: Turning to McLaren's paper: would it be possible for experimenters or Eskimos to make artificial birth lairs — such as igloo-like shelters over holes made in the ice — and so increase the seal population on a stretch of coast?

I. A. McLAREN: This is a nice idea, though it might be difficult to induce a seal to enter a hole smelling strongly of man.

J. B. CRAGG: Are you satisfied with the efficiency of the Eskimo methods for finding lairs?

I. A. McLAREN: The Eskimos certainly do not find most of the lairs. The argument has been based on an *a priori* assumption that a given area has limited sites available, and on an observed correlation between seal numbers and the extent of fast ice.

G. C. VARLEY: Obviously suitable areas are a prior requirement. But what controls the seal density within them? The animals must feed while suckling — can food be a limiting factor?

I. A. McLAREN: There may be some element of competition for food. But the 'best' coast-lines (as defined on arbitrary geographical grounds) have the biggest seal populations although these are very crowded and this correlation suggests that trophic factors are not limiting.

H. R. HEWER: Do these seals feed during lactation?

I. A. McLAREN: Yes, The ringed seal does, in contrast to the harp seal which breeds on the unstable pack ice and often starves during a short suckling period. The ringed seal has a long suckling period, of up to two and a half months, and so must feed during it.

H. R. HEWER: This may not be an absolute necessity, for many bull

seals will, of course, stay ashore without feeding for two to two and a half months.

I. A. McLAREN: But so long a starvation seems unlikely in a female feeding a pup.

H. R. HEWER: When the seals haul out in the spring, are all age-groups represented in the population?

I. A. McLAREN: There is a progressive increase through the spring to a threshold, when more or less the whole population is present on the ice and all age groups are represented.

H. R. HEWER: Of course it is common in Phocids for the younger age groups not to return to the breeding grounds.

I. A. McLAREN: Were this so in the ringed seal an age-group would be evidently missing.

E. D. Le CREN: Laws and Jongsård both mentioned that a rise in growth rate occurred when whale populations had been reduced by exploitation. Does this mean that the whales exert a limiting effect on the plankton populations on which they feed?

R. M. LAWS: The evidence relating to growth rate is circumstantial but I believe it to be correct. There is also a variation in size with longitude, which may suggest that in the best feeding places there is competition between older and younger whales. This size segregation is only seen on the northern feeding grounds, and disappears when the whales move southwards. There are, of course, other animals like crab-eater seals and pelagic birds, which feed on krill and it is possible that their populations have increased as a result of the exploitation of whales.

A. JONGSÅRD: I agree that this could happen in Antarctic fin and blue whales, which feed only on one type of food. But the minke whale is a generalized feeder with many kinds of diet. I know of one animal found with a stomach full of Lofoten cod, a very large fish for a baleen whale to eat. It is unlikely that food is a limiting factor for the minke whale unless some special food is involved, of which a certain intake is nutritionally essential. The complexities of these problems are well shown by Australian work on the humpback whale, whose mean length at puberty was shown to decrease over the period up to 1956. It was thought that this reflected a decrease in growth rate: but it is now known to be due to gunners selecting the largest available animals.

THEORETICAL AND MATHEMATICAL MODELS OF
EXPLOITED POPULATIONS

THE CONCEPTUAL FORMULATION AND MATHEMATICAL SOLUTION OF PRACTICAL PROBLEMS IN POPULATION INPUT-OUTPUT DYNAMICS

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INTRODUCTION

A recent spate of books has focused attention on a spectre that has haunted many thinking men since antiquity. Writers from Plato on have noted the sickeningly destructive effect that civilization can have on the productivity of the environment through shortsighted management practices. Brown (1954), Castro (1952), Cook (1952), Darwin (1952), Ordway (1953), Osborn (1948, 1953), Sax (1955), Sears (1947), Vogt (1948) and many others have tried to alert the public to impending danger through their realistic appraisals of the staggering needs of man's increasing numbers in contrast to the potential productivity of the earth. The effects of mushrooming human populations against an increasingly more exhausted array of natural resources can reduce all mankind to a bestial level of existence more surely than a row of super-bombs stretching from here to Betelgeuse.

It is eminently apparent that two problems are now of crucial importance. First, the maximum amount of renewable natural resources that the world can produce each year must be estimated with a high degree of precision and accuracy. Second, it must be determined how maximum levels of production can be attained and maintained.

Soil science, livestock and crop genetics, silviculture and many other disciplines can aid in the solution of the above two problems. However, two components of the conservation research programme occupy the domain of the population ecologist. For a given population and conditions extrinsic to the population, what age distribution and rate of exploitation will yield a maximum harvest and still leave behind enough reproductive individuals so that a maximum rate of biomass yield can be sustained? Also, what is the maximum thus obtained?

Through a combination of experimentation, field observation and theoretical analysis, population ecologists can determine the form of the interaction of various factors on population productivity, and evaluate the

parameters in a productivity equation. Such analysis leads to the formulation of a specific management routine which will produce maximum sustained yield of the studied resource. A small, but increasing number of workers in this area are attempting comprehensive studies of population productivity in the laboratory and field. Hence the time seems appropriate for considerable effort to formulate a general theoretical model of population productivity.

Many types of mathematical models of productivity have been formulated to date. Four proposed by fisheries workers have been reviewed (Watt, 1956) and applied (Watt, 1959*b*). Many others, often radically different in conception, have been used by specialists in forestry and a variety of other biological fields.

A recent review of optimum yield theories being applied by foresters is found in the *Forestry Handbook* (Forbes, 1955). Analogous thinking applied to pasture grasses is discussed in the treatise by Voisin (1959). However, this author is not aware of any models of exploited biological populations which compare in sophistication with the most advanced models of fisheries. In turn, by far the most comprehensive, realistic and thoroughly tested model put forth by fish population ecologists is that of Beverton & Holt (1957). However, Beverton and Holt are both scheduled to give papers at this Symposium, so I shall not discuss their model further, except to note that this thinking is essentially directed towards analysis of population steady states in a stable environment.

The present paper is intended as a first step in attempting to synthesize a productivity model that will be ubiquitously applicable to renewable natural resources. Various types of biological productive systems will be discussed in order to point out the categories of productivity problems that can arise, and the factors that must be considered in their solution. This will lead to a general statement of the population productivity problem.

TYPES OF EXPLOITED POPULATIONS

The simplest conceivable type of productive system is a regularly exploited population maintained under controlled conditions. Such laboratory studies have been conducted on unicellular algae (Ketchum *et al.*, 1949), blow-fly larvae (Nicholson, 1955), guppies (Silliman & Gutsell, 1957, 1958), *Daphnia* (Slobodkin & Richman, 1956) and flour beetles (Watt, 1955).

In such cases, perhaps the best way to set up a mathematical formulation is to fix attention on maximization of biological productivity, defined as net amount of biomass produced per unit time. Productivity determines the maximum sustained yield per unit time we can remove. The ideal harvesting regimen is that in which the sustained yield per unit time is exactly equal to

the sustained productivity, less the remainder that must be left behind to sustain the yield. Where conditions are controlled, intraspecies competition is the only variable regulating productivity. Up to a certain 'fishing' level, increased yield results in increased productivity in the following time interval due to decreased biomass wastage caused by competition. However, fishing beyond the optimum level causes extinction of the harvested population. How high the optimum is for any species depends on the age structure of the population left behind after harvest, the numbers of individuals left behind and the frequency of harvest. From species to species, the productivity for given treatment depends on the biotic potential of the species.

The effect of biotic potential on optimum yield level shows up clearly when we examine the results from the aforementioned five laboratory studies:

Organism	Rate of yield which results in maximum biomass productivity (all converted to percentage removal per diem)	
Blowflies	.	99 per cent of adults.
<i>Daphnia</i>	.	23 per cent.
Algae	.	13 per cent.
<i>Tribolium</i>	.	3 per cent.
Guppies	.	2 per cent.

Where intraspecies competition is present, my earlier (1955, 1956) formulation of the productivity equation is suitable. That is, we develop an expression in which productivity from time t to time $t + 1$ is equated to the difference between biomass found at the later and earlier times. Then, in turn, we do enough research so that this difference can be expressed as a function of the factors which can regulate the magnitude of the difference, through *their* effect on growth, survival and recruitment. Finally, we use calculus or other mathematical technique to find the values of the independent variables which maximize biomass productivity. In extremely succinct mathematical shorthand, avoiding symbols already defined otherwise by Holt *et al.* (1959),

$P_B(t : t+1)$ represents biomass productivity from time t to time $t + 1$.

B_t represents biomass at time t .

$B_{t+1}(X_1, X_2, \dots, X_n)$ represents biomass at time $t + 1$ as a function of the variables $X_1 \dots X_n$ which governed biomass production over the interval t to $t + 1$.

We may write the forgoing problem statement as that of seeking

$$\text{Max } P_{B(t:t+1)} = B_{t+1}(X_1, X_2, X_3 \dots X_n) - B_t \quad (1)$$

Such equations are discussed in more detail and applied elsewhere (Watt, 1955, 1956, 1959b).

Now such formulations of the exploitation problem will only be useful and meaningful where biomass productivity can in fact be increased by a programme of harvesting. In terms of basic ecological principles, this means that where the rate of conversion of food into biomass by a species is being kept down by intraspecific competition pressure, release of that pressure by thinning can make the species more efficient. However, this state of affairs can only occur where a species is living in an environment that is favourable for its natality, growth and survival.

Where a species is living in an area that is favourable only in certain years, population density may never become great enough for there to be any measurable effects of intraspecific competition. In such cases it is true that competition is the ultimate population regulator, in that if all other regulating factors fail, competition pressure will indeed come into operation. However, where a species is living at the geographical boundary of its favourable range, climate may in fact almost completely regulate numbers of the population.

A case in point is the smallmouth black bass population studied by the author (Watt, 1959b). In this population 94 per cent of the variation in numbers of four-year-olds recruited to the fishable stock is due to temperature in the summer the age-cohort was spawned. Summer temperatures also have a profound effect on weight growth of individuals during their second and third years of life. When we try to find the fishing schedule that will maximize productivity in such a population, applying calculus to the expanded version of an equation such as (1), we find that any fishing at all only decreases productivity. Yet we can fish the population without decimating it. In this instance, the role of fishing in the dynamics of the natural population is to compete for a chance of killing fish that would otherwise be wasted to natural mortality caused ultimately by a rigorous climate.

Clearly equation (1) is not of sufficiently ubiquitous applicability to be of general use.

It should be noted that while smallmouth black bass populations are largely regulated by temperature in north temperate zones, they are probably regulated by intra- and interspecific competition, say, in Georgia or Alabama.

Various other types of populations are found amongst the fishes. Pilchards, sardines, smelt and alewives mature very rapidly, and reproduce within the first two or three years of life or only slightly later. Recruitment must be very sensitive to extreme weather conditions in the year of spawning. Also, biomass productivity must be very sensitive to weather conditions, because mean length of life is not long enough for good growing seasons to compensate for the effect of, say, two successive poor growing seasons. Lake trout

represent the other extreme: the animal lives in a relatively stable environment, has a low biotic potential, and reproduces late in life. The sexually mature individuals may live for many years after the first mating season.

Deer, beaver and cattle populations represent complex exploited systems. Several age-groups are liable to exploitation, growth can occur after reproductive maturity is attained, and the environment can vary from being very favourable to very unfavourable. For example, all other factors being equal, optimum level of harvest of deer (by hunters) would probably have to be lower following a winter of heavy snow cover than a winter of light snow cover.

Competition as well as weather will be important for wheat and trees, and fairly frequent rotation of grazing herds from one pasture to another is necessary to maximize rate of grass growth.

ELEMENTS COMMON TO ALL PROBLEMS OF EXPLOITED BIOLOGICAL POPULATIONS

All the forgoing exploited populations present problems which have certain features in common.

A. Output is to be made as high as possible, with the following qualifications.
B. The ability of the productive system to keep producing at a maximum possible rate must never be impaired by making the yield too high. That is, what we want to determine is the highest possible *sustained* yield the population can produce.

C. Certain restrictions must be imposed on the technique for obtaining maximum yield. For example, it may be economically infeasible to thin out trees or marine fish prior to recruitment age, in order to minimize intra-specific competition. Also, a harvesting technique which would deplete, say, the phosphorus available in an oligotrophic environment would be grossly shortsighted.

D. Productive systems invariably have some kind of built-in rhythmicity. This will be tied to seasonal climate cycles, and hence cycles of growth, reproduction, and the harvesting season.

E. There is always a delay between the time when man manipulates the system for his gain and the time when results of the gain have become significant. Study of the delay period should be an integral part of study of the productive system.

F. The efficiency of conversion into biomass of solar energy cascading through, and matter cycling through a community is different for different species, and for different age-groups within each species. Even within a trophic level, different species have different efficiency rates of biomass production.

G. Biological productivity of a population can be governed by (a) environmental factors extrinsic to the population, (b) the size and age distributions of the population, which regulate competition pressure, or (c), both of (a) and (b). Any species can, and probably will, be under the influence of (a) in the unfavourable or boundary part of its range, and (b) in the central part of its range where climate is favourable for natality, growth and survival. Also, particularly at the fringe of the species range, populations may be largely regulated by (a) in some years and (b) in others.

H. There are many different causal pathways by which population biomass productivity can be governed. Each of intraspecific competition, interspecific competition, food abundance and weather can regulate each of fecundity, fertility, survival and growth. Parasites, predators and diseases can affect growth and survival, and sometimes fecundity and fertility. A mathematical model for a specific exploited population is only realistic and useful in so far as it includes insight into all the relevant causal pathways.

SYMBOLIC FORMULATION OF PRODUCTIVITY MODELS

The foregoing considerations suggest how we must proceed in order to develop a general mathematical model for use in showing how best to exploit biological populations. It is clear that a model designed to show *only* how to maximize productivity will not always be satisfactory, because it will sometimes be impossible to increase productivity by means of a harvesting regimen. On the other hand, it is also clear that a general model must involve a term showing how all relevant factors interact to regulate productivity, for the following two reasons. First, in those cases where a population is not entirely, or at all, regulated by climate, we can in fact increase productivity by judicious choice of harvesting regimen. A model is not general unless it shows how to choose the harvesting procedure in such cases. Second, where a population is entirely regulated by climate, the best harvesting procedure is that which makes best utilization of the productivity allowed by climate. Hence an expression for the productivity which does occur is required in equations for this category of cases also.

Hence I have decided that the best possible statement of the optimum, or maximum yield equation is as follows. 'The maximum biomass yield that can possibly be obtained repeatedly, per unit time, from any biological population is equal to the biomass present at the end of each unit time less the minimum biomass of individuals that must be left behind per unit time to guarantee replacement of the maximum possible yield by the next time exploitation occurs.' It is understood that the age distribution of the remainder is relevant and critical.

Writing the above in mathematical shorthand, and again trying to use notation consistent with that of Holt *et al.* (1959), we have

$$\text{Max } Y_{t+1} = P_{t+1} - P_{(\min)t+1} \quad (2)$$

where P_{t+1} represents the biomass present at the end of the interval t to $t+1$ and $P_{(\min)t+1}$ represents the minimum biomass of individuals that must be left behind at any harvesting time, $t+1$, to guarantee replacement of $\text{Max } Y_{t+1}$.

While a great deal is known now about how to develop expanded versions of equation (2), application of this equation to any particular biological population is still a relatively tricky proposition. I will mention here only a few of the types of technical difficulties that can be encountered.

It may be possible to maximize Y_{t+1} , for example, by removing some individuals prior to their reproductive age. Suppose the optimum yield procedure is to remove all reproductive individuals each harvest, and leave behind individuals that will reproduce between harvests. How many such immature individuals should be left behind? We cannot leave the bare minimum required for reproduction, because natural mortality will reduce this bare minimum between harvest time and the time reproduction takes place. Hence enough immature individuals must be left behind so that even after losses due to natural mortality, there will be sufficient reproducers by the time when reproduction occurs. However, the 'cushion', or extra number of individuals left behind to absorb the effect of natural mortality from one year to the next should vary from year to year, because climate varies from year to year and hence percentage natural mortality differs from one year to another. Since we cannot know what climate will be like in advance, the size of the 'cushion' in such instances should be sufficient to absorb the effect of natural mortality under the worst possible conditions for survival that could occur.

Before proceeding to elaboration of equation (2), let us consider in a general way the strategies of harvest dictated in different situations by this equation.

In cases where the environment is favourable and competition regulates productivity, the equation tells us to fish, harvest, hunt or otherwise exploit the population so that P_{t+1} is a maximum, and this in turn maximizes Y_{t+1} , if exactly $P_{(\min)t+1}$ is left behind. However, where P_{t+1} is entirely regulated by a rigorous environment, and nothing man can do will increase it, the equation tells us to maximize Y_{t+1} by fishing so that no more biomass than $P_{(\min)t+1}$ is left behind at any harvesting time. It follows, of course, that where P_{t+1} is partly determined by competition, and partly by the environment, a mixture of the forgoing two strategies will be required.

It is not necessary to outline here in detail how equation (2) can be expanded, since I have discussed the structure of such equations and components thereof in considerable detail elsewhere (Watt, 1955, 1956, 1959a, b, 1960a, b). Only enough of the symbolic statement of the problem will be given here to indicate the general form of such equations. Again, in so far as possible I shall use the notation proposed by Holt *et al.* (1959).

The number of individuals of the i th year class surviving to the j th birthday may be written as

$$\begin{aligned} N_{ij} &= N_{i0} \cdot S_{i1} \cdot S_{i2} \cdot \dots \cdot S_{ij} \\ &= N_{i0} \prod_{j=1}^n S_{ij}, \end{aligned} \quad (3)$$

where N_{i0} represents the number of the i th year-class hatched, spawned, born or germinated, say.

Where G_{ij} , fractional growth increment of the i th year-class during its j th year of life is defined by

$$G_{ij} = w_{ij}/w_{i(j-1)},$$

we may similarly write

$$\begin{aligned} w_{ij} &= w_{i0} \cdot G_{i1} \cdot G_{i2} \cdot \dots \cdot G_{ij} \\ &= w_{i0} \prod_{j=1}^n G_{ij}. \end{aligned} \quad (4)$$

Hence

$$\begin{aligned} P_{in} &= N_{in} w_{in} \\ &= N_{i0} \prod_{j=1}^n S_{ij} w_{i0} \prod_{j=1}^n G_{ij} \end{aligned} \quad (5)$$

The total biomass present in the relevant universe at any time consists of the sum of the P_{in} 's for all relevant year-classes.

Enough is known now to make a rather reasonable attempt at the detailed form of equation (5) for various kinds of organisms. For example, for sexual animals in a stable environment, where only population density regulates fecundity rate, the best equation we can write for N_{i0} (Watt, 1960a) is as follows.

Where N_{Fec} is the total number of fecund individuals in the population, and we assume a 50 : 50 sex ratio,
 $N_{i0} =$

$$N_{\text{Fec}} \left[a_1 + \frac{2}{a_2 N_{\text{Fec}} t} \left\{ 1 - \exp \left[-a_2 N_{\text{Fec}} t \left(\frac{I_{\min} + e^{a_3 - a_4 N_{\text{Fec}}}}{1 + e^{a_5 - a_6 N_{\text{Fec}}}} \right) \right] \right\} \right] \quad (6)$$

$I_{\min}$, a_1 , a_2 , a_3 , a_4 , a_5 and a_6 are constants and t is the length of time over which reproduction occurs. While the equation is unfamiliar, the family of curves it describes is not. For example, equation (6) is intended to describe stock-recruitment curves as discussed by Ricker (1954), after, of course, suitable terms have been introduced in the pre-recruitment phase.

Equation (6) was derived from three differential equations, which, in turn were developed after an exhaustive examination of entomological literature. However, there is every reason to believe that the three phenomena described by equation (6) operate in the same manner in all sexual animals. The equation states that reproductive rate at any time and at any density of potential reproducers is under the influence of three interacting factors.

These factors are (1) the increased difficulty of potential mates encountering each other as density decreases, (2) the fecundity-depression effect of interference, and (3) the fecundity-depressing effect of competition for oviposition sites. Many experiments have been performed which demonstrate the existence of all three of these factors, particularly by Japanese scientists.

Equations such as equation (6) can be constructed for all the terms in the yield equation. Once the yield equation is developed so that all growth and survival coefficients can be expressed in terms of the factors that regulate these coefficients, our position is as follows. First, since applied mathematics is language, not science, our yield equation does no more than state in succinct symbolic language the extent of our quantitative biological insight into the productivity dynamics of the exploited population under study. The best equation we can write at any time, therefore, is a measure of the precision and accuracy of the data we have collected. Precision and accuracy, in turn, are measures of the volume of replication and ingenuity of design in our data collecting procedures. The yield equation we have written should indicate the magnitude and types of effects on productivity of all the factors which can govern productivity. Second, once we have the appropriate equation, we can manipulate it to find out how to maximize productivity. In general, the yield equation can be thought of as a hypersurface in n -space, yield being the dependent variable, and such factors as water temperatures and fishing pressures in various seasons, and size of spawning stock being the independent variables. (This language can be translated into the appropriate terms for problems in forestry, big game management, algae culture, etc. In fact, the problem as stated and the solutions being outlined are completely general.)

The problem is to find the values of the independent variables over which man has control which give the highest possible yield peak in our hypersurface, which may be thought of as the n -dimensional counterpart of a 3-dimensional mountain range.

Now it so happens that many problems in modern society are essentially analogous to this problem of biological yield, and therefore, happily, the mathematicians have given such problems a great deal of thought. Unfortunately, the fruits of this thought have almost entirely been published in books and journals that the average biologist would not come across in his entire career. A somewhat more complete introduction to this literature is given elsewhere (Watt, 1960b), but I shall attempt a succinct resumé here.

When the biologist is confronted with the problem of finding values of independent variables which yield a maximum or minimum for a complex function, there are three general areas of mathematics to which he can look for help. (The problem under discussion, incidentally, is referred to by modern mathematicians as the 'extremum' problem.)

Briefly, these areas are:

- (1) Classical analysis (e.g. Lagrange multipliers).
- (2) Mathematical programming (more specifically, non-linear and dynamic programming).
- (3) Electronic computer technology (systematic hypersurface-exploring techniques as proposed by Box and associates).

Any good text on advanced calculus will elucidate the theory and application of Lagrange multipliers. Parke (1958) has published an excellent annotated bibliography, complete to about 1955, which will serve the biologist as an excellent guide to the literature in these unfamiliar areas.

Mathematical programming is a very recent branch of applied mathematics created to cope with complex extremum problems arising in the utilization of transportation networks, petroleum refining, and various manufacturing processes, etc.

Specifically, it was invented because classical analysis cannot handle yield, production or allocation extremum problems where there are inequality constraints. That is, suppose we can increase productivity by increasing some variable up to, *but not beyond* a certain value. Our constraint is, in such cases, not of the form

$$V_1 = 2,700,$$

but rather, is of the form

$$V_1 \preceq 2,700.$$

George Dantzig first published on such problems in the volume edited by Koopmans (1951), and there is now a vast literature on the subject. The biologist would be advised to begin his reading in one of the simple introductory texts such as those by Kemeny *et al.* (1957) or Vajda (1956). More complete expositions are by Dorfman *et al.* (1958), Gass (1958) or Vazsonyi (1958). Finally, the biologist (or his mathematical and statistical consultant)

would be well advised to study some of the more advanced literature in this area, by Arrow *et al.* (1958), Bellman (1957) and Kuhn & Tucker (1951). These treatises deal with problems very reminiscent of the actual problems encountered by biologists. The equations may be non-linear and even sequencing of operations in time is considered.

Finally, a variety of electronic computer techniques are available for finding extrema in hypersurfaces as quickly as possible (Box, 1954; Box & Coutie, 1956; Box & Wilson, 1951; Box & Youle, 1955). The computer programme for such problems suggests a blind man trying to find the highest point of the Himalayas. The blind climber would constantly go up the direction of steepest ascent. Unlike the climber, however, a routine can be built into the computer to prevent it from becoming 'lost' on a local maximum.

SUMMARY

Because of burgeoning human populations and limited ability of the earth's surface to produce food, mankind is now confronted with two crucially important problems. The maximum amount of renewable natural resources that the world can produce each year must be estimated with a high degree of precision and accuracy. Second, it must be determined how maximum levels of production can be attained and maintained.

It would be desirable to have some broad unifying theoretical model of the mechanics of exploited populations that would suggest how a great variety of cases could be handled mathematically. The aim of the empirical and subsequent mathematical analysis in each case, for trees, wheat, algae, fish or other exploited resource would be to show how to maximize yield without impairing the ability of the population to replace itself.

A general mathematical model which aims to show how biomass productivity can be maximized is not a ubiquitously applicable theoretical tool. This is because it will only be possible to increase productivity by adjusting a fishing or harvesting regimen in those cases where productivity has been depressed by intraspecific competition. In cases where a population or organisms is existing in an area where the climate is only rarely favourable for natality, growth and survival, competition is not important as a regulator of productivity.

More general and insightful mathematical tools for analysing yield problems are suggested if we think in terms of minimizing biomass wastage, rather than maximizing biomass productivity. Such tools allow us to analyse effects of wastage due to all factors, not just those caused by competition.

Data from, and techniques for various types of cases are discussed.

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THE APPLICATION OF MATHEMATICAL MODELS TO FISH POPULATIONS

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Marine fish populations are among the most intensively studied of natural populations — because of course they sustain commercial fisheries of major economic importance. In these studies a variety of mathematical models of varying complexity have been applied, with varying success.

THE POPULATION TREATED AS A WHOLE

In one class of model the entire fish population, or more strictly in most applications that part of the population vulnerable to fishing, is treated as a unit. The basis of all these models goes back to the classical theories of population growth of authors such as Gause (1934) and Volterra (1931), based on populations of generally very simple organisms. An example of uses of such a model is Graham's (1939) study of the North Sea and more recently Schaefer (1954) has extended it to include the fishing fleet as the predator element of a predator-prey system, and to study the expansions and decline of the size of fleet. Such models assume that the gross rate of increase of a population, i.e. the sum of the growth in weight of the individuals in the population, plus the recruitment, less the natural deaths, is determined directly by the size of the population; i.e. in mathematical terms $dP/dt = f(P)$. The general relation between population and increase will be a peaked curve, the increase being zero at zero population and at the maximum population, and having a maximum at some intermediate value.

The effect of fishing may be readily included in the analysis, so that if $f(P)$ is the gross increase in population, the net increase is $f(P) - C$ where C is the catch (this net increase can of course be negative, indicating a decline in the population).

The population size will remain unchanged, and the fishery may be said to be in a steady state if $f(P) = C$, i.e. the catch equals the gross increase. The greatest steady yield will therefore be taken if the population is maintained at the size giving the maximum rate of increase. Such models have one feature in common with observed natural populations of many kinds —

they are, in the sense used in mechanics, stable. That is, if they are disturbed from the equilibrium state, e.g. by especially good conditions for the survival of young fish in some year, they will return to the original state, while the application of a continuing force, e.g. an established commercial fishery, will alter the population, but only to a new equilibrium level. Though some commercial stocks do show fluctuations, these are usually either short term, due to variable strength in individual year-classes, or long term, due to definite changes in the environment, such as the changes in the abundance and distribution of the cod at Greenland. No fluctuations in amplitude or, especially, regularity comparable to those of some Arctic mammals have been noticed in marine fish.

In most formulations, Volterra's relation between rate of increase and population size has been used, i.e. increase is proportional to population size multiplied by the difference between the present and maximum population sizes i.e. $dP/dt = aP(P_{\max} - P)$. This gives a parabola, with maximum rate of increase at half the maximum population size. However, such observational data as there are, on both natural and artificial fish populations (e.g. Silliman & Gutsell, 1958) suggest that maximum rate of increase occurs at a population size well below half the maximum size, perhaps at a third to a quarter. It would obviously be possible to put forward mathematical equations having these properties, e.g. $f(P) = P(P - M)(P + M)$ has a maximum at $\frac{1}{3}M$ and zero at 0 and M , but none has obvious theoretical qualifications.

The model has other serious disadvantages. No distinction is made about the composition of the stock; populations of a large number of small and young fish, or a small number of old and large fish are considered as the same, though their rates of increase in terms particularly of growth of individuals are likely to be very different. It may be argued that in a steady state only one population composition is possible for a given population size, and that of the two populations with the structures suggested only one at most could be maintained at the same level and with the same structure indefinitely. This may be true, but conditions in the sea are rarely static. The fishing effort is rarely uniform for more than a few years at a time — usually less than the stocks would take to settle to a steady state, even if they could. In most stocks there are considerable fluctuations in the strength of year-classes which mean that the age structure is also fluctuating, the average age being, for example, less than usual when a strong year-class is entering the fishery.

The rareness of any steady state, particularly in the amount of fishing, leads to a further practical difficulty in applying the theory. A large contribution to the gross increase in any stock is due to the entry of young fish — the recruits. These fish will have been born perhaps several years earlier,

and thus the magnitude of the recruitment will be determined by the size of the stock in that earlier year. The observed gross increase in stock in any year is therefore determined in part by the stock in that year, and in part by the stock some years earlier. Unless, therefore, the sizes of the stock in these two years are roughly the same, i.e. the population is in more or less a steady state, the relation between population size and gross increase cannot be simply determined. A somewhat more empirical approach, designed to overcome the difficulties in analysing a rapidly changing fishery, has been used by Gulland (1961). It is assumed that the mortality due to fishing is proportional to the fishing effort, and that the other characteristics of the population (growth, natural mortality, recruitment) are unchanged, even indirectly. This corresponds to the 'constant parameter' model of the analytical type discussed later. Therefore the abundance of an age-group of fish which has been exposed to fishing for, say, five years is determined by the total fishing effort in those five years. The stock at any time will contain fish which have been exposed to fishing for periods ranging from a few days up to perhaps a dozen years, the average duration being, say, four years. The stock, as measured by catch per unit effort, may be plotted against the average effort over the past four years and this will give the steady state relation. By simple multiplication the corresponding relation between catch and effort can be determined. This has given useful results in fisheries where there have been large changes in the amount of fishing, a condition satisfied by most of the important commercial fisheries of the eastern Atlantic, and requires little detailed information beyond statistics of total effort and catch per unit effort. The method may be illustrated by the plot for the hake off the west coast of Scotland (Fig. 1). The average life-span in the fishery has been taken as three years and the index of density as the catch per 100 hours' fishing of English steam trawlers. Such a model has, like the previous one, the inability to distinguish and analyse qualitative changes in the stock or in the catch, due, for example, to changes in the selectivity of the gear, as well as the disadvantages of the constant parameter models discussed later. Some analysis of the effect of gear selectivity changes can be made if they have been in operation long enough to distinguish two separate relations in the plot of catch per unit effort against effort, before and after the change. A further peculiar disadvantage is that the average life-span in the fishery is not constant, but is determined by the level of fishing, being reduced by intense fishing; however this is not likely to have any major effect.

SEPARATION OF GROWTH, RECRUITMENT AND MORTALITY

Another main class of models divides the net change in the population into

its constituent parts, so that in the simple formulation of Russell (1942)

$$S_2 = S_1 + (A + G) - (C + M)$$

i.e. the stock at the end of the year (S_2) is equal to the stock at the beginning of the year (S_1) plus the weight of young fish entering the stock — the recruits — (A) and the growth of fish in the population (G), less the fish removed from the population by fishing (C) and other 'natural' causes of death (M).

FIG. 1.—The relation between stock abundance of hake to the west of Scotland (as measured by the catch in 100 hours' fishing by English steam trawlers), and the amount of fishing. The amount of fishing used is the average amount up to and including the year of observation.

The mathematical exposition is made easier by considering the growth and deaths of individuals of a single year-class. In any steady state the yield from a single year-class during its whole life-span is the same as that in a single year from all year-classes present. The yield during the entire time in the fishery may be computed as the sum of the yield during small time intervals, within which conditions do not alter. This yield in the small time interval is equal to the product:

$$\text{Rate of fishing} \times \text{Number in the stock} \times \text{Average weight of the individual fish}$$

It remains to put these into a suitable mathematical form, and to add them to give the total. Provided that the fishing effort can be expressed in the right units, then the numbers caught per unit time will be proportional to the number in the stock at the time, multiplied by this fishing effort, i.e. in mathematical terms:

$$\left(\frac{dN}{dt}\right)_{(\text{fishing})} = -qfN = -FN$$

where $q = \text{constant}$.

$f = \text{fishing effort, in some suitable units.}$

$F = \text{fishing mortality coefficient.}$

Similarly the rate of death due to other (natural) causes can be expressed as

$$\left(\frac{dN}{dt}\right)_{(\text{natural})} = -MN$$

where $M = \text{natural mortality coefficient}$

from which the numbers at any time t can be expressed in terms of the numbers N_0 at some previous time t_0 as

$$N_t = N_0 e^{-(F+M)(t-t_0)}$$

Various expressions have been used for the weight of the individual fish, but only a limited number can be combined with the expression above for numbers to give an expression which can be handled without too difficult mathematics. These include the exponential ($W = ke^{gt}$) (Ricker, 1948) and the von Bertalanffy $W = W_\infty (1 - e^{-kt})^3$ (Beverton & Holt, 1957). It is not intended to discuss here the relative theoretical merits of various growth equations for which there exists an already over-voluminous literature. However it does seem unlikely that a single formula will give an exact and meaningful fit to growth during the major part of a fish's life, both mature and immature, and in which there are likely to be major changes in diet, as well as marked seasonal changes. For the present purpose the requirements for a growth curve are that, over the range considered it does give a satisfactory fit to the observed growth, and that mathematically it combines with the other expressions easily. In some practical applications, the requirements for a satisfactory fit to growth data are not so much that the theoretical weight at age agrees with the observed weight at age, but that the theoretical and observed growth rates agree, particularly over some critical range. For instance in considering the results of an enlarged trawl mesh size the vital question relating to growth is the time interval between reaching the sizes retained by the old and new mesh size. Using the exponential growth curve

for example, the catch in weight during a small time interval at time t is equal to

$$\begin{aligned} \text{i.e.} \quad \frac{dY}{dt} &= F \times N_t \times W_t \\ dY &= FN_0 e^{-(F+M)(t-t_0)} e^{-gt} dt \end{aligned}$$

and the total yield can be obtained by summation (integration) over the whole time during which the year-class is fished. If necessary, because one or other of the parameters is variable, a more precise formulation can be obtained by splitting this whole period into smaller periods, each with its appropriate parameters. Similarly modifications may be introduced for the analysis of seasonal fisheries, for instance Ricker (1958) has dealt with several forms which the calculations may take, depending on how the fishery season overlaps with the seasons of growth, recruitment and (presumed) natural mortality. The concepts used are the same as already discussed and the mathematics only slightly more complex.

DENSITY DEPENDENT GROWTH AND MORTALITY

In the simpler model of this type it is assumed that the only effects of fishing, both direct and indirect, are on the fishing mortality F , as determined by the fishing effort f , and the range of ages during which fish are liable to be caught, as determined by the selectivity of the gear (e.g. mesh size of the trawl). Explicitly, the growth, natural mortality and recruitment are assumed to be constant, even though changes in fishing may result in large changes in the size of the population. This implies that the mechanism whereby the population is kept within reasonable limits, so that it neither expands without limit nor becomes extinct, lies outside that part of the population so far considered. More exactly, the controlling element, when the numbers of each year-class are determined, occurs in the early stages.

In fact the size of stock must have some effect on the value of the parameters, most probably reducing the growth (e.g. due to pressure on the food supply), with increasing population and increasing the natural mortality (due to disease, though some effects of predation could, at least immediately, reduce the mortality). These effects therefore act against the changes in the population, damping out oscillations, including those due to changes in fishing. Increased parent stock may however increase the number of subsequent recruits; this will exaggerate changes, perhaps very greatly; increased recruits giving a further increase in present stock, and further increase in recruitment, etc. Thus density dependent changes in recruitment are likely to be the most important, in the sense of giving the largest and least predict-

FIG. 2a

FIG. 2.—Density dependent growth of North Sea haddock, showing the relation between the relative density of fish (in numbers) and the increment of length (Fig. 2a), and the growth parameters fitted to these increments (Fig. 2b).

FIG. 2b

able departures between reality and the mathematical model using constant parameters. However, changes in the other parameters, or at least growth, are rather easier to handle both in theory and application. Changes in growth are probably most readily dealt with as growth is easily measurable for most fish, especially when the age of individuals can be determined; further, by using increments put on by fish of different ages in the same year, rather than the complete growth pattern of a single fish during its whole life-span, a growth curve appertaining to any single year can be readily built up. Given a series of pairs of observations of stock abundance and growth an empirical relation between them is not difficult to determine, except for any difficulties with concurrent changes in environmental conditions. Some theoretical forms which the relation between growth and density should take have been put forward. For instance Beverton & Holt (1957) have suggested that in the von Bertalanffy form of the growth equation the changes should be confined to the parameter L_{∞} , the limiting length of fish, while the parameter K , the rate at which this limit is approached, remains constant. They analysed Raitt's (1939) data on the North Sea haddock, and showed a definite density dependent effect. However, while the increase in length during the year shows a significant negative correlation with density, the data do not show whether this is due to changes in L_{∞} or K , or both (see Fig. 2). Plotted in Fig. 2 against the number density in the year concerned, for the haddock in Raitt's western area, are the increments in length during the second, third and fourth years of life, and the values of K and L_{∞} obtained by fitting the Bertalanffy curve to these increments.

The handling of the mathematical expressions is probably easier if it is assumed that changes occur only in L_{∞} , and usually the observed relationship can be adequately represented by a linear relation, i.e. we can write $L_{\infty} = L - aP$.

The effect can then be readily incorporated into the earlier constant parameter model; an approximate value of L_{∞} may be used to compute the population under any desired conditions, hence giving a value of P and from the equation above a better value of L_{∞} . This can be used instead of the original value of L_{∞} to give a further value of P , and hence by such iterative steps the best estimate of L_{∞} and P . In fact the relation found above for haddock related L_{∞} to number density, which is independent of L_{∞} , except possibly where it may affect the age at which the fish becomes vulnerable to the gear, so that no iteration would be necessary.

Density dependent natural mortality is less easily studied, for it is very difficult to get any reliable estimate of natural mortality, and those that are obtained usually refer to the average over a period. Thus changes in the mortality cannot easily be related to changes in density either empirically, or

by the use of some theoretical formula. The use of some formula, such as assuming that mortality is linearly related to density, viz.

$$M = m + kS,$$

where S is measured either in terms of number or weight, may be incorporated into the various equations with but moderate mathematical difficulty. It is more difficult to determine the values of m and k . Some steps towards doing this can be made if natural mortality is split up into its component parts, e.g. disease, parasitization and predation in some proportion, i.e.

$$\begin{aligned} M &= M_{\text{DIS}} + M_{\text{PAR}} + M_{\text{PRED}} \\ M_{\text{DIS}} &= aM \\ M_{\text{PAR}} &= bM \\ M_{\text{PRED}} &= cM \end{aligned}$$

The values of a , b and c are in the first instance estimated (i.e. guessed) from a general impression of the biology of the species concerned. Then reasonable assumptions are

$$\begin{aligned} M_{\text{DIS}} &\propto \text{proportion of diseased individuals in the stock.} \\ M_{\text{PAR}} &\propto \text{proportion of parasitized individuals in the stock.} \\ M_{\text{PRED}} &\propto \text{abundance of predators.} \end{aligned}$$

All these factors could be directly estimated for any short period.

The equation relating to mortality and stock abundance may now be more usefully written in terms of some average or standard conditions, where $M = \bar{M}$, $S = \bar{S}$, and becomes

$$\frac{M - \bar{M}}{\bar{M}} = k^1 \frac{S - \bar{S}}{\bar{S}}$$

which reduces to $M = k^1 \bar{M}/\bar{S} S - \bar{M} (1 - k^1)$.

In this form there is essentially only one constant to be estimated, k^1 , which gives the percentage change in M for a given percentage change in the stock. In particular $k^1 = 0$ gives constant mortality and $k^1 = 1$ mortality proportional to abundance.

In this form the various components of mortality, or numbers proportional to them, can be directly related to population abundance, viz.

$$\frac{M_{\text{DIS}} - \bar{M}_{\text{DIS}}}{\bar{M}_{\text{DIS}}} = k_{\text{DIS}}^1 \frac{S - \bar{S}}{\bar{S}} \quad \text{etc.,}$$

and hence the relation of the total natural mortality given in this form where

$$k^1 = ak_{\text{DIS}}^1 + bk_{\text{PAR}}^1 + ck_{\text{PRED}}^1$$

DENSITY DEPENDENT RECRUITMENT

In the simpler forms of most of the mathematical models described, the numbers of young fish, the recruits, entering the fishery each year are assumed to be the same whatever the size of the parent stock. This is by no means so simple an assumption as that of constant growth or natural mortality and in effect assumes that the mortality of the young is, at some stage, directly related to the number present, increasing at higher abundances. In a contribution to this Symposium Beverton has discussed the various stages at which this effective 'gate' allowing only a fixed number through, can occur, and argues that the most likely mechanism is shortage of food in the larval stages.

While some such factor or factors undoubtedly exist, and probably form the mechanism whereby the population as a whole is kept in balance, their control is likely not to be precise and width of the 'gate' is variable. This is obviously true at very low parental abundances, when the normal recruitment could not be reached even if all the young survived, though with the very high numbers of eggs produced by many marine fish, the same number of recruits could be produced by a wide range of sizes of parent stock. For instance a single female cod (*Gadus morhua*) may produce 10 million eggs in her life; perhaps 1 per cent of young cod entering the fished stock survive to maturity. Thus in a stable stock only 200 recruits need be produced out of 10 million eggs and the same recruitment could be produced by an adult stock one-hundredth of the size, if the egg-to-recruitment survival is 200/100,000, i.e. a mortality of 99.8 per cent compared with the probable present value of 99.998 per cent.

The potentially extremely variable number of recruits obtainable from any one size of mature stock means that the relation between stock and recruitment can in turn be highly variable. The relation may be most easily described by means of a plot of recruitment against parent stock such as that used by Ricker (1954) (Fig. 3). In this diagram the two simplest assumptions are shown, that of constant recruitment (except at the lowest stock abundance) (curve *a*), which is the assumption made so far, and of recruitment proportional to stock (curve *b*). More likely relationships are of the form of curve *c*, with the descending right-hand limb, as favoured by Ricker, or curve *d* which though curved is always increasing and is the form favoured by Beverton & Holt (1957). The important implications of the precise form of this curve in the stability of the population have been discussed at length by both Ricker and Beverton & Holt. The only position possible where the stock is neither expanding nor decreasing is the point where this curve giving the number of recruits produced by a certain adult stock, cuts the constant proportional line, giving the size of stock produced by a given number of

recruits. This latter of course depends on the growth pattern and fishing and natural mortality rates already described. If this point is on the ascending part of the stock-recruitment curve, or on a not too steep part of the descending part, the position will be stable; that is, following any minor disturbances, such as a transitory increase in the amount of fishing, the stock will return to the equilibrium state. If however the point lies on a steep part of the descending limb the position will be unstable, and any disturbances, however brief and small, will cause large and permanent oscillations. With the possible exception of the haddock (*Melanogrammus aeglefinus*) on Georges Bank there are no clear example of such oscillations occurring in a major natural fish

FIG. 3.—Possible relations between stock and recruitment.

population. In many fisheries there are large fluctuations which Hjort (1914) and others have shown to be due to varying numbers of recruits entering the fishery, and though these fluctuations have been believed to be caused by environmental factors this has not often been shown clearly and at least some influence of stock size is possible. In laboratory experiments stock-recruitment curves with right-hand limbs steep enough to cause large oscillations have been shown for several invertebrates. Silliman & Gutsell (1958) kept populations of guppy (*Lebistes reticulatus*) at several fishing rates. Though these exploitation rates were kept at any one value for only a comparatively short time, at rates of 25 per cent and 10 per cent per three-week period the population showed definite signs of oscillations. The control, unexploited populations also showed minor oscillations. In Fig. 4 the data from their

Table 2 of the number of immatures (the recruits) have been plotted against the corresponding number of adults in the preceding period. (For the unexploited populations *C* and *D* the mean number of immature fish has been plotted.) This stock-recruitment curve, though the points are somewhat scattered, definitely has a maximum. A likely curve has been drawn by eye. Straight lines have also been drawn giving the approximate relation between recruitment and stock for the various levels of exploitation. The likely

FIG. 4.—Stock-recruitment relationship for guppies (data from Silliman & Gutsell, 1958), showing adult stock and numbers of immatures three weeks later. Large points are means of several observations. Curve is fitted by eye. Straight lines give the recruitment-stock relation for various levels of exploitation.

equilibrium states for 10 per cent and 25 per cent exploitation lie on the steep descending part of the curve, while the unexploited state is not on so steep a part. The oscillations and their differing amplitude for these varying exploitation rates seem well explained by the stock-recruitment relation, as is the fact that at 75 per cent (and possibly also at 50 per cent) exploitation rate the stock goes to extinction.

This population is perhaps not typical of most marine fish in that a major cause of the stock-recruitment relation lies in the direct predation of the adults on the young. However similar predation, though perhaps on relatively older fish, also occurs in hake (*Merluccius merluccius*) and to a lesser extent in cod (*Gadus morhua*).

While the preceding paragraphs have shown the importance of the stock-recruitment relationship, no mathematical model which could be used in analysis has been suggested. What appears to be required is some function of the form:

$$R = f(S),$$

which could be fitted to the available data and then used in the earlier simple models, together with the relevant values of growth and mortality. As a special case there is the original assumption

$$R = f(S) = \text{constant}.$$

In fact the data usually available from any marine fishery are likely to be highly variable, and the stock-recruitment plot has a very high scatter. Thus even if the form of the curve is known, fitting it to the data is usually difficult. From a different angle this implies that it is equally difficult to determine whether any given form of curve, having been fitted, is indeed a satisfactory description of the data. Thus it is not surprising that Beverton & Holt and Ricker, having developed from different but reasonable assumptions two distinctly different forms of curve ($R = 1/(a + b/S)$ which tends asymptotically to a maximum and $R = cSe^{a-S}$ with a pronounced peak respectively), should be able to fit them satisfactorily to some of the same sets of data.

It appears therefore that this type of model describing the stock-recruitment relationship is not sufficient for most fish; in some ways they are akin to the simplest models of fish populations described at the beginning. Just as a better understanding of the fish population can be achieved by studying it in more detail — e.g. the various growth and mortality rates — so here more details will have to be examined. In particular if indeed food supply is limiting, then the dynamics of the population of food organisms must themselves be investigated.

It is not intended to construct a mathematical model for this analysis, especially as the details of such a model are likely to vary from one fish population to another, depending on the range of foods eaten. However, some points may be mentioned.

If food supply is the factor causing higher mortality among more numerous broods, then not only must shortage of food cause higher mortality, either directly or by lengthening the period of special vulnerability e.g. to predation, but also the higher abundance of young fish must cause a shortage of food. This could be caused by interference or confusion between the fish, but this seems unlikely in the sea and a more probable cause is a direct reduction in the abundance of the food population. An initial guide to the possibility of control by food supply is given by a comparison of the abundance of food

and consumption by the young fish. This may be done for the North Sea stock of plaice. Shelbourne (1957) has shown that, especially during the probably vulnerable stage during and after the absorption of the yolk sac a major food of the young plaice is *Oikopleura* sp., and that probably mortality of plaice larvae at this stage is high when this food is scarce. From Shelbourne's Tables 1 and 3, the abundance of fish and food on his patch of denser food is, *Oikopleura* 37,000 from 30 hauls and 3,153 plaice larvae, of stages 1d and 2a, from 156 hauls; the relative abundance in terms of numbers per haul being $1,200 : 20 = 60 : 1$. It seems well within the power of a single young plaice to eat a large proportion of these sixty *Oikopleura* within a few days. There are therefore all the necessary stages for density dependent control by food. The exact mechanism and final effect will depend on the dynamics of the food population; if there is no reproduction and recruitment into it, then a very abundant plaice population might well wipe out the food and itself die out shortly after. This would give a maximum, perhaps pronounced, in the stock recruitment relation. Alternatively there might be more or less constant recruitment of young *Oikopleura* which would tend to give a rather flat stock-recruitment curve.

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DISCUSSION

M. E. SOLOMON: If there is a high level of competition among small plaice is it a good thing to have a mesh size which allows them to escape fishing?

J. A. GULLAND: There is little evidence of extreme competition among fish of the sizes just escaping.

R. P. SILLIMAN: Watt seems to imply that intraspecific competition does not apply to the populations he is considering.

L. B. SLOBODKIN: In a population which is being held down by climate or predation, intraspecific competition will be unimportant for most of the time. But if and when a large increase occurred, it would become important.

W. EDMONDSON: His Table compares population dynamics, but are the data really comparable? Are the nutrient incomes, for example, the same in all cases?

L. B. SLOBODKIN: It is the yield per unit of nutrient income which is being sought for.

W. EDMONDSON: In the algal populations he uses, the yield per unit of nutrient is itself related to the harvesting system used.

L. B. SLOBODKIN: I think that the figure in the Table will still be of the right order of magnitude.

G. C. VARLEY: I am a little troubled by Watt's use of the term 'regulation' in relation to climatic factors. Isn't this using the word synonymously with 'mortality'? A correlation may be obtained between mortality and climate, but this is not a proof of regulation in the strict sense of the word.

L. B. SLOBODKIN: Watt uses 'regulation', for example, of a population by climate under extreme conditions, to mean that in these conditions the size of the population is predictable from meteorological observations when nothing is known of the population itself. His usage differs from that often adopted in that it does not include a feed-back concept.

J. G. SKELLAM: There are two aspects to the use of mathematical models in biology — the qualitative and the quantitative. In general I rarely expect much more from a model than that it should represent Nature in its broad features and yield a valid pattern of qualitative results. When a model contains several parameters there are great difficulties in estimating them separately, as is easily seen by anyone who attempts to estimate n and p simultaneously in the case of the binomial distribution when p is small.

The individual parameters tend to become fused into a single quantity ($\lambda = np$), a feature which was noticeable in the model considered by Holt earlier. This problem becomes more serious when the mathematical form of the model is not exact, for the parameter values may then suffer considerable distortion in order that the closest fit between theory and observation should be achieved. In general I would stress the importance of attempting to assess population parameters directly wherever possible and to seek confirmation by independent methods of attack. The model Gulland has outlined exhibits oscillatory features (of the kind envisaged by P. P. Moran, 1950, *Biometrics*, 6, 250-8). It must be most gratifying to him to find not merely that this oscillatory property applies also to the fish population studied, but particularly that it comes into operation near to the level of fishing intensity estimated theoretically.

J. A. GULLAND: I do agree that it is essential to look at mathematical models critically, and not just to assume that one is right because it fits.

L. B. SLOBODKIN: Watt's procedure seems to be to set up a programme to learn all the parameters — then to assemble them in a formula, and then to make predictions from it. But if all the parameters are known the formula becomes unnecessary. There must be a distinction between an empirical system giving information about the world and a model in which the output in terms of conclusions is only as good as the input data.

I. A. McLAREN: Models have also a considerable psychological value as an aid to clear thinking.

N. WALOFF: In Gulland's equation there are terms F and M — how is the mortality obtained?

J. A. GULLAND: F is an instantaneous rate. Thus $F = 0.2$ means that fishing mortality is about 20 per cent.

N. WALOFF: But the natural mortality is therefore obtained only by subtraction from the equation term for total mortality, and is not independently assessed?

J. A. GULLAND: It is very difficult to measure natural mortality except as a residual from the known total annual figure. Tagging returns, for example in North Sea herring, give some idea as to how mortality is allocated — in fact the total mortality is 75 per cent and fishing 50 per cent.

S. J. HOLT: I can think of only one case where natural mortality has been estimated directly, by counting shells of *Pecten*. And even here one cannot determine the causes, but only the total time/frequency distribution of dead shells.

J. A. GULLAND: In scallops one can only estimate types of mortality which cause empty shells to remain. If a seal removes whole animals, shells and all, this would not be allowed for.

S. J. HOLT: Referring to Slobodkin's comment on Watt's formula, I agree with what he said but nevertheless believe that the use of an empirical formula can be useful for interpolation.

R. J. H. BEVERTON: Watt is attempting to set up an objective theory for exploited population dynamics, but we cannot overlook the exploiter and the economic factors governing his activities. The maximal yield obtainable may not be the most economic one to take; the last 10 per cent of the yield may not be worth harvesting. The effort input must be taken into account and the yield should be related to it.

L. B. SLOBODKIN: There is no rigorous need to use biomass as the basic parameter in Watt's theory of yield — one could equally use a value parameter and simply adjust the constants.

R. J. H. BEVERTON: Certainly. My point was simply that it is misleading to think only in terms of biomass as it may obscure the fact that the same biomass production may be attained in several ways.

M. GRAHAM: The historical background to the equation described by Gulland is an interesting one. It was produced not by zoologists becoming devotees of mathematics, but because they were forced by policy to look for a more or less rigid equation useful as a guide to factors of first and second magnitude, and as a basis for advice to the Government which was engaging in international negotiations. It was also of value in defining the kind of data which needed to be obtained by such things as marking experiments, to give critical information about important parameters.

R. P. SILLIMAN: There is a philosophical point raised by Beverton's comment on the need to incorporate an economic term in Watt's system. Watt's forecast is most relevant for the time when the human population outstrips its food supply, and when the simple maximal yield will be the important thing.

J. G. SKELLAM: The philosophical problem stated in Watt's abstract just referred to by Silliman is unfortunately considered from only one aspect, maximum sustained productivity. Consideration of this aspect is, however, neither necessary nor sufficient for the solution of the philosophical problem. It is not necessary because the problem vanishes if the human population were maintained by factors other than starvation at a sufficiently low density, and it is not sufficient because the attainment of the maximum level of productivity which the energy of sunlight and the efficiency of chlorophyll can provide implies the maintenance of a still greater human population at a 'bestial level of existence'. It is essential here to consider the ecosystem as a whole, and it is up to man to decide how to control the growth of the human population in the least objectionable way.

SOME EXPERIMENTAL AND THEORETICAL APPROACHES

PREDATION AND EFFICIENCY IN LABORATORY POPULATIONS

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In an earlier Symposium Park (1955) said:

'Research in laboratory population ecology should take its orientation from some phenomenon known or suspected to occur in nature and known or suspected to have significant ecological consequences. Its objective is not to erect an indoor ecology but, rather, to illuminate conceptually the general problem to which it is addressed. The research is thus the handmaiden of field investigation; not the substitute.'

Experimental populations can be thought of as analogue computers for ecological problems. Their only advantage over purely mathematical models is that the significant properties of the experimental animals are likely to be things that would not occur to a mathematician. The corresponding disadvantage is that the results are more difficult to analyse than are those of purely mathematical theories and models.

I will be concerned with two aspects of population dynamics:

1. The effect of predation on the number, size, and age distribution of animals in a population.
2. The efficiency with which yield to a predator is produced from a population.

While the discussion of hybrid populations has never been published a series of papers have appeared on the *Daphnia* work (Slobodkin, 1954, 1959, 1960; Richman, 1958; Armstrong, 1960).

TECHNIQUES

The technique of all the experiments is essentially the same. A small container is filled with a suitable fluid; artificial pond water in the case of hybrid experiments, aged tap water in the case of the *Daphnia*. A feeding regimen is set up under which some constant amount of suitable food is provided per unit time. A few individuals of the appropriate species are added. These animals and their descendants are called a population. The population is free to multiply or die and to adjust itself to living in the experimental container.

The level of food is set initially by the experimenter and as a rule does not change during the history of the population.

The experimenter may act as a predator on the population by removing animals according to some fixed pattern. The most common pattern of predation in these experiments was to remove animals in proportion to the number of births occurring in the population (although the animals removed were not necessarily new-born). The experimenter might act as a source of immigrants (Armstrong, 1960; Armstrong & Slobodkin MS.). In this case animals were added to the populations in proportion to the occurrence of births.

The precise size and shape of the experimental containers and the kind of food and method of feeding varied from species to species. *Daphnia obtusa* was fed *Chlamydomonas moewusii* in early experiments (Slobodkin, 1954). In later *Daphnia* experiments, *C. reinhardi* was used as food for *D. pulex*. The algae were grown separately on sterile agar, washed off into water and the optical density measured with a Klett colorimeter. The *Daphnia* populations were removed from their old medium, counted, sorted and subjected to either predation or the addition of new immigrants, and were then returned to fresh medium. The appropriate amount of food was added and the animals were returned to their incubator. For some populations food was also added on days when the medium was not changed.

Hydrids require live animal food. Eggs of *Artemia salina* can be purchased in sealed cans and hatch readily in salt solution. The *Artemia* nauplii were washed through bolting silk and suspended in graduated centrifuge tubes. When the centrifuge tubes are immersed in ice-water the *Artemia* are immobilized and form a wet pack at the bottom of the tube. An aliquot of resuspended *Artemia* of known concentration can be fed to the hydra. Since hydrids seem very sensitive to the presence of various waste products, the hydrids populations are washed one half hour after feeding. Probably several washings during the day would have resulted in increased population size (Loomis, personal communication).

Flatworms also eat animal food but have difficulty capturing live *Artemia*, since *Dugesia* are repelled by light while *Artemia* are attracted. Armstrong (1960) therefore killed the *Artemia* by dipping the centrifuge tubes in hot water.

The *Daphnia* were grown in wide-mouth bottles, the hydrids in Petri plates and the flatworms in finger-bowls. All of the populations were confined in relatively small spaces. If there was any reaction which would cause these animals to disperse under starvation conditions, or to adjust their distance from their neighbours in some way in response to environmental conditions it would be impossible to manifest under the conditions of these experiments.

Any extrapolation to the field must take into account the geometrically closed nature of the laboratory microcosm.

Three species of hydrid (*Hydra oligactis*, *H. littoralis*, and *Chlorohydra viridissima*), two species of *Daphnia* (*Daphnia obtusa*, *D. pulex*) and one species of flatworm (*Dugesia tigrina*) were used in these studies (Hyman, 1959a, b; Scourfield, 1942). Except where specific differences are concerned I will refer to these simply as hydrids, *Daphnia*, and flatworms.

Further details of the technique are available in the previously cited papers.

POPULATION GROWTH

The *Daphnia* populations came to a fluctuating steady state; the flatworm achieved remarkable numerical stability; the hydrids were much less stable and many of the populations died after an alteration in the laboratory plumbing. Apparently heavy metals or other poisons persisted on the glassware after the plumbing change. The hydrid experiments are being repeated using disposable plastic Petri dishes, and much of the instability seems to have disappeared in the new dishes. I will assume that steady state hydrid populations would have been maintained, had the plumbing been satisfactory. There is an element of doubt in this assumption, so that all of the hydrid results must be considered contingent on repetition of the experiments.

(a) *Daphnia*

If a small number of *Daphnia* are placed in 50 cc of water and fed in the way indicated above, there will be an initial period during which the number of animals will increase and the individuals will all grow and reproduce rapidly. This period of rapid growth may be slightly delayed if the original animals were starved before the beginning of the experiment. In any case, no more than six to ten days after the initial introduction the population will consist of new-born animals and highly fertile adult females, producing fat laden eggs at the rate of from six to fifty eggs per moult. Cladocera do not have elaborate metamorphosis; young animals immediately begin to feed and grow.

After approximately twenty days population growth ceases and the number of animals begins to decline. At this time the population contains mainly small animals. From one-tenth to one-fifth of the animals are reproductive adults. The amount of fat per egg, as indicated by visible fat droplets, the number of eggs per brood and the colour of the eggs have all changed during the early population history. At approximately the sixtieth day no new eggs at all are apparent in the brood pouches of the adults. At this time individual growth rates are low and mortality rates are high.

As the number of animals in the population declines, the size distribution shifts until all of the animals are of reproductive size. Before this, ovaries have begun to reappear. Young animals are now produced, resulting in an increase of population size and a new peak in numbers. This may be followed by a numerical decline. If only adult animals survive, the fluctuation will be repeated. Fluctuation in number and size distribution may persist throughout the history of the population. Occasionally, however, a population may come to a continuous size distribution, with a preponderance of large animals, but at least some smaller animals present at all times. Populations of this sort are numerically constant unless environmental changes occur.

The number of animals in a population that is not fluctuating is a linear function of food supply. The total nitrogen content of *Daphnia* populations is also a linear function of food supply. In the case of *Daphnia*, therefore, the only significant population interactions between the animals are those that alter the food supply for each animal. We can ignore metabolites, conditioning, cannibalism, etc.

If a *Daphnia* population is subjected to predation, population size is reduced, and the amount of food ingested by the population may decrease. The reproductive rates and growth rates of the survivors increase. These effects depend on the kinds of animals that are removed as well as on the rate of predation.

We will define F (fishing rate) as the fraction ((number of animals removed per unit time) divided by (number of animals born per unit time)). This differs from most definitions of predation rates but it is very simple for analytic purposes.

F refers to the rate of taking animals but does not specify the kind of animals removed. For example, if F for a particular population has been set at 25 per cent, the number of animals removed as yield would be one-quarter of the number born. The yield animals might be either new-born or adults or any other category. The kind of animal taken, as well as F , must be specified, to unequivocally describe a predation procedure.

If young animals are preferentially removed from *Daphnia pulex* populations the steady state size of the residual populations (P_F) and the mean yield per unit time are both linearly related to food supply. Fig. 1 shows the relation between population size per unit food and F . Fig. 2 shows the relation between yield of young animals per unit food and F .

The relation between P_F and F can be adequately expressed by the equation:

$$P_F = P_0 \left(1 - \frac{F}{2 - F} \right) \quad (1)$$

FIG. 1.—The relation between residual population size (P_F) per unit food and the intensity of predation (F) in *D. pulex* when young animals are selectively taken as yield.

FIG. 2.—The relation between yield per unit food per four days and F , when young animals are selectively taken as yield (*D. pulex*).

The rationale of this equation is that it has the appropriate limits, so that $F = 0$ implies that $P_F = P_0$, and $F = 1$ implies that $P_F = 0$; has an appropriate curvilinear shape; and is extremely simple.

The removal of a few small *Daphnia* is largely compensated for by an increase in the reproductive rate of the survivors. The lability of reproductive rate is so high that only when F is very high does P_F decline rapidly with F .

Equation (1) is applicable only to the first quadrant. If negative fishing, i.e. immigration, occurs, it is found that P_F increases linearly with $-F$ and not curvilinearly as would be implied by the equation. It seems likely that alterations in reproductive rate are not significant when immigration is occurring. Death rate seems to increase with $-F$. The immigration studies will be presented in detail elsewhere (Armstrong & Slobodkin MS.).

Clearly either the reproductive rate or death rate of at least some of the animals in a population must change as a consequence of predation if a steady state population size is to be maintained. Let

$$R_0 = \sum_0^{\infty} l_x m_x$$

where l_x is the probability of survival up to age x of one individual born at age 0 and m_x is the fecundity of a single live animal during the interval x , $x + 1$. If a population is at a steady state, $R_0 = 1$. Given a steady state population, consider that a system of predation is introduced. The mortality that can be attributed to predation will either compete with other sources of mortality in such a way as to leave the l_x distribution unchanged or, more probably, it will alter the l_x distribution. If the l_x distribution has been altered by predation there must be compensatory alteration in either the l_x or m_x distribution to restore the condition $R_0 = 1$. In a sense this is equivalent to the assertion that only populations which are density dependent can achieve a new steady state under predation (Nicholson, 1954).

When adult animals are removed, the relation between P_F and F is more complex. At low food levels the *Daphnia* completely consume the algae between feedings and equation (1) seems approximately valid. As the concentration of food increases it is found that equation (1) overestimates the size of the standing crop population (Fig. 3).

Microscopic examination of the medium shows that uneaten algae are always present when population size is significantly below the value predicted by equation (1). Experimental studies by Richman (1958) show that assimilation of ingested algae by *Daphnia pulex* is less efficient when algal concentrations are high.

If yield in (animals plus eggs) per unit food is plotted against F for the populations from which adults were preferentially removed, there is a wide

FIG. 3.—The relation between residual population size (P_F) per unit food and the intensity of predation (F) when adult animals are selectively taken as yield (*D. pulex*).

FIG. 4.—The relation between yield per unit food per four days and F when adult animals are selectively taken (*D. pulex*).

scatter (Fig. 4). If we assume that the proportion of the food provided that is consumed by a population is given by

$$\frac{P_F \text{ observed}}{P_F \text{ calculated from equation (1)'}}$$

then the scatter in the relation of yield per unit food to F is greatly reduced (Fig. 5).

FIG. 5. The relation between yield per unit food consumed per four days and F when adult animals are selectively taken, on the assumption that deviation from equation (1) is due to failure to consume all of the food provided (*D. pulex*).

(b) Hydrids

Thirty-two populations of *Hydra oligactis* were maintained, sixteen by each of two technicians. Each block of sixteen included one population at each of four food levels and four fishing levels. The food measuring procedure apparently differed somewhat between technicians so that there was a consistently higher population and yield per unit food from one set of populations.

When the mean of the eight P_F estimates at each level of F is plotted against F (Fig. 6), equation (1) is found to hold.

The relation between yield per unit food and F is also essentially the same as that found in *Daphnia* (Fig. 7.).

Experiments on the interaction between predation and competition in *H. littoralis* and *Chlorohydra viridissima* are still in progress. Some preliminary results will be reported here.

The green hydrid, *C. viridissima*, eats *Artemia* but also contains presumably symbiotic algae. Populations of green hydrid are four times more numerous when grown under a fluorescent lamp than when grown in partial darkness. Complete darkness was impossible since the animals had to be counted under a light microscope. They do not blanch completely in the dark but their

FIG. 6.—Relation between P_F per unit food and F in thirty-two populations of *Hydra oligactis*. The mean values of P_F at each F are indicated by ■. The line is drawn from equation (1).

green colour becomes much paler. Light is of no apparent significance in the population growth of *H. littoralis*.

To the degree that present data permit conclusions, the outcome of competition between the species depends on light. Of the six mixed species populations in the light, two were not subjected to predation and in both of these the green hydrid were the only survivors. Two populations were subjected to predation of $F = 25$ per cent for each species separately. The brown hydrid was eliminated in both of these populations. One mixed

FIG. 7.—Yield per unit food per four days and F (*Hydra oligactis*).

population was subjected to $F = 50$ per cent and in this population *H. littoralis* alone persisted. In a population with $F = 90$ per cent both species persisted. Two mixed species populations were established in the dark. One of these was not subjected to predation and in this one the brown hydrid alone survived. In the other, subjected to $F = 90$ per cent both species survived.

The simplest interpretation of these data is that the green hydrids use light energy in addition to animal food. Darkness alters the outcome of competition by eliminating this extra energy source. It seems possible, however, that green hydrids do not feed as readily in the dark. In most of the populations the green hydrids, when present, were individually smaller and more numerous than the brown hydrids.

A notable feature of the hydrid populations is the relatively high variance between populations maintained under supposedly identical conditions. It seems possible that part of this variance is due to the morphological flexibility of individual hydrids. In hydrids, age and size are almost independent of each other. An individual animal, deprived of food may reduce its size appreciably, before it dies.

(c) *Immigration in Dugesia tigrina populations* (Armstrong, 1960)

The relation between size of individual and steady state population size is most clearly demonstrated in Armstrong's experiments. He added new-born tails to populations of flatworms in proportion to the number of tails that had been produced during the interval between census.

Five populations were grown, two of which served as controls. Each experimental population received either one, two or three new-born tails for every tail that was vegetatively produced by the population. All of the populations reached a steady state in which numerical change was absent and neither deaths nor births occurred.

The number of animals in the populations, when they achieved this static condition, was proportional to the rate of addition of new tails and inversely related to the mass and length of the individuals composing the population. Equilibrium could be attained with either a large number of small animals or a smaller number of large ones. Animals in a population which achieved numerical stability at forty-two animals were more than twice as heavy as those in a population that was stable at 169 animals. The total dry mass of the populations was slightly greater for populations which were more numerous. Possibly food was more effectively utilized when a large number of small animals were feeding.

CONCLUSIONS FROM THE NUMERICAL ANALYSIS

In all of the species examined, the surviving individuals in a population subject to predation are different in reproductive rate, death rate, mean size or some combination of these, from individuals in control populations.

Predation lowers population size in these species. This cannot be expected for all animals, however (cf. Nicholson, 1957).

The degree of population size lability seems to vary from species to species.

Population size in *Daphnia obtusa*, *D. pulex* and *Hydra oligactis* is linearly dependent on food consumption, with or without predation.

Equation (1) or some biologically more meaningful equation of similar form, may prove applicable to many species, since it seems to hold for an herbivorous crustacean and a carnivorous coelenterate.

THE EFFICIENCY OF *DAPHNIA* POPULATIONS

Richman (1958) determined the calories released by combustion of *Daphnia pulex* and *Chlamydomonas reinhardi*. These analyses provide conversion constants for translating the numerical data from *D. pulex* into energy units thereby permitting an analysis of efficiency in *D. pulex* populations.

The term 'efficiency' applied to a natural population is ambiguous. Any dimensionless number which is the quotient of two energies may be called an efficiency. At least three different concepts of efficiency seem of ecological interest. These will be discussed in order of simplicity.

(a) *Ecological efficiency*

The ratio of the steady state rate of production of yield to the steady state rate of food consumption by the population will be called ecological efficiency.

The maximum observed ecological efficiency for the *Daphnia* populations varies from 8.5 to 12.5 per cent. The lower estimate is calculated as calories of yield removed divided by calories of algal food provided. The higher estimate results from correcting for food consumption by use of equation (1). The maximum observed ecological efficiency of a *Daphnia* population from which young animals are preferentially removed is no more than 4 per cent.

Patten (1959) lists twelve estimates of ecological efficiency derived from field data. With the exception of one value of 75 per cent taken from Teal (1957) and one of 21 per cent (Lindeman, 1942) all of these estimates fall in the range 5.5–13.3 per cent. Wright (1958) found an efficiency of 10.5 per cent for a zooplankton population.

The maximum ecological efficiency values derived from the *Daphnia* experiments are therefore in good agreement with observed ecological efficiencies in aquatic environments in nature.

Ecological efficiency is a function of the interaction between three trophic levels; the predator, the prey and the food of the prey. More intense predation or more effective assimilation of food may increase ecological efficiency. There is no direct relation between ecological efficiency and the standing crop of the prey although it may be expected that exploiting a prey population so as to maximize ecological efficiency will tend to reduce standing

crop severely. The upper limit to ecological efficiency is partially set by the necessity of maintaining some minimum standing crop of prey.

(b) *Growth efficiency of individual Daphnia*

In defining individual growth efficiency the relevant time span will be taken as the entire pre-natal and post-natal life of the organism. Growth efficiency is defined as:

$$\frac{(\text{calories in the body of an organism at age } i)}{\left(\begin{array}{c} \text{calories consumed as food} \\ \text{from age 0 to age } i \end{array} \right) + \left(\begin{array}{c} \text{calories consumed by its mother} \\ \text{in producing one young animal} \end{array} \right)}.$$

By this definition the energy utilized in producing young animals relates to the growth efficiency of the young rather than to that of the mother.

Growth efficiency has been computed for *Daphnia pulex* as a function of age and of cell concentration in the medium. The computations were made by Armstrong (1960), using data from Richman (1958) and Slobodkin (1959).

In order to determine the caloric cost of egg production, Armstrong first determined the cost per calorie of growth increment during the period immediately prior to the beginning of reproduction. He then determined the growth increment and food consumption during reproductive life, subtracted the appropriate cost of growth from the food consumption and assumed that the residual food energy was utilized for egg production. The cost per egg was then calculated by dividing the caloric content of the eggs by the food energy available for reproduction and dividing this by the number of eggs produced.

Armstrong's results are summarized in Fig. 8. Growth efficiency up to any age is a decreasing function of age. In excessively low concentrations of algae, growth efficiency is low, since the effort expended in feeding is not adequately compensated by the food acquired. At very high concentrations of algae, growth efficiency is lowered by the inability of the gut to assimilate all of the algae eaten.

Growth efficiency is independent of method or intensity of predation except to the degree that predation may alter the properties of the individual animal and its local environment.

It may reasonably be expected that *Daphnia* in nature are usually at or below the optimal cell concentration for growth efficiency. The values of growth efficiency determined for *Daphnia* seem to conform to comparable determinations from other animals.

(c) *Population efficiency*

It is possible to define a concept of efficiency which takes into account the

FIG. 8.—Growth efficiency contours as a function of cell concentration of the medium and caloric content of the animals in *D. pulex*. Data from Armstrong (1960) — Ordinate — *Chlamydomonas* concentration in thousands of cells per ml. Abseissa — caloric content of *Daphnia*.

effect of predation on standing crop. I have called this concept 'population efficiency'. I believe it is new and must therefore be defined and analysed with caution.

A predator that is not concerned about the size of the prey population may try to simply maximize his yield per unit time, Y , or on a slightly more sophisticated level may maximize ecological efficiency, E :

$$E = \frac{\dot{Y}}{\dot{I}}, \quad (2)$$

in which I is the energy consumed per unit time by the prey population.

A prudent predator may want to maximize the expression:

$$E_P = \frac{Y}{I \left(1 - \frac{P'}{P} \right)} \quad (3)$$

in which P' is the steady state population standing crop in calories maintainable under the given predation system, and P is the standing crop in the absence of predation. If I is independent of predation, it can be shown that

$$\frac{Y}{I \left(1 - \frac{P'}{P}\right)} = \frac{Y}{P' \Delta c} \quad (4)$$

in which Δc is the increase in maintenance cost per calorie day of standing crop that is attributable to predation. Population efficiency is the yield to the predator per maintenance cost increase associated with predation.

Equation (4) is derived from the following argument:

In order to maintain living protoplasm, energy must be expended. The greater the necessary expenditure per calorie day of standing crop the smaller the standing crop that can be maintained by a given energy income per day.

In general, increase of I will imply increase of P , but the precise form of the relation between P and I is not obvious *a priori*. For *Daphnia*, since it has been experimentally demonstrated that P is a linear function of I , we can write:

$$I = Pc \quad (5)$$

and if I is not altered by predation we can write:

$$I = P' (c + \Delta c), \quad (6)$$

which permits us to establish the identity:

$$P' \Delta c = I \left(1 - \frac{P'}{P}\right).$$

The population efficiency, E_{pi} , associated with a predation procedure that removed only one kind of yield animal, i , can be evaluated from the equation

$$I = P'c + \sum_0^{\infty} \frac{Y_i}{E_{pi}} \quad (7)$$

when data from a sufficient number of populations, each subjected to different predation procedures, are available.

This equation was solved using three categories of yield and steady state data from twenty-two experimental *D. pulex* populations (Slobodkin, 1959). A least squares solution for c and the three population efficiencies indicated that a predation system which took only adult animals as yield, would have a population efficiency of 48 per cent, while removal of only young animals would have a population efficiency of 4 per cent. If it were possible to take only eggs as yield the population efficiency would be 6 per cent.

The yield from any real population is typically mixed. The population efficiency associated with a mixed yield is given by:

$$E_p = \frac{1}{\sum_c \frac{Y_i}{E_{pi} \sum_0 Y_i}} \quad (8)$$

For a given population the estimate of E_p from equation (8) ought to be identical with that from equation (3). The relation between the two estimates is shown in Fig. 9. I believe the spread is due to weakness in the estimates of I .

FIG. 9.—Population efficiency estimated for the same population from equation (8) (B) and from equation (3) (A). The line is drawn on the assumption $A = B$.

The value of c , from equation (7) was 1.68 calories per four calorie days. Five control populations consumed 8.1 calories per four days. The expected steady state standing crop, from equation (5), was therefore 4.7 calories. The observed mean standing crop of these populations was 4.5 calories.

Population efficiency depends on life expectancy and growth efficiency of the animals removed and on the interaction between these animals and the other members of the population.

This can be readily visualized by considering that the process of steady state population maintenance consists of producing dead animals at a fixed rate and with a fixed age and size distribution. The cost in calories of producing a dead animal is given by its caloric content, S_x , at the time of death divided by its growth efficiency up to the age of death.

In the absence of predation all of the energy consumed by a population is used for maintenance so that:

$$I = Pc = \sum_0^{\infty} \frac{D_x S_x}{E_x} \quad (9)$$

where D_x is the number of animals dying during the age interval x .

Predation alters the distribution of deaths and may also change growth efficiencies and even the S_x , so that for a population subject to predation:

$$I = P'(c + \Delta c) = \sum_0^{\infty} \frac{D'_x S'_x}{E'_x} \quad (10)$$

Solving for c , using equations (9) and (10), and substituting this solution in equation (4),

$$E_p = \frac{Y_i}{\sum \frac{D'_x S'_x}{E'_x} - \frac{P'}{P} \sum \frac{D_x S_x}{E_x}} \quad (11).$$

E_p , therefore, incorporates almost all the information that may be of interest in exploiting a population.

Growth efficiency of *Daphnia* decreases with age, while the population efficiency associated with selective predation increases with the age of the animals removed. This lack of correspondence is due to the fact that removal of an animal that is about to die of other causes introduces minimal alteration in the population death distribution. A scavenger utilizes a population with infinite population efficiency.

A predator is behaving with maximum prudence when his predatory activities maximize the population efficiency of the prey. This can be done by taking as yield slowly growing animals with a minimal life expectancy and low reproductive value.

CONCLUSION

Despite the dependence of population phenomena on precise experimental conditions, a relatively simple equation predicts the functional dependence of population size on an appropriately defined concept of predation in both

Daphnia pulex, an herbivorous crustacean and *Hydra oligactis*, a carnivorous coelenterate.

Maximum ecological efficiency in laboratory *Daphnia pulex* populations is essentially identical with ecological efficiency estimates in natural aquatic situations. This identity permits the tentative conclusion that the range of ecological efficiencies in nature is relatively narrow. Further laboratory and field work will be required to test this conclusion.

It is possible to define and evaluate a concept of efficiency which takes into account the effect of predation on standing crop size. This has been called 'population efficiency'.

Population efficiency can be defined as a function of death distributions, individual growth efficiency, individual caloric contents, and population size; and their interaction with predation. It may be evaluated for an entire population if energy consumption, yield, and the effect on standing crop are known.

It can also be evaluated in terms of the population efficiency that would be associated with a predation programme that selectively removed some particular kind of animal as yield. This evaluation can be made from data on energy consumption, yield, distribution of the yield among the possible kinds of yield and standing crop in calories, for several independent populations.

When more caloric standing crop data become available it may be possible to solve for population efficiency in field situations.

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LONG-TERM DYNAMICS OF CERTAIN NORTH SEA FISH POPULATIONS

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INTRODUCTION

Despite recent advances in knowledge of the dynamics of marine fish populations, the fundamental questions of whether the populations are in a state of long-term balance and, if they are, of identifying the mechanisms responsible for that balance, remain largely unanswered. There are several reasons for this. One is that the abundance of successive year-classes often fluctuates widely, due primarily to the influence of year-to-year variation in environmental conditions, which makes it difficult to establish the existence of true long-term trends except from a very long series of data. Another is that the natural life-span of many of the species which exist as large population units supporting major commercial fisheries (and therefore for which the records and information are most extensive), extends for at least ten years and in some cases up to thirty years (Brown, 1957; Beverton & Holt, 1959). Consequently, even if many years of reliable data on the size of the population are available, they may cover a span of only a very few generations. A further difficulty is that although commercial fishing records can often provide valuable comparative indices of population abundance, they refer only to sizes of fish which can be retained by the gear and are of commercial importance. In many instances, fish do not reach such a size until they are approaching or have attained sexual maturity; yet the indications are that if compensatory factors are operative their influence may well be confined to the juvenile or even larval phase of the life-history, about which relatively little quantitative information exists.

It is the purpose of this paper to examine the evidence for long-term stability, or lack of it, in certain fish populations of the North Sea for which particularly good records are available, and to attempt to delimit the possible compensating mechanisms in one of these populations about which most is known of the various phases of the life-history, namely the plaice (*Pleuronectes platessa* L.).

LONG-TERM TRENDS IN CERTAIN FISH POPULATIONS OF THE NORTH SEA

The physical nature of the marine environment and certain characteristics of the biology and behaviour of fish often make it possible to identify a particular population as a self-perpetuating unit, to delimit its spatial distribution and, given appropriate data, to obtain reliable comparative measures of its size over long periods. Certain of the demersal fish species of the North Sea exist as identifiable populations of this kind, whose members do not stray to any extent beyond the confines of the North Sea and aggregate consistently for spawning at a particular season and on characteristic spawning grounds.

Early records of catches, when trawling began to spread into the North Sea proper in the first half of the last century, show that the relative abundance of the main species in the catch was broadly similar to that of the present day, despite the major influence which fishing has undoubtedly had. By the beginning of the present century the total amount of trawling in the North Sea for the major species had increased to a level which was probably not greatly different from that prevailing now, and which has not changed much during the intervening period, except for the temporary cessation of fishing during each of the two world wars. From 1906 onwards the International Council for the Exploration of the Sea has published in its *Bulletin Statistique* full records of the total landings of each species by all countries. These constitute a unique set of data which it is possible to use, for certain species, as a fairly reliable indicator of long-term trends in population size.

Five species have been selected for the present analysis, namely plaice, cod (*Gadus callarias*), haddock (*Melanogrammus aeglefinus*), sole (*Solea vulgaris*) and turbot (*Rhombus maximus*). Sole and plaice are typically more southern in their distribution than cod, haddock and turbot, but there is considerable overlap between the five species except between sole and haddock. Data of landings per unit fishing effort would normally be preferable as indices of population size, but these are not sufficiently reliable for all the five species over the whole period to have much advantage over landings for the present purpose. The relative market demand for these species has, however, remained fairly steady and all of them are caught by similar gear. Moreover, the transitory changes in their abundance resulting from the cessation of fishing during each of the two wars were very pronounced in terms of landings per unit effort but are not strictly relevant to the analysis of long-term trends. For this particular purpose it was therefore decided to use statistics of landings rather than of landings per unit effort, although the latter are used for the more detailed interpretation of events in later years when it is known that significant changes in fishing effort have occurred.

The total annual landings of the above five species since 1906 are shown in Fig. 1. They fall broadly into two groups, the landings of plaice, haddock and cod being some ten to twenty times greater than those of sole and turbot. Although the relation between landings and population size is certainly not the same in all five species, there is no doubt that this difference in landings reflects a corresponding difference in order of magnitude of population size. It is also possible to see from Fig. 1 that in certain species, notably haddock,

FIG. 1.—Total international landings of certain species from the North Sea, 1906–57.

there is evidence of a downward trend; whereas in others, such as plaice, the landings have remained at a roughly constant level throughout.

Long-term trends within each population can, however, be examined better by calculating the landings in each year as a ratio of the average landings of the species over the whole period, and plotting these ratios on a logarithmic scale, as shown in Fig. 2. It is now apparent that the most marked trend, an upward one, is in fact shown by sole (at the top of the diagram), the landings of which have increased by some eight times since the beginning of the century. This may be, in some degree, an exaggeration of recent trends in the true population size of sole because fishing for sole has become more specialized in the last decade; but this increased fishing has

itself become possible through a true increase in the size of the population resulting from the very large influx of young fish that is known from age composition data to have occurred since the war, starting with the very large year-class born in 1947. Although the data do not exist that would enable

FIG. 2.—Data of total landings of Fig. 1, expressed as logarithms of ratio ($\times 10$) of mean value 1906-57, for each species.

events before the last war to be examined in this way, it seems difficult to escape the conclusion that the sole population has indeed been increasing throughout the century. If the increase continues at the same rate the sole population of the North Sea will, in some twenty or thirty years' time,

become comparable in size to those of the three major species shown in Fig. 1.

In contrast, the trend in haddock shown at the bottom of Fig. 2 is clearly downward, especially when it is remembered that the removal of fishing pressure during the two wars allowed the population to recover to several times its previous abundance on each occasion. Here again there is little doubt that the impression gained from the trends in landings represents a real change in population size, as during the period there has been a progressive contraction of the main haddock fishing area and it is now rare to find haddock in any quantity south of the Dogger Bank.

The trends in landings of the three remaining species are less marked, but there are signs of an upward one in turbot. It is known that the fishing pressure on both cod and plaice has been rather less since the last war than previously, and that this reduced fishing mortality has allowed the population of adult fish of these two species to increase by something of the order of 50 per cent compared with earlier years. If allowance for this is made in the data of Fig. 2 since 1950, the overall trend in cod becomes a downward one, while the graph for plaice becomes virtually horizontal throughout the period.

Thus, of the five species considered, the plaice shows the greatest degree of stability and the sole the most marked trend. It can also be seen from Fig. 2 that the sole data show the greatest degree of fluctuation about the overall trend and those of plaice the least, with the other three species intermediate. Thus there appears to be an association between the degree of long-term trend and the degree of short-term fluctuation about that trend, a point which is referred to again later. It would have been instructive at this juncture to have attempted a comparative study of the population ecology and dynamics of the five species, but this is not possible in the present state of knowledge. The information on plaice is the most comprehensive (see Wimpenny, 1953, for a general account); on the assumption that the evidence presented in Figs. 1 and 2 indicates considerable stability in the plaice population, an attempt is made below to locate the phase of the life-history during which compensation occurs and to identify the mechanisms which could be responsible for it.

COMPENSATION IN THE ADULT PHASE OF THE NORTH SEA PLAICE POPULATION

Plaice do not appear in the commercial catches until they are about three to four years of age, on the average, and the majority attain maturity within a further year. The age and length composition of the landings of plaice,

which have been sampled regularly since 1930, therefore refer mainly to what may be called the adult phase of the population. These constitute the longest series of quantitative data on the plaice population, and it is appropriate to see first whether there are features of the dynamics of the adult population which could give a clue to the compensating mechanisms.

The fact that the abundance of the adult plaice population has been remarkably steady for most of the period since 1906 does not make it any easier to detect the existence of possible compensating mechanisms. The nearly complete cessation of fishing during each of the two wars, however, caused marked, although temporary, increases in the density of the adult population. These increases are not very noticeable in the landing statistics shown in Figs. 1 and 2 because fishing itself did not recover its previous intensity until a year or two after each war period, but they are clearly shown from the data of catch per unit effort (Margetts & Holt, 1948). In fact, when fishing restarted in the summer of 1945, the density of the adult plaice population, in terms of weight of fish, was something like ten times the average density during the 1930's, and about five or six times higher in numbers. This increase in density was due purely to the absence during the war period of a fishing mortality rate that had previously been in the region of 50 per cent per year, but if density-compensating mechanisms are present in the adult phase they should nevertheless have been detectable in such circumstances; yet the secondary effects do not seem to have been very marked. The growth of the older fish during the war period had indeed been somewhat retarded; thus by 1946 the weight of plaice which had reached maturity before the war was reduced by some 15-20 per cent compared with fish of the same age under pre-war conditions. This is evidence of some compensation of population biomass, but not necessarily of any more far-reaching form of compensation. The growth of fish is remarkably plastic and there are instances both from experimental studies (e.g. Dawes, 1930, 1931, for plaice) and in nature (e.g. Alm, 1946; Deelder, 1951; for perch) in which much greater retardation than this did not have any adverse effect on survival. Moreover, direct measurement of the natural mortality rate of plaice over the whole war period was possible; certain year-classes could be sampled both in 1939 before fishing stopped and again in 1945 when fishing restarted (Beverton & Holt, 1957), and these gave estimates of about 10-15 per cent per year. It is not possible to establish whether this figure is significantly higher than the natural mortality rate under the conditions of reduced population density either before or after the war, but even if it were so the effect would hardly be enough to produce the degree of compensation observed. The retardation of growth may also have influenced the efficiency of the reproductive processes in various ways,

notably by a reduction in the fecundity of females at a given age, but to test the significance of these it is first necessary to examine the relation between the size of the present population and the number of resulting progeny.

COMPENSATION BETWEEN SUCCESSIVE ADULT GENERATIONS IN PLAICE

In plaice, twenty-six pairs of values of adult population weight and resulting progeny are available, the number of the latter being estimated when first recruited to the adult phase of the population at three to four years of age, and these are plotted in Fig. 3.

FIG. 3.—Relation between biomass of adult plaice population and number of progeny surviving to recruitment.

The points to the left of the diagram refer to the low levels of adult population size that occurred during the 1930's and again in recent years; the points to the right resulted from the high densities during the war and up to 1949, by which time the war-time accumulation had been largely fished out. Yet over this tenfold range of adult population size there seems to be no corresponding change in the numbers of recruits; even from the highest adult densities the recruitment was only average. This can be shown more strikingly by calculating the ratio of recruit numbers to adult population — which can be regarded as an index of survival to recruitment — and plotting it against adult population. The result is shown in Fig. 4, where the decrease in this index of survival as adult population increases becomes evident; in

fact, these data fit closely to a hyperbola, which is what would be expected if the data of Fig. 3 are best represented by a horizontal line. Thus it seems that the main compensating mechanisms in plaice are located somewhere between the successive generations of adult fish.

Apart from the lack of a relation between adult population size and subsequent recruitment, the degree of variation in the number of annual recruits is itself not without significance. Thus, in plaice, over the series of twenty-six year-classes whose abundance can be measured fairly reliably, the extreme range of numbers has been about six-fold and the average variation only about 36 per cent above and below the mean (see Fig. 3). The significance of this degree of variation of recruit numbers can be judged from the fact

FIG. 4.—Index of survival to recruitment in plaice plotted against biomass of parent population.

that because of the enormous fecundity of female plaice no more than roughly ten fish can survive from every million eggs spawned, if the size of the adult population is to remain steady. In other words, on average the progeny from about 999,990 eggs out of every million die before reaching maturity; but the observed variation of recruit numbers means that the extreme range of deaths has been only from about 999,970 to 999,995, and the average range only from about 999,987 to 999,993. This indicates a degree of compensation which is remarkably close by any standards. In contrast, recruitment to the haddock population over thirty year-classes has varied over an extreme range of 500-fold (Parrish, 1956, and unpublished data); this would seem to be consistent with the comparative lack of stability

shown by this population (Fig. 2). Although no long series of data are available for sole, it is known that recruitment to this population also can fluctuate widely, and this population is the one which shows the most definite evidence of a long-term trend. Thus the association noted earlier from Fig. 2 between the degree of long-term trend and the degree of short-term fluctuation about that trend, appears to be a function of the degree of compensation that occurs, in effect, between successive adult generations. Representative age-composition data cannot be extended to plaice younger than three years of age from market samples; but Dutch fishery scientists have carried out quantitative research vessel sampling of young plaice on the nursery grounds off the Dutch coast for some years. Their results have shown that the same low natural mortality rate mentioned previously for adult fish, of about 10 per cent per year, is found from the end of the first year of life onwards. The sampling did not cover fish younger than this, but it seems reasonable to conclude from this evidence that if compensation does occur among juvenile plaice it must be restricted to the first year of life, or else that it must be concerned in some way with the reproductive processes.

COMPENSATION IN THE REPRODUCTIVE PROCESSES OF PLAICE

In many fish, including plaice, fecundity is closely proportional to body weight (Simpson, 1951), so that if the sex ratio remains constant the total weight of the adult population can be taken as an index of the total number of eggs deposited during each spawning season. In fact, the increases in adult populations of plaice resulting from the cessation of fishing during the war were made up of a relatively greater increase in males than females, because the former are more susceptible to fishing and so responded more when fishing stopped (Wimpenny, 1953). Nevertheless, the data of total adult population weight shown in Figs. 3 and 4 can be taken as roughly equivalent to the total egg production. When compared with this range of egg production, the effect of the retardation of growth on fecundity noted previously, which probably reduced the fecundity at age by about 15-20 per cent, seems of little practical significance as a compensating mechanism.

It is possible, however, that compensating mechanisms may occur in the spawning processes, quite apart from the total number of eggs produced; one of these is that the extent of the spawning area may itself change with the size of the mature population and give rise to compensation. North Sea plaice spawn in two main areas, in the Heligoland Bight and in the Southern North Sea. The distribution of eggs in the latter has been mapped by Hensen net sampling in a number of years, and it has been established that the eggs

are concentrated towards the centre of an oval-shaped area extending about 100 miles north-eastwards from the Straits of Dover and about thirty miles across at its widest point. This zone coincides with certain clearly defined environmental conditions, notably with the main area of relatively clear and saline Atlantic water that flows into the North Sea through the Straits of Dover, and eventually enables the young metamorphosed fish to reach the inshore nursery grounds along the Dutch and German coasts. It is not unreasonable to suppose that if conditions of high adult population density resulted in a spread of the spawning area, the chances of survival of those larvae outside the normal area might be quite sharply diminished. In the

FIG. 5.—Distribution of plaice eggs at peak spawning in the Southern North Sea, in two contrasting years of total egg-production.

extreme case, if the area of spawning increased in proportion to the total number of eggs deposited, and the survival outside the normal spawning area was nil, complete compensation would result with any increase in adult population above a certain limiting size.

The plaice egg surveys conducted in the Southern Bight by Buchanan-Wollaston and later by Simpson (see Simpson, 1959, for a general account) enable this possibility to be tested. Fig. 5 shows the contours of egg density at peak spawning in two contrasting years, 1937 and 1947, when the total egg deposition was very different. It is seen at once that the total area within which eggs were found was very similar in both years, and that the greater egg deposition in 1947 resulted only in an increased density of eggs, with the centre of concentration at much the same place. The data for all available years are combined in Figs. 6*a-c* to show the same conclusion in graphical form. In Fig. 6*a*, only a slight tendency is seen for the area in which eggs

FIG. 6.—Relation between total egg-production of plaice and (A) egg distribution, (B) egg density and (C) overspill into the English Channel.

are found at peak spawning to increase with total number of eggs. The corollary of this is that there should be a closely proportional relationship between average egg density and egg numbers, which is seen to be the case in Fig. 6*b*. Even the proportion of eggs deposited beyond the Straits of Dover seems to be independent of the total egg deposition (Fig. 6*c*), although this 'overspill' has been surveyed only on a few occasions. Therefore it seems

that the possibility of compensation arising through an increase of spawning area with population size can be rejected, at least for plaice.

There are, however, other ways in which compensation may possibly occur in connection with the spawning processes, although these cannot so readily be tested. Direct interference in one or other stage of the spawning act, if the adults become too crowded, can occur in fish such as salmon, where a fairly elaborate behaviour pattern is involved and the extent of the spawning beds may be very restricted. There is only one recorded observation of the spawning behaviour of plaice (Forster, 1953), but this does not suggest that any very elaborate behaviour pattern is involved. There are also instances in which overcrowding of eggs reduces the efficiency of hatching, as has been shown, for example, by McKenzie (1947), for smelt; but even the peak concentration of plaice eggs, which are dispersed throughout the water column, seldom exceeds two per cubic metre, and this hardly seems likely to be a lethal concentration. A further possibility is that although the growth of adult plaice has not been greatly influenced by large changes in population density, the ability of the females to produce healthy and viable eggs may have been much more affected. Certainly, the condition factor of mature females, i.e. the ratio of weight to length, was some 10 per cent lower immediately before the spawning seasons of 1946 and 1947, when the density was high, than during pre-war years, but it is not known whether such a change could have affected adversely the viability of eggs. It seems, *a priori*, rather unlikely that this could have been solely responsible for the graded degree of compensation which appears to exist over such a wide range of population density, but the possibility that it may be a contributory factor at the highest densities cannot be ruled out.

COMPENSATION DURING THE EARLY LIFE OF PLAICE

Apart from these uncertainties concerning some of the events associated with spawning, it seems therefore that the main compensation in plaice occurs at some time during the first year of life. It has, of course, been suspected for a long time that a very heavy mortality occurs in many marine species during the first few weeks after hatching (Hjort, 1914), when the young larvae are susceptible to relatively small changes in environmental conditions that would be of little or no significance a few months later in life. In a few instances the incidence of larval mortality has been followed quantitatively; for example, by Sette (1943) for Atlantic mackerel (*Scomber scombrus*), and by Ahlstrom (1954) for the Pacific sardine (*Sardinops caerulea*), but there does not yet seem to have been a study in which the contribution of the various causes of death to the total mortality rate has been measured. Yet a distinction

between the causes of mortality is important in the search for possible compensating mechanisms. Adverse water temperature, for example, acting either directly or indirectly (e.g. through a disturbance of osmotic balance) may well be responsible for a substantial part of the mortality of plaice larvae; but unless the mortality *rate* it causes increases with larval density, and vice versa, it cannot act as a compensatory mechanism. Predation is probably another major cause of larval mortality; but again, for predation alone to be an efficient compensating mechanism, the density of predators must be closely correlated with that of the larvae. An obvious way in which this could happen is through cannibalism of the larvae by their parents (Ricker, 1954), which was probably the main cause of compensation in the experimental guppy populations studied by Silliman & Gutsell (1958) and discussed by Gulland (this Symposium). Cannibalism of juveniles is known to occur in a number of the more predatory marine species such as cod and hake, but it is by no means clear whether cannibalism is of any general significance as a compensating factor in natural fish populations. Cannibalism has not been recorded in plaice where, in any event, the adults are demersal but the larvae are pelagic. The possible compensatory nature of interspecific predation of plaice larvae, however, certainly cannot be disregarded. Small planktonic predators such as *Sagitta* may be able to reproduce *in situ* fast enough to have some compensatory action, either through the direct effect on their reproductive rate of the contemporary supply of plaice larvae as food, or else indirectly as the result of variations in the supply of other food organisms that also influence the survival of the plaice larvae. Certain pelagic fish are present in the plaice spawning area when the larvae are present, notably herring returning from their spawning grounds at the entrance to the English Channel. Plaice eggs have been recorded in herring stomachs (Hardy, 1924); plaice larvae have not, but this may only be because most of the observations on the food of herring refer to times and localities at which plaice larvae would not be present, as there are many records of herring eating pelagic larvae or post-larvae of other fish species (Savage, 1937). Whether the abundance of plaice larvae is sufficient to cause herring or other fish to aggregate on them is not known, but it may not be without significance that in the years towards the end of the war and immediately after, when the density of plaice larvae must have been at its highest and the degree of compensation evidently most marked, herring were also several times more abundant than usual in the Southern North Sea.

Another important cause of death among fish larvae in many cases is undoubtedly a shortage of food, and a quantitative relation between larval mortality and abundance of food has been demonstrated for several species (see Beverton & Holt (1957) for a summary of literature). Plaice are highly

specific in their feeding habits, their preferred food being *Oikopleura* which is not particularly abundant in the spawning area when the larvae are present and is rather patchily distributed; Shelbourne (1957) has shown, in fact, that at times when the abundance of *Oikopleura* is lowest the condition of the larvae is poorest.

Intraspecific competition among fish larvae for a limited food supply could act as a compensating mechanism in several ways. Insufficient food could be a direct cause of death, and it is a common experience when attempting to rear marine fish such as plaice from eggs that adequate feeding by the newly hatched larvae is critical for their survival. The effect might also be indirect; a shortage of food that is not severe enough to cause death by starvation but affects adversely the condition of the larvae would be expected to make them more susceptible to other factors which might not have otherwise been lethal. Thus Shelbourne (1957) has shown that starving plaice larvae may die through a loss of their osmoregulatory powers, so that physical factors such as temperature and perhaps salinity, that are not directly density-dependent in their action, might become so in conjunction with a lowering of the condition of the larvae caused by competition for a limited food supply. This is an example of the point made by Chitty (1960) in reconciling the apparently conflicting ideas of Nicholson and of Andrewartha & Birch, that causes of death which in themselves are not directly density-dependent may become so indirectly if the susceptibility of the population to those causes is influenced by its density. Ivlev (1955) has made a detailed experimental study of what he terms 'the ecology of starvation' and has shown, for example, that fish whose condition has been lowered by a shortage of food become more vulnerable not only to adverse physical conditions of the environment but also to predators; again, this means that competition among the larvae for food may cause predation to have a compensatory action without there necessarily being any change in the number of predators. Even if shortage of food did no more than delay the attainment of metamorphosis and so prolong the duration of the pelagic phase, it would allow those causes of death which operate during the larval phase to take a correspondingly greater toll and so to have, indirectly, a compensating effect.

CONCLUDING REMARKS

Although it has been possible to eliminate some of the mechanisms that, in theory, might be responsible for or contribute to the marked degree of compensation that seems to characterize the long-term dynamics of the North Sea plaice population, it is clear that no firm positive conclusions can

be reached at the present time. The weight of available evidence points to the pelagic larval phase as the critical one, with the direct or indirect consequences of competition for food among the larvae as the basic mechanism; yet it has to be admitted that most of the evidence brought forward in support of this is inferential. It has not yet been demonstrated conclusively, for instance, that the consumption of *Oikopleura* by plaice larvae is the main factor responsible for reducing the abundance of *Oikopleura* to the point at which the survival of the larvae is adversely affected, although this is perhaps the essential test. Again, there is little quantitative information about the early demersal life of plaice from the time they metamorphose and terminate their pelagic phase until they first appear in samples taken close inshore some months later. The reason for this is primarily the practical problem of sampling quantitatively for juvenile plaice of only a few millimetres in length while they are still dispersed in relatively deep water, and such relevant information as exists on this phase of the life-history comes, in fact, from experimental studies on the rearing of plaice (Shelbourne, personal communication). These show very clearly, nevertheless, that the mortality rate of plaice larvae is much reduced after metamorphosis; they become progressively more resistant to adverse environmental conditions of all kinds which would have been lethal before metamorphosis, and in particular are much less susceptible to variations in the kind and amount of their food supply. Of course, this does not prove that compensation does not occur during this early demersal phase in the sea, and it may be that the concentration of the juvenile plaice in coastal waters that occurs when they are a few months old gives rise to compensation, despite their greater resistance to adverse conditions. Nevertheless, the evidence is perhaps sufficient to justify exploring more thoroughly in the first instance the dynamics of the pelagic phase which, difficult though it is to attack, is more accessible to quantitative study than is the early demersal phase.

Some of the many questions which need answering in the search for compensating mechanisms in the pelagic larval phase have been touched on previously, but there is one particular feature of the relationship between adult population size and number of surviving recruits in plaice which may be of special significance. It is that over the wide range of adult population size that has occurred, there is no clear evidence of what may be called 'over-compensation', that is, of the higher adult densities resulting in a reduced number of progeny. The same is true for most other marine fish populations so far as can be judged from existing data. There is probably some tendency towards over-compensation in certain salmon populations, where the spawning grounds and environment for the young are much more restricted than in marine populations; but the only striking evidence of this

phenomenon comes from certain experimental populations maintained under conditions which cause certain compensatory mechanisms to become particularly pronounced, such as cannibalism in the case of the guppy populations cited above and fouling of the medium in the case of certain insect populations kept under crowded conditions (Ricker, 1954).

The indication that the compensatory processes in the plaice population are of a kind which tend to result in a roughly constant number of individuals surviving at the end of the phase of compensation, irrespective of the number entering it, has a bearing on the kind of mechanism responsible. It seems that to produce an end-result of this kind, the system must contain elements of heterogeneity. For example, if all the larvae from a year's spawning were competing on equal terms for a limited food supply, it would be expected that above a fairly sharply defined limit of larval abundance there would be mass starvation and something approaching a catastrophic mortality. The fact that this does not appear to happen may be because the larvae are hatching over a period of time, so that the larval population at any one place and time consists of individuals at all stages of development from newly-hatched larvae to those approaching metamorphosis. Thus it may be that the larvae hatching during the first part of the season find sufficient food awaiting them and survive well, whereas the later arrivals find a depleted food supply and suffer accordingly; this could lead to a roughly constant total number of survivors, depending on the variability of the food supply. Again, if competition between larvae for food is indeed the basic mechanism responsible for compensation, whether the effects are direct or indirect, the fact that the competing larvae are in various stages of development may result in the older and more active larvae surviving at the expense of the younger and weaker ones. This might also be expected to reduce the likelihood of a catastrophic mortality at high larval densities, especially when taken in conjunction with the fact that the larger larvae are able to eat the larger *Oikopleura* which the smaller larvae cannot.

Whether the kind of compensatory mechanisms suggested here for the pelagic larval stage of North Sea plaice are likely to be of general occurrence in other marine fish populations cannot be established on present evidence. A high larval mortality rate is probably common to all species which have a high fecundity and whose eggs or larval stages are pelagic; but this is no proof of compensation, as exemplified by haddock and sole where the larval mortality rate is probably of a similar order of magnitude to that of plaice. What does seem to be emerging as something of a generalization among marine fish is that if compensation does occur it is not to be found to any extent within the adult phase of the population as such. Neither does it seem that fecundity alone is of general significance in this respect, despite the fact

that it has been shown to exhibit changes in response to environmental conditions which would seem to have an adaptive value (Nikol'skiĭ, 1950), unless there is also a fairly clear relation between egg-production and number of surviving progeny, and this has seldom been established in fish. The various phases of the life-history of a fish species constitute virtually independent systems. The interactions within a population of larval fish, for example, and between that population and its environment, both physical and biotic, are entirely different from those of the adult fish; and it is evidently possible, as in plaice, for the density of the adult phase to be little influenced by environmental restraints and yet for the population as a whole to be kept closely in check by compensatory processes confined to an earlier stage of the life-history. Quantitative studies on the adult phase of exploited fish populations have advanced a good deal in recent years, due partly to the ease with which age can be determined in many species and to the wealth of information which can be obtained directly or indirectly from commercial catches and fishing activity. Perhaps as much or more is known about their dynamics as about those of any other group of natural populations; yet it seems that a real insight into the long-term dynamics of fish populations can come only from a better understanding of events during the earlier stages of the life-history in relation to the environment.

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DISCUSSION

J. A. GULLAND: Slobodkin's equation for experimental populations gives rise to the following relationship:

$$\frac{P_F}{P} = 1 - \frac{F}{2 - F}$$

Can this be applied to exploited fish populations and the same answer obtained? Some rewriting is necessary since the terminology is different: thus F , which is the proportion of young fish, is equivalent to $F/F + M$, and when re-written in my terms, we have:

$$\frac{P_F}{P} = \frac{2M}{F + 2M}$$

Represented graphically the relationship is comparable with the diagram presented for west of Scotland hake populations (Gulland, Fig. 1, p. 207). For North Sea plaice it is known that exploitation has led to a tenfold decline therefore

$$1/10 = \frac{2M}{F + 2M}$$

hence

$$F = 18M$$

It is also known from age composition data that the total mortality, $F + M$ = 0.7, hence

$$M = 0.039$$

The value of M usually taken, based on other evidence, is 0.1, which is a fair measure of agreement considering the rough nature of the approach.

G. V. NIKOL'SKIĖ: Do you consider that the stock of plaice may be determined very early in life, by the amount of food available for the stages immediately after metamorphosis?

R. J. H. BEVERTON: For the North Sea the data are not sufficient. Certainly once metamorphosis is completed the fish appear much more hardy. It is the pelagic phases which seem, on circumstantial evidence, to be the sensitive ones.

T. B. REYNOLDSON: Beverton does not seem to have taken changes in fishing efficiency into account, and in this his approach seemed to differ from

that of other speakers who related catch to effort. Could efficiency changes be related to changes in his abundance curves?

R. J. H. BEVERTON: I was using catches, and not more refined measures of population, which are not available for the sixty-year period under consideration. There does not seem to have been any great overall change in fishing pressure in this period, and I believe that the trends indicated are genuine ones. The catch per unit of effort could be determined for the past thirty years, but this treatment would emphasize the post-war bulge.

G. V. NIKOL'SKIĬ: I do not agree that Slobodkin is right when he says that the populations he has been studying are of no economic importance. *Daphnia* is a most important food organism for fisheries.

I think that for many predator-prey relationships, however, the mathematical models must be different, to take into account the existence of real predators in contrast to the method of abstraction of animals used by Slobodkin.

L. B. SLOBODKIN: I am using 'predation' in a simple sense. The only biological feature of my predator is that it takes *Daphnia*.

W. EDMONDSON: I am not sure that Slobodkin is a very abnormal predator. It may be that he takes only big or small animals, but many natural predators, like *Chaoborus*, are highly selective.

L. B. SLOBODKIN: But the degree of predation in my case is not related to previous predation. My own population dynamics are in no way dependent upon those of *Daphnia*!

M. E. SOLOMON: One of Beverton's graphs showed a rise in the plaice population during the war. Later, I think he stated that competition for food among the newly hatched animals was the key factor. Surely these statements are contradictory? With less fishing there should be higher egg production and so no population rise, or even a decline!

R. J. H. BEVERTON: The war-time rise in population was due to the fall in adult mortality from 50-60 per cent per annum under fishing conditions, to about 10 per cent per annum. This caused a rise in the total population, but the size of the individual year classes was unaffected: the bulge was thus largely due to improved adult survival.

M. E. SOLOMON: And what happened after the war?

R. J. H. BEVERTON: The sizes of year classes hatched during the war were about average: despite very abundant egg production the same number of recruits came through. Thus there is definite evidence that regulation occurs after hatching.

A MILNE: Is predation, especially on young fish, important?

R. J. H. BEVERTON: Predation on adult plaice is probably slight; at least there are no indications that they are eaten to any significant extent

by other fish. Young plaice, especially in their planktonic phase, must be eaten by a variety of predators, but on present information it is not possible to say whether the mortality from this cause is important or whether it has a controlling influence. For this latter purpose the mortality need not, of course, be directly density-dependent; intraspecific competition among the plaice larvae for food, retarding growth, lowering their vitality and prolonging their pelagic phase, and so exposing them to predation for a longer time, could also act as a controlling mechanism. It is very difficult to assess the likely cause at present.

A. C. SIMPSON: Sette, working on mackerel in America, has shown that a large initial hatch is followed by a steady decline, which makes predation seem probable (Sette, 1943). But more data are needed.

I. A. McLAREN: *Pseudopleuronectes* (winter flounder) populations have been studied at Yale, in parallel to Sette's work. Early mortality has been attributed especially to predation by *Sarsia*, and the loss may reach up to 25 per cent per day, in ten-day-old larvae.

S. J. HOLT: Both Beverton and Slobodkin have described experiments with artificial populations conducted to improve understanding of the dynamics of wild populations. Their experiments are of course of different types — in the former case specific parameters of individual activity are related to other characteristics of the individual: in the latter the experimental population is studied as a whole. Nevertheless there is a common problem of determining which aspects of the experimental results are likely to be applicable to wild populations, and which are not. This problem will become more acute as biologists wish to measure more, and more complex, characteristics of populations, and resort to the use of convenient artificial populations for the purpose. Now by analogy with the subject of anatomy, we see that one result of comparative studies is to conclude that a rat and a man are in many respects more like one another than either is like a turtle, so that since we cannot conduct certain pharmacological tests on men we first test rats. Our problem in population dynamics may be to identify those characteristics of populations which we may extrapolate to other populations, and those which we may not. This particular need may help guide our attempts to establish a comparative method in our field.

L. B. SLOBODKIN: My own experiments are always designed in relation to the field situation. In nature, estimates of the efficiency of ecological processes are only possible with a fairly wide margin of error, owing to the many assumptions necessary, but values from the field fall within a range of 5–15 per cent. This can be interpreted in many ways: it might be held that all estimates of ecological efficiency from nature are essentially the same figure, blurred by the sampling technique. If so, any species taken into the

lab. and studied should yield a steady value lying within the field range but much more definable. This did happen in *Daphnia*. A coarse field estimate may be used to give an idea of a *range*, and a species can then be selected and studied in the laboratory to clarify the picture. Laboratory studies are also valuable if a species or system can, under such conditions, be examined outside its natural range. Furthermore, some phenomena may be demonstrated not to occur in the lab. under conditions which permit the assumption that they also do not occur in the field.

R. J. H. BEVERTON: I think Slobodkin's approach and my own are complementary. His system is a more complete one: mine takes a natural system and attempts to break it into functions.

D. CHITTY: In experimental work on populations of small mammals a great deal of confusion has arisen from failure to appreciate the point made by Slobodkin. It may be possible to refute hypotheses in the laboratory; but it is a serious error to assume that what happens in the lab. is necessarily relevant to the field. Just as field data should suggest experiments, so the experiments should provide lines of thought which should be rigorously tested in the field.

Even in the laboratory it is extremely hard to determine causes of death; in the field it is often impossible to find the corpses. A common error is to suppose that because population size is sometimes related to food resources that surplus animals therefore die of starvation. There is no more justification for such an inference than there would be for saying that animals die of cold or damp simply because population size might be related to temperature or relative humidity.

E. D. LE CREN: It is always hard to tell why an animal dies. But is the precise cause important? Suppose that in a dense population there is a 10 per cent survival of young, and in a sparser one, 50 per cent survival. Then the rate of survival will be proportional to density, tending towards the maintenance of a constant number of individuals. A starved fish larva may survive in a perfect artificial environment when it would fall easy prey to a predator in nature. The slow growth which Beverton showed in a crowded population results in longer exposure to a predator, but the two are alike consequences of limited resources whatever the nature of the actual mortality controlling numbers.

Field experiments may not be feasible working with large populations in the whole North Sea, But under some conditions, as in small streams, or lakes, they are possible and may provide guidance as to the soundness of the extrapolation from the laboratory to the full-scale field problem.

K. R. ASHBY: It is certainly hard to define causes of death. People

working with trout find that even when food is abundant a proportion of the slower growing animals stop feeding, languish and die.

W. E. FROST: I'm afraid this certainly occurs in some hatcheries! Could the cause of mortality among some young fish be however taken one stage further — and looked at in terms of behaviour? Are plaice territorial on the sea bottom? If they are always chivvying one another for niches on the sea bed, the weaker might be displaced to poor feeding stations. Trout are certainly territorial in this way — are plaice?

R. J. H. BEVERTON: We know very little about the first few months in the life of plaice after they have settled. It would be surprising if they were territorial at that age. They are very widespread all along the coastal belts, and while they might be territorial on a micro-scale, they are all very much at the mercy of the currents.

J. G. SKELLAM: It has been indicated that there are four levels of abstraction in the series: model — laboratory experiment — field experiment — observation of nature. The laboratory experiment appeals to the theorist because the correspondence between mathematical model and controlled experiment can often be very close indeed. Though it may be reasonably safe to extrapolate the general pattern of results, caution is required in using the parameter values. Experience gained in the industrial field shows that scale factors do affect the parameter values, for it is known that the optimum conditions for a small-scale laboratory experiment are sometimes markedly different from those which apply to a full-scale industrial plant. My view is that we need to have work done at all four levels.

L. B. SLOBODKIN: Laboratory experiments certainly have many of the properties of mathematical models, but the animal is left with freedom to think of things that would never occur to mathematicians!

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ON SOME ADAPTATIONS TO THE REGULATION OF POPULATION DENSITY IN FISH SPECIES WITH DIFFERENT TYPES OF STOCK STRUCTURE

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The dynamics of the number and biomass of animal populations is a complicated process of adaptive interaction of a population and the changing conditions of its existence: when studying the population dynamics of any organisms the knowledge of the character of adaptive response of a population to the change of the conditions of life is as necessary as the knowledge of the character of the change of these conditions. Unfortunately, until lately the forms of adaptive response of the population to the changes of the conditions of life have not been paid due attention.

Only in the two most recent decades have a number of papers connected with this field been published (Severtsov, 1941; Vasnetsov, 1947; Svårdson, 1949; Monastyrskii, 1949, 1952; Nikol'skiĭ, 1950, 1953 *et al.*; Lack, 1954; Naumov, 1955; Beverton & Holt, 1957; Le Cren, 1957; Alm, 1959; *et al.*). These papers were devoted to the analysis of forms of the adaptive response of the populations of different animals to changes in their conditions of life, primarily to changes in food supply at different developmental stages. (Under food supply I mean not only the food available in the basin, but also the conditions necessary for its procuring and assimilation.)

As far as I know, S. A. Severtsov (1941) was the first to note that the type of dynamics of the stock of a species (i.e. the age composition of the population, the time of maturity, fecundity, the sex ratio) is characteristic of a species and reflects the character of its adaptations to the environment.

S. A. Severtsov was right in saying that the population dynamics of a species could be called a focus at which all its peculiarities were reflected; they were the result of all aspects of its ecology (i.e. reproduction, feeding, growth, mortality) which in turn are determined by the adaptations of the species. The type of stock dynamics, like the other properties of a species, is developed in the course of speciation. The character of the dynamics of the species population, naturally, can undergo changes within certain limits,

in connection with changes in the conditions of life. The changes taking place in the structure of some species populations and in their reproductive rate have not only arisen fortuitously as a result of the effects of external influences on deviations, but are as well the result of the adaptive response of the population to the change of conditions of life.

Fish, like other organisms, establish adaptations which allow the population to increase its density rapidly with an increase of food supply, and to slow down the tempo of reproduction (or to decrease the population density in some other way) with the decrease of food supply (even when the decrease in food is due to an increase in the population density). The ability to change the intensity of reproduction is expressed in different species in different ways. A change in reproductive ability can be realized in different ways: through a change in rate of growth and in the time of maturity, and through an alteration in fecundity in individuals of the same size. Thus there is achieved either an increase or a decrease in the number of eggs laid with the change of food supply.

The timing of approach to the spawning grounds and the difference in the quality of the ova produced by spawners of different sizes and ages is an important adaptation to the regulation of population. Fish possess a diverse system of adaptations for the protection of their population under unfavourable conditions of food supply. This system includes transition to feeding on their own young, the preservation of a high quality of gonad products under unfavourable feeding conditions, the change of variation amplitude of those characters and properties of the population which make it more eurybiotic, as well as others.

ALTERATION OF THE GROWTH RATE AND THE TIME OF MATURITY

The growth of fish was shown by V. V. Vasnetsov in a series of his investigations (1934, 1947, 1953*a*, 1953*b*, 1958) to be an important adaptation, closely connected with the character of the dynamics of the stock. In considering the phenomena in general, one can reveal the following regularities: in fish protected against their predators by various armaments (spines and plates), the growth preceding maturity is as a rule slower than that of fish lacking armament; different populations of one and the same species under conditions of different intensities of predation grow differently. It was shown by V. S. Kirpichnikov (1943), that the young of Aral carp decrease their linear growth under deteriorating food supplies; but during this decrease, reserve substances are accumulating in their organs to provide for hibernation. The young of Amur carp, on the contrary, continue to grow, which growth decreases the

influence of predators, as the Amur predators (especially those belonging to the Chinese lowland complex) feed chiefly on small fish. The absence of the reserve fat products in the organs of young Amur carp makes them feed in winter too.

Thus, the decrease in the growth rate itself usually leads to a decrease in the population, as a result of the increased influence of predators; in the case of the increase in the growth rate, the effect of the predators weakens, which results in increased survival of the population.

V. V. Vasnetsov showed (1934, 1947) that the time of maturity in most fish (excluding the formation of dwarf forms), is connected with the achievement of a definite length. The maturity is correlated to a greater extent with the size than with the age of the fish. This thesis is confirmed by the observations of Monastyrskii (1940) on the Caspian roach and by ample data of Alm (1959) on many fish species.

There are many well-known examples of an alteration of the time of maturity as a result of an alteration in the growth rate under the influence of food supply, including the cases when population density changes under the influence of a fishery. An increase of the growth rate and earlier maturity can be observed in species acclimatized in new water bodies. In the latter instance it ensures a more rapid increase of the population density and its naturalization in the new basin. When the acclimatized population reaches a certain population density, the rate of the fish growth becomes slower, the maturity is attained later and the rate of reproduction decreases.

Apparently, in most species of commercial fish the changes in the population density are connected with changes in the growth rate of individuals and with the time of maturation. This has been noted for sturgeons, herring, salmon, cod, carp and many others. So, according to the data obtained by Chugunov (1927), as a result of the fishery decrease during the war of 1914-19, the growth of sturgeons slowed and the rate of their reproduction decreased.

The growth rate of sterlet and of some other fish of the European part of the U.S.S.R. considerably altered during the period of two most recent millenniums, which is, undoubtedly, connected with the intensification of fishery (Nikol'skii, 1958; Lebedev, 1960) and the increase of their food supply.

In the case of the salmon, the data on the relation of the time of maturity to the stock density are presented by I. B. Birman (1951) for the autumn form of Chum salmon of the Amur.

Some interesting data were obtained on the change of the growth rate and the time of maturity of small whitefish (*Coregonus albula* L.) acclimatized in some Ural lakes; and also on the change of growth rate of Sevan trout (*Salmo*

ishchan infsp. *gegarkuni*) acclimatized in Lake Issyk-Kul in Tien Shan (Luzhin, 1956). The growth rate of both acclimatized species accelerated and the time of maturity became earlier. The change of reproductive ability was observed in a herring stock in the southern part of the North Sea, as a result of the alteration of the time of maturity in post-war years (Cushing & Burd, 1957; Nikol'skiĭ & Belyanina, 1959).

There are many examples of the alteration of reproductive ability in populations of Cyprinoid fishes. There is a direct correlation between the density of North Caspian bream, its rate of growth and its time of maturation. Of course, the growth rate and the rate of maturity of Caspian bream, as well as those of other fish, are connected not only with the density of its population. They depend to a considerable extent on the change of the biomass of its food organisms, which in its turn, is related to the character of the river flow. This interrelation between the stock density and the biomass of food benthos, is shown rather clearly (Zemskaya, 1958). The number of individuals of Caspian bream attaining maturity can be doubled in succeeding years. The same was observed for the Caspian roach by N. L. Chugunov (1928).

The increased rate of maturation and younger age composition of maturing recruits under favourable conditions of development, results in a rapid increase of the population density. At the same time the wider age range of the series of matured individuals provides greater stability in the size of recruitment and decreases the influence of poor brood years.

In fish with a short life cycle, e.g. in lake smelt (*Osmerus eperlanus eperlanus* morpho *spirinchus*) the changes in the rate of maturity can also be rather considerable and can be connected with a serious alteration in the stock structure (Lapin, 1960). In unfavourable years the development of lake smelt can be delayed to such an extent that no spawning takes place. Under favourable conditions of food supply, however, the whole generation can attain maturity in a year, which ensures a rapid increase in stock, the development of the eggs and young being successful.

We have just considered that type of alteration to the reproduction rate of a population when the size of individuals attaining maturity remains more or less the same, but the age of maturity and the age composition of recruitment undergo change. The second form of response of a population to a change in the conditions of life — a lower food supply, and apparently a higher mortality rate — is the change in the size at which maturity is attained.

In this case fish attain maturity at a smaller size and at an earlier age. Such an alteration in stock structure provides a more rapid restoration of the population, which can therefore exist under more variable biotic conditions

and thus ensure its reproduction under a poor food supply. If under conditions of poor food supply a population attained maturity at a size larger than that typical of the given species, then it could not be able to provide for its survival and would perish (Lapin & Yurovitskiĭ, 1959; Alm, 1959).

This case was analysed for the first time in Russian literature by Vasnetsov (1947), who exemplified it by slowly growing populations of a common crucian carp. To this group of phenomenon belongs the formation of dwarf lake and river forms of salmon (both *Salmo* and *Oncorhynchus*) (Kozhin & Protasov, 1959; Moiseev, 1957; Smirnov, 1959 *et al.*) and the formation of freshwater populations of smelts (both *Osmerus* and *Hypomesus*). Among the Cyprinoids, as well as the crucian mentioned above, is the formation of slow-growing precocious forms of semi-migratory roach (*Rutilus rutilus caspicus* Jax.) and bream (*Abramis brama* L.) in the lakes of Uzboi. Unfortunately as yet the physiological mechanism of these changes in stock structure is not exactly clear. It is undoubtedly connected with metabolic changes, but evidently not only with the quantitative aspect of food supply, but also with the alteration of its quality, which, in its turn, somehow alters hormone activity (Alm, 1959). Within these slowly growing populations the same mechanism as that described above continues to act: a rapid growth and an earlier maturity under a better food supply, and a slower growth and later maturity under a poorer food supply.

FECUNDITY ALTERATION IN THE INDIVIDUALS OF A POPULATION

An alteration in the growth rate of fish and the time of their maturity is usually connected with a change in their fecundity. As is shown by many investigators (Svårdson, 1949; Nikol'skiĭ, 1950; Ioganzen, 1955; Yurovitskiĭ, 1958 *et al.*) fecundity of the individuals of a population varies adaptively in relation to changed conditions of life. Many examples are known when a change of food supply is associated not only with a change of growth and the time of maturity but also with an alteration in fecundity in fish of the same size. A similar phenomenon has been noticed in one population of the Sakhalin herring (*Clupea harengus pallasii*) (Piskunov, 1952), in the North Sea herring (Nikol'skiĭ & Belyanina, 1959), in the North Caspian semi-migratory roach (Chugunova, 1951), and in the North Caspian common carp (Sokolov, 1933). In all these cases the improvement of food supply leads to an increase in fecundity in individuals of the same size. This fecundity increase can be reached either by an increase in the volume of the gonads or by a decrease in egg size. In the latter case, if the density of the yolk and the amount of fat in the yolk do not increase, some decrease of food supply for the developing organism takes place during its feeding on the yolk.

TABLE I. *Changes in stock fecundity in (a) Caspian roach in 1946 and 1947 (Chugunova, 1951) and (b) herring of the Southern North Sea (Hickling 1940 and Cushing).*

		Caspian roach							Total
		Size group (lower limit (cm))							fecundity
									of
		16.5	17.5	18.5	19.5	20.5			100 fish
1946	.	34,400	38,500	42,000	45,800	51,900	.		4,903,900
1947	.	19,700	22,800	29,400	32,000	40,200	.		2,460,500

		Herring of the North Sea									Total
		Size group (lower limit (cm))									fecundity
											of
		22	23	24	25	26	27	28	29		100 fish
1933	.	14,315	16,664	19,230	22,074	25,233	28,679	32,434	36,599	.	2,100,000
1956	.	18,000	19,650	28,320	31,590	36,760	40,680	43,400	38,900	.	2,800,000

How great the changes in stock fecundity can be is shown by the fecundity alteration in a spawning fish population (computed to 100 fish), Caspian roach in 1946 and 1947 (Chugunova, 1951) and herring of the southern part of the North Sea (Hickling, 1940 and Cushing's data) given in Table I. When computing fecundity of 100 individuals we have used the observed size composition of the spawning population.

Fecundity of the Caspian pike-perch is shown by A. G. Kuz'min (1958) to undergo some, though rather less, variation from year to year. As the result of these variations and of some changes of spawning population structure the average fecundity of the population of Volga pike-perch can change by as much as 1.8 times. These changes of stock fecundity certainly cannot smooth out all fluctuations brought about by changes in the conditions of existence that determine the survival of a brood, as in some species the size of a generation can vary greatly; but the changes mentioned above can exert a smoothing influence. An increase in stock fecundity, caused by an improvement of food supply which takes place year after year under favourable conditions of survival, provides a more rapid increase in the stock.

Fluctuations are certainly determined not only by the environment factors, but also to a great degree by the state of the population itself, in particular, by the quality of the roe; they also depend on the quantity of yolk and the amount of fat in the eggs, the latter being related to the food conditions of the mother stock in the previous year. As J. I. Cheprakova (1960) showed, for instance, the amount of fat in eggs of Caspian roach is connected to a great extent with the growth rate of fish for the previous year; fish growing more rapidly in the previous year, have a higher percentage of fat in their eggs.

Fluctuation from year to year in productivity is connected with different quantities of yolk and fat in the eggs of different fish species. Fish with a small amount of fat usually have greater fluctuations (e.g. herring, cod). Their larvae at the stage of transition from internal to external food can exist without external feeding for a rather shorter time (Soleim, 1942) than those of fish which have eggs with a considerable fat content (sturgeons, roach and some other Cyprinoid fishes). Naturally, the amount of fat in eggs is important not only as a food supply; it can have rather different functions, and in particular fat plays an important role as a hydrostatic organ in many pelagic eggs and fish larvae (Kryzhanovski, 1960).

The conditions of food supply for the parents in the year before the spawning, particularly the abundance of food (the development of plankton and benthos), has been shown by Nikolaev (1958, 1958a) to determine to a

TABLE II. *Comparison of the fecundity and fatness of 'fat' and 'lean' Baltic herring in different size groups (after L. E. Anokhina, 1959)*

Length of fish (cm)	Groups of fish by percentage of fat in dry weight		Fecundity (in thousands)	Fatness (in percentage dry weight)
10-14	Lean (< 20%)	.	5.9	14.1
	Fat (> 20%)	.	10.6	30.7
15-19	Lean (< 20%)	.	18.4	11.4
	Fat (> 20%)	.	20.8	33.0
20-23	Lean (< 20%)	.	37.9	12.3
	Fat (> 20%)	.	40.9	37.7

great extent the quantity of the generation of the next year in sprat, Atlantic-Scandinavian herrings, Baltic herring and freshwater smelt. The lack of knowledge of the state of the parental stock and particularly of the quality of its roe, makes it difficult to understand the causes of fluctuations. In some fish the fecundity of individuals in the population is connected with their fatness; fatter individuals usually appear to be more fecund. This has been noticed, for example, for Siberian sturgeon (*Acipenser baeri* Brandt) from the Ob' River by Petkevich (1951) and for Baltic herring (*Clupea harengus membras* L.) from Riga Bay by Anokhina (1959). As one can see from the figures presented in Table II fatter specimens of Baltic herring possess a higher fecundity. Hence the food conditions of many species during the preceding year seem to determine to a great extent not only the egg quality but the population fecundity for the next year.

It should be noted that some adaptations appear in fish to provide better conditions for gonad development under unfavourable feeding conditions.

N. P. Makarova (1961) showed that, under conditions of starvation, the fat carp consume to maintain their metabolism comes first from the intestine, then from the muscles and finally from the gonads. During the period of gonad development, the fatness in carp gonads undergoes less fluctuation than the fatness in any other parts of the body. The same phenomenon was noticed in some other fish (smelt, perch). This is an important adaptation, which, in the case of starvation, preserves, for a long time favourable developmental conditions for eggs in the body of the mother.

THE COURSE OF SPAWNING

An important adaptation to the self-regulation of fish population density is the character of spawning and the mode of arrival of the spawners on their spawning grounds. It was determined for some fish that the middle-aged individuals of the spawning population possess the greatest reserve of yolk in the egg and fat in the yolk. F. G. Martyshev (cited by Nikol'skiĭ, 1953) has shown that the diameter of the egg of common carp, the length of the larvae at the moment of emergence, and the weight of the yearlings before the autumn appear to be highest in fish of the mean age group (Table III).

TABLE III. *Size of carp eggs, embryos at the time of emergence, and of yearlings before autumn (after F. G. Martyshev)*

	Fish age (years)				
	17+	15+	8+	4+	3+
Average diameter of the egg (mm)	1.64	1.52	1.71	1.39	1.26
Length of embryo at the moment of emergence (mm)	8.18	6.40	6.41	5.05	4.80
Weight of fingerlings before autumn (g)	25.04	—	34.5	32.08	—

Thus, in common carp, the most viable offspring, best provided with food for the period of yolk feeding, are left by the middle-aged parents. A similar picture is found in the Amur lenok (*Brachymystax lenok* Pall.). The changes in weight of the egg of lenok with fish size are shown in Table IV, and it will be seen that in lenok, as well as in common carp, individuals of the average size in the spawning population have the largest reserve of yolk in egg.

In fish of the spawning population the relative amount of fat in the egg changes with age. Thus in the North Caspian roach the largest reserve of nutritious substances in the eggs is found in middle-aged fish; both in young

TABLE IV. *The change of the egg weight of lenok in the prespawning period (stage IV) in the Amur River*

	Size group of fish (cm)				
	40 — 50	50 — 60	60 — 70	70 — 80	80 — 90
Average weight of egg (mg)	30.0	52.6	62.1	59.9	

and in old spawning fish the fat percentage in the eggs is lower (Cheprakova, 1960) (Table V).

Age changes of sperm quality (and its changes in various portions of milt) are less well known. In Soviet literature the only data known to me were obtained by the workers of the institute of Pond Fishery and concern the sperm quality of roach at the beginning and end of spawning. These workers have shown that the last portions of sperm contain less spermatozoa and possess smaller fertilizing capacity.

TABLE V. *The amount of fat in the eggs of roach of different age (the mouth of the Volga, 1957; after Cheprakova, 1960)*

	Age (years)			
	3+	4+	5+	6+
Percentage of fat from dry weight of eggs	6.8	8.97	8.88	8.03

In connection with the above one can understand the adaptive importance of the character of the approach to the spawning grounds by fish and the order of spawning. The fish of older and middle ages are first to come to spawn in most species; it is they which possess roe of high quality, and their eggs are fertilized by the first portions of the sperm.

If there are many large-sized females, males spend most of the high quality sperm to fertilize their eggs. Younger females, which approach the spawning grounds later, are fertilized by the sperm of lower quality and the percentage of eggs fertilized from younger females often becomes lower. If the number of older females is less, successful fertilization of younger females becomes increased. Thus, individuals of younger age-groups, spawning for the first time, play the role of a reserve by providing stock recruitment when the population density of older fish is reduced. The problem of adaptive significance of the process of spawning has been little studied so far; however, it is of great importance for a rational fishery, particularly for planning the fishery regulation necessary during the spawning season.

FEEDING ON INDIVIDUALS OF THE SAME SPECIES

Accidental or regular consumption of individuals of the same species is known to take place in many fish species; in most cases it is the large-sized individuals which consume their own young (Klyuchareva, 1956). This mass consumption of their own young varies rather strongly from year to year. In years when the production of young is high but the food supply for large fish unfavourable, the consumption of their own young by the adults naturally decreases the density of the forthcoming generation. In some species (cod, navaga, common and Balkhash perch and others) the fry provide more than 50 per cent of the yearly consumption of food. The eating of the young usually takes place after that period of development (usually the period of transition from internal to external feeding) when the size of the generation is being determined. Naturally feeding on the young is not only a method of density regulation; in some species, e.g. in common perch, the feeding on their own young provides food in water bodies where the food supply for the adult fish is insufficient. Consuming its own fry, the adult perch through its young eats such food as small zooplankton which it is unable to assimilate directly.

In the rivers of the Far East the salmon die after spawning and their cadavers are well preserved till spring in the cold water. They then serve as an important food for the young of some species of Far Eastern salmon (e.g. the autumn form of chum salmon) during the river period of their life. But perhaps of much greater importance for the increase of food supply of these young, is not their direct consumption of parental cadavers, but the effect of these latter as fertilizers of feeding grounds. In the places where many cadavers of spawners accumulate in the rivers a rich fauna of the benthic invertebrates develops in the next spring; while in the river the young salmon exist partly on this fauna. As E. M. Krokhin has shown (1959), the amount of phosphates and plankton in the lakes of Kamchatka increase in the years that follow those when large numbers of red salmon (*Oncorhynchus nerka* Walb.) migrated into the lakes for spawning; an increase in the amount of plankton food for the young takes place as a result of the fertilization of the lakes by the cadavers. Thus, the generation of *O. nerka* which descends from a large spawning stock finds itself under more favourable conditions of food supply and its survival rate is increased.

This means that in spawning rivers of the Far East, the young salmon are to some extent provided with food at the expense of the food resources of the sea that have been accumulated in the bodies of their parents during the period of their life in the sea (Vastnetsov, 1953). The feeding of the young of the Far Eastern salmon on the parental cadavers is utilized for practical

purposes by the fish-culturists, who store the cadavers of the spawners and feed them to the young that are reared in hatcheries (Smirnov, 1954).

CHANGES OF AMPLITUDES OF VARIABILITY OF CHARACTERS AND PROPERTIES IN A POPULATION

As it has been shown recently by a number of workers, the amplitude of the variability of the characters and properties in a population changes adaptatively with changes in the conditions of life, including food supply (Nikol'skiĭ, 1955; Nikol'skiĭ & Pikuleva, 1958; Polyakov, 1958; Yurovitskiĭ, 1957).

It also holds for the variability in size in a fish population of the same age. Under favourable conditions the growth of individuals follows a similar course, and the range in size in a population is comparatively small. With the deterioration of food conditions, including an increase of population density, the variability of fish size in the population increases. These changes in size range with deterioration of food conditions can be exemplified by the data of G. D. Polyakov on a common carp population, reared in ponds with different food conditions.

Upon the deterioration of the food supply the range of variability in the size of the fish increases, the modal size shifts to the left part of the curve, but, at the same time, the growth of the largest fish is even faster and their size larger, than in fish under more favourable conditions of rearing. Such extension of the size range within a population of the same age (when some of the fish sometimes pass to the next developmental stage) is an important adaptation, which extends the types of food eaten. Larger fish change to feeding on food other than that taken by the younger ones. In populations reared under good feeding conditions no such deviation in the size and composition of food consumed is observed; all the fish feed on more or less similar food. Knowledge of such changes in the size composition of the fish in a population of the same age allows us, by the amplitude of the variability and by the value of the coefficient of the asymmetry, to judge the conditions under which the fish are being reared, as has been shown by G. D. Polyakov (1960).

An analysis of the year to year changes of amplitude in population variation shows in which year the population has had better or worse feeding conditions. Thus, for example, in bleak of the Uchinsk reservoir, the fish of the age of 1+ are less well provided with food than other age-groups. In fish of this age the range of size is greatest. Thus, one of the most important adaptations that provides for the survival of the population under unfavourable food conditions is the widening of the amplitude of the size variability.

This adaptation is present in marine fish populations as well. Shatunovskii

has shown (1961) that the yearlings of Baltic herring when feeding mainly on the stage V of *Calanus* appear to be better provided with food than those feeding mainly on stages I and II. In the first case the variation coefficient of the size appears to be lower — on average 11.85 (by five tests), and in the second case higher — 15.27 (by four tests). If, for the population as a whole, its density and biomass are determined, as a rule, by the food supply of the fish in the post-larval period of development, the survival of separate generations depends to a great extent on the food supply available for the earlier developmental stages as was found by T. F. Dement'eva (1953). Though naturally these phenomena are interrelated.

One of the forms of the adaptive response of population to the deterioration of the food supply is the increase of the diversity of the egg size, i.e. the increase of the difference in the yolk reserve in the eggs. L. E. Anokhina (1960) showed that the variability of the egg size in the White Sea herring (*Clupea harengus maris albi* Berg) was greater in lean fish than in fat ones (Table VI).

TABLE VI. Differences in the variability of egg size in Onezhskaya herring of different fatness (after L. E. Anokhina, 1960)

Group of fish	Percentage of fat		Egg size		t for difference between standard deviations
	Wet substance	Dry substance	Mean and standard error	Standard deviation	
For all fish between 14.5 and 16.5 cm in length					
Lean . .	3.22	—	4.35±0.23	0.69	3.41*
Fat . .	7.74	—	3.36±0.17	0.44	
For three years' fish between 14.5 and 15.4 cm in length					
Lean . .	3.16	14.82	4.03±0.09	0.24	8.17*
Fat . .	7.12	28.73	3.05±0.08	0.16	

* Both values of t are highly significant.

The mechanism of egg formation with different reserves of yolk was revealed by V. A. Meĭen (1940). He has shown that the difference between the yolk amount in different eggs of one and the same fish depends to a great extent on the position of a given egg with respect to the ovarian blood-vessels. Naturally, the greater the amounts of nutritive substances that enter the egg, the more favourable the conditions of yolk reservation that are created. In fish that are well provided with food all eggs receive a sufficient amount of nutritive substances to accumulate the necessary amount of yolk, and all the eggs appear to be more or less similar in size. Upon the deterioration of the food supply some eggs receive a larger amount of nutritive substances than others and thus the heterogeneity of eggs is brought about which was mentioned above.

What is the adaptive importance of the different sizes of eggs under unfavourable conditions of food provision. It has been shown that the embryos from different sizes of eggs hatch and change to external feeding at different times. Besides that, populations of embryos hatching with a range of different yolk reserves survive better under unfavourable conditions. This is clearly demonstrated by Nikitinskaya (1958) in the development of larvae of Sakhalin herring (*Clupea harengus pallasii* Val.). The same phenomenon was observed by A. V. Morozov (1951) in *Acipenser stellatus* Pall. The different rhythms of feeding at the stage of mixed feeding are connected with the differences in the reserve of yolk in the larvae when they hatch.

As was shown by Pikuleva-Grigorash (1961) for the roach of the Ucha water-body, those larvae that have a significant reserve of yolk at the stage of mixed feeding possess a clearly expressed diurnal rhythm of feeding, while the larvae that have a small yolk reserve continue feeding on the external food uninterruptedly; this also contributes to the more complete utilization of the food supply. A widening of the range of foods eaten is also achieved, as the smaller larvae are feeding on one kind of food, while larger ones are feeding on another kind. If larvae develop under unfavourable conditions of feeding this difference in size increases, while under favourable conditions it becomes less as the smaller larvae overtake the larger ones in size. The ways in which egg heterogeneity has adaptive importance are different with eggs laid in one batch or a single spawning and those laid in part of a spawning (N. V. Lebedev, 1959; G. V. Nikol'skiĭ, 1953) but most of these ways are connected with a better utilization of the food supply and thus with an increase in population density and biomass.

CONCLUSIONS

A knowledge of the forms of adaptive response of populations to changes in the conditions of life, and, particularly, to changes in food supply, is as necessary for a rational organization of a fishery, as is a knowledge of the changes in living conditions of the population. It is impossible to build up a rational fishery industry, based only on studies of the changes in living conditions, without trying to understand the adaptive response of the population. The fishing industry should be planned in such a way that it becomes a component of the environment of the species exploited, i.e. the rate of the industry's influence should not exceed the range of the adaptations of a species. The industry must provide the maximal productivity of the population exploited.

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THE EFFICIENCY OF REPRODUCTION AND RECRUITMENT IN FRESHWATER FISH

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INTRODUCTION

In the major marine fisheries it has been traditional to regard the relationship between the number of parents and subsequent number of young that are available for recruitment into the fished stock to be sufficiently tenuous to be ignored. In the management of freshwater fisheries, however, conservation of spawners has always been considered of great importance, and restrictions upon fishing have often been imposed with the object of protecting the spawning stock rather than preventing overfishing in the sense usually applied to marine fisheries (i.e. catching the stock before they have had time to grow to the optimum size). It is true that legal restrictions on fishing have often aimed at sharing the catch more equitably or preventing fishing by unauthorized persons; but in the background all the time has been the idea that conservation of adult stock is of fundamental importance, and sometimes this idea has become a sacred obligation.

In fact, very little indeed is known about the dynamics of the whole reproductive process in fish populations. Although there is some knowledge of the egg stage in salmonid fish and a considerable literature on the technology of fish culture, few observations have been made on the ecology of the young stages in the wild. Ricker (1954, 1958a) has reviewed the theory and literature on the relationships between number of parents and number of progeny and presented data from year-to-year variations in the runs of various Pacific salmon (*Oncorhynchus* spp.). Beverton & Holt (1957) have discussed this subject again and presented alternative theoretical curves. Real data, however, are still scanty and even where information on the numbers of eggs and resultant recruits are known, information from the intervening period on rates and causes of mortality is usually absent. An understanding of the dynamics of the whole reproductive and recruitment process is urgently needed, and is probably the largest gap in our knowledge of fish population dynamics.

The plasticity of growth rate and adult size in fish renders any considera-

tion of population dynamics in terms of numbers alone of limited value, and growth and biomass must also be taken into account. A useful parameter to estimate, as well as number, biomass, mortality rate, and growth rate, is the 'production', in the sense of the sum of the growth made by all members of the population regardless of their fate and whether they survive to the end of the period being considered. The production can be used as a yardstick for estimates of the efficiency of the 'yield' (whether it be the catch of a fishery, recruits or smolt migrants), and for estimating the food demands of the population. Information on the latter may be of particular relevance to some fresh waters where the size and productivity of the environment may be the main factor limiting the yield of fish.

The following paper discusses aspects and examples of the production of gonad products and the growth, survival and production of young stages, in a few freshwater species, and draws tentative conclusions about the action of some of the controlling factors and their relevance to an understanding both of natural population mechanisms and practical fishery management.

THE PRODUCTION OF EGGS AND MILT

Although growth studies of freshwater fish are numerous, few authors have studied the relationship between gonad weight and body weight, or taken into account the annual production of gonad products by fish as part of their 'production', or as a drain, together with increase in body size, on their assimilatory processes. It is interesting therefore to compute rough approximations of the total weights of gonad products shed by fish and to compare these with the total production in the form of growth in body size.

In Windermere before the fishing experiment started in 1941 the average annual increment in weight for adult perch (*Perca fluviatilis*) was 5 g (Le Cren, 1958). The rate of natural mortality (M) for males was approximately 0.44 and for females 0.32. The eggs just before shedding are 20 per cent of the total body weight and the milt 8 per cent (Le Cren, 1951). The fishing mortality (F) due to traps in 1941 can be estimated as roughly 1.52 for males and the catch for the North Basin is known as about 780,000 males. The average weight of adult males was 26 g and females 35 g, and, allowing for the proportions of II group males that are mature, and the probable relative populations in the North and South basins of Windermere, and assuming, which is reasonable, that growth and mortality are distributed through the year in an approximately similar way, rough estimates can be made of production. These computations give a production of adult perch for the whole of Windermere in 1940 of 23,700 kg, and about 21,000 kg of perch eggs and milt were shed. The total area of Windermere is 14.82 km²

(Mortimer & Worthington, 1942), but the area less than 20 m depth, and thus that normally inhabited by perch, is 7.65 km². On the basis of the latter figures the production of adult perch was 31 kg/ha, and shedding of perch eggs and milt 27.5 kg/ha. These figures must be considered very approximate, but very similar figures were obtained some years ago using a rather different method of computation and the ratio between growth production and shed gonad products is likely to be fairly accurate. Thus, the annual shedding of gonad products for a perch population similar to that in Windermere is nearly as large as the total adult production. This proportion will depend more than anything else upon the growth rate of the fish because the gonad weight as a proportion of the body weight does not seem to vary very much — at least for perch. Before 1941, the perch in Windermere were stunted but the growth was not as slow as several other perch growth rates that have been reported (Alm, 1946). Since 1941 the growth rate has increased greatly, the population decreased and the mortality rate changed as well (Le Cren, 1958). Very rough calculations suggest that production is now about 10 per cent, and gonad products shed about 6 per cent, of what they were before 1941, so that with a fast growth perch gonad shedding would be about half the adult production.

Some of the best data on fish production are those given by Allen (1951) for the brown trout (*Salmo trutta*) of the Horokiwi River. The total production for all but O-group fish from May 1940 to May 1941 was 531 kg. Allen does not give data on gonad weights, only fecundity, but a few data from brown trout from various English sources indicate that the ripe ovary weight is fairly constantly 12.5 per cent of the body weight and the testes vary round 2.5 per cent. If these data are applied to Allen's Horokiwi population the gonad shedding can be estimated at 54 kg or about 10 per cent of the production (of adults). Frost & Smyly (1952) give data on growth and survival in Three Dubs Tarn from which the production of brown trout can be calculated (though the estimate for total population in the tarn is no better than an informed guess). The average production by mature and maturing trout (i.e. III and older) is 1.75 kg and the gonad products shed is 0.42 kg or about 24 per cent of the adult production.

These few examples are enough to show that the annual production of gonad products can be a quantity of significant size, and in some cases as large as the annual growth production of adults. This gonad shedding can be thought of both as a demand upon the productivity of the environment and as a contribution towards recruitment. From many points of view the annual growth of fish should be considered to include the annual spawning of gonad products, and in estimating the food consumption the demands of gonad development should certainly be taken into account, as in terms of

protein and fat gonad development requirements will be relatively larger than simple gonad weight will indicate (Swift, 1955). For the Pacific salmon (*Oncorhynchus* spp.), where the adults die immediately after spawning, the 'production cost' of spawning should also include the weight of the spawners' bodies. The total biomass of the spawning escapement is lost to the stock of salmon; in most other species there is little or no mortality associated especially with spawning.

PRODUCTION IN THE LARVAL AND JUVENILE PHASES

Estimates of production, and indeed any understanding of population dynamics, require measures of the basic parameters; mortality and growth. These have been estimated with reasonable degrees of accuracy for the adult or the exploited phases of a number of fish populations, but data for larval, juvenile or pre-recruit phases are much scarcer. This is partly because young fish have not been studied so much as older fish and partly because the necessary data are much more difficult to obtain. In spite of this, however, the intrinsic interest and importance of the young stages make it worth while attempting some rough estimates of their population parameters, including the magnitude of production in the early phases.

Even though data on population numbers and survival in young fish may not be available, it is frequently possible to estimate the number of eggs from information on the abundance and fecundity of adult females. It is thus possible to pin-point for each brood or year-class its initial abundance as well as the number and size of the survivors when they are recruited into the adult or fished stock. It only remains to fill in the changes in mortality and growth in the intervening period; this may be difficult but a reasonable range of probabilities can often be suggested.

Frost & Smyly (1952) have published data on the brown trout (*Salmo trutta*) in a small lake, that can provide an example of this method of estimating production. The lake was netted to give twelve successive annual samples, each of which averaged roughly half the population, and the fish caught were analyzed for age. The catches of one- and two-year-old fish were subject to net selection and are therefore not representative, but the seine effectively caught fish that were three years old or older and so the age data give a good estimate of the average mortality after the third year. In the fourth year the instantaneous mortality rate, Z , is 0.63. An estimate (based on published and unpublished data) of egg deposition by the number of mature females in the average total population comes to 3,670. If a graph is drawn of survival (Fig. 1) it is clear that survival from the egg to three years old must be less than subsequently. Three possible estimates of the

course of this survival can be made: (1) to assume that the rate of survival is constant from egg to three years old (at a rate of $Z = 1.48$), or (2) to assume that there is very heavy mortality very early in life (before any growth) and that mortality subsequently is the same in the first three years as in the fourth ($Z = 0.63$), or (3) to assume that mortality in the second and third years is the same as in the fourth ($Z = 0.63$) but that the first year starts with a heavy mortality which soon becomes much less. These three possibilities are shown in Fig. 1.

FIG. 1.—Numbers of survivors plotted on a logarithmic scale against age for brown trout in Three Dubs Tarn (data from Frost & Smyly, 1952). Three possible curves of survival from eggs to three-year-old fish are shown.

The growth made in each year of life can be estimated from the scales by back-calculation (as has been done by Frost & Smyly (1952)) and the weight calculated from a length/weight relationship. The production can be calculated in various ways (Allen, 1951; Ricker, 1958*b*). In the present example it has been assumed that both growth and mortality are equally distributed throughout the year and production has been estimated from the product of the mean biomass and the specific growth-rate for the year. In fact this

TABLE I. *Estimates of the production of trout in Three Dubs Tarn*

Age	Population numbers	Mean weight (g)	Production (g)			Cumulative probable production (g)
			Minimal	Probable	Maximal	
0	3,670	0.1	—	—	—	—
1	156-835	6.4	1,072	2,405	7,730	2,405
2	83-190	59	5,377	5,377	17,550	7,782
3	44	105	2,690	2,690	4,210	10,472
4	23	142	—	1,170	—	11,642
5	7.5	180	—	452	—	12,094
6	3.7	202	—	119	—	12,213
7	0.8	211	—	12	—	12,225
8	0.3	220	—	2	—	12,227

assumption is not strictly valid as growth will be confined to the spring and summer months and mortality more evenly distributed, but there is no real information about the seasonal variation in mortality, and the estimates are adequate for the present purpose. The estimates are set out in Table I, giving three estimates for the first three years, based on the three assumptions about the course of early mortality. The third, intermediate, estimate assumes (from independent information) that soon after they hatch most of the alevins migrate down the spawning beck into the tarn, where they grow rather fast but suffer a heavy mortality. They are supplemented in mid-summer by a further immigration of those fry that have remained in the streams and survived better but grown slower.

It will be seen from Table I that, although different assumptions about early mortality can have a profound effect upon the estimates of production, whatever assumption is adopted the rate of production is very much greater in the young fish than in the older. On a similar basis estimates can be made for the production of perch in Windermere. Here, with a pelagic larval phase, early mortality is much greater and a wide range of possible rates could be used, but again the same three assumptions are made and minimal, probable, and maximal estimates calculated (Table II). The maximal estimates are obviously too large and give very high figures for production and surviving biomass, but it is difficult to calculate probable figures without

TABLE II. *Estimates of the production of perch in Windermere before 1941 (metric tons)*

	Minimal	Probable	Maximal
Biomass of hatched larvae	6.0	6.0	6.0
Production in first year	2.5	50	4,000
Biomass when one year old	2.4	7.0	450
Production in second year	10.0	13.0	1,000
Biomass when two years old	10.5	10.5	10.5
Total production to II	12.5	63	5,000
Total production after II	—	24	—

knowing more about the course of mortality; it is possible that a crucial period of high mortality may occur when the larvae are a month or so old, and food becomes in short supply (Smyly, 1952).

Two other estimates of juvenile fish production have been made. One, by Allen (1951), calculated the production of trout (*Salmo trutta*) in the Horokiwi River, New Zealand; the other, by Ricker & Foerster (1948), estimated production for young sockeye salmon (*Oncorhynchus nerka*) in Cultus Lake, Canada. Allen estimated the numbers of eggs deposited from counts of redds and also from estimates of spawning females and their fecundity; the population and growth of the trout were estimated every three months. The early production of fry was thus calculated from an accurately known total growth over the first three months and fairly good estimates of populations when hatching and when three months old. The total survival for the three months averaged 0.0135, which is equivalent to an annual instantaneous mortality rate (M) of 17.2. It is probable, however, that even within this period the mortality rate decreases and much of the mortality takes place within the first month (Le Cren, unpublished data). This will mean that the figures Allen gives for production in the first three months will tend to be over-estimates, though it is difficult to guess by how much without further data. The juvenile phase can be considered to end at the end of the first year, when the largest individuals will be recruited into the fished stock, so the production for the first year can be taken as the juvenile production. For the lower waters of the Horokiwi River this is 1,344 kg, out of a total production for the whole life of a year-class of 1,702 kg (Allen, 1951, p. 180).

Ricker & Foerster's (1948) estimates of production for sockeye salmon in Cultus Lake are notable for (1) being based on a considerable detail of seasonal data on growth and survival, (2) for covering a period of twelve years when, owing to cycles of abundance, the populations of young sockeye varied greatly, and (3) for including an experiment in predator control. Production in the first year of life in the lake varied from 1,320 kg to 40,700 kg (most of the sockeye migrated when one year old). Although most of the seasonal data were collected in one year (1931), Ricker & Foerster produce evidence to suggest that the seasonal incidence of growth and mortality did not vary much from one year to another. It is therefore permissible to examine their data (e.g. Table V, p. 189) for the effect of population density, and especially the number or biomass of newly hatched fry, on the production. The growth rate was affected by population density, especially at high densities (Foerster, 1944) and specific growth rate appears to be roughly inversely proportional to the logarithm of the density of fry at the start of the year. Survival does not appear to be affected so much by population density and there is clearly no significant correlation if the total mortality rate for the year is plotted

against seeding biomass. There is a suggestion, however, that at very high seeding densities (e.g. as in 1927) mortality might increase. When production and surviving biomass are plotted against seeding biomass (weight of fry at the start of the year) (Fig. 2) it is clear that both do not increase propor-

FIG. 2.—Yearling stock biomass and production plotted against seeding biomass of fry for sockeye salmon in Cultus Lake (data from Ricker & Foerster, 1948). The crosses are for the three years after predator control.

tionately but curve away towards a maximum at high seeding densities. Plotting these data on double logarithmic scales (Fig. 3) shows that over the range of densities that occurred the production is roughly proportional to the 0.8th power of the seeding biomass. It is doubtful if much significance can be attached to this actual relationship, but it is interesting that the production for the three years after predator control falls on a parallel line showing a very similar relationship at about twice the production for a given seeding biomass. Ricker & Foerster explain the higher yield of fry (or biomass surviving at the end of the year) after predator control on the basis of a much lower loss from predation and thus decrease in mortality rate. It is clear, however, from plots of production and yield against seeding biomass and seasonal plots of production in 1931 and 1935 that the production itself increased relative to seeding after predator control. This, however, can be explained entirely by the survival of a much greater share of the early

production, leading to a bigger population on hand to grow during the latter part of the growing season. Production was about doubled by predator control, but yield increased between three and four times.

Further data on the effect of seeding (or stocking or spawning) density on juvenile production and 'yield' of recruits is provided by preliminary data

FIG. 3.—The data of Fig. 2 plotted on logarithmic scales.

I have obtained for trout (*Salmo trutta*) in a beck in the English Lake District. Observations on spawning and survival through the first year had indicated survival rates from egg to yearling trout of about 0.06 ($M = 2.8$) with an indication that much of the mortality occurred soon after the fry began to feed. Accordingly in 1959 flood control was installed, and part of the beck divided by fry-proof screens into a number of similar sections. A different

TABLE III. *Growth, mortality and production for four sections of a beck stocked with different numbers of trout alevins*

Period I.—4th May to 4th June

Initial weight (g)	.	.	0.38	.	1.13	.	3.38	.	10.12
Specific growth rate	.	.	2.03	.	1.92	.	1.65	.	1.50
Mortality rate	.	.	2.02	.	2.10	.	1.84	.	2.76
Final weight (g)	.	.	0.38	.	0.96	.	2.81	.	2.87
Production (g)	.	.	0.77	.	2.00	.	5.00	.	8.66

Whole experiment

4th May to 31st August

Calculated data:

Initial weight (g)	.	.	0.4	.	1.0	.	4.0	.	10.0
Final weight (g)	.	.	2.2	.	2.8	.	4.2	.	5.4
Production (g)	.	.	2.9	.	4.2	.	8.3	.	13.5
Final weight/Initial weight	68	.	54	.	34	.	23	.	
+ Production %									

number of eggs or newly hatched alevins was stocked into each section and the survivors counted and measured after removal by electric-fishing approximately 30, 76 and 114 days after they started to feed at the beginning of May.

In the first month after feeding there was a correlation between density of stocking and survival and an inverse correlation between density of stocking and growth. In Table III and Fig. 4 the data for four comparable sections are shown. Some other sections (and some cages placed in the beck with their floors covered with gravel to simulate the beck bottom) gave similar relationships between density and growth and survival.

FIG. 4.—Production, final biomass and final biomass as a percentage of initial biomass plus production, plotted against initial biomass of alevins for trout in experimental sections of a beck.

In the second and third periods a drought and some untoward deaths during sampling precluded exact continuation of the experiment with the same populations of fish but growth, though rather slower, continued to be negatively correlated with population density. The mortality was much less than in the first period, but such as did occur tended to be heavier in the denser populations.

A combination of the data on mortality and growth for each period allows the calculation of the production and its variation with the original stocking density. The data for the first period, and calculated data for four stocking densities for the whole period up to the beginning of September, are shown in Table III and in Fig. 4. The calculated data for four stocking densities are computed from graphs of mortality rates and growth rates plotted against stocking densities for each of the three periods of the experiment, using as a stocking density for each period the surviving density at the end of the previous period.

These data show considerable similarity to those obtained by Ricker & Foerster for Cultus Lake salmon in the relationships between initial seeding or stocking density and resultant production and numbers of survivors. Although the two species are both salmonid fish, the sockeye fry feed on plankton and are pelagic in a lake, but the trout fry feed on bottom and drift fauna in a small stream, so their ecological niches are quite different. It does seem then as if the observed effects of varying population density on the production and yield might be typical of a wide range of kinds of young fish populations.

Inversely density dependent growth-rates are widely known for fish populations but it is perhaps significant that they should be found to operate so early in life. It has been postulated that natural population regulation in fish occurs mainly in the adult phase through the effect of high population density on adult growth rate and thus fecundity, but it appears that there can also be intense intraspecific competition in the early stages with resultant population regulation through density dependent mortality as well as inversely density dependent growth.

DISCUSSION AND CONCLUSIONS

The examples of production estimates quoted above show that the whole reproductive and recruit rearing phase of the life history can involve a large part of the production of fish. If the total production of gonad products and the subsequent body growth up to maturity or recruitment is combined it can then be compared both to the grand total production by a year-class through the whole of its life, and to the biomass of such a year-class on

recruitment. This has been done for the data presented above and is shown in Table IV. From the two lower lines of this Table it will be seen that about

TABLE IV. *Estimates of production, biomass and efficiency*

Species	<i>Salmo trutta</i>	<i>Salmo trutta</i>	<i>Perca fluviatilis</i>
Author	Data from Frost & Smyly (1952)	Allen (1951)	Le Cren
Habitat	Three Dubs Tarn	Horokiwi R.	Windermere
	kg	kg	m/tons
Gonad production	0.4	54	21
Juvenile production	10.5	1,747	63
Adult production	1.7	531	24
Grand total production	12.6	2,332	108
Biomass on recruitment	4.6	519	10.5
Recruitment biomass/gonad and juvenile production %	42	29	13
Gonad and juvenile production/grand total production %	86	77	78

80 per cent of the whole production is involved in reproduction and recruit rearing, and that only a small part of this production (13-42 per cent) may actually survive to the recruitment stage. Additional data for the proportion of pre-recruit production that survives are given by the computations for sockeye salmon and brown trout fry where roughly comparable percentages are 28 per cent and 33 per cent respectively.

There are several practical implications of these findings. Firstly, it is clear that the early part of the life of fish deserves much more study; some of the data presented in this paper are little more than informed guesses. Secondly, the rearing of fish to the recruit stage (or to the migratory stage in the case of anadromous salmonids) is obviously an inefficient process that absorbs much of the capacity of the water to produce fish flesh. This inefficiency is largely due to the mortality suffered by the young, and any management practices that tended to reduce this mortality should be worth while. Sometimes the young fish may act as a necessary link in the food chain ('forage fish') for older and larger individuals of the same population, but this will not normally be so. Thirdly, it is clear that in normal fish populations there is an unnecessarily large expenditure of 'effort' on gonad products and the whole reproductive and rearing process. The data from sockeye salmon and trout show that the 'efficiency' of reproduction and rearing falls with an increase in the density of eggs and young fish, and above a certain level there may be no appreciable increase in the biomass of 'recruits' produced. It is true that for migratory species it may be desirable to produce the maximum number of migrants (smolts) rather than the maximum biomass, but there is some evidence which suggests that survival for salmon in the marine phase

is correlated with size on migration to the sea, so it may not always be advantageous to produce more numerous but smaller migrants.

The biological significance of the normal high levels of spawning and heavy juvenile losses is doubtless connected with the operation of density-independent mortality which tends to cause large fluctuations in survival. The variation in larval and juvenile survival that occurs among many marine fish is well known; freshwater species also show such variations in year-class strength, and these can be correlated with climatic factors (e.g. Le Cren, 1955). These density-independent mortality factors will normally obscure the operation of density-dependent factors, but in the long-run the latter will be important for the maintenance of stable populations, both in natural and fished stocks. The data described above suggest that the 'efficiency' of reproduction and recruitment is greater in less dense populations, and this will tend to be compensatory. The normal overproduction of gonad products and young is an insurance against the heavy independent mortality which may occur on some occasions. It seems that this 'insurance' makes considerable demands upon the production of the species, and often, as well, on the productivity of the environment. It might, therefore, be the aim of fishery managers to reduce the need for such a large insurance. This could be done by trying to mitigate the effects of extremely unfavourable environmental conditions, and using facilities for artificial propagation more for resuscitating stocks that had been decimated by exceptionally unfavourable events in the environment than for adding a small contribution to normal natural propagation. Much could be done as well by measures to reduce juvenile mortality similar to the predator control in Cultus Lake. Every fish that is encouraged to spawn, or allowed to die a natural death, over and above the minimum number necessary for the long-term maintenance of the stock is a fish wasted by the fishery. Above all there would seem to be a great need to reach a real understanding of the processes of propagation and recruitment from the point of view of population dynamics.

SUMMARY

A consideration of some estimates of production from a few species of freshwater fish shows that the production of gonad products can be as large as the growth production of new flesh, and is probably usually a significant proportion of the total production. Little of the production of juvenile fish survives to recruitment and so the overall reproductive and recruitment process is inefficient. However, this efficiency is inversely related to population density and so is a precaution against the occasional catastrophic density-independent mortality. Fishery management should aim to understand these

processes better so that management practices can be designed to reduce unnecessary natural propagation and juvenile mortality.

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DISCUSSION

G. SURTEES: I have worked on West African mosquitoes, especially in southern Nigeria, where one finds well-separated populations isolated in village clearings. Such areas are often up to a quarter mile in diameter, and within them the yellow fever vector mosquitoes breed only domestically, in village water butts. There are no predators on *Aedes aegypti* in these storage butts: their food is algae. The rainy season begins in March and the rains increase to a June-July peak; are less in August, rise to a minor September peak, and terminate in October. The mosquito larvae similarly increase suddenly in March, at the start of the rains, when the eggs hatch (Surtees, 1958, 1959a). They reach a peak in May and by the end of that month the larval populations slump to a very low level despite the abundance of water. There is then a slow recovery. It might be thought that this slump was due to some other organism affecting the adults, but the adult numbers fall off six to eight weeks *after* the larval decline: the decrease in adults thus seems to depend on that of the larvae. In the absence of predators taking the larvae one must look for a direct effect involving them. Laboratory studies show that cultures maintained at a certain high density level show a sudden and high mortality of larvae, and intraspecific larval competition therefore seems to be involved as the control mechanism (Surtees, 1959b).

J. A. GULLAND: Is there any evidence for seasonal periodicity in egg laying?

G. SURTEES: So far as we can see this does not alter significantly. Nor have we been able to correlate larval mortality successfully with any environmental factor.

F. RAW: Many speakers have said that they believed they were dealing with stable populations. Surely entomologists and terrestrial ecologists would agree that such are exceptional. Why should aquatic populations be more stable?

E. D. LE CREN: I think that time relations are important in this. In temperate regions, such as Britain, there is a pronounced seasonal climatic variation and this makes it difficult to study species with a one-year or two-year life cycle. Work is easier on species with a short life cycle, like *Daphnia*, or a very long one, like a fish. In insects the marked seasonal effects may give an impression of population instability.

F. RAW: Fecundity should also be considered. An insect laying say one hundred eggs need experience only the difference between a 96 per cent mortality and a 98 per cent for the population to be halved. In fish the enormous fecundity, despite the stability of population, suggests a remarkable buffering effect.

E. D. LE CREN: Yet often there are fluctuations in the number of young produced per year, due to climatic variations. But if the population includes, say, ten distinct age-groups instead of one (as in most insects) these fluctuations will balance out. One age-group can vary widely without the population as a whole being much affected.

J. B. CRAGG: Referring back to McLaren's paper, he talked about an equilibrium population in his seals. This seems in contrast to the grey seal around Britain: has he any comment?

I. A. McLAREN: I can only say that I accepted the fact of an equilibrium where the numbers seem stable. The reason for the difference may be that whereas my ringed seals have had some 11,000 post-glacial years to reach an equilibrium, the European grey seal has not yet recovered from very heavy exploitation which has only recently terminated.

J. G. SKELLAM: There is a problem about the use of the term 'equilibrium population'. It has been used in two senses:

(a) The total number of animals is more or less constant.

(b) The age structure of the population is of more or less constant form. It is possible to have a rising population which is yet maintaining a constant proportion between its component year groups. Lotka (1925) demonstrated this. If equilibrium be defined in terms of age structure the presence of a slow growth or decline in overall numbers is unimportant.

M. H. WILLIAMSON: Concerning the relative stability of marine and terrestrial populations, there are of course markedly unstable aquatic ones. Plankton commonly vary tenfold in numbers and frequently a hundredfold: thousandfold variations are known.

J. B. CRAGG: I think it is important to compare taxonomically related organisms.

G. C. VARLEY: There are insects with a stability of population comparable with that of fish. For example, ants and termites, in which the reproductive life of a female extends over many years.

R. J. H. BEVERTON: The fisheries work should not be taken as proof that stability is the rule for marine organisms. There are exceptions, such as the Norwegian herring which shows wide variations in abundance.

G. SAETERSDAL: Records are available for several hundred years, but it

is not clear whether some of the changes are due to the herring formerly having been distributed farther from the coast, and so outside fishing range, or to a genuine change in stock. Latterly there has been a rapid fall in catch which could be due to a decrease in population or to an effect of fishing. There is certainly a great variation in the size of year-classes.

T. B. REYNOLDSON: Among terrestrial animals I have been struck by the stability of earthworm populations in undisturbed habitats.

J. E. SATCHELL: Yes, but the variations in moisture content encountered in the terrestrial habitat constitute an additional source of population instability, which we should not overlook when we are comparing terrestrial and aquatic organisms.

T. B. REYNOLDSON: Over a ten-year period, the size of an earthworm population at Bangor does seem to show some correlation with the rainfall.

J. A. GULLAND: There are various forms of stability. Marine populations often remain stable although recruitment varies tenfold or even a hundred-fold. Because these populations include many year-classes such variations are damped down. Apart from recruitment, fishing is the main variable factor.

C. EDELSTAM: Snakes often provide very stable populations, with few major changes over whole decades. Their long life span is a factor — at three years, a grass snake's expectation of life is another three or four years. Such longevity is coupled by necessity with a low reproduction rate; attained for example by giving birth to only a few young each year, or — as in adders in central and north Sweden — by producing young only every two years or perhaps with even longer intervals.

A. C. SIMPSON: Similarly, in Crustacea, lobsters and crabs, which are long-lived, are stable, whereas shrimps, with short life-spans, are more variable in population numbers.

R. J. H. BEVERTON: I think we are confusing fluctuations with trends. Recruitment may fluctuate widely about a constant mean or about a changing trend, and the latter is by far the more significant type of population instability.

J. G. SKELLAM: The length of the period of maturity is more important than the whole life-span, as a factor affecting population stability.

M. E. SOLOMON: Isn't the essential point the degree of overlapping of generations, which commonly means the number of years spanned by an individual? In many insects each year's population is wholly at the mercy of that year's conditions. In other, longer-lived, animals there is a buffering effect. In connection with Le Cren's paper in which he mentioned the high amount of reproductive products liberated by fish, do these serve as diet for

organisms later consumed by the young fish, or otherwise improve the habitat?

E. D. LE CREN: There is no evidence on this. But Professor Nikol'skii has pointed out that in the Pacific salmon dead spawners provide food and also fertilize the water. This may apply to a less extent for milt. The bulk of the weight of these reproductive products, however, is made up of the egg yolk, which is utilized directly by the larvae: in salmonids and perch most of the eggs do hatch.

L. B. SLOBODKIN: Work by Richman, on the populations of a small pond in western Massachusetts, showed that there the amount of phytoplankton varied in direct relationship to the spawning of frogs.

G. C. VARLEY: We have heard a great deal today about populations, but very little about their effects on the organisms which serve them as food supply. In several cases the populations which have been studied are co-existing in the same areas, as Minke whale and fish do off the Norwegian coast. Factors must exist which are common to these two: what is known about these?

A. JONSGÅRD: The Minke whale takes many fish, including young herring. This is especially true in the autumn, when the southward-migrating whales stop for a time in the herring grounds and feed on the young fish. I have also mentioned the discovery of forty Lofoten cod in one whale stomach; translated into terms of herring this would be a vast amount of fish. We kill about 4,000 Minke whale a year: a lot of fish could be eaten by them during their three- to four-week stay in the herring area. Other fish are probably less affected. But we have no actual information on the interaction of these species.

F. RAW: In connection with Le Cren's and Slobodkin's papers, I think we should consider the efficiency of conversion of the food supply. If we consider the actual production of yield, heavy stocking is relatively less efficient than lower stocking. There is surely a carry-over since individuals which die go through a series of cycles returning to the system in three or four years. If energy loss from the system is considered, the number of stages involved in it is important, and it is an asset if these are relatively few. Slobodkin said that *Daphnia's* conversion of food into biomass is 9-12 per cent efficient. He said further that the range for aquatic organisms as a whole was 5-15 per cent. Could he say more about the relation of these figures to organisms and their food habits. Herbivores have a different and usually lower conversion rate than carnivores, and this should be reflected in the figure.

E. D. LE CREN: There are an enormous number of complexities involved

in this question. Consider Windermere perch and pike: the production of pike is about one-tenth that of perch, this agreeing with Slobodkin's bracket. But some young perch go to feed larger perch instead of pike, and occasionally young pike are found in perch stomachs.

L. B. SLOBODKIN: When energy enters an organism, potential energy is assimilated. This can be left as potential energy or converted into heat. Only the former can be re-used either as food, or as a corpse decomposed by other organisms. In *Daphnia* if no animals are removed from the population, about 5 per cent of the algal input is ultimately obtained as dead *Daphnia*, the rest being liberated as heat. I, as a predator can increase this to 10-12 per cent by removing animals.

The efficiency of the population is then:

$$\frac{\text{Potential energy obtained from culture}}{\text{Potential energy consumed in food}}$$

This is not the same as the total energy output of the *Daphnia* population.

All the organisms I have studied are aquatic. The zooplankton itself is consuming phytoplankton, and is being consumed by fish. In such systems there are four or five trophic levels. The top is assumed to have zero efficiency, which is incorrect as the decomposing bacteria do something. Other steps, such as the conversion of zooplankton to fish, range from 5-15 per cent in efficiency.

D. JENKINS: I am not happy about the implications of the concept that if an animal lives longer its numbers are less likely to fluctuate. It must follow that species with a short generation time should all show marked fluctuations. Is this true? Is not the efficiency of adaptation to environment not also highly relevant; If a climatic accident is considered, this is likely to be equally as lethal to an animal with a life expectation of fifty years as it is to a one-year species. It is the capacity to withstand environmental extremes that is vital.

M. E. SOLOMON: Most organisms have at least one exceptionally vulnerable stage in the life cycle. In insects, the whole population may go through this stage more or less synchronously, and thus be more vulnerable than a population of, say a fish, of which only one-fifth the total number are exposed to the adverse conditions at a time.

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PREDATION AND COMPETITION IN RELATION TO
EXPLOITATION

THE EFFECT OF SEAL STOCKS ON SCOTTISH MARINE FISHERIES

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The first Grey Seals' Protection Act was passed in the spring of 1914. Introducing the Bill, the promotor maintained that the grey seal was in danger of becoming extinct and that stocks on the Scottish coast totalled no more than 500. An examination of the available literature and documents has failed to disclose the evidence on which these statements were based, apart from a popular and emotional article by a well-known soldier, hunter and sportsman of the day, H. H. Pritchard, published in the *Cornhill Magazine* in July 1913, in which attention was drawn to the traditional killing of grey seals on a Hebridean island for domestic purposes. No scientific investigation of the matter was undertaken at the time to ascertain whether the statements were true and whether protection was necessary. In this connection it is perhaps significant that in subsequent years, on different parts of the British coast, seal colonies previously regarded as of common seals, have been identified as of grey seals. No consideration appears to have been given to the possible effect of seal protection on fish stocks, nor were its consequences to the inhabitants of the Western Isles, the people most intimately affected, taken into account.

Fourteen years later, Professor J. Ritchie and Mr W. L. Calderwood surveyed the Scottish grey seal stocks and estimated the total population at between 4,000 and 5,000. Ritchie & Calderwood (1928) considered that, in view of the growth of the stocks, the danger of extermination no longer existed, but in spite of this the second Grey Seals' Protection Act was passed in 1932 (protection having been continued in the intervening years under the Expiring Laws Continuance Acts). In the face of some opposition from salmon fishing interests the Bill was accepted, but mainly because it now provided the Secretary of State for Scotland and the Minister of Agriculture & Fisheries with power to make an order curtailing the protective measures if the need should arise. In the years which followed, the grey seal continued to increase in numbers, perhaps aided by the general concern of fishermen with other matters during the second great war.

On resuming full-scale fishing after the war Scottish salmon fishermen began to complain even more strongly and collectively about the growing menace to their fishery — a move which culminated in a request to the Secretary of State for Scotland to have seal stocks reduced. Grounds for complaint appear to have been confirmed by Lockley's (1954) estimate of the grey seal population of the British Isles at 20,000 — an increase to from four to five times the number estimated by Ritchie & Calderwood in the late 1920's.

As a direct result, the wider question of seals in relation to Scottish fisheries generally has been investigated during the past three years. Despite statements to the contrary, a good deal is known about the food of the grey and common seals, the two native British species. After weaning, both species feed for a short period on crustaceans and molluscs and then turn almost entirely to fish (Havinga, 1933; Fisher, 1950; Sergeant, 1951 and others). Almost every fish of economic importance round the British Isles is eaten by seals, including salmon, sea trout, halibut and other flat-fishes. Further evidence was obtained from the examination of the stomach contents of seals killed on the Scottish coast from 1958 to 1960. Of sixty-four examined, forty-one were grey seals and twenty-three common seals. Twenty of the grey seal and fifteen of the common seal stomachs were empty, but of the twenty-one greys containing recognizable food, ten were found to be feeding on salmon and five on cod. Of the eight common seals, one was feeding on sea trout, one on salmon parr, four on gadoids including haddock and whiting, one on mackerel and two on other species. That thirty-four of the sixty-four seals were drowned or killed in salmon nets may give the impression of bias towards the salmon as the grey seal's main food, but in fact seals trapped and killed in nets reveal a higher proportion of empty stomachs than do those shot in the sea, apparently the result of the animals vomiting on finding themselves trapped. From this and other evidence the percentage of seals feeding on salmon could well be higher on the sections of the coast examined. To objections that the examination of stomachs of seals killed in or near salmon nets gives a bias towards salmon in the results, it must also be pointed out that salmon nets are fished over hundreds of miles of the Scottish Coast and that it would be difficult for various reasons, to procure a corresponding number of stomach samples from areas where salmon fishing is not carried on.

From a study of scientific papers dealing with grey seal colonies and from observations on different sections of the Scottish coast it is clear that seals, particularly grey seals, have been increasing in numbers in recent years (Darling, 1939, 1947, 1952; Buxton & Lockley, 1947-8; Davies, 1956; Eggeling, 1957; Hickling, 1958, 1959). There is ample evidence too, of the harmful effect these animals are having on salmon fisheries. Briefly, this may

be summarized as (1) fish mutilated or killed and eaten; (2) nets torn; (3) interruption of fishing time; and (4) diversion of fish from nets.

The impact of seals on Scottish fisheries is dealt with in more detail elsewhere (Rae, 1960), and for the present attention is focused on the effect on marine fisheries.

So far few complaints regarding seals have come from Scottish sea fishermen. The reason for this, however, is fairly obvious. Most marine fishermen employ active methods of fishing such as trawling and seining. Most of the damage attributed to seals abroad has been in respect of passive fishing gears, but in Scotland these methods comprise only a small proportion of the total fisheries. Anchored nets and lines on the west of Scotland, however, have suffered from seal activities for a long time but since the war cod-net and small-line fishermen on the coast of Angus have been troubled by seals tearing their nets and eating or mutilating their fish in a manner similar to the damage sustained by salmon fishermen using bag-nets. Although these passive fishing methods form a small part of Scottish fisheries (drift-netting for herring fortunately is largely carried on outside coastal waters where seals are active) they are nevertheless essential owing to circumstances in particular localities.

This form of damage from seals, however, is small in comparison with the damage apparently done to fish stocks as a whole. This aspect of the problem may be considered by a rough calculation of the quantity of fish eaten by seals. Assuming totals of 20,000 grey seals and 18,000 common seals, and accepting estimates of the daily requirements of these animals as 15 lb and 11 lb of fish respectively (Matthews, 1952 and Havinga, 1933), the daily consumption by both species would amount to 220 tons and the yearly total to 80,000 tons. It is not known whether all this fish would be taken in 'home' waters (see below) but it is noteworthy that this weight is the equivalent of one-fifth to one-sixth of the total British catch of all species of fish from home waters.

It has been estimated that 80 per cent of the seal population is based on Scottish waters for feeding purposes, and, assuming that the quantity of fish eaten is in the same proportion, this means that 65,000 tons of fish are eaten by seals in Scottish waters every year. This weight is the equivalent of between one-quarter and one-fifth of the total Scottish catch from home waters. It is certainly not suggested that in the absence of seals Scottish landings would be increased by that amount, but it does mean that the catches of Scottish fishermen must be reduced to some extent.

Objections may reasonably be raised to this view on the grounds that it is not known if all British seals remain in home waters throughout the year. Tagging experiments on grey seals do show that some migrate to different

coasts on the Continent, including the Faroe Islands (Hewer, 1955; Hickling, 1957). There is, however, as yet no evidence that this movement reaches any great proportion since continental writers do not record any marked seasonal increase in their seal populations.

On the other hand, against this argument it may be stated: (1) that the British grey seal population is now almost certainly greater than 20,000 estimated by Lockley (1954); (2) that seals are known to kill more fish than they eat and that when they do eat they select choice portions and reject the head, skin and tail fin of large fish such as salmon and cod. The 15 lb of fish estimated as being eaten by a grey seal daily must therefore represent a greater weight of fish killed.

TABLE I

Area or locality	Number of cod examined	Number of cod infested	%
Southern North Sea (offshore)	105	0	0
Farne Deep to Berwick coast	322	70	22
East of May Island	208	25	12
Firth of Forth	428	31	7
Central North Sea (offshore)	501	3	0.6
Aberdeenshire coast (eastwards to 1° W)	445	2	0.4
Moray Firth	237	26	11
Orkney (coastal)	62	15	24
Shetland (Balta)	181	47	26
Northern North Sea (offshore)	90	0	0
North coast of Scotland	97	14	14
West of Scotland	350	135	39
Inner Firth of Clyde	60	34	57

Seals are now known to have another harmful effect on fish stocks by the propagation of the parasitic worm, *Porrocaecum decipiens* (Krabbe), which appears in its larval form in the muscles of a number of food fishes but particularly in the cod. In this connection the researches of a number of Canadian scientists are well known (Scott & Martin, 1957; Scott & Fisher, 1958; Templeman, Squires & Fleming, 1957). On the west coast of this country nematode parasites have been known in cod and other gadoids for many years. Until recently, however, North Sea grounds have been regarded as almost free from this parasite. Following representations from the fish trade this problem has been investigated at Aberdeen during the past three years with rather disturbing results. Preliminary figures are given in Table I.

Infestation of cod by *Porrocaecum decipiens* is still either absent or very light on all offshore grounds in the North Sea. In coastal waters, however, it varies from less than 1 per cent off the Aberdeenshire coast to over 20 per cent on the Northumberland and Berwick coasts, round the Orkneys and the Shetlands and to nearly 40 per cent on the west of Scotland, where,

locally, more than 50 per cent of the cod may be affected. The correlation between the areas of high worm infestation and those harbouring dense concentrations of seals is striking. The low infestation of cod on the Aberdeenshire coast may be explained by the fact that this section of the coast is still relatively seal-free.

The infestation percentages have been calculated on all cod from a length of 20 cm upwards. If under-sized fish are disregarded and the percentages based on fish of marketable size only, the proportions of affected fish are even greater. Fortunately, the degree of infestation of individual fish is still low in the majority of cases, but this form of infestation is cumulative so that the bigger the fish the heavier the worm load. Furthermore, the number of seals, on the east coast in particular, has been increasing so rapidly in recent years that it is quite possible that the full effect of worm infestation in cod has not yet been realized. In view of the danger of turning public taste away from cod this threat to the market value of a fish which provides about half the United Kingdom's landings of whitefish must be halted.

Early in the present century it began to be recognized that protection of fish stocks would be necessary to ensure their maintenance in the future, and partly with this aim in view various regulations were drawn up prohibiting or restricting fishing within Scottish coastal waters. With the exception of the war years the stocks of fish round the British Isles have been heavily exploited commercially since the 1920's and, in order to conserve fish stocks, international conservation measures have now been in force for some time. Considerable thought is also being given in different ways to the improvement of salmon stocks.

Meanwhile, however, salmon and marine fish stocks continue to be preyed upon by large numbers of seals which remain almost unexploited. One might reasonably ask not only why no effort should be made to control such a harmful predator as the seal but why, in the case of the grey seal, it should even be protected. Even the most embittered salmon fisherman has never contemplated the extermination of seals and it should be obvious from the present state of the stocks that the grey seal is no longer threatened by this danger.

It may be argued that the protection of the grey seal covers the breeding season only and that fishermen could shoot them outside the closed period. It has even been argued that this is the only necessary remedy! This is done as far as possible, but seals are notoriously difficult to shoot in the water and evidently despite the combined efforts of fishermen, the numbers continue to increase. It is clear that effective action can only be taken against them where they congregate for breeding or resting, but unfortunately such concentrations are often somewhat removed from the fishing grounds.

Moreover, since the passing of the Grey Seals' Protection Acts the extension of Nature Conservancy reserves and of National Trust properties now ensures the protection of large numbers of grey seals throughout the entire year. These are developments which were not foreseen even at the passing of the second Act in 1932. It seems probable, too, that protection of one species has to some extent discouraged hunters who previously made a living by marketing both kinds of seal skins. In the interests of Scottish, and to some extent also of English fisheries, it would now appear important that seal protection should cease, and consideration should be given to whether seal stocks should be reduced and thereafter maintained at a level which will not interfere unduly with fisheries. At present it is not too clear how this can be achieved but a number of conditions seem to be desirable:

- (1) that a start should be made as soon as possible,
- (2) that the reduction must be substantial,
- (3) that the reduction should cover all seal colonies which have increased in size in recent years, and
- (4) that the reduction should extend over a number of years.

It is also important that seal stocks should be put to good use and harvested in a rational manner. Professor Ritchie (1920) refers to the intelligent harvesting of a grey seal colony on one of the Inner Hebrides by the monks of St Columba's day — a procedure which Dr Fraser Darling regards as one of the earliest examples of conservation. In the same way, monks from the Northumbrian coast are known to have exploited the grey seals on the Farne Islands. In view of the facilities now available in this country for the protection of wild life when necessary, it should be possible to reduce the numbers of any harmful predator without endangering its survival.

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SEALS AND SALMON NETS

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About 1,600 tons of salmon valued at £1,250,000 are caught each year by the Scottish commercial salmon nets. The industry employs about 2,000 active fishermen but many more men are employed in the ancillary trades. Commercial salmon nets are operated on the coast, in estuaries and, in a few instances, in rivers above the head of tide. On the coast the three main types of nets used are bag-, fly- and jumper-nets while in estuaries and freshwater, sweep nets are employed.

The three types of coastal nets are basically of the same design. They consist essentially of two parts, a leader and a trap. The leader is merely a curtain of netting which stretches seaward at right angles to the shore and its seaward end is attached to the middle of the entrance to the trap. It has the effect of directing a shoal of salmon moving along the coast seawards into the trap. The main difference between these three types of nets is the way they are set to fish. The bag-net is set to float just below the surface of the water on rocky coasts, it is kept in position by anchors and floats and is fished by coble (boat). The other two types are set on sandy beaches, are held in position by stakes driven into the sand and are fished at low tide without a boat. The bag-net is by far the commonest of these three types of net.

Although bag-nets vary in size at different parts of the coast an average-sized net would be about 50 ft long while the leader would be about 200 ft long. The bag-net proper consists of three chambers. The chamber furthest from the shore, where the fish are caught, is known as the fish court. Very roughly it is 18 ft long, 10 ft deep, 7 ft broad at the seaward end increasing to 13 ft. The entrance to this chamber (the small door) extends down the whole depth of the net and is about 6 in. wide. It lies at the apex of the inscales and this arrangement is thought to prevent fish escaping as, instead of finding the opening, they fall back into the angles created by the sides of the net and the sides of the inscale. The fish court, like the remainder of the net, is made from cotton twine. Bag-nets are very seldom fished singly; two or more are normally set in line extending seawards for perhaps a quarter of a mile.

Jumper- and fly-nets are fundamentally of the same design but may be rather smaller.

Visits to a large number of netting stations made it clear that one of the netsmen's problems was the ease with which seals were able to tear holes in the nets. This resulted in: (a) loss of fish, (b) damage to fish in the net, (c) loss of fishing time, (d) cost of repairs. These additional burdens had already caused the closure of a number of the smaller stations and others, especially in poor years, were being run at a financial loss.

It appears that seals can attack salmon in the fish court either by entering through the small door or by tearing a hole in the netting from the outside. Holes are most often torn in the small scales and in the sides of the net opposite the small scales. The holes are not large, only some three or four meshes being broken, so that they are very difficult to detect and even if they are seen it is a hazardous job to mend them when there is a heavy swell running.

An attempt was therefore made to design a net which would be proof against attack by seals. This experimental net had the following novel features: (a) it was made from nylon twine, (b) the amount of netting in the fish court was increased and set slacker on the ropes, (c) the fish court was protected by an outer curtain of large mesh nylon netting.

This net was first fished at the Altens Station near Aberdeen. The netsmen reported that it fished satisfactorily but they experienced difficulty in getting fish out of the net, especially in rough weather, because of the outer nylon curtain and perhaps because the nylon twine became soft when wet. The net was transferred to the Boddin Station near Montrose where it was fished from 30th June to 12th July, 1958. During this period it seemed that a seal had managed to enter the fish court through the small door and an inspection of the net by frogmen showed that at certain stages of the tide the slack netting of the fish court tended to come across the small door partially blocking it to the entry of fish.

To try to obviate the first difficulty short metal rods were inserted in the sides of the small door between the points of insertion of the horizontal metal door pins. It was thought that this would stiffen the door without making it inflexible and therefore difficult to haul over the gunwhale of a boat. To try and overcome the second difficulty the extra netting in the fish court was removed.

During the 1959 commercial netting season the net was fished at Boddin from the middle of February to the beginning of April and at Burnmouth (Berwickshire) from the end of April till mid-September. At both stations very similar results were obtained, which can be summarized as follows:

- (a) Seals, perhaps with the exception of the very smallest, cannot enter the net.
- (b) Although the other nets in the fleet have been torn and damaged by seals the nylon net has not been affected.

(c) The seals now seem to be destroying the salmon from outside the net. It seems that when a seal detects a salmon in the net, it swims round the outside until the salmon becomes cornered in the angle between the inscale and the side of the net. The seal is then able to kill and even eat the salmon without damaging the net. During the period the net was fishing at Boddin nearly all the fish caught were either eaten or left in an unmarketable state. Very similar results were obtained during the period the net was fished at Burnmouth.

(d) The net was more difficult to fish than a normal bag-net principally because the nylon became soft when wet so that it was very difficult to shake fish from the corner of the fish court and through the additional curtain of netting at the door especially in rough weather.

When this work on net protection was started a number of suggestions were made to the commercial netsmen. Some of them were adopted and some commercial netsmen tested other modifications which they had devised themselves. For example, at Goswick and Cheswick netting stations the following modifications were made, either singly or in combination, to a large proportion of the fly-nets, jumper-nets and bag-nets during 1959:

(a) The fish courts were made of nylon twine.

(b) Screens were stretched across the angles of the fish court so as to eliminate the acute angle between the scales and the side walls of the net.

(c) A curtain of big mesh netting was fixed, either all round the outside of the fish court, or only along each side opposite the small scales.

When fly and jumper nets were modified in the three ways just mentioned the results were encouraging, in that damage to the net and damage to the fish caught in it was much reduced or eliminated. If it proved necessary to replace a modified net by a normal cotton net damage once more became severe. With bag-nets similarly modified, however, the nets were undamaged but the catch was damaged, remains of salmon being left in the net. This would seem to show fairly conclusively that the seals are eating the salmon through the net from outside.

It therefore seems clear that seals can attack salmon in modified bag-nets but not in modified fly- or jumper-nets. It is suggested that this difference arises because, although a bag-net is taut at certain states of the tide, it is slack at other times, whereas a jumper- or fly-net, because it is moored in a different way is taut irrespective of the state of the tide. It is further suggested that it is during the period the bag-nets are slack that seals damage salmon within nets which have been modified to prevent the actual breaking of the netting. Perhaps the seal can, by swimming round the outside of the net, corner salmon in the fish court and then grasp the fish by taking both fish and slack netting in its mouth. Because of the tidal effect on bag-nets it is

not possible to cut off the angle created by the sides of the net and the small scales while it is a simple matter to do so in the case of jumper- or fly-nets.

From these results and observations it is apparent that seals can corner salmon caught in bag-nets because of the design of this type of net and of the way in which it is fished. It therefore seems that the most profitable approach to this problem now is to look critically at the design and mode of operation of this net, to try to discover whether it would be possible to alter it in such a way as to make it more difficult for seals to corner salmon without impairing its fishing efficiency.

GREY SEALS AS COMPETITORS WITH MAN FOR SALMON

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There are two main problems regarding grey seals (*Halichoerus grypus*) and their effect on salmon fisheries; the damage done to nets and their contents, and the influence of seals upon the stocks of the salmon (*Salmo salar*), from which the commercial catch is drawn. The extent of damage to nets on a sample length of coast-line in Northumberland and Berwickshire (NE England) has been considered elsewhere (Lockie, 1959).

This paper explores an aspect of the second problem, by attempting to compare the amount of salmon taken by grey seals with that removed by man. Many new facts — published and unpublished from various sources — have been discovered about grey seals in recent years and, in this paper, these facts are drawn together in order to see how far one may justifiably draw firm conclusions about competition between grey seals and man for free-living salmon.

The study area is 48 km (30 miles) of coast between Goswick, Northumberland, and Cockburnspath, Berwickshire, including the River Tweed; salmon fishing is carried on throughout its length and the Farne Islands seal colony lies 24 km (15 miles) to the south.

NUMBER OF GREY SEALS ASSOCIATED WITH THE FARNE ISLANDS, BASED ON COUNTS OF PUPS

Hewer (1957) has attempted to draw up a life-table for the grey seals of Shillay (Scottish Hebrides) compatible with the known vital statistics of this species. These were: that cow seals have their first pups at three years of age; and that bull seals do not enter the true breeding class until about their eighth year and are probably over ten years before they obtain territory on a breeding ground. The basic facts of reproduction were thus similar to those of the Pribilof fur seals (*Callorhinus ursinus*) for which life-tables have been published (Kenyon & Scheffer, 1954). Using the female life-table, Hewer (1957) then calculated the age structure and size of the Shillay colony from the observed number of pups born. Later work (Hewer, *in progress*) indicates

that cow grey seals do not become sexually mature until they are four or five years of age. Kenyon & Scheffer (1954) show that only 7 per cent of four-year fur-seal cows and 57 per cent of five-year cows have pups. The basic facts of reproduction in the two species are thus perhaps even more similar than was previously thought. Be that as it may, the fur seal life-table applied to grey seals is a useful first approximation.

Hickling (1957) has published figures of the number of pup seals on the Farne Islands in 1956, when there were 747 pups; she has now (1959) given the sex ratio of the pups marked on the Farnes with Monel Metal rings from 1952-7. The ratio of males to females varied somewhat from year to year, even when the numbers of pups involved was large: in 1956 it was 1 : 1.01.

TABLE I. *Possible life-table applied to Farne Islands grey seal population as at June, 1957*

Age in years	Percentage surviving each year	Farnes seals			
		N°	Female class	N°	Male class
$\frac{1}{2}$	40	230	Immatures = 632	230	Immatures = 632
$1\frac{1}{2}$	70	120		120	
$2\frac{1}{2}$	92	100		100	
$3\frac{1}{2}$	94	93		93	
$4\frac{1}{2}$	95	89		89	
$5\frac{1}{2}$	95	82	Mature females = 828	82	Young bulls = 233
$6\frac{1}{2}$	95	76		76	
$7\frac{1}{2}$	95	75		75	
$8\frac{1}{2}$	95	70		70	Mature bulls = 595
$9\frac{1}{2}$	95	67		67	
$10\frac{1}{2}$	95	63		63	
Over $10\frac{1}{2}$	Av. 87	395		395	

Notes:

- (1) The survival figures are adapted from Kenyon & Scheffer, 1954, p. 40.
- (2) The percentage surviving each year refers to the number of seals alive at the beginning of each year.
- (3) The number of mature females is greater than the number of pups born and is based on an 82 per cent pregnancy rate (Kenyon & Scheffer, 1954).

For the purposes of this paper I have taken the sex ratio as unity and the number of pups as 750, and from the information available have drawn up a life-table adapting Kenyon & Scheffer's survival figures as did Hewer for the Shillay colony. The estimates were then plotted against age in years and values for half years were extrapolated to give an estimate of the numbers of each age-group alive in June (i.e. half-way through the 1957 salmon-fishing season). These figures (Table I), give a grand total of 2,920 animals of all age-groups associated with the Farne Islands in June, 1957.

Not all the animals were present at the Farnes at the same time and it is necessary to enquire how the various age groups were distributed.

THE PROPORTION OF SEALS VISITING THE STUDY AREA

Much important information has been obtained as a result of the marking of seal pups carried out by Mrs Hickling and her colleagues on the Farne Islands. After independence, dispersal from the breeding colony is rapid, pups having been recovered on the Aberdeenshire coast, on the Faroe Islands and in Norway only a few weeks after birth. Dispersal is mainly northwards.

I have used the published recoveries (Telfer & Watt, 1953; Hickling *et al.*, 1955; Hickling, 1957, 1959; Coulson & Hickling, 1960) for seals of six weeks of age and over. Of seventy-eight recoveries, four were obtained from the study area.

If the seal pups ringed on the Farnes are representative of all pups from the Farnes, and if marked seals are neither more nor less likely to be recovered in the study area than elsewhere, these figures will indicate the proportion of first-year seals frequenting the study area. Table I shows that 460 first-year seals were alive in June, 1957. The number present in the study area was therefore $\frac{4}{78} \times 460 = 24$.

During 1956-8, twenty-two grey seals were submitted to me by the fishing companies in the study area. The ages of these seals have been determined by H. R. Hewer who has kindly allowed me to use data which will be published. The sex and age distribution of these seals is shown in Table II.

TABLE II. *Sex and age distribution of grey seals caught in salmon nets (Berwickshire and Northumberland coast)*

Age in years	Females	Males
1 .	8 .	1
2 .	4 .	2
3 .	2 .	—
4 .	3 .	—
6 .	— .	1
13 .	— .	1
	—	—
Total .	17 .	5

Even in this small sample two points emerge. First, only one out of twenty-two captured seals was mature. Since mature seals do occur about the nets and the estuary of the river Tweed, the capture of grey seals in salmon nets must be highly selective for immature animals. Second, the ratio of immature females to immature males (including young bulls) was 17 : 4. This is likely to be a real difference in sex ratio in the study area because in Aberdeenshire the sex ratio in first year seals captured in nets was 6

females : 21 males. Presumably males disperse further from the breeding grounds than do female seals.

However, the biased sex ratio does not affect the calculations at this stage since these are based on recoveries and age differences. We may estimate the number of immatures and young bull seals in the study area as follows:

Twenty-four first-year seals are already estimated. From age determinations of the seals captured in the study area, nine were < 1 year old and twelve older but not mature: thus the number of immature seals older than one year plus young bulls was

$$24 \times \frac{12}{9} = 32.$$

This is probably an underestimate, because one would expect seals gradually to become less prone to capture with increasing age, rather than for proneness to capture to cease abruptly at the onset of maturity. As a minimum value, then, there were fifty-six immature grey seals in the study area.

Or, one may proceed differently and assume that the distribution of marked yearlings is the same in relation to the study area as that for all immature animals (including young bulls). The only support for such an assertion is that rather few immature seals are seen on the breeding grounds at any time of year (Hickling, 1957; Farnes) and during the breeding season (Hewer, 1957; Shillay; and others).

The number of immature animals and young bulls in the study area would then be:

$$\frac{4}{78} \times 1,497 = 77.$$

The average of these two estimates is 67. Consisting of twenty-nine yearlings, thirty-five two to five year olds and three young bulls (proportions from Table II). It is likely that the number of young bulls is underestimated.

It is not possible at present to estimate the number of adult seals in the study area. Nor can we say how many seals from other colonies, e.g. from Orkney and North Rona may be present. Three hundred and fifty moulters were ringed on North Rona in 1959 but, so far, there is only one recovery, from Orkney.

FOOD EATEN

Nature of the food. Eight stomachs from seals (age groups one to four years) taken at salmon nets in the study area are available for the months June, July and August, 1956-7. But the study of the food of seals from stomachs alone may be misleading because large fish are often skinned and beheaded.

Scales and otoliths therefore do not appear and in order to identify such remains the seal must be killed before digestion has proceeded far. Again, the food of young seals may be different from that of older seals. Bearing these points in mind, the following food was found (Table III), the identification being from bones, flesh, otoliths and the horny beaks of cephalopods. Dr Bennet Rae has kindly checked the identification of otoliths and has estimated the weight of fish whence they came. Likewise Dr A. C. Stephen kindly provided estimated weights of cephalopods of the size found in these seals.

TABLE III. *Food identified in eight grey seals*
(age groups one to four years, June–August (1956–7))

	Estimated weight of prey (oz)
<i>Gadus</i> spp.	110
Cephalopods (<i>Loligo forbesi</i> and <i>Eledone cinerosa</i>) . . .	296
Salmon or sea-trout (<i>Salmo trutta</i>)	80
Total	406

Proportion by weight of salmon and/or sea-trout = 19.7 per cent.

Amount eaten. The amount eaten by common seals (*Phoca vitulina*) and grey seals per day has been estimated by Steven (1934, 1936) to be 10 lb (4.5 kg) and 15 lb (6.8 kg) respectively. Likewise the sea lions (*Zalophus californianus*) in the Edinburgh Zoological Gardens are given an average of 14 lb (6.3 kg) of haddock (*Gadus aeglefinus*) per day. If 15 lb per day of fish is a reasonable figure for mature grey seals, immatures and yearlings must take less.

Seal pups make little extra growth in their first year (Telfer & Watt, 1953) and may weigh no more than 100 lb (45 kg) at forty-six weeks. 5 lb per day for yearlings and 12 lb per day for immatures may be a reasonable guess of their food requirements.

That being so, we can make a very rough calculation of the amount of salmon eaten by immature grey seals and young bulls in the study area during the 1957 salmon-fishing season (182 days).

Twenty-nine yearling seals at 5 lb per day	= 29 × 5 × 182 =	26,390 lb
Thirty-five two- to five-year-old seals at 12 lb per day	= 35 × 12 × 182 =	76,440
Three young bulls at 15 lb per day	= 3 × 15 × 182 =	8,190
		<hr/> Total 111,020 lb <hr/>

Proportion of this food that was salmon and sea-trout =

$$\frac{19.7}{100} \times 111,020 \text{ lb} \\ = 21,800 \text{ lb (9,875 kg)}.$$

COMMERCIAL CATCHES

This information is based on: (a) confidential information from certain salmon fishing companies; (b) published accounts; and (c) estimates based on the situation and size of the fishery where the catch is not precisely known.

Catches of sea-trout and grilse (salmon that have spent just over one year in the sea) are included in the total. Where the catch is expressed in sterling, the weight has been calculated using the average price wholesale of salmon in 1957 as given by the Scottish Home Department Annual Report (1957).

On this basis the total catch for coastal stations, estuarine fisheries of the Tweed and the rod catch of the River Tweed was in 1957 approximately 731,000 lb (331,580 kg).

CONCLUSION

During the 1957 salmon fishing season, man removed 731,000 lb of salmon and sea-trout. A very imprecise calculation suggests that immature grey seals and young bulls removed 23,000 lb of salmon and sea-trout from the same area, or about 3 per cent of the total catch (range, 0.3 to 30 per cent). In addition, there is an unknown amount eaten by an unknown number of mature seals. Clearly we do not yet know enough to draw conclusions about grey seals as competitors with man for free-living salmon even on this rather well-documented section of the British coast. However, a solution to the problem, while difficult, is by no means impossible.

The more serious gaps in our knowledge which are necessary for this kind of study can be listed as follows:

- (1) The annual mortality of the various age-groups.
- (2) The exact age at which breeding commences in each sex.
- (3) The distribution of immature animals.
- (4) The age-groups frequenting the salmon nets.
- (5) A food study that takes into account the limitations of stomach analysis and the difficulties of sampling in the field.

Happily, some of these are already under investigation and we may expect others to be tackled now that Mr E. A. Smith has been appointed by the Development Commission and based at the Nature Conservancy, Edinburgh, to study the problem of seals and fisheries.

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DISCUSSION

J. B. CRAGG: If seals take an amount of salmon equivalent to one-quarter of the total catch, would this be available to the fishery were the seals removed?

K. A. PYEFINCH (Speaking for B. B. RAE): Rae does not suggest this: his point is that the presence of the seals makes the fishermen work harder for what they take.

J. B. CRAGG: But isn't it true that although the seal population is rising, the salmon catch is rising in parallel?

K. A. PYEFINCH: No marked trend in salmon catch is detectable.

J. C. COULSON: Records go back 150 years of complaints by fishermen of seal damage to salmon, and there is no evidence that this is a recent problem, nor that the recent rise in seal population is as spectacular as has been asserted. Many remote Scottish beaches were omitted from early surveys and two different census methods have been used. One was a direct count of the total number of seals visible and the other a count of the calves and a subsequent multiplication by an arbitrary figure of four. Lockley used the latter procedure: it is possible that the 1929 census was based on a direct count.

I. A. McLAREN: Based on a 1916 total of 400 animals a population rise to 1,500 by 1929 would be reasonable, but 4,000 unlikely.

E. A. SMITH: A great amount of fish of economic importance must be caught away from inshore waters. But to date no analyses have been made of the stomach contents of pelagic grey seals. Therefore Rae's estimate that seals consume one fifth to one quarter of Man's annual catch is based on inshore seals only and is not representative.

Secondly, Lockley's figure of 20,000 seals was arrived at in 1954 — six years ago. No one had been to North Rona — the 'headquarters' of the species in Britain — since Fraser Darling's 1938 visit, and no counting had been carried out in the Orkneys. Lockley's figure is consequently unreal and likely to be an underestimate.

Thirdly, we have been told that common seals consume an average of 11 lb of fish per day, and grey seals 15 lb. I suggest that we have no such information.

The real problem can be put in perspective only by considering the annual total of fish consumed by other predators. There is also competition within the fishing industry. The entrance to a river which it is claimed is robbed of salmon by seals, is frequently 'closed' by drift nets which are very successful at catching salmon before they enter the estuary.

J. MORTON BOYD: No confidence can be placed in any numerical estimates of British seal populations. In the Western and Northern Isles of Scotland there seems to have been an increase in grey seals, and new colonies have been established. This has been accompanied by a decline of local sealing industry.

It seems to me that, due to the economic implications, much more importance is being attached to the percentage of salmon taken or damaged than to the percentage of other species — which yet make up the overwhelming bulk of the grey seal's diet around Britain. Clearly a very small proportion of the grey seal population is associated with the salmon problem. By far the largest numbers of seals in the Western Isles, in my experience, are inshore feeders on rocky coasts, where they probably take saithe, lythe, and Crustacea. Attempts are being made to obtain stomach analyses.

J. DE B. STANSFELD: For twenty-five years I have been concerned with salmon fisheries. The figures we have had presented to us today are all very well, but they contain a large element of guess-work. Day-to-day observations of the actual animals remain of fundamental importance. I would like to emphasize that we handle annually an appalling number of fish which are marketable but are cut and lacerated and so of much lower value. This kind of damage affects a very high proportion of the catch. Secondly, emphasis has been laid on seals catching salmon near net fisheries and damaging nets. But seal kill salmon in places miles away from net fisheries.

H. R. HEWER: I would like to emphasize the complete uselessness of many of the figures which have been presented to us. A lot of them are not estimates: they are not even 'guesstimates'. The idea that numbers were below 500 in 1916 was just an idea, and was brought forward in connection with the Act. When Ritchie said that the population was 4,000–5,000 it was quite impossible for him to know the total even approximately. Lockley's 20,000 is little better: the figure is a compilation which is in many cases based on single brief visits to localities. The inaccuracy of such rough estimates may be shown by our recent data from North Rona: on our arrival we went briskly round the island and guessed a total figure. Later careful census and marking showed this to be 40 per cent too low. There is only one way of estimating reliably, and that is by determining the total number of *pups produced*. (It is no use just going at the end of the season and

counting the *pups surviving*.) Then you have to have accurate knowledge of the life-table for the species under your consideration. It has been estimated that bulls become mature at eight and a half years: I believe that the true figure is higher than that. I deprecate most strongly the use of figures of the degree of unreliability of most of those which we have had today.

E. B. WORTHINGTON: Although the picture is based on 'guesstimates' it seems to be one of interaction between a population with a steady upward trend — the grey seal — and another with extreme fluctuations — salmon.

Rae's paper clearly contains some sweeping conclusions, but I feel that it is most important that we examine it in full, with its supporting data, before agreeing with or rejecting these conclusions.

In spite of the inadequacy of the data and divergent conclusions that have been drawn, some interim decisions must be made about seal populations and salmon fisheries. It is evident that the policy must be based on considerations of the whole populations involved, and not on the isolated study of local aggregations of them.

F. RAW: Surely it is possible to see some figures of the losses (from nets) of salmon destroyed and damaged, the former loss being estimated, if necessary.

K. A. PYEFINCH: One has also to take into account the damage to nets, not just to salmon: such net damage may release unharmed fish.

J. B. CRAGG: Are the data published?

J. DE B. STANSFELD: The figure of the actual catches of salmon are supplied by the fisheries to the Scottish Home Department, but they are not published for ten years. There is no reason why percentage figures should not be given. Any company would be prepared to give these and to indicate the percentage of damaged fish in the catch.

I would emphasize that in Scotland we are suffering considerably from this damage. We are not asking for the extermination of seal: only for a reasonable — and quick — measure of control for an extremely expensive predator.

ON THE COMPETITION BETWEEN WHITEFISH SPECIES

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INTRODUCTION

The concept of interspecific competition has been defined in many ways. For the present purpose the following definition is adopted: competition is every interaction between species populations that adversely affects natality, survival and/or individual growth in these populations. This reading involves slight modifications from the expositions of Darwinian competition given by Elton (1946), Crombie (1947), Solomon (1949), Odum (1953), Nicholson (1954), Park (1954), and others. Competition also means that the general ecological features of the species are affected as ecological 'optima' move apart when species compete (for this modified meaning of 'optimum' cf. Nilsson, 1956 quoted by Kalleberg, 1958).

There are many old and often repeated experiences in fisheries that makes the fisheries biologist inclined to believe in the existence both of intraspecific and interspecific competition. Such experiences are the relation between fish density and growth, and the displacements affecting existing populations in a water as a new species is introduced or as fishing concentrates on some of the populations. More recently it has proved possible to introduce delicate species by poisoning the old populations. Carlander (1955) has shown that the standing crop of some species is lower if other species on the same food level exist in the lake. Most of these demonstrations are hampered by the difficulties of ruling out the effects of changes in the environment other than the changes in the fish fauna and the difficulties of getting a good measure of 'the adverse effect' on all the competing fish populations.

The recent advances in the study of fish behaviour have revealed that many species of fish defend territories also out of the spawning time. This population regulating mechanism leads to a competition that is both intra- and interspecific and also influences individual growth (Newman, 1956; Kalleberg, 1958). Also in schooling fish species such as herring there exist

* The material will be more exhaustively presented elsewhere. The material concerning the first-year biology is mainly treated by Lindström and that concerning the adults by Nilsson. We acknowledge with thanks the assistance of Mr. I. Sasserson in working up some material on stomach contents.

FIG. 1.—Frequencies for different numbers of gillrakers. The best way to identify a whitefish population is to count the gillrakers of the members. Modified from Svårdson, 1957.

ethological community effects other than direct food competition that might influence both survival and individual growth (Blaxter & Holliday, 1958).

The present example of competition belongs to freshwater fish ecology. In a survey of this field, Larkin (1956) concludes that 'many species have a

relatively wide tolerance of habitat type, a flexibility of feeding habits and in general share many resources of their environment with several other species of fish'.

The method employed by the present authors is to study the ecology of some whitefish species when living sympatrically in different combinations and different lakes. Svårdson (1954, 1957, 1958) has shown that there are some indications that a whitefish species restricts its niche when living sympatrically with other whitefish species and that this suggests an effect of competition. Material from such lake studies cannot be expected to be as conclusive as laboratory experiments, when it is considered that the effect of competition cannot be well delimited from the effect of differences in the genetic equipment of populations belonging to the same species, nor from environmental differences between lakes other than the differences in the whitefish fauna.

FIG. 2.—Map. Lake Vojsjön is deep, Lakes Uddjaur and Storavan are shallow. Altitudes 413, 419 and 419 m. Stations A, D and G are the spawning streams of *C. peled*.

The genetic differences between populations of one whitefish species are illustrated by Fig. 1, the number of gillrakers within populations being a stable character according to Svårdson (1957, 1958). Interspecific differences are also illustrated in Fig. 1. Both kinds of differences illustrate Svårdson's

view on the systematic position of the whitefish species: they are so closely related that introgression occurs very frequently (and has gone very far in environments with few niches, reaching replacement or complete fusion of populations).

Darwin pointed out that the intensity of competition must be directly related to the degree of ecological similarity between the species involved. The mechanisms of competition are still very incompletely known, and the present material on the biology of young and adults of closely related and ecologically similar whitefish species allows of only a fragmentary interpretation of the competitive mechanisms working.

COMPETITION DURING THE FIRST YEAR

It is often stated that fish are subject to a heavy mortality in their fry and young stages. As the factors governing this mortality vary between years, the strength of the different year classes varies correspondingly. Most likely the instantaneous mortality coefficient (Beverton & Holt, 1957; Ricker, 1958) typical for the first-year biology of a particular population, varies not only between years but also with the season and the density of the population. If the whitefish species populations adversely affect each other's survival during these early life stages this is an example of competition. A survey of the first-year biology will give some suggestions.

The first-year biology has been studied in Lakes Uddjaur and Storavan (Fig. 2). There exist three species: *Coregonus peled* (Gmelin), *Coregonus lavaretus* (Linnaeus) and *Coregonus pidschian* (Gmelin). The spawning places of *Coregonus peled* — in the streams — are well separated from those of other whitefish populations. *C. pidschian* and *C. lavaretus* have in some cases the same spawning places and the same spawning time.

There is reason to believe that for any of the three species the fraction surviving until hatching could increase in an imagined situation where the species was suddenly left as the only spawning whitefish in the lake. It does not necessarily follow that the relative numbers of the three whitefish species at hatching in the situation which actually exists have any significance for the relative numbers of the adults: this is still an open question.

The hatching times of the whitefish species differ. The different sizes of the eggs of the species result in different sizes at hatching, the fry of *C. lavaretus* being smaller than the others. Strong evidence of the concurrence of large size and good survival during the first year has been gathered for territorial fish (Brown, 1946, 1957; Kalleberg, 1958; cf. Miller, 1959). The same probably also applies to schooling fish (Svårdson, 1949), but the relations between species must be determined in a more complicated way.

The fry and young of *C. peled* are for some time isolated from other whitefish young and occupy the spawning stream and the lake downstream near the inlet. This conclusion is based on observations of the distribution of the spawning parents, since satisfactory identification of the young (by counting the gillrakers) is not possible until late July. The habitat segregation between *C. peled* and *C. lavaretus* is broken down during late summer and

FIG. 3.—Food of young *Coregonus peled* and *C. lavaretus* in Lakes Uddjar and Storavan. Number of stomachs with plankton (white columns) or insects (black columns) forming more than half the stomach content. The intraspecific variation indicated by the figure is probably in part attributable to a diurnal feeding cycle, the young feeding on plankton in the afternoon and insects in the night.

autumn as the *C. peled* young move out in the lakes downstream from the spawning places. Also essential for understanding the first-year biology are the striking similarities in the feeding habits of young *C. peled* and *C. lavaretus* during late summer and autumn (Figs. 3 and 4), and the fact that the growth curves of the two species do not diverge until after the first year, although *C. peled* fry hatch earlier and are longer at hatching (Fig. 5).

These facts are interpreted as follows. There is an urge to grow at a certain rate and to reach a minimum length at the end of the first year. Ricker &

Foerster (1948) have pointed out that a rapid growth can imply that the time decreases during which the young are vulnerable to predation (cf. also Larkin & Smith, 1954 and Foerster, 1954). The interpretation is also consistent with the observations that the first-year growth is fairly stable and does not react in the same way as adult growth (Hile, 1941 and Le Cren, 1958).

FIG. 4.—Food of young *Coregonus peled* and *C. lavaretus* in Lakes Uddjar and Storavan. Mean number of the different food items per stomach. The material indicates pelagic feeding habits. In the left part of the diagram only plankton is represented though insects also existed in the food — cf. Fig. 3. In the samples from 10th October 1954 (represented in Fig. 3) the food consisted only of *Bosmina*. Note: the log. scales for plankton and insects differ.

FIG. 5.—Growth curves for *Coregonus peled* (above) and *C. lavaretus* (below) during the first summer and autumn. The curves are drawn free-hand and based on some data on total length observed from seine-caught young.

The common diet of the *C. peled* and *C. lavaretus* young in the same habitat also calls for an explanation. Lack (1947, 1949) and Crombie (1947) state that a common diet for closely related species in the same habitat can be interpreted either as a sign of a temporary superabundance of food or as an indication that parasites or predators are controlling the numbers of both species. The latter interpretation is the more likely one in the present case but there are certain specific characteristics. The abundance of food should be important if the growth rate affects the length of the predation period. Furthermore, the whitefish young themselves do not perhaps greatly affect the general density, e.g. of zooplankton, but they may very well temporarily deplete rich zooplankton accumulations, and such accumulations are probably important for the growth rate. Mortality is thus brought about through a complex of factors, among which density of food and activity of predators are important. Moreover, the measure of the similarity as regards choice of food and habitat may be crude, particularly as the food-choice mechanism is not yet well developed (see below).

Some sets of circumstances during the first year should favour one whitefish species, other situations should favour another species, but our knowledge on this point is very incomplete. The biology of the whitefish species during this year is, however, so similar that, in an imaginary situation where one species was suddenly left as the only whitefish in the lakes, any one of them would probably have a higher fraction surviving between hatching and the end of the year.

FIG. 6.—In Vojmsjön *C. peled* is a dwarfed plankton- and insect-feeder, but *C. pidschian* mainly a bottom-feeder of medium size.

FIG. 7.—In Uddjaur-Storavan *C. peled* is a fast-growing insect-feeder, *C. lavaretus* a dwarfed plankton-feeder and *C. pidschian* a medium-sized bottom-feeder. *C. peled* has in both lakes an obvious tendency to feed on surface organisms such as emerging and flying insects and ceratopogonid-larvae.

COMPETITION IN THE ADULTS

Turning now to the adult fish, the design of their ecological isolation seems much easier to reveal than that of the younger stages. This is in a way puzzling as the most effective segregating mechanisms should be expected during the time they are most wanted, namely in the early stages when the size of the populations are mainly decided. In contrast, the adults display obvious specific food preferences that are recombined and modified from lake to lake (Figs. 6 and 7). This phenomenon is made possible by a food choice mechanism. This mechanism involves a temporal learning to concentrate on specific food objects as they give the best reward for the energy spent (cf. Allen, 1941; Nilsson, 1955, 1957 and 1958; Hinde, 1959), and first seems to become fully effective when the fish has reached a certain age or size.

C. pidschian displays the most fixed pattern in feeding habits; it has in both cases an intermediate growth (Fig. 8) and is mainly a bottom feeder with strong exploitation of chironomid larvae, caddis fly larvae, *Pisidium*, *Limnaea* and bottom-dwelling crustaceans. *C. peled*, on the other hand, appears in Vojmsjön as a dwarfed plankton-eater (with a diet also comprising some insect-food), in Storavan-Uddjaur as a fast-growing insect-eater. *C. lavaretus*, which is not present in Vojmsjön has in Storavan-Uddjaur on the whole taken over the food niche occupied by *C. peled* in Vojmsjön and appears as a plankton-eater of ciscoe type.

When trying to interpret these facts it should be observed that food competition is difficult to trace in fish, as feeding habits of fish are mostly very flexible and the food niches of different species very often considerably overlapping. To measure the degree of competition by measuring the degree of similarity in feeding habits between sympatric fish species must be wrong as similarity is often rather a sign of superabundance of food (cf. Nilsson, 1955). Nor is it of course correct indiscriminately to interpret dissimilarity as a sign of competition as it might as well often be a sign of what Brian (1956) calls selective segregation, i.e. a segregation most frequently occurring between phylogenetically distant forms, that fundamentally should each keep to the same habitats or feeding habits whether living sympatrically or not, and whether being restricted to limited supplies or not. A better method might be to compare feeding habits as well as other ecological characteristics of closely related species when living allopatrically and sympatrically in different combinations. Moreover it is necessary to study the variations in feeding habits between years, seasons and life stages (cf. Figs. 6, 7 and 9).

The present authors, in agreement with Svärdson (1954) and in analogy with the findings from other food selection studies (cf. e.g. Lack, 1947; Gibb, 1954; Nilsson, 1955) interpret the differences in feeding habits between

FIG. 8.—The growth of *C. peled*, *C. lavaretus* and *C. pidschian* in Uddjaur-Storavan and Vojmsjön.

FIG. 9.—*C. lavaretus* changing from *Bosmina* to other food when reaching a size of 140–155 mm, July 1954.

the three species primarily as a result of interactive segregation (Brian, 1956) that has found different expressions in the two cases because of differences in the species combinations as well as in the general conditions of the lakes in other respects. Genetical differences within species and selective segregation between species are supposed to play subordinate roles. It is thus suggested that interaction between the three species has forced each species to retire from an unrestricted feeding ecology, typical for whitefish in general, to a more specialized one.

The remarkable double existence of *C. peled* as dwarfed plankton eater in Vojmsjön and fast-growing insect-eater in Storavan-Uddjaur where *C. lavaretus* has taken over its place and the role of plankton-eater, gives reason for stressing the differences in the physical conditions of the lakes in question. Vojmsjön is a narrow and deep lake with a narrow littoral zone. In an oversimplified way it could be called a lake with few whitefish niches. Storavan-Uddjaur, on the other hand, which are wide and shallow lakes with wide littoral zones split into mosaic-shaped complexes with islets, sounds, basins and skerries, could be called lakes with several whitefish-niches, that with this interpretation offer several species of whitefish the possibility of living side by side, and, moreover, permit one species that in another situation is dwarfed to surpass the other species in individual growth.

RESTATEMENT OF THE CONCEPT OF COMPETITION

Following the survey of the factors acting in the competition between the whitefish species, a closer analysis of the competition concept will now be attempted. In the Introduction, competition has been defined with special regard to the general theme of the Symposium. If a population obtains a bad individual growth, it is certainly adversely affected from the viewpoint of human beings exploiting that population. If for a moment we consider intraspecific competition, the only indication of the success of a particular type is that its offspring attain a supernormal numerical proportion of the population in a sequence of generations. The success in interspecific competition is more complex. Without entering into the question of evolutionary trends, one can state that it is often justifiable to use number as a measure of the success in interspecific competition also. This, however, is not always an adequate method. From Elton's exposition (1946) it is possible to derive the idea that the success in competition may also be judged by the amount of the environmental resources that the species utilizes. This is at least easy to realize when one regards the problem from the point of view of the situation of the species losing resources. Other things being equal, a change in growth (length or weight) involves a change in the utilization of the resources. Again,

if the life-span is short and sexual maturity soon attained — as in the case of *C. lavaretus* in Lakes Uddjaur and Storavan — the demand on the resources is greater than for a population with a longer life-span and retarded maturity but with equal standing crop in weight and an essentially equal length distribution.

These points of view may also prove useful when discussing 'optima' (Lindström, 1958). 'Optimal conditions' do not necessarily characterize those habitats with the highest average density, as other habitats may induce a faster rate of turnover and a greater demand on the resources and hence a more successful competition with other species.

EXPECTED CONSEQUENCES OF INTERSPECIFIC COMPETITION FOR EXPLOITATION

During the course of exploitation of a particular species the decreased density of adults decreases intraspecific competition with better individual growth and perhaps also decreased natural mortality rate for adults of that species as a result. To the extent that the species itself cannot take care of the released resources, the competition with other species also decreases, resulting in a gradual breakdown of the limits of the niches with consequences for individual growth and survival also in the interacting species. An important question arises in this connection: is it possible to affect in any significant degree the growth of a dwarfed plankton-eater by hard exploitation of that species only, if it coexists with competing species that have occupied all food niches that give fast growth? Hypothetically the answer is no, but we have no material to illustrate this point.

Exploitation of one species may also affect the survival in young stages of all whitefish species in the lake, but the details are difficult to envisage.

SUMMARY

The first-year biology of three *Coregonus* species has been studied. *C. pidschian* and *C. lavaretus* have the same hatching places in some cases. The habitat segregation between *C. peled* and *C. lavaretus* is broken down during late summer and autumn; their feeding habits are similar and their growth curves do not diverge until after the first year. These similarities are such that it is difficult to envisage how the necessary isolation is established during this year of high mortality.

In the adults there is an obvious segregation into different feeding niches. It is suggested that this segregation is made possible by a behaviour mechanism, resulting in a changeable food specialization and that the segregation is primarily the result of species interaction. The interaction also has effects on

the growth of the fish, some species being forced to eat food that causes slow growth (plankton).

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DISCUSSION

M. GRAHAM: Is the taxonomy of the species described secure, and are the differences between them marked?

T. LINDSTRÖM: Identification of species is based on gillraker structure, there being no other significant character to use. I am convinced that they are species as described by Svärdson in the papers cited above.

G. V. NIKOL'SKIĬ: The data presented are a very good example of the general rule that in the same faunistic complex, the different fish species present take different food, at least in the adult stage. But if we wish to determine the nature of their interrelations, or competition, we must consider not only the composition of the diet but also the rate of growth and the stomach index. The variability of the food resources in the Arctic is reflected in the variability of food in the stomach contents. From north to south in the northern hemisphere, it is found that the northern forms have more varied stomach contents than the southern ones. This phenomenon is connected with differences in the stability of the food organisms. There is a need for the quantitative estimate of food demand. In sparse feeding times there are several foods: in times of rich food specialization may occur.

E. D. LE CREN: I agree entirely. We certainly need really quantitative estimates of food consumed. For example, when I estimated the consumption of food by pike of different ages, it appeared that the pike population as a whole may consume as much plankton as fish.

I. A. McLAREN: Does the nature of the food organism affect the number of gillrakers in larval fish?

T. LINDSTRÖM: No evidence of this for young fish is available. There is a suggestion that the number of gillrakers affects the food of the adults.

W. E. FROST: I had understood from previous work that each plankton animal is taken individually in the adults of these species, as it is in char. The gillrakers are therefore unlikely to have much connection with planktonic feeding.

THE EXPLOITATION AND CONSERVATION OF LARGE
TERRESTRIAL MAMMALS

THE CONSERVATION OF AFRICAN PLAINS GAME AS A FORM OF LAND USE

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As a land-hungry human population crowds in more and more on the remaining wild places of the world, the problem of what is to become of the remaining populations of indigenous plants and animals assumes a greater and greater urgency. The naturalist-scientist and big-game hunter are both easily satisfied that samples of these organisms should be preserved. Often the novelty of seeing wild animals in their natural surroundings has created a tourist interest and a trade which has persuaded even governments to set aside nature reserves and national parks (in Africa) in which to concentrate this interest.

It is unfortunately true that little attention has been paid by ecologists to the scientific basis of these measures, and I propose to record some reflections on the problems which are involved in one type of game conservation — taking as an example the plains game in East Africa and to limit the scope somewhat particularly, to those visiting the Serengeti Plains.

PLAINS GAME AND THEIR HABITAT

In the Serengeti one may still see some of the remaining herds of African plains game animals and their attendant predators; on the one hand the wildebeest, zebras, gazelles, buffalo and numerous forms of antelope, large and small, and on the other, lions, leopards, cheetahs, hyenas and the like.

Most of the plains game are migratory animals and as far as is known they are now confined to arid areas with seasonal and uncertain rainfall. Three types of locality are thus involved in the typical habitats — wet-season grazing, dry-season grazing and migration routes between. In Northern Tanganyika the wet-season grazing lies on the famous Serengeti Plains — deep sediments with, in the east, a covering of fertile volcanic ash, lying at an altitude of some 1,650 m (5,500 ft) in the lee of the Crater Highlands.

These are a typical Tertiary volcanic upland area with peaks of between 3,000 and 4,200 m (10,000 and 14,000 ft). The estimates of rainfall that are available for all this region show averages of 760 ± 50 mm (30 ± 2 in.) per annum with some regularity, but the rainfall on the plains is known to be uncertain, falling below the minimum for arable husbandry (*c.* 500 mm) in one year out of five (Glover & Robinson, 1955). The rainfall in the Crater Highlands, though of the same average order, leaves a margin for charging ground water springs and rivers owing to the lower evaporation rates at higher altitudes. This may be illustrated by a figure showing the variation in potential evaporation with altitude (Sansom, 1955). At about 2,100 m (7,000 ft) the annual potential evaporation falls to 760 mm and thus at and above this height there is a rainfall which would maintain permanent forest vegetation and which at higher levels still, supplies a considerable margin for maintaining springs and rivers throughout the year. The Crater Highlands are thus a suitable dry-season grazing for the plains animals, with a short migration path of about 15–25 km through the intervening *Acacia* woodlands and scrub. Unfortunately the native Africans are the Masai, a pastoral tribe that lives on blood and milk from their herds of cattle. They have similar migratory habits to the plains game. They compete directly for pasture and water and are rapidly replacing the plains game in this area. The Masai, moreover, are steadily destroying the high level woodlands by fire. There is much, though not absolutely conclusive, evidence that this forest destruction is having an adverse effect on the water regime, a vital matter in an arid climate.

Most of the plains game in the Serengeti region possess a very much longer migration cycle. They follow the river valleys running from the plateau of the Serengeti Plains down to Lake Victoria, where there are alluvial pastures at about 1,350 m (4,500 ft) near the lake. These are 'dambos' or 'mbugas' (see Michelmores, 1939), waterlogged in the wet season so that there is little or no tree growth, but good pasture in the dry. The better drained sites among and surrounding these alluvial pastures are 'savannah', now being heavily occupied by African cultivators. They are encroaching on the pastures and, as is usual, the carbohydrate-rich and protein-poor diet derived from their 'shambas' (gardens) leads to an intense desire for meat, so that the game animals are heavily poached for this purpose. Both the normal dry- and wet-season grazing grounds of the plains game animals are thus becoming subject to severe human pressure, in the former case from arable cultivations, in the latter from pastoral competitors.

The intervening migration routes are mostly 'bush' of various types, often heavily infested by tsetse-fly, varying from 'savannah' through *Acacia* scrub to thorn-scrub. The proper form of land use of this type of country is not

known. Whatever it may be, the soils and vegetation here are being heavily punished by indiscriminate burning, and as a result the vegetation almost always shows signs of being a fire-climax (cf. Shantz & Marbut, 1923), lower in nutrient status and in water status than it should be.

The possibility of maintaining the plains game thus depends on sacrificing to them a useful proportion of the dry-season grazing, a share of the wet-season grazing, and probably also on maintaining the fertility of the intervening 'bush'.

It will be seen that the proposals necessary to preserve the migration cycle of the plains game here involve an area of something like 5,175 square km (2,000 square miles). Some of the ecological problems involved may now be considered.

RIVAL METHODS OF PROTEIN PRODUCTION

There is much evidence that protein production is often a desirable form of land use in these arid climates. In East Africa generally, the soils show very rapid nitrogen turnover, organic matter decays very quickly and the high calcium status of the rooting levels and vegetation in the plains is a feature normally associated with a protein-rich vegetation as it is here. The marginal level of the rainfall in the Serengeti and its uncertainty, however, preclude the regular use of cereal crops for protein production, as on an average the rainfall is likely to be insufficient in one year out of four or five (Glover & Robinson, 1955). Animal cropping is thus considered to be the present alternative, and it is evidently also the natural ecological form of land use. We can in the Serengeti contrast this natural form of land use in what we can call the plains-game eco-system with the human pastoral form evolved and followed by the Masai.

DIFFICULTIES OF THE HABITAT

In addition to the seasonal scarcity of water, an obstacle to the use of domestic stock and especially to human occupation in the Serengeti is the character of many of the sources of water. As the dry season develops, the surface waters accessible to animals become extremely saline and in the foothills of the Crater Highlands and on the volcanic dust areas, the waters may contain quantities of fluorine which would be highly deleterious to human beings and harmful to most forms of domestic stock. A concentration of fluoride of the order of three parts per million of water is accepted as the desirable limit for human beings and 15 p.p. mill. is usually regarded as the limit for cattle, while 18-25 pp. mill. are known to give harmful effects in Tanganyika. Amounts of this order or above are frequent in the Serengeti surface waters (Pearsall, 1957).

The wild animals use these waters for only a short period if at all, and do not appear to suffer from them in any way. On the other hand the Masai cattle in this area, though apparently able to survive, often show remarkable signs of fluorosis including softened bones and deformed jaws, which are attributed to the continual use of this quality of water in wet season and dry. It must be supposed that this is a factor which would prevent the use of more normal breeds of stock as it is known to do further east in the Meru district. The wild game are either immune or their mode of seasonal migration enables them to avoid the effects of the toxic waters.

ADAPTATIONS TO EXTREME HABITATS

This example may illustrate a general feature involved in the use of any extreme or 'difficult' habitat. Are not the organisms making up the natural eco-systems likely to be better adapted to existence there than would be any domesticated or imported animal or plant? A biologist might well argue that the natural eco-system has taken ages to evolve and its successful existence shows that the dominant organisms have at least achieved survival value. Imported organisms are likely to lack the essential adaptations unless brought from a closely similar environment.

One of the striking features of the plains game in my experience has been the magnificent condition in which they appear even under arid conditions which seem to be far from ideal for grazing animals. Physiologists and veterinary officers have discussed the possibility that some features of the diet might exist on these arid grasslands which particularly improve the protein metabolism or act in the animal body in a protein-sharing role. This would be a favourable factor in addition to the fairly high protein content of some of the grasses eaten. A difficulty is that even the native breeds of cattle do not flourish in the same way, and their condition is generally markedly inferior to that of the wild game — even though they can survive in conditions which would rapidly prove lethal to European cattle. In the case of the African buffalo, it has been found (Harthoorn, 1959) that these animals will thrive and gain in weight on natural grasses which will not serve to maintain weight even in the native cattle. The buffalo will give larger gains in weight than either native or European domesticated animals on most forms of native herbage.

There seems to be little doubt that domestic cattle suffer from various physiological disadvantages in this environment. The improved European breeds, for example, suffer from the fact that the hair length or coat length is controlled by daily light duration. In the relatively short 12-hour day of the tropics, breeds from temperate climates produce their long 'winter'

coats. They are unable to alter their metabolism accordingly, especially in respect to heat loss, so that in a warm climate they lose condition to a remarkable extent, becoming also predisposed to any disease infection which may be in the vicinity.

The wild game are adapted to this environment also in their immunity from many if not most of the cattle diseases, and especially to those associated with trypanosomiasis. Domestic breeds of cattle are susceptible to these diseases and, with sheep and goats, are regularly attacked by the *Glossina* species found in the tsetse-infected bush which forms the migration paths of the game. In recent surveys of the blood types present in *Glossina* spp. in East Africa, no flies were found to have fed on the commonest forms of plains game, wildebeest, zebra, hartebeest and topi, and very few on impala, eland, waterbuck, duiker and buffalo; even where these were numerous (Hindle, 1959). Domestic animals were always attacked. These various lines of enquiry suggest that the wild game may have adaptive advantages in arid and disease-infested country such as that we are talking about, and thus it might well be ecologically justifiable to think of using them and of harvesting them as the protein crop. This could make their preservation a justifiable method of land-use.

COMPARISON OF SIMILAR FORMS OF LAND USE

If the arguments used earlier are correct, then the comparative basis of rational biological forms of land use would be the amount of protein they would yield from a given area. As an illustration I shall attempt to estimate the yield given by wild game in the Western Serengeti with that given by the Masai pastoral economy in and around the Crater Highlands, where it excludes most of the game. The game use the western bush and the river valley in the dry season, where there are no Masai. Both the game and the Masai share the Serengeti plain in the wet season. The main game migration routes as we have seen take in some 5,000 square km of country. The data for the Masai refer to an area which must be generally similar in size, but it includes some forest and some high mountain, and as I wish to avoid any reduction of the apparent value of the human economy, it will be wiser to regard the Masai as using definitely and intensively not more than 3,875 square km (1,500 square miles). Thus the attempt to estimate the stocking intensity for Masai cattle, sheep and goats, which follows will give rather overestimates than underestimates. In this area of about 1,500 square miles there are about 9,000 Masai (Grant, 1954) and they own some 120,000 cattle, each about the size of a Jersey cow. There are also some 200,000 sheep and goats of large breeds (Pearsall, 1957). By weight this will give about one

human being to forty to fifty herbivore units, the human animals being directly dependent on the herbivores for milk and blood (flesh is not eaten; a cow can be blooded about once a month). Putting the matter in another way, the stocking intensity used in the Masai pastoral areas, where there are the best supplies of water and the most luxuriant vegetation, is somewhat less than 80 cattle and 133 sheep or goats per square mile and this would support between four and five Masai. (Compare this with the 300 small sheep per square mile which is the typical stocking intensity on a sheep walk in Highland Britain.)

In the 2,000 square miles given over mainly to plains game, the available estimates, probably more approximate, suggest about 100,000 wildebeest, about 55,000 zebras and some 175,000 (Thomson's) gazelles. Each of these figures could vary by 10,000. The wildebeest and zebra weigh about as much or rather more than Masai cattle, the gazelles rather less than the domestic sheep or goats. These figures, however, take no account of the heavy game in the area, buffalo and giraffe (to say nothing of rhinoceros and elephants), each unit of which would weigh perhaps three times as much as one cattle unit, nor do they estimate the many other types of large buck, some of which are numerous, e.g. topi, impala, hartebeest, and others less common. I thought that collectively these did not much exceed zebra in number, so that we can be as accurate as our knowledge will allow, but probably underestimating if we say that all these additional species would not exceed another 50,000 individuals of an average size of about that of a zebra. We thus arrive at a total of about 200,000 large and possibly 180,000 small herbivores, that is about 100 large and 90 small herbivores per square mile. As the gazelles are smaller and lighter than Masai sheep, the total weight of stock produced is evidently not greatly different from the 80 cattle and 133 sheep and goats per square mile of the Masai economy. Although the latter is based on what looks to be more fertile and better-watered country and is an over- rather than an underestimate. Both types of stock, of course, use the Serengeti grasslands in the wet season.

I confess that when I first arrived at this type of comparison from very rough field estimates I was somewhat surprised. It means that the natural eco-system on the *poorer* part of the area is as biologically productive as the human pastoral system in the *better* regions. Moreover, while on the whole the Masai have been extending their area of occupation in recent years, the numbers of cattle in the Masai territory have not varied greatly. They have been approximately constant in the six years for which figures are available since mass inoculation for rinderpest was introduced. At any rate I think it must be asked why with more intensive occupation and the better habitats, the man-controlled pastoral system does not manage to produce a much

greater head of stock. It has been suggested that the stock numbers are now limited by drought not disease, but I think the real answer is a nutritional one. It may well be that the plains game are (as was suggested above) better adapted to this country.

But there is also a probability of habitat deterioration under the Masai pastoral use. I believe, though detailed evidence is lacking, that the Masai have continually used fire in attempting to control vegetation, to enlarge the grasslands and (they say) especially to remove ticks and to get an early bite for their herds and flocks. Much of the area they have used in the Crater Highlands is thus covered now by fire-climax vegetation which is little used by stock except when it is very young. One grass present in the native woodlands, *Eleusine jaegeri*, which grows in large tussocks and as a result is almost undamaged by burning, has become dominant over large areas of former woodland. Another tough and tufted species which is now dominant over large areas, *Pennisetum schimperi*, also appears to represent a vegetation of the fire-climax type in places where there has been continued over-grazing. These plants are species of relatively low protein content, in contrast to other types of grass, *Cynodon*, *Digitaria*, *Themeda*, which have been unable to survive the continued fire-damage and the lowering of the nutrient status of the soils.

GAME-CROPPING AS A PROTEIN HARVEST

The main point, however, is that the uncared-for game apparently produce as much or more protein as domestic stock, even if confined to areas which are mostly tsetse-infested bush. It seems fair to ask whether the direct cropping of the game for protein for feeding indigenous Africans is not a method of land use which is worthy of trial.

In Uganda, even now, wild game yields 13 per cent of the total meat used and in some country districts from 60 to 70 per cent of the meat is derived from this source. About 1,000 tons of this meat comes from a single animal, the African buffalo, which in addition to immunity from disease, including trypanosomiasis, will thrive on grasses which do not support native cattle. It is believed that the numbers of buffalo used could be raised fivefold without depleting the existing stock (Harthoorn, 1959).

In Uganda also (around the Queen Elizabeth National Park) it has become necessary to limit the numbers of hippopotami. In a comparatively limited area adjacent to the Park, it is expected that it will be necessary to market some 1,200 animals a year, averaging over 3,000 lb each in weight, if the required limitation in numbers is to be maintained (Bere, 1959).

No good data are yet available for the plains game. There is, however, already a considerable cropping effect in the western Serengeti from the

poaching prevalent there, and if this is eliminated I should be surprised if it were not possible to harvest much more than 5 per cent of the present population without reducing the gross numbers. It must, of course, be recognized that the balance of predators to herbivores will also need supervision as in effect any method of harvesting simply substitutes a human predator for a wild animal.

ECOLOGY OF PROTEIN PRODUCTION

Both the harvesting of game as human food and the provision of tourist facilities would help to justify the maintenance of national parks as a form of land use. Nature conservation of this type in East Africa is scientifically justifiable on much stronger economic grounds. We want to know, before they are destroyed, how these eco-systems work and remain productive under adverse and arid conditions.

Their productivity is, of course, a balance between two things:

- (i) The primary productivity — the amount of energy (sunlight) which can be fixed by plants in the form of dry matter and especially of protein.
- (ii) The conversion ratios — how much of the primary production can then be got into the form of herbivorous animal or higher.

The losses in both cases seem to be tremendous, and in conclusion, a brief consideration of these subjects may be of value.

Primary production in the Serengeti depends very much on water and this in turn means getting the water into the soil as Perriera (1954) has shown. Low soil temperatures (due to a sufficient shade from vegetation) and a good soil texture (associated with the above and with a rather unknown effect due to the incorporation of vegetable residues into the soil surface) largely determine whether the rain penetrates or runs off on the surface, leading to soil erosion.

Any form of extreme destruction of the vegetation cover is thus harmful to the water relations and the common statement that East Africa is drying up is true in as far as it describes the widespread results of over-grazing and over-burning.

The second important feature of a protein-producing system is the conservation of nitrogen, the element drawn from the soil in largest proportion. Much energy is used in converting gaseous nitrogen into organic forms, and when so converted it should be conserved. To burn the vegetation doing the conversion and containing the converted nitrogen — the protein — usually results in diminishing the proportion of nitrogen in the nitrogen cycle by more than can be taken out in the form of a protein crop. Nevertheless fire is almost always used in African pastoral economies — so much

so that a great part of the so-called 'bush' is believed to represent fire-climax vegetation (Shantz & Marbut, 1923), degraded and often thorny forms of fire-resistant bushes which have replaced more luxuriant woodlands and which represent lower levels both of water status and nitrogen status.

Much could be said about the possible effects of unsuitable practices on the vegetation. The main thing to be emphasized is this — that the amount of production depends on the amount of energy absorbed and used. Bare earth, whether from over-grazing or from burning, is useless and the vegetation cover ought to be maintained at a depth sufficient to absorb all or most of the incident light and to fix all the available nitrogen.

Turning now to the conversion ratios, a major ecological problem is how much of the energy and nitrogen so fixed can be converted into animal population in an eco-system which is in a steady state. We are accustomed to think of stall-fed beasts as requiring about eight times their own dry weight of food in growing to maturity. Thus one might expect that expressed as standing crops in the best conditions the balances of plants : herbivores : carnivores might be represented as 100 : 10 : 1.

In Masai land we have seen that the ratio of herbivore to man is something like 120 cattle and 200 sheep or goats to nine human beings of all ages. In terms of weight this means about forty parts of herbivore to each human being. There is reason to believe also that the ratio vegetation : herbivore is at least 50 to 1 in equivalent weights, and possibly as high as 100 to 1. One of the difficulties of giving a better approximation here is that no actual measurements of herbage weight are available. One can only say that the ungrazed grasses, for example, suggest an annual dry-weight production of the order 5-10,000 lb/acre (7-14,000 kg/hectare) by comparison with English examples. Much of the vegetation considerably exceeds this figure. Let us therefore take the estimates to be of the order of magnitude of

Vegetation	Herbivore	Carnivore
100	: 2	: 0.05

recognizing that these are probably optimistic and underestimate the conversion losses. Ratios of this order of magnitude show, however, that very large losses of protein and energy take place in these conversions in a semi-natural system like this. Clearly here is a point at which thought on conservation should start.

Deevey (1956) has suggested that such ratios may well indicate the insurance necessary in an adverse habitat. The argument could be that the fluctuating secondary population will only occasionally build up to the level at which damage to the primary or 'food' population takes place. When this happens there will of necessity be a subsequent decline in the grazing population.

The average level of the latter will tend to remain below that representing the average amount of food it is possible to take without damaging the food population. The fraction representing the conversion ratio will thus always be less than one-tenth say (if this is the best possible) and the fraction will be smallest where the habitat is in other respects most severe.

There are, of course, other possible explanations of variations in the conversion ratio. It seems probable that well-adapted animals, well adapted to a particular habitat, would give a larger conversion ratio than unadapted ones. This at least seems to be the implication of Harthoorn's data for buffalo, that they flourish on diets on which domestic animals cannot maintain themselves. This also would explain how it may be that the plains game give as high a stocking intensity in a less favourable habitat as Masai cattle do in a more favourable one.

But in the latter case we have already seen what may be still a third explanation of a low conversion ratio — the unsuitable and unpalatable character of much of the fire-climax vegetation which has resulted from bad land use. This means that only a fraction of the vegetation is used as food.

We are thus brought back to what many distinguished conservationists have emphasized as the first necessity of wild-life management — the conservation of the habitat. In semi-arid Africa this is, I believe, first and foremost — the maintenance of a natural vegetation cover or else its replacement by one which possesses similar qualities in respect of light absorption, protein synthesis and soil protection — throwing useful shade, maintaining soil structure and the nitrogen cycle, and preventing soil erosion.

Secondly, if we are to use animals for protein harvesting, we shall need suitably adapted species, even if they are wild, in order to get a high yield. The criterion of suitability is adaptability in that particular habitat and not herdability or any of the other traits characteristic of many domesticated breeds.

In conclusion, I think the greatest need is for the fullest possible study of the eco-systems in these somewhat arid habitats. The ecology of 'bush' and the neighbouring seasonal grasslands is practically unknown in spite of its quite reasonable natural production. No satisfactory form of land use for it by man has been devised. A study of the natural biological potential would undoubtedly be of the greatest value both from scientific and economic points of view. Here is the real reason for national parks and for a trained biological service to maintain them and study them.

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DISCUSSION

J. B. CRAGG: I think it is fair to point out that the Masai do use their cattle to produce protein in the most economic way — by bleeding them. My second point is to ask whether the redesigning of the park has interfered with game migration routes.

W. H. PEARSALL: The redesigning of the park was done hurriedly and it is now clear that the best dividing line was not found. We chose a provincial boundary: in fact nomadic peoples and game alike transgress such lines. A considerable proportion of the wildebeest calve east of the boundary. But the park is a viable unit, and would be even if limited rigidly by fencing.

J. B. CRAGG: Are the Masai increasing?

W. H. PEARSALL: They will do so slowly. They are traditionally a raiding people. Nowadays they cannot raid for wives, but buy wives from adjoining regions. These have a pastoral tradition and consequently maize plots are now being made near to the settlements and a change in the pattern of life is likely.

W. BANAGE: Professor Pearsall has said that the Masai use the land disastrously and that their cattle tend to cause more deterioration than the wild game. One wonders how far these processes have been accentuated by the pressure of marginal tribes on the Masai. Some of these, like the Kikuyu, have increased greatly in the adjoining lands that the Masai used to roam.

W. H. PEARSALL: To some extent this is true, but there is also the question of the methods used by the Masai. I think there is no doubt of the causes of damage, as pictures of cattle trails radiating from huts, and unpalatable fire-resistant grasslands on burnt land, will demonstrate. [Professor Pearsall showed further slides to illustrate these points.]

G. SURTEES: The rainfall in this area is said to be about 30 in. per annum.

I understand that you feel that annual burning is unsatisfactory under these conditions. In West Africa cleared ground recolonizes to forest very quickly: surely much the same would happen here, were there no burning, and this would lead to an even lower stock-carrying capacity than at present.

W. H. PEARSALL: Forest is preferable to unpalatable grassland and is also useful because it is a natural protective unit. Because land is not immediately useful agriculturally, it does not mean that it is being wasted. Water is the prime need in much of Africa — and the place where it is needed is in the ground. Forests check evaporation and conserve water. The Masai, in contrast are burning forests which are essential for water conservation. If the land is ever to become productive the useless fire-climax vegetation must be eliminated. There is a twofold need in these regions: fuel and food, and population density depends on the rate at which these can be produced in a manner which is also consistent with conservation.

J. B. CRAGG: There is one practical snag which strikes me. Surely to harvest the game one would have to alter the way of life of the Masai?

W. H. PEARSALL: I see no reason why the Masai should not conform to the basic natural principles of the region.

W. BANAGE: The greatest problem which we have in East Africa is to maintain a balance between pastoralists and agriculturalists. I cannot see that we shall solve any problem by confining the Masai in one region and the game in another. There may be a solution through technological advances in the Masai areas — for example in irrigation and the introduction of better nutrient grasses.

W. H. PEARSALL: In East Africa two sorts of people are messing about with the habitat — Native and European agriculturalists — both aiming at using the bush country in a wholly inappropriate way. There is a need to find a new method of utilization, since the present methods are wasteful, dangerous, and indeed seek to do something which cannot be done. Until then, the best solution would be to leave the area alone, deriving the protein harvest from native game which is as productive as native cattle and less harmful.

A. M. JORDAN: One of the great dietary deficiencies over much of Africa is protein. This is despite the fact that much of Africa is suitable for grazing, and it is mainly due to the presence of the tsetse-fly and trypanosomiasis. There is one experimental area in southern Nigeria where zebu cattle imported from the north of the country have thrived in an area of high tsetse density, owing to a two-monthly protective Antrycide pro-salt regime. Until veterinary trypanosomiasis can be controlled there does seem

much to be said for cropping the resistant natural bovid populations of these areas to provide protein for the human population.

This is not, however, a solution applicable to all Africa. Professor Pearsall has described an area in East Africa with abundant game animals. In contrast, West Africa, which I know personally, has far less game and mere conservation of the existing fauna, even if possible, would be far less productive. Here, the correction of the severe protein deficiency must probably await the solution of the trypanosomiasis problem.

It is important to remember that game animals form the natural reservoir of the trypanosomes pathogenic to cattle. Different species of tsetse seem to have different host preferences: various species of wild pig are widely fed on by both East and West African flies, and bushbuck are also used as hosts in both areas. Conversely, other common antelopes are apparently rarely bitten by tsetse, for no clear reason.

T. B. REYNOLDSON: Is the population turnover rate of wild and domestic stock comparable? Is it wise to use standing crops as a measure of productivity?

W. H. PEARSALL: No other methods are available.

R. J. H. BEVERTON: What possibilities might there be for producing vegetable protein in these areas? Professor Pearsall has dismissed the ground-nuts scheme as not being the solution, but I believe I am right in saying that with a bit less bad luck the scheme might have been a resounding success. With such an adverse conversion chain through cattle as is shown on the board, might it not be that even a relatively inefficient and uncertain production of vegetable protein, which would eliminate one stage entirely, would be worth considering as complementary to animal protein production.

W. H. PEARSALL: Yes, but the real problem in this case is the instability of the climate. One year in five will bring a certain crop failure; three in five a balance, one in five a good crop. Cereals were tried in the war and were a complete failure. There is no clear future agricultural use except the replacement of bush carefully by trees or perennials of similar ecological requirements. Bush, when rain falls, allows this to soak into the ground: when bush is cleared, the runoff is vastly more rapid. It has been found that land clearance is followed by the washing away of bridges which were quite adequate when the land was under natural vegetation. The water thus draining away is lost to the land. The modern policy of water conservation is to get it into the land and keep it there. The answer therefore is a system of agriculture which will keep the ground covered and allow water to soak into the soil, yet be productive. In the Mediterranean the olive was one solution: in East Africa no suitable plant is yet available.

The general problem is that these regions are ecological tension zones and it is virtually impossible to define good land uses for them. This has been tried and failed in such zones all over the world. The Scottish Highlands, a similar low productivity zone have been wrecked in a comparable manner.

E. M. NICHOLSON: I would like to confirm the dangers inherent in wishful thinking. We have seen two examples of this in East Africa. Attempts to grow wheat during the war failed so disastrously that two grain ships had to be sent to avert a famine among the grain growers. The ground-nut scheme lost £50 million, which would have financed scientific surveys of Africa sufficient to put us half a century ahead of our present position.

Can we fix 'danger limits' — critical population density levels — for soils of this type? Can we set up controlled experiments now on other possible land use methods? Is anyone trying to eliminate cattle and go back to game? These are the kind of immediate points which need attention.

J. B. CRAGG: I wonder whether Dr Jordan can inform us how many people in the whole of Africa are working on tsetse control? I suspect it is below a hundred.

A. M. JORDAN: That is certainly true for the research side. There are more involved in practical tsetse control measures in the various veterinary and medical departments.

M. E. SOLOMON: Where in the world have these 'ecological tension zones' been properly used?

W. H. PEARSALL: Probably nowhere.

V. VALDEZ: In Angola we have used sheep very successfully to obtain valuable skins and good protein yields from semi-desert areas. We have run Astrakan/Angola and Persian/Angola hybrid sheep for ten years and what was once an uninhabited hunting ground with no sanitary control now has many farmers. The same has been done in South-West Africa, Pakistan and near the Aral Sea.

D. JENKINS: The expression 'protein crop', as applied to wild game is not altogether satisfactory. In what practical way can this game be harvested? The locals may not eat the meat. In Scotland it would be easy enough to kill the game at an economical crop rate: the difficulties begin when you try to get it down from the hill to the main population centres and to sell it.

W. H. PEARSALL: This cropping is none the less being done throughout these areas. Africans, now living on poor food, take all the game they can get. On the margins of the Serengeti, more poached wild game is probably being eaten by natives than all the other protein that is going into the Masai. Cropping is not very difficult. In Southern Rhodesia two farmers are

actually eliminating cattle and farming game, and it is said to pay. Around the Queen Elizabeth National Park a plague of hippopotamus is at present causing grave alarm. It is planned to shoot hippo on the margins of the park; the minimum estimated crop being 1,600 per year, each of average weight 3,000 lb. This will constitute a very considerable local meat asset. In Uganda 30 per cent of all the meat sold comes from wild game. Cropping is in fact inevitable and often desirable. Strict conservation prevents at the same time other forms of land use in the neighbourhood. It may be well more satisfactory to harvest game as a form of land use.

GENERAL DISCUSSION

GENERAL DISCUSSION

INTRODUCTION

The programme of the Symposium included three 'general discussions' on the subjects:

- (1) Is it relevant to construct a comparative population dynamics?
- (2) The response of populations to exploitation and the operation of density related factors.
- (3) The management of exploited populations (intended as a summary of the Symposium).

Discussion on these three topics was opened by brief, prepared statements by D. H. Chitty, M. E. Solomon and G. C. Varley and M. Graham respectively. In practice, the discussions tended to depart from the intended topics, to overlap with each other, and often to develop ideas first put forward in the discussions following the papers. The records have therefore been combined and rearranged and are presented here under the seven headings listed below. Some of the remarks made were repetitive or irrelevant to a printed version and so have been omitted; otherwise the spontaneous spoken remarks have been subject to only minor editing.

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I. CHARACTERISTICS OF STABLE POPULATIONS

S. J. HOLT: I think that today, when we were discussing the 'damping effect' of age-groups, we were confusing 'life-span' and 'mature life-span'. In fact the critical relation is that between the mature life span and the frequency of reproduction. For example, an anchovy in tropical waters with a two-year life-span, shows no more fluctuations than does a cold-water

population with a four-year life-span. This is reasonable because the warm water species may spawn twice a year but the cold water species only once. But even so, the damping caused by the presence of several age-groups in the population may be only a second-order effect.

M. GRAHAM: Why?

S. J. HOLT: Because despite this damping effect real variations in population are usually due to differences in numbers in a few age-groups only. This happens even when there are many year-classes present, as in the North Sea plaice where the bulk of the fluctuation depends on that of individual year-classes.

S. W. HURRY: Many population cycles, like those in arctic mammals, surely occur near the limit of range of a species?

D. H. CHITTY: No, that is not really true.

J. A. GULLAND: I think we must distinguish critically between regular and predictable cycles like the mammalian ones and irregular fluctuations such as we have in fish.

D. H. CHITTY: There are certainly two separate phenomena here. First, chance fluctuations such as those due to bad weather, often seen among insects whose short life-span makes them especially vulnerable. Secondly, fairly regular variations like those in lemmings or snowshoe hares. It is the first type that we are really concerned with.

G. E. WOODROFFE: Could the distinction be made in terms of the controlling mechanism? Comparatively stable populations are tied down by self-regulatory systems whereas irregularly fluctuating ones are controlled by external factors like food and environment.

R. P. SILLIMAN: I am sure that in large populations those with the largest number of year-classes are the most stable: this is well seen in the Pacific halibut.

J. G. SKELLAM: It is unfair to relate the fluctuations of a species to that species alone. A species is a component of a system which itself may be oscillatory, as is the classic predator-prey relationship. Others may form part of a stable system with no oscillation — again one must relate this to the whole system and not just to a part of it.

M. E. SOLOMON: But generally it is practical to study only part of the system.

J. G. SKELLAM: Then you can only expect to get part of the answer!

2. OSCILLATIONS AND TRENDS

M. E. SOLOMON: Ordinarily, 'stability' means fluctuation about a mean population level which is regarded as constant, as in Fig. 1a, with the assumption that when the population density is either above or below the line there are forces tending to restore it to the mean level.

FIG. 1.—(M. E. Solomon): Fluctuations and trends in populations with time — see text.

In some cases a gradual change in the mean level about which the population fluctuates can be detected (Fig. 1b). This can be termed 'stability' in a sense, comparable with the physicist's concept of 'moving balance'. Nicholson goes further than this, and envisages oscillation about an 'equilibrium density' which is continually changing with environmental conditions (Nicholson, 1954b). Of course, until we know a lot more than just the counts of abundance, the choice of a line and the relating of the fluctuation to it must be largely arbitrary.

In a 'horizontal line' population (Fig. 1a) the stability of the adult numbers may be partly or even wholly the result of regulation of the earlier stages. Le Cren has said that fish populations tend to have a constant number surviving independently of the number of eggs produced, and Gulland has suggested that the number of young recruited may be independent of the adult stock. Beverton states that a tenfold variation in plaice egg production has no effect on year-class size.

G. C. VARLEY: It is most important to show the scales on the axes of population fluctuation curves. For example, a seasonal peak of enormous dimensions will appear if the total number of eggs is counted as individuals, while the adult numbers may yet persist at a steady low level (Fig. 2).

Where adults overlap several seasons there is a comparative stability: on the other hand, in insects with a life cycle of one year the peak of adult

FIG. 2.—(G. C. Varley): Figs. 2 and 2A show different methods of presenting the same information. The total population curve (upper line of Fig. 2) is the sum of the partial population curves for eggs, larvae, pupae and adults. Fig. 2a is a generation curve for the adults, in which the total number reaching the adult stage in a generation is plotted against generation number.

numbers will show variation possibly correlated with that year's egg production and always well below the peak of numbers represented by the total eggs laid.

We must therefore separate:

- (1) *Total population curves* of the whole species, including all stages, against time.
- (2) *Partial population curves* in which the actual number of (say) adults is plotted against time, and there are many observations during the life-span of an individual.
- (3) *Generation curves* in which the total number of individuals reaching a particular stage (e.g. larval or adult) in any generation is plotted against generation number. No individual is counted more than once.

M. E. SOLOMON: My diagrams do not show the ups and downs of reproduction and juvenile mortality, only the numbers of adults. The fish data I quoted could indeed be displayed better in a diagram like Varley's. Mine show only the results of such relationships, or others, in terms of adult numbers.

W. T. EDMONDSON: I am worried about this averaging of populations: how relevant is it to real biological conditions?

K. P. ANDERSON: There is a mathematical model for a population assumed to show a constant mortality rate and a constant birth rate. This model consists of:

$$P_t(N=0) \rightarrow 1$$

This means that under certain conditions there is a tendency to population decline, and to maintain a constant mean the number of animals must be very large.

In such a system, N , the number of animals tends to 0 as t , time, tends to infinity. The whole system can originate from one specimen.

J. G. SKELLAM: This is a well-known property of Markovian stochastic processes. If the Markovian framework is not assumed, this kind of extinction process need not occur. In fact doubts have been raised whether biological stochastic processes are necessarily Markovian.

M. H. WILLIAMSON: Assuming that Markovian stochastic processes were operating, how long would be needed for the chance extinction of a species?

J. G. SKELLAM: It depends on generation time. If n , the number of animals is low, the processes can be quite rapid. If very large, t — the time involved — tends towards a geological time scale. In fact, Thomas Park's experimental *Tribolium* populations, though containing very few animals initially, showed extinctions in only a tiny proportion of cases. It is unlikely that random extinction is of practical importance in many ecological experiments.

L. P. SLOBODKIN: The formula implies that variance at a given time is cumulative or multiplicative. It is important to know whether populations are Markovian or not. Thus Smith, working at Harvard, took Andrewartha's thrips data and related the annual censuses to mortality. The variances in the same month from one year to the next should be the same as for any other month, and all should increase with time if a Markov system was applicable. It was found that this was not so. Variances may well be able to throw a system out of a Markovian framework and make chances of stochastic extinction nil.

T. B. REYNOLDSON: One must remember that the population in the field is far from being a simple unit.

C. W. HUME: Surely the theory is also out in assuming that the population can start from a single individual?

J. G. SKELLAM: Bacteria probably can. Sex has not yet been found everywhere!

M. GRAHAM: There are some questions which can at present only be answered empirically. A complex population can only be dealt with in a simple way because the treatment works. The yield of North Sea fisheries has fitted the theoretical predictions; despite great changes in gear and methods, the cessation of fishing during six or seven war-time years did have much the effect predicted. This suggests that however complex the parameters, they can yet be handled in a simple way.

It is quite evident, for example from the data that Beverton presented, that some populations can fluctuate about stable, and others about rising means. Sole, for example, follow the latter, and plaice the former pattern.

S. J. HOLT: We have tended to think of the relationship between recruitment and the preceding stock in terms of a basic assumption that recruitment in succeeding generations is not affected by stock size. Le Cren has now stated that whatever the amount of eggs produced, the number of recruits remains the same. It has also been suggested that recruit numbers and stock size are independent. But this is not the same thing from the point of view of regulatory mechanisms. In the first case we have fluctuating egg numbers but constant recruitment; in the second the stock size or egg number may vary little but the recruits considerably. Yet fisheries biologists perhaps wrongly take these two patterns as comparable.

FIG. 3.—(S. J. Holt): Mortality and recruitment in fish — see text.

The difference is that the process controlling the fluctuation operates at different stages of the life cycle. In Le Cren's example it occurs before recruitment; in other instances after it. In the second case the damping through the presence of a succession of age-groups in the population is the sole influence.

Thus on Le Cren's pattern, whatever the number of eggs laid, the same number of recruits result, as in Fig. 3*a*. While on the other hand in Fig. 3*b*,

there is no correlation between egg laying and recruitment, and the regulation of numbers occurs in the post-recruitment phase.

For a fisheries biologist these may come to the same thing — the number of recruits need in neither case depend on stock size.

M. GRAHAM: There are species of fish in which recruitment does depend on the stock size: e.g. salmon and perhaps herring. Certainly to say they are unrelated is not a valid generalization.

J. G. SKELLAM: Stock density rather than the total number is the important factor in this connection.

J. B. CRAGG: In Holt's two models, in the first (Fig. 3a) is self-regulation considered to be operating prior to recruitment, while in the second (Fig. 3b) is it active afterwards, bringing the population down to a steady state?

S. J. HOLT: No. Regulation occurs in the early stages in both. The damping down of oscillations, however, occurs in the post-recruitment stage in the second case. Damping is not itself a regulatory process and may occur elsewhere in the life history.

E. D. LE CREN: The timing of density effects is important. Consider two generations: in the first instance, as suggested by Nikol'skiĭ, these may have different adult numbers but lay the same number of eggs — regulation here occurring by a variation in the level of fecundity. Alternatively, there is the system in which regulation occurs in the pre-recruitment stages of the larvae, leading to the same result but depending on another stage of the life cycle.

S. J. HOLT: Looking at the system in these two ways leads us to contemplate different regulatory mechanisms. Yet all result in the population derived from eggs coming to a constant average level related to the available niches.

D. A. HANCOCK: Shellfish show very irregular recruitment. The answer to poor oyster fisheries is to improve the stock by aiding settlement, yet this does not eliminate the irregularity in the process. The cockle also shows very variable settlement. Yet examples of regulation at the recruitment level can be seen in invertebrates, starfish giving an example. In one instance a big settlement of starfish was followed by good growth, and then to a stoppage in growth or actual shrinkage. Mortality rose at this stage. After a year the animals were about the size of a normal three-month-old starfish, and these competed for food and prevented the establishment of the following year group of recruits.

G. V. NIKOL'SKIĖ: Is the amplitude of variation the same at all points

in the diagram? Surely not. In all species many regulatory mechanisms operate at many stages, some before and some after recruitment.

J. G. SKELLAM: Distinguishing between trends and oscillations is a major problem.

E. BROADHEAD: Does this mean that populations under many independent influences, such as predators and the like, can show several variations of this kind?

J. B. CRAGG: Is this the meaning of Cole's work?

L. B. SLOBODKIN: Cole took a system of random numbers and smoothed them to get a pattern comparable with population fluctuations. Field data for fluctuations at least seem of the same type. Yet the random numbers, once smoothed, are no longer random but in a sense a proper oscillating mechanism. The cycles in his paper give a superficial impression that because random numbers that have been smoothed give an apparent oscillation comparable with the population, therefore natural oscillating populations are oscillating randomly.

M. E. SOLOMON: It should be possible in suitable cases to measure regulation and random fluctuation against each other by raising or reducing the population density and observing the rate of return towards the normal level.

J. G. SKELLAM: The tendency to come back is equivalent to the stability of the population.

N. WALOFF: How many generations are needed before a population can be considered in a stable state? The environment itself is often not stable — this is so for insects. What is a stable population related to?

M. E. SOLOMON: This cannot be laid down in general. It must be made clear with reference to the particular case.

3. THE INFLUENCE OF ENVIRONMENTAL CHANGE

E. B. WORTHINGTON: I notice that whenever a fishery biologist comes to the blackboard he draws even lines to represent population numbers, while terrestrial biologists draw irregular ones. Surely there are in fact fundamental differences between land and water environments, and one cannot divorce a population from its environment. In water, there is much more stability of habitat; things are buffered so much that slow changes occur as compared with gross oscillations on land.

E. D. LE CREN: I am not convinced by Worthington's distinction between terrestrial and aquatic habitats. Isn't an undisturbed tropical forest —

i.e. a climax situation — comparable for stability with the sea? If you are not a pest entomologist, will you find more examples of instability on land than will a marine biologist in the sea?

M. E. SOLOMON: Instability of some terrestrial populations seems not to be due to human influence. For example, it is probable that epidemics of the spruce budworm in Canada have always been associated with the maturing of large areas of balsam fir (Greenbank, 1956 and references therein).

M. J. WAY: I agree with Le Cren that most entomologists concentrate on species tending to oscillate violently owing to human modification of their habitat to the benefit of a particular species. Climatic changes are, however, unlikely to cause a downward trend in a well-adapted animal. Tropical forest environments are nearest to the sea among terrestrial areas in their constancy: in temperate zones seasonal cycles, reflected in population cycles mediated, for example, by diapause will cause some tendency to unbalance.

M. E. SOLOMON: But can it be shown that non-pest species do not fluctuate?

E. BROADHEAD: Often the rarer species are not studied.

E. B. WORTHINGTON: Tsetse-fly may maintain a constant area of occupation in their environment but their abundance within it may fluctuate widely. I can think of no single land environment with any degree of stability. Aquatic biology is hence easier to tackle and fisheries workers can draw straight lines. Land ecologists are generally behind the aquatic workers in progress as a result.

S. J. HOLT: I wonder if it is really true that aquatic species don't fluctuate. What about the 'red tide' and analogous phenomenal outbreaks among planktonic organisms?

E. B. WORTHINGTON: I defy anyone to produce curves for population levels for any land animal comparable with those for fish.

I. A. McLAREN: Stability for a buffalo is not the same thing as stability for a mouse. A cod, being large and long lived, is in this comparable with a buffalo.

L. M. DICKIE: I suggest that there are differences related to the stability of the environment. Gause (1947), working with his experimental populations, suggested an inverse relationship between capacity for phenotypic and genotypic variation. Consider the relationship between land and sea: the former is more variable as an environment and has complex animals showing more genotypic variation but perhaps less phenotypic which are therefore more readily thrown into resonance-type oscillations. Marine

animals need less genotypic variation. Surely there is no marine animal showing the regular oscillations drawn as type for terrestrial environments?

R. J. H. BEVERTON: Haddock in the North Sea show wide fluctuations in the size of year classes over a period. The environment may influence young and adults very differently and the two groups should be considered separately.

G. C. VARLEY: I dispute the allegation that more is known about aquatic than about terrestrial animals. Aquatic animals are in many respects hard to study and the few data available often give a wholly spurious smoothness to the curves. In terrestrial organisms there is often a trend to more violent instability in simpler environments, as in the spruce budworm in northern regions, where adult populations may vary by as much as 10^4 year by year. Similar wide variations are known in the tropics, as in pests on coconut palms in Fiji where synchronous generations may build up to high levels after escape from parasitic control.

4. BEHAVIOUR AND COMPARATIVE POPULATION DYNAMICS

M. GRAHAM: I do not think that ecology has yet reached the stage where a Symposium of this kind can lead to the expression of a few clear general principles. We are unlikely to reach much greater clarity than has been obtained in this afternoon's discussions.

I should like to hear more about the studies on populations of birds and mammals — what have workers in these groups got out of the Symposium?

E. M. NICHOLSON: I am somewhat worried that the behavioural aspect of regulation of numbers has so rarely been brought up. In birds there are many short-term distributional changes, exemplified by the 'eruptions' of tits. The distance of movement in these birds is normally small — rarely exceeding ten miles. In some years, however, an 'explosive' outburst of population can occur over hundreds of miles. Behaviour changes are of great importance in these.

D. H. CHITTY: Tinbergen (1957) refers to dispersion as 'the state of living dispersed, as opposed to crowded and as distinct from being distributed at random'. Many animals have dispersion mechanisms which operate through hostility, either as a threat to or as an avoidance of, members of the same species, and both these factors serve to limit numbers.

One can see how this might operate by considering bird species in which, due to territorial behaviour, surplus members are driven out into unfavourable habitats. Where there is a resistance to moving out there will be selection

in favour of aggressive individuals (up to the point at which aggressive behaviour occupies too much time and energy at the expense of other biological demands), and it is to be expected that crowded populations differ fundamentally from expanding populations in the frequency of certain genotypes.

A. WATSON: Behaviour is recognized as important in birds, where it is easy to see. It may also be of great significance in other species where it has escaped notice because these are more difficult to watch. Trout might provide an example, and be fairly easy to watch. Have the fisheries people any data?

E. D. LE CREN: There has been a lack of emphasis on behaviour studies in much fisheries work simply because of the difficulty in observing the animals. There are certainly evidences of changes and mass movements in some species, such as herring, and of territorial behaviour in others such as the trout.

E. M. NICHOLSON: Changing distribution, and not only mortality, is relevant here.

D. JENKINS: Fish exist in a truly three-dimensional environment. This may possible lead to major differences in their use of the habitat, as compared with non-aquatic forms.

M. GRAHAM: Many fish can certainly inhabit levels in the habitat other than that at which they are commonest.

D. H. CHITTY: I think the fishery results are of the greatest value, and are in many aspects well ahead of those in terrestrial ecology. Le Cren's point about behaviour is, however, important, suggesting that fisheries workers may miss data vital to the understanding of population regulation owing to technical difficulties. Only recently have we come near enough to defining the points on which to look for detailed information.

It is gratifying to find that work on one organism can be checked or paralleled by work on another from an entirely different field. It is very important that we try to arrange data so that hypotheses based on one species can be tested on another.

G. C. VARLEY: I think that workers with different taxonomic groups make use of very different concepts; for example, where there is no overlap in generations, as in many insects, problems of age distribution are enormously simplified. Both the methods and the models used vary from group to group, and before beginning a study it is essential to be clear as to what model is being proposed and what observations are required to test its relevance. Thus, if one is looking for the common factors in comparative

population dynamics one should choose animals which do not show irrelevant properties such as phases of distribution. Too many studies are isolated from their essential ecological context such as position in a food chain.

I. A. McLAREN: I would plead that it is not the phenomena of population dynamics but the tools — the methods of analysis — which will provide us with a common basis.

J. G. SKELLAM: I consider that there is already a body of information on comparative population dynamics, as for example the population consequences of particular types of life history such as parasitism etc. (Cole, 1954). Many apparent differences are merely the result of vast variations of time scale. I agree with McLaren that it is not the features of species but of systems which should concern us; that is to say the relation between species.

Several people have spoken of populations regulating their own numbers by reducing fertility. There is nothing in the theory of natural selection which could favour such behaviour. As Haldane (1932) showed no gene which induces altruistic behaviour of this kind would survive. This means that population regulation is not controlled from within.

L. B. SLOBODKIN: (a) I suggest that what we cannot expect is a single model or formula to apply to all species. Any model will depend firstly on its mathematical form and secondly on the values of the functions in the formula. What we can expect is that there will be a limited range of such functions and of such values.

(b) The reply to Skellam's argument which I have put forward before is that natural selection may not always favour the production of the greatest number of children if this is associated with a lower number of grandchildren — or great-grandchildren. This mechanism demands a labile environment and a number of small, mainly isolated populations. If in such circumstances there are many local extinctions the populations having the features producing more grandchildren would be the ultimate survivors.

N. WALOFF: In the desert locust the high mobility of the gregarious phase results not only in dispersal but also in regulation by dispersion.

In this connection, surely Chitty's 'aggression' mechanism of dispersion must apply only to gregarious species?

D. H. CHITTY: Tinbergen included purely chemical mechanisms under dispersion.

M. E. SOLOMON: Some insects are definitely very intolerant of their own kind — for example grain weevils in a jar. This may even interfere with successful mating.

D. H. CHITTY: Voles as a rule only show the reaction between strangers.

G. M. DUNNET: There can be no doubt that many species have surplus animals moving around and unable to settle due to population pressure. I have observed this in opossums.

G. V. NIKOL'SKIĬ: (a) There are two aspects to intraspecific relationships: on the one hand competition, and on the other co-operation, as for example the schooling of fish which results in improved defence against predators. Shoals may disperse at night when this is no longer effective.

(b) We should remember that population properties like other properties of the species are adaptive.

(c) Host/parasite relationships in fish are of two types; those in which the host is killed — in which case only a proportion can be parasitized — and those in which it is not — where parasitism can be complete. Improved adaptation results in a change from the first to the second.

5. THE RESPONSE OF POPULATIONS TO EXPLOITATION AND THE OPERATION OF DENSITY-RELATED FACTORS

M. E. SOLOMON: Most ecologists who have been concerned with the question would agree with the view that the abundance of animals is regulated, at least in a rough way, by density-related factors. These factors (or processes, as I prefer to think of them) are not considered as operating independently of the general environment, but rather as gearing the size of a population to the capacity of its environment (or to this capacity as modified by the presence of predators, competitors, etc.).

On the other hand, a few of the theorists of insect ecology have claimed that certain insect populations simply fluctuate in response to changes in the environment, in a manner not related to population density (Thompson, 1956; Andrewartha, 1957; Birch, 1957). That is to say, if regulation means control through density-related processes, they claim that these populations are not regulated. Some of us have objected that the chances of a population remaining for a long period within the observed limits of abundance seem too remote, unless there is at least occasional regulation by density-related processes.

Supposing, however, that such an unregulated population did exist, it seems clear that any exploitation would impose a reduction from which such a population would in a sense never recover: whatever its subsequent fluctuations, it would always be larger if it had not been exploited. Moreover, the effects of successive imposed reductions would be cumulative.

Going to the other extreme, imagine a population in which each adult female produced 100 female offspring yet the numbers of adults were kept at a constant level by density-related processes. Clearly, a high rate of exploita-

tion, with a theoretical maximum of 99 per cent of the juveniles of each generation, could be maintained without reducing the population of adults.

Presumably it would be agreed that with most natural populations the state of affairs must be somewhere between these two extremes. Some fluctuate rather wildly and may be only intermittently regulated (cf. Schwerdtfeger, 1958). Others seem more closely regulated but still with a good deal of variation in response to environmental changes.

To unravel all the significant processes influencing the abundance of any particular population is difficult, slow work. Before this has been done, is there any way of assessing to what extent a population is under the influence of density-related processes? It has been suggested that such an assessment could be made by testing experimentally the readiness with which the population recovered from an artificially imposed reduction (cf. Nicholson,

FIG. 4.—(M. E. Solomon): Population growth and exploitation — see text.

1957; Hairston, 1957). In the field of exploitation, has not this very experiment been performed whenever a population has been reduced by over-exploitation and its powers of recovery observed?

Moreover, exploitation studies offer other ways of assessing the degree of regulation of a population. I propose to formulate some of them as questions for discussion, in the hope that examples will be forthcoming. They can be clarified by means of diagrams depicting the changing numbers of animals in an imaginary population in a stable environment.

Fig. 4a represents the curve of increase from small numbers to saturation level, in the form of the familiar sigmoid (but not necessarily logistic). It will be assumed that if the numbers are reduced to any level below saturation, they will increase again (so long as there is no exploitation) according to this curve. Fig. 4b shows this and suggests recovery curves for populations capable of different rates of recovery. Hence (Question 1): *What have*

exploitation studies revealed about the degree of density-related regulation in particular populations, as measured by their speed of recovery after artificial reduction?

This question refers to drastic reductions of the standing crop. But presumably in the exploitation of a natural resource the aim is often to exploit the potential turnover without reducing the standing crop (or without reducing it below a level from which it soon recovers), i.e. to employ a regime of frequent rather small 'takes'. We may enquire (Question 2): *What is known of the degree of density-related regulation in particular populations, as measured by the rates of exploitation they can sustain without reduction of the standing crop?* Fig. 4c illustrates the sort of test envisaged.

A glance at Fig. 4a suggests that the procedure of conserving the level of the standing crop may not necessarily give the maximum yield. For if the numbers are kept down by cropping to a level where the curve of increase is steeper (being not so subject to density-related hindrances as at the upper levels), then, in this model at least, the yield should be greater (Fig. 4d). This leads to the enquiry (Question 3): *How is yield affected when exploitation is increased to a rate which keeps the standing crop well below its natural level?*

In formulating these elementary questions, I have not tried to anticipate the difficulties that no doubt arise when one tries to apply them to real populations. These difficulties vary with the circumstances; I hope that they are not too often insuperable.

For analogies, on an exaggerated scale, of what the above considerations lead us to expect in natural populations, it may be appropriate to refer briefly to some of the laboratory experiments on insect populations as examples of the relationships I have been discussing. In one of the experiments Nicholson (1954a) performed with populations of the blow-fly *Lucilia cuprina*, the main limiting factor was the supply of food provided for the larvae. When he systematically removed 99 per cent of all emergent adults, the consequent alleviation of adult crowding and of larval competition allowed greater numbers to develop through to the adult stage — about six times as many as before. This is an extreme example of the principle of Fig. 4d — severe exploitation evoking an increased rate of production of exploitable individuals.

Watt (1955) used populations of flour beetles as a model for the study of the optimum yield problem. As with Nicholson's flies, the productivity of *Tribolium* cultures increased with the rate of exploitation, sometimes up to an exploitation rate of about 90 per cent; the result varied according to the age-distribution of the residual population.

The foregoing questions represent aspects of one approach to population dynamics — an attempt to assess the degree of regulation of some natural populations whose ecology is not exhaustively known, using the information

gained from exploitation studies. Equally, they suggest preliminary tests by means of which the exploitation ecologist might explore aspects of the capacity of particular populations to withstand artificial reductions.

G. C. VARLEY: May I enquire if anybody has thought of a population which shows an increase following exploitation?

M. GRAHAM: I know of no case apart from the rabbit, and here the rise during exploitation was probably due simply to more predators being destroyed than the prey which they would have taken.

In general, exploitation often leads to higher production, but not to a higher total biomass.

H. V. THOMPSON: I am surprised that no populations of species other than the rabbit are said to increase under exploitation. I am also surprised that the removal of predators is said to be responsible for the success of the latter. In fact predators are markedly inefficient at catching rabbits. Foxes proved useless in Australia, and Mustelidae in New Zealand. Resistance to exploitation is in fact a characteristic of 'pests': in the grey squirrel 40 per cent may be taken and still the population will go on rising.

M. E. SOLOMON: I have been told that in dense rabbit areas the number surviving the winter is inversely proportional to the number entering the winter, owing to food shortage. Are there any data showing that more rabbits follow an autumn trapping campaign than if no exploitation goes on?

C. W. HUME: Surely one would expect that a trapping campaign killing 30-40 per cent of the population would aid the remainder to survive the winter?

H. V. THOMPSON: Unfortunately it is impossible to test such a hypothesis by doing the converse experiment.

H. KLOMP: I would like to illustrate the relation of population numbers to the level of exploitation by a simple model (Fig. 5). Mortality is density-dependent because of competition. Reproduction decreases at very low population density due to the fact that an increasing part of the females does not contact a male.

Consider the situation in which the unexploited population is in equilibrium at density P_1 . Here the position is a stable one. If exploitation now occurs the mortality is raised, e.g. independently of density to the line M_2 or dependently of density to the line M_3 . This causes a shift of the stable equilibrium to a lower population density (P_2).

With very great exploitation, however, population density may reach the level P_3 . Then the population is in danger because a small random fluctuation in density can cause a permanent decrease in numbers, due to the fact that mortality is in excess of reproduction. However, if density has not yet

decreased to a level lower than P_4 , the population may be saved by stopping the exploitation.

The regulatory mechanism may precede exploitation, or exploitation may precede the operation of a regulatory system. In the former case the mechanism plotted above operates. In the second, exploitation is buffered by the regulatory mechanism.

D. H. CHITTY: Do you suppose that if one exploits a population after it has established stable numbers through a natural regulatory process the results will be bad, while if exploitation precedes regulation it will be less deleterious?

FIG. 5.—(H. Klomp): A model of an exploited population — see text.

H. KLOMP: Regulation precedes exploitation in some cases, for example where it operates on the larval stages but the adults are exploited.

E. D. LE CREN: But life cycles are cyclic processes: the regulation of the following generation, in their larval stage, will follow the exploitation of the adults of the first generation so that a balance will be attained.

E. M. NICHOLSON: There is a simple example available in North American duck populations. Two things have been done: firstly, protection in certain regions, and secondly a controlled exploitation. The result has been firstly a steady rise in numbers, despite an increase in exploitation, and secondly a concentration in the protected areas leading ultimately to overstocking there and natural regulation. This fits with Klomp's model. Where there was heavy cropping the population never reached the point at which

natural regulation comes in. Where protection operated, this was not the case.

D. H. CHITTY: This may be paralleled by the work on grouse, which Jenkins and Watson have described. The main losses there are in late winter, and cropping prior to this may perhaps not affect the spring population density.

G. C. VARLEY: Domestic hens show a very simple case. If you allow them to accumulate eggs they stop laying and become broody. If you continually abstract the eggs they continue to lay.

J. G. SKELLAM: There is an interesting point about Klomp's model. The growth curve associated with the graphs of production and mortality employed is in two parts. Populations initially above a critical level grow in a typical sigmoidal manner very similar to the logistic. Below the critical level of unstable equilibrium the population declines to extinction. In most applications I should imagine that this lower strip is very narrow indeed, as many populations, natural and experimental, are known to survive and recover if the habitat is favourable even when reduced artificially to levels many times lower than those at which the animals normally prevail.

D. H. CHITTY: My work suggests that in dense populations the 'quality' of the animals is different from that in expanding populations. In the vole there is one year only in a four-year cycle in which a maximum rate of increase prevails. Predictions from my data are the exact opposite of those expected from Solomon's scheme. Since there is only one year in which population increase occurs at a rate such as would be expected from studies on captive animals, it should be possible to maintain a steady population if they are exploited during that year, whereas exploitation during the other years of decline would presumably accelerate the decline.

M. GRAHAM: There is a tendency in talking of this sort of topic to assume that all situations are reversible. This is not the case.

6. TERMINOLOGY

G. C. VARLEY: Some considerable divergence has become apparent in the way in which we use words like 'control' and 'self-regulation'. I think we should attempt to agree on a uniform and consistent definition for such terms.

D. H. CHITTY: Nicholson used the term 'self-regulation' for populations which induce changes in other species such as predators that increase the level of mortality in the population.

D. JENKINS: I think it implies a behavioural mechanism, whereby a

surplus of animals is excluded from the population to maintain steady numbers. What do the fisheries people think?

G. V. NIKOL'SKIĬ: In some cases an adaptive response to the food supply may be involved. Either density of population or availability of resources may be an influence. In most cases the reasons for population increase cannot be ascertained: changes in even the nature and rate of metabolism may be involved.

R. J. H. BEVERTON: 'Self-regulatory' is not a term to which fisheries people have attempted to give a standard definition, and indeed I do not think it is much used in fish population literature. But if any generally applicable definition can usefully be made — and I am not sure that it can — it would seem to me to have to do with processes by which a tendency for the size of the population to increase or decrease is opposed by factors which are inherent in the population itself — in effect by intraspecific density-dependent factors.

J. G. SKELLAM: The present confusion in population dynamics is largely due to inadequate definition. Personally, I find much of the literature meaningless or even self-contradictory. Admittedly, all sciences appear at some stage to have difficulty in giving definition to concepts which initially appear intuitive, and this kind of confusion has even arisen in mathematics. The use in population dynamics of such terms as oscillation and periodicity is bewildering to the mathematician, who has used these terms in a rigorous way for a long time. If ecologists intend that mathematicians take an interest in their problems it is essential that some of their terminology be clarified. It would be a substantial advance if only some of the most frequently used terms could be defined objectively, freed as far as possible from theoretical content or implication.

M. GRAHAM: Objective uses can in a few cases be found. 'Self-regulatory' could be restricted to cases like that of cannibalism where an organism regulates its own species directly. Similarly processes of dispersal in which surplus members of the population are driven out into marginal habitats would provide an instance of a self-regulatory mechanism.

J. G. SKELLAM: I am not satisfied by the definition of self-regulation just given, or by the example. For it still remains to be proved that the behaviour pattern in question (cannibalism) does in fact regulate. Before we define 'self-regulation', should we not define 'regulation'?

A. MILNE: Graham's example was really one of intraspecific competition, and this is really the only self-regulating mechanism. But all these terms have a very large theoretical component, from which, if objectivity is to be

attained, they must be separated. We should certainly define 'regulation' first, and then see if 'self-regulation' exists.

I. A. McLAREN: The connotation in 'self' implies a behavioural system. Regulation is usually thought of as an environmental effect.

M. E. SOLOMON: It seems generally assumed that regulation is the control of numbers by means of some type of feed-back system. As numbers rise, this mechanism bears on the population more heavily. Self-regulation is generally used as convenient shorthand, and if it is to be used more seriously it needs careful definition. Logically, it involves the fallacy of abstracting the population from the environment. Even intraspecific competition always results from a limited supply of something in the environment.

D. H. CHITTY: Surely it is conceded that a self-regulatory mechanism must be a part of a larger framework?

B. B. PARRISH: Any attempt at definition involves building upon prior terms. 'Population' is a case in point. In fisheries research the dynamic unit is the 'stock', which is treated as a unit for management purposes not necessarily equivalent to the total 'population'. Some 'populations' include several species, and in such instances 'self-regulation' could involve inter-specific competition.

L. B. SLOBODKIN: Skellam seems to be seeking for words with 'no theoretical content'. I feel that in this he is looking towards mathematical expressions. But the mathematician is clearer about what he is trying to do. In our case, we can easily define a word and then spend years looking for a case which fits our rigorous conditions. If, however, we first observe a phenomenon and then derive a word to describe it, our terms almost inevitably have a 'theoretical content'.

Solomon has said that regulation implies feed-back. In that case, can we not say that 'A population shows *self-regulation* when some property of the population participates in the feed-back system'?

D. H. CHITTY: I think that is too broad a definition. In that case surely any property of the population which leads to feed-back would be self-regulatory?

L. B. SLOBODKIN: I do not think so.

G. C. VARLEY: I think this discussion has made it plain that we are *not* clear about the terms we use. Surely we should set up a mechanism to obtain a clarification? Something should be attempted, to obtain concise and useful definitions.

7. MATHEMATICAL MODELS

G. C. VARLEY: Even those who have little mathematical understanding must inevitably use some type of model, directly or indirectly. In this context I feel that we have not heard enough about the use of such models in planning research. In fact, there is a kind of sequence of processes in the study of a problem:

Natural history	Theoretical	Test of	Interpretation.
observations. —→	model. —→	assumptions.	—→ Prediction.
		Measurement of parameters in field.	

J. G. SKELLAM: There is a feature of Varley's diagram which deserves emphasis. Between the observation of nature on the one hand and the estimation of population parameters on the other, there stands a model. For the estimation of parameters it is logically necessary to have a model, even if this is only a set of common-sense assumptions scarcely deserving the epithet 'mathematical'. The testing of models against observations rarely takes place directly. More commonly we compare the logical consequences expected from the operation of the model against observation. There is here a deductive phase which is the real province of the biometrician, but it is up to the biologist to provide him with at least the outlines of a model on which to work.

G. C. VARLEY: The biologist's main problem is often the choice between a profusion of models.

A. C. SIMPSON: The 'natural history' phase in Varley's scheme should be divided into two subsections. Firstly, there is a qualitative process of observation on stocks, spawning areas and the like. Secondly, there is a quantitative element in which parameters are assessed.

W. H. PEARSALL: I am not happy about Skellam's approach. Surely the basis of modern studies is a preliminary qualitative description, a subsequent quantitative assay, and then the formulation of a model based on these data, from which deductions can be drawn. The model thus *follows*, not precedes, the estimation of population parameters.

E. D. LE CREN: An important key to success in research is the ability to ask the right questions of nature. Even at the 'natural history' stage one must look for the right things and when measurements are made, measure the right things. For this some theoretical 'model', even if an unwritten one, is essential.

M. GRAHAM: I am becoming more and more impressed with the

achievements which have been made by uneducated men unaided by mathematics or Markov stochastic processes and allied concepts. I doubt if the deviser of the wheelbarrow knew the theory of levers: Brindley, who made vast advances in the engineering practice, was an uneducated man. Does this imply that we should follow Simpson's principle of emphasizing the non-quantitative observational phase of natural history as the basis of research, rather than adopt Skellam's precept that we should compose a mathematical model before attempting to measure any parameter? If theory is needed prior to any advances, how is it that great new advances come from the work of uninformed people? Early workers in fisheries collected vital data before anybody knew how it was to be used. Intuitive mathematical and mechanical models (not necessarily hydrostatic!) can be of great value. But in any field of biological research one can blunder on and hit upon important discoveries simply because one is blundering on in the right field of investigation.

D. H. CHITTY: The transition from natural history to model does not arise automatically. There is a gap only bridged by intuition, not by logic. In this sense discovery parallels the invention of the wheelbarrow, but a mathematical model is harder to test than a wheelbarrow. As a rule models cannot be tested directly, but only used by seeing if they lead to predictable results.

G. C. VARLEY: The model can in fact be recognized quite easily, and discarded if it is inapplicable. Nicholson & Bailey's model, for example, can easily be seen to be inapplicable to fish with a long life-span, and Lotka-Volterra systems to insects with a short life-span. One can achieve something by blundering on — by 'trial and error' processes — but this approach is uneconomical of effort. It may involve much hard work in counting and assaying parameters, and these, when a model is ultimately arrived at, may prove to be inapplicable — while the vital parameter was omitted from the study. To have a model earlier in the process makes the whole scheme much more efficient.

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