Historical Document: Life History and Fisheries of Atlantic Bluefin Tuna

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Frank J. Mather, III
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts 02543

John M. Mason, Jr.
New York Department of Environmental Conservation
Division of Marine Resources
East Setauket, New York 11733

Albert C. Jones
U.S. Department of Commerce, NOAA
National Marine Fisheries Service
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, Florida 33149

U.S. Department of Commerce
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southeast Fisheries Science Center
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Albert C. Jones
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75 Virginia Beach Drive
Miami, Florida 33149

U.S. Department of Commerce
Ronald H. Brown, Secretary

National Oceanic and Atmospheric Administration
D. James Baker, Undersecretary for Oceans and Atmosphere

National Marine Fisheries Service
Rolland A. Schmitten, Assistant Administrator for Fisheries

¹ Formerly with Woods Hole Oceanographic Institution.

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AUTHORS' NOTE AND ACKNOWLEDGMENTS

This report is based on extensive studies of Atlantic bluefin tuna carried out over many years by the senior author. The report was prepared in the late 1970s but not published. It is published now to provide a historical review of the biology and fisheries of bluefin tuna, based on knowledge available at that time. More recent studies have expanded the information base for bluefin tuna; however, that information is available, mostly in reports of the International Commission for the Conservation of Atlantic Tunas (ICCAT). Consequently, we have not attempted to include a review of that information in this document.

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Copies may be obtained by writing:

National Marine Fisheries Service
Southeast Fisheries Science Center
75 Virginia Beach Drive
Miami, Florida 33149

or

National Technical Information Service
5258 Port Royal Road
Springfield, Virginia 22161
(703) 487-4650
FAX: (703) 321-8547
Rush Orders: (800) 336-4700

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I. INTRODUCTION

The objective of this work is to review and summarize available information on the fisheries, distribution, and other aspects of the life history of the Atlantic bluefin tuna, *Thunnus thynnus thynnus* (Linnaeus 1758) (Figure 1). The need for such a review is emphasized by the concern over the status of the Atlantic bluefin tuna stocks and the recent enactment of measures for the conservation of this species by the International Commission for the Conservation of Atlantic Tunas (ICCAT).

The wastefulness of harvesting Atlantic bluefin tuna at extremely small sizes was recognized intuitively by d'Amico (1816, cited by Pavesi 1887). Sicilian laws of 1796 and 1801 prohibited the catching of small bluefin tuna (Avolio 1805 in Parona 1919). This restriction was apparently dropped during revisions of Italian fishery regulations in 1877 and 1882 (Pavesi 1887), but a minimum size limit of 60 cm was imposed in 1927 (Mussolini and Belluzzo 1927). In the 1960s, a minimum size limit of 90 cm was in effect in Italy (Sarà 1968, Miyake 1976, Maldura 1965).

The effect of harvesting bluefin tuna at small sizes was estimated theoretically by Shingu et al. (1975) and empirically by Mather (1974). Both works indicated that the capture of one thousand tons of young bluefin tuna precluded the subsequent capture of many thousand tons of larger individuals.

Action in 1975 by ICCAT in regulating the bluefin tuna fisheries finally recognized in principle the need to manage the fisheries for this economically important species. The regulations which became effective August 10, 1975, are as follows (Miyake 1975):

First — That the contracting parties take the necessary measures to prohibit any taking and landing of bluefin tuna (*Thunnus thynnus thynnus*) weigh-

ing less than 6.4 kg. Notwithstanding the above regulation, the contracting parties may grant tolerances to boats which have incidentally captured bluefin tuna weighing less than 6.4 kg, with the condition that this incidental catch should not exceed 15% of the number of fish per landing of the total bluefin tuna catch of said boats or its equivalent in percentage by weight.

Second — That as a preliminary step, the contracting parties that are actively fishing for bluefin tuna (*Thunnus thynnus thynnus*) or those that

ment (National Marine Fisheries Service, 1975, 1976) Canada, France, and Japan have also put the ICCAT regulations into effect (Caddy and Burnett 1976, Kume 1976, 1977).

Whether these regulations were enacted in time, and are adequate to restore the Atlantic bluefin tuna fisheries to their potential and former importance, is questionable. It is certain, however, that better knowledge of the life history of the bluefin tuna is a prerequisite to effective management of its fisheries. By general consensus, knowl-

Figure 1. Atlantic bluefin tuna (*Thunnus thynnus thynnus*).

incidentally catch it in significant quantities shall take the necessary measures to limit the fishing mortality of bluefin tuna to recent levels for a period of one year. At the 1975 meetings of the ICCAT Commission, this second item was extended for an additional two years, with provision for its review at the 1976 meetings of the ICCAT Council.

The member nations are responsible for enforcement of ICCAT regulations within their territorial waters. For the United States, the Atlantic Tunas Convention Act of 1975 empowered the Secretary of Commerce to implement regulations established by ICCAT. The National Marine Fisheries Service (NMFS) drew up a set of regulations, and is responsible for their enforce-

ment of stock identity and migratory patterns is of prime importance.

The aspects of the fisheries and life history herein discussed include: age and growth information; catch statistics; size, sex, and age composition of the landings in various areas; spawning and development; migration; and stock identification. Environmental parameters and their possible influences on the distribution, migrations and spawning of the species are also considered. Hypotheses on the migrations of bluefin tuna and stock identity are discussed. Finally, we state our own conclusions in regard to these matters and make some recommendations for future research.

II. METHODS AND DEFINITIONS

A. METHODS AND MATERIALS

Personal research by the authors during 1950-1976 has produced much of the knowledge which is summarized herein. Extensive additional information was obtained from the literature, by participation in meetings, and through correspondence and conversations with scientists, fishery experts, and fishermen.

The authors and their colleagues obtained a great mass of data and information on the species and its fisheries directly. They examined the landings and often observed or participated in the operations of various commercial and recreational fisheries over a great geographical range. They also participated in many exploratory fishing cruises of U.S. and foreign research vessels.

The Cooperative Game Fish Tagging Program of the Woods Hole Oceanographic Institution (a joint program with the National Marine Fisheries Service since 1973), initiated by the senior author in 1954, has provided much of the information on migrations and mortality rates of Atlantic bluefin tuna. Exchange of information and cooperation with marking programs of other nations has been extensive.

Also, much information has been obtained through participation in meetings of a variety of groups. These include international regulatory agencies and advisory groups, such as ICCAT, the Panel of Experts for the Facilitation of Tuna Research of the Food and Agriculture Organization (FAO) of the United Nations, and national, regional and state fishery agencies. We have also attended numerous meetings of non-governmental research and fishery groups or associations.

Further knowledge was obtained by correspondence and conversations with representatives of agencies of the types mentioned above, and with indi-

viduals concerned with the Atlantic bluefin tuna in many areas and several nations.

An important additional source of information was a thorough search of the literature. This was most intensive

B. DEFINITIONS

1. Bluefin Tuna

The subject of this paper is the Atlantic bluefin tuna, *Thunnus thynnus thynnus*, as distinct from the southern

Figure 2. Fork length measurement.

at the initiation of our studies and has been continued since then to the extent that time has permitted. This experience has enabled us to locate many important and little known references.

Our extensive contacts and data sources, increasing over the years, have enabled us to maintain close connection with the entire Atlantic bluefin tuna situation.

In the course of our investigations it became increasingly apparent that this species cannot be studied successfully on a piecemeal or limited area basis. Our approach, therefore, has been an attempt to observe and describe the species and its fisheries over its entire geographic range and during each stage of its life cycle. Our methodology has been a combination of original research and a review of the findings of other investigators in all the nations concerned with Atlantic bluefin tuna.

bluefin tuna, *Thunnus maccoyii* (Castelnau 1872) and the Pacific bluefin tuna, *Thunnus thynnus orientalis* (Temminck and Schlegel 1844). The ranges of the Atlantic and the southern bluefins overlap off South Africa and in the South Atlantic, whereas those of the Atlantic and the Pacific bluefins are apparently separate (Gibbs and Collette 1967, Talbot and Penrith 1968, Fisheries agency of Japan 1974, 1975, 1976, 1977).

Throughout this report, the terms Atlantic bluefin tuna, bluefin tuna, bluefin, tuna, fish, and individual refer to *Thunnus thynnus thynnus* unless otherwise identified.

a. Length

The most widely used measurement of length for bluefin tuna over 12 cm is fork length (FL). This is the straight line length, measured by calipers or equivalent instruments, from

Table 1. Size-age groups used to discuss much of the biological and fisheries data for Atlantic bluefin tuna in this report.

Group	Length		Weight		Approximate Age
	(cm)	(in)	(kg)	(lbs)	
Very small	< 50	<20	< 2.5	< 5	0
Small	50-120	20-48	2.5 - 32	5 - 70	1 - 4
Medium	120-185	48-76	32 - 122	70 - 270	5 - 8
Large or Giant	>185	>76	> 122	> 270	> 8

the snout (tip of upper jaw) to the posterior medial margin of the caudal fin (**Figure 2**). In this paper, length measurements exceeding 12 cm are fork lengths unless defined otherwise. An alternative method of measuring fork length is with a tape and following the lateral contour of the body. Lengths measured by this method have been referred to as tape lengths, curved lengths or flank lengths. The slope of a linear regression which Schuck and Mather fitted by inspection to a plot of straight lengths against curved lengths for each of a series of western north Atlantic bluefin tuna from 35 to 270 cm long indicated that the straight length was 0.958 times the curved length. Several other authors have published conversion factors for these parameters. Of course this relationship would vary slightly with the length-girth (or length-weight) ratio of the fish.

The lengths of juvenile specimens less than 12 cm long and of larvae are usually measured in standard length (SL). This is the length from the snout to the end of the vertebral column. In this paper, length measurements of bluefin tuna less than 12 cm long are standard lengths unless defined otherwise.

b. Weight

Weight data for fish are presented in this paper in terms of round, whole, or live weight (the weight of the entire fish) unless otherwise stated. In some fisheries, it is necessary to collect weight data for fish in the condition in which they are sold. This may be in several forms depending on the extent to which

the fish have been butchered. Conversion factors for obtaining round weights from weights in the various other conditions are available in the literature and at the Woods Hole Oceanographic Institution.

Weights of individual fish and average weights of fish are recorded in kilograms, unless otherwise stated. Weights of landings and catches (of numerous fish) are recorded in metric tons unless otherwise stated.

2. Size-Age Groups

Much of the biological and fisheries data for the Atlantic bluefin tuna will be discussed in terms of the size-age groups shown in **Table 1**. The limits of these groups were selected to

correspond as closely as possible to sizes and estimated ages at which the migratory and distributional patterns of the species undergo distinct changes (Mather 1964b). The ages for the respective sizes are from Mather and Schuck (1960). These size groups were set up on the basis of data from the summer fisheries in the northwestern Atlantic and the spring fishery off the Bahamas. They appear, however, to be reasonably applicable to bluefin in the eastern Atlantic and the Mediterranean Sea.

3. Trap Fishery Terminology

Specialized terms have been used to describe the bluefin tuna trap fisheries of the eastern Atlantic and the Mediterranean Sea. Since these terms are often misunderstood or poorly translated in the literature, an explanation of them seems desirable.

The true bluefin tuna traps are very large, complex installations set at special locations to harvest runs (periodic migratory passages) related to the spawning of these fish. "Arrival" fish are essentially fat, maturing individuals, generally traveling eastward in late April, May, and June. "Return" fish are essentially lean, spent individuals, gen-

Table 2. A glossary of some of the more important tuna fishery terms in English, French, Italian, Portuguese, and Spanish.

English	French	Italian	Portuguese	Spanish
True Tuna Trap	Madrague Thonaire ¹	Tonnara ¹	Armacoa	Almadraba
Minor Tuna Trap	Petite Madrague Thonaire Mixte	Tonnarella		Almadrabilla
Arrival	Arrivé Course	Corsa	Direito	Derecho Arribada
Return	Retour	Ritorno	Revez	Reves
Genetic	Genetique	Genetico		Genetico
Erratic	Erratique	Erratico		Erratieo

¹The words thonaire and tonnara are also used locally for other gears which catch tunas or tuna-like fishes.

erally traveling westward in July, August, and early September. Some of the younger spawners, which have not yet discharged their eggs, are sometimes taken with the return fish. The arrival fish are not only more robust than the return ones, but their flesh is fattier and usually commands a higher price.

In most areas, traps were fished for only one run — either as arrival or return traps. However, along the south-

ern Atlantic coasts of Portugal and Spain, many traps were altered to fish for each season, and in this way they fished both runs.

Smaller and less important traps take bluefin tuna throughout much of the year, but these fish are mainly immature individuals or larger ones which have completed their spawning cycle and are more widely dispersed, presumably in search of food.

Roule (1914a, 1914b) proposed the terms “genetic” for maturing bluefin tuna, and “erratic” for those which had spawned and whose behavior was dominated by search for food. These terms occur in many works on these fisheries. A brief glossary of some of the more important terms, in English, French, Italian, Portuguese, and Spanish is listed in **Table 2**.

III. AGE AND GROWTH

A. INTRODUCTION

Knowledge of the age-size relationship is not only important from the biological viewpoint but is also essential for effective management of a fishery. Until recently, there has been general agreement on the sizes of Atlantic bluefin tuna at ages up to 12-14. Preliminary results for ages up to 26 have been presented in 1975 and 1976, but these are controversial.

B. METHODS OF DETERMINING AGE AND GROWTH AND THEIR APPLICATION TO BLUEFIN TUNA

1. Size Frequencies

Age groups show up as modes when the sizes of sufficient numbers of bluefin tuna are plotted. These modes are usually distinct for small individuals (up to 125-150 cm long), but become less distinguishable with larger fish. The length-weight ratio of large bluefin fluctuates greatly with the seasons (Tiews 1963). Therefore length measurements are more suitable for size frequency analyses than weights. Growth may be estimated from the progression of modes in plots of size data for consecutive time intervals.

Size-frequencies were evidently used, although the methodology was not described, by d'Amico (1816, in Heldt 1930) and Bourge (1908, in Roule 1917), in estimating the sizes of juvenile Mediterranean bluefin tuna in their first four months of life. Piccinetti and Piccinetti-Manfrin (1970) presented a more detailed and precise study of their growth through this period, describing the methods they had used.

Westman and Gilbert (1941) and Westman and Neville (1942) were

evidently the first to study the growth of larger bluefin tuna by this method. They traced the growth of young individuals taken off Long Island, New York, in the summers of 1938 and 1941 by analyzing their length frequencies. They established the age in years of each size group by counting annuli on scales.

Buser-Lahaye and Doumenge (1954) and Doumenge and Lahaye (1958) likewise analyzed length frequencies to estimate the ages of small bluefin tuna caught off the Mediterranean coast of France during 1953 and 1954. They used Sella's (1929a) data, however, to establish the estimated age of each size group.

More extensive studies of the summer growth of western Atlantic bluefin tuna, using counts of annuli on hard parts as well as size frequencies, were presented by Mather and Schuck (1960).

Furnestin and Dardignac (1962) were the first authors to trace the growth of *T. thynnus thynnus* through most of the first two years of its life. They used size frequencies of young fish taken off the Atlantic coast of Morocco, where, after attaining a length of about 32 cm, they are available throughout the year.

Tiews (1960) used the frequencies of eye diameters, which he assumed to be related to the age of the fish, as well as to its length, to estimate the ages of large bluefin tuna caught in the North Sea in the summer and fall of 1959.

2. Counts of Marks on Hard Parts

Ages of bluefin tuna have been estimated by counting marks, usually called annuli, which were thought to have been laid down annually, on certain hard parts of the fish. The parts used included scales, vertebrae, and otoliths (Figure 3).

The relative merits of these methods were extensively discussed at the "conférence d'experts pour l'examen des méthodes scientifiques et techniques à appliquer à l'étude des poissons de la famille des Thonidés" (hereafter referred to as "Conference of experts") held at Madrid and Cadiz, Spain, 16-22 May 1932 (Anonymous 1932b), and by others as cited here.

a. Scales

Age determinations from scales are based on counting the "checks" or areas where two or more circuli are close together, instead of being more widely and evenly spaced as they are on most of the scale's surface.

Corson (1923a, 1923b) presented the first age determinations for Atlantic bluefin tuna of which we have knowledge. These were based on scales taken from a small number of young fish caught off Long Island, New York, in September 1923. He used scales from the posterior part of the fish, having found those from the shoulder to be unreadable because of streaks and globules of oil within them.

At the "Conference of experts" (Anonymous 1932b), F. de Buen and Sella said that scales did not furnish

Figure 3. Bluefin tuna vertebra showing two annuli.

interesting information on the age of the bluefin tuna, but Frade showed that growth lines were clearly indicated on scales of young individuals. The experts concluded that scales were not useful for determining growth in this species, except for young individuals.

Spagnolio (1938) estimated ages of from 3 to 6 years from scales of bluefin tuna caught in traps off southern Italy and northeastern Sicily. She presented illustrations of these scales but did not report the sizes of the fish. She concluded that readings from scales should be checked against readings from vertebrae of the same individual. She maintained that if the method were validated, scales would be preferable to vertebrae for determining ages of small bluefin tuna, up to 40-58 kg or 5-6 years of age, since scales were easier to collect and to examine than vertebrae. Spagnolio used scales from the caudal and lateral parts of the body, rejecting those from the corselet because they were too thick and opaque. The scales which she used were preserved in formalin, and later were soaked in water or an alcohol solution or glycerine before examination. She found no marked advantage in using either of the last two fluids instead of water.

Westman and Gilbert (1941) and Westman and Neville (1942) used readings of annuli on scales, as well as analyses of length frequencies, to determine ages of young (1-7 year old) bluefin tuna taken off Long Island, New York, during the summers of 1938 and 1941. These authors also offered tentative age determinations from scales for a few much larger bluefin tuna, up to 250 cm and 275 kg, with an estimated age of about 18 years. They used carefully selected thin and round scales from the side of the body, just below the lateral line in the area below the base of the second dorsal fin. Projected impressions of the scales facilitated their readings of those with more than five annuli.

Mather and Schuck (1960) estimated ages of 0-4 years from scales of bluefin tuna taken off the northeastern United States during several summers. They relied more heavily on length frequencies for studying the growth of young individuals, however, and on vertebral annuli for the older ones. These authors used scales from the general part of the tuna's body where Westman and Gilbert (1941) and Westman and Neville (1942) collected theirs. They made impressions of the scales on celluloid (Arnold 1951), and counted annuli on magnified projections of these impressions.

None of the above authors used the large and thick scales of the corselet for age determinations, but F.S. Russell mentioned (personal communication) that he had found a possible method of determining ages from these scales. He found that they were built up of lamina, like the pages in a book, which might represent years of growth. These lamina could be separated after the scales had been soaked in a weak solution of acetic acid.

The most important use of scale readings in aging bluefin tuna has been in validating determinations made by other methods (Westman and Neville 1942, Mather and Schuck 1960).

b. Vertebrae

F. de Buen (1925) estimated, by counting its vertebral rings, that a male bluefin tuna 206 cm long (from snout to tips of caudal) and weighing 119 kg was 12 years old. This fish was caught July 4, 1923, in the Barbate trap near Cadiz, Spain.

Sella (1929a) presented mean lengths and weights of Mediterranean bluefin tuna for ages 1-14, as estimated by counting the rings in the centra of vertebrae. This was the first study which described the growth of bluefin tuna through most of the size range ordinarily encountered.

At the "Conference of experts" (Anonymous 1932b), Sella and the

other experts discussed the use of vertebrae for age determination. Several methods of preparing vertebrae for examination were described, and it was noted that they could be examined without special preparation. He described three instruments which he used in the study of vertebrae and stated that the annuli were generally better defined in vertebrae from the caudal trunk. Heldt reported that, in each of five bluefin tuna of different sizes which he had examined, the number of annuli on each of the vertebrae was the same. He also noted that double rings, which should not be counted as two years, sometimes occurred. Sella and F. de Buen maintained that the vertebral rings represented years of age, but the latter noted that, because of the time of spawning, the first ring did not correspond exactly to one year. Frade reported finding 16 vertebral annuli for a 263 cm fish, which exceeded the maximum age reported by Sella (1929a).

Several workers reported on the growth of bluefin tuna from different areas as determined from readings of vertebral annuli in the period 1956-1962. These include Hamre (1958, 1960) (Norway), Rodríguez-Roda (1960) (Spain), Vilela and Pinto (1958), Vilela (1960), and Frade and Vilela (1962) (Portugal), and Mather and Schuck (1960) (northeastern United States). Mather and Schuck used the technique of Galtsoff (1952) to stain many of the vertebrae which they used for age determinations. Rodríguez-Roda (1964a) presented thorough mathematical interpretations of his 1960 results.

Butler (1971, 1975) counted the rings in the vertebrae of large bluefin tuna taken in Canadian waters in 1966 and in 1974 and estimated their ages as 11 to 22 or more years. Myklevoll used this method to determine the ages of bluefin tuna taken in Norwegian waters in 1974 (Caddy and Butler 1976). These estimates ranged from 14 to 21 years.

Butler and Myklevoll were the first investigators to estimate the ages of significant numbers of bluefin tuna more than 14 years old.

Berry et al. (1977) discussed in great detail the techniques of aging bluefin tuna by reading annuli on vertebrae and otoliths. They described methods of storing, staining and examining vertebrae, and their interpretation of the markings on them. They found that immediate freezing and freezer storage produced better results than the other methods of preservation which they tested. Immediate staining and reading, however, was probably the most satisfactory procedure. They noted that staining time varied with the size of fish, and that the inner rings, particularly in large fish, stained before the outer ones.

Their interpretation of marks on vertebrae was complex. It involved ridges, grooves, fimbriated lines, and stained and unstained rings. They noted that several stained rings might occur early in the staining process within an annular zone, and that these might coalesce in various ways as staining progressed.

Berry et al. (1977) did not include size-for-age data or age data for individual fish, but they presented extreme and average vertebral ages, determined from readings of vertebral annuli, for bluefin tuna in various weight ranges. They tentatively recommended the use of vertebrae for estimating ages up to about 10 years for this species.

From 1932 until 1974, counting vertebral annuli was generally regarded as the most satisfactory method of aging large Atlantic bluefin tuna.

c. Otoliths

The use of otoliths in determining ages of *T. thynnus thynnus* was first investigated in the 1920s, but important results did not appear until 1975.

Despite the fact that F. de Buen (1925) had been discouraged by the

difficulties encountered in extracting otoliths, Frade (1925) described procedures for their relatively rapid removal, and the nature of the growth zones on them. These descriptions, accompanied by excellent illustrations, suggested that this was a practical method of age determination.

At the "Conference of experts" (Anonymous 1932b), however, Frade reported that, although he had found zones of growth in thin sections of otoliths, he was not sure that these sections included all of the years of growth. He attributed his uncertainty to the irregular shape of the otoliths. The experts concluded that growth zones were laid down on otoliths, but that it was difficult to assign absolute ages by counting these zones. They therefore recommended that this technique be used mainly to confirm age determinations obtained by other means.

Frade and Vilela (1962) referred to age determinations from otoliths by Frade (1950), but we have not seen the latter work. No further references to Frade's early work with otoliths have come to our attention.

The next attempt to determine ages of bluefin tuna from otoliths was by Nichy (Nichy and Berry 1976). They developed techniques for estimating the ages of bluefin tuna similar to those of Frade (1925). They used otoliths from large individuals caught off Prince Edward Island in the Gulf of St. Lawrence, Canada, in 1974. Caddy and Butler (1976) classified large bluefin tuna taken in Canadian waters in 1974 and 1975 by year classes, using Nichy and Berry's techniques and some of their determinations in addition to their own. They did not report the sizes of these fish.

Caddy et al. (1976) present the most complete study available on the growth of bluefin tuna as determined from otoliths. They used this method to determine the ages of large individuals (age 10 and over) caught in Canadian waters during the summer and fall of 1975. They calculated pa-

rameters for von Bertalanffy growth equations for males and females, using their data for fish of ages 10 or greater and Mather and Schuck's (1960) results for fish of ages 1-4.

Their work was the first to indicate different growth rates for the two sexes. Butler et al. (1977) reproduced the above material with the addition of preliminary age data from the otoliths of 60 large bluefin taken in Canadian waters in 1976, and presented some modifications of the Nichy and Berry (1976) and Caddy and Butler (1976) techniques.

Berry et al. (1977) discussed the removal, storage, measuring, mounting and sectioning of otoliths. They described the sections and their interpretation of the markings on them. They found that, at ages greater than 10 or 11, hyaline bands occurred in pairs which represented a single annular zone.

They discussed definitions of annuli on vertebrae and otoliths, and proposed the following tripartite hypothesis:

- a) Major discernible markings on vertebrae and otoliths of Atlantic bluefin tuna do not have to be presumed to be annuli.
- b) Within each year of life, multiple markings are successively formed on vertebrae and in otoliths. These multiple markings may appear in prepared specimens of vertebrae and otoliths as irregular combinations. Single markings that represent the end of a year of life (annuli) may be distorted by variations of the within year multiple markings.
- c) Annuli may be deciphered by considering the nature in which they form and by interpreting the variations that may exist within and between individual prepared samples.

Berry et al. (1977) did not present age data based on readings of annuli on otoliths.

3. Release-Recapture Data for Tagged Fish

When size data at release and recapture of a given fish are avail-

able, its growth during the period at liberty is established. If age at the time of release can be determined, age at the time of recapture can likewise be calculated. Positive age and growth information thus obtained can provide a valuable check on estimates based on indirect methods (Mather 1980).

C. RESULTS

1. Sizes of Fish at Determinable Ages

The first objective of most age and growth studies is to determine the mean sizes of fish at each year of age for which this is possible. Ideally the sizes should be determined at one year intervals after the date of spawning. This was done by Sella (1929a) and Rodríguez-Roda (1960, 1964a), but most other investigators have been limited to seasons in which sufficient material was available.

Sella (1929a) presented the first important study of the age and growth of bluefin tuna. This was based on counts of annuli on vertebrae from more than 1,500 bluefin tuna caught in June, during the spawning season. The individuals whose ages were assessed as 3 or more years had been taken off Tripolitania (western Libya). Sella noted that these results did not differ noticeably from those for bluefin tuna taken in other parts of the Mediterranean. He assessed ages of 1 and 2 years for individuals which had been captured in the Adriatic Sea, since fish of these sizes were not available off Libya. He presented his results in terms of mean length and mean weight for each year of age from 1 through 14.

Westman and Gilbert (1941) and Westman and Neville (1942) produced the first important information on the growth of bluefin tuna taken in the western Atlantic. Their works provided well supported

information of the sizes of fish of ages 1-4 taken during the summers of 1938 and 1941 off Long Island, New York, and sizes based on small samples or individual specimens, for young of the year and for various ages of 5 years or more.

Several additional works on the age and growth of bluefin tuna taken in various parts of the Atlantic Ocean were published between 1958 and 1962. Tiews (1963) plotted the sizes for ages obtained by Sella (1929a), Westman and Gilbert (1941), Hamre (1960), Vilela et al. (1960), Tiews (1960), Rodríguez-Roda (1960), and Mather and Schuck (1960) (Figure 4). As Tiews observed, the results of these studies, using material from several widely separated areas, are remarkably similar.

Rodríguez-Roda (1960, 1964a) presented the following formula for back-calculating the fork length of a bluefin tuna at ages previous to that of its capture:

$$l = 17.88 + \sqrt[4]{v} (L - 17.86)$$

where:

L = fork length in cm of the fish,

V = radius in mm of the fourth or fifth precaudal vertebra,

l = fork length in cm of fish at age x , and

v = radius (mm) of vertebral ring corresponding to age x .

The back-calculated lengths were considerably less than those obtained directly for fish of the same ages. This was due in part to the fact that the vertebral rings were laid on during the winter, but the direct age determinations were made from material collected in late spring and early summer.

Rodríguez-Roda presented revised size-for-age data (1969c) and the following von Bertalanffy equation for the relation between age and size:

$$l_t = 355.84 (1 - e^{-0.09 (t + 0.89)})$$

Figure 4. Sizes for ages as estimated by various authors (Tiews 1963).

Caddy et al. (1976), using otoliths from 225 large (over 220 cm long and 230 kg in weight) bluefin tuna taken in Canadian waters in the summer and fall of 1975, produced preliminary size for age data for fish up to 15 years old. They also calculated the following parameters for von Bertalanffy growth curves (Figure 5) for males and females:

	Males	Females
K	0.134	0.116
L_{∞}	286.64	277.315
t	0.3278	0.7999

Additional growth and size at age data have been obtained from the lengths at release and recapture for three tagged fish which had been at liberty for periods of 13-14 years. (Table 3) (Mather 1980). Points corresponding to these sizes have been plotted with the growth curves of Butler et al. (1977) (Figure 5). All of the points lie very near the curve of Butler et al. (1977) for male bluefin. Although the sexes of these recap-

Table 3. Growth and sizes of three tagged fish recaptured after periods of 13-14 years at liberty.

Return Number	Release		Years at Liberty	Recapture		
	Length (cm)	Age ^a (years)		Age (years)	Length (cm)	Weight (kg)
1	197 ^b	8.8	13	21.8	279	288
2	78 ^c	2.2	14.1	16.3	256	397
3	75 ^c	2.2	13.1	15.3	251 ^b	329

^a Assuming birth date June 1 (Richards 1976) and ages as estimated by Mather and Schuck 1960.

^b Estimate coinciding with modal size of 21 fish caught on same longline set.

^c Measurements converted to "caliper" length from "tape" length, assuming: caliper length = .958 tape length.

tured fish were not determined, the agreement between results obtained mainly by direct methods and those obtained from counts of age marks on otoliths is good.

The results of some of the more important studies of the sizes at ages of Atlantic bluefin tuna are shown in Table 4.

Berry et al. (1977) did not provide size for age data, but they presented age ranges and average ages for selected weight ranges of bluefin tuna captured off Massachusetts in 1975 (Table 5).

2. Growth of Bluefin Tuna in Its First Year of Life

There has been much interest in determining the growth of the bluefin tuna during its first year of life, since this information is a prerequisite for validating the determinations of all older ages. Data on this subject, starting with the early observations of d'Amico (1816) have been recapitulated in detail by Scaccini et al. (1975). The less extensive data from the eastern Atlantic (Furnestin and Dardignac 1962) and the western Atlantic (Rivas 1954, Mather and Schuck 1960) are in good agreement with those from the Mediterranean.

The growth in weight of larval and small juvenile bluefin (up to 1400 g, or about four months of age) spawned in the central Mediterranean has been described by Piccinetti and Piccinetti Manfrin (1970) (Figure 6). These authors estimated growth by assuming that the largest individuals in each collection made as the season progressed represented the group which was hatched earliest (about June 15). Thus it is possible that their

Figure 5. Fits of von Bertalanffy growth curves to mean fork length at age (as determined from otolith readings) for male and female bluefin tuna taken in Canadian waters in 1975 (bracketed values omitted). Mean sizes at age (series combined) from Mather and Schuck (1960) for ages 1-4 (closed squares) were used in fitting both curves (from Butler et al. 1977). Points in circles represent lengths of three tagged fish at ages when recaptured.

Table 4. Sizes of Atlantic bluefin tuna at ages as determined by various authors.

Age	Sella 1929a		Hamre 1960	Rodríguez- Roda 1969	Vilela 1960	Westman, Neville 1941	Mather, Schuck 1960	Caddy et al. 1976*	
	(cm)	(kg)	(cm)	(cm)	(cm)	(cm)	(cm)	Males (cm)	Females (cm)
1	64	4.4		55.3		65.0	57		
2	81.5	9.5		79.0		85.0	77		
3	97.5	16		116.2		105.2	95		
4	118	25		130.1	120.5	117.6	114		
5	136	40	135	146.9	136.0	147.8	133		
6	153	58	153	165.1	146.9	148.3	149		
7	169	76	166	178.1	163.9	157.5	163		
8	182	95	180	192.9	187.2		177		
9	195	120	195	206.5	196.1		190		
10	206	145	207	220.3	217.7		201		
11	216	170	221	221.5	223.0			223	
12	227	200	228	244.0	232.8			231	
13	239	235	239	246.0				239	
14	254	280						245	
15								250	238
16								254	242
17								258	244
18								262	246
19								266	248
20								270	250
21								273	252
22								275	255
23								276	257
24								278	258
25								279	259

*Estimated from curves (Figure 5).

Table 5. Age ranges and average ages for selected weight ranges of bluefin tuna captured off Massachusetts (Berry et al. 1977).

Weight Range (kg)	Age Range (years)	Average Age (years)
136-181	6- 9	7.3
181-226	8-10	8.6
227-272	8-14	11.1
272-317	12-14	12.7
318-362	13-17	14.9

Ages determined by counting vertebral annuli.

Figure 6. Growth in weight of bluefin tuna collected in Sicilian waters in their first months of life (Piccinetti and Piccinetti Manfrin 1970).

results apply to the fastest growing, rather than the average, individuals.

Rivas (1954) and Mather and Schuck (1960) presented very similar curves of estimated linear growth for the first eight months of life of bluefin tuna collected in the western North Atlantic. Mather and Schuck's curve (Figure 7) was based on a limited number of measurements, including those of Rivas, from various areas along the Atlantic coast of the United States and in the Gulf of Mexico. The date of spawning was assumed to be May 15. Although spawning probably occurs earlier in the western Atlantic than in the Mediterranean (see Section V), the estimated mean sizes attained by the young of the year by mid-October are about the same in both areas—38 cm or 1,100 g. Data for age 0 bluefin caught off the Atlantic coast of Morocco (Furnestin and Dardignac 1962, Aloncle 1964) are similar. Individuals taken in the first half of October were 31 to 34 cm long, in November, 39 to 43 cm, and at the end of December, 44 to 45 cm.

Figure 7. Lengths of bluefin tuna less than 50 cm long (young of the year) collected in the western Atlantic and the Gulf of Mexico. The curve of estimated growth was fitted by inspection (Mather and Schuck 1960).

Figure 8. Estimated growth of young bluefin tuna. Broken lines indicate estimated lengths in periods for which data are lacking. The lower scale shows ages assuming that hatching occurs at mid-May (Mather and Schuck 1960).

In all three areas, growth is extremely rapid in the spring, summer and early fall, and considerably slower during the first winter of life. At twelve months of age, eastern and

western Atlantic fish are about 50 cm long, according to Furnestin and Dardignac (1962) and Mather and Schuck (1960). Larger sizes are reported for 1-year-old tuna by Rodríguez-Roda (1960) for eastern Atlantic fish (55 cm) and Sella (1929a) for specimens from the Mediterranean Sea (64 cm).

3. Growth of Young Bluefin Tuna

Westman and Seville (1942) were the first to show that young bluefin tuna grow much more rapidly during the summer than during the winter. They reached this conclusion by tracing the growth of young fish taken off Long Island, New York, through the period July 1-October 16, 1941, from length frequency data.

Mather and Schuck (1960) studied this matter in greater detail. Their data included some specimens taken during both summer and winter in their first year of life (age 0), but data were available for ages 1-4 for the period July-October 16 only. The growth rates in the latter period were very rapid (about 3.8 cm per month), and it was evident that their average

Figure 9. Curve of linear growth of young bluefin tuna (caught off the Atlantic coast of Morocco) up to the beginning of their third winter (Furnestin and Dardignac 1962).

growth rate during the remainder of the year must have been much slower (about 0.8 cm per month)(Figure 8).

Furnestin and Dardignac (1962) were able to collect material of ages 0-2 throughout most of the year along the Atlantic coast of Morocco. Their data for winter sizes fitted very well with corresponding data for January obtained by extrapolation from Mather and Schuck's (1960) results. It also showed that growth virtually ceased from January to March at age 0, and at the end of November, when the fish were about 63 cm long, at age 1. Data for age 2 were incomplete, but suggested that in autumn they had practically reached their winter length of about 85 cm (Figure 9).

4. Seasonal Changes in the Length-Weight Relationship of Large Bluefin Tuna

Extensive seasonal changes in the length-weight ratio of large bluefin tuna have been found by many investigators working in different areas which collectively represent a

considerable part of the coastal habitat of the species.

In the North Sea area Bahr (1952), Tiews (1957) and Luhmann (1959) observed an increase in weight in relation to length during the fishing season of August to October. Tiews (1957) showed that tunas of 215-240 cm increased their weight during their 2-3 month stay in the North Sea by about 11.0 kg in 1954 and 17.4 kg in 1955. This worked out to about 34% to 54% of their yearly weight increase. Luhmann (1959) pointed out that variations in the length-weight relationship in different years might be directly associated with variations in feeding conditions.

Rodríguez-Roda (1964) observed that during the spawning season, from May to August along the south Atlantic coast of Spain, mature fish lost about 14.73% of their weight between the pre- and post-spawning state.

In the western Atlantic, Rivas (1955) studied records of the weights of giant tuna from the Bahamas in

May and June and from Nova Scotia in July to September. He estimated a 7.5% per month increase in weight of these fish during their sojourn in Nova Scotia waters.

Butler (1974) supported Rivas' findings for the northern fish. He examined giants taken near Prince Edward Island between July and October 1974. By calculating weekly mean weights during this period Butler showed an approximate weight gain of 70 kg in 12 weeks. He refined these data and calculated a 30 kg per month gain between August 19 and October 4, 1974, or about 10% per month.

The present authors have calculated length-weight relationships for various monthly periods for bluefin tuna taken during the fishing seasons in two parts of the western North

Figure 10. Seasonal ratios of fork length to maximum girth and fork length to total weight by sex for all areas combined. (Caddy et al. 1976)

Table 6. Factors derived from the length-weight formula for Area 1 (north of latitude 35°N and west of longitude 50°W) and Area 2 (Straits of Florida and adjacent waters).

Season	A	B	Length (cm)
Area 1:			
June	- 4.2571	2.7871	50-260
July	- 4.3893	2.8497	50-260
Aug.	- 4.5540	2.9290	35-270
Sept.	- 4.5651	2.9391	35-270
Oct.	- 4.7330	3.0192	35-270
July-Sept.	- 4.4989	2.9044	35-270
Aug.-Oct.	- 4.0333	2.8606	35-270
Area 2			
May-June	- 4.8070	2.9044	185-260

Atlantic. Area 1 comprised waters north of latitude 35°N and west of longitude 50°W. Area 2 included the Straits of Florida and adjacent waters. Factors derived from the following length-weight formula are shown in **Table 6**:

$$W = A + B \text{ Log } L$$

where:

W is the live (whole) weight of the fish (kg), and

L is the fork length (cm)

Unpublished data collected by Schuck and Mather showed that although there was a marked increase in the length-weight ratio of large bluefin from June through October, the length-weight ratio of individuals less than 100 cm long did not change noticeably from month to month during the summer.

5. Differential Growth of Males and Females

Although some authors noted that male bluefin tuna attain larger sizes than females, only two studies, those of Caddy et al. (1976) and Butler et al. (1977), showing a consistent difference in growth rate have

come to our attention. Few of the publications on the growth of the species present data in terms of sex of fish. Hamre (1960) found no significant difference in growth between males and females.

Tabulations of age determinations by sex of fish (Rodríguez-Roda 1964) indicate that males attain larger sizes than females. The data suggest, however, that this difference is due to greater longevity for males, rather than a difference in growth rates. Rivas (1976) reported that, on the average, the males in samples of large bluefin taken off the Bahamas and in the Gulf of Mexico in various years were 4 % longer and 13 % heavier than the females.

As noted in part 1 of this subsection, Caddy et al. (1976) found consistent differences in length for age between large male and female bluefin caught in Canadian waters in 1975 (**Figure 5**). These authors also found differences in the length-weight relationship between males and females in the period July-November (**Figure 10**). Males are heavier than females of the same length. Since, as this figure shows, there is very little difference in maximum girth between

the sexes, the males must be considerably heavier posteriorly than the females.

6. Ultimate Length

The asymptotic or ultimate length (L_{∞}) of Atlantic bluefin tuna has been estimated from some growth studies. Rodríguez-Roda (1964a, 1971) presented an L_{∞} of 355.8 cm, derived from his age determinations for bluefin tuna collected off the southern Atlantic coast of Spain. Caddy et al. (1976) derived an L_{∞} of 447.88 cm from the age-size data of Mather et al. (1974), an average of several previous works, and an L_{∞} of 286.64 cm for males and 277.315 cm for females from their own determinations for fish taken in Canadian waters. The longest bluefin tuna entered for record consideration by the International Game Fish Association as of December 1976, weighed 540 kg and was 312 cm long (FL) (the method of length measurement used was not specified) (E. K. Harry, personal communication). Larger bluefin tuna have been reported in the literature. For example, Hamre et al. (1971) reported an individual in the 310-315 cm range measured at the Istanbul (Turkey) fish market in January 1967. Unfortunately, the weights of many large bluefin are reported without any information on their length. Sarà (1969) mentioned bluefin tuna of 625 and 685 kg taken in traps off Sardinia in 1969 and Scaccini et al. (1975) cited fish weighing up to 600 kg taken in the Favignana trap off western Sicily in June 1974.

7. Discussion

There has been good agreement on the size for age of Atlantic bluefin tuna for ages 1-11 (**Table 4**). There is less confidence in determinations for older ages. Caddy et al. (1976) extended estimated age determinations to 25 years, and also provided separate von Bertalanffy growth curves for males and females (**Figure 5**). These authors note that ear-

lier age determinations had ascribed fish smaller than 245 cm to age group 8, whereas their own determinations indicated that 245 cm was roughly equivalent to ages 14-15 for males and age 18 for females. They also asserted that apparent underestimates of the ages of fish more than 240 cm long had resulted in estimates of L_{∞} based primarily on data from fish less than 12 years old, which were in excess of any sizes recently recorded for Atlantic bluefin tuna. If their results should be validated, considerable revisions of recent estimates of the age composition of the Atlantic bluefin tuna stocks (Sakagawa and Coan 1974) would be required.

Berry et al. (1977) questioned previous age determinations for large Atlantic bluefin tuna. In the size ranges for which they provided average ages (136-181 kg, 181-226 kg,

227-272 kg, 272-317 kg and 318-362 kg), their ages were 2-3 years less than those of Mather and Schuck (1960), 3-4 years less than those of Butler (1975), and 4-5 years less than those of Caddy et al. (1976). They attributed these discrepancies to the interpretation of growth marks on otoliths and vertebrae, mainly in fish more than 10 years old. In these older fish, they often found double or multiple markings which, they believed, represented subdivisions of a single year's growth. They assumed that other workers had counted each such mark as representing a year's growth, resulting in a tendency to overestimate ages.

It is most important that the actual age composition of the "relict" population (as described by Caddy et al. 1976) of giant Atlantic bluefin tuna be determined.

It is also important that the linear growth rate of the early stages of bluefin tuna be determined for the various spawning areas. This information is needed in terms of length, rather than weight, to permit better estimates of spawning dates and localities from the collection data for these stages of the bluefin tuna.

Seasonal variations in the growth rates of bluefin tuna up to 4 years old are reasonably well known (Mather and Schuck 1960, Furnestin and Dardignac 1962), but the data now available should permit extension of this knowledge to older ages. The possibility that the growth rate of the Atlantic bluefin tuna has increased as the size of the stock has decreased should also be investigated. This possibility is suggested by the remarkable number of extremely large bluefin caught since 1970 (see Section IV).

IV. DISTRIBUTION AND FISHERIES

A. GENERAL DISTRIBUTION

The bluefin tuna has been reported at one season or another over an extraordinarily large area of the Atlantic and the adjacent seas, and in a wide variety of water types (Figures 11 and 12). In recent years it has ranged off the Atlantic coasts of Europe and Africa, from the North Cape, inside the Arctic Circle, to the Cape of Good Hope, and off the American coasts from Newfoundland to 40°S latitude, and also in most of the intervening oceanic areas. It also has been present in most of the adjacent seas, the North, Mediterranean, Black and Caribbean Seas, and the Gulf of Mexico.

The distribution of the bluefin tuna has varied greatly with the seasons and with the size of fish (Figure 13). Seasonal variations are influenced by the requirements of spawning and feeding, and by water temperature. Tiews (1963) concluded that distribution was limited by the 12°C (surface temperature) isotherm. Distributional changes with size of fish are probably related to the change from a planktonic diet to one of small fishes during its first few months of life, to its first spawning at 3 to 5 years of age, or, possibly, to the full development of its swim bladder at ages 8 to 10 years (Sella 1929b, Sarà 1973). Year-to-year changes in distributional and migratory patterns are frequent. Variations in environmental conditions and the availability of food are regarded as the major causes of these changes.

B. DEVELOPMENT OF THE MAJOR FISHERIES

Large scale fisheries for bluefin tuna have existed in the Mediterranean and its approaches for centuries, but those in the remainder of the Atlantic are of more recent origin. Several methods and gears have been used. The oldest large scale method is the tuna trap, which has been used through most of the Christian era and perhaps much earlier.

Figure 11. Bluefin distribution (longline catches off southwestern Africa probably consisted mainly of southern bluefin, *Thunnus maccoyii*).

Figure 12. Bluefin regions of capture by seine, live bait, and trap

(Pavesi 1889, Parona 1919). These were set near the coasts and the more important ones depended on the spawning migrations of the bluefin in the Mediterranean and its approaches. An eastward or "arrival" run of prespawning fish occurs in May and June in many localities, and a westward or "return" run of spent fish occurs in July and August in some of these, and in some other locations. Most of these tuna traps were designed to catch fish coming from one direction only, but a few were reversed between the seasons and fished both runs. Less elaborate traps have taken bluefin tuna in many localities during other seasons.

Handline and harpoon fisheries have existed in many areas, in some cases for centuries, taking relatively small catches. Specialized gears, such as the "thonaille" (a drifting entangling net) and "seinche"

Figure 13. Lengths of bluefin tuna by region ("+" on graph means less than 0.5%).

(a complex multi-boat seine) of southern France (Doumenge 1953) and the "cianciolo" (a modified seine) of Sicily (de Gaetani 1948), have been used locally, and generally on a small scale.

Since World War II, great changes have occurred in the Atlantic and Mediterranean bluefin fisheries through the introduction of three much more productive methods: live-bait, pelagic longline, and purse seine. In addition some fisheries using the older methods were initiated or expanded.

The traditional trolling fishery for small bluefin and albacore, *Thunnus alalunga* (Bonnaterre 1788), in the Bay of Biscay was largely converted to the much more productive live-bait method between 1947 and 1949 (Navaz 1950a, 1950b; de la Tourrasse 1951). The French catches increased from 600 tons in 1948 to from 1,900 to 3,500 tons per year in 1950-1959. In 1960-1970, however, they declined to between 400 and 1,600 tons, exceeding 1,000 tons only once (Aloncle 1972). The 1970 and 1971 catches were also below 1,000 tons (Bard et al. 1972). The live-bait method has also come into use in the fishery for small bluefin off the Atlantic coast of Morocco (Lambocuf 1972).

The highly effective purse seine method has also been widely introduced in the Atlantic and the Mediterranean. The first important step was the development of a seine fishery for medium sized and giant bluefin off Norway in the late 1940s. The annual Norwegian bluefin catches increased from a few hundred tons in the middle 1940s to about 10,000 tons in the middle 1950s (Hamre 1971). Catches declined greatly after 1962, varying from 200 to 2,500 tons per year in 1963-1971, collapsing to about 100 tons in 1972 and 1973, and rising to 800 tons in 1974 (Miyake and Tibbo 1972, Miyake and Manning 1975).

A handline fishery for giant bluefin tuna in the North Sea was originated by German and Danish fisher-

men in 1950. Catches peaked at 2,400 tons in 1952 and amounted to 1,800 tons in 1959 (Tiews 1975). Thus two virtually new fisheries began to take great quantities of large bluefin in the northeastern Atlantic at the same time that the only important fishery in the area for small bluefin, in the Bay of Biscay, greatly increased its catches by adopting the live bait method. The German handline catches declined to 200 tons by 1962 and the fishery was abandoned after the 1963 and 1964 seasons produced only one fish each.

Purse seining for bluefin tuna also became widespread in the Mediterranean. Yugoslavian fishermen evidently introduced the method in the Adriatic in 1929 (Tihc 1954). Joined later by Italian fishermen, they have seined small bluefin extensively in the Adriatic (Scaccini and Biancalana 1959, Morovic 1961). Seining of small bluefin has also been carried out by Italian fishermen in the Tyrrhenian and Ligurian Seas, but with less modern equipment. Very small bluefin are seined by sardine boats with "cianciolo." In 1972 Italian fishermen began to take considerable quantities of giant spawning bluefin in the Tyrrhenian Sea and the Sicilian channel with large modern purse seiners (Paini 1975).

The seining of bluefin tuna off the Mediterranean coast of France was authorized in 1960 and developed rapidly (di Meglio 1962). Sardine boats occasionally seine bluefin tuna, including extremely small ones, off the Mediterranean coasts of Morocco and Spain (Rodriguez-Roda 1964a, 1964b). Small bluefin tuna are also seined off the Atlantic coast of Morocco (Aloncle 1964, Lambocuf 1972) by sardine vessels, sometimes with the assistance of chumming by live-bait boats.

Purse seine fishing for bluefin tuna, practiced in Cape Cod Bay by only one or two very small vessels in 1958-1961 (Squire 1959), expanded to an oceanic fishery ranging from Cape Hatteras, North Carolina, to

Cape Cod, Massachusetts, in 1962 (Wilson 1965). The catch of small bluefin rose to 5,600 tons in 1964, along with an almost equal quantity of skipjack tuna, *Katsuwonus pelamis* (Linnaeus 1758). The largest fleet in the history of the fishery, 21 vessels, including some of the world's largest, was responsible for this catch. Subsequent annual catches have varied considerably between a low of 600 tons in 1966 and a high of 3,600 tons in 1971.

The Japanese longline fishery entered the Atlantic in 1956, and subsequent expansion was rapid (Shiohama et al. 1965). By 1962, most of the ocean between latitudes 25°N and 25°S was being fished by Japanese longliners. In 1969, the fishery had expanded so that most of the waters between 40°N and 40°S were being fished (Wise and Davis 1973). The catches of bluefin tuna were small (less than 7,000 fish per year) in 1956-1961, but increased to 53,000 to 67,000 fish per year in 1962-1965. They then declined to less than 1,000 per year in 1969 and 1970. The 1971 catch was 8,000 fish, however, and the catch had risen to about 46,000 fish by 1974 (Fisheries Agency of Japan 1976). This was due mainly to the entry of the fishery into areas which had formerly been unexploited, or exploited only by inshore gears — the oceanic eastern Atlantic, the Bay of Biscay, the Ibero-Moroccan Gulf, and the Mediterranean.

Japanese longliners entered the bluefin tuna fishery in the Bay of Biscay in 1974, reportedly affecting the operations of the local Spanish fleet (Cort and Cendrero 1975). Their catches in the area in that year totalled about 11,215 fish (Fisheries Agency of Japan 1976).

Japanese longliners entered the Mediterranean in 1972. Their total catch that year included 112 tons of Atlantic bluefin tuna. This increased to 246 tons in 1973 and 2,195 tons in 1974 (Miyake and Manning 1975). Much of this catch was taken in the vicinity of Sicily in June and July, during the spawning season (Shingu et al. 1975, Shingu and Hisada 1976, Fisheries Agency of Japan 1975, 1976). The concentration of longlines around Sicily reportedly made it al-

most impossible for the Italian seiners to set their nets (Paini 1975). In 1975 the Japanese government prohibited their longliners from fishing in the Mediterranean as part of its compliance with the ICCAT regulations (Kume 1976).

Numerous longline vessels of South Korea, Nationalist China, Cuba, Venezuela, and the Soviet Union have also caught bluefin tuna, along with other species, in the Atlantic in recent years (Miyake and Tibbo 1972).

Offshore big game fishing for bluefin tuna and other large oceanic fishes (chiefly billfishes) became popular in parts of the northwestern Atlantic during the 1930s (Farrington 1939) and expanded to a highly developed pursuit after World War II (Farrington 1949). Centers of intensive sport fishing for bluefin tuna have been off the northwestern Bahamas in spring, and along the United States coast from Virginia to Maine and in Canadian waters off southwestern Nova Scotia, eastern Newfoundland, and in the Gulf of St. Lawrence in summer and early fall. Thousands of private and charter boats have participated in this fishery, with as many as a thousand anglers in two hundred boats entering a single tournament. Sport fishing for bluefin tuna has also been popular in eastern Atlantic and Mediterranean waters. Centers have been the Oresund off Denmark, the North Sea off England, the Canary Islands, the Bay of Biscay off northern Spain, the Italian Riviera, and the Mediterranean coasts of France and Spain. Recent low availability of fish has reduced interest in sport fishing in several of these areas.

The northeastern Atlantic fisheries for large and medium sized bluefin tuna began a decline in 1963 which reduced several of them to extinction by 1973. Bluefin tuna production in the Japanese oceanic longline fishery peaked rapidly in 1962-1965 but declined to a low level by 1967.

The reported total catches of the Mediterranean fisheries, on the other hand, appeared to be maintaining themselves satisfactorily as recently

as 1971. Apparently, however, central Mediterranean (Italian, Tunisian, and Libyan) trap fisheries, have recently undergone a collapse similar to that experienced by those in the eastern Atlantic. Catches were fairly good through 1969, but in 1972 and 1973 traps which had formerly produced thousands of fish per year yielded only a very few hundred. Only a handful of the once numerous Italian traps survive. This decline has been offset recently by the entry of the Japanese longline fishery into the area and the development of the Italian purse seine fishery for giant bluefin in the central Mediterranean. It should be noted that both of these fisheries also use spawning concentrations.

Another notable trend in nearly all of the Atlantic and Mediterranean fisheries for large bluefin for which data are available has been the virtually complete absence of medium sized (32-122 kg, ages approximately 5-8) and a marked scarcity of small giant (123-200 kg, ages approximately 9-11) bluefin from the catches. This trend has been reversed in the central Mediterranean fisheries in 1975 (Miyake 1976).

In the following section, we will discuss the distribution of Atlantic bluefin tuna and the fisheries for it in detail.

C. DISTRIBUTION AND FISHERIES BY AREAS

I. Introduction

In this section we will discuss the following information, by area:

- 1) Times and locations of occurrences of bluefin tuna, and their variations with size of fish

- 2) Fisheries and fishing methods.

- 3) The volume and size composition of the catches, and their trends

The size composition by years of samples of the catches of most of the major fisheries is illustrated by histograms. The tables from which most of these histograms were plotted have been reproduced, with the sources of the data, in ICCAT Data Record, Vol. 3, Madrid, 1974.

2. Western Atlantic

The major fisheries for bluefin tuna on the western Atlantic continental shelf are concentrated between Cape Hatteras, North Carolina, and Newfoundland, Canada (**Figure 14**). The small fish have been predominant in the area between Cape Hatteras and Cape Cod, Massachusetts, but medium sized and giant fish have also occurred there in numbers on occasion. Giant fish have been predominant in the region between Cape Cod and Newfoundland in recent years. Until 1966, medium sized bluefin were often abundant between Cape Cod and Nova Scotia. In some years during the 1950s, small bluefin were the most numerous size group in northern Massachusetts waters, but we have never heard of their occurrence in significant numbers off Canada.

The gears used for bluefin tuna in this area include harpoons, hand lines, traps, rods and reels, and purse seines.

Some giant bluefin have also been taken by sport gear off the northwestern Bahamas and by small-scale commercial fisheries off some Cuban ports. Captures of bluefin tuna elsewhere in western Atlantic coastal waters have been insignificant.

a. Newfoundland to Cape Cod

i. Newfoundland

There has been little commercial fishing for bluefin tuna off the Canadian island of Newfoundland (**Figure 15**), but good sport fishing for the species was enjoyed there from 1961 through 1972.

This fishery was initiated at Conception Bay in 1956, and was well developed there by 1961. Another productive ground, Notre Dame Bay, was opened in 1967, with most of the boats based at Lewisporte. The fishing usually extended from mid-July to mid-October. From 1961 through 1972, catches of up to 635 fish were taken in Newfoundland waters each season. Many of these fish were tagged and released. The catch has declined drastically since 1972, with less than 100 fish being taken each season. Nearly all of the catch consisted of giants, and their modal

Figure 14. Geographical references in the northwestern Atlantic.

length increased from about 220 cm in 1961 to about 240 cm in 1971 (Figure 16). Their mean weight rose likewise, from 220 kg in 1961 to 314 kg in 1975 (Caddy and Butler 1976).

ii. Gulf of St. Lawrence

In recent years, more extremely large bluefin tuna have been taken on rod and reel in the Gulf of St. Lawrence (Figure 17) than in any other area. No less than 36 out of 487 tuna caught in the Gulf in 1975 exceeded 1,000 lbs (454 kg) in weight (D. A. MacLean, personal communication).

The sport fishery was initiated at Prince Edward Island in 1966. The season originally extended from late July into October, but the high prices offered for large bluefin tuna caught in the late season resulted in its extension into November, and also in an increase in the number of boats fishing from 30 in 1972 to about 72

in 1973 (Anonymous 1974). Almost all of the fish taken have been giants (Figure 18). The average weight of the fish caught has remained consistently over 300 kg, and rose sharply to 382 kg in 1975 (Caddy and Butler 1976). With increasing fishing effort, the total catches rose to a peak of 1,048 fish in 1974, but declined sharply to 343 fish in 1975 (D. A. MacLean, personal communication). In 1972, the Canadian Minister of Fisheries restricted bluefin tuna fishing in the Gulf of St. Lawrence to rod and reel, using lines of not over 130 lb (59 kg) test (Anonymous 1974). In 1975 the Minister restricted the fishing to 10 week seasons and the catch to two fish per boat per day, using rod and reel only. In addition, licenses were limited to boats which had fished in 1974. These restrictions, which were part of Canada's compliance with the ICCAT regulations, combined with poor abundance

of fish to reduce the catch in 1975 (Caddy and Burnett 1975).

The success of the Prince Edward Island fishery and exploratory efforts by visiting United States anglers resulted in the extension of the sport fishery in 1973 to Chaleur and Gaspé Bays, New Brunswick. This fishery increased rapidly and took 93 fish with an average weight of 801 lbs (363 kg) in 1974 and 148 fish with an average weight of 858 lbs (389 kg) in 1975 (D. A. MacLean, personal communication).

Potential world record rod and reel bluefin weighing 1,190 lbs (540 kg) and 1,200 lbs (544 kg) were taken in Chaleur Bay in 1976 (E. K. Harry, personal communication).

The continuing increase in the sizes of the bluefin taken in the Gulf of St. Lawrence, and the lack of recruitment to the fishery, are vividly illustrated by the weight composition of the 1974-1976 catches (Figure 17).

iii. Nova Scotia

Bluefin tuna have long been taken by traps and harpoons in Nova Scotian waters, but the only historical size data are from the sport fishery. The sport fishery was first developed in 1935 at Wedgeport south of Yarmouth (Figure 19) where it was very successful for many years. In the mid 1950s, however, the fishing there deteriorated, and Nova Scotian fishing has been centered at Cape St. Mary (north of Yarmouth) since then. Our data extend from 1946 through 1955, and also include 1959. The size composition of the catches varied considerably over these years (Figure 20). Giants dominated the catch in 1946, but medium sized fish became more important in succeeding years, dominating the catch in 1949 and providing over 40 percent of those in 1948 and 1950. The year class of 1942 was dominant in 1948, and that of 1943 was dominant in 1949-1950, and important in 1951 (Mather and Schuck 1960). Giants again dominated through 1955, excepting an important showing of mediums (year class of 1949) in 1954. In 1959 mediums were again dominant (year classes of 1952 and 1953). The few catches in recent years have

Figure 15. Geographical references off Newfoundland and Labrador

been of very large giants. Their average weight has also increased in recent years, reaching 761 lbs (345 kg) in 1974 and 824 lbs (394 kg) in 1975 (D. A. MacLean, personal communication). The fishing off southwestern Nova Scotia usually extended from early July to late September or October. The giants have been most abundant in August and September, but the medium fish, which arrived and departed later than the giants, have been most abundant in September and October. Nova Scotia has been the locale of the prestigious International

Tuna Cup matches since their inception in the 1937 season. As documented by Farrington (1974), these competitions were held at Wedgeport through 1957, except for one at Liverpool and an interruption caused by World War II. Subsequent matches were held at Cape St. Mary in 1958 and from 1965 through 1975.

Bluefin tuna have been an important incidental catch in the mackerel trap fishery at St. Margaret's Bay (near Halifax) Nova Scotia (**Figure 19**). Young (1974) briefly reviewed the history of the fishery, and Butler

(1977) has provided details on its recent trends and developments, and its status in 1976. Additional data are available in Butler (1975), Caddy and Butler (1976) and statistics of Environment Canada (D. A. MacLean, personal communication).

Young (1974) stated that landing statistics for the fishery have been recorded since 1918, but the fishery predated the establishment of statistical systems. The recorded annual catches of large fish have been in the order of 400, but have ranged as high as 1,500. There was also a second later run of much smaller fish, in the 20-70 kg range.

None of the small fish have been seen in recent years, and the average weight of larger fish increased considerably, reaching 295 kg in 1974. The weight composition of the 1973-1975 catches (**Figure 21**) shows a considerable increase in sizes of fish taken each year, and only fragmentary recruitment of younger fish to the fishery.

The estimated numbers of fish caught in the period 1964-1975 varied between 104 (in 1972) and 865 (in 1974) (Butler 1977). In June 1974 an additional 150 tuna caught in the traps were tagged and released. Tonages in the years 1971-1975 ranged from 23.6 mt in 1972 to 256 mt in 1974 (Caddy and Butler 1976, Butler 1977, D. A. MacLean, personal communication). The average weight of the fish increased from about 227 kg in 1971-1973 to 295 kg in 1974 and 319 kg in 1975.

Butler (1977) described a most interesting development in this fishery — the holding of giant bluefin in impoundments, and fattening them, to secure optimal prices. Japanese interests offer very high prices for fresh giant tuna in the fat condition which they attain in late summer and fall through heavy feeding. The prices offered for the typically lean fish taken in the early season are much lower. Butler stated that the average price per pound offered to Canadian fishermen for giant bluefin in 1976 varied from \$0.20 in July-August to \$1.40 in October. The St. Margaret's Bay traps normally take most of their catch of giant tuna in the early season, when the price is low. In an

Figure 16. Lengths of bluefin tuna captured off Newfoundland (1960-1971) ("+" on graph means less than 0.5%).

Figure 17. Weights of giant bluefin tuna caught by rod and reel in the Gulf of St. Lawrence (1974-1976).

effort to capitalize on the high late season prices, two impoundment nets were constructed in the Bay in 1975. Each impoundment measured about 100 m x 50 m, and was in water about 20 m deep. Fifty bluefin were transferred from neighboring traps to the pounds. They were fed on trash fish and held for a period of two or three months. Then they were killed in small batches, to avoid depressing the price, and sold on the Japanese market. The experiment was so successful that nine impoundments were constructed in 1976, and about 300 bluefin were held and fattened.

Butler (1977) showed the locations of the traps and impoundments in St. Margaret's Bay and discussed past and proposed research activities in this unique situation.

iv. Cape Cod to Maine

Bluefin tuna have occurred in many sizes and been fished by many

methods in the New England area (**Figure 22**) (Bigelow and Schroeder 1953, Wilson 1965). The traps, which were formerly numerous in Cape Cod Bay, took considerable quantities of these tuna in years of abundance, but the fishery there was terminated in 1975. Operators of various types of commercial fishing craft, such as lobster boats and small trawlers, occasionally harpooned bluefin or caught them with handlines. This activity was usually incidental to their normal pursuits or undertaken temporarily during periods when tuna were readily available and commanded a reasonable price.

Sport fishing for bluefin tuna developed in the area in the 1930s (Farrington 1939) and increased in popularity after World War II (Farrington 1949). Pre-war activity centered in Ipswich Bay, Massachusetts, and Casco Bay, Maine. After the war the popularity of sport tuna fishing spread into Massachusetts and Cape Cod Bays as well. Some of the most successful giant tuna tournaments ever held have taken place in

Figure 18 Lengths for bluefin tuna captured off Prince Edward Island (1969-1971).

Figure 19. Geographical references of Nova Scotia.

these waters in the years 1972-1976. Large bluefin were remarkably available in those years, and their average size was increasing steadily.

The purse seine fishery for bluefin tuna off the east coast of the United States originated in Cape Cod Bay and its vicinity (Wilson 1965). After initial experiments in 1951 and 1954, a continuing purse seine fishery began in 1958 with a single small vessel operating out of Provincetown, Massachusetts. Very high catch rates were obtained from the schools of medium sized bluefin which were then abundant in the Bay (Sakagawa 1975). In 1962 the carrying capacity of the fleet was greatly increased by the purchase of additional vessels by local fishermen and visits by larger ones from other areas, and the fishing area was expanded southwestward to include the New York Bight and more southerly areas. The large fleets which entered the fishery in 1963 and 1964 made considerable portions of their catches of small and medium bluefin in Cape Cod Bay and vicinity, especially toward the end of the season. Very few small or

medium fish have been found in the Gulf of Maine since 1964. For several years thereafter, seining in the area was limited to occasional trips by one or two vessels after the season for small bluefin southwest of Cape Cod had terminated. This situation was altered by the high prices offered from 1972 on by Japanese interests for the fat bluefin which were caught late in the season. A local seiner, who specialized in catching giant fish, had fished in the Bay for the Japanese market toward the end of each season since 1972. In 1976 a second vessel joined the fishery.

The prices offered for large bluefin tuna also caused a dramatic increase in fishing effort by the harpoon, handline and sport fisheries. The "sport" fishery differed only in the gear used, since virtually all of the anglers were fishing for the market. Boats of all types and sizes, from small outboard motor boats to large trawlers and party fishing boats, participated.

Mather and Mason attempted to gather catch records during the be-

ginning of this period of increased effort and estimated catches of 3,000 and 3,500 fish in 1972 and 1973, respectively.

In 1974, the Commonwealth of Massachusetts regulated the fishery for large bluefin in its waters and collected data on the landings. The National Marine Fisheries Service also initiated a data collection program for the fishery. The resulting data are shown in Table 7 (F. H. Berry, personal communication). The data for the rod and reel and harpoon and handline catches were estimated.

Since 1975 quotas have been imposed on these fisheries to control the number of large fish taken each year and to prevent the capture of the surviving small fish (National Marine Fisheries Service 1975, 1976). Under the 1975 quotas, the recorded catch by hand gears (harpoon, handline and rod and reel) was 2,277 fish weighing 693.5 tons, with an average weight of 305 kg. The recorded seine catch was 1,017 fish weighing 267.2 tons with an average weight of 263 kg (Aloncle et al. 1976, ICCAT 1976).

The time of the best fishing in Cape Cod Bay has varied considerably — partly according to the sizes of the fish which entered the area. The giant fish usually arrived early, in June or early July, and stayed into September or October. Peak fishing was usually in August or September.

Medium sized fish have usually arrived later, and also stayed in the Bay later than the others, being abundant in August-October. Exceptions occurred when the smaller (age 5) individuals of this group accompanied early summer runs of small (age 2-4) bluefin. Small bluefin were unpredictable. Some strong runs peaked in early summer, as in 1951 and 1953, but others have occurred in late summer, as in 1950.

As noted above, fishing techniques in the area have changed over the years. Also, catch records have not been kept in a consistent manner. We do have sporadic records of the sizes of fish landed for Ipswich Bay and the Maine coast for 1947-1951 (Figure 23) and more comprehensive ones for Cape Cod Bay and vicinity (including Ipswich Bay from

Figure 20. Lengths for bluefin tuna captured off Nova Scotia (1946-1959) ("+" on graph means less than 0.5%).

Figure 21. Weights of bluefin tuna captured from St. Margaret's Bay ("+" on graph means less than 0.5%).

1960 on) for 1947-1975 (**Figure 24**). As the latter figure shows, the size composition of the samples has varied drastically over the years. In 1947, giants were dominant, with a fair proportion of mediums in Cape Cod Bay. The mediums, mainly the year class of 1943, which was also outstanding in the Nova Scotia catches of 1949-1950 (Mather and Schuck 1960), became dominant in Cape Cod Bay in 1948 and 1949. They would have been dominant in 1950 also but for an apparently unprecedented influx of small bluefin. This 1948 year class remained dominant through 1957. The mediums became dominant again in 1958-1960, mainly because of the progression of the very strong year class of 1952 through this size category. This year class was also prominent in the 1959 Nova Scotia catches. In 1961, small, medium, and giant bluefin were all represented, but another strong year class (1957) had become dominant. The progression of this class made the medium group

Figure 22. Geographic references in the Gulf of Maine region

preponderant in 1962-1963. Giant tuna have dominated the catches in all the subsequent years (1964-1975), with only negligible numbers of small and medium sized bluefin being recorded between 1966 and 1970. As in Newfoundland, the modal lengths of the giant bluefin taken in this area in the late 1960s reached high values, over 220 cm, and the size of the smallest fish taken increased significantly. The latter trend changed in 1970-1971, indicating some recruitment of younger fish. In subsequent years, however, the catches have consisted almost entirely of very large fish, and the mean size has been steadily increasing. Catches of bluefin less than 8 years old have been insignificant.

The available data for 1973-1975 show a continuing increase in the size of the fish taken, especially by the hook and line and harpoon methods. The average weights of fish caught by nets (traps and purse seines) are somewhat lower, possibly because of the tendency of smaller fish to

school together in greater numbers than the larger ones

There has been a fairly close relationship between the occurrences of medium sized bluefin in Cape Cod Bay and off Nova Scotia, but the important runs of small fish which have occurred in the former area have had no counterpart in the latter.

The runs of small bluefin in Cape Cod Bay have comprised ages 2-4, and we are aware of only one individual of age 1 having been reported from this area. The age composition of these size groups has often overlapped, with age 4 fish associating with runs of medium fish, and age 5 fish with runs of small bluefin.

b. Cape Hatteras - Cape Cod (Coastal Waters)

The "Middle Atlantic Bight" (Figure 25) is the usual summer habitat of the small (age 1-4) bluefin of the western North Atlantic, although they have occasionally ranged into the Gulf of Maine (chiefly Cape Cod Bay) as noted above. Many traps in this area took bluefin tuna occasion-

ally, but very few of these are now in operation. The bluefin tuna has been one of the most abundant and popular big game species supporting the offshore sport fishery of this area, particularly in its northeastern part. Since 1961 it has also been the object of a seasonal purse seine fishery which also takes skipjack tuna in some years. Bluefin usually arrived in the area in late June or early July and departed in the early fall, but they sometimes departed as late as November. The size composition data available to us for this area (Figure 24) are mainly from the sport fishery for years before 1961, and from the purse seine fishery for later years.

As indicated by these histograms, the sport catches have consisted almost entirely of small bluefin, mostly of ages 1-3. Sport fishing for these bluefin has been very successful in some years off New York Harbor (Westman and Neville 1942, Moss 1967) and elsewhere between New Jersey and Cape Cod (Farrington 1939, 1949). The best season is unpredictable. Sometimes the early season produces the best fishing, whereas in other years there is excellent fishing in late summer and early fall, particularly in the grounds off New York Harbor.

The purse seine fishery began to harvest this stock in 1962. In the first three seasons (1962-1964) considerable quantities of medium sized bluefin were taken, but in subsequent years, fish of this group have been rare in this area, as well as in the more northerly waters which they formerly frequented (see above). Trends in the catches are shown in Figure 27. Wilson (1965) and Sakagawa (1976) give details of this fishery and its catches.

The size composition data (Figure 26) suggest some variation in the sizes taken by the various gears. In the years when most of the data were from rod and reel catches, 1941-1960, age 1 fish were often important. In the years from 1962 on, when the seine fishery was the chief harvester of young bluefin in this area, age 1 fish were important only in some years, notably 1966. In the first three years (1962-1964) of intensive seine fishing, fish of ages 4 and 5 were

Figure 23. Lengths of bluefin tuna captured in Maine and Ipswich Bay, Massachusetts ("+" on graph means less than 0.5%).

important. Many additional fish of ages 5 and over were taken in this period but were discarded because they were not acceptable to most of the canneries (several eyewitness reports, personal communications). Also many fish were lost when nets burst, or were discarded when the catch exceeded the remaining carrying capacity of the vessels (the data sources are the same as above, in addition to incidents witnessed by some of the authors and their colleagues). After 1966, fish of age 2 usually dominated the catch. Since 1974 the New England based seiners have generally avoided age 1 fish as a voluntary conservation measure. Since midsummer 1975, their capture has been prohibited in conformance with the ICCAT regulations. It appears, however, that in most years full recruitment to the fishery does not occur until age 2.

The size composition data give indications of strong-year classes. The year class of 1938 was dominant in the New York Bight in 1941. In 1951 the year class of 1950 showed up very strongly in the catches, but no sampling was carried out. It was very prominent, however, in the 1952 sample. The class of 1958 was conspicuous in the 1960 and 1962 samples. The class of 1965 was dominant in the 1966 seine fishery, and showed up strongly in 1967 and 1968. Data for 1974, 1975, and 1976 indicate a very strong year class of 1973.

Sport fishing for giant bluefin off New York Harbor was fruitful in the 1930s (Farrington 1939), but declined after World War II. Late in the 1940s, a new giant tuna ground was discovered near the western coast of Rhode Island (Farrington 1949). This was productive for some years, but after 1960 successful seasons became infrequent. More recently, giant tuna have been caught farther off the Rhode Island and eastern Long Island shores, in areas where the tunas follow the nets of trawlers as they are being hauled to the surface. This fishing has usually been most successful in late summer and early fall. After being absent for many years, some giant bluefin have been taken off northern New Jersey or during the later part of some recent seasons

Table 7. Landings data from the Commonwealth of Massachusetts in 1974.

Gear	Number of fish	Metric Tons	Average Weight (kg)
Trap	37	9.1	245.6
Seine	167	48.1	287.5
Rod and reel	200	63.5	317.5
Harpoon and hand line	900	349.2	317.5

These sport catches of giant tuna were usually unimportant in numbers, but did document their seasonal occurrence in the area.

At the other end of the size range, runs of very small (age 0) bluefin (1-2 kg) occasionally occur in this area from late July into October. These are most common in late summer and early fall, and from northern New Jersey southward to Cape Hatteras. They are of no significance to the fishery, but the biological information obtained from them has been a very important step in understanding the life history of the species.

c. Atlantic Ocean outside 200 meter contour N of 35°N and W of 40°W

During the cold season, the bluefin tuna disappear from the summer habitats described above. Since 1956, however, exploratory and commercial longline activities have revealed much about their oceanic distribution in this period (Wathne 1959, Wilson and Bartlett 1967, Wise and Davis 1973). The only substantial size composition data for oceanic bluefin tuna catches are from the area north of 35°N and west of 40°W (**Figure 28**). The most important exploratory catches were near the northern edge of the Gulf Stream in spring, and in the canyons along the edge of the continental shelf in fall (Mather and Bartlett 1962). The majority of the fish taken were in the medium (120-185 cm) size range. As in the inshore fisheries, however, the average size of the fish taken, as well as the size of the smallest fish taken, increased markedly during the 1960s.

Japanese longline catches in this area have indicated a predominance of the larger medium sized fish (about 100 kg) during the period from April

through October (Shingu et al. 1975). Shingu and Hisada (1976), however, reported that medium-sized bluefin tuna (ages 5-8) were scarce throughout the Atlantic Ocean. They also noted that, during the winter months, December-February, considerable proportions of small fish (ages 2-5) have appeared in the catches of recent years in the waters off New England.

d. Bahamas and Southeastern Florida

The only bluefin fishery in the western Atlantic south of 35°N for which there is significant size composition data is the sport fishery off the northwestern Bahamas (Cat Cay and Bimini) (**Figure 29**). All the fish taken are giants, over 185 cm and 122 kg (**Figure 30**), and are caught in May and June. Usually the fish are caught from schools which are travelling northward along the edge of the Great Bahama Bank, but on rare occasions they are taken from schools which are "smashing" (feeding on the surface, often jumping clear of the water) farther offshore. This fishery has varied somewhat in recent years, with a general tendency to decline. Many of the fish have been released after being brought to the boat. We have some weight records for more recent years, however, which, although few in number, constitute representative samples. These samples indicate that the modal sizes and minimum sizes of the fish taken in this fishery have increased steadily in recent years. Rivas (1976) showed that the mean length of the males which he had measured in the years 1972-1973 at the Bahamas was 25 cm longer than the mean of those which he had measured in the years 1952-1955. For the same periods, the

Figure 24. Lengths of bluefin tuna captured in Cape Cod, Massachusetts bays and vicinity (1947-1975) ("+" on graph means less than 0.5%).

Figure 25. Geographic references for the Cape Hatteras to Cape Cod areas.

mean length of the females which he had measured increased by 20 cm. Similar fishing occurs, with fewer boats participating, along the western edge of the Little Bahama Bank (West End to Matanilla Shoal).

Giant bluefin have also been taken off the eastern Bahamas, from Cat Island to Walker Cay (Anonymous 1962), in the same season. A few have been taken off southeastern Florida on rare occasions during the winter and spring.

Small and medium sized bluefin are very rare or nonexistent in the vicinity of the Bahamas, but runs of very small (less than 2 kg) fish sometimes occur off southeastern Florida in July-September, and individuals are sometimes taken through the fall

and into early winter (Rivas 1954, Mather and Schuck 1960, Mather 1963).

c. Gulf of Mexico and Caribbean Sea

Bluefin tuna are caught by longline, and occasionally by sport fishing, in the Caribbean Sea and the Gulf of Mexico (Figure 31). Catch records, aside from those of the Japanese longline fishery, and size data are sparse, but sufficient to give a good idea of their distributional pattern. Most of the catches have been in the first two quarters of the year. United States exploratory catches (Wathne 1959, Anonymous 1962) and commercial catches (H. R. Bullis, Jr., personal communication) have

been mainly in the Gulf of Mexico and the northwestern Caribbean. The Japanese effort, which has been much more extensive, has shown that the species occurs occasionally throughout most of the Caribbean (Fisheries Agency of Japan 1967a).

A small scale Cuban longline fishery for giant bluefin has operated in the spring, over the Bartlett Deep between Cuba and Jamaica. This fishery was initiated in 1969 and the largest catch of about 360 tons (including incidental catch of other species) was taken in 1970. The landings were smaller, but good, in the next three years, but the 1974 catch was extremely poor (Ubeda 1974). Cuban handliners occasionally catch giant bluefin off Havana in the spring (Rivas 1954).

All of the longline catches in the Gulf of Mexico and the Caribbean Sea for which we have size data were giants, over 185 cm long. Similar size fish have been encountered occasionally by sport fishermen between Cozumel Island and the Yucatan Peninsula and off the Mississippi delta in late spring on the surface, sometimes in large schools (Nakamura and Rivas 1972).

We had virtually no records of occurrences of medium sized or small bluefin tuna in these waters until Shingu et al. (1975) reported catches of bluefin tuna weighing less than 10 kg by Japanese longline vessels in the Gulf of Mexico in June and July 1973. We have had several reliable reports and records, however, showing that very small (age 0, 2 kg or less) individuals have occurred in the Gulf of Mexico from July into November.

3. Atlantic Oceanic Waters

Extensive data on the seasonal distribution of bluefin tuna in the oceanic waters of the Atlantic have become available from the records of the Japanese longline fishery (Shiohama et al. 1965, Fisheries Agency of Japan 1965, 1966, 1967a, 1967b, 1968, 1969, 1970, 1971, 1972, 1973, 1974, 1975, 1976, Wise and Le Guen 1969; Wise and Davis 1973) as well as from exploratory fishing (Wathne 1959, Anonymous 1962, Wilson and Bartlett 1967). The gen-

Figure 26. Lengths of bluefin tuna captured from Cape Hatteras to Cape Cod ("+" on graph means less than 0.5%).

Figure 27. Annual catches of small and some medium size bluefin tuna from the northwest Atlantic purse seine fisheries, 1958-1973, in tens of thousands of fish and thousands of tons.

eral seasonal distribution pattern, based on Japanese catch rates for 1956-1969, is illustrated by **Figure 32** (Wise and Davis 1973). This figure, however, includes southern bluefin, *Thunnus maccoyii*, as well as the Atlantic bluefin, *T. thynnus thynnus*. The records south of latitude 20°S, and perhaps also the one in the first quarter centered at 12°S, 2°E, are probably of southern bluefin. Catch rates for individual years and areas (**Table 8, Figure 35**) (J. P. Wise, personal communication, Wise and Davis 1973) suggest that the abundance has varied considerably over the years. The catches declined pre-

Figure 28. Lengths of bluefin tuna captured in the Atlantic outside the 200 meter contour north of 35°N and west of 40°W ("+" on graph means less than 0.5%)

Figure 29. Geographic references for the Bahamas and southeastern Florida.

cipitously from 1965 through 1970 but have risen rapidly since then (Figure 33).

The following description is based on the 1956-1968 catches (Figure 32):

In the first quarter of the year, the highest catch rates occurred around the easternmost part of Brazil, and the greater Antilles.

In the second quarter, the area of relatively high catch rates off Brazil extended farther to the northwest, and catch rates were high in the northern Gulf of Mexico, and off the Bahamas and the eastern United States northward to latitude 40°N and eastward to longitude 65°W. The concentrations off easternmost Brazil and off the Bahamas appeared to be connected (Figure 32, Appendix Figure 62 in Fisheries Agency of Japan

Figure 30. Lengths of bluefin tuna captured from the Bahamas ("+" on graph means less than 0.5%).

Figure 31 Geographical references for the Gulf of Mexico and Caribbean Sea.

1967a) Small areas of high catch rates also occurred about midway between easternmost South America and westernmost Africa.

In the third quarter, the only areas of high catch rates were off New England and the Grand Banks of Newfoundland, and again in the narrow part of the Atlantic, midway between the most western part of Africa and the most eastern part of South America.

In the last quarter, the concentration south of the Canadian banks was farther west and extended southward to latitude 30°N. The concentration between South America and Africa had moved northward to 20°-32°N. The concentration off easternmost Brazil had formed again, and

Figure 32. Distribution of oceanic catches of bluefin tuna (per 10,000 hooks) in the four quarters of the year, 1956-1968.

Figure 33. Annual catches of Japanese longline fisheries in the Atlantic Ocean for large and medium size bluefin tuna in tens of thousands of fish and in thousands of tons.

extended northward to 16°N, almost joining the mid-ocean one mentioned above.

Considerable size data are available from exploratory fishing and commercial catches in the western North Atlantic. These records indicate that most of the bluefin taken in oceanic waters south of 35°N and west of 70°W (catches north of 35°N and west of 40°W have been discussed in a previous section) were giants.

Unfortunately, little size data are available for the much more extensive Japanese catches. Hayasi et al. (1970) reported that the Japanese longline fishery took "small" bluefin off Florida (25°-35°N, 70°-80°W), but no size data have been provided. Hayasi and Shingu (1972) and P. C. Wilson (personal communication) provided lengths for about 220 Atlantic bluefin caught in oceanic waters. Most of these were giants, but a considerable number were medium sized, although mostly of the larger sizes (ages 7 and 8) occurring in that group. It appears that nearly all of the bluefin over one year old taken in the westernmost

part of the North Atlantic south of 35°N, and in the Gulf of Mexico and the Caribbean Sea, were giants, but that there have been considerable numbers of medium sized, as well as giant, bluefin in mid ocean catches in the 1960s (Shingu et al. 1975).

After the decline of their Atlantic bluefin tuna catches in the late 1960s and early 1970s, the Japanese shifted much of their effort to the eastern Atlantic and the Mediterranean. The remaining effort in the western Atlantic was concentrated in the northern Gulf of Mexico in May and June, when giant bluefin spawn there, and in the area south of the Grand Banks through much of the year (Shingu et al. 1975).

The move into the eastern Atlantic brought new pressure on stocks of larger fish which had previously been fished mainly by the declining trap and seine fisheries, and on medium sized fish which had been previously fished mainly by the Spanish and French bait boats in the Bay of Biscay. The fishery also provided indications of a previously suspected wintering ground around the Canary Islands (Aloncle 1964) for the large

bluefin which were fished in European waters in the warm season.

The effect of these shifts in effort was to restore the catches to levels approaching those of the mid 1960s. Whether they will follow the pattern of rapid rise and rapid decline illustrated for other areas by the combination of **Figures 34** and **35** remains to be seen.

Shingu and Hisada (1976) showed the length compositions of samples from longline catches taken in waters west of Gibraltar in May-August 1973 and April-June 1975. The former was dominated by large fish 190-240 cm long with a mode at 205-215 cm, but also included a significant number of medium sized fish 135-155 cm long. Larger fish, 185-300 cm long with a broad mode at 225-255 cm, were even more preponderant in the latter sample, with only a scattering of fish 110-175 cm long.

4. Eastern Atlantic Islands

Bluefin tuna occur in the vicinity of the Azores, Madeira, and the Canary Islands (**Figure 36**), but there has been little information on the fisheries and the sizes of fish until recently.

a. Azores

Ferreira (1932) reported on the tuna fisheries of the Azores for the years 1924-31. The principal catch was bigeye tuna, "*Parathunnus obesus*", with bluefin tuna being much less frequent.

Seven of 219 tunas caught in 1930 and 5 of 1404 caught in 1931 were bluefin. The fishing seasons usually extended from mid-April or early May until July or August. Ferreira does not state the sizes of fish taken, but mentions that very small (50 cm) tunas occurred, as well as adults. Figure 5 in his work, which is described as a young "*Parathunnus obesus*" of 51 cm, shows, in our opinion, a young bluefin tuna.

During cruise 63-4 of the Bureau of Commercial Fisheries M/V "Delaware", six giant bluefin were taken by longline off the Azorean Island of Santa Maria in May 1963, and another was lost alongside the

Table 8. Catch rates (numbers of fish per 1,000 hooks) for bluefin tuna of the Japanese Atlantic longline fishery, 1956-71, by year and area. The BEN and RIO areas are not included since it is believed that the bluefin caught in them were predominantly southern bluefin. Note: 0.00 = <0.005 but > 0, 0 = effort but no catch; - = no effort.

Year	GM	NOW	NOE	CAR	GUI	CV	GG	BALI	Total
1956	-	-	-	-	0.01	-	-	0	0.01
1957	0	-	-	0	0.14	0.11	0	0	0.07
1958	-	-	-	0	0.01	0.01	0.00	1.17	0.06
1959	-	0.51	0	0	0.19	0.08	0.00	0.94	0.22
1960	-	0	0	0	0.81	0.15	0.17	0.32	0.33
1961	-	0	0.13	0	1.11	0.08	0.01	0.36	0.16
1962	-	0.02	0.13	0.01	3.12	0.36	0.21	0.83	1.11
1963	0.02	0.18	0.05	0.03	3.94	0.25	0.01	3.82	1.42
1964	0.18	0.99	0.21	0.19	1.78	0.12	0	1.07	0.88
1965	0	2.98	0.16	0.07	0.76	0.07	0.00	0.26	0.76
1966	0.10	3.39	0.07	0.03	0.30	0.01	0.00	0.02	0.58
1967	0	0.72	0.03	0	0.11	0.04	0.00	0.00	0.17
1968	0.31	0.34	0.02	0.01	0.02	0.00	0	0.00	0.08
1969	0.01	0.18	0	0.00	0.02	0.00	0	0.00	0.04
1970	0.00	0.04	0.06	0	0.02	0	0.00	0.02	0.02
1971	0	0.43	0.12	0	0.00	0.00	0	0	0.19
1956-71 TOTALS									
Thousands of Fish:									
	0.7	94.0	2.0	0.8	130.0	9.9	3.2	52.3	293.0
Millions of Hooks:									
	8.9	87.5	17.3	19.6	96.4	91.2	92.6	58.4	471.8
Fish per Thousand Hooks:									
	0.08	1.07	0.12	0.04	1.35	0.11	0.03	0.89	0.62

vessel (Anonymous 1963). In the same period, six bluefin tuna were observed among the landings of the local fishery at Ponta Delgada, and all of these were also giants (observations by Dr. B. B. Collette, Dr. D. de Sylva, and F. J. Mather).

b. Madeira

The numbers of bluefin tuna sold in the market in Funchal, Madeira, in the years 1954-1962 were furnished by J. Maul (personal communication). These ranged from six to 268 fish per year, averaging 104. The most numerous landings were in March-June and in October, with the least in November-January. Catches of other tunas, notably bigeye, were much more numerous. Maul has stated that the bluefin is relatively low in abundance off Madeira, and that the catches are

from two size groups: 6-7 kg, and 150-200 kg (Aloncle 1966)

c. Canary Islands

Early information (Frade 1929) indicated that *T. thynnus thynnus* was rather rare at the Canary Islands, but more recent developments indicate that the species may occur there in considerable numbers, and in various sizes. Aloncle (1964) reported a wintering area for small and young adult bluefin tuna (0.5-60 kg) between Lanzarote, one of the easternmost of the Canaries, and the Moroccan coast. The senior author directed the tagging of four 45 cm (age 0) fish off Gran Canaria in December 1974. Catches of large bluefin tuna have been made by sport fishermen off Tenerife in the Canary Islands, where the "European" record was broken

twice in two years, with 374 kg and 392 kg fish (Anonymous 1975, 1976). Several additional catches of large bluefin, off Gran Canaria, were reported by C. H. Roncoroni (personal communications). It appears that most of these giants were taken in late fall and winter (L. F. de Gamboa, personal communication). The distribution of Japanese winter (January-March) longline catches in 1974 (Fisheries Agency of Japan 1976) indicates that the Canary Islands are in a wintering area for bluefin tuna.

Santos (1976, 1977a, 1977b) has provided the first detailed information on commercial catches of bluefin tuna in the Canary Islands. The 1975 landings, excluding longline catches, were 932 metric tons. Catches and catch per unit of effort were greatest in the period June-No-

Figure 34. Areas of the Atlantic Ocean (Wise and Davis 1973).

vember, peaking in August and September. In 1976, however, Santos reported that catches were frequent in the first four months, but declined during the summer. The estimated catch through September was 641 mt. L. F. de Gamboa (personal communication, November, 1976) informed us that the sport fishing off Tenerife followed the same trend, and that the excellent fishing which had occurred in the fall of 1975 had not materialized in 1976.

5. Eastern Atlantic

Bluefin tuna fisheries in the eastern Atlantic (Figure 36) have been distributed in a manner somewhat similar to those in the western Atlantic. Large and medium-sized individuals have been taken during summer and early fall in Norwegian waters and the North Sea. The largest fishery for small bluefin, with some mediums, has been in the Bay of Biscay, mainly in summer. Less important fisheries for small bluefin occur off Portugal in the fall, and off Morocco during much of the year. Trap fisheries in the Ibero-Moroccan Bay have taken important catches of large bluefin, along with usually lesser amounts of medium and small individuals, in late spring and early summer.

The fisheries in Norwegian waters and the North Sea are of comparatively recent origin, as is the one for small bluefin off Morocco. The Bay of Biscay fishery is over a century old, but was modernized about 1950. The trap fisheries in the Ibero-Moroccan Bay, on the other hand, are of extremely ancient origin.

The Japanese longline fishery has become active in the Bay of Biscay and the waters off Gibraltar and northwestern Africa since 1970.

Figure 35 Japanese longline catch rates of bluefin tuna in areas of the Atlantic Ocean (Note: Bluefin in areas RIO and BEN are assumed to have been southern bluefin, *Thunnus maccoyii*, while those in other areas are assumed to have been Atlantic bluefin, *Thunnus thynnus*.)

Figure 36. Geographic references in the eastern Atlantic

a. Northeastern Atlantic

Le Gall (1927, 1929) described the distribution of bluefin in the northeastern Atlantic and the North Sea (Figure 36). The species was recorded in abundance off the southwest coast of Ireland in July and off the north coast in July and August. They were also observed off the west coast of Scotland in July, and off the south and west coasts of Norway, and in the Skagerrak and the Kattegat from July to October. Herring boats encountered them in July and August east and south of Fair Isle, then north and west of Dogger Bank. In late September and October, bluefin

were observed on the west edge of Dogger Bank. In November and December, trawlers on the Great Sole at the edge of the continental shelf encountered schools of them surfacing. Le Gall related the occurrences of bluefin in the North Sea and its tributaries to the seasonal "transgressions" of Atlantic and Atlantic slope waters, with salinities of about 35 o/oo.

b. Norway

Bluefin tuna have been taken by harpoon and angling gear in Norwegian waters for many years, but the introduction of the purse seine method in the late 1940s greatly increased the catch. The fishery, includ-

ing the catch and its size composition (Figure 37), has been described by Hamre (1971). The catch increased from a few hundred tons in the 1940s to over 11,000 tons in 1952, but decreased after 1962 to 2,500 tons or less per year. Hamre attributed the decrease to lack of recruitment. He showed that the seasonal movement of bluefin tuna through the fishery varied with age of fish. The largest fish (age 7 and older) arrived off Bergen in early July and migrated to the northern Norwegian coast. After feeding there for three or four weeks, they migrated southward into the bank area of the North Sea. Fish of ages 6-12 arrived in mid-July south of 62°N latitude, and migrated southward along the coast. Catches of fish of this size in late autumn by Swedish and Danish fishermen in the Kattegat, including one fish which had been tagged earlier in the same season in Norwegian waters, indicated that the migration continued to that area. Five and six year old bluefin arrived in the southern area in September and migrated to the east coast of Norway (Skagerrak).

This general pattern was followed as long as new year classes were recruited. Since 1958, when the 1952 year class was recruited, there has been no recruitment of younger age groups to the stock (Figures 37-39). This resulted in a decline in the annual catch, and a change in the migration pattern of the fish after the 1962 season. The largest bluefin now rarely migrate to the northward, but usually follow the southerly route previously travelled by the intermediate size (6-12 year old) fish. A few large fish, however, were taken in the northern area in 1967-1969 (Figure 38). No bluefin have been caught in the German North Sea fishery since 1962, probably because of this change in migratory pattern, but a few have been caught in the Kattegat. Medium sized bluefin have failed to appear in the Norwegian fishery since 1962 (Figures 37-39). The annual catch since 1967 has been less than 1,000 tons. It fell to a low of 90 tons in 1972 and even less in 1973. An increase in the modal and minimum sizes of fish taken since 1957 is evident for both the northern and south-

ern Norwegian areas, but is especially striking for the southern area (Figure 39)

c. North Sea

The German bluefin tuna fishery in the North Sea was carried out by handline, with the capture sometimes facilitated by an electrocuting system (Meyer-Waarden 1951). The landings reached a maximum of 1,286 tons in 1957 but declined to 194 tons in 1962 (Tiews 1975). The fishery was then abandoned because of lack of fish. The catch consisted entirely of giant fish (Figure 40). An increase in the modal size of the fish taken since 1952 is apparent. A similar Danish fishery took catches of from 800 to 2,100 tons in the years 1950-1955, but became negligible after 1959 (Tiews 1975).

Small catches of bluefin tuna have been taken in the approaches to the Baltic by Danish fishermen using various gears. Yearly catches since 1960 have been less than 200 tons. The fish taken have been large, with the modal size increasing in recent years. Sport fishing in the Oresund near Elsinore, Denmark, in 1948-1954 and 1960 produced yearly catches of from 18 to 119 fish with average weights of from 120 to 260 kg (L. R. Crandall, personal communication).

English sport fishermen have occasionally taken giant bluefin tuna in the North Sea. The British Tunny Club (Anonymous 1937) reported that tuna appear off the Shetland Islands in June and between Scarborough and the Dogger Bank off the Yorkshire coast from July to October. Sport catches in the latter area from 1932 to 1936 were listed as 21, 80, 54, 53, and 33, respectively. The very difficult conditions for this sport, combined with the lack of fish in recent years, have prevented its growth.

d. Bay of Biscay

The most important fishery for small (2.5-35 kg) bluefin tuna in the eastern North Atlantic has been in the Bay of Biscay (Figure 36). This Bay is therefore, presumably, the major nursery ground for young bluefin in the region and is a major source of recruitment to the fisheries for me-

Figure 37 Weight distribution of bluefin tuna captured from Norwegian waters by area and year. The columns to the left show number of fish landed with one unit equaling 5,000 fish (from Ilamre 1971).

Figure 38. Lengths of bluefin tuna captured off Norway (north of 63°N) ("+" on graph means less than 0.5%).

dium sized and large bluefin in the eastern Atlantic. Considerable numbers of medium sized (32-122 kg) and some large bluefin have also been taken in the Bay of Biscay (Le Gall 1954, Shingu et al. 1975).

French tuna landings from this bay began about 1840, when pilot boats from La Rochelle began taking considerable catches of tuna by trolling while waiting for ships. Tuna fishing did not become important there commercially, however, until a crisis in the sardine fishery about 1860 caused the French fishermen to turn their attention to tuna. The success of the trials exceeded expectations, and the fleet of sailing trollers increased year by year (Grandbesançon 1909). The major catch of this fishery was albacore, *Thunnus alalunga*, with

bluefin usually being taken incidentally. The introduction of the live bait method in Spain and France in the years 1947-1949 (Navaz 1950a, 1950b; de la Tourrasse 1951), however, resulted in a specialized fishery for bluefin. The catches of this species consequently increased greatly in the 1950s, but were much lower through most of the 1960s and have remained at intermediate levels in the 1970s (Figure 41). Statistics for this fishery are very confusing, but it appears that the landings varied between 1,000 and 1,500 tons in 1945-1949, then rose to between 2,700 and 5,500 tons in 1949-1959. The catches in the 1960s were much smaller, generally varying between 1,000 and 1,900 tons, but attained 2,100 and 3,300 tons in 1965 and 1966, respectively.

Catches in the early 1970s have evidently been somewhat over 2,000 tons per year.

Bluefin tuna apparently occur in the Bay of Biscay in every month of the year (J. Le Gall 1950, 1954; Navaz 1950b), but the active fishing season has usually extended from May or early June into October or November. Individuals weighing more than 30 kg are usually taken between mid-July and early September (Hamre and Tievs 1964, Hamre et al. 1966, 1968, 1971; Aloncle et al. 1974).

Research on bluefin tuna in the Bay of Biscay has been divided between two periods — 1949-1954 and from 1972 to the present. This division of research effort leaves a gap of

Figure 39. Lengths of bluefin tuna captured off Norway (south of 63°N) ("+" on graph means less than 0.5%).

Figure 40. Lengths for bluefin tuna captured from the North Sea ("+" on graph means less than 0.5%).

almost two decades for which very few data are available.

Length frequency data in 5 cm groups for Bay of Biscay catches in 1949 (J. Le Gall 1950) (French catches only) and 1972 (Bard et al. 1973) and 1975 (Cort 1976) (for both French and Spanish catches) are presented in **Figure 42**. Additional size frequency data, in different size groups, are furnished by Dao and Bessineton (1974) and Cort and Cendrero (1975).

These data indicate that age 2 fish are usually the most important in the Bay of Biscay catches, with age 3

the next in order, and age 1 fish occurring episodically in recent years (Dao and Bessineton 1974). Age 1 fish were important in the 1949 sample, but no data for other years in the peak period of the live-bait fishery are available. There has been a decrease in the importance of age 4 and larger fish in the catches since 1972. This has been attributed to the entry of Japanese longline vessels into the area in 1974 and subsequent seasons (Cort and Cendrero 1975, Cort 1976).

Much additional data is available for weekly (or daily) landings at

St. Jean de Luz, the principal port of the French bluefin tuna fishery, in terms of fish weighing less than 30 kg and more than 30 kg (Hamre and Tiews 1964, Hamre et al. 1966, 1968, 1971, Aloncle et al. 1974). Eighty percent of the 1962-1972 landings by weight were in the class weighing less than 30 kg (Dao and Bessineton 1974). The percentage by numbers would, of course, be considerably higher.

The Spanish fishermen, however, take more of the larger fish than the French. Dao and Bessineton (1974) found that only 52% of the

total French and Spanish catches of 1972 and 1973 consisted of fish weighing less than 30 kg, whereas 67% and 80%, respectively, of the French catches for those years were of fish weighing less than 30 kg. They found two apparent causes for this difference.

- the French sought out the smaller fish, which command a higher price,
- the baits used by the Spaniards were larger than those used by the French.

In view of the virtual disappearance of medium sized bluefin tuna from the landings of the Norwegian fishery since 1962, and their relatively poor showing in the trap fisheries of the Ibero-Moroccan Bay (subpart g of this section), it is unfortunate that size composition data for Spanish landings prior to 1972 are not available.

In addition to the commercial fisheries, there has been an active sport fishery along the north coast of Spain for bluefin tuna and albacore. Reportedly (L. F. de Gamboa, M. R. Borrell, personal communications) this fishery has declined greatly in recent years because of lack of fishing success. In addition, giant bluefin have been taken by Michael and Helen Lerner in August 1947 off Trehurden (Normandy, France) (Farrington 1949) and in the Bay of Biscay by the late Generalissimo Franco and Max Borrell (Max Borrell, personal communication).

c. West Coast of Portugal

Small bluefin were taken by trolling in the vicinity of Cape Espichel (south of Lisbon), Portugal, in late summer and early fall. The season usually started in September-October (Vilela and Monteiro 1961, quoted in Tiews 1963). In 1960 the entire catch of 5,500 fish (34.65 tons), averaging 6.3 kg, was taken in November. The 1961 catch was 7,859 fish totalling 36.01 tons (4.6 kg average) (Hamre and Tiews 1964). Both years' catches consisted of a large group of age 1 fish (50-70 cm) and a smaller group of age 2 fish (75-85 cm), as shown by histograms for each year and a sample of 128 fish from September 1961 catches presented by Hamre and Tiews (1964).

The 1965 catch is illustrated by the length frequencies of a 363-fish sample tabulated by week of capture (weeks 40-46, September 26-November 13). All of the 363 fish measured were age 1; their total weight was 2,047 kg and the average was 5.6 kg. The total catch of about 13,000 fish weighing 75 tons was taken mainly between early October and early November. The 1966 catch was small and irregular and was not recorded (Hamre et al. 1968). In 1968, 26,199 fish averaging 5 kg were taken (Hamre et al. 1971).

f. West coast of Morocco

Small bluefin are taken off the west coast of Morocco by hook and line, live bait, and seine fisheries (the trap fishery will be discussed separately). Catches ranged up to 2,000 tons in the mid 1960s, but have been less than 1000 tons in recent years (Figure 43). Fish are present during most of the year, but the largest catches occur in autumn (Aloncle 1964).

Aloncle (1966) gave the length composition of a 91-fish sample from a purse seine catch of 700 kg of bluefin taken September 9, 1967, at 30°40'N, 10°05'W (off Cape Ghir). The lengths ranged from 50 to 67 cm, with nearly all the samples in a modal group extending from 56 to 65 cm, and having its main peak at 62 cm. This indicates that nearly all the fish were age 1. Aloncle stated that bluefin of this age were common in the region at this season. This catch was made during a series of experimental cruises of the seiner "Danguy," which extended from September 1964 to July 1965, and covered the area bounded by the African coast from Tangier to Cape Bojador, the south coasts of Spain and Portugal, the Canary Islands, and the Madeira archipelago.

The first few weeks of the cruise resulted in the capture of age 0 and age 1 bluefin and sightings of age 2 and possibly age 3 bluefin. The few bluefin taken by trolling during the winter were in the 62-cm class. In late April and early May two individuals, one 70 cm and one 43.5 cm long, were taken northeast of the Salvage Islands. These would have been

ages 2 and 1, respectively, in the ensuing summer.

In November and December 1960, fishing boats from Barbate, Spain, seined a great quantity of bluefin about 42 cm long and 1.7 kg in weight, along with young albacore of about the same size (Rodríguez-Roda 1964a). A histogram of a sample of 100 of these showed a range from 38 to 45 cm, with a mode at 41.9 cm. This author states that the fishermen of Barbate often seine bluefin of 40 to 60 cm in length off the Moroccan coast from Larache to Casablanca and even to Safi and Agadir in October, November and December.

g. Ibero-Moroccan Bay Trap Fisheries

As noted previously, trap fisheries for bluefin tuna have existed in the Ibero-Moroccan Bay (Figures 44 and 45) for centuries. The recorded histories of the Spanish and Portuguese fisheries date back to the 15th and 16th centuries, respectively (Pavesi 1889). On the other hand, we have found no records of Moroccan Atlantic traps prior to the 20th century. The Phoenicians and Carthaginians who fished intensively for bluefin in all these areas in the pre-Christian era (Parona 1919), however, probably operated traps similar to those still in use (Thomazi 1947).

The specialized tuna traps are very large and complex structures, with a leader extending up to 5 km, and sometimes even more, from the shore to the body of the trap. In many cases an additional leader extends diagonally up to 2 km farther offshore (Figure 46). Traps have been described and illustrated by several authors (Pavesi 1889, Parona 1919, Rodríguez-Roda 1964a, Sarà 1964, de Cristofaro 1970). Two basic types of tuna traps have been used extensively, the "Atlantic" or "Spanish" trap and the "Mediterranean" or "Sicilian" trap. Fodera (1964) and de Cristofaro (1970) described the design, construction and relative advantages and disadvantages of each type. The traps in the Ibero-Moroccan Bay were of the Atlantic type.

Most of the traps along the Spanish and Portuguese coasts faced west and fished the "arrival" (eastward)

Figure 41. Annual catches by Bay of Biscay fisheries for small and some medium size bluefin tuna in hundreds of thousands of fish and in thousands of tons.

run from late April through June. Some of these were reversed at the end of June and fished the "return" (westward) run in July and August. The Moroccan traps faced southward and fished the "arrival" run, which was northward in that locality, only. After the 1976 season it appeared that, of all these traps, only one or two located off the Spanish coast would continue to operate.

These fisheries, and the biology of the fish which supply them, have been the subject of a great many investigations and scientific papers.

There are two maxima in the fishery, one near the middle of the "arrival" run, and the other near the middle of the "return" run. Spawning is presumed to occur between these maxima (Sella 1929a, 1929b; Vilela 1960). Sella (1929b) provided generalized diagrams showing the variation of the catches with dates and the movements of the fish in the vicinity of the traps during the spawning cycle (Figure 47).

For fish of the same length, those taken in the "arrival" run average about 15% heavier than those taken in the "return" run (Rodríguez-Roda 1964b) (data from fish taken at Barbate, 1956-1961). Vilela et al. (1960) found that females lost about 21 percent of their weight between the two runs, when most of the spawning takes place, while males lost only about 10 percent of their weight.

Length frequency data for the Spanish fishery for the years 1956-1959, 1961 and 1963-1975 are presented (Figure 48). The catch consisted mainly of medium and giant

fish, with small ones (ages 1-2) significant in 1958 and 1959 only. Medium sized bluefin were dominant in 1957 and important in 1956, 1958, and 1959. Since 1960, however, giants have constituted over 70 percent of each year's sample. One year class, probably that of 1954, dominated the samples for the years 1963-1965 (Rodríguez-Roda 1969b). Length frequency data are not available for the Portuguese trap catches, but the yearly catches for the years 1931-1972 (Vilela and Cadima 1961, Hamre and Tiews 1964, Hamre et al 1966, 1968, 1971) are shown in the size groupings traditionally used in this fishery (Figure 49).

Fish of the "atuns" size were usually dominant, but in three years the cachorretas, nearly the same sizes as our "small" group, considerably outnumbered them. These fish were generally most

Figure 42. Lengths of bluefin tuna captured from the Bay of Biscay ("+" on graph means less than 0.5%).

Figure 43 Number and weight of fish for the Morocco fisheries for small and medium size bluefin tuna.

numerous in late August (Vilela 1960). The albacoras and atuarros (ages 4-7, including most of our "medium" group) were important in some years but, as has happened with the medium group in most other areas, have generally decreased in importance in the most recent years.

Size composition data for Spanish trap catches by week (Rodríguez-Roda 1964b) showed a tendency for the largest individuals to be taken near the beginning of each "run." Alonele (1964) observed the same tendency in the catches of the Moroccan traps. Similarly, Vilela (1960) showed that the smaller tunas tended to be most important in the catches toward the end of each run, but especially in the "return" run.

Vilela (1960) found 300 males (38.1%) and 487 females (61.9%) in a sample of the bluefin taken in the Portuguese fishery in the years 1958-1960. There was little year-to-year variation from this proportion. There was also little difference between the sex ratios for the "arrival" and "return" runs, except in 1960, when the sample from the "arrival" run consisted of 44.4% males and 55.6% females. Rodríguez-Roda (1964b) presented the figures for the sexes determined from samples of the 1956-1961 catches of the Barbate trap, and the 1961 catches of two others (Table 9).

Lozano Cabo (1958) pointed out that the average size of the bluefin caught in the Portuguese and Spanish traps increased according to how

far east (near Gibraltar) the traps were located. The average was smallest in the Portuguese traps, and the greatest in the trap at Tarifa, near Gibraltar. He reported that the average size of the bluefin taken in the Moroccan traps was even greater than the average of those taken at Tarifa. Alonele (1964) showed that in Morocco the average weight of the fish caught also increased with the proximity of the traps to Gibraltar. The largest fish

were taken at Cape Spartel, at the entrance to the Strait and opposite Tarifa.

Statistics for most of the Ibero-Moroccan Bay trap catch are shown in Figure 50. These do not include all of the Moroccan catch. We were unable to obtain continuous data for the important trap at Cape Spartel (in the former International zone of Tangier) for 1933-1953, or for the three more ephemeral traps near Kenitra (in the former French Protectorate) for 1939-1955. Therefore we have omitted their catches and used those of the Larache group (in the former Spanish Protectorate) to represent the Moroccan catch. The catches of this group, which varied from one to five traps in the years 1927-1954 and stabilized at three from 1955-1966, have been recorded, in numbers of fish, for 1927-1962 (Lozano Cabo 1958, Ilamre et al. 1966). Data for subsequent years are available, in various forms, in Alonele (1964), Collignon (1964, 1965, 1966, 1967, 1968, 1969, 1972), Lambocuf (1972), and personal communications from M. Lambocuf and R. Sarà. Since 1966 only one or two of the Larache traps, if any, have been set. Data for

Figure 44 Geographic references for the Ibero-Moroccan Bay area.

Figure 45. Trap fishing locations for bluefin tuna in the Ibero-Moroccan Bay area.

the Spanish traps, provided by Lozano Cabo (1958), Rodríguez-Roda (1964a, 1973, 1974), and Aloncle et al. (1976), are believed to be complete, but are somewhat biased by the inclusion of some records of the La Linea trap, which is actually just inside the Mediterranean. Its

catches, however, were relatively small. From four to seven Spanish "Atlantic" traps were listed for 1941-1971. Since then, only one or two, if any, have been set. The Portuguese data, provided by Vilela (1960), Lima Dias and Barraca (1972) and Republica Portuguesa (1957, 1958,

1959, 1960, 1961, 1962, 1963, 1964, 1965, 1966, 1967, 1968, 1969, 1970, 1971) are believed to be complete. Five traps were set in most of the years 1931-1965, three in 1966-1968 and two in 1968-1972. Due to these discrepancies and omissions, the data in **Figure 50** are not exact. They are presented to illustrate trends in the catches rather than exact totals.

Pavesi (1889) estimated the mean annual production of the Spanish traps for the period 1884-1887 at 70,000 tuna, or quintals (100 kg). He derived a corresponding figure of 30,000 tuna for the Portuguese traps. Roule (1917) calculated the average yearly catch of the Portuguese traps in the years 1896-1912 at 43,983 tuna. In the period from 1930 through 1960, the Spanish catches occasionally surpassed Pavesi's figures, with 106,000 fish in 1930, 76,200 in 1943, 63,500 in 1944 and 80,500 in 1949. The average for the period, about 55,000 fish per year, was considerably below Pavesi's figure. The Portuguese traps only attained Pavesi's average of 30,000 fish in 1943, with 32,400 fish, and never approached the 1896-1912 average of nearly 44,000 fish. The 1931-1960 average of the Portuguese fishery was 17,400 fish per year. The Larache group in Morocco produced a peak catch of 29,000 fish in 1958 and averaged 13,500 fish per year for 1930-1960. The addition of the Cape Spartel and Kenitra catches would increase these figures considerably. Data for Moroccan catches before 1930 are too meager to permit any deductions in regard to long-term trends.

The total annual catches of the samples of the three fisheries remained above 48,000 fish and 7,000 tons per year through 1962. A decline which began in 1963 became disastrous after 1967. Estimated catches varied from 16,000 to 24,000 fish (2,400-4,300 tons) in 1963-1967, and fell to 700 to 12,600 fish (100 to 1,600 tons) in 1968-1973. The Portuguese traps caught just one fish in 1971 (Lima Dias and Barraca 1972) and only 176 kg in 1972 (Y. F. Barraca, personal communication). They have not been set since. In 1972, the only Spanish trap set in the Atlantic, Barbate, which had averaged

Figure 46. Schematic diagram of the type of specialized tuna trap used in the Ibero-Moroccan Bay area: (a) body of trap, divided into compartments, (b) leader from shore to trap, (c) leader extending offshore from trap. Solid lines show trap arranged to catch fish traveling from right to left. Dashed lines show trap modified to catch fish traveling from left to right.

about 20,000 fish per year from 1946-1961 (Sakagawa and Coan 1974), took only 388 fish and the company which had operated the Spanish traps since 1929 was dissolved (Rodríguez Roda 1973). Barbate took 1,952 tuna in 1973 (Rodríguez Roda 1974). Two Moroccan traps, the only others set in the Atlantic in that year, caught 12 fish (R. Sarà, personal communication). Two Moroccan traps were also set in 1974, but took only seven bluefin (M. Lambocuf, personal communication). The situation had become such that when Barbate, which had not been set in 1974, took 1,842 fish (less than one tenth of the 1946-1961 average) in 1975, it was regarded as encouraging (Aloncle et al. 1976)!

The decline in the Barbate catches was accompanied by a marked increase in the average weight, indicating that poor recruitment to the fishery was a major cause of the decreased catches. Although the annual catch fell from 19,000 fish in 1961 to 2,500 in 1971, the average weight per fish increased from 145 kg to 223 kg. (Sakagawa and Coan 1974). Rodríguez-Roda (1964a) had already noted the drastic decrease in the numbers of the smaller bluefin taken in the Spanish traps since 1953, and attributed it to either a high mortality on young fish in previous years, or unknown variations in oceanographic conditions which might have caused them to go elsewhere

h. Trends in Eastern Atlantic Fisheries

The decline in the northeastern Atlantic fisheries for large and medium bluefin tuna is illustrated in **Figure 51**. This trend has been reversed to some extent by improved catches off Norway, and more significantly by the entry of the Japanese longline fishery into the area in 1971 (Shingu and Hisada 1976). Concern has been expressed over heavy catches of very young bluefin as a possible cause for the decline in the fisheries for larger individuals (Rodríguez-Roda 1964a, 1964b, 1969d).

6. Mediterranean and Black Seas

The fixed trap has been the prime producer of bluefin tuna in the Mediterranean Sea (**Figures 52 and 53**)

Table 9 Sexes determined from samples of the 1956-1961 catches from the Barbate trap, and the 1961 catches of two others

Trap	Barbate	Sancti-Petri	Isla Cristina
Males	403	123	46
Females	756	215	66

for centuries. The most important traps were the large ones in the central Mediterranean. The majority of these fished the "arrival" run in May and June; the remainder fished the "return" run in July and August. Some of the smaller traps also fished these migratory passages and similar runs in the Bosphorus between the Sea of Marmara and the Black Sea. The majority of the smaller traps, however,

fished mainly for bluefin which were too young to spawn, or which were in the feeding, rather than the spawning, phase of their annual cycle. Therefore the fishing seasons of these traps were not limited to the May-August spawning cycle, and extended through much of the year. These smaller traps for non-spawning tuna were widely distributed along the coasts of the Mediterranean, but were

Figure 47 Schematic diagram of bluefin tuna movements in the vicinity of traps during the spawning cycle

Figure 48. Lengths of bluefin tuna captured in the Spanish fishery (1956-1959, 1961, 1963-1975) ("+" on graph means less than 0.5%).

Figure 49. Annual catches of the Portuguese trap fishery (Hamre and Tiews 1964, Hamre et al. 1966, 1968, 1971).

most concentrated off France and what is now Yugoslavia (Pavesi 1889, Parona 1919, Belloc 1961).

The history of the Mediterranean tuna traps dates to the pre-Christian era. Thomazi (1947) believed that the Phoenicians introduced this method throughout their colonies, and that some of the French traps had probably operated continuously from pre-Christian times until their demise near the end of the 20th century. He thought that the Sicilian traps were of equally early origin, but had fallen into disuse during the Arab occupation. The Normans revived the fishery soon after their conquest of the island toward the end of the 12th century (Pavesi 1889, Parona 1919, Thomazi 1947). The numbers of tuna traps operating in the Mediterranean declined greatly during the 19th and 20th centuries (Pavesi 1889, Parona 1919), and especially since 1950 (de Cristofaro 1970).

Until recently, the major tuna traps in the central Mediterranean have been of the "Sicilian" type. Since World War II, however, changing conditions have caused the abandonment of many traps and the conversion of others to the "Spanish" type, usually with modifications (Gaudillière 1954, Fodera 1964, Sarà 1964, de Cristofaro 1970).

Various types of nets, hook and line gears, and harpoons have also been used for bluefin tuna in many parts of the Mediterranean-Black Sea system (Pavesi 1889, Parona 1919, Doumenge 1953, Iyigüngör 1957). Until recently, however, their catches were small in comparison with those of the traps.

Developments after World War II have altered this situation drastically. While the trap catches have declined catastrophically (Sarà 1973), catches of small (Tilić 1954, Seacchini and Biancalana 1959, di Meglio 1962) and large (Paini 1975, Miyake 1976) bluefin by purse seine have become important. Also, Japanese longliners took increasing quantities of bluefin in the Mediterranean in the years 1972-1974. The catch declined in 1975, when the Japanese government prohibited their longline vessels from fishing in the Mediterranean during the spawning season as a conservation measure.

Meanwhile, promising sport fisheries for bluefin tuna have developed along the French and Spanish coasts from the mouth of the Rhone to Castellon and along the French and Italian Rivières (Ligurian Sea), where albacore are also taken (Gianelli 1969, Cesario 1972, M. R. Berrell, A. Cesario, L. F. de Gamboa, and E. K. Harry, personal communications).

a. Western Mediterranean

Although located between the formerly important trap fisheries of the Ibero-Moroccan Bay and the central Mediterranean, the bluefin tuna fisheries of the western Mediterranean have produced modest tonnages (Miyake et al. 1976), consisting mainly of small and medium fish. Various gears have been used, some of which are of ancient origin. Others have been introduced recently. Among the most ancient are the traps, which were formerly wide-spread but now survive in a few locations off Spain and Africa only (Parona 1919, Belloc 1961). Hook and line gears and specialized nets have also been in use since long ago. Purse seine and longline fishing have been introduced in the area since World War II. Sport fishing has also developed there in this same period.

The French traps are of historical interest only. Thomazi (1947) stated that they reached their apogee in the 17th century. Gourret (1894) reported those traps near Marseille took bluefin tuna from late July to late November. In 1851 there were 10 traps in the area, but in 1891 only three were operating. Their catch of bluefin in 1891 and 1892 (1,500-2,000 fish, 41-43 tons) was about half of the total catch in the same area by other gears. Parona (1919)

Figure 50. Annual catches of Ibero-Moroccan Bay trap fisheries for bluefin tuna in tens of thousands of fish and in thousands of tons.

showed locations for 23 traps, of which eight were active, along the coast of Provence (France) between the mouth of the Rhone and Monaco. Thomazi (1947), however, reported that the last of the French traps disappeared between 1892 and 1900.

The Spanish and Moroccan Mediterranean traps have taken only small catches of bluefin tuna in recent years. Parona (1919) showed 23 trap locations, of which nine were active, along the Spanish coast east of La Linea. Belloc (1961) listed five in that area, with maximum annual catches of 60 tons of all species combined for a single trap in the years 1954-1958. In 1975 only one of these

traps was set, and it took no bluefin tuna (Rey et al. 1977). Most of these traps fished from early February to mid October, and took feeding (non-spawning) tuna. Other species were more important in their catches (Belloc 1961).

Return traps have been set at La Linea, on the Spanish coast near Gibraltar; at Ceuta, a Spanish city on the opposite side of the Strait of Gibraltar; and at three nearby locations on the Mediterranean coast of Morocco (Belloc 1961, Sará 1964). These traps take bluefin in July and August, but again they depend mainly on other species

Yearly catches of bluefin tuna at La Linea since 1961 have ranged from 0 in 1968 up to 2,400 fish weighing 340 tons in 1965. Their average weights have varied from 128 to 186 kg, probably excluding the numerous age 0 (1 kg) fish which are taken in some years (Rodríguez-Roda 1964a, 1964b, 1969d, 1973; Rey et al. 1977).

The trap at Ceuta and those along the Mediterranean coast of Morocco may be considered together. Only one or two of the Moroccan traps have fished in most recent years. The bluefin tuna catches have ranged up to a maximum of 172 tons for a trap, but have usually been 50 tons or less

(Collignon 1964, 1965, 1966, 1967, 1968, 1969, 1972, Lambouf 1972, Crespo and Rey 1976, M. R. Borrell, personal communication). Little information is available on the sizes of bluefin taken. F. de Buen (1927) stated that 4-5 kg bluefin were taken in the Ceuta trap in early winter. Rodríguez-Roda (1964b, 1969c) estimated that 500,000 age 0 bluefin were taken by the traps at Ceuta and Mediterranean Morocco and the Ceuta fishing fleet in September-October 1963, but stated that such extremely numerous catches of these fish were exceptional. Crespo and Rey (1976) showed that the catches of age 0 bluefin were much greater numerically than all other sizes combined in eight of the 14 seasons from 1961-1974, with significant highs in 1963, 1967 and 1973. Rey et al. (1977) reported that 22 bluefin were caught in the Ceuta trap in 1975.

Twenty of these were reportedly more than 4 years old, and weighed 12,500 kg. Perhaps there is an error in these figures, as the average weight would be 625 kg.

We have little information on the bluefin tuna trap fisheries of Algeria. Heldt (1932a) listed six traps set in 1930 and two in 1931, but with little success in most instances. Belloc (1961) named three in the vicinity of Oran, and listed their individual yearly catches for 1953-1958. The largest such catch was 69 tons (all species) and the average was about 30 tons (all species).

Specialized nets used off the French coast, and their catches, have been described by du Hamel de Monceau (1769-1782), Doumenge (1953), di Meglio (1962) and Farrugio (1977). These included fixed and drifting gill nets and beach and pelagic multiboat seines, called

"thonnaies" or "thonaires," "combrieres," "courantilles," and "seiches." In some cases the same name was applied to various gears, according to the locality. The name "thonnaire" appears to have been used for several types of gear.

Hook and line gears used off the French coast were described or mentioned by du Hamel de Monceau (1769-1782), Doumenge (1953), di Meglio (1962) and Farrugio (1977). These included longlines, trolling gear, poles, and sport gear. Dieuzeide (1931) described handline fishing for large and medium bluefin in the Bay of Castiglione, Algeria. Thomazi (1947) and Dieuzeide (1949) detailed an interesting method of hook and line tuna fishing utilizing small fishes, which had gathered around a moored branch of a tree, as live baits. They reported that this method was used off the Mediterranean coasts of Spain and Morocco, as well as off Algeria.

Recreational fishing for bluefin tuna has been developed off the Mediterranean coasts of France and Spain. Commercial fishermen have been catching medium and giant bluefin by trolling with rod and reel gear off Port de Bouc, at the mouth of the Rhone, since 1959. The season extends from late June into early November. Annual contests, in which sport as well as commercial fishermen participate, have been held. In one which took place August 27-31, 1969, 15 boats landed 40 tuna with an average weight of 105 kg, even though the weather permitted fishing on only two days. The largest bluefin taken weighed 220 kg. The above information is from Gianelli (1969). Another French port where recreational fishing is developing is La Grand Motte, on the Gulf of Lions, where tuna up to 30-40 kg are taken (Cesareo 1972). Sport fishing off the French Riviera will be discussed in the following subsection.

Recreational fishing has also become popular on the Spanish Mediterranean coast at Rosas, near the French frontier, and at Castellon. Catches at Rosas include small tuna and giants of 150-180 kg (Cesareo 1972). Tuna tournaments are held annually at Castellon in late August and early September. Catches totaled

Figure 51. Annual catches of northeastern Atlantic fisheries for large and medium size bluefin tuna (Scandinavian and North Sea seine and hook-and-line fisheries and Ibero-Moroccan Bay trap fishery) in tens of thousands of fish and in thousands of tons.

Figure 52. Geographic references for the Mediterranean and Black Seas.

Figure 53. Geographic references for the northwestern Mediterranean Sea.

47 fish weighing 4,536 kg with maximum, average and minimum weights of 161, 96.5 and 38.2 kg, respectively, in 1973, and 32 fish with maximum, and minimum weights of 180 and 37.8 kg, respectively, in 1974

(M. R. Borrell and E. K. Harry, personal communications). In 1976, however, only one fish was caught (I. F. de Gamboa, personal communication). Tuna of the above sizes were taken in August and early Sep-

tember, but after they disappeared, great quantities of age 0 bluefin (about 1 kg) were taken from late September to early November (J. Bexnat Ortiz, personal communication).

The authorization of seining for bluefin tuna in French Mediterranean waters in 1960 brought about a considerable increase in the catches of the species. The development of the fishery in the Gulf of Lions was described by di Meglio (1962) and Farrugio (1977). Some old boats, mainly trawlers, were fitted with this gear. The first seines, "cinciole", were derived from the Italian type and the second, "cerco", from the Portuguese type used off Morocco. The annual catch in the Gulf of Lions immediately increased from about 500 tons in the years 1950-1961 to about 1,000 tons in 1961 and 1962 (Maurin 1964). Most of the 1962 catch was taken in the beginning of the year in the region of Marseille and Rousillon. The French seine fishery for bluefin off Provence and in the Gulf of Genoa began in 1967 (Patania 1967) and has produced more than half of the total French Mediterranean catches of this species since then (Farrugio 1977). Hamre et al. (1971) reported that from July 1969 through January 1970 purse seine catches off the Mediterranean coast of France totalled 1,500 tons, with most catches occurring in October and November. Catches have fluctuated around 1,500 tons since 1966 with lows of 1,100 tons in 1970 and 1972 and a high of 2,200 tons in 1971 (Farrugio 1977). Miyake et al. (1976) reported generally smaller catches in this period. For some years, their figures differed considerably from those of Farrugio (1977).

The best pre-seining fishing in the Gulf of Lions was from early April to mid-June and from late July to the end of September, with a lull from mid-June to mid-July. Scattered fish were caught in late February and March, and from October into early December. Late December and January were periods of scarcity (Doumenge 1953). Data on the 1963-1965 catches (Hamre et al. 1968) showed minor peaks in March and major peaks in September-October. Farrugio (1977) reported that the seine fishery was active in the Gulf of Lions from early March to late May and from October into December and in the eastern area (St. Tropez

to Capo delle Mele) from July to late September or early October.

Farrugio (1977) described the seine fishing areas. In the Gulf of Lions, fish were taken in September and October in two areas, one between Port Vendres and Leucate and the other between Sète and Marseille. Beginning in November or December, they tend to concentrate in the northern part of the Gulf, between Sète and the mouth of the Rhone. At all seasons, the fish are generally less than 20 miles (33.3 km) from the coasts, in waters whose depths rarely exceed 100 m. Off Provence and in the Gulf of Genoa, the fishing occurs from 5 to 50 miles (8.3 to 83 km) off the coast between Cap de St. Tropez and Capo delle Mele.

Until recently, little information on the sizes of fish taken in these fisheries has been available. Gourret (1894) showed that the average sizes of bluefin taken near Marseille in 1891 and 1892 by traps and other gears ranged from 18 to 28 kg. Samples of catches taken in the Gulf of Lions (off Languedoc, France) in 1953 and 1954 consisted of bluefin of ages 1, 2, 3, and 4 (about 48, 80, 97 and 119 cm long, respectively) (Doumenge and Lahaye 1958). Little variation in sizes of fish with method of capture was indicated by either of these studies. Samples of the 1968 and 1969 catches showed that most of the fish were in the "small" size group, with age 3 dominant in both years (**Figure 54**). Since then, this predominance of age 3 fish has remained relatively constant (**Figure 55**). In 1970 and 1971 a significant showing of medium (ages 6-8) and small giant (ages 8-10+) bluefin occurred but this has not happened since (Farrugio 1977). The 1971 catch consisted partially of 120 tons of bluefin weighing from 100 to 150 kg (ages 8-10), which were reportedly taken off Sète, France, in April by three sardine-tuna seiners (Anonymous 1971). The possibilities of seining bluefin off the Mediterranean coast of Spain were mentioned by Bellon (1954), but, apparently, they have not been developed significantly. In their review of the fisheries for tunas and related species in the Mediterranean and Atlantic waters off southern

Spain, Laboratorio Oceanografico Palma et al. (1976) do not mention seining, even among the minor gears. Rodríguez-Roda (1964a), however, noted that considerable numbers of age 0 bluefin (0.5 kg in September, October; 1 kg in November, and 2 kg in December) were often taken by sardine seiners off Alicante, Spain, mixed in with the sardines. Considerable catches of age 0 bluefin in the same season during 1976 were also reported (F. L. de Gamboa and J. Bexnat Ortiz, personal communications). Rodríguez-Roda (1964b) also reported considerable catches of age 0 bluefin in the fall of 1963 off the Mediterranean coast of Morocco by Spanish seiners based at Ceuta.

Spanish and Japanese longline vessels have also taken bluefin tuna in the western Mediterranean. Annual catches of the Spanish Mediterranean longline fleet, which fishes primarily for broadbill swordfish, *Xiphias gladius* Linnaeus (1758), included from 16 to 274 tons of bluefin in the years 1968-1974 (Laboratorio Oceanografico Palma et al. 1976). Japanese longliners took 238, 427 and 7,980 bluefin tuna in Mediterranean waters west of longitude 10°E in 1972, 1973, and 1974, respectively. Fish were caught from April into October, with the highest catch rates, up to 24 fish per 1,000 hooks, occurring in June. Good catch rates were also attained in May and August (Fisheries Agency of Japan 1974, 1975, 1976).

Rodríguez-Roda (1969d) expressed concern over massive catches of very young bluefin in the western Mediterranean, as well as off the Atlantic coast of Morocco, which he had described previously (Rodríguez-Roda 1964a, 1964b). He reported catches of large numbers of age 0 fish in the fall by seiners off Alicante and the trap at La Linea in Spain, and by seiners and traps off the Mediterranean coast of Africa just east of Gibraltar. He reported that, in the period September 15-October 19, 1963, about 500,000 age 0 bluefin were taken by the Ceuta seiners and the traps in the vicinity. This was, however, an exceptional year, according to his informant. We have been advised that comparable catches of

age 0 bluefin were taken off Castellon, Spain, in the fall of 1976, mainly by sardine seiners, but also by sport fishing boats. Rodriguez-Roda (1969d) believed that the decline in the Spanish Atlantic trap fisheries for larger bluefin might have been caused by excessive fishing of immature fish.

Bluefin tuna catches in the western Mediterranean were evidently unimportant prior to the development of the French seine fishery in 1960. Combining the data of Miyake et al. (1976) and the Fisheries Agency of Japan (1974, 1975, 1976), it appears that the total western Mediterranean catches varied between 1,000 and 2,500 tons (approximately) in the years 1965-1973, but rose to about 4,200 tons in 1974. The latter figure was due mainly to exceptionally large catches by the French purse seine and Japanese longline fisheries. The fishing of age 0 bluefin in this area, which apparently is very poorly recorded, appears to be a cause for concern.

b. Central Mediterranean

The central Mediterranean (Figure 56) has traditionally been the area of the major bluefin tuna catches in that Sea. The tuna trap has been the dominant gear in the area until recently. The oldest trap fisheries were around Sicily and Sardinia, and off the southwestern coast of Italy itself. Additional traps were subsequently installed off Tunisia and western Libya. All of these traps were originally of the Sicilian type (Fodera 1964). Changing conditions have necessitated their modernization through the use of better materials and the adoption of the Spanish design. This process began in Tunisia in 1950 (Anonymous 1952) and in Sicily in 1956 (de Cristofaro 1970). In addition to the ancient trap fisheries (Pavesi 1889, Parona 1919, Belloc 1961, Sarà 1964), bluefin tuna are taken in the central Mediterranean by purse seine (Seaccini and Biancalana 1959, Paini 1975), hook and line (Scordia 1931, 1932; Genovese 1965; Cesarco 1967) harpoon (Scordia 1932, Sarà 1968) and longline (Sarà and Arena 1967, Shingu et al. 1975). In the early

Figure 54. Lengths of bluefin tuna captured in France in 1968 and 1969 ("+" on graph means less than 0.5%).

1970s, the traps were failing (Sarà 1973) and the purse seiners were becoming dominant (Paini 1975, Miyake 1976). Catches of the Japanese longline fishery increased from 1972 through 1974, but conservation measures which were introduced in 1975 curtailed the catch in that year (Kume 1977). Italian longliners whose primary catch is broadbill swordfish also take some bluefin tuna (Sarà and Arena 1967).

Most of the major traps, located off the coasts of southwestern Italy, Sardinia, Sicily, Tunisia and Libya, fished the arrival (prespawning) run of maturing bluefin in May and June. A few, along the eastern and southern coasts of Sicily, fished the return (postspawning) run of spent fish in July and August. Most of the smaller traps fished "erratic" or feeding bluefin at various localities off the Italian mainland and Yugoslavia. The Mediterranean trap fisheries have been described and discussed by Cetti (1777), Pavesi (1889), Parona (1919), Sella (1929a, 1929b, 1932a, 1932b), Belloc (1961), Sarà (1964), de Cristofaro (1970) and others. Parona (1919) (this work was actually completed in 1914)

showed locations for some 100 traps in Italian waters. These included many which were inactive or unimportant, or did not fish specifically for bluefin tuna (Sarà 1968). By 1950, only 30 real tuna traps were active, only 14 in 1965 (de Cristofaro 1970) and just seven in 1973 (Miyake 1976; R. Sarà, personal communication).

Catches of the Sicilian and Sardinian traps for 1938-1939 and 1946-1973, based on statistics from the Istituto Centrale di Statistica (1949, 1951, 1954, 1957, 1960, 1963, 1966, 1969, 1972, 1974) are shown in Table 10. Although data from sources which are probably more accurate are available for certain years, this extensive series of records seems most suitable for illustrating the long-term trends in the catches. A few traps in the Gulf of Sant' Eufemia, Calabria, (Figure 56) also caught prespawning tuna. Three of them formerly took very large numbers of small fish. Pavesi's (1889) data show that the average annual catch per trap for two of these was 4,674 fish with an average weight of 44.4 kg, or 208 tons, in 1879-1883. Parona (1919) listed seven annual catches of over

Figure 55. Estimated age composition of samples of bluefin tuna taken in France in 1964-1965, 1967, and 1969-1975.

100 tons (129-260 tons) for one of them in the period 1896-1914. One or two of these traps were set in each of the years 1938-1939 and 1946-1963 (*Annuario Statistico Italiano*). Their annual catch per trap varied from 25 to 1,329 fish, averaging from 16 to 65 kg each, or 0.4 to 75 tons. The numbers of fish caught by the more important traps in recent years are compared with their average pro-

duction in the years 1879-1883 in **Table 11**. Pavesi (1889) used the latter figures as a basis for classifying the Italian traps in orders as shown in **Table 12**:

The trap catches have been diminishing gradually over a long period, but this decline became catastrophic in the 1970s. Pavesi (1889) reported the average annual catch of these traps in the years 1879-1883, a

good period, as 68,029 tuna, probably at least 6,000 tons. The catches for 1894-1914 varied between 1,624 and 8,160 tons, with an average of 4,643 tons (Parona 1919). Roule (1917a) showed that the Sicilian and Sardinian traps took totals of from 2,342 to 5,329 tons per year in 1909-1913. Sella (1927) listed the Sicilian and Sardinian catches in 1926, in a period which was then regarded as disastrous, as 9,800 fish.

The catches in 1938-1939 and 1946-1969, while not approaching the pre-World War I levels, were generally better than those of the crisis period in the late 1920s and early 1930s. The catch did not decline in proportion to number of traps fishing, partly because the least efficient traps dropped out, and the most productive ones were improved (de Cristofaro 1970). The catches deteriorated drastically after 1969. Figures for the Sicilian and Sardinian traps for 1970-1975 provided by P. Arena and R. Sarà (Miyake 1976) and for the Sicilian traps in 1976 (P. Arena, personal communication), which differ considerably from those in the *Annuario Statistico Italiano* for 1970-1972, are shown in **Table 13**. These data show considerably smaller catches than those indicated in **Table 10**, especially in numbers of fish for 1970-1972, and correspondingly higher average weights in those years. These figures indicate that the greatest decline in the Italian trap fishery was accompanied by a great increase in the average weight of the fish taken, just as it was in the Spanish fishery.

The failure of the Italian trap fisheries (**Table 12**) has followed a rather distinct geographical pattern, moving from east to west. The first order (**Table 11**) trap of Pizzo, the last one set in the Gulf of Sant' Eufemia (compartment of Catanzaro, Calabria), was abandoned after 1963. Another previously productive group in the Gulf of Patti (compartment of Messina, northeastern Sicily), virtually ceased operating after 1967. One of them, San Giorgio, was set for the last time in 1973, after nine years of inactivity, but took only five fish (R. Sarà, personal communication). The group of return traps off the east coast

Figure 56. Geographic references for the central Mediterranean area

of Sicily also became extinct after its two most productive ones, including the first order trap of Marzamemi, took little or nothing in 1969. Less important return traps on the southern coast of Sicily had failed in the 1950s. One at a new location off Cape Granitola, at the southwestern corner of Sicily, fished successfully through 1966. After poor seasons in 1967-1969, it was set for the last time in 1972 with no success (R. Sarà, personal communication). Its failure marked the end of the Sicilian return fishery. The last traps in the Palermo (northwestern Sicily) district were also abandoned after the 1972 season (R. Sarà, personal communication). This left two or three traps being set each year in the Trapani district at the western tip of the island,

and two in the Aegades Islands west of there, as the only survivors of the once flourishing Sicilian trap fishery. In Sardinia, the first order trap of Saline (compartment of Sassari, at the northwestern tip of the island) took very poor catches (1-366 fish per year) in 1967-1972, and evidently has not been set since. The three first order traps of the Carloforte group (department of Cagliari, southwestern Sardinia) averaged about 1,000 fish each per year through 1971, but took only 1,174 tuna in all in 1972. In 1973, only two were set, and they caught only 295 fish. The first order trap (5,000 fish per year) of Favignana in the Aegades Islands is the only one in Italy which has even come close to a second order perfor-

mance (2,000 fish per year) (Pavesi 1889) since 1970 (Table 11).

Pollution and the disturbing effects of increased coastal traffic and other fisheries (trawling and fishing with lights) are regarded as contributing factors, along with reduced numbers of fish, in the decline of the Italian tuna trap fisheries (Sarà 1969, 1973; de Cristofaro 1970, Cesareo 1973). This fits in with the progressive decline of the fisheries from Calabria and eastern Sicily to western Sicily, while the traps in Sardinia, perhaps less subject to these effects until recently, continued to produce good catches. The production of the Sardinian traps, however, has also collapsed since 1972 (Table 11). Sarà (personal communication) advised us that the 1974 catch of the three southwestern Sardinian traps was only 300 tuna. He noted that the entire coast had been contaminated with the wastes of an aluminum plant.

The sizes of fish taken varied with the location of the traps, or with the water temperature at the traps during the fishing season (Sella 1929a) as well as from year to year. Sella (1929a, 1932a) considered the traps off western Sicily and those off southwestern Sardinia as "cold" traps (surface temperature 18.0-19.0°C, salinity 37.37-37.65 o/oo) and producers of large fish, and those off Calabria and Tripolitania as "hot" traps (surface temperature 20.8-21.8°C, salinity 37.48-37.66 o/oo) and producers of medium sized and small fish. The relationships between occurrences of tuna in traps and environmental conditions are discussed in detail in section VI.

The numbers and weights of the bluefin tuna taken by traps in each compartment of Italy in each of the years 1951-1957 were presented by de Cristofaro (1970). The mean weights of the fish taken in each compartment in each year were calculated from these data. The maximum, minimum and average of these mean weights over this period, for each compartment which contained important tuna traps, are shown in Table 14.

These data support Sella's (1929a) findings in regard to western Sicily and Calabria, but the traps off

Table 10 Number and weight of bluefin tuna caught in traps off Sicily and Sardinia by year as reported by the Istituto Centrale di Statistica

Year	Traps	Fish (x1000)	Tons (x1000)	Fish per Trap	Tons per Trap	Average Wt. (kg)
1938	25	16.7	1.6	667	63	95
1939	29	17.4	1.6	600	54	89
1946	32	21.2	2.1	662	64	97
1947	28	20.3	2.1	724	75	104
1948	30	11.4	1.1	381	35	93
1949	32	18.1	2.1	565	67	118
1950	31	18.2	1.7	588	56	95
1951	30	19.3	1.8	644	61	94
1952	29	9.4	1.0	324	33	103
1953	30	13.3	2.0	443	65	147
1954	27	12.2	1.7	451	62	138
1955	28	12.5	1.5	447	54	121
1956	25	10.8	1.5	434	60	139
1957	22	15.2	2.5	694	112	162
1958	27	17.9	2.6	663	96	146
1959	24	13.5	1.8	566	74	131
1960	21	11.7	1.2	560	58	104
1961	21	11.6	1.4	553	67	122
1962	19	12.5	1.3	661	66	100
1963	17	2.2	1.2	540	71	132
1964	15	12.3	1.4	819	106	130
1965	14	10.2	1.3	732	122	89
1966	15	9.2	0.9	611	62	102
1967	13	16.4	1.9	1,63	148	118
1968	13	13.2	1.7	1,016	132	130
1969	12	8.9	1.3	741	109	148
1970	9	6.6	1.0	733	106	144
1971	9	6.8	1.0	852	115	151
1972	8	4.6	0.8	576	103	120
1973	7	1.6	0.4	236	52	219

Sources: Istituto Centrale di Statistica 1949, 1951, 1954, 1957, 1960, 1963, 1966 1969, 1972, 1974

southwestern Sardinia did not produce especially large fish in this later period.

Sarà (1965c, 1968) discussed the historical importance of the smaller bluefin (40-50 kg, ages 5-6) locally known as "golfitani" (Cetti 1777) in the Italian trap fisheries. In the years before 1920, when the fisheries were flourishing, these smaller fish formed a large percentage of the captures,

sometimes as high as 90%. When the catches of large tuna were poor, as they often were, substantial catches of golfitani kept the fishery solvent. About 1925, the catches of these fish began to decrease gradually until they virtually ceased about 1935. This caused a real crisis in the industry. In 1943-1945 (the first post-war years) there was a transitory appearance of golfitani possibly because of the de-

crease in fishing effort during the war. In 1964, these fish appeared again in the catches, increasing year by year. Sarà thought that this occurrence was not transitory, because of the local abundance of herring, anchovies and mackerel, on which they fed. Consequently he believed that the future of the trap fishery was good. Sarà (personal communication, 1973), however, reported that the

Table 11. Italian traps grouped in orders according to the average number of fish caught in 1879-1883 and their catches in numbers of fish since 1966. Only the first three orders are shown.

Order	Trap	Location	Average 1879-83	Year	Last Record ^b Catch	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976
First Order	Saline	NW Sardinia	7,719			77	1	368	204	165	58	X	-	-	-
	Porto Paglia	SW Sardinia	4,423					1,425 ^b				200	50	-	-
	Porto Scuso	SW Sardinia	6,597			3,769 ^c	3,862 ^c		3,060 ^c	2,778 ^c	1,174 ^c	15	0	-	-
5,000 Avg.	Isola Piana	SW Sardinia	5,691					2,100				364	250	-	-
	Pizzo	SW Italy	5,641	1963	26	X	X	X	X	X	X	X	X	X	X
	Marzameni	SW Sicily	4,939			70	X	0	X	X	X	X	X	X	X
10,000 Max.	Favignana	W Sicily	9,018 ^b				4,217	3,250	2,894	1,368	2,340	2,023	970	1,772	2,0891,436
Second Order	Bivona	SW Italy	3,702	1953		X	X	X	X	X	X	X	X	X	X
2,000 Avg.	Flumentorgiu	W Sardinia	2,165	1939	505	X	X	X	X	X	X	X	X	X	X
5,000 Max	Formica	W Sicily	2,165 ^b			2,359	1,997	1,094	980	1,197	505	184	594	960	503
Third Order	Marciana	Elba	1,810			-	-	-	-	-	-	-	-	-	-
	Scopello	NW Sicily	1,000			792	372	178	279	372	270	68	X	203	600
1,000 Avg.	Solanto	NW Sicily	2,000	1961	220	X	X	X	X	X	X	X	X	X	X
	Oliveri	NE Sicily	1,000			105	X	X	X	X	X	X	X	X	X
3 000-	Santa Panagia	SE Sicily	1,392	1959	27	X	X	X	X	X	X	X	X	X	X
4,000 Max	Cape Passero	SE Sicily	1,851			X	X	0	X	X	X	X	X	X	X

Legend:

0 = set but no catch; X = not set; - no information.

^aFor traps not set after 1966. More recent settings may have occurred for some.

^bPorto Paglia and Porto Scuso combined

^cPorto Paglia, Porto Scuso and Isola Piana combined.

^d9,018 is average for Favignana and Formica combined.

Sources:

Pavesi (1889), Hamre et al. (1966), Aloncle et al. (1971a), Istituto Centrale di Statistica (1972, 1974), P. Arena (personal communications), R. Sarà (personal communications). Data are often inconsistent; some mean values have been used.

Table 12. Pavese's (1889) classification of Italian traps.

Order	Number of Tuna per Year	Number of Traps
First	5,000 or more, sometimes 10,000	7
Second	2,000 or more, sometimes 5,000	3
Third	1,000 or more, sometimes 3,000-4,000	6
Fourth	500, not exceeding 1,500	11
Fifth	Rarely exceeding 500	12

Table 13. Catches for the Sicilian and Sardinian traps for 1970-1975, as reported by Miyake (1976) and P. Arena (personal communication).

Year	Traps	Fish (x1000)	Tons (x1000)	Fish per Trap	Tons per Trap	Average Weight (kg)
1970	?	3.3	0.7			205
1971	?	3.9	0.7			191
1972	9	3.3	0.7	364	74.1	204
1973	7	1.4	0.3	193	45.3	234
1974	5	2.6	0.7	522	141	270
1975	6	3.7	0.7	624	119	190
1976	4	3.2	0.6	793	161	203

Table 14. Maximum, minimum, and average weights per Italian compartment which contained important tuna traps for 1971-1957.

Compartment	Area	Location	Annual Average Weight (kg)		
			Minimum	Maximum	Average
Trapani	Sicily	(W)	106	178	140
Palermo	Sicily	(NW)	71	184	121
Messina	Sicily	(NE)	33	160	104
Siracusa	Sicily	(E)	20	174	114
Agrigento	Sicily	(SW)	66	133	101
Cagliari	Sardinia	(SW)	67	115	93
Sassari	Sardinia	(N)	75	181	126
Catanzaro	Mainland	(SW)	16	78	46

golfitani which had appeared in good numbers in 1967-1968 had been practically annihilated by 1972, and that the typical mean weight of the catches had consequently increased from about 150 kg in 1967-1968 to about 270 kg in 1972. He characterized the 1972 fishery as depending on "the remnants of ancient year classes, with no possibility of compensating for their loss with the younger classes which should have constituted the strength of the catches." Sarà (personal communication) also informed us that the early landings in 1973

consisted of enormous fish, including one "matanza" (removal of fish from the trap) of 111 fish whose average weight was 470 kg! The catches at the end of the season, on the other hand, were mainly of fish weighing about 80 kg. Despite this recruitment of smaller fish, however, the annual catch had still declined drastically and the average weight of the fish caught had increased remarkably (Table 10). Sarà (personal communication) advised us that the 1975 catches consisted of large fish up to June 7-8, after which they continued

with very small tuna weighing 25-30 kg. The season ended about June 10 rather than at the usual date, about June 24-25. The figures for this year (Miyake 1976) indicated the first real improvement in the stock since 1970. The size of the catch had increased for the second time, and the average weight of the fish had decreased significantly for the first time, since 1973.

Samples of the Sicilian trap catches in 1958 and 1965-1971 (Figure 57) suggest that giant fish were most important in all but two years, constituting from 35 to 100 percent of the individual samples. The medium fish, or golfitani, made up the majority of the catch in two years, and contributed from 0 to 65 percent of the respective samples. Small fish were apparently insignificant in the catches, never exceeding 2 percent of a sample. The golfitani were most important in 1958 and 1967, and were less so from 1968 on.

The 13 available samples of individual catches of Sicilian traps (Aloncle et al. 1974, Miyake 1976) provide striking evidence of the tendency of the bluefin to school by size. Six samples consisted entirely of medium fish, 122-185 cm long, and six consisted entirely of giants, over 195 cm long. Only one contained a mixture of the two groups, including fish from 147 to 233 cm long. The spreads between the minimum and maximum lengths ranged from 28 to 39 cm, with an average of 33 cm, in the samples of medium fish, and from 34 to 52 cm, with an average of 46 cm, in those of large fish. The 1958 sample (Figure 57) consisted of two catches, taken two days apart. One consisted entirely of giant fish, and the other entirely of medium fish. The same situation existed for samples of two different catches taken in a single trap on the same day in June 1965. This tendency to school by size indicates that size data must be collected on a more continuous basis than has been possible in the Italian fishery to permit accurate estimates of the composition of the annual landings.

The use of purse seines for bluefin tuna was introduced into the Italian waters of the Tyrrhenian and

Adriatic Seas in 1950 (Scaccini and Biancalana 1959). These authors indicated that the early fishing occurred mainly along the Tyrrhenian coast from Salerno to Gaeta and along much of the Adriatic coast between Barletta and Trieste. They reported that the season extended from the end of March to mid-November, and that the bluefin tuna taken weighed from 4 to 30 kg. Their statistics showed that the total Italian purse seine catches from 1950 through 1957 ranged from 351 to 722 tons per year, amounting to from 23 to 72 percent of the corresponding catches of the traditional trap fishery.

Purse seines, including a modified type called the *cianciole* (de Gaetani 1948) have also been used extensively to catch small fishes, including young bluefin tuna, in Sicilian waters. This seining often takes place at night, with the aid of a light to attract the fish. Despite the regulation prohibiting the capture of bluefin tuna less than 90 cm long (Sarà 1968), great numbers of bluefin less than a year old (55 cm long) have been caught (Sarà 1965c, 1968; de Cristofaro 1970, P. Arena, personal communication). Sarà (1973) attributed the decline in the numbers of large bluefin to the heavy fishing of young individuals.

The French seiners which began fishing small bluefin and albacore in the Ligurian Sea (see subsection a) in 1967 were soon joined by their Italian counterparts (Cesareo 1973, 1974a). According to Cesareo, these vessels had reduced the stock to such an extent by 1970 that there was no incentive to fish in the area for the next two years. The stock apparently recovered, or returned to the area, in 1973 and the seiners were present in 1974.

A most important innovation in the central Mediterranean tuna fishery was the creation of a fleet of modern Italian seiners which began fishing for large spawning and postspawning bluefin in 1972 (Paini 1975, Miyake 1976). According to Paini, these vessels fished for two months off the Aeolian Islands and for one month in the Sicilian Channel. Afterward, they went north and fished for small tuna and albacore.

Miyake (1976) stated that the season started in May and peaked in June-July. He indicated that the fishing area was in the southwestern Tyrrhenian Sea, from the north coast of Sicily to Salerno. Data for the catches in 1972-1976 are shown in Table 15. P. Arena also furnished data (Miyake 1976) on the size composition of the catches, as shown in Table 16.

The seine catch in 1975 thus approached that of the traps in their better years early in this century. It is uncertain whether the concentration of large tuna in offshore waters is a new phenomenon, or one which simply had not previously been observed and used. The decline of the trap catches encouraged the exploration of offshore waters, and the use of active gears. The development of the modern purse seine and longline provided the necessary equipment. It had been generally agreed that the bluefin move offshore from the area of the traps to spawn (see Section VI), and the use of pelagic gears to increase the catch had been advocated many years ago (Scordia 1942).

The average weight and size composition data provided by Arena confirm the indications, also noted in the average weights of the trap catches, that there was a substantial recruitment of younger fish to the central Mediterranean spawning stock in 1975. The size composition data suggests a strong influx of fish in the 40 to 100 kg class in that year. This is most encouraging, but whether the stock can withstand the massive impact of the new seine fishery remains to be seen.

As noted above, Paini (1975) reported that the large seiners, after completing their fishing in the Tyrrhenian Sea and the Sicilian Channel, moved north to fish small tuna and albacore. P. Arena (personal communication) advised us that seiners had taken about 2,600 tons of bluefin weighing from 10 to 100 kg in the northern Tyrrhenian and Ligurian Seas in September and October 1976. Thus very heavy pressure is also being put on the stock of young fish just as it appeared to be furnishing urgently needed recruit-

ment to the spawning stock of large bluefin.

Although Ninni (1921a) and Scordia (1939) had reported occurrences of bluefin tuna off the Italian Adriatic coast near Venice and near Manfredonia and Molfetta, respectively, it was not until 1950 that an Italian Adriatic tuna fishery was initiated (Scaccini and Biancalana 1959). This purse seine fishery has been described by Levi (1977). The season extended from the end of March to mid-November, and the fishing area covered most of the coast between Barletta and Trieste (Figure 58). The most successful fishing occurred in March-April off Pescara and Punta Penna, in the central Adriatic, for fish between 10 and 50 kg and in August-October, to the north, off Porto Garibaldi and Cattolica-Cesenatico for 6 to 10 kg fish. The fishing originally took place about 15 miles (24 km) or less from the coast, but this distance has gradually increased to 30-40 miles (48-64 km). The yearly catches have varied between 83 and 434 tons, with an average of 186 tons, from 1955 through 1971. Levi (1977) reported that two of the larger and more modern Italian seiners had entered the Adriatic fishery in 1976. P. Arena (personal communication) advised us that the 1976 Italian seine catch in the Adriatic had reached about 1,000 tons in October.

Hook and line fisheries have existed in several parts of the central Mediterranean, but the most important was in the Strait of Messina. Scordia (1931, 1932, 1934, 1935) and Genovese (1965) have described this fishery, which embraced two distinct seasons. The fall-winter fishery (September-March) occurred in the northern part of the Strait of Messina, and took small or medium sized fish between spawning seasons. The summer (late June-August) fishery occurred in the southern part of the Strait, and took giant fish which were maturing or recently spent. Scordia believed that the winter fish came from the Tyrrhenian Sea, and the summer ones from the Ionian. She provided extensive data on the catches for 1928-1935. Genovese presented the size composition, by

Figure 57. Lengths of bluefin tuna taken in the Sicilian trap catches in 1958 and 1965-1971 ("+" on graph means less than 0.5%).

weight groups and months, of the catches for most of 1948-1950 and 1953-1954, with the sex ratios for some samples. The bluefin taken in the winter fishery were mostly in the medium size group, but with many small fish and a few giants. The introduction of live-bait chumming in 1950 increased the catch from a few hundred fish per year to as many as 1,500 in a month, but after 1953 the catch declined. The summer catches were nearly all giant fish, with a few mediums. Only from 23 to 44 fish per year were taken in 1948-1950, and none were caught in 1953-1954.

The sex ratios of the tuna taken in these years showed a very slight predominance of females (about 52% females), which did not vary greatly between months and years. Arena (1959a) described a productive line fishery off the Aeolian Islands (north of eastern Sicily). Up to 27 fish were taken per boat day under favorable conditions. It was necessary to use fine lines baited with sand launces, *Ammodytes cicirella*. The fish taken generally ranged from 30 to 40 kg. Much larger individuals, 200 kg and over, were often hooked, but usually broke the light lines. The Italian

longliners fished primarily for broadbill swordfish, but caught bluefin tuna incidentally (Sarà and Arena 1967). Their tuna catches have not been recorded in the statistics. R. Sarà (personal communication) estimated that the swordfish longliners might have captured "not over 500" tuna with an average weight of about 150 kg during the 1972 season. Sarà and Arena (1967) noted that smaller longlines used primarily for dolphin (fish), *Coryphaena hippurus* Linnaeus (1758), also took unrecorded numbers of small bluefin.

The Japanese longline fishery entered the Mediterranean in 1972, taking 459 bluefin between 10°E longitude and 20°E longitude. Its catches in this area increased to 748 fish in 1973 and 4,914 in 1974 (Fisheries Agency of Japan 1973, 1974, 1975). Assuming that the weight of these fish was the same as the average for the entire Mediterranean, the corresponding tonnages would be about 74 in 1972, 156 in 1973, and 835 in 1974. The numbers of fish taken in 1975 are not available, but the total Japanese Mediterranean catch declined from 2,192 tons in 1974 to 1,100 tons in 1975, because of conservation measures (Kume 1976). The largest catches were taken south of latitude 40°N in May and June, corresponding to the "arrival" run of maturing bluefin in the area. Catch rates, in fish per thousand hooks, varied from 0 to 12.8 in May, 7.8 to 14.6 in June, and 0 to 19.5 in July. Thus the most consistent catch rates were obtained in June, during the arrival run when the maturing bluefin are believed to be reluctant to feed (see Section VI). The highest catch rates, 14.6 and 19.5 fish per thousand hooks, were obtained in the Ionian Sea in June and July, respectively.

Sport fishing for small bluefin tuna and albacore (*Thunnus alalunga*) in the Ligurian Sea was initiated by French and Italian anglers in 1962 and 1963. This fishery was very successful in the years 1964-1968, with daily catches in 1964 averaging 30 tunas a day for a well crewed boat with expert anglers. This average declined to 0 in 1971, reportedly because of heavy fishing by Sicilian and French seiners in 1968-1971.

Some improvement in the fishing was noted in 1972 and 1973, after the seiners had left the area. The schools were much less numerous than before the seining, however, and were present for a much smaller portion of the year (Cesareo 1973, "A.C." personal communication). This improvement has evidently continued; nine boats took 680 kg of bluefin and albacore in a day and a half in a tournament off San Remo, Italy, in September 1975 (di Sant' Ignazio 1975). Friction between seiners and recreational fishermen was also men-

Table 15. Catch data for the Italian purse seine fishery in the southeastern Tyrrhenian Sea and the Sicilian Channel (Miyake 1976, P. Arena, personal communication).

Year	Boats	Fish	Tons	Average Weight (kg)
1972	8	9,000	2,300	256
1973	11	8,500	2,200	259
1974	15	13,000	3,500	269
1975	16	32,000	5,800	181
1976			4,120	

tioned in this report. Cesareo (1974b) stated that there had always been giant bluefin along the Italian Adriatic coast from the delta of the Po southward, from Punta Pila to Porto Corsini (Figure 58). They were especially numerous in 1968-1970. Catches were scarce, however, because of the lack of sport fishing effort. Cesareo's comments were in response to a letter from a sportsman who reported the capture of a giant fish weighing 176 kg off Punta Pila in 1974, and recalled taking one weighing 152 kg in the same area in 1971.

Scaccini (1961) discussed the distribution of young bluefin tuna in the Adriatic in relation to physical, chemical and dynamic conditions of the environment (Figure 58). Very small fish (11-20 cm, 40-100 g) occurred in summer close to the coast from north of Rimini to Ancona over sandy bottom. Fish 40-60 cm long (3-5 kg) and larger ones 10-12 kg and up to 1 m long were fished by seine from April to September in the north Adriatic from the mouths of the Po to just north of Ancona, always from 6-7 to 12 miles offshore.

On the other hand fish of the same size were found from one half to five miles off the coast in very shallow water in the middle Adriatic between San Benedetto de Tronto and the Gargano promontory. They also occurred in the mid-Adriatic, always on the surface, north of the island of Pianosa over the trench of Pomo. Bluefin of 30-70 kg and more than a meter long, rare in the western Adriatic, were caught habitually in the eastern Adriatic, and in summer and early fall north of the mouths of the Po near Venice. Scaccini showed that this apparently strange pattern was based on currents whose waters were more favorable than the surrounding ones for the tuna of the sizes in question.

The oldest bluefin tuna fishery in the Adriatic is by traps situated along the northern coasts of Yugoslavia and the adjacent islands. As elsewhere in the Mediterranean, the number of traps fishing off Yugoslavia has decreased greatly. Whereas Parona (1919) listed 38 active emplacements, only 21 existed in 1957 and 17 in 1958-1959 (Belloc 1961).

Table 16. Size data for catches of the Italian purse seine fishery in the southeastern Tyrrhenian Sea (P. Arena, personal communication).

Size Range (kg)	Percentage of 1974 Catch	Percentage of 1975 Catch
40-100 kg		30%
100-200 kg	20%	25%
200-300 kg	50%	35%
300-500 kg	30%	10%

Figure 58. Geographic references and movements of bluefin tuna along the Italian Adriatic coast.

A Yugoslavian purse seine fishery for bluefin tuna was introduced in 1929 (Tilic 1954), with seven vessels fishing in the period 1936-1940 and 11 in the period 1947-1951. Like the trap fishery, this occurred mainly off the northern coasts and the adjacent islands (Morovic 1961). Total yearly bluefin tuna catches in Yugoslavia averaged 127 tons for 1936-1940 but increased to 468-873 tons in 1947-1951 (Tilic 1954). In 1952-1974, the total yearly catches varied from less than 100 to 700 tons, but have not exceeded 350 tons since 1959 (Hamre et al. 1966, Miyake et al. 1976).

Trap fisheries have long been important in Tunisia (Figure 56). Although as many as 11 traps have operated in some years (Gaudillière 1954), Roule (1924) recommended that studies of the bluefin tuna stocks in the area be concentrated on the catches of the Sidi Daoud trap on the west side of the Cape Bon peninsula. This trap has been by far the most productive in Tunisia, and has fished

almost continuously since 1863 (Figure 59). The other traps have fished intermittently and their catches seemed to follow the same trends as those of Sidi Daoud. Its catches for 1863-1923 (excepting 1874 when it was not set) averaged about 8,000 bluefin tuna per year (Roule 1924). In the years 1928-1937, regarded as a period of crisis, its annual catches ranged from 1,000 to 3,400 fish (Heldt 1932, 1934, 1937, 1938). In 1955 it took 3,600 fish with an average weight of 128 kg (Postel 1956). In the period from 1962 through 1976, its approximate average annual catches declined from 1,500 fish weighing 180 tons in the first five years to about 300 fish weighing 40 tons in the last five (M. Zaouali, personal communication). Thus, the Tunisian trap fishery for bluefin has apparently suffered a collapse similar to that of the Italian trap fisheries. Sella (1929a) pointed out that the trends of the Sidi Daoud catches were remarkably similar to those of the important traps off southwestern

Sardinia. Roule (1924) concluded that the Sidi Daoud catches varied inversely with the amount of rainfall in the area. He felt that the runoff from the Lake of Bizerte reduced the salinity of the waters around the trap, making the area less attractive to the bluefin.

Total catches of the Tunisian traps in 1910-1923 ranged from 4,300 to 34,400 fish with the larger catches being taken before 1916 (Roule 1924). In 1927-1938 catches ranged from 2,200 to 9,000 fish weighing 200 to 800 tons with yearly average weights of 71 to 108 kg (Heldt 1932, 1934, 1937, 1938). The three traps operating in 1955 caught 3,985 bluefin averaging 119 kg (Postel 1956). This constituted only 47 percent of the total catch of the traps, by weight. The annual total catches of all species by the three Tunisian madragues active in 1952-1958 ranged from 677 to 1,013 tons (Belloc 1961). Postel's (1956) data suggest that about half of these tonnages might have been bluefin. Total Tunisian bluefin catches for 1964-1974 ranged from 200 to 900 tons with smaller catches occurring since 1970 (Miyake et al. 1976) but no breakdown by gear is available. Heldt (1932, 1934, 1937) reported that catches of up to 40 tons a year were taken in the "winter fishery", mainly with seines.

The Tunisian traps all fish in the "arrival" run, except for some experimental fishing of the "return" run by the Cap Zebib trap in 1924 (Gruvel 1926) and an experimental trap at Ras Mustapha (Bellon 1954). For 1931-37, the first trap catches were from May 19 to June 9, and the last from June 20 to July 6 (Heldt 1932, 1934, 1937, 1938). Heldt (1929) supplied average weights of the bluefin caught by the Sidi Daoud and Ras el Ahmar traps and for all the Tunisian traps for 1904-22. The average for all traps ranged from 50 to 89 kg. The average for Ras el Ahmar (59-126 kg) was higher than that for Sidi Daoud (50-89 kg) in every year but two. Since Ras el Ahmar is situated north of Sidi Daoud, nearer the tip of the Cape Bon peninsula, Heldt concluded that the larger bluefin travelled farther offshore than the smaller individuals. Heldt's (1932, 1934,

1937, 1938) data for individual Tunisian traps showed that those on the north coast (Cap Zebib, Sidi Daoud, Ras el Ahmar and El Aouaria) caught larger fish than those on the east coast (Monastir, Kuriat, Conigliera, and Bordj Kadidja). Yearly average weights for the western traps varied from 42 to 246 kg, whereas those for the east coast traps ranged from 47 to 62 kg. Postel's (1956) data for 1955 catches showed the same trend: 125 and 115 kg for Sidi Daoud and El Aouaria, respectively, and 52 kg for Kuriat.

Sella (1912a) reported that there were quantities of bluefin tuna along the Libyan coast, and the installation of traps began in 1914 (Parona 1919, Ninni 1921b). Data are available for the catches in Tripolitania (western Libya) in 1915, 1919-1936, 1939, 1951, 1955, 1959, 1972, and 1973, but not all on a comparable basis. The most complete data are for 1921-34 (Anonymous 1928a, 1929a, 1932a, 1934a, 1934b, 1935a, 1935b, 1936). In 1915 and 1919-20 from one to three traps were set each year, and annual catches ranged from 1,160 to 6,206 fish per trap. In 1921-34, from six to 13 traps were set each year, and annual catches varied from 285 to 1,200 tons per year, consisting of from 547 to 2,067 fish per trap with average weights of from 56 to 110 kg per fish. In 1935, 1936 and 1939 from seven to 10 traps fished each year and took from 1,133 to 1,737 fish per trap year. The average weight of the fish caught in 1936 was 75 kg. Catches totalled 1,120 tons in 1951 (Anonymous 1952), 6,403 fish averaging 86 kg in 1955 (Postel 1962), and 1,950 tons in 1959 (Anonymous 1960). Recent landings have been considerably smaller, with four traps taking 1,550 fish in 1972, and three taking 2,360 in 1973 (R. Sarà, personal communication). The total yearly bluefin tuna catches of Libya for 1964-1974 varied between 300 and 2,000 tons (Miyake et al. 1976), with the largest catches occurring in 1968 and 1969.

The Tripolitanian traps fished the "arrival" run only, although evidence of a potential "return" fishery has been noted (Anonymous 1932). First catches for 1927, 1928, and 1931

occurred between May 29 and June 23 (Anonymous 1928a, 1929a, 1932). Belloc (1961) reported that the fishing began at the end of May, peaked in the first half of July and ended during the last half of July. Sarà (1964) stated that the Libyan traps fished about 15 days later than those of Sicily, Sardinia and Tunisia. In 1964, the fishery extended from the 22nd to the 26th week (about May 25-June 23) (Hamre et al. 1966).

The only size sample available for the Libyan fishery is for the 1964 catches (Figure 60). About three-quarters of the fish were in the "medium" category, with the remainder in the "large" group.

Except for an ephemeral attempt near Tobruk (Sella 1932a), the easternmost tuna trap which fished spawning bluefin in the Mediterranean was at El Mongar near Bengasi in Cyrenaica, Libya. Information on this trap is meager. In 1924-27, it took from 1,039 to 3,286 bluefin tuna per year (Anonymous 1928b). The latter figure, attained in 1927, was reportedly the highest for any trap in the Mediterranean in that year. In 1928, only 197 tuna were taken (Anonymous 1929b). Catches of from 112 to 436 tuna per year are listed for Bengasi or Cyrenaica for 1930-33 (Anonymous 1932a, 1934a).

In 1927, the first and last bluefin catches at El Mongar were on May 31 and July 18, respectively (Anonymous 1928b), and in 1928, on June 26 and July 14 (Anonymous 1929b). The latter season was regarded as unusually late in starting.

No quantitative data are available on the sizes of the fish taken, but Sella (1932a) stated that they were small or medium size, and that their gonads were ripe. Anonymous (1929b) reported that the tuna caught in 1928 were very small.

Because of the irregularity of its catches and the small size of the fish taken, Sella (1932a) did not regard El Mongar as a true "arrival" trap. Since it did not catch large spent fish, he also felt that it did not qualify as a "return" trap. It appears to have been abandoned soon after this information was published. He pointed out that this trap was east of the 38 o/oo isohaline, which he regarded as the

upper limit of salinity for large "arrival" (maturing) bluefin. He added that, had he known what he then did about the sensitivity of maturing bluefin to salinity, he would not have attempted to establish a trap east of El Mongar (in water of higher salinity) near Tobruk.

c. Eastern Mediterranean and Black Sea

Bluefin tuna are extensively distributed over the eastern Mediterranean (Figure 52), except its south-east corner, but the only fisheries of any importance are those of Greece and Turkey. Annual catches reported for Greece since 1952 have ranged from less than a ton to 1,220 tons, and those for Turkey since 1957 from less than a ton to over 1,500 tons. Catches in Greece since 1968 and in Turkey since 1970 have been negligible (Hamre et al. 1966, Miyake and Manning 1975, Miyake and Tibbo 1972).

Eleven traps were active in Greece in the period 1954-1958 (Belloc 1961). The maximum annual catch (all species) per trap was 21 tons; few catches exceeded 10 tons and many were less than one ton. All of the traps were located on the Aegean (eastern) coast of Greece (Figure 61), with all but two on the Peloponnesus. Ninni (1922) quoted Vinciguerra (1896) to the effect that the only bluefin tuna fisheries in the Aegean were at Melina in the Gulf of Volos and Gialtra on the island of Euboea. Ninni concluded that in spring bluefin tuna migrated northward in two groups through the Aegean from a wintering area around Crete. The major group skirted the coasts of Asia Minor and the adjacent islands and a smaller one traversed the channel between Euboea and the mainland to enter the Gulf of Volos. Athanassopoulos (1923, 1924, 1926) considered the bluefin to be a rare fish in Grecian waters, particularly off its western (Ionian Sea) coast. Oren et al. (1959) reported trolling catches of very small (45-53 cm total length) bluefin tuna in several parts of the Aegean during an exploratory fishing cruise September-December 1952.

Figure 59. Annual catch of bluefin tuna from the Sidi Daoud trap in Tunisia in thousands of fish and hundreds of metric tons.

Turkish fishing for bluefin tuna is by trap, handline and harpoon (Ninni 1922, Devedjian 1926, Hovasse 1929, Lebedeff 1936, Akyüz and Artüz 1957, Iyigüngör 1957, Belloc 1961). Lebedeff (1936) described sport fishing near Istanbul in the winter of 1935-36. The favorable situation for developing a sport fishery there was also mentioned by Iyigüngör (1957), but we have no further information on this subject.

Parona (1919) showed 26 locations for traps in the eastern Sea of Marmora and the Bosphorus. Belloc (1961) noted that Devedjian (1926) showed 225 emplacements for Turkish traps in the Black Sea, Bosphorus, Marmora and Dardanelles, but his charts show only 19 in the Bosphorus and eastern Marmora and two in the Dardanelles. Only a few of these were noted for catching bluefin tuna. Ninni (1922) noted that there were some "summer" and some "winter" traps,

but Iyigüngör (1957) said that the traps fished from early April to the end of August. He estimated the average season's catch per trap at 100-150 tuna. Opinions also differed as to the periods of passage. Ninni described an "arrival" (northward) run from late March to mid-August and a "return" (southward) run from early August to December or even February. Hovasse (1927), on the basis of catch records for the years 1915 and 1921-1923, found three maxima in

Figure 60. Length composition of samples of bluefin tuna taken along the Libyan coast in 1964 ("+" on graph means less than 0.5%).

the landings: one with maturing fish in February, March and April, one with spent fish in July and August, and a lesser one in December. Hovasse believed that the first run was an "arrival" migration into the Black Sea, where spawning took place and the second was a "return" run from the Black Sea. He did not understand the significance of the third maximum. Iyigüngör (1957) listed three rather similar runs: March-April, July-autumn, and November-January. Akyüz and Artüz (1957) specify an "arrival" run similar to Ninni's, from April to early August, and a "return" run from late October into December. These authors show the average volume of bluefin tuna sales in the Istanbul market, by month, for 1935-1955. These show a maximum in March and another in July, with good volume in April, February, and August and a minimum in June. The yearly volume of bluefin tuna sales in the Istanbul market varied from 85 to 537 tons in 1909-1916 (Ninni 1922), from 15 to 112 tons in 1928-1938 and from 40 to 764 tons in 1953-1955 (Akyüz and Artüz 1957). The allocation of catch by gears is not shown.

Harpooning is practiced both from the shore and from small boats (Devedjian 1926). Handlining is also practiced from small boats (Devedjian 1926, Iyigüngör 1957).

The hook-and-line fishing seasons are November-January and March-April; the fish do not take bait July-October (Iyigüngör, 1957). Both of these fisheries are centered around Istanbul.

Ninni (1922) concluded that the quantity of bluefin tuna available was much greater than was indicated by the catches of the traps, since the latter did not extend into sufficiently deep water to fish tuna effectively, and also were too weak structurally to hold any considerable quantity of bluefin. He noted that a trial setting of an Italian style trap at Touz Burnum in 1913 had not produced satisfactory results, but did not consider this experiment conclusive.

Evidently most of the bluefin taken near Istanbul are large. Most of the fish examined by Akyüz and Artüz (1957) at the Istanbul market (1955-1956) were in the 170-280 cm range, with the smallest 120 cm and the largest 330 cm. Samples examined there in 1967 and 1968 (Hamre et al. 1971) ranged from 85 to 320 cm, with most of the fish from 155-290 cm (Figure 62). Lebedeff (1936) mentions that hook and line catches in 1936 included 40 bluefin over 400 kg, 10 over 600 kg, and some from 700 to 775 kg. He noted that fish over 200 kg were taken only in the fast current, whereas 100 yards away only individuals of 20-50 kg were caught. In early April, the large and small bluefin left, but medium sized

ones stayed near Prince's Island. During a few days of sport fishing, from December 25, 1935 to late March 1936, Lebedeff caught tuna of 120, 230, 350, 380 and 400 kg. He also lost several large bluefin which broke his lines or leaders. One of these, which was later caught in a net and identified by the hook and leader which had remained attached to it, weighed 450 kg.

Hovasse (1927) noted that bluefin tuna occurred in the Aegean Sea-Marmara-Black Sea area in waters of extremely different salinities, from 18.3 o/oo in the Black Sea to 39 o/oo in the southern Aegean. In the vicinity of Istanbul tuna are found simultaneously in deep waters with salinity of 38 o/oo and shallow waters with only 17 o/oo to 18 o/oo. He stated that tuna in the area were found in considerable ranges of temperature—as low as 14°C to 19°C, according to depth—in the Black Sea at the time of the "arrival." These findings conflicted with Roule's (1924) hypothesis of a stenothermic and stenohaline tuna.

Small bluefin tuna range along the Mediterranean coasts of Turkey and Syria, and occasionally occur off Cyprus (Carp 1951, Oren et al. 1959, Sarà 1964). Carp reported a Turkish fishery for bluefin (apparently 10-30 kg) along the Anatolian coast and in the Gulf of Mersin. Oren et al. (1959) reported captures of very small (45-

Figure 61. Geographic references in the Aegean Sea area.

Figure 62. Length composition of samples of bluefin tuna taken in Turkey in 1967 and 1968 ("+" on graph means less than 0.5%).

53 cm) individuals in various localities in the northeastern corner of the Mediterranean in November and December. They also noted catches of young tuna off Haifa, Israel, in waters with salinities of 39.58 o/oo or more. Sarà (1964, Figure 1) indicated that the northeastern corner of the Mediterranean (Haifa, Israel, to the Gulf of Mersin, and around eastern Cyprus) is a year-around habitat of 5-25 kg bluefin and an August-November habitat of 0.2-3 kg bluefin.

The southeastern corner of the Mediterranean (coasts of Egypt and southern Israel) is evidently devoid of bluefin tuna. The stranding of a single bluefin near Alexandria (Heldt 1937) was regarded as an extraordinary event.

d. Summary.

Sàrà (1964, 1973) summarized the distribution of bluefin tuna in the Mediterranean Sea. From August through November, almost all of the Mediterranean is filled with large schools of very young tuna born in the year. After November, when they have attained a weight of about 2 kg, few are taken, probably because of bad weather rather than because of their absence. With the return of good weather in late winter, they are found in practically the same places, weighing 4-5 kg. These young tuna remain in the areas where they were born, making small movements in response to changes in environmental conditions, and in search of food, until they reach sexual maturity. Sarà's (1964) distribution chart indicates scattered concentrations of bluefin weighing 5-25 kg near most of the islands and coasts in the western and central Mediterranean, except the African coast between Morocco and Tunisia. In the eastern Mediterranean, concentrations are shown in the Aegean Sea, around the Bosphorus, and off the northeastern coasts.

Medium-sized tuna (30-100 kg) are found off many of the coasts throughout the year. Sarà's (1964) chart locates these fish along the African coast from Gibraltar to Bengasi (mainly from Tunisia to Cape Misurata), along the Spanish and French coasts and around the Balearic Islands, in the central, eastern and southern Tyrrhenian Sea, along the

east coast of Sicily and around the islands in the Sicilian Channel, in the Adriatic Sea and in the northwestern Aegean Sea. Sarà (1973) said that these fish are especially visible in late summer and autumn, when they chase prey relentlessly on the surface near the coasts.

Large tuna (over 150 kg) are abundant, except in certain local areas, only from April to September (Sarà 1964, 1973). The principal areas of abundance indicated in Sarà's (1964) chart are off western Sardinia, Sicily, Tunisia and western Libya.

Other occurrences are shown near Gibraltar, in the Gulf of Lion, in the Bosphorus, and off Bengasi. Sarà (loc. cit.) believed that the major occurrence of large bluefin in the Mediterranean is the spawning run from the Ibero-Moroccan Bay, whose volume and movements are greatly influenced by the inflowing Atlantic Current. Occurrences in other seasons consist of relatively small numbers of fish which stay in areas where food is plentiful, such as the Gulf of Lion (off the mouth of the Rhone), the Tuscan Archipelago, the Aeolian Islands, the Strait of Messina and the Dardanelles.

The fisheries for large bluefin were historically the most important in the Mediterranean, and laws prohibited the capture of young fish in Italian waters more than a century ago. Catches of young bluefin have increased since 1920, and this tendency has accelerated after World War II. Perhaps in consequence of this, the landings of large bluefin by the traditional trap method declined, especially in the 1970s. The introduction of longline and purse seine fisheries for large bluefin in this period, however, had restored the catches of large fish to their earlier level by 1974.

V. SPAWNING

A. INTRODUCTION

Considering the amount of research which has been devoted to the Atlantic bluefin tuna, positive information on its spawning habits is surprisingly incomplete. The earliest and most extensive information on this subject is from the Mediterranean, but even there much remains to be learned. The situation is far worse in the important eastern North Atlantic region, since, to our knowledge, no larvae or small (less than 12 cm) juveniles have been collected in any of its areas which have been assumed to be spawning grounds. Greater advances have been made in the western North Atlantic, but positive information there is limited to relatively small areas. Aside from a few larvae collected near the Equator, we found no information whatsoever on the spawning of the species in the South Atlantic. The paucity of knowledge concerning this vitally important phase of the life of the bluefin tuna may be attributed to the serious limitations inherent in the methods used to obtain this information.

B. DEFINITIONS

Larva: Matsumoto et al. (1972) stated that the larval stage of nearly all tuna species ends when the larva has attained 10 to 13 mm standard length (SL) (Figure 63). We have arbitrarily selected 12 mm SL as the size at which the bluefin tuna passes from the larval to the juvenile stage.

Juvenile: Postlarval fish may be regarded as juveniles until they reach maturity-- a considerable size, in the case of the bluefin tuna. In this section on the spawning of this species, however, we have arbitrarily limited the term "juvenile" to include individuals from 12 to 120 mm. Bluefin tuna only slightly larger than 120 mm are active predators and are taken in some fisheries.

Index of Maturity: The numerical index of maturity most frequently used in this section is the weight of the entire fish divided by the weight of the

gonads. This index is therefore inversely proportional to the maturity of the fish. Other indices are defined where they first occur in the text.

C. CRITERIA FOR DETERMINING SEASONS AND AREAS OF SPAWNING, AND THEIR LIMITATIONS

I. Presence of Ripe Adults

The evaluation of the condition, or degree of maturity, of the gonads of adult fish is one of two approaches

used to determine the spawning seasons and areas of the bluefin tuna. The presence of fully ripe adults is assumed to indicate spawning.

Stages of maturity have been evaluated by several methods, some subjective and some objective. The appearance and physical characteristics of the ovaries and the ovarian eggs are among the subjective criteria used for this purpose. Visual diagnosis may be based on the color of the ovaries and the extent and color of their external veining. Their consistency (hardness or softness) and their size and shape are

Figure 63. Early life history stages of *Thunnus thynnus* of the western central Atlantic (Richards 1989).

important physical factors. The size and consistency of the ovarian eggs, and the tenacity of their adhesion to one another and to the walls of the ovaries also provide indications of maturity.

The more objective criteria include indices of maturity, usually expressed as a relationship between the weight of the ovaries and some measurement of the fish from which they were taken. Examination of histological sections of gonads permits more exact assessment of stages of maturity, but few such studies on bluefin tuna have been published.

Estimates of spawning areas and seasons from gonad condition are subject to many limitations. Unless the specimen is fully ripe, serious errors may be involved, as these fish can travel great distances in short periods (Mather 1962, 1969). Also, fully ripe bluefin tuna are difficult to catch on hook and line as they are reportedly reluctant Sarà to feed (Sella 1929a, Rivas 1954, Sarà 1964, 1973). Their capture in traps is extremely rare. Sanzo (1910a) found a ripe female in a trap near Palermo, Sicily, in 1908, but had not encountered another when he produced his final (1932) work on the eggs and larvae of the bluefin. Likewise Rodríguez-Roda (1964a, 1967a) had observed only one ripe female in his extensive studies at Barbate, the most productive tuna trap in this century, and other sites. He remarked that the oviduct of this individual might have been obstructed. The recently developed purse seine fishery in the central Mediterranean spawning grounds (Section IV) has made more mature bluefin available (R. Sarà, personal communication), but no studies based on these catches have appeared.

Bluefin tuna spawn fractionally, by several separate emissions of eggs over a period of several days, rather than by a single emission (Sanzo 1910a, Frade and Manaças 1933). Thus, even when ripe fish are taken, the localities of capture may not indicate the total area over which the fish have spawned.

The fractional nature of their spawning also adds to the difficulties in determining when bluefin tuna are fully ripe. As noted above, many of the criteria used to determine stages of maturity are subjective. In addition, even the seemingly objective indices of maturity may be subject to error.

Maturing and post-spawning fish may have the same indices as the size of their gonads increases and then decreases. Also, maturing fish are considerably heavier than spent ones of the same length. This fact introduces errors when indices for fish in these different phases are compared. In addition, the testes of males decrease in size much more than the ovaries of the females after spawning has been completed. Thus comparison of indices for fish of different sexes may be misleading. Frade (1937) pointed out these sources of error and used corrections for the differences in gonad weight between sexes and in total weight between maturing and spent individuals of the same length. These refinements in the method, however, have apparently been ignored. We have observed another possible source of error in indices of maturity for bluefin tuna in the western North Atlantic. When large bluefin tuna arrive in New England waters in July (Section IV), they are spent and their gonads are small. Toward the end of their feeding season, in late summer and early fall, their gonads become almost completely encased in adipose tissue. If this tissue is not removed before weighing the gonads, the maturity index may be almost as high as for a ripe fish, even though the gonad proper is small and dormant. Baglin (1976) noted that the average weight of the adipose tissue attached to the ovaries of six giant bluefin taken off New England in August 1975, was 1,152 g, while the average weight of the gonads themselves was 1,114 g.

The well documented presence of fully ripe fish may therefore be a good indication of a spawning area, but conclusions based on nearly ripe fish may be very misleading.

2. Presence of Pelagic Eggs and Larvae

The times and locations of collections of pelagic eggs and larvae form another basis for the determination, or estimation, of the seasons and areas of spawning. When eggs or extremely small larvae can be identified, it may be assumed that spawning occurred not very long before the time of collection and not very far from the collecting locality. Estimating the time and place of spawning when larger larvae or ju-

veniles are collected, however, requires knowledge of their growth rate, and also of the currents in the collecting area.

Although this approach is very logical, its execution has not proved to be easy. The collection and identification of eggs and larvae is difficult. Bluefin eggs cannot be positively identified unless they are hatched and the larvae are reared to an identifiable size (Piccinetti and Piccinetti Manfrin 1970), which is a most difficult process. The identification of larvae has been controversial (Sella 1924, Dieuzeide 1951, Duclerc et al. 1973, Richards 1976). Sella and Richards questioned Ehrenbaum's (1924) tentative identifications of "*Orcynus thynnus* L.", and Richards reidentified several of Ehrenbaum's larvae of tunas and tuna-like species. Duclerc et al. (1973) found it impossible to distinguish eggs and larvae of "*Thunnus thynnus* L.", from those of "*Auxis thazard*", even after the eggs had been hatched and the larvae reared to lengths of 5.0 mm. Duclerc et al. (1973) and Richards (1976) questioned Sanzo's (1932) descriptions of the egg and larval stages of "*Orcynus thynnus* Ltkn.", and felt that they should be verified. Some encouraging progress has been made recently, however. Duclerc et al. (1973) and Scaccini et al. (1975) have reared larval bluefin tuna for periods of up to eight days from eggs collected at sea. Richards and Potthoff (1974) have produced a most thorough description of larval bluefin tuna more than 3.0 mm (SL) long.

The accuracy of estimates of spawning seasons and areas based on the collection data for young stages, their length and growth rates, and current systems in the collecting area, declines rapidly with the passage of time from the hatching of the specimen. Not only does the error in calculating passive transport increase, but juvenile bluefin tuna become active swimmers at a surprisingly early age. They attain their full complement of caudal rays at about 16 mm SL (Potthoff 1975). Sella (1929a) stated that the bluefin tuna could already be considered an active fish at the age of 15 days.

Most of the available data on the growth of the early stages of the bluefin (Section III) have been presented in terms of weight. Growth data in terms

Figure 64. Bluefin spawning areas in the Mediterranean and Black Seas and the eastern Atlantic.

of length would be much more useful for back-calculating the localities where larvae or juveniles had probably been spawned.

Collection data for eggs and small larvae which have been reared to identifiable sizes furnish good indications of spawning dates and areas. Estimates based on collection data for larger larvae or juvenile stages, however, must be regarded only as approximations.

Unfortunately, most of the available data on the growth of early stages of bluefin tuna (d'Amico 1816, Bourge 1908, Heldt 1930, Piccinetti and Piccinetti Manfrin 1970) were presented in terms of weight (a characteristic which is seldom reported in this size range), rather than length. Length-age data for early stages of bluefin tuna are needed to reduce the error in estimating the probable date and location of hatching from the collection data of early stages.

D. SPAWNING AREAS AND SEASONS

I. Mediterranean and Black Seas

a. General Information

The spawning habits of *T. thynnus thynnus* have been more extensively

studied and are better known in the Mediterranean than elsewhere.

Bluefin tuna spawn over extensive areas of the Mediterranean and Black Seas (**Figure 64**). The larger individuals, to which most of the research has been devoted, spawn mainly in the last half of June and the first half of July. There is considerable evidence that the smaller bluefin which have reached maturity (the older small bluefin and the medium-sized fish) spawn later, throughout July and into August, and occasionally even into September.

The principal known spawning areas were in the southern central Mediterranean, around Sicily, off western Sardinia, and off northeastern Tunisia. Additional reproduction has occurred around the Balearic Islands, off Tripolitania (western Libya), off Algeria, and in the Black Sea. It is believed that additional research would show that the species spawns over a much broader area.

The relationship between eastern Atlantic and Mediterranean bluefin tuna has been debated for centuries. An ancient theory, proposed by Aristotle (circa 325 B.C.), has been believed for centuries by the Mediterranean fishermen and repeated by many authors. His hypothesis was that the bluefin tuna lived in the Atlantic for most of the

year, but entered the Mediterranean in the spring, travelled along its northern shores to the Black Sea to spawn, then returned to the Atlantic, following the southern coasts of the Mediterranean, in the summer. Scientific findings in the sixteenth and seventeenth centuries, however, raised questions about this theory and from 1875 to 1925 most authorities believed that spawning bluefin did not pass through the Strait of Gibraltar in numbers. They felt that the Mediterranean bluefin tuna comprised an autochthonous population, which made only limited local movements to and from the spawning areas. Since 1925 evidence of migrations from the Atlantic into the Mediterranean has reopened the question.

A recent hypothesis (Sarà 1964, 1973) satisfies many of the arguments used by both sides in this debate. Sarà maintains that most of the large bluefin which spawned in the Mediterranean were migrants from the Atlantic and spent the rest of the year in that ocean, but that most of the medium sized and small fish which spawned in the Mediterranean had been born in that sea and had remained there until they attained about 150 kg. These problems are discussed in detail in Sections IV and VI.

b. Specific Occurrences

The first positive indication that bluefin tuna spawned in the Mediterranean was presented by Cetti (1777) from observations made along the coasts of Sardinia. He found eggs, which he believed to be those of bluefin tuna, on the ropes of the traps, and also in the water around the traps. He also stated that the ovarian eggs of fish taken in the traps in May were very well developed, but that those of fish taken in June had degenerated. He concluded tentatively that more large bluefin tuna spawned in the Mediterranean than in the Black Sea. Even though his data are questionable, in view of present knowledge, his conclusions were correct. His work eventually led to the first doubts about the Aristotelian theory.

This was followed by d'Amico's (1816) revelation that bluefin spawned off Sicily. He noted that juveniles of the species weighed about 42 g in June, 122 g in August and 840 g in October. These data and those of Sella (1929a) enabled Heldt (1930) to present the first growth curve for the early stages

of this species. Sanzo (1909, 1910b) described eggs taken from ripe bluefin caught off Sicily. Later Sanzo (1929, 1932) described pelagic eggs which he collected in the Strait of Messina in May and June, and larvae which were hatched from these eggs and reared for six days. Sanzo concluded that these were the eggs and larvae of bluefin tuna, because the eggs matched those taken from a ripe female, and the six-day-old larvae hatched from them matched the smallest of the identifiable bluefin tuna larvae which he had collected off Messina. More recently, however, several authors who have examined Mediterranean material have concluded that bluefin tuna eggs could not be identified positively unless they were hatched and the larvae were reared to an identifiable size (Piccinetti and Piccinetti Manfrin 1970, Duclerc et al. 1973, Scaccini et al. 1975). Collections of larger larvae and juveniles were also reported (Sella 1924, 1929a; Sparta 1933, Padoa 1956, Scaccini 1965, Piccinetti and Piccinetti Manfrin 1970). Although Sella (1924) explained the differences between juvenile *T. thynnus thynnus*, *T. alalunga* and *Auxis bisus*, these early collections were not thoroughly described or illustrated. Recently Scaccini (1961) and Scaccini et al. (1975) published a photograph of some of Sella's material and reproduced drawings of larvae 4-12 mm long prepared under his guidance as well as their own photographs of eggs, larvae and juveniles.

Watson identified and described, with illustrations, larval and juvenile bluefin from 11.4 to 37.8 mm long collected off Messina, Sicily, during the summer months of 1958, 1959 and 1960 (Watson and Mather 1961). These identifications, based on external characters (Sella 1924) and osteological characteristics examined by radiography, were subsequently verified by T.C. Potthoff (personal communication) of the Southeast Fisheries Center of the National Marine Fisheries Service, who examined additional vertebral characteristics after clearing and staining the specimens.

Many additional identifications of juvenile Mediterranean bluefin tuna were obtained after the Woods Hole Oceanographic Institution collection was donated to the Southeast Fisheries

Center of the National Marine Fisheries Service at Miami, Florida. T.C. Potthoff (personal communication) identified 60 of the specimens which had been collected in Sicilian waters during the months of July, August and September as *Thunnus thynnus thynnus*. The lengths and the dates and localities of capture of these specimens, which include the four largest ones reported by Watson and Mather (1961), are shown in Table 16.

The most numerous records of larval and juvenile bluefin tuna are from Sicilian waters, but these forms have been encountered in several other parts of the Mediterranean.

Roule (1917) cited Bourge's (1908) records which showed the apparent growth of juvenile bluefin collected off Tunisia. These young fish weighed about 150 g in August, attained 900 g in September, and exceeded 1 kg in October.

Richards (1976) reidentified two of Ehrenbaum's (1924) larval specimens, originally identified as "*Euthynnus alliteratus* Raf. (?)", taken near the Balearic Islands in late August 1910, as *Thunnus thynnus thynnus*. Roule (1917) had tentatively listed these islands as a spawning area for this species. In 1972 Duclerc et al. (1973) collected eight bluefin tuna larvae near the Balearic Islands between June 20 and July 7. They also collected pelagic eggs which fitted Sanzo's description of those of bluefin tuna, but, even after hatching some of these and raising the larvae for periods of up to four or five days, they were unable to distinguish eggs of *T. thynnus thynnus* from those of "*Auxis thazard*".

Dieuzeide (1951) listed the captures of three bluefin tuna larvae off the coast of Algeria June 7-8, 1940. He provided drawings of two of these, which were 5 and 6 mm long.

Table 16. Collection data and lengths of bluefin tuna from Sicilian waters. M.E. Watson originally identified most of the specimens. T.C. Potthoff subsequently confirmed her determinations and identified the remaining individuals.

Collection Area	
Collection Date	Standard Length (mm)
1. Straits of Messina	
July, 1949	17.4, 19.4, 24.9, 34.3, 36.8, 37.1
July 15 - Aug 31, 1958	33.7
July - August, 1959	30.5, 31.0, 31.0, 32.0, 34.2
June 30 - July 1, 1960	16.9
July 18 - 20, 1960	17.0, 17.7, 19.5, 22.5, 24.8, 25.1, 26.3, 26.9
July 24 - 25, 1960	17.7, 18.9, 20.9, 21.0, 25.9, 28.0, 28.9
July 26 - 27, 1960	32.4, 33.4, 34.5, 38.5
August 20 - 21, 1960	45.3, 50.4, 50.5
August - September, 1960	17.6
August 10 - 20, 1963	62.0, 64.6, 66.4, 71.3, 74.0, 76.1, 87.5, 99.6
Unknown	12.6, 15.5, 16.7
	16.9, 16.9, 17.1, 17.3, 18.7, 19.5, 20.1, 20.3, 20.5, 27.3, 30.4
2. Palermo	
August 1, 1963	107.8, 117.5

The Messina specimens were purchased by the Woods Hole Oceanographic Institution from G. Arena of Messina. The Palermo specimens were donated to the Institution by F. Tarantino of Dorchester, Massachusetts. All of the specimens were subsequently donated to the Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, Florida, and are now in its collection.

Recently, Piccinetti (1973), Piccinetti and Piccinetti Manfrin (1973), and Piccinetti et al. (1976b) reported on occurrences of larval and juvenile *Thunnus thynnus thynnus* in the Adriatic Sea, the first positive indication that the species reproduced there.

Richards (1976) thought that a larval specimen collected off Cape Matapan, Greece, on August 26, 1911, and originally identified by Ehrenbaum (1924) as "*Orcynus germo* Lacep. (?) " was probably *Thunnus thynnus thynnus*.

Richards agreed with Sella (1929a) that the specimens identified by Ehrenbaum (1924) as "*Orcynus thynnus* L. (?) " were not of that species.

Several scientists have reported on eggs and larvae of bluefin tuna collected in the Black Sea in mid and late summer. Vodyanitskii and Kazanova (1954) reported that eggs and larvae were encountered there repeatedly in the second half of the summer, but mainly in the beginning of August. Vodyanitskii (1936) and Oven (1959) described eggs found in the latter part of July and in early August, off Sevastopol and Karadag, respectively. Oven hatched some eggs and reared the larvae for up to eight days.

Many authors have presented indices of maturity for bluefin tuna taken in the Mediterranean traps; we cite those of Sarà (1964, 1973) because they are among the most recent. He found that the first maturing fish taken in the Sicilian "arrival" traps in early May had maturity indices of 70-60, whereas those taken toward the end of this fishery in mid June had indices of about 25. An index of about 40 was the most frequent within the entire period. The females were generally in a less advanced state of maturity than the males in this period. During the "return" run of presumably spent fish, the first captures, in early July, were of fully mature fish with indices of about 50. By late July, this had increased to 91, and in early August, to 198. This decrease in maturity was much more regular than the increase during the "arrival" run. Sella (1929a), as well as Scordia (1932) and Sarà (1973), noted that small maturing or ripe fish were sometimes taken in the Sicilian return traps, along with the spent large ones, in July and even in August. Sella and Sarà also pointed out that the "arrival" traps in Tripolitania

took relatively small maturing fish for a considerable period after the conclusion of the "arrival" fisheries for larger maturing individuals in the Italian and Tunisian traps.

Heldt (1938) summarized the results of Frade's histological studies of gonads of bluefin tuna taken in various Tunisian traps. Heldt had collected this material and furnished it to Frade. Frade concluded that, if this small sample was representative, the various groups of tuna which frequent the Mediterranean do not mature simultaneously. The fish taken off Tunisia were, in general, less mature than those taken in the eastern Atlantic at the same time.

Gonad studies related to the spawning of bluefin tuna in the Black Sea depended mainly on material collected near Istanbul, Turkey. Hovasse (1927), after analyzing statistics of landings at that city in 1915 and 1921-1923, found two significant maxima in the catches, one in the spring (March-April) and one in the summer (July). There was also a minor maximum, whose significance Hovasse did not understand, in the winter (December). He believed that the spring peak corresponded to a northward migration into the Black Sea and the summer one, to a southward passage back from the Black Sea into the Sea of Marmara. He found that the ovaries of the females taken in the spring were full, whereas those taken in July contained no eggs. Akyüz and Artüz (1957) stated that bluefin started to run through the Bosphorus into the Black Sea in April, and that this run peaked in July and ended in September. The return migration occurred from late October to November. Their studies of gonad condition indicated that spawning occurred in late July, August, and possibly September. İyigüngör (1957), however, listed three periods of passage: November-January, March-April, and July-autumn. Thus there are considerable differences in the interpretations of the catch records in regard to migrations and spawning.

The above research shows clearly that spawning in the Mediterranean by large bluefin tuna starts about mid-June and ends about mid-July. The reproduction of the smaller (the medium-sized and some of the larger "small" individuals) fish has not been investigated as thoroughly. The available evi-

dence indicates that they begin to spawn later than the large ones, and that their spawning extends through July well into August, and sometimes even into September. This information is based mainly on observations made in the south-central Mediterranean. The spawning periods in other parts of the Mediterranean and in the Black Sea, are not as clearly defined. Reproduction off the Balearic Islands evidently extends from mid-June at least to late August. Collections of eggs and larvae indicate that spawning in the Black Sea is at its maximum in the second half of July and early August, but conclusions based on catch records and gonad condition are inconsistent.

The most completely documented bluefin tuna spawning areas in the Mediterranean are off northeastern and western Sicily, and off the Balearic Islands. Another apparently well documented area is in the Black Sea. There are also strong indications of spawning off western Sardinia, northern Tunisia, and Tripolitania. More fragmentary data suggest reproduction in the Adriatic Sea, off Algeria and Greece, and in the Aegean Sea. Scaccini et al. (1975) concluded that additional intensive research will show that the spawning areas of *T. thynnus thynnus* cover much more of the Mediterranean than was then believed.

2. Eastern and Central North Atlantic and the South Atlantic

a. General Information

Many experts have assumed that the Ibero-Moroccan Bay (west of Gibraltar) contains the major, or the only, spawning grounds for *T. thynnus thynnus* in the eastern Atlantic. Extensive research in this area, dating from the late nineteenth century, has produced much information on the condition of the gonads of the bluefin tuna taken in the once flourishing trap fisheries in this bay. As noted in Section IV, this fishery was divided into two periods, the "arrival" (late April, May and June) and the "return" (July and August). During the "arrival" period, the fish are apparently travelling along both coasts of the bay in the general direction of the Strait of Gibraltar. In the "return" fishery, which occurs only along the Iberian coast, they seem to be travelling westward. The "arrival" traps

which have been used within recent years were distributed from Cabo de Santa Maria in Portugal to Tarifa, Spain, and along the Moroccan coast from Kenitra to Cape Spartel, Morocco (Figure 44). It should be noted that the two latter localities are at the very entrance of the Strait of Gibraltar. Some of the Portuguese and Spanish traps were rearranged at the end of June to fish in the "return" period.

The gonad studies showed that the "arrival" fish were maturing and that their indices of maturity became lower (indicating more advanced maturity) as the season progressed. On the other hand, the "return" fish were generally spent, with their indices of maturity increasing (indicating shrinking of the gonads) toward the end of the season. Since the more mature ovaries were an important by-product of the fishery (F. de Buen 1928), these facts were known to the fishermen for centuries before the scientists arrived on the scene. In fact, they may have played a role in the development of Aristotle's migratory theory.

This simple combination of circumstances was interpreted in opposite ways by the proponents of the "Atlantic-Mediterranean migration" or "migratory" theory and the advocates of "separate Atlantic and Mediterranean populations" or "sedentary" theory. The former maintained that these facts indicated that many of the "arrival" tuna entered the Mediterranean to spawn, and that the "return" run included many individuals which had spawned in the Mediterranean and were returning to feeding areas in the Atlantic. The latter believed that few, if any, of the "arrival" fish passed through the Strait of Gibraltar and that most of them spawned in the Ibero-Moroccan Bay.

Despite the many decades of intensive research on bluefin tuna in the area, however, no identifiable eggs, larvae or juveniles (as defined here) of bluefin tuna have been collected in the Ibero-Moroccan Bay.

In addition to the gonad studies, a great deal of other biological information pertinent to the possible spawning of the species in this area has been published. Extensive data on the properties of the environment are also available.

Evidence of reproduction of the species in other parts of the eastern Atlantic, and in the central and the South Atlantic (Figure 65), is very meager. Some larvae have been collected in the eastern equatorial Atlantic. A few occurrences of ripe bluefin in the Bay of Biscay have been reported. Spawning in the vicinity of the Azores has been suggested. A spawning area between Lanzarote, one of the Canary Islands, Conception Bank, and the Moroccan coast has been hypothesized, but not investigated.

b. Specific Occurrences

From numerous studies of the condition of the gonads of bluefin tuna caught in the Ibero-Moroccan Bay, we have selected for discussion those of Frade and Manaças (1933) and Frade (1937a) for Portugal, F. de Buen (1927) and Rodríguez-Roda (1964a) for Spain, and Lozano Cabo (1957, 1958) and Furnestin and Dardignac (1962) for Morocco.

Frade and Manaças (1933) presented one of the few histological studies on the stages of maturity of the gonads of bluefin tuna which are available. Their observations confirmed the fractional nature of the spawning of the species. This accounts for the lack of completely ripe fish in the traps, because all the eggs destined to be emitted in a given season do not mature simultaneously. A large number of the individuals entering the traps in the "arrival" period may have already emitted part of their spawning products. In addition the small bluefin 1 m long (about 3 years of age) behave differently according to their sex. The males are in active or terminated spermatogenesis, whereas the females are in very retarded ovulation.

Later Frade (1937a) described a simple method for determining stages of maturity consistent with the absolute ones established by his histological studies (Frade and Manaças 1933). To offset the effect of seasonal variations in the length-weight ratio, his index of maturity was the quotient of the weight of the head, rather than the total weight of the fish, divided by the weight of the ovaries. He also used a factor K (the ratio of the weight of ovaries to the weight of testes at the same stage, as determined by histological studies, usu-

ally about 1.5, to make the indices for males comparable to those for females at the same stage of maturity. Even though these corrections did not prevent the occurrence of similar indices, in the intermediate stages, for pre-spawning and post-spawning fish, he felt that this procedure clearly showed the progressive emptying of the gonads, or the fractional emission of the spawning products. His stages are shown in Table 17.

Frade (1937a) presented the indices obtained for 171 bluefin tuna examined at Vila Real de Santo Antonio, Portugal, from May 31 to August 18, 1933 (Table 18). These same values are shown graphically in Figure 66. Frade reached the following conclusions:

- 1) Ripe and intermediate stages (A-D) of both sexes are represented in June, but in decreasing frequencies.
- 2) In July intermediate stages (C and E) predominate among the females, and in the males, late intermediate and spent stages (E and F) appear.
- 3) In August intermediate stages (D and E) are predominant for the females while ripe and intermediate stages (B and C) are still predominant among the males. Some fish of both sexes have attained the fully spent stage (G) and females in the fully ripe stage (A) have disappeared from the catches.

F. de Buen (1927) noted that bluefin tuna which had arrived to spawn were caught in the southern Spanish Atlantic traps in April, May and June, and that they also entered these traps beginning in July, after spawning. After examining a large number of specimens from these traps in 1923, he concluded from the data that in 1923 the bluefin spawned in the Ibero-Moroccan Bay in the months of June and July, and that the males had attained sexual maturity before the females (Table 19).

In one of his major works on the biology of the bluefin tuna taken in the traps off the southern coast of Spain, Rodríguez-Roda (1964a) provided much information on the variations in gonad condition through the spawning season. He set up the following scale

Figure 65. Bluefin spawning areas in the Eastern Atlantic and the Mediterranean and Black Seas.

for stages of maturity, based on the color of the ovaries:

- I. Immature: Gonads of rosy color.
- II. Prematuration: Male gonads of a violaceous color, and female of a rose color.
- III. Maturation: Male gonads of a rose or a rosaceous white color, and female yellow rose or yellowish.
- IV. Prespawning: Male gonads of a milky violaceous color.
- V. Spawning.
- VI. Postspawning: The male and female gonads are of a violet color.

Very swollen ovaries with most of the eggs transparent were considered to be in stage V. Only one such female was observed during the "return" pe-

riod and it was concluded that its oviduct was probably obstructed.

During the "arrival" run in May and June the bluefin tuna appeared with turgid gonads in a state of prematuration or maturation and in the "return", in July and August, the gonads were already flaccid and with obvious signs of having emitted the eggs. Between these two phases, at the end of June and early in July, when spawning should actually occur, the bluefin disappeared from the coast and its captures were very limited.

To define the spawning period, the monthly percentages of the sexual stages for 779 males and females examined at the Barbate trap from 1956 to 1959 are shown in **Table 20**.

The majority of the fish were in a prespawning state (stage III) in May and June and in the post-spawning stage (stage VI) in July and August. The small percentage of tuna of both sexes

which were in stages I and II were not large individuals. Those in stage I in June were 95 and 80 cm long, respectively. Those of both sexes in stage II were 115 to 140 cm long, excepting two females 170 and 175 cm long. In July and August a few bluefin were in the prespawning state. One male 135 cm long was in stage II in July. Males and females from 125 to 220 cm long in July, and 125 to 135 cm long in August, were in stage III. The only specimen in stage IV was a male 170 cm long taken in June.

Rodríguez-Roda (1964a) also used an index of maturity, the "gonosomatic relation", equal to 100 times the ratio of the weight of the gonads to the total weight of the fish, to evaluate relative fecundity. He also provided plots and formulae showing the relationships between the weight of the gonads and the fork length of the fish for bluefin tuna during the "arrival" and "return" periods.

He tabulated the gonosomatic relation for males and females, by 5-cm length groups and 10-day periods, for 260 "arrival" and "return" fish examined in 1956, and also for 198 examined in 1958 (**Tables 21a and 21b**).

This index generally increased with size of fish. Its mean value also increased during the "arrival" period in June, for both sexes, then descended abruptly in the months of July and August, in the "return" period. All this confirmed spawning in early July. In general, the index was higher for females than for males.

The condition of the gonads of bluefin tuna taken off the Atlantic coast of Morocco was examined by Lozano Cabo (1957, 1958) and Furnestin and Dardignac (1962). Lozano Cabo (1958) tabulated, by sex and 10-day period, the minimum, mean, and maximum indices of maturity of samples of bluefin tuna taken in 1955 by the trap at Los Cenizosos (near Larache) in 1955 (**Table 22**).

The mean index for females decreased from 80.8 in the last ten days of May to values between 46.2 and 40.0 in the three ten day periods in June. In the second ten days of May a few females with very low maturity (indices averaging 105.3) were examined. When these fish were being taken, the catch was very small. The fishery did not

Table 17. Indices of maturity and condition of gonads (Fraide 1937a).

Stage	Indices of Maturity		Condition of Gonads
	Female	Male	
A	Up to 7	Up to 10.5	Full
B	7 - 12	10.5 - 18.0	"
C	12 - 17	18.0 - 25.5	"
D	17 - 22	25.5 - 33.0	Intermediate
E	22 - 27	33.0 - 40.5	"
F	27 - 32	40.5 - 48.0	Empty
G	32 - 37	48.0 - 55.5	"

Table 18. Stages of maturity for 171 bluefin tuna examined at Vila Real de Santo Antonio, Portugal, May 31-August 18, 1933 (Fraide 1937a).**FEMALES**

	A	B	C	D	E	F	G	
29 Tuna	13	11	4	1	—	—	—	May 31-June 5
%	45	38	14	3	—	—	—	
21 Tuna	3	5	7	4	2	—	—	
%	14	24	33	19	10	—	—	July 7-18
54 Tuna	—	3	10	15	14	6	6	
%	—	6	19	28	26	11	11	August 5-18

MALES

	A	B	C	D	E	F	G	
16 Tuna	9	3	2	2	—	—	—	May 31-June 5
%	56	19	13	13	—	—	—	
17 Tuna	3	8	4	—	1	1	—	July 7-18
%	18	47	24	—	6	6	—	
34 Tuna	1	8	9	4	6	3	3	August 5-18
%	3	24	26	12	18	9	9

Figure 66. Plot showing the changes in sexual maturity of Atlantic bluefin tuna by month. The data are the same as in Table 18.

become productive until the index reached 63.6 (Lozano Cabo 1957). The maturity of the females decreased slightly (index rising from 40.0 to 43.9) from the second to the third ten days of June. This was caused by the capture of some spent, post-spawning, or "return" fish in this "arrival" trap. The only indices for males, taken in the last ten days of May, ranged from 42.7 to 131.2, with a mean of 76.8. These figures do not differ greatly from those for females taken in the same period.

Furnestin and Dardignac (1962) tabulated the mean "gonado-somatic indices" (evidently the "gonosomatic relation" of Rodríguez-Roda 1964a) for males and females taken in the trap at Moulay-bou-Selham (near Kenitra) in the first and second halves of May and the first half of June (Table 23).

The indices for males increased rather regularly from 1.10 in the first half of May to 2.04 in the first half of June. Those of the females followed a similar trend, from 1.52 to 1.99 over the same period. These values showed a more consistent increase in maturity through the season than those of Lozano Cabo (1958). Furnestin and Dardignac (1962) also plotted the gonado-somatic indices for each sex against the length of fish. Those for females increased with length, but those for males only increased up to a length of 210 cm and decreased slightly in longer individuals. The authors attributed this to the fact that the largest fish were caught at the beginning of the season, when their maturity would normally have been less advanced. The maturity of the fish taken in the first half of June at Moulay-bou-Selham is generally comparable to that found by Rodríguez-Roda (1964a) for fish taken at Barbate, Spain, in the first twenty days of June. Lozano Cabo (1958), however, reported that the bluefin tuna which he examined at Los Cenizosos were less mature than those which he had examined at Barbate.

There is strong circumstantial evidence that bluefin tuna spawn in the Ibero-Moroccan Bay, but conclusive proof of this is lacking. Great numbers of maturing individuals occur there in May and June, and recently spent fish are abundant in July and August. The stages of maturity of these fish have been verified by many investigations. On the other hand, much research and

Table 19. Bluefin maturity by month from the trap fishery along the southern Atlantic coast of Spain (F. de Buen 1927).

Month	Males			Females		
	% Not	% Fully	% Spent	% Not	% Fully	% Spent
	Mature	Mature		Mature	Mature	
May	100	0%	0	100	0	0
June	32	60	8	67	30	3
July	1	33	66	26	12	62
August (beg.)	0	0	100	0	0	100

two intensive surveys have failed to produce a single identifiable egg or early stage (less than 10 cm long) of the species from the area.

O. de Buen (1924) and F. de Buen (1924, 1925, 1927) failed to find any eggs or early stages of bluefin tuna during their intensive 1923 survey of the Ibero-Moroccan Bay, west of Gibraltar, and the Alboran Sea, east of it. They explained this apparent contradiction of their theory that the Ibero-Moroccan Bay was a major spawning ground for bluefin tuna, and that the maturing fish did not enter the Mediterranean to spawn, as follows. The bluefin spawned in this Bay, but the eggs and larvae were carried from it by the surface (Atlantic) current into the Mediterranean before they attained full mobility. There they accumulated off the Moroccan coast between Punta Almina and Cape Tres Forcas, where the rich plankton provided food for the early stages. Roule's (1923) contrary view, that bluefin larvae were abyssal and were passively transported from the Mediterranean into the Atlantic by the deep outflowing (Mediterranean) current will be discussed in Section VE2. More recently, Spanish scientists in the research vessel "Cornide de

Saavedra" conducted an intensive planktonic and hydrographic survey of the waters east and west of Gibraltar in 1972. The period of the survey, 19 June-16 July, was chosen because this was regarded as the period of maximum spawning of bluefin tuna in the area (Rodríguez-Roda 1975). During this cruise 66 stations were occupied in the Atlantic, four in the Strait of Gibraltar, and 82 in the Mediterranean (Rodríguez-Roda 1975). No identifiable larval or juvenile bluefin tuna were collected.

Until eggs or early stages collected in the Ibero-Moroccan Bay are positively identified as those of bluefin tuna, this area must be regarded as only a hypothetical spawning area for this species.

F. de Buen (1937) proposed a second spawning area for the eastern Atlantic bluefin in the southeastern corner of the Bay of Biscay. This hypothesis was based on reports of bluefin with ripe ovaries being taken there in June. Le Gall (1952) reported similar findings there during the 1950 and 1951 seasons. Creac'h (1952) described the sizes of bluefin tuna landed at Saint-Jean-de-Luz through the 1951 season (April 12-October 26) and the condi-

tion of their gonads. The ovaries of very few specimens among the bluefin landed in the period June 16-30 were ripe. The fish landed in this period were in the 15-25 kg weight range. Creac'h (1952) noted that a similar situation had been observed for the first time, in about the same period, during the 1950 season. No observations of mature fish during the remainder of the season were reported.

Cort et al. (1976) and Cort (1977) provided the first detailed information on the gonads of maturing bluefin taken in the Bay of Biscay. These authors examined four bluefin 125-149 cm long taken in the Bay of Biscay June 25-26, 1976, and seven 111 to 161 cm long taken there on July 15, 1976. On the basis of color (Rodríguez-Roda 1964a), they estimated that the two males in the first group were fully mature, whereas one female was in pre-spawning condition and the other specimen was spent. They classified three females in the second group as pre-spawning and two as spent, and considered one male to be fully mature and the other spent.

Cort et al. (1976), using the technique of Rodríguez-Roda (1967), measured the diameters of eggs from two females, 148 and 152 cm long, of the second group. The diameters for the 148 cm specimen ranged from 0.10 to 0.66 mm, with many from 0.22 to 0.58 mm and the highest mode at 0.50 mm. Those from the other ranged from 0.14 to 0.58 mm, with most between 0.30 and 0.53 mm and a wide mode between 0.40 and 0.46 mm. They classified these fish as in stage IV (pre-spawning) or between stage III (maturation) and stage IV, since the diameters were greater than those of the ova and oocytes of the specimens placed by Rodríguez-Roda (1967) in stage III. Cort (1977) noted that these observa-

Table 20. Monthly percentage of the sexual stages (years 1956-1959) of tuna at Barbate (Rodríguez-Roda 1964a).

Month	Sexual Stages of Males. Number = 284						Sexual Stages of Females. Number = 495					
	I	II	III	IV	V	VI	I	II	III	IV	V	VI
May	—	—	100.00	—	—	—	—	—	100.00	—	—	—
June	0.62	3.09	95.06	—	—	1.23	0.41	3.26	96.33	—	—	—
July	—	1.85	5.55	1.85	—	90.74	—	—	9.46	—	—	90.54
August	—	—	3.17	—	—	96.82	—	—	1.06	—	—	98.94

Table 21a. Variation of gonosomatic relation* with length of fish and period of capture for male and female bluefin tuna taken in the Barbate trap in 1956 (Rodríguez-Roda 1964a).

Fork Length:	95-99.5	100-104.5	105-109.5	110-114.5	115-119.5	120-124.5	125-129.5	130-134.5	135-139.5
Males (Arrivals)									
June 1-10	0.11	-	-	-	-	0.55	-	-	-
June 11-20	-	-	-	-	-	-	-	1.44	-
June 21-30	-	-	-	-	-	-	-	-	1.37
Males (Returns)									
July 10-20	-	-	-	-	-	-	-	-	-
July 20-30	-	-	-	-	-	-	-	-	0.33
Females (Arrivals)									
June 1-10	-	-	-	-	-	-	-	1.44	0.93
June 11-20	-	-	-	-	1.14	-	-	1.55	1.19
June 21-30	-	-	-	-	-	-	-	-	1.16
Females (Returns)									
July 10-20	-	-	-	-	-	-	-	-	-
July 20-30	-	-	-	-	-	-	-	-	0.51
Fork Length:	140-144.5	145-149.5	150-154.5	155-159.5	160-164.5	165-169.5	170-174.5	175-179.5	180-184.5
Males (Arrivals)									
June 1-10	1.30	-	-	1.35	1.89	-	1.21	-	-
June 11-20	1.28	-	-	-	1.66	0.80	1.19	1.18	2.28
June 21-30	0.96	-	-	-	-	2.00	0.97	-	-
Males (Returns)									
July 10-20	-	-	-	-	-	-	0.69	0.71	-
July 20-30	-	-	-	-	1.00	0.54	0.84	-	0.51
Females (Arrivals)									
June 1-10	1.36	0.80	1.39	-	1.46	1.18	0.96	-	-
June 11-20	1.38	1.71	1.33	2.03	1.09	1.38	1.33	2.50	1.41
June 21-30	-	-	-	1.90	-	1.71	-	-	-
Females (Returns)									
July 10-20	-	-	-	0.98	-	1.07	0.84	-	-
July 20-30	0.73	0.80	-	0.74	0.69	0.78	0.75	0.79	0.82
Fork Length:	185-189.5	190-194.5	195-199.5	200-204.5	205-209.5	210-214.5	215-219.5	n	Mean
Males (Arrivals)									
June 1-10	-	1.37	1.62	1.13	1.45	1.91	-	20	1.31
June 11-20	-	1.43	2.48	1.71	2.28	-	1.22	22	1.48
June 21-30	-	1.22	2.57	1.96	-	-	1.31	10	1.63
Males (Returns)									
July 10-20	-	1.17	0.69	-	-	-	-	5	0.89
July 20-30	0.63	0.44	-	0.57	0.66	-	-	16	0.63
Females (Arrivals)									
June 1-10	1.80	1.53	1.25	2.06	1.14	1.71	1.83	37	1.53
June 11-20	-	1.85	1.01	2.34	1.69	-	1.55	36	1.51
June 21-30	1.54	2.02	2.07	-	-	1.24	-	24	1.73
Females (Returns)									
July 10-20	1.03	1.06	0.94	0.93	0.79	0.82	-	26	0.92
July 20-30	0.76	0.82	0.75	0.79	0.85	-	-	64	0.77

*Maturity index obtained by multiplying the ratio of the weight of the gonads to the total weight of the fish by 100 (Rodríguez-Roda 1964a).

Table 21b. Variation of gonosomatic relation* with length of fish and period of capture for male and female bluefin tuna taken in the Barbate trap in 1958 (Rodríguez-Roda 1964a).

Fork Length:	120-124.5	125-129.5	130-134.5	135-139.5	140-144.5	145-149.5	150-154.5	155-159.5	160-164.5		
Males (Arrivals)											
June 1-10	-	2.67	-	1.90	1.48	1.54	1.29	1.63	-		
June 11-20	-	-	-	2.58	1.92	-	-	-	1.39		
June 21-30	-	-	-	-	-	-	-	-	-		
Males (Returns)											
July 20-20	-	-	-	-	-	-	-	0.87	-		
Aug 1-10	-	-	-	-	-	-	0.60	0.52	-	-	
Females (Arrivals)											
June 1-10	0.95	-	1.54	1.04	2.47	1.25	0.72	2.13	2.02		
June 11-20	-	-	-	1.10	1.78	1.70	1.26	1.40	1.62		
June 21-30	-	-	-	-	-	-	-	-	-		
Females (Returns)											
July 20-30	-	-	-	-	-	0.77	-	-	1.04		
Aug 1-10	-	-	0.77	-	-	-	0.81	0.69	0.80		
Fork Length:	165-169.5	170-174.5	175-179.5	180-184.5	185-189.5	190-194.5	195-199.5	200-204.5	205-209.5		
Males (Arrivals)											
June 1-10	-	1.32	1.30	2.41	1.69	-	1.38	1.22	-		
June 11-20	-	2.02	-	-	-	1.73	2.06	1.87	1.86		
June 21-30	-	-	-	-	-	-	-	-	-		
Males (Returns)											
July 20-30	1.10	-	-	-	0.80	0.63	-	-	-		
Aug 1-10	0.66	1.00	0.68	0.55	-	-	0.81	0.44	0.60		
Females (Arrivals)											
June 1-10	2.14	1.95	-	1.50	2.13	1.46	1.33	1.60	1.00		
June 11-20	1.37	1.64	1.34	1.75	2.05	1.75	1.53	-	3.14		
June 21-30	-	-	-	-	-	-	-	-	-		
Females (Returns)											
July 20-30	-	1.18	0.90	1.19	1.00	1.16	-	-	-		
Aug 1-10	0.67	0.80	0.92	-	0.84	0.69	0.88	-	-		
Fork Length:	210-214.5	215-219.5	220-224.5	225-229.5	230-234.5	235-239.5	240-244.5	245-249.5	250-254.5	n	Mean
Males (Arrivals)											
June 1-10	2.51	2.13	1.30	-	1.99	-	-	-	-	31	1.73
June 11-20	1.07	2.25	1.73	-	-	-	-	-	-	15	1.91
June 21-30	-	2.64	2.76	-	-	-	-	-	3.06	6	2.87
Males (Returns)											
July 20-30	-	-	0.64	0.90	0.72	-	0.47	0.61	-	12	0.72
Aug 1-10	0.42	-	-	-	-	-	0.48	0.47	-	13	0.59
Females (Arrivals)											
June 1-10	1.98	1.89	2.11	-	-	-	-	-	-	41	1.65
June 11-20	2.49	2.47	-	2.17	-	-	-	-	-	38	1.68
June 21-30	-	-	-	-	1.94	-	-	-	-	1	1.94
Females (Returns)											
July 20-30	-	0.72	0.74	0.89	0.94	-	-	-	-	17	0.96
Aug 1-10	-	-	-	-	-	-	-	-	-	23	0.89

*Maturity index obtained by multiplying the ratio of the weight of the gonads to the total weight of the fish by 100 (Rodríguez-Roda 1964a).

Table 22. Indices* of maturity for 140** bluefin tuna taken in the Los Cenizosos trap (near Larache, Morocco) in May and June 1955 by sex and 10-day period (Lozano Cabo 1958).

Month	Indices for Females			Indices for Males		
	Min.	Avg.	Max.	Min.	Avg.	Max.
May 20-30	37.1	80.8	142.8	42.7	76.8	131.2
June 1-10	25.4	46.2	62.7	—	—	—
June 11-20	30.0	40.0	52.0	—	—	—
June 21-30	—	43.9	—	—	—	—

* The index of maturity is the ratio of the total weight of the fish to the weight of its gonads.

** Seventy-six were examined individually in the first three periods. The index for the last period was obtained by dividing the total weight of 64 fish by the total weight of their ovaries

tions were too few to be conclusive, but hoped that future research might determine the possible existence of a bluefin spawning ground in the Bay of Biscay.

Aloncle (1964) found that many 30-60 kg bluefin wintered between the Canary Islands and Morocco and hypothesized that one group of them spawned between Lanzarote Island (Canaries), Conception Bank, and the Moroccan coast. Distributional data support this hypothesis, but studies of gonad condition and collections of eggs and early stages are required to verify it.

Ferreira (1932) reported that ripe bluefin were sometimes landed in the Azores in spring, but his statistics indicated that the species was not abundant there.

The only reports of larval bluefin taken in the eastern Atlantic are from equatorial waters off Africa. Fourteen small larvae (mostly 2.5-4.5 mm long) were taken in the area bounded by latitudes 6°N and 8°S and longitudes 0° and 15°30'W. One of these was collected in February, eight in March and five in August (Richards 1969, Richards and Simmons 1971, unpublished NMFS data reports for *Geronimo* cruises 3, 4 and 5). The surveys in which these collections were made were carried out in the periods February-April and August-October, missing most of the period in which the eastern

Atlantic bluefin are believed to spawn. The oceanic distribution of bluefin tuna (Wise and Davis 1973) in the first quarter of the year shows concentrations of bluefin near where these larvae were found, but the distribution in the third quarter does not. It would be desirable to conduct a survey in this area in the second quarter, and also to examine the gonads of bluefin caught there in the months of February through August.

Much remains to be learned about the spawning of bluefin in the eastern Atlantic, and about the possible role of the Mediterranean, both as a spawning ground and a nursery area for bluefin tuna from the eastern Atlantic. The degree of mixing of adults and new-born

Atlantic and Mediterranean tuna, if they are indeed separate, is another important matter about which there is no quantitative information. In view of the possible passive transport of spawning products from the Ibero-Moroccan Bay into the Mediterranean, the technique of collecting pelagic eggs, hatching them, and rearing the larvae to identifiable size appears to be the most promising approach to solving the important problem of whether bluefin tuna actually spawn there. The failure to find identifiable eggs or early stages of bluefin in the Alboran Sea (westernmost Mediterranean) as well as in the Ibero-Moroccan Bay during the 1923 and 1972 surveys, however, does not support the theory of passive drift of spawn from the latter area to the former.

3. Western North Atlantic

a. General Information

Important information on the spawning of *Thunnus thynnus thynnus* in the western North Atlantic has been obtained through collections of larvae and juveniles. Ripe or nearly ripe fish have been captured over extensive additional areas.

The great majority of the captures of larvae and juveniles have occurred in the Gulf of Mexico and the Straits of Florida. Scattered occurrences farther north include one larva east of northern Florida and seven juveniles (17.5-33.2 mm SL) off the Carolinas, Maryland and New Jersey (Figure 67).

Occurrences of ripe or nearly ripe fish have spread over some additional

Table 23. Variations in the mean gonado-somatic indices^a of bluefin tuna^b taken in the trap at Moulay-bou-Selham (near Kenitra, Morocco) in May and June, 1955 (Fumestini and Dardignac 1962).

Sex	May 1-15	May 16-31	June 1-15
Males	1.10 (n = 21)	1.25 (n = 9)	2.04 (n = 75)
Females	1.52 (n = 8)	1.42 (n = 18)	1.99 (n = 91)

^aThe gonado-somatic index is 100 times the ratio of the weight of the gonads to the total weight of the fish. ^bThe term n is the number of fish in each sample.

areas. They include several medium-sized (32-125 kg) bluefin as well as a few larger individuals, in the area bounded by latitudes 37°30'N to 40°30'N and longitudes 66°20'W to 70°00'W, well north of nearly all of the recorded captures of larvae and small juveniles in the western North Atlantic. Nearly ripe large bluefin tuna have also been encountered in the northwestern Caribbean Sea and northeast of the Bahamas, where no larvae or small juveniles have yet been found.

The capture of larvae depends not only on their abundance but also on the intensity and seasons of the collecting effort. Additional planktonic surveys in the proper seasons would probably have extended the areas of known occurrences of larvae and small juveniles considerably.

b. Specific Occurrences

The most numerous and widespread collections of larval and juvenile bluefin tuna from the western North Atlantic area were taken in the Gulf of Mexico. During extensive ichthyoplankton surveys of the Gulf by the Centro de Investigaciones Pesqueras of Cuba in April to May 1973, and in May to June 1974, numerous bluefin tuna larvae were taken over extensive

areas (Juárez, M. 1974b, Montolio and Juárez, M. 1977) (Figure 68). The relative abundance of larvae per 100 m² was calculated by the formula:

$$NT/V \times 100$$

where:

N is the number of larvae per tow,

T is the depth of the thermocline and

V is the volume of water filtered in m³.

In the 1973 cruise, which covered the eastern half of the Gulf, larvae were taken in varying numbers at 13 of the 46 stations which were occupied (Juárez 1974a, 1974b). Most of the larvae were captured in the north central Gulf at 11 stations within the area bounded by latitudes 25°N and 30° N and longitudes 87°W and 91°W. Others were taken at a station at about 26°N latitude and 84°30'W longitude, and another at about 24°N latitude and 88°W longitude.

The April to May collection data indicated relative abundances of bluefin larvae of up to 2,000 per 100 m².

Relative abundance of larvae (number per 100 m² of sea surface) were 2,000 for one station, 649 at an-

other, 101 to 331 at three stations, and 100 or less at eight stations. No bluefin were captured at the other 33 stations. The estimated number of larval *T. thynnus thynnus* in the area, on the basis of Juárez's (1974b) data, was 31,442 X 10⁵ (Richards 1976). Bluefin tuna constituted 24.6 percent of all of the larvae of the family Scombridae collected during this cruise (Juárez 1974b).

Bluefin tuna larvae were much more available during the May to June 1974, cruise, which sampled nearly all of the deep (over 200 m) waters of the Gulf. Larvae of this species were collected at 23 of the 61 stations occupied (Montolio and Juárez 1977). All of the successful stations were between latitudes 23° and 28°30'N, and longitudes 84°30' and 94° 30'W. Nearly all of them were between 40 and 140 nautical miles (74 and 140 km) from the 200 m contour. Five stations yielded more than 1,000 bluefin per 100 m² each. These stations were rather scattered, with one at 24°N, 87°W, another at 28°N, 87°W, one at 27°30'N, 90°W, and two near 26°N, 94°30'W. From 501 to 1,000 per 100 m² *T. thynnus thynnus* larvae were taken at five stations well spread over the area. Ten stations produced 101-500 per 100 m², and only two of the successful stations yielded 100 or less. Results at one positive station were not reported. No bluefin larvae were collected at the 38 remaining stations. The larvae of *T. thynnus thynnus* constituted 47.7 percent of all of the larvae of the family Scombridae which were collected during this cruise (Montolio and Jaurez 1977).

The May to June 1974 cruise showed that the spawning of bluefin extended over much of the deep water of the Gulf of Mexico north of 23°N latitude in that period. Comparisons with the results of the April to May 1973 cruise suggest that bluefin tuna larvae are much more available in the Gulf in May and June than in April and May, and consequently that spawning is more intense in June than in April. This is in agreement with other available indications, but this comparison might have been biased by better spawning success in one year than the other.

"Numerous" bluefin tuna larvae 4.2-10.2 mm SL were collected at

Figure 67. Collection locations for larval and juvenile bluefin tuna in the western North Atlantic.

23°50'N latitude, 88°40'W longitude on May 17, 1972 (Juárez 1972). Considerable quantities of these larvae were also collected near this location in the subsequent surveys of April to May 1973 and May to June 1974.

T.C. Potthoff (personal communication) reported the collection of one larval *T. thynnus thynnus* 5.5 mm SL June 29, 1969, and four larvae 3.6-4.2 mm SL on July 6, 1969, in the northern Gulf of Mexico near 29°N latitude and 87°W longitude. Thus, these were captured near the northeastern boundary of the area where Juárez (1974) and Montolio and Juárez (1977) took most of their specimens, but the dates of capture extend the time of occurrence of the bluefin tuna larvae in the Gulf of Mexico into July.

Richards (1977) provided additional data on occurrences of bluefin tuna larvae in the Gulf of Mexico. Nineteen larvae ranging from 3.9 to 7.4 mm SL were collected near 27°N latitude, 96°W longitude, on May 6, 1975, and May 30-June 6, 1976.

Another important series of collections of bluefin larvae was made off Miami, Florida, with surface tows (from 1969 to 1971) and on a transect from Miami to Bimini, Bahamas, with surface tows and oblique tows to 200 m depth (in 1975) (Richards 1976). The cumulative numbers of surface tows and captures of larval bluefin tuna are listed by half-month periods in Table 24. In total, 93 tows were made, and 164 identifiable bluefin tuna larvae of 3.3 to 7.2 mm SL were collected, an average of 1.8 larvae per tow. The tows extended over a period from April 2 to July 8, but bluefin larvae were taken between April 22 and June 26 only. The number of larvae per tow was only 0.1 in the second half of April, but rose to 1.8 to 3.5 in the half month periods of May and June, with maxima in the first half of May and the last half of June.

During the transects in 1975, 39 larvae 3.4-7.3 mm SL were collected in 61 surface tows at five stations, and 23 were collected in 47 oblique tows at

four stations (oblique tows at station number 1 near the Miami harbor entrance buoy were omitted because the depth of the water was insufficient). The catch rates in numbers of larvae per tow (both types combined) were maximum, 0.8 and 0.6, at stations 2 and 3. Lower catch rates, 0.1 and 0.2, were obtained at stations 1 and 4, and no larvae at all were caught at station 5 on the Bahamas side of the Straits. This distribution is rather surprising, as large bluefin tuna are observed and caught in considerable numbers along the edge of the Great Bahama Bank near Bimini in May and June but are a rarity on the Florida side (Rivas 1954, Mather 1963a). A single larva (8 mm SL) collected off St. Augustine, northeastern Florida, (Figure 67) in May 1968 (T.C. Potthoff, personal communication) completes our knowledge of the distribution of bluefin tuna larvae in the western North Atlantic system.

The known range of small juvenile (12-120 mm SL) bluefin tuna includes much of that covered by the larvae, but extends considerably farther north (Figure 67). Rivas (1954) collected a 45 mm SL juvenile off Miami on June 9, 1953. Potthoff and Richards (1970) identified 40 juvenile bluefin 22-118 mm long which had been regurgitated by terns during a tern-banding operation at the Dry Tortugas, Florida, in June and the first half of July 1960-1967. None were found in May, although juveniles of other scombrids were collected. No scombrids less than 20 mm long were collected in this manner. Twenty additional juvenile bluefin in the same general size range and season have been obtained from terns at the Dry Tortugas subsequent to the 1970 publication (T.C. Potthoff, personal communication). T.C. Potthoff (personal communication) also informed us of five juvenile bluefin 22-33 mm long collected in the Gulf of Mexico in late May and early June, and four others, 16-21 mm long collected off the Carolinas in May. A most surprising record, also provided by Potthoff, was of a 17.1 mm SL juvenile collected off Mobile, Alabama, on August 19, 1954. This specimen must have been spawned long after adult bluefin have usually left the Gulf, and also in a month when the extensive Cuban ichthyoplankton survey in 1973

Figure 68. Bluefin tuna larvae sampled in the Gulf of Mexico.

failed to collect a single larva of this species (Juárez 1974b). Three juveniles 21-33 mm long collected off Maryland (37°42'N latitude, 73°10'W longitude) and New Jersey (38°45'N latitude, 71°00'W longitude) July 27-28, 1959, have been identified as bluefin tuna by Watson (Watson and Mather 1961) and this identification has been verified (T.C. Potthoff, personal communication). These records are the most northerly in the western Atlantic for small juvenile bluefin. They are of special interest because they are from the area where medium-sized bluefin may spawn (Mather 1974, Baglin 1976). The spawning habits of these fish in the western Atlantic are little known, but they do not occur in numbers anywhere near the known spawning areas of the large bluefin (Mather 1963a; also see Section IV).

Examinations of gonads suggest that the spawning grounds of the bluefin tuna in the western North Atlantic may be much more extensive than is indicated by the distribution of catches of larvae, or even of juveniles (Mather 1974, Baglin 1976).

Rivas (1954) examined the gonads of 95 large (199.7-255.0 cm long) bluefin tuna caught near Bimini, Bahamas, all in the month of May, but in three different years, 1952, 1953 and 1954. He classified the specimens, by the color and consistency of the gonads, the nature of the ovarian eggs, and the amount

of milt present, as recently spent, partly spent, or ripe.

All of the 29 males examined were classed as recently spent. He also considered that 61 of the 66 females examined were recently spent, but one was judged to be partly spent, and four were considered ripe.

The smaller eggs of ripe females were non-spherical, opaque and measured 0.4 to 0.7 mm in diameter, with a mode at about 0.6 mm. The larger eggs were spherical, translucent, yolk-filled, and measured 0.7 to 1.1 mm in diameter, with a mode at about 0.9 mm. Rivas (1954) offered two possible explanations for the small number of ripe individuals (about 4%) found in comparison with the larger number (about 96%) of spent individuals. Since the fish which are observed in the area are nearly always travelling northward, it was possible that they had spawned in an area south, or southwest, of the fishing area near Bimini and were caught when spawning had been nearly completed. He assumed that they had migrated to this area through the Straits of Florida, passing close to Havana, Cuba, and the western edge of Cay Sal Bank. The other possible explanation which Rivas offered was that the rod and reel fishing method used at Bimini selected spent rather than ripe fish. He quoted previous authors on the reluctance of spawning fish to feed.

During cruise 57-5 of the Bureau of Commercial Fisheries M/V "Dela-

ware", R. H. Gibbs and B. B. Collette, then of Woods Hole Oceanographic Institution, macroscopically examined the gonads of 48 bluefin tuna caught during the period June 8-14, 1957, in the area between latitudes 37°30'N and 40°30'N and longitudes 66°W and 70°W. Their observations were reproduced by Baglin (1976). Two age-3 (95-105 cm) individuals were considered immature. The testes of one male of age 4 (121 cm) contained abundant milt. Two other males and two females of this age group were classed as immature, but the ovaries of another age-4 female were "much vasculated," a sign of ripening. Milt was squeezed from the testes of a 5-year-old (140 cm) male. The ovaries of a female of the same age-size group were preserved for laboratory examination, presumably because of signs of maturity. Six males and six females, probably 6 years old (143.5-157.2 cm), were examined. The testes of all of the males contained abundant sperm; those of one individual were much enlarged, and another was classified as ripe. One female was classed as "near ripe." The ovaries of another contained eggs which seemed to be nearly ripe, but were not loose. Those of two others were well developed and loose, indicating imminent spawning. The ovaries of the last two females of this group contained no eggs, and were believed to be spent.

These observations, and less numerous ones from later catches of the

Table 24. Number of surface tows and number of larvae collected 25 nautical miles (4.0 km) from the Miami harbor entrance (Station 1) (1969-1971 and 1975) and additional stations (2-5) completing a transect of the Straits of Florida from Miami to Bimini, Bahamas, in 1975*. Data are from Richards (1976).

Date	Station 1 (1969-71, 1975)			Stations 2-5 (1975)			Total		
	Tows	Larvae	Larv./Tow	Tows	Larvae	Larv./Tow	Tows	Larvae	Larv./Tow
April 1-15	6	0	0	8	0	0	14	0	0
April 16-30	5	1	0.2	4	0	0	9	1	0.1
May 1-15	8	45	6.7	8	7	0.9	16	52	3.2
May 16-31	6	6	1.0	8	20	2.5	14	26	1.8
June 1-15	8	23	2.9	8	10	1.2	15	33	2.0
June 16-30	10	52	5.2	5	0	0	15	52	3.5
July 1-12	4	0	0	5	0	0	9	0	0
Total	47	127	2.7	46	37	0.8	93	164	1.8

*The vessel and nets used in 1969-1971 differed considerably from those used in 1975

“Delaware” in this area and season, indicate that at least some of the medium-sized and the larger “small” bluefin have spawned in May and June in the waters north of the Gulf Stream off the northeastern United States. We have noted (Section VC1) that ripe or nearly ripe bluefin may have travelled considerable distances in short periods before their capture. In this case, however, Wathne (1959), Wilson and Bartlett (1967), and all the additional data we have been able to collect on bluefin tuna catches in the western North Atlantic, indicate that medium-sized bluefin have occurred north of the Gulf Stream during the winter and spring but have been only rarely captured south of it and west of 60°W longitude. It therefore seems unlikely that these fish had migrated from southerly areas immediately before their capture.

Baglin (1976) presented a histogram showing the “gonadal-somatic index” (the “gonosomatic relation” of Rodríguez-Roda 1964a) by months for 67 bluefin tuna weighing over 100 kg (Figure 69). The specimens were from various areas, but nearly all of those captured in May and June, when the index was at its maximum, were from the vicinity of Bimini and Cat Cay in the Bahamas. The mean gonadal-somatic indices were about 1.5 in May and 1.0 in June, as against values of from 0.25 to 0.5 in other months.

The sex ratio for 237 large bluefin tuna which had been captured near the Bahamas in the years 1950-1966 and examined by Woods Hole Oceanographic Institution and National Marine Fisheries Service personnel (unpublished data) and Rivas (1954) was 72% females and 28% males.

Baglin (1976) also showed the frequency distributions of ovum diameters for bluefin taken at various dates and in various conditions. He found no developing eggs in bluefin tuna less than 10 years old. He set up a maturity scale based on the gonadal-somatic index, the diameter and morphology of the ova, and the appearance and physical properties of the gonads. He concluded that the bluefin spawned in May and June, and probably in April also. He observed that spawning must start south of Bimini and, on the basis of the data from “Delaware” cruise 57-5, might extend as far north as off New

England, and might involve smaller fish.

Characteristics of the gonads of giant bluefin tuna collected during exploratory fishing cruises of United States and Russian research vessels indicate that these fish may spawn in the northwestern Caribbean, the Windward Passage, the old Bahama and Santaren Channels, and a large area east and north of the Bahamas (Figure 70). Their presence in numbers in the latter area during the spawning season is confirmed by catches of the Japanese longline fishery (Fisheries Agency of Japan 1971, Wise and Davis 1973). The collection data and sizes of the fish, and their gonad weights and maturity indices are shown in Table 25.

Zharov (1965) observed that large bluefin taken by longline in late May and early June 1963 north of the Bahamas and east of central Florida (near 29°00'N, 79°00'W, and 30°00'N, 77°30'W) were “typically spawning, since their sexual products were in stages IV to VI-II” (these stages were not defined). The fish were from 198 to 238 cm (average 219.4 cm) long, and weighed from 140 to 220 kg (average 177.5 kg).

The information summarized above defines some positive locations

and periods of spawning of the bluefin tuna, and more extensive tentative ones.

The best documented spawning area is in the Gulf of Mexico (Figure 68). Bluefin larvae have been collected over much of the deep (more than 200 m) area of the Gulf north of 25°N, and also off the northern edge of the Campeche Bank, near 23°30'N and 94°30'W, and at 23° 30'N, 85°W. The most thorough and extensive surveys of the area were carried out in April-May 1973, and May-June 1974 (Juárez 1974b, Montolio and Juárez 1977). A few specimens have been collected in early July, and one, reportedly, in August. The last specimen, a 17.1 mm SL juvenile collected in the northern Gulf in August, almost certainly represented an aberrant occurrence, or a case of incorrect collection data, since the northward migration of spent adult bluefin through the Straits of Florida ceases before the end of June (Rivas 1954, Mather 1963a), and no adults of the species have been recorded in the Gulf of Mexico in late July or August, to our knowledge. These same considerations, and the fact that the authors did not list the characters on which they based their larval identification, also cast doubt on Gorbunova and Salabarría's (1967) reports of bluefin tuna larvae in the Gulf

Figure 69. Seasonal variation in mean gonadal-somatic indices of western Atlantic bluefin tuna greater than 100 kg (number of fish indicated above bars) (Baglin 1976).

of Mexico in September, and in Cuban waters in September and October (Potthoff and Richards 1970, Richards 1976). The major spawning of giant bluefin in the Gulf of Mexico most probably takes place in May and June, with lesser occurrences in late April and early July.

The distribution of catches of larval bluefin tuna along the transect of the Florida Straits from Miami to Bimini, with the largest catches at the western and central stations, and none in the station off Bimini, seems very significant. It suggests that the majority of the larvae have been transported by the Florida current from areas in the southwestern part of the Straits, and possibly even in the southwestern Gulf of Mexico. Conversely, it does not indicate extensive spawning in the area of the fishery for adult bluefin along the northwestern edge of the Great Bahama Bank. This in turn strongly supports the belief that the majority of the large adult bluefin which pass Bimini in May and June have spawned before arriving there, as did the studies of their gonads (Rivas 1954, Baglin 1976). Rivas' (1954) alternative suggestion that the northward migration might include schools of spent fish, which may take bait, and schools of ripe fish, which do not, seems less probable in view of this new information on the distribution of larvae. It thus appears that this migratory passage off the northwestern Bahamas is actually a spent fish run, analogous to the "return" runs which occurred regularly along the north coast of the Ibero-Moroccan Bay and in some Mediterranean localities. Rivas (1954), Potthoff and Richards (1970), Richards (1976) and Baglin (1976), on the basis of their studies of gonads, larvae and juveniles collected in or near the Straits of Florida and the occurrences of spent adults along its eastern edge, reached slightly different conclusions about the probable dates of spawning in that area. All of their estimates, however, fell within the months of April, May and June. The total evidence suggests that some spawning may have occurred in late April, but that the bulk of it has taken place in May and June. The termination of spawning may well have coincided with the disappearance of the

adult fish, which has usually occurred during the last half of June.

As noted above, the collections of bluefin larvae in the central and western parts of the Straits of Florida off Miami suggest that spawning may have occurred in the Straits south and west of there, off the Florida Keys or possibly in the southwestern Gulf of Mexico. Bluefin tuna have very rarely been observed off the Florida Keys (Section IV), but, as Juárez (1974b) pointed out, the species tends to spawn in offshore waters. Most of the very large sport fishing effort exerted off the Florida Keys has taken place on or close to the continental shelf. This might explain the scarcity of observations of bluefin, even if they had been spawning in the deep waters off the Keys.

E. RELATIONSHIPS BETWEEN ENVIRONMENTAL FACTORS AND SPAWNING BEHAVIOR

1. Introduction

Biologists agree that the spawning behavior of bluefin is strongly affected by environmental factors and that its sensitivity to these factors is intensified during the reproductive period. Opinions as to the importance and the nature

of the effects of various conditions, however, are extremely diversified.

Among the environmental factors most frequently considered are the temperature, salinity, density, transparency and oxygen content of the water, winds, tides, currents, atmospheric pressure, rainfall, and abundance of plankton. Most of this research has centered on mature individuals. Less attention has been paid to the effects of environmental conditions on the hatching of eggs and the survival of the early stages. With the present decrease in the spawning stocks, however, knowledge of these factors may also be very important.

2. Mediterranean Sea

Since the ancient trap fisheries in the Mediterranean Sea depended on the spawning behavior of the bluefin tuna, much attention has been paid there to the effects of environmental factors on this behavior.

Roule (1914a, 1914b, 1917), a pioneer in these studies, concluded that the bluefin tuna was "stenothermic" and "stenohaline." These beliefs were the basis of his "halo-thermic" theory. Roule did not specify the limits, or averages, of the temperatures and salinities which were suitable for the bluefin. He did, however, note that the sen-

Figure 70. Collection locations for the large, mature bluefin tuna collected during exploratory fishing cruises of United States and Russian research vessels (see Table 25).

Table 25. Collection data and sizes of large, mature bluefin tuna taken in the area bounded approximately by latitudes 20°N and 33°N and longitudes 69°W and 81°W, with their gonad weights and maturity indices. Temperatures of the ambient water are shown.

Sample Number ^a	Collection Date	Collection Location	Fish		Fish Weight (kg)	Gonad Weight (kg)	Index of Maturity	Water Temperature °C	
			Length (cm)					Surface	55 m
1	IV-12-55	20° N 81° W	245.6		(250.5)	11.8	21		
2	IV-23-55	19° 55' N 74° 10' W	(227)		(195.0)	4.8	41		
3	IV-24-55	19° 45' N 74° 45' W	223.9		(187.3)	5.5	34		
4	IV-27-60	20° 21' N 73° 47' W	203.1		(137.3)	1.5	94	27.2	
4	IV-27-60	20° 21' N 73° 47' W	211.9		(157.3)	3.1	51	27.2	
4	IV-27-60	20° 21' N 73° 47' W	214.5		(163.6)	5.3	31	27.2	
4	IV-27-60	20° 21' N 73° 47' W	224.6		(188.6)	5.3	36	27.2	
4	IV-27-60	20° 21' N 73° 47' W	250.5		(266.8)	6.0	45	27.2	
5	IV-23-61	32° 39' N 68° 34' W	244.5		(187.7)	4.8	39	18.6	18.4
6	IV-24-61	30° 14' N 69° 17' W	236.5		(221.8)	8.6	26	20.8	19.6
7	IV-25-61	29° 18' N 71° 17' W	213.7		(160.5)	3.4	47	20.8	19.7
7	IV-25-61	29° 18' N 71° 17' W	214.8		(163.2)	3.2	51	20.8	19.7
8	IV-28-61	26° 52' N 76° 10' W	215.3		(164.1)	5.8	28	23.6	22.4
9	IV-29-61	25° 48' N 77° 07' W	218.6		(172.7)	2.8	61	23.6	22.4
10	V-15-61	20° 06' N 73° 40' W	212		(157.3)	9.2	17	27.9	26.3
11	V-17-61	24° 25' N 74° 26' W	(204)		(139.6)	2.0	68	26.5	25.3
11	V-17-61	24° 25' N 74° 26' W	211.3		(155.5)	5	31	26.5	25.3
12	V-18-61	26° 30' N 75° 08' W	203.8		(136.4)	1.6	86	25.5	24.6
12	V-18-61	26° 30' N 75° 08' W	208.6		(149.1)	2.3	65	25.5	24.6
12	V-18-61	26° 30' N 75° 08' W	209.3		(151.4)	1.8	83	25.5	24.6
12	V-18-61	26° 30' N 75° 08' W	213.5		(160.0)	3.4	47	25.5	24.6
13	V-19-61	28° 02' N 76° 34' W	208.5		(149.1)	3.8	40	24.2	20.8
13	V-19-61	28° 02' N 76° 34' W	211.0		(154.5)	2.5	62	24.2	20.8
13	V-19-61	28° 02' N 76° 34' W	211.8		(156.4)	1.6	98	24.2	20.8
13	V-19-61	28° 02' N 76° 34' W	214.1		(161.8)	5.7	28	24.2	20.8
13	V-19-61	28° 02' N 76° 34' W	222.7		(183.2)	3.3	56	24.2	20.8
14	V-20-61	27° 39' N 78° 20' W	198.5		(127.7)	6.1	21	25.6	24.1
14	V-20-61	27° 39' N 78° 20' W	209		(150.5)	4.9	31	25.6	24.1
14	V-20-61	27° 39' N 78° 20' W	209		(150.5)	2.5	60	25.6	24.1
15	V-22-61	23° 40' N 79° 08' W	213.1		(159.6)	3.0	54	26.7	26.1
15	V-22-61	23° 40' N 79° 08' W	226.5		(193.6)	6.1	32	26.7	26.1
15	V-22-61	23° 40' N 79° 08' W	230.7		(204.6)	6.2	33	26.7	26.1

Sample numbers refer to station locations shown in Figure 70. Figures in parentheses are estimated.

sitivity of the fish to these properties of the water were heightened during the period of gonadal maturation. He concluded that, in this period, the bluefin sought the warmest and most saline waters of the western Mediterranean. This conclusion is somewhat inconsistent with his use of the terms "stenothermic" and "stenohaline."

In support of his "halo-thermic" theory, Roule (1924) showed that the direct route from a wintering area for bluefin tuna off the Mediterranean coast of France to a spawning area off Tunisia followed the path of maximum thermal increment, crossing isotherms of successively higher temperatures at right angles. The isotherms at a depth of 10m had been traced during an oceanographic survey made in the spring of 1923.

Roule (1924) also studied the relationship between the bluefin catches of the trap at Sidi Daoud, Tunisia, and the rainfall in spring at Bizerte, over a 35 year period. He found that the trap catches generally declined in years of heavy rainfall. He attributed this to the decrease in the salinity of the waters near the trap caused by the increased outflow of fresh water from the large Lake of Bizerte. He used these two examples to demonstrate the stenothermic and stenohaline characteristics of the bluefin.

Roule (1914a, 1917) believed that the relatively cold waters of the Strait of Gibraltar prevented the passage of any significant numbers of bluefin tuna, particularly during the spawning season when their sensitivity was increased, from the Atlantic into the Mediterranean. He therefore strongly supported Pavesi's (1887) and de Bragança's (1899) opinion that the Mediterranean bluefin constituted an autochthonous stock, completely independent of the Atlantic bluefin which spawned very near the Strait of Gibraltar.

The influence of winds on the movements of the fish near the Sardinian traps was slight, according to Roule (1914a). He concluded from his observations there, however, that increases in the density of the water favored increased catches. Roule (1914a) stated that all of the traps for spawning bluefin were designed to capture fish which were swimming against the fishable current.

Sella (1927, 1929a, 1929b, 1932a, 1932b) disputed the almost unanimous views on the movements and effects of environmental factors by the scientists who studied the biology of the eastern Atlantic and Mediterranean bluefin tuna. Most of these supported the views of Pavesi (1887), de Bragança (1899), Sanzo, (1910a) and Roule (1914a, 1917, 1924). Sella traced migrations of bluefin tuna by a new method. He collected many hooks and lures which had been found in fish caught in traps. He then determined the areas where the hooks and lures, which were then handmade in distinctive local patterns, were in use. His findings indicated that several bluefin tuna had migrated from the Atlantic into the Mediterranean, and that others had made extensive migrations within that sea.

Sella also disagreed with Roule's view that the species was absolutely stenothermic and stenohaline. He pointed out that feeding bluefin tuna occurred in numbers in many localities whose waters included a very wide range of temperature and salinity. He agreed with Roule in regard to the increased sensitivity to environmental factors of maturing bluefin tuna, but showed that even these fish did not seek maxima of temperature and salinity. As an example, he pointed out that no spawning occurred in the eastern Mediterranean, where the salinity was the highest. He supported this statement by pointing out that all of the "arrival" traps, whose catch consisted almost entirely of maturing fish, were west of the 38 o/oo isohaline, where the salinity was lower, whereas only "return" traps, whose catch consisted mainly of large spent fish, were east of it, where the salinity was higher. He felt that, instead of maxima, the maturing bluefin tuna sought specific hydrological conditions. He maintained that maturation occurred in the period of the most rapid thermal increment. He also showed that the larger maturing bluefin evidently favored somewhat colder and less saline water than the smaller ones. The important Favignana trap off the western end of Sicily, and the group of three equally productive traps off southwestern Sardinia, where the water temperature (about 18.0-18.8°C) and salinity are relatively low, took mainly large maturing fish. The

traps off Calabria (southern Italy) and Tripolitania, where the water is warmer (about 20.8°C - 21.8°C) and more saline, caught mainly small and medium-sized fish.

Sella (1927) refuted Roule's (1924) hypothetical migration of bluefin tuna along the line of maximum thermal increment from off southern France to off Tunisia. He showed that the tuna taken in the former area averaged less than 20 kg, whereas those taken in the Tunisian traps averaged 70 kg. Sella also differed with Roule (1914a) in regard to the influence of currents. Sella (1932b) showed that successful fishing of the very productive traps off southwestern Sardinia depended on having their leaders reach beyond the local northeasterly counter-current into the main southwesterly current, which was farther offshore. This main current was deflected upward by the bottom topography, resulting in colder water at the traps than elsewhere in the vicinity. Sella offered the hypothesis that the tuna followed this deep current from a distant area, and favored its water over the local waters with different characteristics. He emphasized the importance of studying currents in research on the behavior of the species.

Scordia (1937, 1938, 1942) conducted extensive studies at the traps off eastern Sicily and Calabria, and also of the hook and line fishery in the Strait of Messina (Scordia 1932, 1934). She maintained that density *in situ* was an important factor in controlling the movements of spawning bluefin tuna. She also found that atmospheric depressions and "zoo currents" (currents containing large quantities of zooplankton) and water temperature strongly influenced local movements of maturing fish in the vicinity of the traps. A requirement for successful fishing of the traps in the Tyrrhenian Sea was the presence of a "hypothermia barrier" of water with a temperature of 14°C at depths of 35-40 m. Although she did not believe that bluefin from the Atlantic spawned in the Mediterranean, she concluded (1938) that the arrival ("transgression") of Atlantic current waters was the determining cause of the reproductive migration of the bluefin tuna, and consequently of their entry into the traps. In Scordia's opinion environmental conditions, rather than

the state of the gonads, determined the movements of the species during the spawning season.

Sarà (1964, 1973) also maintained that the entrance of bluefin tuna into the traps depended greatly on the position of the Atlantic currents, which in turn was influenced by the prevailing winds before and during the spawning season. He believed, however, that most of the large maturing bluefin taken in the traps had followed the Atlantic current from the ocean into the Mediterranean. He found that layers of water with temperatures of 16°C to 19°C, at suitable depths, were most favorable for the approach of maturing bluefin tuna to the traps. The depth of the suitable layer varied, in different parts of western Sicily, from 5 to 25 m. Sarà felt that the vertical thickness of the 17°C layer was a determining factor. He agreed with Scordia that the 15°C isotherm, which usually occurred at depths of 50-60 m in the areas which he studied, constituted a barrier to the maturing fish. He further noted that the bluefin in different groups, usually consisting of individuals of the same, or nearly the same, size, tended to remain together in the traps, with each group staying at a depth where a favorable environment existed. He believed that the conditions selected by each group depended on the conditions in the area from which it had come to the trap, and the degree of acclimatization it had undergone during this migration and while being held in the trap. Sarà also studied the transparency of the water in the vicinity of the traps. He found no relationship between this factor and the occurrences of bluefin tuna, despite the firm belief of the local fishermen that clear water was a prerequisite to their presence.

Arena (1964) also made detailed studies of the behavior of bluefin tuna in and around the traps, and of related environmental factors. His research was conducted at traps at Milazzo (Gulf of Patti, northeastern Sicily) in 1961-1962, and at San Cusumano (near Trapani, western Sicily) in 1958. He found that the fish entered the traps at various depths (40 meters to the surface) and in waters of various temperatures, ranging from 15.5°C to 21.5°C. In general, however, his findings supported Sella's (1929a) view that the larger fish pre-

ferred the cooler waters. Like Sarà (1964, 1973), he noted that groups of tuna which entered the traps at different times sought different depths and temperatures. There was some tendency, however, for the groups to acclimate to warmer waters nearer the surface as their period of confinement increased. He did not note any relationship between the occurrences of the bluefin with the salinity, density *in situ*, or transparency of the water.

As noted above, little research on the important subject of the effects of the environment on eggs and early stages of bluefin tuna has been carried out. The difficulty in collecting these early stages at the tuna traps led Roule (1923) to conclude that they were photophobic and occupied abyssal waters. He extended his hypothesis to the possible passive transport of larval bluefin from the Mediterranean into the Atlantic by the deep outflowing current. Sella (1929a) refuted this idea, pointing out that larval and juvenile bluefin were photophilic and that he had collected thousands of them at the surface with the aid of lights. He believed that, if there was any passive transport of early stages of bluefin through the Strait of Gibraltar, it would be from the Atlantic to the Mediterranean, with the inflowing surface current. Sparta (1933) and Sarà (1973) supported Sella's opinion that juvenile bluefin were attracted to light.

Scaccini et al. (1975) concluded that the early stages of the bluefin tuna could withstand a wide range of hydrological conditions, even when changes occurred rapidly. They believed that an abundant supply of food, consisting of zooplankton, was the prime requisite for the survival of the larvae and small juveniles.

3. Eastern Atlantic

a. Distribution, Objectives and Nature of Research

Environmental research related to the spawning behavior of bluefin tuna in the eastern Atlantic has been intensive in the Ibero-Moroccan Bay, especially at the sites of tuna traps, and in the Strait of Gibraltar, but sporadic in the remainder of this large area.

Some of these studies were of a local nature, in the vicinity of particular traps, but others covered most or all of the Ibero-Moroccan Bay, or even

extended eastward into the Mediterranean Sea or southward to the Canary Islands.

The immediate purpose of these investigations was to determine the environment in which the tuna matured and presumably spawned, and the effects of the various factors on the spawning behavior and related movements of the tuna. The ultimate objective was to improve the fisheries, or at least to permit better estimates of their potential and predictions of their fluctuations. The effects of the environment on the early stages of the bluefin tuna were also investigated.

Frade and Vilela (1962) summarized the environmental factors considered by various authors as follows:

Intrinsic factors: Temperature of the water at various depths and thermocline topography, density of the water, salinity, pH, transparency, currents, etc.

Extrinsic factors: Air temperature, atmospheric pressure, irradiation, light intensity, wind, rain, etc.

Other factors considered include dissolved oxygen and tides (Lozano Cabo 1957, 1958, 1970) and chlorophyll productivity (Rodríguez-Roda 1963).

b. Portugal

Don Carlos de Bragança, king of Portugal, conducted what was probably the first methodical study of environmental conditions, the spawning behavior of the bluefin tuna, and the catches of tuna traps in the eastern Atlantic. We have not seen his report (de Bragança, 1899) but have found quotations from it, and discussions of its contents, in Pavesi (1889), Roule (1914b, 1917), Parona (1919), F. de Buen (1925) and other sources.

During the fishing season of 1898, de Bragança collected hydrological and meteorological data, and attempted to observe the behavior of the tuna themselves, from his yacht "Amelia" in the Ibero-Moroccan Bay. He also had detailed data on the catches of the Portuguese tuna traps collected concurrently. These traps were located in the province of Algarve on the country's south coast, which forms the northwestern boundary of the Ibero-Moroccan Bay (Figure 44). He examined the com-

bined information in an effort to determine the spawning behavior and the related movements of the tuna, and the influences of environmental factors on them.

De Bragança concluded that variations in meteorological conditions—waves, strength and direction of wind, barometric pressure, and air temperature—had no effect on the movements of the tuna during the trap fishing season (May–August). He believed that variations in their displacements in this period were caused by changes in the marine environment itself, mainly in its temperature. He observed that the bluefin tuna was not found in waters with temperatures of less than 13°C, and believed that the tunas' choice of limited areas in the trap fishing and spawning season was explained by variations in the temperature of the water.

He also concluded that the same groups of tuna which had passed the Algarve coast in the "arrival" fishery re-appeared there from 50 to 52 days later in the "return" fishery. In the meanwhile, he believed, they had spawned in the eastern part of the Ibero-Moroccan Bay, with only insignificant numbers of them entering the Mediterranean. He noted that, although some bluefin tuna occurred in Portuguese waters throughout the year, the Algarvian trap fishery was the only one in which these fish were abundant and followed a regular migratory pattern.

Vilela and Pinto (1958) presented monthly maximum, minimum and average sea surface temperatures and salinities taken near the tuna trap off Cabo de Santa Maria, on the southern or Algarve coast of Portugal during the trap fishing season, from April 24 through August. Although this was not specified, we presume from the context in which they were presented that these determinations were made in 1958. They also listed the portion of the 1958 catches of the Algarvian traps which was used by the canneries (about 80 percent of the total) by months in numbers and weight of fish in each of the traditional Portuguese size groups. These data are shown in Table 26.

c. Spain

From April to August 1923, an extensive dual survey of the oceanog-

raphy and the tuna fisheries of the Ibero-Moroccan Bay (westward to Cape St. Vincent and southward to Casablanca, Morocco) and the western Mediterranean, or Alboran Sea (eastward to Cape de Gata, Spain, and the Mulaya River, Morocco) was carried out (F. de Buen 1924, 1925, 1927; O. de Buen 1924; R. de Buen 1927). The most important of these reports, from the biological point of view, is that of F. de Buen (1925). This work was conducted under the terms of international accords reached at the meetings of the International Commission for the Scientific Exploration of the Mediterranean Sea in Paris, January 11, 1923 (O. de Buen 1924, F. de Buen 1925).

A general oceanographic survey of the area, including 540 operations, was conducted under the direction of Dr. O. de Buen on the Spanish naval transport "Almirante Lobo." A party on the smaller vessel "Principe Alberto de Monaco" concurrently collected biological and statistical data from the tuna fisheries in the area. Dr. F. de Buen was in charge of the biological work of the entire campaign.

To determine the causes of the arrival of the tuna on the Spanish coasts, data were gathered on the winds, the surface currents, and the transparency of the water. F. de Buen (1925) maintained that the general oceanographic conditions were the unique local causes of the spawning concentration of tunas off the Atlantic coast of southern Spain. Water transparency was a very important factor, as was demonstrated by the catches of two traps near the mouth of the Guadiana River at the Portuguese border. About 90 percent of the fish were caught in clear water. The remainder were taken in "regular" or "dirty" water, without a consistent difference between the catches in these two types. The clarity of the water, however, seemed more critical during the "return" (westward) movement than during the "arrival" (eastward) transit. It was difficult to find a definite relationship between winds, or wind-driven currents, and the catches of the traps. De Buen concluded that the direction, intensity and frequency of the winds might act as a secondary factor influencing the local movements of the tuna by altering the temperature of the surface waters.

In discussing the results, F. de Buen (1925) stated that the bluefin tuna was a typically stenothermic fish, whose distribution was exactly limited by temperature. In the spawning season, its sensitivity to temperature increased. In his opinion, the tuna was a surface-dwelling fish, submerging occasionally to depths of only a few meters. He rejected the abyssal winter habitat proposed by Pavesi (1887) and supported by Sanzo (1910a). He believed that the adult tuna which inhabited the western Mediterranean basin were altogether independent of those occupying the adjacent parts of the Atlantic. He postulated that the colder waters of the Strait of Gibraltar separated the two basins oceanographically and prevented the intermingling of these two groups of tuna.

De Buen concluded, from his own observations, that the water temperature was the main factor influencing the movements of the tuna, and proposed a thermic theory, as opposed to the hydrodynamic theory of Bounhiol (1911) and the halothermic theory of Roule (1914a).

F. de Buen (1925) found, by comparing the Spanish trap catches of May 1923 with oceanographic observations made concurrently in the same area, that the maturing "arrival" tuna preferred the warmer and less saline waters near Cadiz to the adjacent colder and more saline waters, which are typical of the open ocean to the west and the Strait of Gibraltar to the east.

After the peak of the "arrival" fishery along the coast, the fishery diminished. This coincided with the greatest intensity of spawning. In general, the conditions causing variations in the water temperature, such as the persistence of certain winds and the influence of coastal currents, were secondary factors affecting the local movements of tuna.

Fresh waters carrying suspended materials might have caused the tuna to leave the coast and temporarily prevented their capture by certain traps. The spawning areas coincided with the centers of high temperature, varying constantly under the effect of coastal factors on one side, and the high seas on the other.

F. de Buen stated that after spawning, the tuna, no longer subject to such

close constraints in regard to temperature, dispersed in the Ibero-Moroccan Bay, contributing another period of great catches for the traps (the return). The maximum catches in the "return" fishery, however, were concentrated at the western and eastern ends of the southern Spanish Atlantic coast, at or near areas where the temperature and salinity were considered the least favorable during the "arrival" period.

O. de Buen (1924), in a preliminary report on this survey, presented the following conclusions:

The moment of spawning changed from year to year according to changes in environment.

Increases and decreases in water temperature exercised a great influence on the development of the gonads.

High temperature, high salinity and agitated waters with high dissolved oxygen content were sought by the tuna for spawning.

The temperature of the surface water in the Strait of Gibraltar was 3°C lower than that of the coast of Cadiz, and 5°C less than that of the Mediterranean coast of Morocco from Ceuta eastward. These conditions were unfavorable for spawning tuna, and constituted an obstruction to their migration through the Strait. On the other hand, the currents and winds in the Strait increased the dissolved oxygen in its waters, a favorable factor for such migrations.

The tuna spawned west of Gibraltar before reaching Tarifa, where the salinity became lower.

The next important survey of the environment in relation to the occurrences of spawning bluefin tuna in Spanish waters was by Lozano Cabo (1957, 1958). He studied oceanographic conditions at the Barbate trap east of Cadiz and the biology of its catches during the 1954 fishing season. He made similar studies in the Moroccan trap fishery (Section VE3d) in 1954, providing the basis for interesting comparisons of data from the two areas.

The surface temperature at Barbate in June and July varied from 17°C to 21°C (18.9° ± 0.089°), increasing progressively despite small local alterations. There were greater fluctuations, from 14°C to 19°C (16.83° ± 0.146°), in the temperature at a depth of 35 m, which decreased, instead of increasing

as did the surface temperature, in the final days. The water was colder at 35 m than at the surface.

Lozano Cabo found a negative correlation index of -0.29 with a probable error of ± 0.11 between the surface temperature and the catch. There was no correlation between the temperature at 35 m and the catch. The "arrival" tuna preferred water temperatures from 18°C to 21.5°C off southern Spain and Morocco, with a more specific preference for 18.2°C to 18.7°C at Barbate.

The transparency of the water, measured by Secchi disc, varied from 5 m to 17 m, with a mean of 13.04 m, at Barbate. There was a correlation index

of 0.40, with a probable error of ± 0.10, between the transparency and the catch. The best catches occurred at transparencies of more than 13 m and especially over 15 m. Minimal catches always occurred at transparencies of less than 14 m.

The fishermen believed firmly that the catches of the traps depended intimately on the lunar phases and the tides. Lozano Cabo could not confirm this, except that, when tuna were present, they tended to enter the trap with rising tides. This might signify a negative rheotaxis, at least during their pre-spawning migration. The correlation coefficient of +0.10 with a prob-

Table 26. Surface temperatures and salinities at the trap off Cabo de Santa Maria and catches of the traps in the Algarve (southern Portugal) in the period from late April through August by month.

TEMPERATURE AND SALINITY OF THE SURFACE WATER OFF CABO DE SANTA MARIA						
Month	Temperature (°C)			Salinity (‰)		
	Min.	Max.	Avg.	Min.	Max.	Avg.
April ^a	15.0	19.5	17.4	35.93	36.02	35.97
May	15.0	20.5	17.3	35.77	36.15	35.99
June	15.0	20.0	17.4	35.77	36.22	35.96
July	15.5	20.0	18.7	35.82	36.11	35.96
August	17.0	26.0	22.3	35.73	36.29	36.04

FISH ^b RECEIVED BY THE CANNERIES.						
1958		"Atuns"	"Atuarros"	"Albacoras"	"Cachorretas"	Total
May	Weight kg	73,166	8,713	723	115	82,717
	No. of fish	439	119	12	7	577
	Average kg	166.7	73.2	60.3	16.4	143.4
June	Weight kg	307,071	130,658	3,052	500	441,291
	No. of fish	2,330	1,903	68	78	4,379
	Average kg	131.8	68.7	44.9	6.4	100.8
July	Weight kg	65,870	4,746	244	-	70,860
	No. of fish	457	64	5	-	526
	Average kg	144.1	74.2	48.8	-	134.7
August	Weight kg	21,282	1,149	932	-	23,363
	No. of fish	157	15	17	-	189
	Average kg	135.6	76.6	54.8	-	123.6

^aApril 24 - 30

^bSize groups of fish (Vilela 1960): Atuns > 90 kg, Atuarros = 50 - 89 kg, Albacoras = 30 - 49 kg, Cachorretas < 30 kg.

able error of ± 0.12 between the state of the tide and the catch of Barbate was not significant.

Salinities and dissolved oxygen were also observed at Barbate by Lozano Cabo. Although measurements of both were taken from the surface and at depths of 30 m or 35 m, he did not study the correlation with the catches. He had found no correlation between salinity and catch at the Los Cenizosos trap in Morocco. Salinities at Barbate fluctuated between 35.39 o/oo and 35.53 o/oo at 35 m. Dissolved oxygen levels were abnormally high varying from 6.9 to 8.1 cc/l at the surface and 5.0 to 9.0 cc/l at 30 m.

Rodríguez-Roda (1963, 1965, 1969c, 1970a, 1970b) collected environmental data at the Barbate trap from 1961 to 1969, and discussed their possible relationships to its catches and the movements of the maturing and post-spawning bluefin tuna. His 1963 publication presented monthly values of the temperatures, phosphate production, and salinity, of the water at various depths from the surface to 30 m, and its transparency and optical absorption.

Rodríguez-Roda (1969c) presented the mean temperatures at 10 m intervals from the surface to 30 m in the Barbate trap in August 1967. Rodríguez-Roda (1970a) collected daily temperature measurements of the water temperature at 10 m intervals from the surface to 30 m for the months of May through August 1968. He compared the weekly averages of these temperatures graphically with the corresponding numbers of tuna caught in the trap. He (1970b) collected corresponding data and presented a similar graphical comparison for the same period in 1969. In that year he also measured the transparency of the water each day, and he compared these values graphically with the daily catch of the trap in numbers of tuna.

The temperature during the most productive months, May to July in 1961 and 1962, ranged from 18.0°C to 21.4°C at the surface and 16.5°C to 18°C at a depth of 30 m. During the "arrival" run in May and June 1968, the highest catches occurred with mean surface temperatures of 17.2°C to 18.9°C and temperatures of 16.6°C to 17.6°C at 30 m. The best catches dur-

ing the 1969 arrival run were taken in a week with mean temperatures of about 18°C at the surface and 16°C at 30 m. During the "return" period in July and August 1968, the best catches took place with temperatures of 19.5°C to 19.9°C at the surface and 16.3°C at 30 m. In 1969, the best "return" catches were taken with mean surface temperatures of 21.0°C to 22.5°C, and temperatures of 18.5°C to 20.2°C at 30 m. Rodríguez-Roda noted (1969a), that the August temperatures in 1961, 1962 and 1967 were about the same, and that the total production of the Spanish Atlantic traps in those years did not vary greatly. In his 1970b publication, he observed that the catch of these traps was greater in 1969, when the water was warmer, than in 1968. Rodríguez-Roda (1971) concluded that the maturing "arrival" period begins at temperatures of 16°C to 17°C, and is most productive at temperatures of 18°C in the upper 10 meters, 17°C at 20 m and 16°C at 30 m. In the post-spawning "return" period, optimum temperatures are 20°C to 21°C in the upper 10 m and 19°C at 30 m.

The average salinities during the months of May, June and July in 1961 and 1962 varied from 35.88 o/oo to 36.34 o/oo at the surface and 36.01 o/oo to 36.21 o/oo at 30 m (Rodríguez-Roda 1963).

The transparency of the water ranged from 11 m to 21 m in May and June of 1961 and 1962, and from 2 m to 25 m in May-August 1969, (Rodríguez-Roda 1963, 1970b). The author found a high positive correlation, during intensive periods of the fishery, between the transparency and the catches of the trap.

Phosphate production in May, June and July, the months of maximum tuna catches, varied from 0.54 to 0.59 mg/l at the surface.

Chlorophyll production was generally greater in the cold months than the warm ones, with a large maximum in October and lesser ones in January and April.

Zooplankton was predominant in the warm months, although undergoing many variations during the year, due to the influences of Atlantic waters.

Rodríguez-Roda (1963) concluded that the Barbate area, in regard to its

oceanography and the plankton in general, could be said to be under the influence of Atlantic waters, especially in its surface layers.

d. Morocco

Lozano Cabo (1957, 1958, 1970) conducted thorough studies of the environment at the Los Cenizosos trap, north of Larache, Morocco. Our account generally follows his 1970 summary, with some details added from the earlier reports.

The water temperature varied from 17°C to 22°C at the surface, from 15°C to 20°C at 15 m, and from 14°C to 18°C at 35 m. The correlation between the surface temperature and the numbers of fish caught was negative (-0.72 ± 0.06). Fish were caught at temperatures between 17°C and 21°C, but mainly between 18°C and 19.7°C.

The transparency of the water ranged from 8 m to 19 m, with an average value of 13.7 m. A high positive correlation, $+0.59 \pm 0.08$, existed between the transparency and the numbers of fish caught in the trap. The catches were poor when the transparency was less than 13 m and good when it was over 15 m, especially at 15 m to 16 m.

The salinities were between 36.00 o/oo and 36.34 o/oo at the surface, 36.11 o/oo and 36.33 o/oo at 15 m, and 36.06 o/oo and 36.25 o/oo at 35 m. The correlation between surface salinity and the numbers of tuna caught in the trap, -0.078 ± 0.13 , was not significant.

Likewise, no correlation was found between the height of the tide (above the daily low water level) and the number of tuna caught, even though the captains thought that the tides strongly influenced the catches. There was a clear relationship, however, between the velocity of the tidal currents and the presence of tuna. Good catches coincided with tides of large amplitude, during which the coastal currents were stronger and farther from shore.

The dissolved oxygen content varied from 5.9 to 7.9 cc/l at the surface, from 5.7 to 7.9 cc/l at 15 m, and from 5.5 to 7.7 cc/l at 30 m.

Aloncle (1964, 1969) developed a hypothesis on the migrations and spawning of bluefin tuna, and the influences of water temperature upon

them, in the waters between the southern Iberian coasts and the Canary Islands. This hypothesis was derived from studies of the tunas and their fisheries off the Atlantic coast of Morocco, and a hydrographic survey of the above waters. In early June 1964, tuna were found between Lanzerote Island (Canaries) and the African coast in water with a temperature of 20.06°C and salinity of 36.40 o/oo at the surface, and 18.37°C and 36.56 o/oo at a depth of 50 m. Aloncle believed that these tuna were pushed northward with the seasonal warming of the water, and kept away from the Moroccan coast by isotherms of temperatures greater than 21°C. In the course of this movement, he believed that they spawned in the area between Lanzerote, Conception Bank and the Moroccan coast.

e. Other Eastern Atlantic Areas

The only other parts of the eastern Atlantic where bluefin tuna are believed to spawn are in the vicinity of the Azores (Ferreira 1932) and in equatorial waters south of Sierra Leone (Richards 1969, Richards and Simmons 1971, unpublished data reports for *Geronimo* cruises 3, 4 and 5).

In May and June, the months in which bluefin reportedly spawn around the Azores, the surface temperature in the area varies between about 17.0°C and about 19.7°C, while the salinity remains at about 36.1 o/oo.

In the area bounded by latitudes 7°N and 8°S, and longitudes 13°W and 15°W, three larval *T. thynnus thynnus* were collected in March 1963, in waters with surface temperatures exceeding 27°C and surface salinities of from 36.4 o/oo to 38.8 o/oo (Richards 1969). These temperatures are much higher than those in other reported spawning areas of the species in the eastern Atlantic and the Mediterranean.

4. Western Atlantic

a. Introduction

In comparison with what is available for the eastern Atlantic and the Mediterranean, very little has been published on the relationships between the spawning of bluefin tuna in the western Atlantic and environmental conditions. Therefore our discussion of this correlation depends almost entirely on ob-

servations which were made concurrently with investigations, but have not been synthesized or analyzed, and data in atlases or survey reports.

b. Gulf of Mexico

The best documented spawning of bluefin in the western Atlantic takes place in the Gulf of Mexico in from late April to early July (Section VD3). The heaviest concentrations of larvae evidently occur in the deep (more than 200 m) area between latitudes 23°N and 30°N and longitudes 84°W and 94°W (Figure 68) (Juárez 1974b, Montolio and Juárez 1977). During April, May and June the surface temperature of these waters increases from between 22°C and 24°C to a little over 27°C (Galtsoff 1954). The temperature in the upper layer is fairly constant down to 30 m. The salinity in the upper 50 m layer is typically 36.00 o/oo. In contrast, the salinity of this layer over the Campeche and Florida Banks, where few larvae have been collected, is 36.25 o/oo, possibly because of upwelling.

c. Straits of Florida

The Straits of Florida at the Miami-Bimini line present an unusual situation in that adult bluefin are found in numbers, and almost exclusively, on the eastern (Bahamas) side (Section IVC2), but the abundance of larvae is minimal on the eastern side and maximum near the Florida side (Section VD3). Most of the fish examined at Bimini were spent, with a very few ripe ones among them (Rivas 1954). Evidently most of the spawning occurs south of this line.

The surface water temperature across the Straits of Florida between Miami and the Florida Keys and the Bahamas (25°N to 26°N and 79°W to 80°W) is fairly uniform in the deeper central area. On the edges of the Strait where the bottom rises sharply temperatures are cooler (Sverdrup et al. 1942). The surface temperature in the deep water is about 26°C to 26.5°C in April, increasing to about 27°C in May and about 28°C in June (Pyle 1962).

Nearly all of the catches of bluefin tuna in the Straits of Florida have been taken by rod and reel from schools traveling close to the surface (Rivas 1978). The fish are seen near the surface in this area only under certain con-

ditions of wind and current, however, and it is presumed that they must spend much of the migrating period at deeper levels. A male with milt was taken by longline at an estimated depth of 55 m on the eastern side of the Straits just north of Bimini (Mather and Bartlett 1962). The water temperature at the location was 26.7°C at the surface and 25.7°C at 55 m. The salinity in the upper 50 m layer in this region ranges from 35.5 o/oo to 37 o/oo, with an average of about 36.2 o/oo, from April through June 1977. The average phosphate and oxygen levels in this period were about 0.1 and 4.65 ppm, respectively.

d. East and North of the Bahamas

In the waters east of the Bahamas the research vessel *Crawford* caught bluefin with maturity indices from 28 to 126 (mostly 60-90) at several locations in May 1961 (Figure 70, Table 25). The surface water temperatures ranged from 23.6°C to 26.5°C, but most of the fish were taken in waters of 25°C. At 55 m the temperature range was 22.4°C to 25.3°C, but most of the fish were taken where the temperature was about 24°C.

A little north of the Bahamas the *Crawford* caught eight fish with maturity indices of 21 to 98 (Table 25) in water with surface temperature between 24.2°C and 25.6°C and temperature at 55 m between 20.8°C and 24.1°C. Zahrov (1965) reported that spawning fish caught north of the Bahamas (Figure 70) at the end of May and the beginning of June were in water with surface temperature of 25°C to 26.4°C.

e. Northeastern United States

The bluefin showing signs of spawning taken by the *M/V Delaware* about 500 km off southern New Jersey and the Delmarva Peninsula during cruise 57-5 (Section VD3) were generally in cooler waters than were any of the previous fish. These catches were made in waters of surface temperatures between 18.3°C and 25.5°C. The most successful catches were in water with a temperature around 20°C or 21°C. Fishing depths were estimated to be 52 m to 57 m and most of the fish were taken where the water temperature at this depth ranged from 15.5°C to 21.1°C.

F. Feeding Activity During the Spawning Season

Different opinions have been expressed in regard to the feeding activity of bluefin tuna during the spawning season. Many of the studies used individuals caught in traps. It has been argued that the lack of food in the stomachs of "arrival" fish might have been caused by digestion while the fish were awaiting removal from the trap, or by regurgitation resulting from their struggles during this removal. Food is frequently found in the stomachs of "return" fish, however, even though they undergo the same treatment.

F. de Buen (1925) and Sella (1929a) were of the opinion that the bluefin continued to feed during their period of maturation and spawning, but at a reduced rate. De Buen believed that they ate food which they happened to encounter, and could catch without undue effort, but seldom exerted themselves in the pursuit of difficult prey.

Rodríguez-Roda (1963, 1964a, 1969) found that stomachs of tuna taken in the Spanish "arrival" traps were usually empty. Some contained a few swimming crabs, *Polybius henslowi* Leach, which they had presumably consumed before entering the trap. Small fish which had been caught in traps with the tunas were occasionally found in their stomachs. He emphasized the limitations of his findings because of the possible losses of stomach contents of trapped fish mentioned above.

Sarà's (1964, 1973) studies of stomach contents of "arrival" fish taken in the traps off western Sicily and observations of their behavior when confined in the traps with species on which they normally fed, led him to believe that maturing bluefin tuna abstained from eating. He found increasing amounts of food in the stomachs of post-spawning fish, however, as the season advanced and their gonads became smaller.

Arena (1964) found stomachs of "arrival" fish caught in the western Sicilian traps to be empty, or nearly so. Those of others caught off the eastern part of the island, however, contained considerable quantities of food. A large quantity of swimming crabs, *Polybius henslowi* Leach, was found in the stomach of the first group of bluefin tuna caught at Milazzo in 1961. Several other

authors have reported observations of food in the stomachs of maturing bluefin caught off eastern Sicily (Genovese 1960, Genovese and Alonzo 1961, Li Greci 1961).

The considerable longline catches of bluefin tuna in the central Mediterranean during the spawning seasons of 1973 and 1974 (Fisheries Agency of Japan 1975, 1976) prove that significant numbers of these fish feed during the spawning season. As Sarà (1973) noted, the trophic (feeding) tendency may on occasion overcome the tendencies which are usually dominant during the spawning period, including the tendency to reduce, and finally stop, feeding as the volume of the gonads increases.

G. The Spawning Act

The only published accounts of the actual spawning of bluefin tuna which we have encountered described occurrences in the central Mediterranean. Some of these activities occurred while the fish were being held in traps, but others, probably more important because the fish were under no constraint, took place in the open sea.

Sella (1911) and Heldt (1932) described the spawning actions of fish in traps off Sicily and Tunisia on the basis of accounts which they considered reliable. Sarà (1964) personally observed the reproductive acts of tunas in the vicinity of traps off Sicily. Arena (1964) likewise witnessed the spawning of bluefin tuna in the open sea off Sicily.

These accounts show that spawning occurs at the instant when a pair of fish turn on their sides and make contact, or appear to, with their ventral surfaces. This refutes the previous supposition (Tiews 1963) that tuna spawned by saturating an area with randomly discharged eggs and milt.

Arena and Sarà, however, reported that small groups of tuna sometimes engaged in communal mating. In a spectacular observation, Arena (1964) saw files of 10-12 giant fish overtake other files of about the same number, with the fish of one file mating with those of the other as they passed.

P. Arena (personal communication) provided the following information on spawning, based on his more recent observations. The mating of fish in large schools may involve nearly all

of the fish in the school at the same time. This causes an enormous bright flash under the surface, with a very spectacular effect. The school, which usually travels at from 2 to 7 knots (3.7 to 13 km/hr), leaves a rather milky trail behind it, due to the emission of sexual products.

H. Maturity and Fecundity

The ages at which bluefin tuna spawn, and the variation in the fecundity of females with their size and age, are two elements of the biology of the species which are especially important for the management of its fisheries.

1. Age and Size at First Maturity:

Research on bluefin tuna in the eastern Atlantic and Mediterranean indicated that they first spawned at ages 2-4 (lengths of about 75-125 cm, weights of about 12-40 kg). Sella (1929a, 1929b) reported that the species usually spawned first at age-3, or at a weight of about 15 kg. He added that a few age-2 fish which had attained weights of 12 kg through rapid growth might also spawn.

Frade and Manaças (1933) found that young bluefin 1 m long taken in the "arrival" (May-June) fishery off southern Portugal developed differently according to their sex: the males were in active or completed spermatogenesis, whereas the females were in a very retarded oögenesis. Arena (1964) and Sarà (1973) have observed that bluefin tuna school by size, even during the spawning season, and that fertilization is accomplished by paired emissions within these schools. Therefore the reported difference in the times of maturity of 3-year-old males and females implies that their spawning efforts might be ineffective. Rodríguez-Roda (1929a) concluded from his fecundity studies that females attained their first maturity at a length of about 97.5 cm, and males at about 105 cm, corresponding to ages of 3 years. Frade and Vilela (1962) concluded that first maturity usually occurred at age 3, but occasionally at ages 2 or 4.

Scaccini et al. (1975) reported the smallest mature bluefin tuna observed by any of them was an individual weighing 27 kg (4 years old) examined by Sarà at the Solanto trap in Sicily in mid-June 1959.

Less information is available on the age of first spawning of western Atlantic bluefin, but these fish have apparently been less precocious than their eastern Atlantic and Mediterranean counterparts.

Westman and Neville (1942) examined many small and medium sized bluefin tuna landed by the coastal sport fishery at Freeport, Long Island, New York. They reported that nearly all of the "school tuna" (fish averaging less than 30 kg) were immature. They found some evidence of approaching maturity in a few tuna of the 3-year-old age group, and signs of maturity in a larger percentage of the 4-year-olds. They considered all of the fish of both sexes which were 5 years old (about 130 cm long and weighing about 40 kg) or older to be adults, but found no indications of eggs or sperm in their gonads.

The present authors have conducted macroscopic examinations of the gonads of numerous small bluefin tuna caught in traps or by sport fishing in southern New England coastal waters and by purse seines in coastal waters between southern New Jersey and New England in the summers of 1950-1975. We concur with Westman and Neville's conclusions. We found signs of maturity in less than 1% of the 3-year old fish but in a considerably larger percentage of the tuna of age group 4. Nearly all age 3 fish, like all the 0, 1, and 2 year-old individuals examined, had very small gonads which were almost uniformly slender throughout their length, like very flat shoestrings. The gonads of the older fish which were considered to show signs of maturity were distinctly enlarged for at least part of their length. The testes of a few age 4 males taken in Cape Cod Bay, Massachusetts, in early July 1953, contained milt. Those of a 4-year-old specimen, 110 cm long and weighing 25 kg, weighed 27.5 g and contained milt. A photomicrograph (970x) taken by R. F. Vaccaro, an Associate Scientist of Woods Hole Oceanographic Institution, showed that this milt contained fully developed sperm. The gonads of most of the 5-year-old tuna (about 133 cm long and weighing about 45 kg) were generally better developed, and most of these fish had probably spawned.

We believe that the mature members of the "small" bluefin group (less than 120 cm long) spawn in offshore waters north of the Gulf Stream, along with fish of the "medium" size group, in May and June. As noted in Section VD3, a few small bluefin and several medium sized ones taken by longline in this area and season were examined. The results of macroscopic examinations of their gonads were as follows: **Age III.** Two fish were examined. Both were classified as immature.

Age 4. Three males and three females were examined. One fish of each sex showed definite signs of maturity.

Age 5. One male was examined. Some milt was squeezed from its testes.

Age 6. Twelve fish (six of each sex) 143.5-157 cm long and probably of this age were examined. Two of the females were classified as spent. The other ten fish appeared to be approaching spawning condition.

We conclude tentatively from all of these data that the first spawning of bluefin tuna in the eastern Atlantic occurs at age 3, in exceptional cases, and more frequently at age 4. By age 6 all, or nearly all, of the fish are spawners. Probably the first spawning of western Atlantic bluefin tuna occurs most frequently at age 5, but more research is required to establish this.

2. Fecundity

Rodríguez-Roda (1967a) found that the estimated fecundity of bluefin tuna caught near Cadiz, Spain, in May and June generally increased with size of fish, from 5.2×10^6 for an individual 130.5 cm long and weighing 54 kg to 32.2×10^6 for one 230 cm long and weighing 235 kg. The minima and maxima, however, were 5.0×10^6 for a fish 160 cm long and weighing 96 kg, and 45.9×10^6 for one 214 cm long and weighing 191 kg. He calculated the following relationships between F , the fecundity or number of maturing eggs, and (1) L , the length of the fish in cm; (2) and (3) P_1 , the weight of the fish in kg; and (4) P_2 , the weight of the ovaries in kg:

$$(1) F = 2.29245 L^3$$

$$(2) F = 53,451 P_1^{1.159489}$$

$$(3) F = -1,220,717 + 138,068 P_1$$

$$(4) F = 553 P_2^{1.337073}$$

In the size range studied, the estimated fecundity was thus roughly proportional to the weight of the fish, or the third power of its length.

Baglin (1976), studying six bluefin tuna taken near Bimini and Cat Cay in the northwestern Bahamas in May and June and ranging from 222.5 cm in length and 188.4 kg in weight to 260.6 cm in length and 271.5 kg in weight, found that their estimated fecundity increased from 16.7×10^6 for the smallest to 31.4×10^6 for the largest. The maximum, however, was 33.0×10^6 for an individual 240.8 cm long and weighing 247.4 kg. Where F is the estimated fecundity, L is the length of the fish in cm, W is its live weight in kg, and W_1 is the dry weight in g of all of the eggs from both of its ovaries, Baglin calculated that:

$$F = 65.4214 L^{2.35326}$$

$$F = 6,245,010 + 95,132.3 W$$

$$F = 3,051,104 + 18,916.4 W_1$$

He concluded that fecundity increased with size of fish in the length range from 222.5 cm and to 260.6 cm, and that, therefore, larger fish contribute more to the reproductive potential.

No significant difference in the slopes or adjusted means was found by Baglin in a covariance analysis between the fecundity-length and the fecundity-weight relationships found in his study of western Atlantic bluefin tuna and those found by Rodríguez-Roda (1967a) for eastern Atlantic individuals. Baglin noted, however, that the samples were small, and that more extensive studies might reveal significant differences.

The studies of Rodríguez-Roda (1967a) and Baglin (1976) indicate clearly that the fecundity of Atlantic bluefin tuna increases with size of fish, in both the eastern and western parts of the Ocean. Baglin's study shows that this relationship extends to the very large size of 260 cm. Pending actual determinations of the fecundity of larger fish, there is no reason to suppose that the fecundity does not also increase with size of fish for the relatively few larger individuals which are captured. Baglin and Rivas (1977) estimated the fecundity of 17-year-old Atlantic bluefin as 44.6×10^6 eggs.

3. Maximum Size at which Bluefin Tuna Spawn

The only authors who have discussed the largest size or age at which bluefin tuna spawn, to our knowledge, are Scaccini et al. (1975). They state that the species spawns "up to the maximum weight and the maximum age" and cite Sarà's observation of bluefin tuna estimated to be about 18 years old and weighing up to 600 kg, caught in the trap at Favignana (Aegades Islands, just west of the western end of Sicily) in June 1974, as the largest individuals in spawning condition which had been examined by any of them. Since the number of recorded catches of bluefin tuna weighing over 600 kg is negligible, it is most unlikely that any significant number of these fish attain a size at which they cease to spawn.

I. Discussion and Conclusions

A discussion and a presentation of our tentative conclusions seem appropriate, since much of the information in this section is inconclusive and, in many instances, even contradictory.

1. Mediterranean and Black Seas

The Mediterranean and Black Seas have traditionally been regarded as prime spawning grounds for the bluefin tuna. Despite a preponderance of scientific opinion against this concept which developed in the last quarter of the nineteenth century and the first quarter of the twentieth, it still appears to be valid. The information now available, however, indicates that the principal reproduction of the eastern Atlantic and Mediterranean bluefin takes place in the south central Mediterranean, instead of occurring in the Black Sea as Aristotle and his followers supposed.

Small juvenile bluefin were first reported from the Mediterranean by d'Amico (1816). The eggs and larvae were first described briefly by Sanzo in his 1910b publication, and more completely in his 1929 and 1932 works. Some authors have stated that the characters presented by Sanzo do not differentiate the eggs and very small larvae of bluefin from those of other tunalike fishes, especially *Auxis*. Ehrenbaum's tentative identifications of larval *T. thynnus thynnus* have been questioned by Sella (1929a) and Richards (1976). Despite these uncer-

tainties over identifications, there is no doubt that young stages of bluefin have been collected in great numbers in the south central Mediterranean. It is unfortunate, as noted by Heldt (1930) and Dieuzeide (1951), that Sella did not describe the "thousands" of early stages of bluefin which he (1929a) reported that he had collected. His 1924 publication, however, convinced Richards (1976) of the accuracy of his identifications. Scaccini (1961, 1968) and Scaccini et al. (1975), to whom Sella's material was available, also agreed with these identifications. The most numerous collections have been made in the Strait of Messina and in waters north and west of Sicily (Sanzo 1932, Sella 1924, 1929a; Sparta 1933, Scaccini 1968, Piccinetti and Piccinetti Manfrin 1970, Scaccini et al. 1975). The detailed study of Duclerc et al. (1973) showed that larval bluefin also occurred around the Balearic Islands. Dieuzeide (1951) described three larval bluefin collected off Algeria, and Piccinetti (1973) and Piccinetti et al. (1976b) presented preliminary reports on occurrences of early stages in the Adriatic Sea.

Several authors (Vodyanitskii 1936, Vodyanitskii and Kazanova 1954, Oven 1959) have reported on eggs and larvae of bluefin collected in the Black Sea, but have not produced detailed descriptions. The difficulties of identifying eggs and small larvae of bluefin, even after hatching the eggs and rearing the larvae, have been fully explained by Duclerc et al. (1973) and Scaccini et al. (1975).

The regular occurrences of great numbers of maturing bluefin along the coasts of western Sardinia, Tunisia and Tripolitania suggest that spawning occurs in those areas as well. Although the traps on the eastern (Ionian Sea) coast of Sicily were known as "return" traps, some maturing individuals were caught in them, along with the more numerous spent fish (Sella 1929a, Scordia 1938). Scordia's extensive studies (summarized in her 1938 and 1942 publications) indicated that large numbers of bluefin tuna passed through the Strait of Messina from the Tyrrhenian Sea to the Ionian Sea, spawned there, and then returned through the Strait to the Tyrrhenian. It appears that the

spawning of bluefin tuna in the Mediterranean is most intense in its south-central part, but also extends into the western Mediterranean and the Adriatic Sea. As Scaccini et al. (1975) concluded, additional research will probably show that bluefin spawn in other parts of the Mediterranean. Some spawning must also occur in the Black Sea. The absence of a commercial fishery for the species there, however, and the relatively small catches taken in its approaches, the Bosphorus and the Sea of Marmara, suggest that the reproduction there is not comparable, quantitatively, to that in the central Mediterranean.

2. Eastern Atlantic

The situation in the eastern Atlantic is dramatically different from that in the Mediterranean and Black Seas. Despite extensive research efforts over many decades, no identifiable early stages of bluefin have been collected in the Ibero-Moroccan Bay, which has been regarded as the prime spawning ground in the region, or in the more recently suggested areas of reproduction off Morocco and in the Bay of Biscay. The only identified early stages from the eastern Atlantic were collected near the Equator between longitudes 0° and 15°30'W (Richards 1969, Richards and Simmons 1971). This was a totally unexpected area on the basis of existing knowledge of the distribution of maturing bluefin. It certainly merits further investigation to determine the seasonal and areal extent of the occurrence, and also to make certain that the larvae are actually those of *T. thynnus thynnus* rather than those of *T. maccoyii*, which also occurs in the South Atlantic.

Regular seasonal occurrences of very numerous maturing and spent bluefin in the Ibero-Moroccan Bay have been abundantly documented. Small numbers of maturing or ripe bluefin in the Bay of Biscay have been reported occasionally (Creac'h 1952, Le Gall 1952) and detailed studies of the gonads of a few individuals have just become available (Cort et al. 1976, Cort 1977). The occurrence of small numbers of mature bluefin at the Azores has been reported (Ferreira 1932), but no details on their gonad condition were presented.

3. Western North Atlantic

The western North Atlantic is the only part of that ocean from which extensive collections of early stages of *T. thynnus thynnus* have been obtained. The most important occurrence documented up to now has been in the Gulf of Mexico. Bluefin larvae and small juveniles have been collected over much of the deep (more than 300 m) part of the Gulf, especially in the area north of latitude 23°N (Juárez 1972, 1974b; Richards 1976, 1977; Montolio and Juárez 1977, T.C. Potthoff, personal communication). Important collections have also been made in the Straits of Florida, particularly at the Dry Tortugas and off Miami (Potthoff and Richards 1970, Richards 1976, T.C. Potthoff, personal communications). Scattered individuals have been collected off the east coast of the United States up to latitude 38°45'N. These collections show that the Gulf of Mexico is the most important bluefin tuna spawning ground yet discovered in the Atlantic, and that spawning also occurs in the Straits of Florida and probably for an unknown distance farther north.

The condition of gonads of captured fish suggests that spawning may also take place in the northwestern Caribbean, the Windward Passage, the Old Bahama and Santaren Channels, and a large area east and north of the Bahamas. Virtually all of the mature bluefin taken in these southerly parts of the western North Atlantic and adjacent waters for which we have size data were large (over 185 cm long) individuals, weighing over 125 kg. Examinations of gonads suggest that at least some smaller bluefin spawn near the

northern edge of the Gulf Stream, or the Gulf Stream front, north of latitude 37°N and east of longitude 70° W.

4. Overall Situation

On the most positive evidence available, the occurrence of larvae and very small juveniles, one can only conclude that the most important spawning areas of *T. thynnus thynnus* are in the south central Mediterranean Sea and the Gulf of Mexico. This in itself is an interesting parallel, as the Gulf of Mexico and the Caribbean Sea are often referred to as the "American Mediterranean."

The major spawning occurs earlier in the western Atlantic (probably about May 15-June 15) than in the Mediterranean (about June 15-July 15).

The smaller bluefin spawn later than the larger ones in the Mediterranean, and probably do in the western Atlantic also. Studies of spawning in both areas have centered on the larger fish. Some information is available on the spawning of the smaller individuals in the Mediterranean, where they mix to a considerable extent with the larger ones during the spawning season. The two groups evidently reproduce separately in the western Atlantic, and much less is known about the spawning of the smaller fish (all of the "medium" size group, and the mature members of the "small" group) there.

The only occurrence of early stages of bluefin in the eastern North Atlantic, or the South Atlantic of which we have knowledge is the collection of a very few larvae near the Equator and longitude 7°W. Much more information will be needed to determine the significance of this unexpected finding.

Other collections of larvae, although less important than those from the Gulf of Mexico and the central Mediterranean, indicate that bluefin spawn around the Balearic Islands, in the Black Sea, in the Straits of Florida and, probably, north of the Bahamas.

Studies of the maturity of gonads suggest spawning over more extensive areas. These would include major spawning along the coasts of Tunisia and Tripolitania, and in the Ibero-Moroccan Bay (by the fish which do not enter the Mediterranean to spawn). Spawning in the Bay of Biscay is also indicated but this is probably less important. Gonad studies in the western Atlantic suggest, extensive additional spawning areas off Cuba, the Bahamas, and the southeastern United States along the Gulf Stream front north and east of Cape Hatteras.

Juárez (1974b) and Montolio and Juárez (1977) provided quantitative estimates of the numbers of bluefin larvae in extensive areas of the Gulf of Mexico. Richards (1976) estimated the number of fish in the spawning stock from the estimated number of larvae (Juárez 1974b). His figure was in reasonable agreement with those calculated by other methods.

No quantitative estimates of the abundance of bluefin tuna larvae in the Mediterranean have been published. C. Piccinetti (personal communication), however, informed the senior author that the relative abundance of larvae in the Gulf of Mexico, as indicated by Montolio and Juárez (1977), was much less than that which he and his colleagues had found in parts of the Mediterranean.

VI. MIGRATIONS AND STOCK IDENTIFICATION

A. INTRODUCTION

Identification of Atlantic bluefin tuna stocks is regarded as one of the most important prerequisites to the efficient management of its fisheries. The studies of stock identification and migrations are so closely related as to be almost inseparable. Some methods, such as the visual or electronic tracking of fish, and the analysis of the seasons and localities of catches, relate primarily to migrations. Others, such as biometric and biochemical studies, are more directly concerned with stock identification. Tagging is one of the most positive methods of studying both problems. In difficult cases, however, it is necessary to use all available means to achieve either objective. This is especially true of the bluefin tuna, whose long, rapid and variable migrations make their migratory patterns and populations especially difficult to identify.

Until 1954, when sustained tagging of the Atlantic bluefin was initiated, scientists were limited to deductive, or indirect, methods of studying its migrations. Likewise, until the development of biochemical methods at about the same time, they depended mainly on biometric studies to identify its populations. Even with the aid of these and other advanced techniques, the migratory patterns of bluefin tuna are not completely understood and the stocks have not been positively identified.

In this section we will consider the migrations and stocks (without a priori implication that they are separate) in the Mediterranean-eastern Atlantic area and in the western Atlantic. Finally, we will consider the implications of trans-equatorial and transatlantic migrations and present our conclusions in regard to the identity of stocks.

B. METHODS AND MATERIALS, AND DEFINITIONS

1. Methods and Materials

a. Deductive Methods

Deductions in regard to migrations and the identity of stocks have been based on observations or information of the following types:

- (1) The times of appearances and disappearances of the fish in fishing areas and the observed movements of the fisheries for it.
- (2) The size or age composition of the catches.
- (3) The sex ratio of the catches.
- (4) The observed behavior of the fish in specific areas and seasons.
- (5) The apparent preferences of the fish for environmental conditions, and their seasonal changes.
- (6) Deductions as to the localities where specially constructed hooks and lures found in bluefin tuna caught in traps had originated.

b. Methods Used Mainly for Identifying Stocks

Just as many of the above methods have been used to identify stocks as well as to study migrations, the following ones, which have been used primarily for stock identification, have also been applied to the study of migrations:

- (1) Anatomical comparisons.
- (2) Biometric comparisons of morphological characters.
- (3) Comparisons of biochemical properties.
- (4) Comparisons of areas and seasons of spawning.
- (5) Comparisons of growth rates.

c. Methods Used Mainly for Studying Migrations

Most of the methods listed below were developed to study migrations, but tagging is equally useful for identifying stocks:

- (1) Visual tracking from aircraft. [Visual observations from vessels or shore come under item a(4).]
- (2) Tagging.
- (3) Tracking with sonar.
- (4) Tracking with sonic tags.

d. Development of Bluefin Tuna Tagging

Tagging is the only positive method of determining that an individual fish has gone from one place to another. The desirability of tagging Atlantic bluefin tuna was recognized long ago (Sella 1912b), but the technical difficulties were such that it was not accomplished on a continuing basis until 1954 (Mather 1960, 1963). Sella (1927) tagged 20 bluefin tuna weighing from 4 to 20 kg off Gallipoli (southern Italy) in 1912 with bands around the caudal peduncle, but no returns resulted. His (1927, 1929a) deductions of migrations from hooks and lures found in tuna caught in traps, however, aroused new interest in the problem. Methods of marking were discussed extensively at the "Conference of experts—" (Anonymous 1932b), and the tagging of bluefin tuna was strongly recommended. Large and small bluefin tuna were tagged off Portugal in the years 1931-1935 and 1960 (Frade and Dentinho 1935, Heldt 1938, Vilela 1960). Some large individuals were also tagged off Tunisia and Morocco (Heldt 1943). In addition Heldt (1932) distributed marked hooks to tuna fishermen at Groix, France, on the Bay of Biscay in 1927, 1928 and 1929. Many of the hooks and lures retrieved by Sella (1929a) from tuna which had been caught in Mediterranean tuna traps

were of the type ordinarily used in that bay. English sport fishermen, co-operating with F. S. Russell (1934a), left marked hooks in a number of giant bluefin tuna in the North Sea in 1933. Since no returns resulted from all of these efforts, interest in the matter subsided again.

The first successful tagging of Atlantic bluefin tuna was achieved by Westman and Neville (1942), who marked 23 small bluefin tuna with celluloid disc tags off New York Harbor during the 1941 fishing season. They obtained two returns in the same locality and season, after periods of less than 75 days at large. Interest in such matters of course ceased with the outbreak of World War II.

Cooperating sport fishermen used numbered hooks furnished by Schuck and Mather to mark giant bluefin tuna off the Bahamas in 1950 and 1951, and off Rhode Island in 1952 (Mather 1963). Rivas (1954) also used the numbered hook method to mark giant tuna off the Bahamas in 1952 and applied strap tags to the opercles of some of these fish, likewise utilizing the cooperation of rod and reel anglers. The only result from all these efforts was the return, about fifteen years after its recovery, of a numbered hook from a fish recaptured from Wedgeport, Nova Scotia. The release data for this hook, which had been sold by a tackle dealer in eastern Long Island, New York, had not been reported, and our efforts to retrieve this information were unsuccessful. The fish probably had been released, or broken free, off eastern Long Island, but of course this is uncertain.

Interest in tuna tagging was revived when the California Department of Fish and Game developed the dorsal loop tag and used it successfully on small Pacific tunas (Wilson 1953). Mather, with the cooperation of a few interested sport fishermen, proved the feasibility of marking small Atlantic bluefin with the dorsal loop tag in Massachusetts waters during the 1954 fishing season. He concurrently developed the dart tag, with which even very large fish could be marked rapidly once they were brought alongside the boat (Mather 1960, 1963). The successful

Cooperative Game Fish Tagging Program of the Woods Hole Oceanographic Institution, which has been conducted jointly with the National Marine Fisheries Service since 1974, developed from these beginnings. Subsequently agencies in other Atlantic and Mediterranean nations have marked bluefin tuna and other large pelagic species with interesting and important results.

e. Summary of Bluefin Tuna Tagging Programs

A summary of the more important programs, with the major areas and dates of operation and major literature references for each, follows:

Canada — Fisheries Research Board of Canada (now Environment Canada).

St. Andrews Biological Laboratory — Northwestern Atlantic-1963-present, Beckett (1970), Burnett et al. (1977).

France — Institut Scientifique et Technique des Pêches Maritimes-Bay of Biscay and Portugal-1968-present, Aloncle (1973).

Italy — Centro Sperimentale della Pesca-Tyrrhenian Sea-1962-present, Arena and Sarà (1967), Arena and Li Greci (1970).

Morocco — Institut des Pêches Maritimes du Maroc-Atlantic coast of Morocco-1972-1973, Lamboeuf (1975).

Norway — Fiskeridirektoratets Havforskningsinstitutt-West coast of Norway-1957-1962, Hamre (1965).

Spain — Instituto de Investigaciones Pesqueras — Cadiz area, Spain-1960-1967, Rodríguez-Roda (1963, 1964c, 1969a).

United States of America — Woods Hole Oceanographic Institution and National Marine Fisheries Service — Northwestern Atlantic and adjacent waters-1954-present and 1974-present, respectively, Mather (1960, 1962, 1969, 1974a), Mather et al. (1967, 1974b), Mason et al. (1977).

The results of tuna tagging have been summarized and briefly described by the FAO Panel of Experts

for the Facilitation of Tuna Research (1972), Mather and Mason (1973, 1976), Mason (1975), and Mason et al. (1977).

2. Definitions

Direct migration—This term is used to designate the movement of a fish which presumably could not have been repeating an annual migratory pattern when recaptured. It does not imply that the fish has travelled on a straight course from one point to another.

Trap fisheries—Special terms of the trap fisheries have been defined in Section IIB4.

3. Hypothetical Migration Model

Subject to some variations between successive ages and overlaps between age groups, and some regional differences, we believe that the basic migratory behavior of the bluefin, through its life in the Atlantic, may be summarized by age groups as follows:

Very Small Fish (Less Than 2.5 kg, and Age 0) — Development from egg to active predator is extremely rapid. Hatching occurs within two days. The larvae become active swimmers in 15 days, and a length of 30 cm may be attained within three months. The first important movement of the newborn fish is one of concentration. They migrate from extensive spawning areas to limited nursery (feeding) grounds. Growth during their first winter is much slower than it was during the warm season.

Small Fish (2.5-32.0 kg, Ages 1-4, Immature) — These fish make annually repeated two-phase migrations between limited warm season coastal nursery areas and little known, but presumably more extensive, cold season wintering areas. The warm season occurrence is typically in the surface layers, with heavy feeding and rapid linear growth, but no decrease in the length-weight ratio. The winter sojourn, on the other hand, occurs at deeper levels, and growth virtually ceases.

Consequently, feeding and general activity are presumed to be greatly reduced. The migratory behavior of mature individuals in this group often resembles that of the medium fish.

Medium Fish (32-122 kg, Ages 5-8, Mature)— These fish make annually repeated three-phase migrations between warm season feeding areas, deep water wintering areas, and late spring spawning areas. The warm season distribution is more extensive than that of the small fish, and not as limited to coastal waters. This occurrence is again frequently in the surface layers, but not as predominantly so as that of the small fish. Feeding is heavy. Seasonal linear growth has not been determined, but is presumably rapid. The length-weight ratio decreases considerably during this period. The cold season distribution is much wider than that of the small fish, extending far into oceanic waters. These fish then remain in the subsurface layers and it is assumed, but has not been demonstrated, that their feeding, activity and growth are reduced. In late spring and early summer, many of these fish concentrate in spawning areas which are little known. After spawning they return to the warm water season feeding areas.

Large or Giant Fish (Over 122 kg, Age 9 or Older, Mature)— The fish make three-phase migrations basically similar to those of the medium size group, but their distribution and migrations are much more extensive. Their spawning and migratory periods, as well as the areas concerned, while differing somewhat from those of the medium group, overlap or coincide with them to a considerable degree. The seasonal linear growth of these fish is not known, but their length-weight ratio decreases greatly during the feeding season, and increases correspondingly during spawning and their post-spawning migrations. As with the smaller groups, their feeding, general activity and

growth are presumed to be reduced during their wintering period in deep waters. Movements within some of these seasonal habitats have been observed, as well as the migrations between them.

We shall discuss the migratory patterns of the different size groups of bluefin tuna in terms of this simplified model.

C. STUDIES OF MIGRATIONS AND STOCK IDENTITY

1. Mediterranean and Eastern Atlantic

a. Introduction

The earliest speculations and hypotheses about the migrations of bluefin tuna, and in fact nearly all of those before 1920, were concerned with the Mediterranean and eastern North Atlantic areas. In fact, the study of these migrations undoubtedly developed from observations made during fishing operations in the Mediterranean and its approaches during the pre-Christian era. Traps similar to those still in use apparently existed then, but movable nets, whose successful operation required the assistance of watchers (*thynnoscopi*) situated at coastal vantage points, were probably more numerous (Parona 1919, Thomazi 1947). Both methods depended on the movements of schools of fish along the coasts, which occurred mainly during the runs of maturing (now known as "arrival") tuna in May and June, and post-spawning (now known as "return") fish in July and August. Therefore, before recapitulating the development of hypotheses on the migrations and populations of tuna in this region, we will summarize some of their local movements which have been indicated over the ages by the operations of the traps which have harvested these periodic passages. Basic data which will be considered include the location of the traps, the direction from which fish must approach them, and the periods when they catch tuna. The relative importance of their catches will be discussed in special cases.

Sarà (1964, his Figure 5) showed the approximate locations of the significant traps still in use in the early 1960s, indicating, for each, the fishing period and the direction from which the fish entered the trap. The data for those in the Ibero-Moroccan Bay and the extreme western Mediterranean (Figure 45) strongly suggested eastward movements from the Atlantic into the Mediterranean ("arrival") in May and June, and movements in the opposite direction ("return") in July and August. The arrays of "arrival" traps on the sides of the Bay terminated at Tarifa (north coast) and Cape Spartel (east coast), showing that the "arrival" run extended at least up to the very threshold of the Strait of Gibraltar.

Data for the "return" traps suggested that some west-bound tuna followed both coasts of the Mediterranean as they approached the Strait. In the Ibero-Moroccan Bay, however, they occurred in much greater strength along its northern (Iberian) coast, in contrast to the complete absence of a "return" trap fishery along its eastern (Moroccan) coast.

The other important group of traps shown by Sarà (1964) was in the central Mediterranean. Most of these fished the "arrival" run only. The indications from the dates and directions in which the fish entered the traps were as follows.

Off Tunisia, the "arrival" tuna apparently travelled eastward from Bizerte to the Cape Bon peninsula, which they rounded, then moved southward to Ras Kapudia. "Arrival" bluefin also evidently moved eastward along the Libyan coast, from Zuara near the Tunisian border to Cape Misurata (longitude 15°E).

The situation around Sardinia, Sicily, and Italy differs because of the disjointed configuration of the coasts. The "arrival" fish tended to move in southerly directions along the western shores of Sardinia, and also along the Calabrian coast in the Gulf of Sant' Eufemia. With local exceptions at its two extremities, "arrival" fish travelled westward along the north coast of Sicily, following the western sides of bays and the eastern sides of promontories along the way. This westward movement is

directly opposite to the usual "arrival" pattern.

The "return" situation is much simpler. Tuna apparently swam southward along the southern half of the east coast of Sicily, and westward along the western half of its southern coast.

The above discussion is obviously simplified, and is only intended to show trends in the movements of the tunas. There have been many varying opinions on how the tuna approach the coasts and enter the traps (Scaccini and Pacagnella 1965). We do not mean to imply that the entire mass of fish in a given area follows the route described, but only that many fish in the respective areas tend to travel in the stated directions.

Most of the early theories on the migrations were based mainly on information of the type which has been summarized above. It should be noted, however, that the European fisheries have a very ancient history, whereas most of those in Africa originated in modern times.

The theories on migrations of bluefin, developed largely from studies of the trap catches, and later from consideration of environmental factors as well, varied from Aristotle's (circa 325 B.C.) view that the bluefin was an Atlantic species which occupied the Mediterranean only on its way to and from its supposed spawning grounds in the Black Sea, to the concepts of Pavesi (1889), Sanzo (1910a), Roule (1914a), F. de Buen (1925), and Scordia (1938) that the Mediterranean and Atlantic bluefin constituted entirely separate populations. Pavesi (1889) thought that the Mediterranean bluefin was an abyssal animal, rising from the depths of that sea and moving to nearby surface waters only to spawn. Bounhiol (1911) shared in the concept of a strictly Mediterranean bluefin stock but believed that its apparent migrations were actually the result of a tendency to swim against the wind-driven currents. Roule (1914a) felt that the bluefin was a pelagic creature which migrated only within the basin of the Mediterranean in which it lived. He believed that its spawning migrations were controlled by the temperature and salinity of the wa-

ter. Scordia (1938) and others (Ninni 1922, Genovese 1957) thought that there were two or more stocks of bluefin within the Mediterranean, each native to its particular basin. Some authors even questioned whether bluefin tuna actually occurred in the Atlantic (except in the Ibero Moroccan Bay) in significant numbers, or whether the bluefin reported from the Atlantic were of the same species as those in the Mediterranean.

These theories were predominant in the late 1800s and early 1900s, until Sella (1926a, 1926b, 1927, 1929a, 1929b, 1930, 1932a, 1932b) hypothesized several migrations from various Atlantic areas and from the Sea of Marmara into the Mediterranean, as well as between the different basins of that sea. He deduced these migrations by determining the localities where hooks and lures found in bluefin, which had broken lines or leaders and subsequently been caught in traps, were in general use. In that period, tuna fishermen used hooks and lures which were handmade locally. Distinctive designs and methods of attachment to lines or leaders made hooks and lures from different localities easily recognizable. Thus it might be assumed that a fish found carrying a hook or lure typical of a given area had come from that area. In some cases, this probability was greatly increased by many findings, indicating similar migrations. This somewhat uncertain method was followed by the more positive ones of sonar tracking (Lozano Cabo 1959a, 1959b) and tagging (Rodríguez-Roda 1964c, 1969a; Hamre 1965, Arena and Li Greci 1970, Aloncle 1972, Lambouef 1975). Studies of the effects of environmental conditions on the occurrences and behavior of tunas, particularly during the spawning season, and analyses of the time, location, quantity and size composition of catches, continued to provide deductive indications in regard to migrations concurrently (J. Le Gall 1929, J.Y. Le Gall 1974, Hamre 1958, 1962, 1965; Lozano Cabo 1958, Rodríguez-Roda 1963, 1964a, 1969b, 1970a, 1970b; Aloncle 1964, Arena 1964, Sarà 1964, 1973; Tiews 1964).

Numerous biometric comparisons of morphometric and meristic characters of bluefin tuna from various areas were carried out to identify populations or races (Frade 1931, Arico and Genovese 1953, Nedelec 1954, Genovese 1957, 1958). More recently, some genetic and biochemical research has been undertaken for the same purpose (Keyvanfar 1962, Lee 1965, 1968).

Despite all of these efforts, uncertainties about the migration patterns and the identity of the stocks in the eastern Atlantic and the Mediterranean still exist.

b. Migrations Between the Mediterranean and the Eastern Atlantic

Unit stock or two stocks? — The question of whether the bluefin tuna constitute a single stock which migrates from the Atlantic into the Mediterranean to spawn and then out again, or comprise two stocks — one Atlantic and one Mediterranean — has been debated for decades. This discussion led to such terms as the "migratory" or "sedentary" tuna, (referring to the supposed habits of the fish) and the "unitists" or "dualists" (referring to the theories on the number of stocks).

Ancient trap fisheries in the Mediterranean Sea and its approaches were based on the spawning runs of the larger bluefin: an eastward "arrival" run, mostly of fat fish with ripening gonads, in May and June and a westward "return" run, mostly of lean spent fish, in July and August. These runs were the basis of the Aristotelian theory, that the bluefin was essentially an Atlantic species, but passed through the Mediterranean in May and June to spawn in the Black Sea, and returned to the Atlantic in July and August. This theory has been accepted, wholly or in part, by nearly all of the trap fishermen to this day, and also by many scientists.

Objectors (Pavesi 1887, 1889; de Bragança 1899, Sanzo 1910a, Roule 1914a, 1914b, 1917, 1924; F. de Buen 1925, 1931; O. de Buen 1924, Scordia 1938) noted that bluefin spawned in the Mediterranean and that individuals of all sizes were present in it throughout the year. They also maintained that the lag which

would have occurred between catches in "arrival" traps located in westerly areas and those in easterly areas, if all were fishing a single group of fish moving eastward, did not exist. Roule and F. de Buen used the relatively poor bluefin catches in the Sea of Alboran (just east of Gibraltar) as another argument against a large scale spawning migration of bluefin from the Atlantic into and out of the Mediterranean. Both of these scientists cited the sensitivity of the bluefin tuna to environmental conditions as evidence that they could not pass through the relatively cold (R. de Buen 1927) waters of the Strait of Gibraltar, especially during the spawning season. Roule (1917) proposed the "halothermic" theory, maintaining that the bluefin were "stenotherms" and "stenohalines", and sought the warmest and most saline waters during the spawning season. F. de Buen (1925) opted for the "thermic" theory, considering water temperature to be the dominant factor controlling the tunas' movements. Both agreed, as did most students of the subject in the Mediterranean and adjacent Atlantic waters, that the sensitivity of the bluefin tuna to the environment increased during the period of maturation.

Scordia (1938) also believed in the "sedentary" tuna theory and felt that few, if any, bluefin tuna entered the Mediterranean from the Atlantic. Like Roule (1914a, 1914b, 1917) and F. de Buen (1925), she stressed the increased sensitivity of the maturing tuna to its environment.

Sella (1929a) showed, however, that bluefin tuna could withstand extreme changes in temperature and salinity during their feeding period. He maintained that even during the spawning period they sought specific conditions which varied with size of fish, rather than maxima as proposed by Roule (1917). He further argued that the "thermic" or "halothermic" barrier of F. de Buen (1925) and Roule (1917) did not constitute proof that bluefin could not pass through the Strait of Gibraltar, but would be an explanation of such a situation, if its existence were substantiated.

Sella noted, as Sarà (1964, 1973) and Scaccini et al. (1975) did later,

that there were relatively few large bluefin in the Mediterranean except during the spawning migrations and that the arrival fishery actually did begin later in the season in proportion to how far east the traps were located.

After this long period of indirect studies, Sella's (1927, 1929a) finding of 25 Atlantic hooks and lures in tuna caught in Mediterranean traps revived the "migratory" or "unit stock" theory. The items recovered included 13 from Tarifa, seven certainly and two probably from the Bay of Biscay, two from the Azores, and one from south of Ireland. These startling revelations did not pass unchallenged in this period when the "sedentary tuna" theory was deeply rooted in the minds of nearly all the scientists concerned with the problem. F. de Buen (1931) and Scordia (1934) questioned Sella's deductions, on the grounds that fishermen from the localities where the hooks and lures were made might actually have used them while travelling in other areas. Although they admitted that a few such migrations might occur, they maintained that they probably were not related to the spawning cycle, and were relatively insignificant numerically. Sella (1929a) had already pointed out, in support of his hypothesis, that the findings of the hooks varied according to the intensity of fishing in the area of their origin. When the fishery off Tarifa was important, numerous hooks of the very distinctive type used there were recovered in the Mediterranean. After the fishery off Tarifa had declined drastically, and the one in the Bay of Biscay had increased greatly, hooks of the former area were no longer found, but hooks of the Biscay type appeared in numbers. Sella also noted that, considering the enormous odds against recovering a lost hook in a tuna, the numbers of findings indicating these migrations were too large to be attributable to casual fishing by transients.

Detailed information on the movements of bluefin tuna in the Strait of Gibraltar obtained by echosounder was reported by Lozano Cabo (1959a, 1959b). In 2,000 miles of cruising in the Strait, and as far as

Barbate and Cadiz, Spain, and Larache, Morocco, in June and July 1957, he obtained data which he considered sufficient to provide interesting conclusions on the biology of the species.

Lozano Cabo (1958) had suspected that bluefin, at least during their spawning migration, might be negatively rheotactic (tending to swim with the currents). The detection of schools confirmed this. The greatest number of "arrival" schools were found in the middle of the Strait, where the current always favored their eastward passage. Many schools were also found on the northern side, where the current was usually favorable, but they were very rare on the Moroccan side, where the currents tended to vary with the tides. The depth at which the schools traveled was difficult to determine, but appeared to be somewhat less than 60 m.

The migration route of arrival at the Strait when departing from the Atlantic followed the Spanish coast. Some schools were located between Cape Spartel and Cape Malabata (on the southwestern side of the Strait), but none were detected south of Cape Spartel during numerous cruises between Tangier and Larache. Perhaps the tuna which came from the African coast partially crossed the Strait from off Cape Spartel toward Tarifa, and joined those coming from the Spanish coast, or followed routes similar to theirs through the Strait. The schools which had tended to concentrate in the center of the Strait while traversing it appeared to disperse as they entered the Mediterranean at the Ceuta-Algeciras line.

In general, the migrating tunas appeared to prefer temperatures of 18°C to 21°C, but deviations from the preferred temperature were more frequent in the Strait than at the traps. Lozano Cabo attributed this to the overcoming of temperature sensitivity by the reproductive urge. Nearly all previous scientists (Roule 1914a, Sella 1929a, Scordia 1938) had maintained that the sensitivity of the bluefin to temperature and salinity was greatly increased during the spawning period in contrast to the "erratic" (feeding) period. In any case, Lozano

Table 27. Release and recapture data for bluefin tuna tagged in the Gulf of Cadiz, Spain and off Sicily with size at recapture and months* at liberty.

Return Number	Release Area	Release Location	Release Date	Recapture Area	Recapture Location	Recapture Date	Length (cm)	Weight (kg)	Months at Liberty
1	Sancti-Petri	36° 22' N 06° 16' W	V-1960	Portugal	37° 00' N 07° 36' W	V-1960	170	110	0.0
2	Barbate	36° 09' N 05° 56' W	V-1960	Spain	36° 09' N 05° 20' W	VII-1960	173	90	2.1
3	Barbate	36° 09' N 05° 56' W	VII-1960	Spain	37° 07' N 07° 07' W	VIII-1960	174	70	0.4
4	Barbate	36° 09' N 05° 56' W	V-1960	France	43° 30' N 03° 56' E	VIII-1960	136	41	2.8
5	Barbate	36° 09' N 05° 56' W	VII-1960	Portugal	36° 50' N 07° 54' W	V-1961	190	120	10.0
6	Barbate	36° 09' N 05° 56' W	VII-1960	Morocco	35° 12' N 06° 10' W	VI-1961	—	100	10.4
7	Barbate	36° 09' N 05° 56' W	VI-1961	Spain	35° 52' N 05° 15' W	VII-1961	195	83	0.6
8	Barbate	36° 09' N 05° 56' W	VII-1961	Portugal	37° 00' N 07° 36' W	VII-1961	—	90	0.1
9	Barbate	36° 09' N 05° 56' W	VII-1961	Spain	37° 07' N 07° 07' W	VII-1961	—	—	0.2
10	Barbate	36° 09' N 05° 56' W	V-1962	Portugal	37° 00' N 07° 36' W	V-1962	133	44	0.1
11	Barbate	36° 09' N 05° 56' W	VII-1960	Morocco	35° 12' N 06° 10' W	V-1962	199	136	22.1
12	Barbate	36° 09' N 05° 56' W	VII-1960	Morocco	35° 12' N 06° 10' W	VI-1962	185	162	22.5
13	Barbate	36° 09' S 05° 56' W	VIII-1962	Portugal	37° 00' N 07° 36' W	VIII-1962	—	70	0.4
14	Barbate	36° 09' N 05° 56' W	VIII-1962	Morocco	31° 30' N 09° 50' W	XII-1962	—	175	3.2
15	Barbate	36° 09' N 05° 56' W	VII-1965	Portugal	37° 00' N 07° 36' W	VII-1965	220	270	0.2
16	Barbate	36° 09' N 05° 56' W	VIII-1967	Spain	37° 30' N 01° 00' W	VIII-1967	165	120	0.8
17**	Barbate	36° 09' N 05° 56' W	—	Libya	32° 58' N 13° 12' E	V-1965	—	—	—
18**	Barbate	36° 09' N 05° 56' W	—	Libya	32° 58' N 13° 12' E	V-1965	—	—	—
19	Punta Raisi	38° 08' N 13° 22' E	V-1968	Spain	40° 00' N 00° 00'	X-1969	—	45	16.6

*0.0 indicates less than 1.5 days.

** These tags were not returned. The recoveries were reported without the tag numbers.

Figure 71. Geographic distribution of bluefin release and recapture data shown in Table 27.

Cabo has apparently provided first-hand evidence against the existence of the thermal or halothermic barrier to maturing bluefin at the Strait postulated by Roule (1914a), F. de Buen (1931) and others.

The sizes of schools were also difficult to determine. Lozano Cabo estimated that one of the largest schools, observed on June 21, 1957, between Algeciras and Tarifa, Spain, occupied about 7,200,000 m³. If the fish were 20 m apart in all dimensions, their number would have been 1,922. If the spacing were reduced to 10 m, the number would be 11,163.

Lozano Cabo estimated the average speed of the schools at less than 7 knots (13 km/hr). He pointed out that, although the schools observed in the Strait were numerous and large, it should be recalled that 1957 was a very good tuna year.

Some uncertainties may exist in regard to the actual origin of Sella's (1927, 1929a) hooks and the identity of Lozano Cabo's (1959b) sonar targets, but Rodríguez-Roda (1963, 1964c, 1969a) provided indisputable proof of bluefin tuna migrations from

the Atlantic into the Mediterranean. He marked 312 bluefin tuna, ranging from 60 to 220 cm in length, from catches in traps near Cadiz, Spain, in 1960-1968. Four of these fish were recaptured in the Mediterranean and 15 in Atlantic waters off southern Spain and Portugal and western Morocco (Table 27, Figure 71).

The Mediterranean returns are of special interest, in view of the long debate as to whether or not important numbers of bluefin tuna migrated through the Strait of Gibraltar. Two of the fish were recaptured at La Linea and Ceuta, Spanish ports on the north and south sides of the Mediterranean outlet of the Strait, respectively, and about 40 nautical miles (64 km) from the release point. The other two, recaptured off Cartagena, Spain, and Palavas, France, had penetrated much more deeply into the Mediterranean, 270 and 675 nautical miles (431 and 1,080 km) respectively, from the release point. Three of the releases were in May and June, during the "arrival" run when the fish are supposed to be travelling eastward. The fourth, how-

ever, was during the "return" run, when they are thought to be travelling westward. The recaptures were all in July or August, during the "return" run. Times at large varied from 19 to 23 days, and the weights of the fish were 41, 83, 90 and 120 kg (medium size range). These returns demonstrate conclusively that some bluefin enter the Mediterranean from the Atlantic. They also suggest that some of these fish return to the Atlantic, since the traps at La Linea and Ceuta, at the extreme western end of the Mediterranean, are designed to fish the "return" (westward) run only.

The recovery of two Spanish tags from bluefin tuna caught in a trap near Tripoli, Libya, was reported, but the tags have not been returned, nor have their numbers been ascertained (Rodríguez-Roda 1969a).

The Atlantic recaptures (15) were much more numerous than those in the Mediterranean (4), but the probability of recapture of a tagged bluefin seems to have been much greater in the Ibero-Moroccan Bay than in the western Mediterranean. The fisheries in the former area took many more bluefin in the period 1960-1967 than those in the latter. Much more tagging is needed to evaluate the migrations between the Atlantic and the Mediterranean quantitatively.

Much meristic and morphometric data on bluefin tuna from various areas of the eastern Atlantic and the Mediterranean are available, and several comparisons of the data for fish from different localities have been made (Tiews 1963). Sella (1929a, 1930) noted that he had made several observations on tuna from Spain, Calabria (Italy) and Tripoli (Libya), without finding differences sufficient to justify any racial demarcation. He did not, however, publish these data. Frade (1931) concluded that there were significant differences between the tuna which he had examined on the Portuguese coast and those which Heldt (1927b) had measured in Tunisia. Nedelec (1954) compared morphological data from bluefin tuna captured in the North Sea, off southern Portugal and off Tunisia. He concluded that the North Sea samples were close to those from Portugal, but that both differed considerably

from those from Tunisia in many characters. Arico and Genovese (1953) and Genovese (1957, 1958) compared morphological data for spawning and feeding tunas taken off northeastern Sicily with similar data for bluefin taken off Tunisia and southern Portugal and in the North Sea. They concluded that the two Sicilian samples were from a single Tyrrhenian stock which was distinct from the fish from the other three areas and also from smaller samples taken off the Mediterranean coast of France, and off Algeria.

Tiews (1963) summarized, compared and discussed these data and studies. He found that only the differences in head length, pectoral fin length and number of finlets support the case for the existence of separate stocks on the European side of the Atlantic. In view of the long and rapid migrations of bluefin demonstrated by tagging experiments, however, he did not believe that the above differences would stand up under critical inspection. He predicted that further studies would prove the existence of a single bluefin population in the eastern North Atlantic.

Genetic and biochemical characteristics of bluefin tuna from the eastern Atlantic and the Mediterranean have also been investigated and compared. Keyvanfar (1962) studied the serology and immunology of bluefin tuna from the Atlantic and Mediterranean coasts of France. Individual differences in immunology between Mediterranean samples were found but the samples were too few in number, particularly those from the Atlantic, to furnish any interpretation on migratory tendencies. Lee (1965) provided further information on the serology and immunology of the bluefin from the French Mediterranean coast and (1968) comparisons of the immunology of bluefin tuna from the eastern Atlantic (30 specimens) and the Mediterranean (72 specimens). Lee found individual differences even within the samples from the Atlantic and those from the Mediterranean. She also found that the percentage of individuals with no antigens and those with one or several differed in the two lots. She concluded that one might consider the

presence in the Gulf of Lion (Mediterranean) of certain individuals which belong to a race or to a population different from that observed in the Bay of Biscay.

These biometric and biochemical studies provided interesting information, but, in our opinion, they were inconclusive in determining whether the bluefin in the Mediterranean and eastern Atlantic constituted a single or separate stocks, or to what degree mixing occurred.

In summarizing his extensive studies of the fisheries and migrations and other aspects of the biology of the species, Sella (1929a, 1930) proposed the following four phase migratory cycle for bluefin tuna:

- a. Gathering of bluefin in May-June in relatively limited spawning areas in the southern part of its range (Mediterranean, Ibero-Moroccan Bay)
- b. Post-spawning dispersion, mainly northward, with the maximum extension of their habitat occurring in the warmest part of the summer and autumn.
- c. New reduction in habitat with the coming of winter. This distribution was not well known, because the fish were farther below the surface, but was presumed to be considerably reduced, with major withdrawal from the more northerly area.
- d. In March-April, immediately preceding the reproductive period, the tuna made another northward migration which was much more limited than that in summer-autumn. They appeared en masse off the north coasts of the Mediterranean and the Spanish coast of the Bay of Biscay.

The subsequent development of fisheries covering nearly all suitable waters of the Atlantic, and modern research, including tagging and tracking with sonar, have shown how accurate Sella's concept was. The only dubious point is his fourth phase, the pre-spawning northward migration. This probably consists of immature fish and the younger mature ones, concerning whose spawning habits little was known then (Sella 1929a),

or indeed, even now (Sarà 1973). Both authors indicated, however, that these smaller reproducers spawned later than the larger ones.

Sarà (1964, 1973) has proposed a hypothesis which reconciles many of the seemingly contradictory facts in regard to the relationships between eastern Atlantic and Mediterranean bluefin tuna. He believed that a number, determined by the environmental conditions existing then and in the preceding few weeks, of large (over 100 kg) bluefin tuna gathered in the Ibero-Moroccan Bay in late April and early May, "hesitating" (Lenier 1959) there. Then a portion of these, the number again dependent on environmental conditions, entered the Mediterranean to spawn, and subsequently returned to the Atlantic.

Lozano Cabo (1958) and Aloncle (1964) showed that the average sizes of the bluefin taken in the Atlantic traps, both in Morocco and along the south coasts of Portugal and Spain, varied inversely with the distance of the trap from the Strait of Gibraltar. The largest bluefin (by average weight) have been taken by the traps of Tarifa and Cape Spartel, at the very entrance to the Mediterranean. Actually, more small fish were taken in the more westerly and southerly traps. This was a good indication that the larger bluefin were more apt to enter the Mediterranean than the smaller ones, just as Sarà (1973) hypothesized.

Sarà (1973) stated, moreover, that daily catch records collected continuously during the fishing seasons for several years showed that the first catches of the Cape Spartel trap, at the entrance of the Strait, consistently preceded the first of the traps off western Sicily by from seven to nine days. This 900 nautical mile (1,675 km) itinerary would require average speeds between 4.2 and 5.4 knots (7.7-10.0 km/hr). This range does not differ greatly from the migrating speeds observed by Lozano Cabo (1959b), less than seven knots (13.0 km/hr), and by Rivas (1955, 1976), four knots (7.4 km/hr), or from the average speed of a giant bluefin which migrated from the Bahamas to Norway in 50 days (Mather 1969), 3.5

knots (6.5 km/hr). These facts refute the argument that no lag between the catches in the respective localities existed, or that it was so short that impossible speeds would have been required for a tuna to have accomplished the implied migration (Pavesi 1887, 1889, Roule 1925). This information, combined with Sella's (1929a) findings of Atlantic hooks and lures in tuna caught in the Mediterranean and the tag returns showing similar migrations by Rodríguez-Roda (1969a), strongly supports the old concept that numerous large bluefin migrate from the Atlantic into the Mediterranean in May and June. The departure of large bluefin from the Mediterranean in the "return" period, July and August, has been indicated by rather small catches in the "return" traps near the eastern end of the Strait (see Section IVC6a). The modest size of these catches in comparison with those of the Ibero-Moroccan Bay traps may be explained by Sarà's (1973) hypothesis in regard to the depths at which the bluefin travel in the respective migratory periods. He maintained that the "arrival" fish swam in the surface layers, following the inflowing Atlantic current. This is in accord with the findings of Lozano Cabo (1959b) during his sonar survey of the Strait. Sarà (1973) assumed that, on the other hand, the "return" fish swam at deeper levels, following the outflowing Mediterranean current. He cited a new fishing technique used in the Sicilian Channel as evidence of this (see Section VIC). Sarà believed that this tendency to follow the deep current persisted until the gonads had shrunk and the feeding urge became predominant. This might occur more readily after the fish had emerged from the Strait into the Atlantic, where the velocity of the Mediterranean current diminishes rapidly. The Mediterranean "return" trap at La Linea, on the European side of the Strait, usually caught more large bluefin than those on the African side. This is in accord with the tendency of the "return" tuna to follow the European coast of the Ibero-Moroccan Bay closely, as evidenced by the formerly large "return" catches taken there, in contrast to the lack of "re-

turn" trap fisheries along its African coast.

Sarà (1973) believed that the smaller bluefin (less than 100-150 kg) did not participate in this Atlantic-Mediterranean migratory pattern. He felt, as did Sella (1929a), that the immature individuals were relatively sedentary. He concluded that the individuals in this size range made longer migrations after reaching maturity but that those in the Mediterranean spawned there and those in the Atlantic reproduced in that ocean. At some period in their development as their weight approaches 150 kg, groups of these fish tend to join the groups of larger ones in their Atlantic-Mediterranean migrations. Sarà (1973) speculated that this change in life style is related to some change in the physiology of the animal, most probably the attainment of the full development of the swim bladder.

The sizes of the four fish tagged by Rodríguez-Roda (1969a) near Cadiz and recaptured in the western Mediterranean do not fully support Sarà's view in regard to the sizes of fish which usually follow this route. One of them weighed 120 kg, but the weights of the other three ranged from 41 to 90 kg. Only one of these smaller fish, however, could have accomplished this migration during the "arrival" period which Sarà (1973) was discussing. The results indicate that casual migrations through the Strait by bluefin of various sizes may occur at any time, but that the mass periodic movements are carried out mainly by large individuals.

One fact not explained by Sarà's (1973) theory is the continued productivity of the fisheries for small bluefin off the Atlantic coast of Morocco and in the Bay of Biscay (Section IVC5). Since there is no hard evidence of extensive spawning of bluefin tuna in the Eastern Atlantic (Section VD2), important recruitment to these fisheries from the Mediterranean seems logical. F. de Buen (1925) hypothesized a migration of small bluefin from the Mediterranean to the Atlantic in the autumn of their second year of life when they weighed 4-5 kg. We believe that it is more probable that this migration occurs mainly in the autumn of their

first year of life, when they weigh about 1 kg. This ties in with the disappearance of age 0 bluefin weighing about 1 kg from the Mediterranean coast of Spain in October, and the regular appearance of age 0 bluefin weighing about 1.5 kg off the Atlantic Moroccan coast in the second half of November (Section IVC5). The massive catches of age 0 bluefin in the fall by the "return" traps and purse seiners at the western end of the Mediterranean (Rodríguez-Roda 1964b, 1969d; Crespo and Rey 1976) also suggest such a migration. In 1963, captures around Ceuta increased sharply in mid-September and remained high until late October, when they declined.

c. Migrations and Stocks Within the Mediterranean

Much has been written about the migrations and stocks of bluefin tuna in the Mediterranean Sea, but the tagging results required to reach definitive conclusions are still lacking. Deductive studies have led to widely diverging opinions, but a reasonable working hypothesis has emerged.

Since many of the pertinent studies have already been discussed in parts a and b of this section, they will be recapitulated briefly here, stressing the aspects which are relevant to migrations within the Mediterranean. According to Aristotle's (circa 325 B.C.) theory, the bluefin was essentially an Atlantic fish, but spawned in the Black Sea. Therefore it made the circuit of the Mediterranean by passing through it once, en route to the spawning ground, and again to return to the ocean.

Little new information was added until Cetti (1777) made two very important discoveries. One was that bluefin spawned near Sardinia. He surmised correctly, moreover, that more of them spawned in the central Mediterranean than in the Black Sea. His other major finding was that medium sized bluefin occurred in the Gulf of Sardinia throughout the year. He named these fish "golfitani", a term which is still in common use. He adhered to Aristotle's basic concept, however, and described several distinct routes by which he believed that the larger bluefin reached the

central Mediterranean. This last finding was criticized (Pavesi 1887), but recent evidence (Sarà 1973) indicates that it was surprisingly accurate.

Pavesi (1887, 1889), who was the first to seriously challenge the migratory theory, believed that the Mediterranean (and eastern Atlantic) bluefin spent most of the year in abyssal waters near their spawning grounds. His theory restricted their migrations to a vertical ascent to superficial water and a short horizontal migration to a nearby spawning ground in spring, and short horizontal return and a vertical descent into the abyss after spawning.

Sanzo (1910a) agreed with Pavesi (1887) in regard to the complete separation of the Atlantic and Mediterranean bluefin stocks. He had doubts, however, in regard to Pavesi's hypothetical bathymetric migrations. He recommended investigating the darkness or lightness of the coloration and other characteristics of the tuna when they first arrived at the traps to determine whether they had come from the abyssal depths or from the surface layers. He believed that spawning was independent of the coastal movements of the tuna, and that other causes of their comings and goings in the Mediterranean should be sought.

Bounhiol (1911a, 1911b) also believed that the Mediterranean bluefin tuna stock was separate from that of the Atlantic. He introduced a new concept, however, that the bluefin in the Mediterranean always moved against the wind-driven surface currents — the “hydrodynamic” theory. This theory has received scant support.

Ninni (1922) discussed hypothetical populations and migrations of bluefin tuna in the Mediterranean in considerable detail. He believed that the Tyrrhenian bluefin were independent of the Adriatic ones and that both were independent of those of the Aegean Sea, and that the last were at least partly independent of those of the Sea of Marmara. Ninni assumed each group had its own well defined wintering area. He shared the opinion of Pavesi (1887) that the bluefin tuna wintered in deep waters.

Ninni believed that the major eastward migration of bluefin tuna must have departed from the wintering area between Sardinia and Tunisia, passing along the northeastern coast of Tunis then along or offshore from the Tripolitanian coast toward Bengasi. There Ninni's personal observations ended, but he felt that the bluefin avoided the Nile outflow and turned toward Crete. Ninni thought that there was a wintering area around Crete, and possibly another between Crete and Alexandria, Egypt.

Ninni hypothesized that when the fish left the Cretan wintering area they split into two groups. The smaller group went up the western Aegean, passing between Euboea and the mainland of Greece and entering the Gulf of Volos. The larger group followed the Asiatic coast to the Dardanelles and into the Sea of Marmara and the Bosphorus, always leaving the islands on their left. They passed through the Bosphorus and “lost themselves” in the Black Sea. The passage into the Black Sea began March 15 and lasted into August, after which the “return” began, but not all of the bluefin went back into the Aegean. A large proportion of them wintered in the Sea of Marmara. Ninni's hypotheses do not lead to an annually repeated migratory cycle; in successive years the same fish might winter once between Sardinia and Tunisia, once near Crete, and once in the Sea of Marmara. Such shifts of habitat (or migratory pattern) are unusual.

Roule (1914a, 1914b, 1917, 1924) believed that the bluefin were pelagic or bathypelagic rather than abyssal, but he felt that their migrations were restricted to the particular basins of the Mediterranean which they occupied. He (1924) studied temperature and salinity observations made during the season of spawning assembly (May-June) in 1923 between southern France and Tunisia. He found that the line of maximum thermal increment ran directly from southern France to Tunisia, fitting his (1917) hypothesis that when the bluefin were absent from the former area, they were in the latter to spawn. He found that these observations supported his halothermic theory in re-

gard to water temperature, but showed no correlation in regard to salinity.

Sella (1927) disputed Roule's (1917, 1924, 1926) hypothesis that the tuna which occurred off the southern coast of France during the remainder of the year spawned in May and June near the traps off Sardinia, Sicily and Tunisia. He showed that the tuna caught off the southern coast of France averaged only about 20 kg, whereas those caught in the traps averaged from 70 kg to 130 kg. The differences between Roule's and Sella's opinions in regard to the sensitivity of the bluefin to the temperature and salinity of the water, and the effects of these factors on its distribution and migrations, have been discussed in Section VE2.

Scordia (1938) maintained that the bluefin tuna which she studied off eastern Sicily and the west coast of Calabria (southern Italy) were of a distinct and separate stock which she called the Tyrrheno-Ionian stock. She observed that these tuna remained mainly in the deep waters of the lower (southern) Tyrrhenian in autumn and winter, sometimes rising to the surface near Messina in the fall to feed. They surfaced in the spring with the warming of the waters to 18°C. When increased warming reduced the density *in situ*, from between 1.02700 and 1.02800 to about 1.02500, the tuna moved from the Tyrrhenian through the Strait of Messina into the Ionian Sea, where the density was higher. This occurred toward the end of May and in the first half of June. During June the continued warming reduced the density in the Ionian Sea. The tuna then returned to the deep waters of the Tyrrhenian where the density was suitable for them. They went a few at a time, with the large fish departing first, followed by smaller ones up to September. These movements, which constituted the “arrival” and “return” runs, were based on the sensitive reactions of the fish. At the beginning of their period of sexual maturity they underwent a reversal of their thermo-tactic reaction. During the winter they chose a water temperature of about 13.5-14.5°C, but with the approach of the spawning period, they became

thermophiles and sought surface waters of at least 18°C. The migrations were probably provoked by the "transgressions" of Atlantic water, which controlled their period and volume, and were independent of gonad condition (Scordia 1932).

The biometric studies of Arico and Genovese (1953) and Genovese (1957, 1958) supported Scordia's hypothesis of a distinct and separate Tyrrhenian-Ionian stock of bluefin tuna.

Sella (1929a) maintained that the Mediterranean bluefin could not be separated into autochthonous stocks corresponding to the various basins, as proposed by Roule (1917) and Ninni (1922). In addition to his Atlantic-Mediterranean results, Sella's (1927, 1929a) hook recoveries indicated that bluefin tuna were constantly moving from one place to another within the Mediterranean (see Heldt 1930a, his unlabeled figure). These findings will be considered in terms of three general areas of origin: the western Mediterranean, central Mediterranean, and the Bosphorus (Istanbul, Turkey). Hook items of Atlantic origin which were retrieved in the Mediterranean will be considered with those of the western Mediterranean, since the fish in which they were found could only have entered the Mediterranean through the Strait of Gibraltar.

Hook recoveries indicated extensive eastward migrations within the Mediterranean. Numbers in parentheses following deduced migrations show the number of such migrations revealed, if more than one. Items from Malaga were recovered at Arzeu, Algeria, and near Tripoli, Libya. One from Arzeu was found off southwestern Sardinia. Another, from Philippeville, Algeria, was retrieved at Sidi Daoud, Tunisia. More numerous and extensive eastward migrations were deduced from recoveries of fish with Atlantic hooks, whose Mediterranean movements must be considered to have begun at Gibraltar. These retrievals occurred off Sardinia (10 + 1 probable), Sicily (5), Gallipoli, Italy southeast of Taranto (1), Tunisia (4 + 1 probable) and Tripolitania (3). Thus movements from Gibraltar as far east as the heel

of the Italian boot on the north coast (longitude 18°E) and nearly to Cape Misurata on the south coast (longitude 15°E) are indicated.

Recoveries of single hooks or lures of central Mediterranean origin suggested that bluefin moved freely between the various fishing centers: Sardinia to Tunisia, Messina to Sardinia, and Palermo, Sicily, to the Aegades Islands. More numerous reported findings showed movements from the Strait of Messina to the "return" traps along the southern part of the east coast of Sicily, which captured fish travelling southward along the coast. The only movements to other regions were a westward one from Messina to Arzeu, Algeria, and a longer migration to the east and north, from Sicily or Tunisia to the upper Adriatic near Trieste, Italy.

More dramatic findings resulted from six recoveries of very distinctive and easily recognized lures used only in the vicinity of Istanbul, Turkey. Two of these recoveries indicated migrations to eastern Tunisia and southwestern Sardinia. Sella (1929a) considered the finding of four lures, each in a different individual caught in the same season and in the only trap operating in the area around Bengazi, Libya, as proof of the arrival of several schools coming directly from the Sea of Marmara and the Bosphorus. Despite these impressive findings, the tendency to split the Mediterranean bluefin into separate stocks continued for another 30 years.

The taggings of bluefin in the Mediterranean have not been sufficiently numerous to answer the questions which have been raised by deductive research. Arena and his colleagues marked 288 bluefin tuna off Sicily and the Aeolian Islands in the years 1963-1968 (Arena and Sarà 1967, Arena and Li Greci 1970, Arena 1971). Most of these were very small individuals (age 0, lengths 28-42 cm), but eight were adults weighing 28 to 60 kg (ages 4-5). Returns from four small fish and one adult have been recorded. The recapture of another small fish was reported but the tag was not returned.

The returns for small fish were from releases in October 1967. The

recaptures occurred after periods at liberty of 65 days or less and within distances of 150 km from the release points. One had passed through the Strait of Messina into the Ionian Sea, but the others had remained in the southeastern corner of the Tyrrhenian Sea. The unconfirmed recovery from a small tuna reportedly occurred within the general release area after a time at large of about 18 months. The adult tuna had made a longer migration, from off Punta Raisi near Palermo at the end of May 1968, to off Castellon, Spain, in mid-October 1969 (Figure 71). Its weight was estimated as 28-30 kg when released, and reported as 45 kg when recaptured 17 months later.

The returns from small fish suggest that their movements are quite limited, but the times at liberty were not sufficient, except in the case of the one unconfirmed recapture, to establish this as a definite tendency. The migration from Sicily to Spain by the larger fish, which was probably age 4 when released and age 5 when recaptured, supports Sella's (1929a) view that the mature bluefin travel freely about the Mediterranean, and refutes the concept of a distinct Tyrrhenian stock (Ninni 1922, Scordia 1938, Arico and Genovese 1953, Genovese 1957, 1958). Obviously, much more tagging in various parts of the Mediterranean is needed to solve the complex problems of the migrations and stock structures in that sea.

Sarà (1964, 1973) studied the behavior of bluefin tuna in the Mediterranean extensively. He believed that age 0 bluefin made only very limited local movements in the area where they were spawned. As they grew larger, they migrated farther, but always within the same basin, until they attained a weight of about 100 kg and joined in the Atlantic-Mediterranean migration. The results of tagging in the Mediterranean cast doubt on the hypothesis of a separate Tyrrhenian-Ionian stock (Scordia 1938, Arico and Genovese 1953, Genovese 1957, 1958).

Sarà (1973) described the migratory and distributional patterns of bluefin in the Mediterranean in terms of the size groups. He used size

groupings recommended at the "Reunion sur le Developpement et la Coordination de Programmes de Recherches sur le Thon en Mediterranee, Palermo 22-24/5/1967" (Anonymous 1968). These size ranges, which are quite similar to those we have used, were as follows:

large spawning tuna of over 150 kg,
medium spawning and feeding tuna of 15 to 60-70 kg,

very small tuna and small tuna of up to 15 kg which have not yet attained their first maturity.

Sarà believed that most of the large spawners which were observed from the end of April through all of August, were of the same stock, of which a portion, greater or smaller in relation to certain oceanographic conditions, entered the Mediterranean to spawn and, having accomplished this, returned to the Atlantic to reconstitute their biological reserves (Section VIC1b). The numbers of tuna "hesitating" in the Ibero-Moroccan Bay and the volume of water entering the Mediterranean determine how many of these tuna enter in a given year. These "arrival" tuna swim in the surface layers, following the branches of the Atlantic currents or its counter currents. These usually follow routes quite similar to the much-criticized ones proposed by Cetti (1777). Displacements of these branches of the currents by the winds, toward or away from the traps, has a critical effect on their catches.

These currents were illustrated by Sarà (1964, his Figure 1). The main current generally followed the African coast, bringing the tuna within range of the traps of Tunisia and Tripolitania. A west-flowing counter current brought the "arrival" tuna into the traps along the north coast of Sicily from the east, rather than from the usual westerly direction.

According to Sarà (1973), the "return" tuna swim in deeper layers, following the westward flow of the Mediterranean water. This current flows southward and westward along the east and south coasts of Sicily, where "return" traps were set until recent years. Sarà (1973) found evidence of this in the new night fishery

practiced in waters from south to southwest of the western end of Sicily. Dead bait was thrown into the water (chumming) to attract the tuna to the surface. There they fed on small live fish which had previously been drawn to the boat by powerful lights. The tuna were then vulnerable to capture by seining. These catches took place from late July until mid September.

Some large tuna remain in the Mediterranean through the fall and winter in areas of rich and available food, such as the islands of the Tuscan Archipelago, the area between the Aeolian Islands and the Strait of Messina, the Dardanelles, and Port de Bouc in the Gulf of Lion. The numbers of these fish are inconsequential in comparison with the great mass of migrating fish which occur in the period of reproduction.

The schools of large "Atlantic" tuna remain separate, according to size of fish, during the period of maturation. During the time of actual spawning, however, they mix temporarily with each other, and with younger Mediterranean fish of ages 4-7. The latter at other times remain altogether aloof from the larger fish, and, even during the reproductive processes, occupy other layers and areas when constrained together with them.

Medium and small fish weighing from 20 to 50 kg, with fringes of larger and smaller individuals, are seen and captured along the coasts of the Mediterranean countries throughout the year (Sarà 1973). These fish school very strictly according to size. They are seen closer to the coast in late summer and autumn, often on the surface in constant and furious pursuit of prey. They are present all year in certain locations near the coast where they can be observed and fished, even in bad weather, and the currents and geomorphology of the bottom are favorable, as at the Straits of Bonifacio, in the Adriatic, at the Aeolian Islands, at the Strait of Messina, at the Kerkennahs, and at the Dardanelles.

These fish have a different migratory pattern from the large ones and make limited spawning and trophic (feeding) migrations, within the

limits of each basin. Apparently it was their contemporaneous presence in several localities, and their habit of remaining off this coast or that one, that, years ago, led to the concept of various populations differing at the racial level. In the spawning period, they approach the coasts, aggregating with the schools of large Atlantic tuna with which they can mix only during the limited period of reproduction.

Sarà (1973) considers the small and very small tuna next. In the months from August through all of November, almost all of the Mediterranean Basin is occupied by great schools of young of the year. Remaining for a few months along any coast, one can see them grow day by day until in November they attain about 2 kg. After this, probably more because of bad weather than because of their departure, they are rarely captured. With the return of good weather, they are found again in the late winter months in almost the same places where they had been seen earlier, but now weigh 4-5 kg. The young tuna stay in the same areas, making small movements in response to meteorological conditions and in search of food. They remain sedentary until they attain their first sexual maturity, when they begin their first migrations about the Mediterranean.

Sarà's (1973) concept of the migratory and distributional patterns of bluefin tuna in the Mediterranean is very similar to Sella's (1929a) in regard to the large bluefin, which both consider to be essentially migratory, and the immature fish, which both consider to be relatively sedentary. They differ somewhat concerning the behavior of the intermediate (medium) fish. Sella (1929a) felt that these were constantly moving, and could not be separated into groups in the various basins, whereas Sarà (1973) believed that their aggregations tended to remain stationary for considerable periods, and migrated only within the basin which they occupied. Both scientists agreed that knowledge of the spawning behavior of these intermediate bluefin was inadequate.

The few details available on the trap fisheries of Tripolitania, and the ephemeral one in Cyrenaica (Bengasi) may provide clues in regard to this important subject. Both Sella (1929a) and Sarà (1973) cited the later fishing of the Libyan traps, compared to those in Tunisia, as evidence of the eastward "arrival" run of the bluefin from the Atlantic. Sella (1929a) noted, however, that the fish taken in Tripolitanian and Cyrenaican traps were medium and small. In a later work, Sella (1932a) stated that the fish taken by the El Mongar trap near Bengasi, Cyrenaica, although mature, were too small to justify its classification as an arrival trap. Anonymous (1929b) described the fish which it caught in 1928 as very small ("piccolissimi"). These data indicate that the Libyan traps may have been harvesting the intermediate (Mediterranean) mature fish rather than the large (Atlantic) migratory spawning group.

Another unsolved question concerns the migration between the Mediterranean and the Black Sea. Hovasse (1927), Akyüz and Artüz (1957) and Iyigüngör (1957) all cited passages of maturing fish through the Bosphorus into the Black Sea, and of spent fish in the opposite direction (Section VD1). They differed, however, in regard to the dates of these runs. Hovasse (1927) and Iyigüngör (1957) set the northward migration in March and April, and the beginning of the southward one in July. Akyüz and Artüz (1957) postulated a longer northward passage, starting in April, peaking in July, and extending into September, and a "return" run occurring from late October into November.

Sella (1929a), on the other hand, cited what he considered to be clear evidence of a massive migration of tuna from the vicinity of Istanbul to spawning grounds off Cyrenaica. Four lures, of special types used only in the Bosphorus and its approaches, were retrieved from the few hundred tuna caught during the 1929 season in the El Mongar trap, the only one set in Cyrenaica. Such a migration would be consistent with Sella's (1929a) hypothesis of spring spawning concentrations in the southern

parts of the bluefin tuna's range (Section VIC1b).

These apparently inconsistent findings might be reconciled if it could be shown that the larger fish in the Sea of Marmara entered the Black Sea to spawn, whereas the smaller mature individuals reproduced off the African coast.

Another probable spawning area for the intermediate bluefin is in the Adriatic Sea, where these fish are much more abundant than giants (Section IVC6, Section VD1). This would be more in keeping with Sarà's (1973) concept of limited spawning migrations, within basins, for the smaller mature fish.

The configuration of the Mediterranean and its approaches is such that many important problems could be solved quickly and definitively by tagging, or by tracking with sonic equipment.

d. Migrations and Stocks in the Eastern Atlantic

i. Large and Medium Fish

In addition to the four fish recaptured in the Mediterranean (Section VIC1b), 15 of the 312 fish tagged in the years 1960-1967 near Cadiz have been recaptured in Atlantic waters (Rodríguez-Roda 1969a). These recaptures provided information on several migrations within the area of the Ibero-Moroccan Bay trap fisheries, and one to a more distant locality (Figure 71).

Since the periodic migratory passages through the trap fisheries extend over only about four months, short-term tag returns are required to study them in detail. All of the six recoveries from 140 fish tagged during the "arrival" period occurred within 85 days of the releases. As noted in part b of this section, three of these recoveries took place in the Mediterranean, representing a continuation of the expected easterly movement. One of the other recoveries was irrelevant, since the fish was recaptured almost immediately by the trap from which it had been released. The other two recoveries, however, indicated rather rapid "backward" (westward) migrations of 79 miles (146 km) in one day and 100 miles (185 km) in two days, respectively,

into Portuguese waters. These fish were 170 cm and 133 cm long, respectively. Seven of the 13 recaptures from the 172 fish released during the "return" run occurred after from three to 23 days at large. One recapture, as noted in part b of this section, had "backed" to the eastward, well into the Mediterranean. Another, recaptured where it had been released three days previously, provided no information. The remaining five made rather rapid migrations of 90 to 100 nautical miles (167-185 km) in from four to 11 days, traveling in the expected direction into, or approaching, the waters south of Portugal. Three of these fish weighed from 70 to 90 kg, one weighed 270 kg, and the weight of the remaining fish was not reported. These short term recoveries suggested that fish tagged during the "arrival" period were more apt to deviate from their expected migratory pattern than those marked in the "return" period. This is rather surprising, since the "arrival" fish are believed to be concentrating to spawn, whereas the "return" fish are thought to be dispersing to feed.

The approximate times at large for the remaining six recaptures of fish marked in the "return" period were 4 months for one fish, 10 months for three fish and 22 months for the other two fish. The longest Atlantic migration revealed by this set of releases near Cadiz, about 370 nautical miles (685 km), was from off Barbate, Spain, in August to off the Moroccan coast between Essaouira and Agadir four months later (Figure 71). This movement supported Aloncle's (1964) hypothesis of seasonal migrations of bluefin tuna between waters off southern Morocco and the Ibero-Moroccan Bay. This fish, however, weighed 175 kg, considerably more than the group which Aloncle was discussing.

All of the long-term (10 months or 22 months at large) recaptures of fish marked during the "return" run were in traps fishing the "arrival" passage. Three recaptures occurred near Larache, Morocco, about 40 to 60 nautical miles (74-112 km) south of the release point, one off Portugal and another at Sancti Petri, about 100

nautical miles (185 km) and about 20 miles (37 km) west of the release point, respectively. These long-term recoveries suggested that the Moroccan and Iberian trap fisheries in the Atlantic harvested the same stock.

Comparison of the return rates and times at liberty for fish tagged from the "return" run (7.6%, five recaptures after 302-683 days at liberty) with those for fish marked during the "arrival" run (4.3%, no recaptures after more than 85 days at liberty) suggests that fish tagged from the "return" run were more viable than those released from the "arrival" run.

Giant and medium-sized bluefin occurred in Scandinavian and North Sea waters during the summer and fall. It was generally believed that these came, at least in part, from the "return" run which was fished by the traps off southern Spain and Portugal in July and August (Sella 1929a, Sarà 1964). Le Gall (1929) projected a northward migration route west of Ireland and north of Scotland into the North Sea and the Scandinavian waters, on the basis of observations of tuna from fishing boats along the way. Sella (1929a) identified a hook found in a bluefin tuna caught in Oslo Fjord, Norway, as of the type used in the Bay of Biscay. This finding supported the concept of a northward migration of bluefin tuna from Iberian waters to those off Scandinavia. Le Gall (1929) also noted indications of a southward migration passing north and west of the British Isles in the fall. Le Gall (1927, 1929) noted that the presence of bluefin in the North Sea was controlled by influxes of Atlantic or Atlantic slope waters with salinities of about 35 o/oo. These waters entered the North Sea from the north. Records of bluefin in the English Channel were scarce, although fish occurred frequently off its western entrance, and off the western end of Cornwall. Le Gall (1927) noted that these fish were in the feeding phase, and speculated that they had spawned in the Ibero-Moroccan Bay.

The accuracy of this assumption was proved by the tagging experiments of Hamre (1965). Hamre tagged 242 medium and large (150-

250 cm long) bluefin tuna in August and September 1957-1962 near Bergen, Norway. Six of these fish have been recaptured near Cadiz, Spain, and 26 in Scandinavian waters (Figure 72) (Hamre 1965 and personal communication). Four of the Spanish recaptures occurred after less than 10 months at liberty ("direct" migrations). The other two took place 23 and 45 months after release, respectively. If we exclude nine of the local returns which were recovered in the season of their release, and thus had no opportunity to emigrate, 26% of the returns were from Spain, as against 74% from local waters. Bluefin were tagged off Norway in each of the years 1957-1962, but the tags used in 1957 were evidently defective and produced no returns at all, and only 13 fish were marked in 1962. One more of the fish tagged off Norway in each of the other years was subsequently recaptured off Spain. These results suggest strongly that substantial numbers of the bluefin tuna which occurred off Norway in summer and early fall also occurred off southern Spain in spring and early summer, presumably there to spawn. Studies of the size composition of the landings in Norway and southern Spain (Hamre et al. 1968), however, indicated that the fisheries in these two areas did not harvest the same stock in every year. In 1955 through 1960, the size composition of the Norwegian and Spanish catches were quite similar, but in 1961 through 1964, they were quite different. In 1965 they were similar again. Hamre et al. (1968) attributed these changes to a subdivision of the northeast Atlantic tuna population into two contingents with different migratory habits in 1961 through 1964.

Although it has not been demonstrated by tag returns, Hamre agreed with Le Gall (1927, 1929) that the bluefin entered the North Sea and Scandinavian waters from west and north of the British Isles, rather than through the English Channel (Figure 73).

After the disappearance of medium-sized bluefin from the Norwegian fishery in 1963, the northward migration of the giant bluefin along

the Norwegian coast ceased and most of these fish followed the southward migratory route previously used by medium-sized fish (Hamre 1965). Tiews (1964) and Hamre (1965) agreed, on the basis of the locations and periods of fishing and the sizes of fish taken, that the large bluefin which had arrived in July and travelled northward along the Norwegian coast from Bergen eventually left that coast and migrated southward into the North Sea. There they were vulnerable to the German and Danish fisheries (Section IVC5 b and c). When these large fish reversed their migration route in 1963, predominantly following the Norwegian coast southward rather than northward, the North Sea fisheries disappeared (Hamre 1971, Tiews 1975).

The local tag returns (Hamre 1965, personal communication) confirmed migratory patterns (Figure 73) in Norwegian waters which Hamre (1962) had also deduced from studies of the size composition of catches. The bluefin tuna reached the coast at about 62°N latitude. The larger individuals, which arrived in July, migrated northward and the smaller ones, which arrived in August, migrated southward. One of the latter which had been tagged near Bergen was recaptured off the island of Anholt in the Kattegat. In addition to the nine returns in the release season, nine tags were recovered after about one year at liberty, three after about two years, as well as single ones from fish which had been at large for about three, five, six, seven and eight years.

In recent years, most of the bluefin tuna in Norwegian waters, all of which have been very large, have left there early in the fall. Prior to 1963, when medium fish were abundant there, many of these fish did not depart until late autumn. The ensuing migration of the large bluefin apparently takes them north and west of the British Isles to their wintering area. This probably lies between latitudes 25°N and 40°N and between the African and European coasts and longitude 35°W (Shingu et al. 1975, Fisheries Agency of Japan 1976). The size distribution of the fish in the area is not known. Aloncle (1964), however, reported that small to me-

dium fish occurred between the Canary Islands and Morocco in winter.

Many medium and some large bluefin are captured in the Bay of Biscay from mid-July to mid-August, or early September (Creac'h 1952, Le Gall 1954, Bard et al. 1973, Dao and Bessineton 1974, Cort 1975, 1977). Some of the smaller fish may spawn on their arrival in the Bay (Cort 1977), but this is primarily a feeding concentration. Where these bluefin go after they leave the Bay of Biscay is uncertain. Cort (1976) conjectured that those in age groups 6 to 9 continued their northward migration to Norwegian waters, whereas those in age groups 4 and 5 followed a different, probably more southerly, route. The migration of age groups 6-9 to Scandinavian waters may well have taken place in years prior to 1963, but fish of these ages have not been important in the Norwegian catches since then (Hamre 1971).

The European landings of medium bluefin in the Bay of Biscay have increased markedly since 1973, perhaps in consequence of substantial fishing effort by Japanese longline vessels in the area (Cort and Cendrero 1975, Cort 1976, Fisheries Agency of Japan 1976, Shingu and Hisada 1976).

It is unfortunate that adequate size composition data for Bay of Biscay landings in the 1960s are not available. It would have been of interest to note whether the departure of the medium fish from the Norwegian fishery in 1963 through failure of recruitment (Hamre 1971) was reflected by any increase in their availability in the Bay of Biscay.

The medium and large bluefin which leave the Bay of Biscay in August or early September presumably reach the wintering area described above in late fall or early winter, but their whereabouts in the meantime is unknown. Possibly some of them join the concentration off the central Moroccan coast, along with others which may have gone there directly after spawning in the Ibero-Moroccan Bay (Aloncle 1964).

In April the medium and large bluefin begin to migrate from their wintering area to their spawning

grounds. Most of the large fish and some of the older mediums participate in the "arrival" run, assembling in the Ibero-Moroccan Bay in May and June. One contingent of them, mainly the individuals weighing less than 150 kg, presumably spawns there, along with a portion of the larger fish. Apparently many of the latter, however, enter the Mediterranean, spawn there in June or early July, and make a "return" run into the Atlantic in July and August. Most of the larger fish which have remained in the Ibero-Moroccan Bay also join this "return" run.

Some of the smaller individuals may spawn off the Moroccan coast

while en route to the Bay of Biscay (Aloncle 1964). Others may spawn after arriving there (Cort 1977), thus actually spawning in their feeding area.

Most of the large "return" fish migrate from the Ibero-Moroccan Bay around the British Isles to their summer feeding area in Norwegian waters. Many of the smaller ones, including most of those which have spawned in that Bay, proceed to the Bay of Biscay, but others may join the concentration off the central Moroccan coast. This gathering is occasioned when the impingement on the northern coast of Morocco of a tongue of warm (over 21°C) tropical water

Figure 72. Geographic distribution of bluefin tag release and recapture data from Norwegian tagging studies and hook recovery data in the eastern Atlantic.

from offshore inhibits the further progress of some groups of small and medium tuna travelling northward from the wintering area. These fish eventually find themselves in the cooler upwelling waters off the central Moroccan coast, but completely surrounded by tropical water. Most of them stay in this cool water rather than continuing northward through the warmer water (Aloncle 1964).

The return to summer feeding areas completes the migratory cycle of the medium and large bluefin of the eastern Atlantic. The hypothetical three phase migration is complicated by the entrapment of some medium fish off central Morocco, and the entry of larger fish into the Mediterranean to spawn.

ii. Small Fish

Thirty-four small bluefin tuna have been tagged in the Bay of Biscay and off Portugal since 1960 (Aloncle 1973). Three of these were recaptured locally, and two off the north-eastern United States. One of the local returns was from a small bluefin tagged off Cape St. Vincent (south-western corner of Portugal) in early June and recaptured in the Bay of Biscay 83 days later (Figure 74). This migration supports Aloncle's (1964) hypothesis that small bluefin migrate seasonally from the Ibero-Moroccan Bay in spring to the Bay of Biscay in summer. The transatlantic returns will be discussed in part 3 of this section.

The results of tagging off the Atlantic coast of Morocco (Lamboeuf 1975) also support Aloncle's (1964) theory. During 1972 and 1973, 63 bluefin, 41-73 cm long, were tagged and released there: 15 in June, one in July, 25 in August and 21 in November. Eleven returns resulted, including five from Moroccan waters and six from other areas (Figure 74).

During 1973 two fish, of which one had been marked in June and the other in August (at ages of approximately 11 and 14 months, respectively), were recaptured off the south-western coast of Portugal in October and September, respectively. Four others, of which three were tagged in August 1972 (at ages of about 13 months) and one in November 1972, (age about 17 months) were recap-

tured in the Bay of Biscay in June-August 1973. These important results indicate that both the minor fall fishery off the west coast of Portugal and the much more important one which takes place in the Bay of Biscay during the warm season draw recruits from off the Atlantic coast of Morocco. These few returns suggest that fish recruit to the former fishery at age 1 and to the latter at age 2. These ages of recruitment are in accord with the age groups which have been predominant in the landings of the respective fisheries. The tendency for the maximum catches of "cachorretas" (age 1 bluefin) in the Portuguese trap fishery to have occurred in late August suggests that the indicated migration from off Morocco in summer to off western Portugal in the fall may sometimes have passed along the south coast of Portugal en route.

Local returns showed two south-westward movements from the Larache-Casablanca area toward Cap Blanc in August-September 1972 and two northward migrations from off Agadir to off Essaouira in November-December 1972.

Lamboeuf (1975), considering these results and observations of the movement of the fishery and the sizes of fish caught, formulated the following hypothesis:

Bluefin spawned off Morocco by the adult "arrival" tuna in spring or early summer remain offshore in favorable waters (18°C-22°C). They occasionally approach the coast when hydrological conditions allow this. Having attained 1 year of age and 50 to 60 cm in length, they frequent the coast from June through August, moving from north to south during this period. They then disappear, having been driven offshore by the cold waters in the Safi-Essaouira region,

Figure 73. Possible paths of bluefin tuna entering the North Sea and Scandinavian waters from west and north of the British Isles, rather than through the English Channel.

Figure 74. Geographic distribution of bluefin tag release and recapture data from Moroccan and Bay of Biscay tagging studies.

only to reappear in the Bay of Agadir in November and December. These bluefin which have attained a mean length of 67 cm then undertake a longer migration, passing along the Portuguese coast and penetrating deeply into the Bay of Biscay.

In certain years, as in 1973, when the cold waters of the central sector extended far offshore, the tuna may have migrated earlier in the season, bypassing the Agadir area.

These results of tagging off Portugal and Morocco and Lamboeuf's (1975) hypothesis explain Furnestin and Dardignac's (1962) observation that young bluefin become scarce along the Moroccan coast in November, when they have attained a length of 64 cm, and confirm Aloncle's (1964) hypothetical migration of young bluefin from Moroccan waters to the Bay of Biscay.

After feeding in the Bay of Biscay through the remainder of the warm season, the age 2 fish depart, along with fish a year or two older, mainly in October. Their next destination is their wintering area, which is little known. There is a wintering

zone between the Canary Islands and Morocco, but the total winter habitat is probably much larger, with the fish spreading over greater areas as they attain older ages.

Age 3 and 4, and older, bluefin move northward again in the spring; probably the majority of them eventually enter the Bay of Biscay. Many of the older individuals in this group are mature. Some of these may spawn during this northward migration, and others may split off from it and spawn with the larger fish in the Ibero-Moroccan Bay. During late summer and fall, considerable aggregations of small and medium bluefin occur off the central Moroccan coast, as noted previously. Some of these fish may have been trapped there by a warm water mass during their northward movement and others may have migrated there after spawning in the Ibero-Moroccan Bay. Most of the small bluefin which have spawned there, however, probably proceed to the Bay of Biscay, entering it during the last half of July or early August. Thus the hypothetical two-part migratory pattern of this group may be

interrupted by local hydrological conditions, and the mature individuals are inclined toward the three-part migratory pattern proposed for the older age groups.

iii. Very Small Fish

Eastern Atlantic bluefin (applying this term to individuals which are recruited to stocks in the eastern Atlantic as juveniles) are hatched mainly in the Mediterranean Sea and/or the Ibero-Moroccan Bay. Those born in the former area, however, would have to pass through the latter to reach their nursery areas. Supplementary hatching may extend to the area between the Canary Islands and Morocco, and also into the Bay of Biscay. The principal hatching occurs from about the middle of June to about the middle of July, with reproduction by the smaller individuals occurring up to the end of July or later. By mid-November, when they are about 40 cm long, the bulk of the new-born tuna have converged from their various birth places to concentrate off the Atlantic coast of Morocco, where they complete their first year of life in the following June or July.

2. Western Atlantic

a. Introduction

Tag returns, data on the fisheries, and knowledge of oceanographic conditions must be used in combination to establish hypothetical migration patterns for bluefin tuna. Since 1954, about 2,760 giant, 490 medium, and 14,630 small bluefin have been tagged in the western Atlantic and 63, 9, and 3,000 returns, respectively, have resulted. These returns have not only provided important information on movements within the area, but have also revealed surprising migrations to distant regions. Extensive data on the coastal and oceanic fisheries are available (see Sections IVC2 and IVC3) to complement the pattern disclosed by tagging. Also, comprehensive works on the oceanography of the Atlantic, with details of its circulatory system, have been published (Sverdrup et al. 1942). Those concerning the Gulf Stream system (Fuglister and Worthington 1951, Von Arx et al. 1955) are of special interest in relation to the distribution and migra-

tions of bluefin tuna in the north Atlantic (Sella 1931, Rivas 1955, Squire 1963). Since the economic importance of the species in the western Atlantic has been slight until recent years, the history of research on its migrations there is brief in comparison with that in the eastern Atlantic and the Mediterranean.

b. Large Fish

Few deductions about the migration of large bluefin tuna in the western Atlantic have been published. The summer and early fall occurrences of bluefin tuna off northeastern North America (off the United States coast from New Jersey to Maine, and off Nova Scotia and New Brunswick in Canada) have long been known (Farrington 1939). A periodic northward migration of "giant" bluefin through the Straits of Florida (mainly along the northwestern edge of the Great Bahamas Bank near Cat Cay and Bimini) was discovered by sport fishermen in the 1930s and it was soon concluded that these fish were among those which subsequently occurred off northeastern North America in summer and early fall (Farrington 1939, Mowbray 1949).

At the Oceanic Fisheries Conference held at the Bermuda Biological Station for Research, May 28-31, 1951, (transcript of tape recordings available at Woods Hole Oceanographic Institution) Schuck and Mather presented their views on several aspects of the biology of bluefin tuna in the western North Atlantic. They described the behavior of the giant bluefin tuna in the Straits of Florida as observed during flights made with L. R. Rivas in U.S. Coast Guard aircraft. These observations confirmed that the visible schools were virtually all travelling northward, as reported by the sport fishermen. Schuck and Mather also showed that the times of the passage of the giant tuna through the Straits of Florida and their arrival in New England waters were consistent with a migration between the two areas. Finally, they presented preliminary results of biometric studies which showed that the fish taken in the Straits of Florida were similar to those taken in New England waters, except

in regard to body condition. The fish taken off New England in the beginning of the season were similar in body proportions to those taken in the Straits of Florida. As the season advanced, however, the fish off New England fed heavily and gained weight rapidly. Therefore the fish taken there in August, September and October became progressively heavier in proportion to their length than those taken in the Straits of Florida. The ratios of their girth and depth to their length consequently also became greater than the corresponding ratios for fish taken in the southern area.

Rivas (1955), in a similar study, compared the morphological characteristics of samples of bluefin tuna of similar sizes taken in the Straits of Florida in May 1952-1954 (19 specimens) and at Wedgeport, Nova Scotia, in October 1952 and August 1953 (nine specimens). He found no significant differences between these samples, except those attributable to the normal seasonal change in body condition experienced by bluefin tuna. These fish lost considerable weight during the spawning process and related migrations, then fed so heavily during the summer and early fall that their length-weight ratio was at a minimum in September-October. The lean condition of the fish taken in the early part of each season at Wedgeport was consistent with their having come from the Straits of Florida. In addition, Rivas showed that the times of arrival of giant bluefin tuna off Cape Cod, Massachusetts, and Wedgeport were consistent with the time of departure and estimated average speed (3.5 knots, or 6.5 km/hr) and direction of travel of the individuals passing the Bahamas. Thus he presented a case, which he considered strong, but not conclusive, for a northward migration of giant bluefin from the Straits of Florida in May-June to New England and Nova Scotia waters in summer or early fall.

Exploratory and commercial longline fishing has provided important information on the temporal and areal distribution of bluefin in the oceanic waters of the western Atlantic since 1956 (see Sections IVC2

and IVC3). The records of occurrences during the cold season (November-April), when their whereabouts had previously been virtually unknown, were especially valuable. This information has been used in conjunction with tagging results in developing new hypotheses on the migrations of the species (Mather 1969, 1974, Mather et al. 1974).

Continuous tagging of western Atlantic bluefin began in 1954. Since then, about 1,100 giant fish have been marked off the northwestern Bahamas (Straits of Florida) and 15 of these fish have been recaptured over a very extensive area — four off northeastern North America, two off eastern South America, and nine off Norway (Table 28) (Mather 1962, 1969; FAO 1972, Mason et al. 1977). Cooperating sport fishermen provided the effective tagging in this effort. A few fish have been marked during exploratory fishing cruises in this general area, but none of the tags have been returned.

The four returns off North America were from off Maryland to off the Nova Scotian banks (Figure 76); only one was from an area known as a tuna fishing ground. This return was from a giant released in early June 1973, in the Bimini-Cat Cay area (northwestern Bahamas) and recaptured about 18 nautical miles (33 km) northeast of Gloucester, Massachusetts, a well-known center for small boat tuna fishing, in early July 1974. Since it had been at liberty for 13 months, this was not a "direct" migration. If it is regarded as a second retracing of an annual migratory cycle, however, the fish would have passed through the Straits of Florida again in May or June 1974, and its ensuing migration would have fitted the proposed pattern. The other three recaptures were incidental or accidental catches by vessels fishing for other species. While they could be interpreted as representing incomplete migrations toward the New England or Canadian feeding areas, there is an element of doubt in each case. One return was from a fish recaptured about 48 nautical miles (89 km) east-southeast of Ocean City, Maryland, in April 1973, 23 months after it had been released off the

northwestern Bahamas in May 1971. The inshore location of its recapture suggests that it might have eventually entered New England or Canadian coastal waters. Its recapture date, April 4, however, indicates that, if it had come from the Straits of Florida, it must have left there in March, well ahead of the usual May-June passage. The other two recaptures occurred in offshore waters, from 40 to 65 nautical miles (74 to 120 km) outside the 2,000 m contour. One fish, which was recaptured 135 nautical miles (250 km) southeast of Nantucket Island, Massachusetts, in June 1970 had been released four years previously, in May 1966, in the Cat Cay-Bimini area. The fourth tuna had been released in the same locality in early June 1970, and was recaptured just 30 days later 100 nautical miles (185 km) southeast of Sable Island, off Nova Scotia. Thus it had travelled at least 1,500 nautical miles (2,800 km) in a maximum of 30 days, requiring a minimum average speed of 2.1 knots (3.9 km per hr). It is uncertain whether these fish, had their journeys not been terminated, would have proceeded to the feeding grounds off the American coasts, completing the hypothetical migration, or continued across the ocean to Norwegian waters, as so many other bluefin released off the Bahamas have done. It is widely believed, however, that these animals have a strong tendency to follow favoring currents when migrating (Sella 1929a, Rivas 1955, Lozano Cabo 1958, 1959b; Sarà 1964, 1973; Rodewald 1967). Since both of these fish were recaptured far north of the Gulf Stream, which would have favored a migration to Norway, it seems more probable that they would have proceeded to the nearby American feeding grounds than that they would have wandered out into the less productive waters of the open ocean.

Two giant bluefin tagged off the northwestern Bahamas have been recaptured in the South Atlantic (Table 28, Figure 75) (Mather 1974). One fish was marked in May 1963 and recaptured southeast of Recife, Brazil, in March 1965. The other fish, released in June 1969, was recaptured off Argentina in February 1973.

This migration of at least 6,600 nautical miles (12,250 km) is the longest ever recorded for an Atlantic bluefin.

These surprising recoveries provided the first clues to the relationships between the bluefin tuna stocks of the North and South Atlantic. Catch records of the Japanese longline fishery (Fisheries Agency of Japan 1965, 1966, 1967a, 1967b, 1968, 1969, 1970, 1971, 1972, 1973) show that, in some years, an area of intensive bluefin fishing develops in March and April off easternmost Brazil, moves northwestward toward the Bahamas and then northward to off

Cape Hatteras in May and June. In July, the longline catches of large fish diminishes. The capture off Recife of a giant bluefin which had been tagged off the Bahamas increases the probability that a group of large fish does actually migrate from off the Bahamas in May-June to off Cape Hatteras by early July, thence to various summering areas farther north (Figure 75), and southward in the fall to wintering areas around the Antilles and off South America. It had been generally believed (Wise and Davis 1973) that bluefin tuna concentrations north of

Table 28. Releases and returns for giant bluefin tuna (over 120 kg) tagged off the Bahamas by year of release, months at large, and area* of recapture. Also shown is the estimated percentage of German North Sea bluefin tuna catches in late season (September 15 - October 31) recruited from the western Atlantic (Tiews 1964).

Year Releases		Returns by Month at Large						%
		0-5.9	6-17.9	18-29.9	30-41.9	42-53.9	78-89.9	
1954	21	0	0	0	0	0	0	8
1955	14	0	0	0	0	0	0	4
1956	41	0	0	0	0	0	0	6
1957	0	0	0	0	0	0	0	0
1958	0	0	0	0	0	0	0	7
1959	25	0	0	0	0	0	0	0
1960	13	0	0	2 N	0	0	0	11
1961	34	2 N	0	0	0	0	0	33
1962	45	1 N	0	0	0	0	0	2
1963	147	0	0	1 B	0	0	0	
1964	41	0	0	0	0	0	0	
1965	54	0	0	0	0	0	0	
1966	105	0	0	0	0	1 A	0	
1967	82	1 N	0	0	0	0	0	
1968	57	0	0	0	0	0	0	
1969	50	0	0	0	0	1 B	1 N	
1970	182	1 A	0	0	0	0	—	
1971	49	0	0	1 A	0	0	—	
1972	32	0	1 N	0	0	0	—	
1973	47	0	1 A, 1 N	0	0	—	—	
1974	31	0	0	0	—	—	—	
1975	18	0	0	—	—	—	—	
1976	5	0	—	—	—	—	—	

Areas: A = Northeastern North America, B = Brazil and Argentina, N = Norway.

Figure 75. Geographic distribution of bluefin tag release and recapture data illustrating transatlantic and transequatorial migrations.

latitude 20°S consisted mainly of Atlantic bluefin tuna *T. thynnus thynnus*, and that those south of 20°S consisted mainly of southern bluefin tuna, *T. maccoyii*. The recapture off Argentina of a giant bluefin which

had been tagged off the Bahamas indicates that the already tremendous migratory circuit suggested above for Atlantic bluefin occasionally extends much farther south, well into the habitat of the southern bluefin.

The nine recoveries in Norwegian waters from the releases in the Straits of Florida will be discussed in part 3 of this section.

Giant bluefin tuna have also been tagged successfully during the sum-

Table 29. Releases and returns for giant bluefin tuna (over 120 kg) tuna tagged in St. Margaret's Bay, Nova Scotia, by year of release, months at large and area* of recapture.

Year	Releases	Returns by Months at Large						Total
		0-5.9	6-17.9	18-29.9	30-41.9	42-53.9	54-65.9	
1963	18	0	0	0	0	0	0	0
1964	6	0	0	0	0	0	0	0
1965	52	2L	1L	0	0	0	0	3L
1966	71	0	2N	0	0	0	0	2N
1967	193	5L,1W	0	1N	0	0	0	7LWN
1968	0	0	0	0	0	0	0	0
1969	15	1L	0	0	0	0	1G	2LG
1970	3	0	0	0	0	0	0	0
1971	45	0	0	0	1N	1G	1G	3NG
1972	12	0	0	0	0	0	0	0
1973	0	0	0	0	0	0	0	0
1974	8	0	0	0	0	0	0	0
1975	148	3G	1L	0	0	0	0	4GL
1976	12	1G	0	0	0	0	0	1G

*Areas: L = Local, G = Gulf of St. Lawrence, N = New England, W = Wedgeport, Nova Scotia

Gulf of St. Lawrence had been at liberty for 49, 60 and 63 months. These six migrations were therefore "indirect". The recaptures off New England occurred in June (1 recapture) and August (3 recaptures); the one at Wedgeport occurred in September. Those in the Gulf of St. Lawrence occurred in July (1 recapture), August (2 recaptures), September (3 recaptures) and October (1 recapture). The two local recaptures after a winter at liberty took place in August and October.

Sport fishermen cooperating with United States and Canadian programs have tagged 962 giant bluefin in eastern Newfoundland waters, and of these nine tags have been returned (**Table 31**). Four of these were recovered locally, but five were returned from other areas (**Figure 77**). The longest migrations recorded were from Notre Dame Bay, Newfoundland, in August 1970 and 1971, to Cape Cod Bay, Massachusetts, in July 1974, and October 1973, respectively. These two fish had moved nearly 1,000 nautical miles (1,850 km). Two

mer off northeastern North America. Since 1961, 583 giant bluefin tuna have been tagged and released from traps in St. Margaret's Bay near Halifax, Nova Scotia, (Beckett 1970, Caddy and Burnett 1975, Burnett 1977), and 22 of these tags have been returned (**Table 29**, **Figure 78**). Ten of the recaptures were local (in St. Margaret's Bay), eight in the release season and two in the following summer. The other 12 recoveries indicated longer migrations (**Table 30**), one to the area off Wedgeport, Nova Scotia, four to New England waters and seven into the Gulf of St. Lawrence. The fish recaptured off Wedgeport had been at liberty for only 49 days and four of those recaptured in the Gulf of St. Lawrence for from 63 to 84 days, so that all five migrations were "direct". The four fish whose tags were recovered off New England had been at large for from 12 to 35 months and the other three which were recaptured in the

Figure 76. Geographic distribution of bluefin tag release and recapture data from Bahamas tagging studies.

Table 30. Release and recovery data for bluefin tuna tagged in St. Margaret's Bay, Nova Scotia and recovered elsewhere, with size at recapture and months at liberty.

Return Number	Release		Recapture		Weight	Liberty
	Location	Date	Location	Date		
1	St. Margaret's Bay 44° 37' N 64° 00' W	VIII-1966	Cape Cod, Massachusetts	VIII-1967	—	11.3
2	St. Margaret's Bay 44° 37' N 64° 00' W	VII-1966	Cape Cod, Massachusetts	VIII-1967	—	13.5
3	St. Margaret's Bay 44° 37' N 64° 00' W	VII-1967	Wedgeport, Nova Scotia	IX-1967	—	1.6
4	St. Margaret's Bay 44° 37' N 64° 00' W	VII-1967	Cape Cod, Massachusetts	VI-1969	—	23.3
5	St. Margaret's Bay 44° 37' N 64° 02' W	VIII-1969	Prince Edward Island, Canada 46° 40' N 63° 50' W	VII-1974	278	60.0
6	St. Margaret's Bay 44° 37' N 64° 03' W	IX-1971	Cape Elizabeth, Maine 43 30' N 70° 06' W	VIII-1974	—	34.7
7	St. Margaret's Bay 44° 39' N 63° 59' W	VII-1971	Chaleur Bay, New Brunswick 48° 08' N 64° 56' W	VIII-1975	412	49.8
8	St. Margaret's Bay 44° 37' N 64° 02' W	VI-1975	Prince Edward Island, Canada 47° 06' N 63° 55' W	IX-1975	388	2.4
9	St. Margaret's Bay 44° 30' N 63° 56' W	VI-1975	Prince Edward Island, Canada 46° 29' N 62° 01' W	IX-1975	301	2.7
10	St. Margaret's Bay 44° 36' N 64° 03' W	VI-1975	Prince Edward Island, Canada 46° 31' N 62° 07' W	IX-1975	374	2.8
11	St. Margaret's Bay 44° 38' N 63° 59' W	VII-1971	Prince Edward Island, Canada 46° 28' N 62° 44' W	X-1976	427	62.8
12	St. Margaret's Bay 44° 38' N 64° 00' W	VI-1976	Chaleur Bay, New Brunswick 48° 09' N 64° 54' W	VIII-1976	395	2.1

others travelled from Notre Dame Bay to St. Margaret's Bay, Nova Scotia, one in 47 months and the other in 59 months. One tuna moved from Notre Dame Bay in August 1972 to the southern extremity of the Grand Banks in December 1973. The times at liberty for the recaptured fish varied from a few days to nearly six years.

Cooperating sport fishermen also marked 117 giant tunas in New England waters, and 17 returns have resulted (Table 32). All but one recapture were local, after periods of from a few days to about three years. The exception was a fish released July 22, 1974, in Massachusetts Bay off Boston and recaptured May 13, 1975, in the Gulf of Mexico off south-

western Florida (Figure 79). All the giant bluefin marked in New England and Canadian waters were tagged during the summer-fall feeding season (July-October), and all but two of the recaptures occurred in the same general area and season. This group of recaptures shows that large bluefin move freely within the waters between Cape Cod and Newfoundland, and return to them year after year.

Evidently fish off northern New England and off Canada are of a single stock, or of stocks which are only partially separated. The only "direct" migrations, however, have been one from St. Margaret's Bay to Wedgeport and four from that Bay into the Gulf of St. Lawrence. None of the recorded movements from

Nova Scotia to New England and from Newfoundland to Nova Scotia or New England have occurred within a single season.

The two returns from outside Canadian and New England coastal waters provide more significant indications of migratory patterns. The December recapture, at the southern end of the Grand Banks, of a giant bluefin which had been tagged in Newfoundland coastal waters 16 months previously may show the initiation of a southerly migratory route even though it was not a direct migration. The migration from New England coastal waters in July to the Gulf of Mexico in the following May provides the first definite and "direct" connection between the giant bluefin

Table 31. Releases and returns for giant (over 120 kg) bluefin tuna tagged in Newfoundland waters, by year of release, months at large, and area* of recapture.

Year	Releases	Returns by Months at Large						Total
		0-5.9	6-17.9	18-29.9	30-41.9	42-53.9	> 54	
1962	6	0	0	0	0	0	0	0
1963	3	0	0	0	0	0	0	0
1964	41	0	0	0	0	0	0	0
1965	49	0	0	0	0	0	0	0
1966	49	0	0	0	0	0	0	0
1967	6	0	0	0	0	0	0	0
1968	217	1L	0	0	1L	0	0	2L
1969	195	0	0	0	0	0	1N	1N
1970	96	1L	0	0	0	1M,1N	0	3L,MN
1971	94	0	0	1M	0	0	0	1M
1972	112	0	1G	0	0	0	0	1G
1973	4	0	0	0	0	0	0	0
1974	14	0	0	0	0	0	0	0
1975	0	0	0	0	0	0	0	0
1976	0	0	0	0	0	0	0	0
Unknown	1	0	0	0	0	0	0	1L

*Areas: L = Local, M = Massachusetts, N = Nova Scotia, G = Grand Banks

which feed in New England and Canadian waters in summer and early fall and those which spawn in the Gulf of Mexico in spring (Section VD3). As noted previously in this section, an "indirect" northward migration from the Straits of Florida to Massachusetts coastal waters has also been recorded.

Another important tag return, which was not from the above release groups, connects the feeding area off New England and Canada with the spawning area for giants in the Gulf of Mexico. This fish, which was tagged when it was in the small size group, was released August 4, 1966, 38 nautical miles (70 km) south by west of Martha's Vineyard, Massachusetts, and was recaptured April 18, 1976, in the north central Gulf of Mexico, 135 nautical miles (250 km) south by east of the Mississippi River entrance (Figure 79). Its length when released was about 56 cm and after nearly 10 years at liberty, the longest such period of which we have knowledge for a tagged Atlantic bluefin tuna, it was reported as 218 cm. Thus the fish was age 1+ when tagged, and

age 11, or slightly less when recaptured. Although this fish was in the small size group when tagged, it must have been a giant when it made its

last southward migration. Since less than 1 percent of the returns from bluefin tagged in New England waters have been from outside the western North Atlantic, it is highly probable that this final migration was from the New England or Canadian feeding grounds. The main significance of this return is the establishment of a connection between the nursery area south of Cape Cod and the spawning grounds in the south. Moreover, it most probably also represents the seasonal migration of large bluefin from the northwestern Atlantic feeding area to their spawning areas.

This is the third important link between the spawning area in the Gulf of Mexico and the summer feeding grounds off the northeastern United States. As noted previously in this section, a large bluefin made a "direct" migration from waters north of Cape Cod into the Gulf of Mexico, where it was recaptured during the spawning season. Another fish made an "indirect" migration, which might well have originated in the Gulf of Mexico, from the Straits of Florida, where post-spawning bluefin are prevalent, to New England waters.

Thus tag returns have produced considerable information on movements of large bluefin within the western North Atlantic, and from it

Figure 77. Geographic distribution of bluefin tag release and recapture data from Newfoundland tagging studies.

Figure 78. Geographic distribution of bluefin tag release and recapture data from Nova Scotian tagging studies.

into the eastern North Atlantic and the South Atlantic. Although connections have been established between spring spawning areas in the Gulf of Mexico and the Straits of

Florida and summer nursery and feeding areas off northwestern North America, a complete migratory pattern has not emerged. We shall use the temporal and areal distribution of

longline catches and the observed relationships of the bluefin's distribution and migratory habits to the ocean currents in completing a hypothetical model for the migrations of large western Atlantic bluefin.

The limits of the western Atlantic area in which large bluefin spawn have not been established, but the spawning grounds may include most of the deep (over 200 m) waters between latitudes 18°N and 33°N, and longitude 17°W and the coast (see Section VD3).

The only thoroughly documented migration of large bluefin within this supposed spawning area is their northward passage through the Straits of Florida in May and June. This movement may be traced visually from boats or aircraft for about 65 nautical miles (120 km) along the northwestern edge of the Great Bahama Bank from Orange Cay to Great Isaac (**Figure 29**) when conditions are favorable (Farrington 1939, personal observations from U.S. Coast Guard Aircraft by L. R. Rivas, H. A. Schuck and F. J. Mather in May-June 1951, Rivas 1955, Mather 1964b). A continuation of this migration along the 40 nautical mile (74 km) western edge of the Little Bahama Bank has also been observed (personal observations by the senior author at Memory Rock and Matanilla Shoal, June 1966, catches off West End, Grand Bahama, personal communications). The senior author also sighted and baited schools of giant bluefin which were traveling northward on the surface at the western end of the Northwest Providence Channel, between the Great and Little Bahama Banks, in May-June 1968. This unusual observation was a good indication of the continuity of this migratory route.

Other migrations within the spawning areas may be deduced from the times and locations of catches, sightings and/or the destruction of equipment of anglers fishing for billfishes and other less powerful game, as well as occasional appearances of schools of bluefin.

The Windward Passage appears to be a focal point in the migrations of giant bluefin into the spawning area. Large fish, including some with

Table 32. Releases and returns for giant (>122 kg) bluefin tuna, *Thunnus thynnus*, tagged in New England coastal waters by years of release and time at large.

Year Releases		Returns by Month at Large				Total	%
		0 - 5.9	6 - 17.9	18 - 29.9	30 - 41.9		
1966	2	0	0	0	0	0	
1967	0	0	0	0	0	0	
1968	6	0	0	1	0	1	16.7
1969	1	0	0	0	0	0	
1970	4	0	0	0	0	0	
1971	10	0	0	1	0	1	10.0
1972	17	1	1	0	2	4	23.5
1973	15 ^a	5	1	1	0	7	46.6
1974	9 ^b	2	2	0		4	44.4
1975	19	0	0	0			
1976	34	0	0				

^aIncludes 6 releases of, and 4 1973 and 1 1975 returns from fish tagged while free swimming.

^bIncludes 3 releases of, and 3 returns from, fish tagged while free swimming.

Figure 79. Geographic distribution of bluefin tag release and recapture data from northeastern North America tagging studies with recovery sites in the Gulf of Mexico and Caribbean Sea.

maturing ovaries (Table 25), have been caught there by longline in April 1955, April 1960, and May 1951 (Bullis and Mather 1956, Anonymous 1960, 1962). There are three major routes along which tuna might migrate from the Windward Passage through the spawning areas and northward toward their summer feeding grounds (Figure 31).

The best documented of these routes, although it is the longest, is through the northwestern Caribbean, the Gulf of Mexico, and the Straits of Florida. This pattern is indicated by the distribution of longline catches of bluefin during cruise 30 of M/V "Oregon" in the spring of 1955 (Bullis and Mather 1956). Bluefin were taken in the Windward Passage, at stations south of the eastern end of Cuba and near the Cayman Islands and Cozumel Island in the northwestern corner of the Caribbean, but not one was taken at several stations in the Caribbean east of the Windward Passage. A migration between eastern Cuba and Jamaica was also indicated by the existence of a Cuban-based spring longline fishery for giant bluefin in this area (Ubeda 1974). Schools

of large bluefin have been observed occasionally during this same season in several consecutive years on the surface between Cozumel Island and the Yucatan Peninsula. Many of these fish have been hooked, but very few landed, by billfish anglers (personal communications). Similar occurrences off the Mississippi River delta have been reported (Nakamura and Rivas 1972). The catch rate distribution charts of Wise and Davis (1973) (Figure 32) and Le Gall (1974) indicate that the winter concentration around the Greater Antilles and in the southeastern Gulf of Mexico moves westward and northward in the spring, occupying the northern Gulf as well as waters north of Cuba, Hispaniola, and Puerto Rico. The abundance of bluefin tuna larvae in the Gulf of Mexico in April, May and June also implies the presence of large numbers of adults (Richards 1976, Montolio and Juarez 1977). The connection between the disappearance of this concentration of adults from the Gulf by the end of June (Shingu et al 1975) and the northward migration of large numbers (Tyler et al. 1979) of giant blue-

fin through the Straits of Florida in May and June seems obvious. It is also indicated by occasional catches of deep swimming bluefin off Havana (Rivas 1955) and by the sightings of schools off Cay Sal, at the southwestern corner of the Cay Sal Bank (P. Pierce, T. Sanchez, personal communications).

There are also strong indications that many bluefin follow the north coast of Cuba westward from the Windward Passage, through the Old Bahama and the Santaren Channels to the "tuna alley" in the Cat Cay area. We have received reports of sightings of schools moving through the Old Bahama Channel from persons who operated aircraft there, but were unable to obtain precise details. During cruise 62 of *RV Crawford* in April-June 1961, which had been planned to study these migrations, additional evidence of such a migration was obtained. Giant bluefin were taken by longline in the Windward Passage (sample 10, Table 25, Figure 70), near Cay S. Domingo off the eastern end of the Old Bahama Channel, and at the edge of the Great Bahama Bank on the eastern side of the Santaren Channel (sample 15, Table 25, Figure 70) (Anonymous 1962, unpublished data). Sample 14 was taken about 60 nautical miles (110 km) northwest of the western end of the Old Bahama Channel and about 110 nautical miles (204 km) south by east of the center of the Cat Cay sport fishery for giant tuna. The capture of eight giant bluefin and the loss of many hooks, leaders and branch lines, all at the inshore end of the line, indicated a heavy concentration of the fish close to the steep drop-off at the edge of the bank at this station. Radio telephone reports from participants in a tuna tournament at Cat Cay bewailed a prolonged dearth of fish. Two days later, they reported one of the best catches in many years. The distribution of these four catches and the subsequent catch off Cat Cay strongly suggests that contingents of bluefin migrate from the Windward Passage through the Old Bahama and Santaren Channels and continue northward through the Straits of Florida. Because of the rupture of diplomatic relations between

the United States and Cuba it was impossible to verify this migration route completely by fishing in the Old Bahama Channel itself.

The third and most direct possible route from the Windward Passage to the northern feeding grounds is through the Crooked Island Passage (**Figure 31**). Bluefin tuna are abundant east and north of the Bahamas in spring (Shingu et al. 1975) and some of them probably spawn in these waters (**Table 25, Figure 70**). It also appears that these fish move northward in May and June (Shingu et al. 1975), as do those in the Straits of Florida. Several exploratory longline sets were made in the Crooked Island Passage and west of Great Inagua island from research vessels of the Woods Hole Oceanographic Institution in May and June of 1958 and 1961 (Mather 1959, Anonymous 1969). No bluefin tuna were caught on any of these sets, nor did we note any of the gear damage which these fish often cause when they have been hooked and subsequently escaped. This, of course, did not prove that no bluefin follow this route, but, in our opinion, the fishing results and other data indicate that they follow the other two routes in much greater numbers.

After the giant bluefin have spawned in these southern areas, they migrate northward to feeding grounds off northeastern North America and, in some years, large contingents of them go on to feeding areas off Norway.

The evidence for these migrations has been discussed in preceding paragraphs. Daily records of catches at Cat Cay for numerous pre- and post-World War II years (personal communications) show that the passage through the Straits of Florida occurs in strength, as indicated by availability to surface fishing from early May to about June 20.

As noted previously, longline catch records (Anonymous 1962, LeGall 1974, Shingu et al. 1975) indicate that a parallel but much more dispersed migration takes place in about the same period along the oceanic edges of the Bahamas, and for considerable distances east and north of them. After passing north of these

islands, this migration merges, at least partially, with the one moving northward from the Straits of Florida. The migration through Atlantic waters east of the Bahamas has not been observed visually, to our knowledge, and sightings of large bluefin between the Bahamas and Cape Hatteras have been extremely rare. In fact, the occurrence of surface schools of giant bluefin travelling steadily in one direction off the northwestern Bahamas is a strictly local phenomenon which is unique in the western Atlantic. It is quite similar to the periodic runs of bluefin on which the traps at many localities in the Ibero-Moroccan Bay and the Mediterranean depended, particularly the "return" run of spent fish in July and August.

In addition to the lack of sight records, no tag returns revealing the movements of giant tuna between the Bahamas and Cape Hatteras have been obtained to date. Exploratory longline fishing results (Anonymous 1962, Zharov 1965) indicate that these fish are much more available in waters east of the Gulf Stream than in those west of it, just as they are in the northern Straits of Florida. Because of the tendency of bluefin tuna and other large pelagic fishes to travel in favoring currents when migrating for great distances (Sarà 1973), we assume, in the absence of more precise data, that many large bluefin swim in the Gulf Stream northward to the vicinity of Cape Hatteras. After the Stream has passed the Cape and turned eastward, aggregations of fish leave it successively, according to our hypothesis. We speculate further that the distance that a given group has travelled in the east-flowing current may be an important factor in determining where it enters the coastal waters. The first fish to leave the Stream after it passes Cape Hatteras may approach the coast anywhere from off the Chesapeake Bay entrance to Cape Cod. This is indicated by a tag recovery off the Chesapeake Capes (**Figure 76**), catches in traps off northern (peninsular) Virginia, New Jersey, and Long Island, and occasional sightings by fishermen off southern New England of giants travelling eastward, singly or in small schools, in late June and

early July (personal communications). We believe that the majority of these fish eventually enter the Gulf of Maine. Larger contingents probably follow the easterly current farther and tend to enter the Gulf of Maine more directly, presumably through the Great South Channel in many instances. Giant tuna usually arrive off northern Massachusetts in June, and off southern Maine and southwestern Nova Scotia in July. They often arrive in the Halifax area, however, in June. The latter may have left the Gulf Stream at about the same time as those which entered the Gulf of Maine, but followed a more direct course to this area. Large aggregations which have remained in the easterly current even longer may eventually enter the Gulf of St. Lawrence and Newfoundland waters in the latter half of July. The times of arrival in American waters are from Section IVC2. In some years, considerable numbers of bluefin persist in following the Stream much farther and eventually reach Norwegian waters in August, September or October (**Figure 75**).

These transatlantic migrations are discussed in the following Section C3. The local movements within the feeding area between Cape Cod and Newfoundland have been described previously in our discussion of tagging results.

The southward migration of large bluefin in late fall from their warm season feeding areas to their southern wintering areas (**Figure 14**) around the Greater Antilles and off Brazil is one whose details are unknown. Most of the large bluefin leave their coastal feeding areas between late September and early November (Section IVC2). As previously stated, tag returns (**Figure 79**) show a "direct" migration by a giant fish from the southwestern Gulf of Maine in July 1974 to the western Gulf of Mexico in May 1975 and a long term "indirect" migration from the nursery area for young bluefin off southern New England in August 1966 to the north central Gulf of Mexico in April 1976. These two returns show movements from the feeding area to the spawning grounds, but do not tell us where the fish spent

the winters. Two other returns, which may be more pertinent, were from releases off the northwestern Bahamas in May 1963 and June 1969 and recaptures off Recife, Brazil, in March 1965 and off Buenos Aires, Argentina, in February 1973, respectively (**Figure 75**). These two migrations were definitely to wintering grounds (in the northwest Atlantic frame of reference) and one even extends the probable wintering area far south of what was inferred from distributional data. The information available leads to the assumption that each of these fish had migrated southward from the northern feeding grounds in the fall preceding the winter in which it was recaptured. Since they had been at liberty for periods of 21 and 45 months respectively, however, they might possibly have entered a different migratory pattern of which we have no knowledge. In any case, these returns do not provide information as to the routes which they followed in their final migrations.

The recapture in December 1973 at the "tail" of the Grand Banks of a giant which had been released in northeastern Newfoundland coastal waters in August 1972 might indicate a starting point for southward migrations, but, since this fish had been at large for about 16 months, this was an "indirect", or presumed, movement from coastal waters.

Japanese longline catch rates in November 1965 (Le Gall 1974) were relatively high (one to three fish per 1,000 hooks) in a narrow area between longitudes 59°W and 60°W and extending from 44°N to 32°N. Although data on the sizes of the fish have not been published, this area might well represent the first part of a southward migration of large bluefin from Canadian coastal waters to their wintering areas.

Consideration of the North Atlantic circulatory system (Sverdrup et al. 1942) and the tendency of bluefin tuna to follow currents, however, leads us to suggest that many of the giants may follow a hypothetical migratory pattern following the North Atlantic gyre around the Sargasso Sea, first eastward, roughly along latitude 40°N, then southward and li-

nally westward over a rather broad front. The proposed migrations from the wintering areas through the spring spawning areas to the summer feeding grounds generally follow the remainder of this gyre. Sella (1929a, 1929b) was most likely the first to discuss the probable influence of the Gulf Stream system on the distribution of bluefin tuna in the Atlantic Ocean. We consider the southward migration of large bluefin tuna as one of the most challenging problems which remain to be solved.

The wintering grounds of the large bluefin which feed in northwestern Atlantic coastal waters in the warm season have not yet been clearly defined. The giant tuna are less concentrated, and presumably less active, during the cold season than in their spawning and feeding periods. They are dispersed over great areas, and are almost always too far below the surface to be seen, or to be caught by surface gears. Moreover, the opportunities for bluefin from different spawning and feeding areas to mix with each other may be at their maximum during this period. Except for a very few tag returns, the major sources of information on the distribution and migrations of giant bluefin during the (northern) cold season are the records of oceanic longline fisheries. As already stated (Section IVC3, and in this section), extensive catch and effort data for the Japanese longline fishery are available, but there is little published information on the sizes of the fish which it captures. This deficiency increases the uncertainties inherent in deducing migratory patterns from these data. In addition, the temporal and areal coverage of the vast potential range of the giant bluefin is incomplete, even if the data from all years combined are considered collectively for each month.

The contours of relative abundance, as indicated by longline catch rates (**Figure 32**), show two areas of maximum abundance in the first quarter of the year (January-March). One of these is centered on the Greater Antilles and includes the southeastern Gulf of Mexico, the northwestern Caribbean and Atlantic waters north of central and eastern Cuba and

Hispaniola. The other centers around the "bulge" (the easternmost part) of Brazil. It extends northeastward nearly halfway to the nearest parts of Africa, northward to latitude 15°N, eastward to longitude 40°W and southward, near the Brazilian coast, to latitude 10°S. Tag returns (**Figure 75**) show that giant bluefin do, at least occasionally, migrate from the western North Atlantic into the South Atlantic.

The distributions of monthly catch rates for individual years (Le Gall 1974) and of average monthly catch rates for groups of years (Shiohama et al. 1965, Shingu et al. 1975) permit more detailed estimates of seasonal distributions and migrations.

Examination of the catch rates in the Antilles area on this basis led us to believe that the winter distribution centered on these islands actually covered all of the Gulf of Mexico and the Caribbean Sea, and the adjacent Atlantic waters up to latitude 25°N and eastward to longitude 60°E. Data for United States exploratory and commercial fishing in this area (Wathne 1959, H. R. Bullis, Jr., personal communications, personal observations of the senior author) indicate that nearly all the bluefin taken in these waters have been giants.

The Japanese longline coverage in this area during the cold season has been light. The data indicate, however, that bluefin were scarce during most of the fall, but become more abundant in December, January and February. Coverage in March was minimal, but bluefin were taken in nearly half of the areas fished. In April, catch rates rose drastically in the Atlantic waters of the area, evidently because of the arrival of spawning fish.

Catch rates of more than one fish per 1,000 hooks were rare until April. They occurred in only four instances, each of which was in a different locality.

Wathne (1959) reviewed United States exploratory and commercial longline fishing in the Gulf of Mexico and adjacent waters. The commercial fishery was directed toward yellowfin tuna, *T. albacares*. Wathne noted that giant bluefin occurred in

the northern Gulf in January and February.

The available evidence indicates that the distribution of bluefin in this wintering area is rather sparse and patchy. This estimate may be biased, however, since most of the longline fishing effort in the area was probably directed toward yellowfin tuna rather than bluefin.

The situation off the "bulge" of easternmost Brazil and in the narrow "waist" of the Atlantic between there and western Africa was more complex. Concentrations of bluefin occurred off the "bulge" in each quarter of the year (**Figure 32**). Examination of the monthly charts suggests that two separate concentrations developed there, and then dispersed, during each year.

Bluefin were thinly distributed across the "waist" in July and August. In September a concentration (bounded approximately by the Equator and latitude 15°N and by longitudes 25°W and 40°W) formed in this area. The maximum catch rates exceeded one fish per 1,000 hooks. In October and November this concentration moved slowly southward, until its southern edge was at about 15°S latitude. In December, bluefin were still present in the area, but the catch rates were all below one fish per 1,000 hooks. This concentration probably did not consist of recent migrants from the North Atlantic. The giant bluefin do not usually leave their feeding grounds there until late September or October (see Sections IVC2 and IVC5) and this concentration had already developed in tropical waters in September.

The distribution of bluefin in the "waist" was generally thin in January, with more fish off the "bulge" than elsewhere. In February, however, the catch rates in the latter area increased, and a new concentration had definitely formed by March. This extended approximately from 20°S to 5°N latitude, and from 25°W longitude to the South American coast. Catch rates in this area were especially high in the years 1962 through 1965, sometimes exceeding 20 fish per 1,000 hooks. Since then, fishing in the area has been infrequent, and catch rates have generally been low.

The available information indicates that the bluefin taken in this area were giants. Zharov (1965), reporting on exploratory and commercial catches taken in the period from February through June 1963, off the South American coast from 11°S to 11°N latitude, stated that the bluefin ranged from 205 to 254 cm in length, with an average of 224 cm, and from 151 to 283 kg in weight, with an average of 183 kg. Thus all of them were in our "large" category. Shingu et al. (1975) also reported that the bluefin taken by longline in the equatorial Atlantic off northeastern Brazil were of large size.

The April catch rate distributions (Le Gall 1974) show that the area of high apparent abundance had expanded northeastward into the Gulf of Guinea, and northwestward almost to southeastern Florida. The latter extension of high catch rates, in our opinion, represents a major migration of giant bluefin from the wintering area described above to the spawning grounds in the "American Mediterranean" and in Atlantic waters east of the Bahamas and Florida (Section VD3). This route would follow the major branch of the North Equatorial Current off the northwestern coast of South America (Sverdrup et al. 1942) for much of the 3,500 nautical mile (6,575 km) distance. As stated previously, large bluefin tend to travel with favorable currents when they are migrating for long distances. The change in the areas of high catch rates from March to April indicates that this migration might have been completed in about a month. This would have required an average speed of about 5 knots (9 km per hour), with considerable help from favorable currents. This rate of migration is not inconsistent with those cited previously in this section for migrations between other areas, or for estimates of observed migratory speeds.

This hypothetical migration has not been verified by tag returns, since no bluefin have been tagged in the South Atlantic. As noted previously, however, two fish tagged off the Bahamas have been recaptured off eastern Brazil, or south of there. The sizes given by Zharov (1965) for fish

caught off eastern Brazil and along this proposed migration route, moreover, are in close agreement with the corresponding figures for fish taken in the Straits of Florida in May and June, prior to the recent increases in the sizes of giants taken there and elsewhere (Rivas 1955, 1976, Mather 1963a, 1974; Mather et al. 1974a).

Other contingents probably follow more northerly branches of the North Equatorial Current from mid-Atlantic wintering areas, where their relative abundance is lower than off the "bulge", and join this migration off northeastern South America or the Antilles. Still others may migrate directly westward, or even southwestward, from more northerly oceanic winter habitats to the spawning grounds.

While many giant bluefin evidently make lengthy migrations between their wintering and spawning areas, others, which have wintered farther north and west, east of the Bahamas, or in the American Mediterranean may reach their spawning grounds with relatively little movement. In the extensive areas where the proposed wintering and spawning areas overlap, the fish might reproduce wherever they happen to be when the spawning period occurs.

The distributions of the higher spring longline catch rates (LeGall 1974) suggest that most of the giant bluefin which migrated northwestward along the South American coast subsequently followed the Antilles Current in the Atlantic east of the Antilles and the Bahamas, instead of the North Equatorial and Florida Currents which flow through the Caribbean, the Yucatan Channel, the Gulf of Mexico and the Straits of Florida (Sverdrup et al. 1942).

As noted previously, these catch data may have been biased by spotty fishing effort in the Caribbean and the Gulf, and its possible direction toward yellowfin, rather than bluefin, tuna. Even allowing for these factors, the spring catches of bluefin in the eastern and southern Caribbean have been very scarce. In recent years, on the other hand, effort directed toward bluefin in the northern Gulf of Mexico during the spawning season has produced consider-

Table 33. Releases and returns by months at large for bluefin tuna tagged in the northwestern Atlantic, north of 35°00'N latitude and outside the 100 fathom (183 m) contour (offshore tagging ceased in 1968)

Year	Releases	Returns by Months at Large								
		0-5.9	6-17.9	18-29.9	30-41.9	42-53.9	54-65.9	66-77.9	78-89.9	90.0-101.9
1957	5	0	0	0	0	0	0	0	0	0
1958	0	0	0	0	0	0	0	0	0	0
1959	97	1	0	0	0	0	0	0	0	0
1960	204	0	0	0	1	0	0	0	0	1
1961	2	0	0	0	0	0	0	0	0	0
1962	1	0	0	0	0	0	0	0	0	0
1963	42	4	1	0	0	0	0	0	0	0
1964	25	1	0	0	0	0	0	0	0	0
1965	37	0	0	0	0	0	0	0	0	0
1966	67	0	0	0	0	0	0	0	0	0
1967	8	0	0	0	0	0	0	0	0	0
1968	4	0	0	0	0	0	0	0	0	0

able catches (Shingu et al. 1975, Shingu and Hisada 1976).

If "equatorial" bluefin did leave the Atlantic proper in significant numbers during their northward migration, there is a good chance that they did so through the Windward Passage instead of through the channels between the Lesser Antilles. Evidence that giant bluefin migrated from that Passage to the Straits of Florida by two routes — one through the northwestern Caribbean, the Yucatan Channel, and the Gulf of Mexico, and the other through the Old Bahama and Santaren Channels (**Figure 14**) has been presented previously in this section. We have found no indications, however, of the route by which the bluefin reached the Windward Passage.

It will be impossible to even estimate the percentage of the fish from the equatorial Atlantic which complete their northward migration in Atlantic waters, and the percentage which pass through the "American Mediterranean" or the adjacent channels and straits, until significant numbers of bluefin have been tagged in equatorial waters.

The return to their spawning areas completes the prodigious migratory cycle of the giant "western Atlantic" bluefin, as we now envisage

it. In our opinion, however, this extremely long circuit, extending from latitudes 40°N to 50°N to latitude 10°S, or even to 40°S, is the outer perimeter of a very broad pattern. Although many fish may follow something resembling this route, others which winter farther north make correspondingly shorter circuits. Some individuals may not even reach the latitudes of the Bahamas

c. Medium Fish

Direct information provided by tag returns from medium sized (32-122 kg) bluefin tuna, and deductions based on their occurrences in the coastal and oceanic fisheries (Mather 1964b) enable us to offer a preliminary hypothesis on their migrations in the western North Atlantic. These fish are the only ones, among the three major size groups, which have been extensively tagged in this region but never recaptured elsewhere.

The most important tagging information resulted from 491 releases in offshore waters, from which nine returns have resulted (FAO 1972) (**Table 33**). Seven of the recaptures occurred on the continental shelf from off Maryland to just north of Cape Cod, one near Yarmouth, Nova Scotia, and finally one at the edge of the continental shelf south of Cape Cod (**Figure 80**). All of these tags

were recovered during the normal tuna fishing season, June through October. Six of the recaptures near the United States coast, each of which took place after less than four months at large, represented "direct" migrations. Most of these, and a seventh which could be regarded as repeating its migratory pattern after 13 months at large, suggested that medium-sized bluefin approached the coast off Maryland and New Jersey in late June or early July from the east, and then worked northeastward toward Cape Cod as the summer advanced. The seasonal progression of the recoveries in coastal waters resembled that for the larger of the "small" bluefin tagged in those waters. They also coincided with the movements of the medium group through the coastal fisheries (Mather 1964b). The other two returns represented much longer times at liberty, 31 and 93 months, respectively. The former was released in November 1960 off the east end of Georges Bank and recaptured in June 1963 at Veatch Canyon, south of Nantucket Island. The recapture location coincides closely with the possible inshore migration route of the five fish tagged at 40°N latitude, 68°W longitude in the same month and eventually recaptured in coastal waters (**Figure**

Figure 80. Geographic distribution of bluefin tag release and recapture data from North Atlantic tagging studies, illustrating offshore-inshore movements and one transatlantic migration

80). The last fish of this group was tagged at Atlantis Canyon (south of Cape Cod) in November 1960 and recaptured off Cape St. Mary's (near Yarmouth), Nova Scotia, in August 1968. In its nearly eight years of freedom, its weight had increased from 69 kg (estimated) to 185 kg, bringing it into the "giant" category. This return was the first to show a migration from New England to Canadian waters.

Movements during the summer feeding season in coastal waters, as indicated by the seasonal progression of the returns from offshore releases and also by the movement of the fisheries, is from southwest to northeast. This general pattern could be observed from off Maryland to the southern part of the coast of Maine. Medium fish have also been abundant in Nova Scotian waters in some years, off Wedgeport (near Yarmouth) and, more regularly, in

St. Margaret's Bay (near Halifax). The years of abundance at Wedgeport generally coincided with those in Cape Cod Bay, as did the ages of the fish taken. The medium fish were often abundant in Cape Cod Bay through most of August, but did not usually occur in numbers off Wedgeport until September. These facts suggest a continuation of the northeastward movement from Cape Cod to Nova Scotia. However, fish were usually numerous in Cape Cod

Table 34. Releases and returns for bluefin tuna 50 - 150 cm (mostly 50 - 100 cm) tagged on the continental shelf between Cape Hatteras, North Carolina and Cape Ann, Massachusetts, June - October, by year of release, months at liberty, and recapture area.*

Year	Releases	Area*	Returns by Months at Large								Total	%
			0-5.9	6-17.9	18-29.9	30-41.9	42-53.9	54-65.9	66-77.9	???		
1954	169	1	1	0	0	0	0	0	0	0	1	0.6
		2	0	0	0	0	0	2	0		2	1.2
1955	215	—	0	0	0	0	0	0	0		0	0
1956	58	—	0	0	0	0	0	0	0		0	0
1957	34	1	0	0	1	0	0	0	0		1	2.9
1958	38	—	0	0	0	0	0	0	0		0	0
1959	25	—	0	0	0	0	0	0	0		0	0
1960	15	1	0	0	1	0	0	0	0		1	6.7
1961	150	1	0	2	3	2	0	0	0		7	4.7
1962	77	1	0	4	0	0	0	0	0		4	5.2
1963	29	1	7	2	0	0	0	0	0		9	31.0
1964	483	1	100	36	0	0	0	0	0		136	28.2
1965	1938	1	182	60	37	0	1	0	0		280	14.4
		2	0	14	5	1	0	0	0		20	1.0
1966	3959	1	529	569	50	8	4	0	2	1	1163	29.4
		2	0	12	3	0	1	0	0		16	0.4
1967	628	1	97	59	15	13	0	0	0		184	29.3
		2	0	1	1	0	0	0	0		2	0.3
1968	260	1	88	19	8	0	0	0	0		115	44.2
1969	341	1	12	85	12	2	1	0	0		112	32.8
1970	460	1	50	118	9	7	1	0	0		185	40.2
1971	622	1	38	99	16	1	0	0			154	24.8
1972	195	1	9	53	5	0	0				67	34.4
1973	511	1	59	23	8	1					91	17.8
1974	1733	1	73	127	50						250	14.4
1975	309	1	23	26							49	15.9
1976	2308	1	142								142	6.0

*Areas: 1 = Northwestern Atlantic, 2 = Bay of Biscay

Bay in October. This movement, if it did occur, represented a range extension, rather than a migration, of the entire mass of fish. Since 1964 catches of medium-sized tuna in all waters north and east of Cape Cod have been small or negligible.

Information on the fall and winter migrations of the medium-sized bluefin is limited to deductions from results of exploratory oceanic fishing (Mather and Bartlett 1962, Mather 1964b, Wilson and Bartlett 1967). Commercial longline fishing in the area has been much more extensive

and provides valuable data on the relative abundance of tuna in the area by seasons (Wise and Davis 1973), but size composition data for the catches are limited, and have usually been presented in such large temporal and areal strata as to be of little value for this purpose.

Offshore exploratory longline catches of bluefin north of latitude 35°N have consisted mainly of medium fish, and dense seasonal concentrations have been encountered (Squire and Mather 1963). Considering these data collectively, the fol-

lowing pattern for medium fish emerges. After leaving the coastal waters in mid autumn, fish of this size concentrate in great numbers in the canyons along the edge of the continental shelf, from the Hudson Canyon off New York Harbor to the northeastern end of Georges Bank. In winter, few were encountered in these canyons, and the oceanic exploratory catch rates in this season have been relatively low. The data indicate, however, that the bluefin tend to accumulate in loose aggregations along the Gulf Stream front,

from east of Maryland and south of Cape Cod to south of the Grand Banks. In May and early June the fish tend to concentrate in the western part of this area, at least. The eastern part has not been sampled in these months. The highest catch rates occurred in the area bounded by 38°N and 40°N latitude and 68°W and 70°W longitude, where some fish which appeared to be in advanced stages of maturity were taken (Section VD3). In June, this distribution spreads westward to the edge of the continental shelf, and thence to the coast, completing the migratory cycle of this size group. Since the exploratory fishing may not have covered all of the eastward part of the winter and spring distributions, the migratory pattern may extend farther to the east in those seasons.

d. Small Fish

Over 14,600 small and medium bluefin have been tagged in coastal waters between Cape Hatteras, North Carolina, and Cape Cod, Massachusetts, in the period July 1954 through October 1976, and 2,992 returns have resulted (**Table 34**) (Burnett et al. 1977, Mason and Baglin 1977). Most of these fish were in the small group, 50-120 cm long, but a few were mediums, 120-160 cm long. The majority of the fish were released from purse seine catches, a procedure which may incur very high tagging mortality (Beckett 1974). The return rates from hook and line releases were considerably higher than those from seine releases in nearly all years (unpublished data at Woods Hole Oceanographic Institution). Lenarz et al. (1973), utilizing the results of the double tagging experiments which have been carried out in this area since 1971, estimated the instantaneous rate of tag shedding, on an annual basis, to be 0.31.

The returns included 2,944 from the release area, seven from oceanic waters in the western North Atlantic, one from the Gulf of Mexico, and 40 from the Bay of Biscay. Since times at large ranged up to six years, and even 10 years in one case, several of these fish were in the medium size group when recaptured, and one was definitely a giant. The migration of

the last individual, which has been described previously in this section, was the first to connect the only known nursery area for juveniles in the western Atlantic with the major spawning ground of giants in the Gulf of Mexico. The returns from the Bay of Biscay will be discussed in Section VIC3.

The local recaptures included 1,408 in the fishing season in which the fish were released. The 1,536 local recaptures in subsequent seasons, after up to six years at large, indicate that many of these young bluefin visit this nursery and feeding area for two or more consecutive seasons, sometimes returning even after they entered the medium group (ages 5-8).

Less has been learned about the migratory pattern of this size group than might have been expected from the large number of returns, because so many of them were from the release area. Therefore deductions from the movements of the fish through the coastal fishery, and from the limited information available on longline catches in oceanic waters will be used to supplement the tagging results in describing its migrations.

The 2,944 local returns show that the young bluefin have generally tended to migrate from southwest (Virginia, Maryland and New Jersey) to northeast (southern New England) within this nursery and feeding area during the fishing season (Mather et al. 1974b). This is also indicated by the movement of the fishery (Mather 1974b, Sakagawa 1975).

Migrations to waters north of Cape Cod (into Cape Cod and Massachusetts Bays) have been recorded for only a few of the larger (when recaptured) individuals. As noted in Section IVC2, however, small and medium-sized bluefin tuna have not been caught in numbers in the Gulf of Maine for many years.

In the later part of some seasons (September-October), considerable numbers of small bluefin have reversed the usual migratory pattern, moving from off southern New England into the approaches of New York Harbor. In some years, such as 1966, this "reverse" migration has been followed by exceptionally good

fishing for "school" tuna, which has extended later into the fall than usual, off western Long Island and northern New Jersey (Moss 1967).

Until recently, little has been known about the migration of small bluefin from their coastal nursery ground, from which they disappear in late September or October, to their wintering area, which was presumed to be in offshore waters. An interesting description of their behavior prior to this movement, however, has been received from R. Hillhouse (personal communication), an experienced air spotter of tuna in the area. He has observed "hesitating" behavior (Lenier 1959) of small bluefin off southern New England in late September and early October. Hillhouse reported sighting schools of small bluefin traveling together in a very large circle, which other schools joined successively until a substantial aggregation of fish had been built up. Then they all left the area together. This behavior is identical to that observed by Sarà (1973) off the Strait of Messina.

The six winter recoveries off the edge of the continental shelf east and southeast of Georges Bank, near latitudes 40-41°N and longitudes 65-66°W (**Figure 81**), have provided the most significant progress in migratory studies of small northwestern Atlantic bluefin in recent years. Two of these indicated "direct" migrations. These fish had been tagged in the coastal feeding grounds off the northeastern United States in August 1973 and July 1975, and recaptured in the above wintering area after five to six months at large, in January 1974 and January 1976, respectively. Three of the other recaptures occurred in January after about 17 months at large, and one in February after 30 months. The extent of this wintering area is not known. Catches of bluefin taken during extensive exploratory fishing from the research vessel "Delaware" in the slope water between the Gulf Stream and the continental shelf during winter and early spring (Wilson and Bartlett 1967) consisted mainly of medium fish (size data obtained by Woods Hole Oceanographic Institution personnel on board the "Delaware" and from J. L. Squire,

Figure 81. Geographic distribution of bluefin tag release and recapture data from middle Atlantic tagging studies, illustrating inshore-offshore movements.

Jr., W. F. Rathjen and P. C. Wilson, personal communications). The presence of small bluefin in the area bounded by latitudes 40° and 45°N and longitudes 45° and 70°W has been documented, however, by Shingu and Hisada (1976). About 90 percent of their sample of Japanese longline catches in this quadrilateral in January-February 1975, consisted of small (less than 32 kg) fish, about half of which were in their third year of life.

While in this wintering area, the small bluefin remain at subsurface levels (perhaps about 50-100 m). Their growth almost ceases during this period (Section IIIC3), and their feeding and other activities are probably minimal.

The remaining offshore migration was by an individual which was released about 40 nautical miles (75 km) south by east of Martha's Vineyard in August 1966, and recaptured off the southern end of the Grand Banks (about 42° 30'N, 71° 00'E) in August 1972. In six years at liberty, its length had increased from 58 cm (estimated age 1), to 180 cm, with a reported weight of 120 kg. This fish

was approaching "giant" size, and might have been entering the migratory pattern proposed for giants earlier in this section.

Tagging has produced no information on the late spring migration of small bluefin from this wintering area into the coastal feeding grounds.

In the first half of June 1959, however, an experimental longline fishing operation conducted from the fishing vessel "Golden Eagle", in cooperation with the Bureau of Commercial Fisheries (Wilson and Bartlett 1967), obtained high catch rates (up to 170 fish per 1,000 hooks) of small (estimated sizes provided by J. L. Squire, Jr., personal communication) bluefin tuna in the vicinity of latitude 39° 20'N, longitude 68° 15'W. Since the first appearances of small bluefin in coastal waters in recent years have occurred between the Chesapeake Bay entrance and Long Island (Sakagawa 1975, personal observations of the authors), their approach to the coast may have been quite similar to that indicated by tag returns for medium bluefin (Figure 80).

The return to the nursery area completes the migratory cycle of the

young bluefin tuna. Since it appears that few western Atlantic fish in the small size group (ages 1-4) have attained sexual maturity, this pattern is not as greatly complicated by spawning activity as is that for small bluefin in the eastern Atlantic, which evidently spawn at younger ages (Section VII).

The summer and winter habitats of the young bluefin, however, tend to expand with age of fish. Age 1 bluefin have very rarely been recorded in the Gulf of Maine, but age 2, 3 and 4 fish have occurred in Cape Cod Bay, at the southwestern end of the Gulf, in great numbers in some years. Age 3 and 4 fish have been caught in Nova Scotia waters. In winter and spring, fish of ages 3 and, especially, 4 have been captured much farther offshore than the wintering area mentioned above, but usually in small numbers.

e. Very Small Fish

Less is known about the migrations of age 0 bluefin in the western Atlantic, since no areas where they concentrate regularly have been found there. Hatching occurs extensively in the Gulf of Mexico in May and June. It also must spread widely over waters adjacent to the Greater Antilles and the Bahamas, and far to the east and north of those islands. The limits of these areas in which bluefin are born have not been defined, but we estimate that they may extend over most of the deep (>200 m) waters between latitudes 18°N and 33°N and between longitude 67°W and the coast and islands. Another probable hatching area is north of the Gulf Stream and east of New Jersey and Maryland. Age 0 bluefin from all these areas must converge by various routes on the nursery grounds between Cape Hatteras and Cape Cod, since that is the only western Atlantic area in which age 1 bluefin are known to occur regularly en masse.

The only route by which it seems obvious that such a migration occurs is from the Gulf of Mexico and adjacent waters through the Straits of Florida to the northern nursery area. The timing of this migration is uncertain.

The meager information available (Rivas 1954, Mather 1963a, Mather et al. 1974) indicates that the passage of these young of the year through the Straits peaks in late July and August. Since no age 0 fish have been tagged in these waters, this migration is strictly hypothetical. It does, however, fit the known facts of extensive spawning in the Gulf of Mexico and the tendency of age 1 bluefin to concentrate almost exclusively in the Cape Hatteras-Cape Cod area in the summer. Age 0 bluefin do occasionally appear in numbers, for a few weeks at a time, between late July and early November in some part of this northern nursery area, but there has been no way to determine where these fish had been spawned.

Thirty age 0 bluefin (42-48 cm long) were marked during an unusually strong concentration of young of the year off Brielle, New Jersey, in October 1973. Four of these have been recaptured off New Jersey, one in August 1974, and the others in June or July 1975 (Mather and Mason 1976). These returns proved that bluefin which visited the nursery area at age 0 were actually recruited to the group of small (ages 1-4) fish which supported the fisheries there in ensuing seasons.

The first sustained and regular concentration of these very small bluefin known to us begins in late June or early July between Cape Hatteras and Cape Cod, when the fish are almost exactly one year old. The important question of how they reach that area remains to be answered.

3. TRANS-ATLANTIC AND TRANS-EQUATORIAL MIGRATIONS, AND ATLANTIC STOCKS

a. Introduction

Transatlantic migrations of bluefin tuna have been demonstrated by tag returns showing migrations of 40 small (ages 1 and 2 when tagged) individuals between the New York Bight (New Jersey to Cape Cod) and the Bay of Biscay (**Table 34**, and migrations of 9 large (over 122 kg)

individuals from the Straits of Florida to Norwegian waters (**Table 28**).

Two transequatorial migrations have been recorded for giant bluefin which were tagged off the northwestern Bahamas and recaptured off the South Atlantic coasts of South America (**Table 28**).

Biometric comparisons of bluefin tuna from various parts of the Atlantic and the Mediterranean have been made and biochemical characteristics of bluefin tuna from various parts of the Atlantic have been compared.

In the following parts of this section we will present the data for these migrations (**Figure 75**) and some related factors, and consider their implications. Finally we will discuss the identity of the stocks in the Atlantic Ocean.

b. Trans-Atlantic Migrations

i. Giant Fish

Nine giant bluefin which had been tagged off the Bahamas have been recaptured in Norwegian waters. Four of these recaptures represented "direct" migrations since the fish had been at liberty for less than four months. The other five indicated longer periods at liberty, which were approximately as follows: 15.3 months for two fish, 26.5 months for two, and 86.6 months for the remaining one. Thus when the fish in the second group ("indirect" migrants) had crossed the Atlantic, or whether they had done so more than once, is uncertain. The release (May 9-June 15) and recapture (August 4-October 6) dates show that the "direct" migrants had crossed the Atlantic during the warm season. One of these made the trip of at least 4,200 nautical miles (7,800 km) in a maximum of 50 days, at a rate of 84 nautical miles (155 km) per day, or 3.5 knots (6.5 km per hr).

These transatlantic migrations of giant bluefin were not randomly distributed over the years. Five of the nine fish were released in the years 1960-1962, two in the years 1972-1973 and only two in the other 15 years in which bluefin tuna were tagged in the Bahamas.

Four of these migrations definitely occurred in the following years

(numbers in parentheses indicate number of migrations, if greater than one): 1961(2), 1962, 1967. The other five could have occurred in the following years 1960-1962(2) (migrations in 1962 are considered improbable because of the fat condition of the fish when they were recaptured), 1969-1976, 1972-1973, and 1973-1974. Unfortunately, no body condition data have been reported for the tagged fish recaptured since 1962. Likewise, the weekly distributions of body condition data for the landings in northwestern Europe since then are not available. The tag return data, however, suggest another pulse of west to east migrations in the period 1972-1976. This may account for the somewhat increased availability of giant tuna off Norway since their virtual disappearance in 1973.

The fish which made the direct migrations, between May and early October, must have spent much of this time in deep oceanic waters where food is relatively scarce. Normally, large bluefin tuna are concentrated in the coastal areas in the more northerly part of their ranges in summer and early fall, where they are feeding heavily (Sections IVC2 and IVC4).

The two "direct" transatlantic migrants which were examined after recapture were very lean, in contrast to the fat condition typical of large bluefin which have spent the summer in coastal waters (Rivas 1955, Mather 1962, Tiews 1964). Such lean bluefin, called "long-tailed bluefin" (J. Hamre, personal communication) by the local fishermen, had previously been observed among late season catches off Norway and in the North Sea, but there had been no explanation for their unusual body condition.

Hamre (in Mather 1962) and Tiews (1964) assumed that the lean condition of the recaptured fish resulted from their having passed much of the summer in relatively barren oceanic waters, instead of the rich coastal feeding grounds. They concluded that the "long-tailed bluefin" were actually fish which had been recruited from the western Atlantic during the years in which they were captured. Using extensive body con-

dition data from German North Sea catches of bluefin tuna, Tiews (1964) estimated the percentage of the yearly late season (September 15-October 31) catches there which probably were recruited from the western Atlantic in the years 1952-1962. The percentage recruited varied from 0.39 of the 1953 catch to 0 in 1957 and 1959. After 1954, the first year in which bluefin were tagged in the Straits of Florida, the maximum estimated recruitment of western Atlantic fish to the northeastern Atlantic occurred in 1960 (11%) and 1961 (33%) (**Table 28**). Two tagged fish migrated directly from the western Bahamas to Norway in 1961. Two others, released in 1960 and recaptured in 1962, were in the normal late-season fat condition when recaptured, indicating that they had probably crossed the Atlantic during a previous year (1960 or 1961), and spent their last summer in the feeding grounds off northern Europe. Thus the results of the tagging, limited as they are, are quite consistent with the estimates of recruitment based on body condition (**Table 28**).

To sum up, even though the majority of the returns from releases of giant bluefin in the Straits of Florida have been from Norwegian waters, the following facts, or deductions, suggest that these returns do not represent a part of a normal annually repeated migratory pattern:

1. The fish are in waters where food is scarce during the period when giant bluefin are normally feeding heavily in rich coastal areas and regaining the weight they have lost during their spawning activity and the related migrations.

2. The transatlantic migrations have not been randomly distributed over the years, but have occurred in clusters in certain periods.

3. Tiews' (1964) estimates of annual recruitment of giant bluefin from the western Atlantic in the late season North Sea fisheries, based on body condition data, also show that this recruitment is very irregular, with peaks of high recruitment separated by long periods of negligible recruitment.

4. The variations in annual recruitment, as estimated by Tiews

(1964), are consistent with those in transatlantic migrations indicated by tag returns, for those years in which both types of data are available.

5. Rodewald (1967) has shown that the volume of west-east transatlantic migration may have been influenced positively by anomalies in the atmospheric circulation over the North Atlantic which produce exceptionally strong west winds in the middle latitudes in certain years. His findings were generally consistent with the tag return data and Tiews' (1964) estimates of annual recruitment.

6. The two giant bluefin tuna which were recaptured in Norwegian waters in August and September 1962, 26-27 months after they had been tagged off Bahamas, were in the normal fat condition which is typical of fish which have been feeding heavily in coastal waters. Rodewald (1967), moreover, found that atmospheric conditions over the probable migration route in July 1962 were distinctly unfavorable for movements from west to east. It is highly probable that these fish had crossed the Atlantic in a previous year, and then entered into the migratory pattern followed by large bluefin in the eastern Atlantic.

On the basis of this evidence, we conclude tentatively that recruitment of large bluefin to the northeastern Atlantic from the western Atlantic is variable, being important in some years and negligible in others. We speculate further that at least some of these recruits remain in the eastern Atlantic through the next annual feeding period, or longer.

No east-west transatlantic migrations of large bluefin tuna have been recorded. Although 554 large and medium-sized bluefin were tagged in the eastern Atlantic off Norway and Spain prior to 1968, none of the 51 recoveries has been west of longitude 10°W (FAO 1972). A renewed and sustained tagging program is required to determine whether such migrations occur.

ii. Medium Fish

While there is no direct evidence of medium sized fish making the migration from North America to Europe, there remains the possibility

that several fish tagged and released as small sized fish could have made the migration and been recaptured as medium sized fish.

iii. Small fish

Tag returns have demonstrated transatlantic migrations of 40 small (less than 20 kg when tagged) bluefin tuna from west to east, and two from east to west (**Figure 75**).

All of the west-east migrations were from the New Jersey-Cape Cod area to the Bay of Biscay (Mather 1960, 1969; Mather et al. 1967, FAO 1972). All of the releases took place in July and August, and the recaptures extended over the period from June through October in subsequent years. Therefore, these migrations evidently occurred mainly in the cold seasons between the departure of the small bluefin from American coastal waters in late September or October, and their arrival in the Bay of Biscay in late May or early June. The minimum distance travelled was about 3,000 nautical miles (5,500 km) and the minimum time at large was 11 months. The average speed required would be only 0.4 knots (0.7 km/hr). It is possible, however, that the times at large were influenced by the eight month period (October-May) in which there was little or no fishing for small bluefin.

The 40 west-east transatlantic migrations of small bluefin have not been randomly distributed over the years. Thirty-eight of them could have occurred in a minimum of three, and a maximum of five cold seasons between 1965 and 1969. The other two could have taken place in a minimum of one, and a maximum of two periods between 1954 and 1959. Thus, over a 22 year period, all migrations of this nature revealed by tag returns could have occurred in a minimum of four, and a maximum of seven winter periods. All of the returns were from only four of 22 yearly release groups. Two of these groups, however, 1,938 in 1965 and 3,959 in 1966, were the largest. On the other hand, the 169 releases in 1954 yielded two transatlantic returns at a time when tuna tagging was a relatively unknown practice, and larger numbers of releases in 1955, 1964, and in 1968-1975 after tagging had been

well publicized, have produced no transatlantic returns at all.

In comparing the numbers of local and transatlantic returns, the 1,396 local recaptures which occurred in the release season have been eliminated. This leaves 1,517 local recaptures after eight months or more at large, in comparison with the 40 in the Bay of Biscay. Transatlantic returns have exceeded 1 percent of the releases for only two years, 1954 and 1965. These figures indicate a much stronger tendency for young bluefin in the western Atlantic to return annually to their usual nursery ground, rather than to migrate across the Atlantic. Also, the data indicate that when such migrations do occur, they take the form of pulses, rather than a constant small flow. Finally, the fact that the fish are in a given area in one summer and in such a distant one in the next does not support the concept of an annually repeated cyclical migration.

Deviations from established migratory patterns may be caused by changes in environmental conditions. Rodewald (1967) showed that the transatlantic migrations of small bluefin recorded prior to 1967, like the corresponding ones of giant tuna, might have been positively related to anomalies of the atmospheric circulation pattern over the North Atlantic which caused unusually strong westerly winds in the middle latitudes.

Two east to west transatlantic migrations of small bluefin tuna have been recorded (Aloncle 1973). These fish were tagged in or near the Bay of Biscay in September 1968 and September 1969. The former was recaptured in August 1970 south of Cape Cod, and the latter in July 1970 in the New York Bight (**Figure 75**). These migrations, in regard to dates and localities of release and recapture, constituted an almost exact reversal of the west to east transatlantic migrations just described. These results show that small bluefin sometimes cross the Atlantic from east to west as well as from west to east. The transatlantic returns constitute a much higher proportion of the total number (40%) for the eastern Atlantic taggings, than for those in the western Atlantic (0.4%). The numbers of

releases in the eastern Atlantic (34 fish from 1967 through 1972) and of returns from these (5 fish) (Aloncle 1973), however, are so small that this comparison may not be statistically significant. Likewise, they give no basis for estimating the annual frequency with which east-west transatlantic migrations occur.

We lack the data required to estimate the approximate total numbers of fish which have made transatlantic migrations from these tag returns. There are indications, however, that the volume of these migrations has sometimes been sufficient to affect the fisheries in the respective areas.

As noted above, the most important west-east transatlantic migrations of young bluefin tuna were from the release groups of 1954 and 1965. Catch records for young bluefin in the Bay of Biscay in this period are somewhat confusing, but some data indicate considerable increases in the landings there between 1954 and 1955 and between 1965 and 1966. There was also a great decrease in the western Atlantic purse seine catch in 1966. Fourteen tag returns furnish fairly strong evidence for a significant west-east transatlantic migration between the 1965 and 1966 seasons. The case is less clear for the 1954 releases. Since these fish had been at large for five years, the actual date of their transatlantic migration is uncertain. These fish were of age 2 (year class of 1952) when released, however, and nearly all subsequent small bluefin which have made similar migrations were recaptured in European waters before they had reached age 4. Therefore, it is most probable that these two migrants had actually crossed the Atlantic between the 1954 and 1955 seasons. On the basis of these returns, Hamre et al. (1966) suggested that the great contribution of the 1952 year class to western European catches might have been due to a major movement of fish of this year class from the western to the eastern Atlantic.

The only certain period of east-west transatlantic migration was 1969-1970. New England purse seine fishermen informed us that tagged fish were scarce among the early catches in 1970 in comparison with the numerous returns obtained in previous

years from earlier local taggings. The senior author attributed this situation to a probable influx of fish from European waters, where very few small bluefin had been marked. The subsequent recovery of two French tags verified this conjecture. This immigration may have been at least partially responsible for the increase in the northwestern Atlantic purse seine catch of small bluefin from 1,565 tons in 1969 to 4,200 tons in 1970.

c. Trans-Equatorial Migrations

The two South Atlantic recaptures of giant bluefin which had been tagged in the Straits of Florida (**Figure 75**) have been discussed in the context of the migratory pattern proposed for the large bluefin which occur in the western North Atlantic during the warm season (part 2b of this section). As noted there, however, bluefin are widely distributed in the tropical Atlantic during this same period. Among the possible explanations of this situation are the following:

1. Some large bluefin may switch their summer feeding grounds from the northwestern Atlantic coastal waters to the frontal zones of the Equatorial Currents. Concentrations of tunas of various species have been observed in the frontal zones of the Pacific Equatorial Current system (Blackburn 1965, Laurs and Lynn 1977, Murphy and Shomura 1972).

2. A separate stock of large bluefin may exist in the tropical Atlantic.

Neither of these explanations would be ruled out by the transequatorial tag returns, if fish of the hypothetical tropical stock reproduced in the western North Atlantic spawning area. These possibilities will be discussed further in the conclusion of this section (Section D).

d. Stock Identification

i. Biometric Studies

Preliminary biometric comparisons (Ginsburg 1953, Schuck and Mather 1950, Mather 1959) of morphometric and meristic data suggest that there are slight morphological differences between bluefin tuna of

the same sizes from the eastern and the western Atlantic. These studies indicated that the heads and the pectoral fins of individuals from the eastern Atlantic were slightly shorter than those of individuals from the western Atlantic, and that the maximum depths of the former were slightly less than those of the latter, even allowing for seasonal changes in this characteristic. Comparisons of meristic data, particularly gill raker counts, by Robins (1957), Mather (1959) and Tiews (1963) showed no significant differences between large samples of fish from the two areas.

In a more recent study, Rivas (Rivas and Mather 1976), however, did not find significant differences in the characteristics noted above between the samples from the two areas. He did, however, show divergences in the pectoral ray counts and in the counts of gill rakers in juveniles 27 to 118 mm long. He also found that the average length of the second dorsal fin was significantly greater for bluefin from the western Atlantic than for those from the eastern Atlantic. Previous authors had not noted this difference. Since Rivas and Mather have been in contact for many years, and have followed the same methods as closely as possible, these discrepancies show how difficult it is to obtain consistent results from biometric studies. The preliminary results suggest, however, that there may be distinct stocks of bluefin tuna on the two sides of the Atlantic. Extensive data for more ex-

haustive studies are available at the Woods Hole Oceanographic Institution and the Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, Florida, and in the literature: Heldt (1927) [Tunisia], Frade (1931) [Portugal], Russell 1934a [North Sea], Navaz (1950a) [Bay of Biscay], Nedelec (1954) [North Sea], Buser-Lahaye and Doumenge (1954) and Doumenge and Lahaye (1953) [Mediterranean coast of France], Arico and Genovese (1953), and Genovese (1957, 1958) [Tyrrhenian Sea], and Morovic (1968) [Adriatic Sea]. European workers have taken their measurements with tapes, following the contour of the body (Anonymous 1932b), whereas United States workers have taken "straight line" measurements with calipers (Marr and Schafer 1949). Factors for converting "straight" measurements of northwestern Atlantic bluefin to the "curved" system are available at the Woods Hole Oceanographic Institution.

ii. Biochemical Studies

Edmunds and Sammons (1971, 1973), after studying the genic polymorphism of tetrazolium oxidase in bluefin tuna from the western North Atlantic and from the Atlantic coast of France using electrophoretic techniques, concluded that no differences could be found between the samples from the two areas. On this basis, and the indications of sporadic transatlantic migrations from tagging, they

tentatively concluded that the bluefin tuna of the two areas belonged to a single breeding population rather than two geographically distinct stocks. They noted that the evidence was not conclusive and that other hereditary characters might reveal a degree of racial separation that was not apparent from a comparison based on the Ox-I enzyme system.

iii. Conclusions

In our opinion, neither the biometric nor the biochemical studies have provided conclusive evidence in regard to the identity of the stock, or stocks, of bluefin tuna in the Atlantic Ocean and adjacent seas. Furnestin and Dardignac (1962) have previously expressed this opinion in regard to the biometric studies available at that date. Tiews (1963) did not believe that the differences between samples of bluefin tuna from different areas which had been proposed by various authors would stand up under critical inspection. The biochemical studies now available are admittedly of a preliminary nature and were based on samples which were not sufficiently numerous to provide definitive results.

It is our opinion that the identification of stocks must be based largely on distributional studies and tagging results. Hypotheses in regard to the identity of stocks, as well as migratory patterns, will be discussed in Section VII E, the concluding part of this work.

VII. DISCUSSION, RECOMMENDATIONS, AND CONCLUSIONS

A. INTRODUCTION

In this section we review and present our conclusions on the aspects of the life history of the Atlantic bluefin tuna. Since the fisheries in each area have been described and their trends have been summarized in Section IV, we shall not refer to them further except as necessary to elucidate the life history of the species. Our opinions on stock identity will conclude our discussion of the material in the preceding sections.

Although much information on the biology of the Atlantic bluefin tuna has been compiled in this work, we have not attempted to cover all of the aspects of its life history, nor have we been able to cite all of the works on the topics which we have discussed. We shall point out the areas in which the existing information seems to be deficient, and make recommendations in regard to future research.

B. AGE AND GROWTH

There has been good agreement on the sizes of Atlantic bluefin tuna at ages 1-11 (Table 1). There is less confidence in determinations for older ages. Caddy et al. (1976) extended estimated age determinations to 25 years, and also provided separate von Bertalanffy growth curves for males and females. These authors noted that earlier age determinations had ascribed fish smaller than 245 cm to age group 13, whereas their own determinations indicated that 245 cm was roughly equivalent to ages 14-15 for males and age 18 for females.

They also asserted that apparent underestimates of the ages of fish more than 240 cm long had resulted in estimates of L₄, based primarily on data from fish less than 12 years old, which were in excess of any sizes recently recorded for Atlantic bluefin tuna. If their results should be validated, considerable revisions of recent estimates

of the age composition of the Atlantic bluefin tuna stocks (Sakagawa and Coan 1973) would be required. Berry et al. (1977), however, questioned previous age determinations for Atlantic bluefin tuna. They concluded that medium size tuna (defined as fish weighing between 56.7 and 136.1 kg) might have been overaged by one or two years, and that giant fish might have been overaged by from one to 10 years. They attributed this alleged overaging to the counting of double or multiple markings on vertebrae or otoliths as representing two or more years' growth rather than a single year's.

It is most important that the actual age composition of the "relict" population (as described by Caddy et al. 1976) of giant Atlantic bluefin tuna be determined with certainty.

It is also important that the linear growth rate of the larval, postlarval and early juvenile stages of bluefin tuna be determined for the various spawning areas. This information is needed in terms of length, rather than weight, to permit better estimates of spawning dates and localities from the collection data for these very small bluefin tuna.

Seasonal variations in the growth rates of bluefin tuna up to 4 years old are reasonably well known (Mather and Schuck 1960, Furnestin and Dardignac 1962) but the data now available should permit extension of this knowledge to older ages. Information on this subject could be greatly increased by more systematic and extensive collections of size frequency data and biological material, especially from catches of the oceanic longline fisheries.

The possibility that the growth rate of the Atlantic bluefin tuna has increased as the size of the stock has decreased should also be investigated. This possibility is suggested by the remarkable number of extremely large bluefin caught since 1970 (see Section IV).

C. DISTRIBUTION, MIGRATIONS, AND SPAWNING

1. Introduction

Although there are differences in details, the general patterns of distribution, migrations and spawning on the two sides of the Atlantic fit the hypothetical migratory model presented in Section VI B3, which may be summarized as follows:

a. Very Small Fish (<50 cm, < 1 year old)

Convergence from various spawning areas to concentrate in nursery and feeding areas.

b. Small Fish (50 cm-120 cm, 1 to 4 years old)

i. Immature Individuals

Two-way migrations between warm season nursery and feeding areas and cold season wintering areas.

ii. Mature Individuals

Three-way migrations between warm season feeding areas, cold season wintering areas, and late spring-early summer spawning areas.

c. Medium Fish (120 cm -185 cm, 5 to about 8 years old)

More extensive three-way migrations between warm season feeding areas, cold season wintering areas, and spring-early summer spawning areas.

d. Large Fish (> 185 cm, > 8 years old)

Maximum three-way migrations between warm season feeding areas, cold season wintering areas, and spring-early summer spawning areas.

Except in certain situations related to the reproductive cycle and/or the configuration of the coasts, the bluefin migrations are not confined to narrow routes but spread over wide areas. The species is very widely distributed, and capable of long and rapid movements

in response to various stimuli. Changes in the currents, in the water temperature, or in the availability of food may affect its migratory behavior. Population pressure, either within the species itself or from competing species, may also be an influencing factor. Even in apparently stable conditions, the distributional behavior of the bluefin does not confine it to strictly limited seasonal habitats. These proposed migratory patterns should, therefore, be regarded as tendencies with which a major portion of the fish are apt to conform in a general way, rather than fixed routes followed by entire size groups.

2. Western Atlantic

a. Very Small Fish

During their first year of life, bluefin tuna (less than 50 cm long) in the western North Atlantic migrate considerable distances from extensive and incompletely defined spawning grounds to the warm season nursery area for small (50 cm-120 cm) bluefin in the Middle Atlantic Bight. They form their first regular and stable concentration there in late June or early July when they are approximately one year old. The net movement during this first year is basically one of concentration. The routes are unknown, but they are probably varied and devious.

Their wide distribution in their first weeks of life has been established by collections of larvae and small (less than 122 mm long) juveniles over much of the Gulf of Mexico and off the coast from southern Florida to New Jersey. Their movements during the intervening period are not known. Small and usually brief concentrations of newborn fish occasionally occur in the Cape Cod-Cape Hatteras area between late July and November. Tag returns have shown that some of these fish, at least, return to the area when they are one or two years old. Scattered occurrences suggest distribution along the United States coast from Cape Cod to the Mexican border during the warm season, and from Cape Hatteras to southern Florida in the colder months. Thus these fish may visit various areas during their first year of life. Occasional mid-summer schooling in the Straits of Florida suggests a migration from the Gulf of Mexico to the Cape Hatteras-Cape Cod area. Such a migration seems reason-

able, since the most important reproduction of bluefin in the western Atlantic evidently occurs in the Gulf, and the only known warm concentration of yearlings in the region takes place in the Middle Atlantic Bight.

There is a great need for extensive tagging of age 0 bluefin when they appear in the Straits of Florida. Any same season recoveries from fish tagged in this area would give a much more definite indication of their distribution during the first year. This is one essential gap in our understanding of the bluefin's life history.

b. Small Fish

Small bluefin (50 cm to 120 cm long, ages 1-4) concentrate in the nursery and feeding area between Cape Hatteras and Cape Cod during the warm season. They tend to move northeastward along the coast as the season advances, and their range has extended into the southwestern Gulf of Maine in some years. The oldest fish in the group tend to pass through this area first, followed by successively younger age groups. When the waters cool in October and November, they move offshore. Their wintering area, as indicated by recent tag returns, is in oceanic waters not far from the edge of the continental shelf off New England, Long Island and New Jersey. They occupy subsurface waters in this period and grow much more slowly than during the warm season. During late May and June they tend to concentrate and move inshore to their summer habitat. A few of these fish may attain their first maturity near the end of their third year of life, and many more near the end of their fourth year. These fish probably spawn in this same wintering area in late May or June. Thus a special spawning migration is not required and all of the fish in this group follow a two-phase migratory pattern between their feeding and wintering areas, with the ranges of the fish increasing slightly with each additional year of age. The available facts show that this is an east-west migration, in contrast to the north-south pattern which has been, and continues to be, surmised.

In a few years, tag returns have revealed migrations of small bluefin (one or two years old when released) from the Middle Atlantic Bight to the Bay of Biscay. These appear to have

been unusual occurrences, rather than part of a regular migratory pattern, as noted in Section VIC. They will be discussed further in the context of stock identification.

c. Medium Fish

The distribution pattern of the medium (120 cm to 185 cm long, 5 to about 7 years old) bluefin in the western Atlantic differs mainly from that of the small fish in its eastward extent. In recent years, their warm season distribution and movements have been very similar to those of the small fish, extending from Cape Hatteras to Cape Cod. Until 1966, they were often abundant in the southwestern Gulf of Maine from early August through October and sometimes into November and also along the Nova Scotian coast from Yarmouth to Halifax. They usually arrived in, and departed from, these northern waters later than the larger and smaller fish which were present. Fish of this size, however, have very seldom been taken north of Cape Cod in significant numbers since 1966. Their maximum seasonal abundance south of Cape Cod is rather unpredictable, occurring early in the season in some years and as a late season concentration in others.

These fish, like the small ones, move offshore when the water cools in the fall. Many of them concentrate in the canyons along the edge of the continental shelf in November, and then resume their offshore movement. Part of their wintering area coincides with that of the small fish. It extends eastward between the edge of the continental shelf and the Gulf Stream north of Cape Hatteras at least to the southern tip of the Grand Banks.

Most, if not all, of the fish in this group are mature, but their spawning area has not been defined. Limited explorations have located concentrations, including maturing fish, near the northern edge of the Gulf Stream south of southern New England and George's Bank in late May and early June, but this probably is only a part of the spawning area. As in the case of the small fish, spawning apparently does not require much deviation from the direct routes between the summering and wintering areas. The concentrations which form near the Gulf Stream in May and early June move inshore and

enter their feeding area in late June or July. In recent years, they have tended to enter the coastal waters in the southern part of this area, off Virginia, Maryland, or southern New Jersey. Again, this is basically an east-west migratory pattern, in contrast to the generally accepted concept of northerly and southerly movements. At least 500 medium bluefin have been tagged in the northwestern Atlantic; all of the returns were consistent with the above pattern and not one tag was returned from any other area.

d. Large Fish

The distribution and migratory patterns of the large (more than 185 cm, usually more than 7 years old) bluefin in the western Atlantic are much more extensive than those of the smaller fish. The main warm season habitat of this group includes much of the coast from Cape Cod to the east coast of Newfoundland, including the southwestern Gulf of St. Lawrence, but usually excluding most of the Bay of Fundy. Secondary concentrations, usually of brief duration, occur in the Cape Hatteras-Cape Cod area. In the 1930s, the late 1940s, and the 1950s, however, giant fish were often quite abundant in parts of that area. The large fish usually arrive in their southern feeding grounds between early June and early July, and in their northern ones in late July. The movements of fish within this large area are not well known, except that some fish released in St. Margaret's Bay, near Halifax in June or July have been recaptured in the Gulf of St. Lawrence in August or September.

The giant fish usually leave this feeding area in October and migrate to their very extensive wintering areas. Routes of this migration can only be surmised. They probably spread over a very wide front, with some fish traveling eastward and then southward with the currents, while others follow more direct routes south. Since bluefin, most of which are large individuals, are distributed almost all over the Atlantic between latitudes 35°N and 10°S during the northern cold season, the limits of this wintering area cannot be determined with certainty. There are indications, however, that it extends eastward to longitude 40°W and southward, in some cases, to latitude 40°S. These fish are dispersed; the relative

abundance is usually highest off easternmost Brazil in late winter and early spring, and around the Antilles. There are indications of an important northeastward migration along the South American coast from the former area to the latter in April. This would be a spawning migration, since the prime known reproductive area in the western Atlantic is in the Gulf of Mexico. There is evidence that spawning also occurs in the enclosed waters adjacent to the Gulf, and in the ocean east of the Bahamas and the southeastern United States. These spawning grounds are actually a part of the much more extensive wintering area. Thus the giant bluefin may move from their wintering areas to their spawning ground by migrations of various lengths and directions; some may not have to move at all.

The spawning season in the western Atlantic area extends from late April through June, with the maximum emission probably occurring in May and early June. When spawning is completed, the spent fish migrate northward toward their feeding grounds. This is most dramatically illustrated by the northward passage of spent bluefin through the Straits of Florida, close to the northwestern Bahamas. The duration of this run, which usually occurs in strength from early May to mid June, is consistent with the period of maximum spawning stated above. Soon after it leaves the Straits of Florida, this northward migration is joined by a similar, but less concentrated one which follows the Antilles Current along the oceanic side of the West Indies and the Bahamas. The combined contingents of giant fish tend to concentrate along the eastern edge of the Florida Current and follow it to beyond Cape Hatteras, where it becomes the Gulf Stream and gradually turns eastward. Contingents probably cross the Gulf Stream at various distances east of the American coast and resume their northward course. These groups of fish follow various routes to different parts of their feeding grounds. Their arrival there completes a prodigious circuit where distance may vary for different groups of fish. This is, for most of the fish at least, a three phase migration.

In some years, substantial contingents of fish remain in the Gulf Stream

and its continuation, the North Atlantic Current, until they reach the Norwegian coast in late summer or early fall. We believe that this is unusual behavior, rather than part of an annual pattern, for reasons enumerated in Section VIC. These migrations will be discussed later in the context of stock identification.

3. Eastern Atlantic and Mediterranean

a. Very Small Fish

Very small (less than 50 cm long, less than 1 year old) bluefin are very widely distributed in the Mediterranean, but are known from only a very small part of the eastern Atlantic. Larvae and very small (less than 10 cm long) juveniles have been collected in many parts of the central and western Mediterranean, and in the Black Sea. In amazing contrast, not one has been captured in the supposed reproductive areas in the eastern Atlantic, despite prolonged and sometimes intensive efforts. The Ibero-Moroccan Bay has long been regarded as the prime or only bluefin tuna spawning ground in the region on the strength of the massive catches of maturing and spent fish which were formerly taken by numerous traps along its coasts.

Age 0 bluefin are observable in great numbers over much of the Mediterranean, and are often available to fisheries, from August through November. Then they usually disappear, probably by simply remaining below the surface during the cold season. In April they reappear, supposedly in or near the same localities, and finish out their first year of life without having moved extensively.

These fish, along with older immature bluefin in the Mediterranean are believed to be sedentary, remaining near their birthplace until they attain maturity. Their distribution, however, is even more extensive than that of the known and supposed spawning areas. Reproduction is known or supposed to occur off most of the western, northern and eastern coast of Sicily and in much of the south Tyrrhenian Sea; off western Sardinia; around the Balearic Islands; off western Libya, Tunisia and Algeria; and in the Adriatic and Black Seas. The distribution of age 0 bluefin, however, extends into the Ligurian and Aegean Seas, and the northeastern

Mediterranean. Dense concentrations often occur in September and October in the waters just east of the Strait of Gibraltar. No evidence of spawning has been reported from any of these areas. Therefore these fish must have moved some distance from their birthplaces, or there are several undiscovered reproductive areas. A migration from the Black Sea might explain their occurrences in the Aegean and northeastern Mediterranean Seas. In any case, if bluefin do move about the Mediterranean during their first year of life, the net result of these movements is dispersion, in contrast to the strong tendency to concentrate, which is typical in the Atlantic.

The situation in the eastern Atlantic is, as noted previously, dramatically different. Not only are the early stages virtually unknown, but there is very little information on the distribution of the young of the year until October, when they are over 30 cm long. They concentrate off Morocco in that month and in November and remain in the area, usually some distance away from the coast, through the cold season. In June, when they are nearly a year old, they enter coastal waters, where most of them remain through the summer. This appears to be the only regular and important occurrence of age 0 bluefin in the eastern Atlantic. Isolated occurrences off the Canary and Salvage Islands and Cape St. Vincent have been reported. No one knows from where the young of the year which concentrate off Morocco come. It is generally assumed that they were hatched in the eastern Atlantic, but we have stated our reasons (Section VIC) for believing that many of them may have migrated from the Mediterranean. The tendency of bluefin to concentrate during the first year of life appears to apply in the eastern Atlantic, just as it does in the western side of the ocean, and in contrast to the dispersion which persists through this phase of life in the Mediterranean. The eastern Atlantic concentration forms when the fish are only three or four months old, whereas in the western Atlantic it does not occur until the fish are about a year old.

b. Small Fish

The distribution of small fish (50 cm-120 cm long, ages 1-4) in the east-

ern Atlantic somewhat resembles that off North America, but these fish, like the young of the year, are much more widely distributed in the Mediterranean than in the eastern Atlantic.

The concentration of bluefin which became one year old in late spring or early summer while in the Atlantic coastal waters of Morocco generally remains there, gradually working southward along the coast, until late summer or early fall. Then many of them migrate northward, arriving off southwestern Portugal in October or November. Many of these fish spend the cold season there and then continue their northward migration in June, entering the Bay of Biscay when they are about two years old.

In some years, concentrations of age 1 fish occur in the Bay of Biscay but, again, no one knows whence these fish came. Bluefin of all the ages included in the small size group, as well as older fish, feed in the Bay of Biscay during the warm season. This is the prime nursery and feeding areas for small bluefin in the eastern Atlantic and is analogous to the Middle Atlantic Bight on the ocean's western side. The youngest fish, which are immature, usually remain there for the longest period. When three-year-olds and most of the four-year-olds are mature, their appearances in the Bay are usually brief. Some spawning reportedly occurs in the Bay, which may combine the functions of a feeding and a spawning ground for some fish. A few bluefin are reportedly present in the Bay throughout the year, but the fishing season usually extends from early June through October. With the advent of the cold season, the small bluefin leave the Bay and migrate southward to their wintering area, which probably centers on the waters between Morocco and the Canary Islands. When the warm season begins, they migrate northward. During this movement, numerous fish are often trapped in a hydrological pocket off the central coast of Morocco and remain there through the season. The fish which avoid this entrapment may follow various courses. The immature fish probably proceed directly to the Bay of Biscay to feed. Some of the mature fish may accompany them and spawn and feed there. Other mature fish may spawn in the Ibero-Moroccan

Bay, or, possibly, off the Moroccan coast before reaching the Bay. Most of the spent fish probably proceed to the Bay of Biscay, completing the migratory cycle, but others may join the concentration off central Morocco. Presumably, all of them return to the wintering area there when the next cold season arrives.

Movement patterns of the small bluefin are thus considerably more complex in the eastern than in the western Atlantic. Separate summer nursery areas are available, one mainly for age 1 fish and the other mainly for older fish. In addition, more than one spawning area is apparently available to the mature fish. Thus a variety of migratory patterns may be followed, in contrast to the simple "offshore-inshore" arrangement in the western Atlantic. Also, the small bluefin appear to follow a basically north-south migratory pattern in the eastern Atlantic, whereas those in its western waters move seasonally in east-west directions.

Small bluefin concentrate in more localities in the Mediterranean than in the Atlantic, and are more available there to year-around fishing.

Most of the concentrations occur in association with current systems, islands, straits, or promontories. Some of these which endure through all, or most, of the year are at the Strait of Messina and Bonifacio (between Sardinia and Corsica) and the Bosphorus, the Aeolian Islands and the islands of Malta and Kerkennah, and in the Adriatic Sea. Seasonal concentrations occur in the Gulf of Lions, the Gulf of Adalia, the Alexandretta-Haifa-Cyprus triangle, the Ionian and Aegean Seas and the Sicilian Channel. Most of these are available during most of the warm season, but diminish or disappear during the spawning season in late spring and early summer and during the winter. Little is known about the migrations of tuna of this size. They are believed to be relatively sedentary until they attain maturity, usually at ages of three or four years. They then undertake migrations related to reproduction, but the extent of these is unknown. They may be confined to the basins to which the fish are native, or they may range throughout the Mediterranean. The spawning areas of the mature small fish are not well known. Probable areas include the

southeastern corner of the Tyrrhenian Sea and the Ionian Sea off Sicily, the coast of Libya eastward to Bengasi, and the Balearic Islands. The small fish spawn considerably later than the larger ones. Their reproductive season extends through July and well into August; some even spawn in September. As with the young of the year, the distribution of the immature small fish is much greater than that of the known spawning area. Again, this implies some migration by these fish, unless the reproductive areas are much more extensive than is now known. The tendency for small bluefin to concentrate seasonally in one or two relatively small areas, which is so pronounced on both sides of the Atlantic, is not evident in the Mediterranean.

c. Medium Fish

While the bluefin in the eastern Atlantic and the Mediterranean are in the medium size range (120 cm-185 cm long, from 5 to about 8 years old), their ranges begin to overlap. This greatly complicates the tracing of their life histories and adds correspondingly to the uncertainties of existing knowledge about their life cycles. The distribution and migratory patterns of the medium fish in the eastern Atlantic are, or have been, more extensive than those of the small fish. It is more difficult to assess these differences in the Mediterranean.

Virtually all of the medium fish in this region are mature, but their spawning habits are not well known. They spawn later than the large individuals—probably through all of July in the eastern Atlantic, and into August in the central Mediterranean.

In recent years, the migrations of medium fish in the eastern Atlantic have been similar to those attributed to the mature small fish, with the exception that some medium fish, at least, enter the Mediterranean. Most of these fish migrate from their wintering area off northwestern Africa (which probably extends from latitude 35°N to latitude 15°N and from the coast to longitude 20° W) to the Ibero-Moroccan Bay or nearby waters, where the majority of them presumably spawn. Some of them, in numbers which vary from year to year, migrate along the coasts of the bay in the “arrival” run in which large fish are usually predominant. An un-

known, but probably small, percentage of these medium fish enter the Mediterranean with more numerous large fish and spawn there. These fish, and most of those which have spawned in the Ibero-Moroccan Bay or adjacent Atlantic waters, then migrate to the feeding grounds in the Bay of Biscay. Some of them participate in the “return” run with the large spent fish and others migrate separately. Still other fish may travel directly from the wintering area to the Bay of Biscay and reproduce in the secondary spawning area which apparently exists there. The medium fish are usually most abundant in the Bay of Biscay from mid July to mid August or September. Their whereabouts thereafter is unknown until they presumably return to their wintering area in late fall. A secondary feeding area exists off the central coast of Morocco. Some medium fish may go there, rather than to the Bay of Biscay, after spawning in the Ibero-Moroccan Bay or the Mediterranean. Others possibly visit this area after leaving the Bay of Biscay. All of these fish probably return to the same wintering area in late fall. Until 1962, large numbers of medium bluefin migrated from their spawning ground to feeding grounds also used by large bluefin off the southwestern coast of Norway, passing west and north of the British Isles en route. They usually arrived there in mid or late July, and departed in late October. They rounded the British Isles again en route south to their wintering area. Since 1962, few medium fish have been taken north of the Bay of Biscay. Their coastal feeding thus became similar to that of the small fish. As noted previously, a comparable change in the summer distribution of medium bluefin in the western Atlantic occurred in 1962. These range reductions may have been related to the great decline in the apparent abundance of fish of this size group which occurred all over the Atlantic in this period, and has subsequently affected the Mediterranean.

The distribution of medium bluefin in the Mediterranean Sea is quite similar to that of the small fish. Both groups often share the same habitats, or adjacent ones. Medium fish are usually predominant, however, off the east coast of Spain. The medium fish presumably migrate farther than the small ones, but their migratory patterns are

not known. Their concentrations tend to remain more or less stationary in a given area for a few weeks and then disappear. One of these absences occurs during the spawning season, which probably extends from late June into August. Spawning migrations begin earlier, in May or June. The directions and distances of these migrations are probably quite variable. Many medium fish participate in the eastward “arrival” run of maturing bluefin in May and June. This run is believed to include many large and some medium fish from the eastern Atlantic, but more medium fish than large ones from the Mediterranean. The medium fish are usually most numerous in the later part of this run, and favor the more easterly areas, such as the southeastern Tyrrhenian Sea and the waters off eastern Tunisia and Libya. The waters in these areas are somewhat warmer and more saline than those in the more westerly areas favored by the large fish. “Resident” medium fish also participate in the westward “return” run of spent fish in July and August. Probably many of the oldest fish in this group accompany this migration into the Atlantic, shifting into the wider ranging pattern of the “giant” fish. This would occur when the fish are about 185 cm long and about 9 years old. Most of the younger “resident” fish probably remain in the Mediterranean.

d. Large Fish

Under the hypothesis which we regard as the best explanation of the available facts, the large bluefin in the eastern Atlantic and the Mediterranean may be regarded essentially as a single aggregation of fish.

The wintering area occupied by the majority of this group has not been defined. Probably most of the fish winter in the Atlantic between latitudes 20°N and 35°N and the African coast and longitude 30° W, but the total wintering area may extend much farther, especially to the south.

Relatively small groups of large bluefin winter in certain localities in the Mediterranean-Black Sea system where food is plentiful, particularly off the mouth of the Rhone and in the Bosphorus. There are two possible explanations of these occurrences. The groups may comprise a resident Mediterranean stock (or stocks). On the other

hand, they may simply be contingents of the main aggregation which have chanced upon satisfactory feeding grounds after spawning in the Mediterranean, and stayed there rather than returning to the Atlantic. At present, there is no basis for determining which explanation is correct.

The main group of fish leaves the Atlantic wintering area in late March or April and migrates to the Ibero-Moroccan Bay forming the "arrival" run (see Section VIC1di for details) which moves along both shores of the Bay toward the Strait of Gibraltar in May and June. A fraction of these fish continue to migrate eastward and spawn in the Mediterranean. The others presumably remain in the Ibero-Moroccan Bay and spawn there. Further study is necessary to determine what percentage of the "arrival" fish do remain and what percentage spawns in the Mediterranean.

The major spawning grounds of the large fish in the Mediterranean are probably off western and northern Sicily, western Sardinia and western Tunisia, where the waters are somewhat cooler and less saline than those farther east, which are predominantly the spawning areas of the smaller fish. Spawning is believed to occur between mid-June and mid-July in the Ibero-Moroccan Bay and central Mediterranean. The numbers of fish which concentrate off Gibraltar and the fraction of these which enter the Mediterranean depend considerably on the environmental conditions in and over the eastern Atlantic during the preceding weeks. The number of fish entering the Mediterranean depends greatly on the strength of the inflowing Atlantic surface current, in which they travel.

After spawning, the fish in the Mediterranean initiate the westward return run, which occurs through July and August. They follow the deeper Mediterranean current, skirting the east and south coasts of Sicily, and go out through the Strait of Gibraltar, contributing relatively small catches to the traps on either side of the eastern entrance. There they evidently join, or follow, the fish which have remained in the Ibero-Moroccan Bay in their westward migration along the southern coasts of Spain and Portugal, forming the "return" run.

The positions where these reproductive migrations come near the coasts are clearly indicated by the traditional locations of the traps. Those which fished the arrival run in the Ibero-Moroccan Bay extended along the Iberian coast from Cabo de Santo Maria in Portugal to the Strait of Gibraltar, and along the Moroccan coast from near Kenitra to the entrance of the Strait. The traps nearest Gibraltar took the largest fish. In the Mediterranean, the traps off western and northern Sicily, western Sardinia, and western Tunisia have usually taken larger fish than those off eastern Sicily, Calabria, eastern Tunisia and Libya. The waters in the latter areas are somewhat warmer and more saline than those in the latter and the 38 o/oo isohaline, which runs from the Gulf of Sirte to Sicily, has been proposed as the eastward limit of the spawning of large bluefin. Pelagic fisheries have recently indicated that large bluefin are extensively distributed in the western and central Mediterranean from late April into September, and that spawning occurs extensively in off-shore waters of the south Tyrrhenian Sea. The fish of the "local" groups in the western and central Mediterranean, presumably spawn with the more numerous migrant aggregation, but this is conjectural. Larvae and/or small (less than 10 cm) juveniles have been found in many of these central and western areas. It seems very probable, however, that the large bluefin which feed and winter in the Sea of Marmara spawn in the Black Sea, where collections of bluefin larvae have been reported. Since large maturing fish are said to be rare in the Mediterranean east of the central Libyan coast and the eastern Ionian Sea, it seems improbable that the very large fish taken near Istanbul are migrants from the Atlantic. The Bosphorus would be an ideal location for tagging and sonic tracking experiments.

The "return" passage is completed along the northern shores of the Ibero-Moroccan Bay in July and August and then the fish turn north toward the feeding grounds. Some of them follow the Iberian coast into the Bay of Biscay, where they usually remain for only a month or six weeks. The majority, however, has usually proceeded to feeding grounds off the coast of Norway and in the North Sea. They reached these

northern areas by a circuitous course passing west and north of the British Isles, rather than following the more direct route to these areas through the English Channel. Until 1962, most of the larger giant bluefin moved northward along the Norwegian coast and subsequently migrated southward into the North Sea. Since then, however, nearly all of them have moved southward along the Norwegian coast with the smaller members of this group, and the species has been scarce or absent off northern Norway and in the North Sea. These large bluefin usually enter Norwegian waters in July, spend the remainder of the warm season there, moving southward along the coast and feeding voraciously, and depart from them in October. They again pass north and west of the British Isles and reach their wintering grounds east of northern Africa and the Ibero-Moroccan Bay in November or December, completing their migratory cycle.

The south central Mediterranean appears to be the prime reproductive area for the bluefin of the Mediterranean. Its importance to the reproduction of eastern Atlantic bluefin is more difficult to assess. This is one of the most important questions in regard to the spawning, and the identification of stocks that remains unanswered.

The Ibero-Moroccan Bay has been generally regarded, at least in this century, as the prime bluefin tuna spawning ground in the eastern Atlantic, but not one bluefin larva, or small (less than 10 cm long) juvenile, has been collected in its waters. Research, including plankton collections, has been carried on there almost continually for many decades by scientists of several nations, and the waters of the Bay, as well as adjacent parts of the Atlantic and the Mediterranean, have twice been surveyed very thoroughly during the spawning season. The failure to collect any early stages of bluefin there cannot be attributed to lack of effort. It has been suggested that the products of spawning in the Ibero-Moroccan Bay might have been passively transported into the Mediterranean by the inflowing surface current before the early stages had attained full mobility. This seems unlikely, since the surveys mentioned above covered all, or most of, the Alboran Sea (the westernmost part

of the Mediterranean) as well as the Ibero-Moroccan Bay, and also failed to collect any early stages of bluefin there. It seems inconceivable that bluefin do not spawn in the eastern Atlantic. On the other hand, the collection of bluefin larvae in so many parts of the Mediterranean and the collection of "thousands" (Sella 1929a) of juveniles less than 10 cm long in Sicilian waters offers a striking contrast. It is difficult to escape the conclusion that the Mediterranean is most important to the reproduction of the bluefin tuna of the eastern Atlantic.

4. Comparison

The distribution and migratory patterns of the bluefin on the two sides of the Atlantic are quite analogous (Table 35). The extension of its range to much higher latitudes off Europe than off North America may be explained by the warmer temperatures in northern European waters.

The similarity in the patterns is especially evident during the warm season when the distributions are best known. The Norwegian coast and the North Sea correspond to the Gulf of Maine and Canadian waters, being occupied principally or entirely by large and medium bluefin. The surface temperatures and salinities of these waters, excepting the salinity in the North Sea, are relatively low. South of these areas, we find the principal summer habitats of the small bluefin, the Bay of Biscay and the Cape Hatteras-Cape Cod area. The surface temperatures and salinities in these areas are somewhat higher than those farther north. The northerly distribution of small bluefin in the eastern Atlantic is limited by the English Channel and the British Isles, and the North Sea. Some large and medium fish are taken in the Bay of Biscay, however. The summer habitat of the small bluefin in the western Atlantic, on the other hand, is contiguous with that of the larger fish at Cape Cod. In some years, great numbers of small fish have entered the southwestern Gulf of Maine. Large and medium tuna also occur frequently in the Cape Cod-Cape Hatteras area, but usually in moderate numbers and for short periods.

Small bluefin gather off the southwest coast of Portugal from October through June, and very small or small ones are found off the coast of Mo-

rocco throughout the year. There are no counterparts of these occurrences in the western Atlantic, since the species is rarely encountered in United States coastal waters south of Cape Hatteras.

The cold season occurrences of the bluefin are not as well known, but some differences between the patterns on the two sides of the Atlantic are evident. In the western Atlantic the small and medium fish winter separately from the large ones, north of latitude 35°N, whereas in the eastern Atlantic, the medium and small fish share the northeastern part of the winter habitat of the large ones. The medium fish occur farther offshore than the small ones in both areas and the large ones are distributed all the way across the ocean from about 35°N latitude to the equatorial region. Therefore, there is no clear cut separation between the western and eastern groups, but the distributions of relative abundance suggest that the former group is more extensively distributed than the latter.

The spawning seasons and areas of the Atlantic bluefin, especially for the medium fish and the mature individuals of the small group, are far from completely known.

The most important spawning grounds which have been described are in the Gulf of Mexico (part of the American Mediterranean) and in the south central part of the European Mediterranean Sea. These locations are analogous geographically, but the surface temperatures and salinities of the waters differ considerably. They are about 23°C - 27°C and 36.0 o/oo, respectively, during the late April-early July spawning season in the Gulf of Mexico, and 18.0°C - 22°C and 37.5 o/oo in the mid June-August spawning season in the south central Mediterranean. The stock structure is much simpler in the Gulf than in the Mediterranean. The former area is occupied only by large bluefin during the winter and the spawning season, and by newborn fish from the time of their birth through the fall and perhaps into the winter. The spawning fish presumably come from various parts of the western Atlantic. Bluefin of all sizes occur in the Mediterranean throughout the year, but large fish are relatively scarce there except between the "arrival" run of

maturing fish in May-June and the "return" run of spent fish in July-August. These runs include many giant fish and lesser numbers of medium ones from the eastern Atlantic. Maximum spawning of large fish takes place from mid-June to mid-July, but the reproduction by medium fish is later and may extend into August.

Thus spawning occurs earlier in the western Atlantic than in the eastern-Atlantic-Mediterranean system. Also, the stock structure appears to be less complicated in the former area than the latter.

The occurrences of larvae and juveniles less than 10 cm long are much better known in the western Atlantic, where they are widely distributed, than in the eastern, where their supposed range is relatively small. The larger age 0 fish form a stable and regular concentration off Africa at least six months earlier than any known occurrence of this nature off the American coasts. The routes which these fish follow from their birthplaces to their earliest concentrations in the respective areas are not known. It seems probable, however, that analogous post-spawning migrations of large and new-born bluefin occur in the Straits of Florida and the Strait of Gibraltar. After spawning has taken place in the Gulf of Mexico on the one hand, and the Mediterranean on the other, the large spent fish pass through the respective straits into the Atlantic. These migrations may be followed, after a few weeks, by similar migrations of their offspring.

The migratory patterns joining these seasonal occurrences are likewise quite analogous, insofar as they have been determined. The longest migrations are carried out by the largest fish.

After feeding in the northern part of their range, they make long southward and generally offshore migrations to their vast winter habitats which extend, in the western Atlantic at least, into the South Atlantic. The fish in the North Sea and in Scandinavian waters pass north and east of the British Isles, instead of going directly south through the English Channel.

Shorter northward and more inshore migrations in the spring bring them to concentrations in spawning areas which are in the northern parts of their wintering areas, or between their

Table 35. Patterns of spring and summer-early fall distribution of bluefin tuna on the two sides of the Atlantic.

Season	Fish Size	Eastern Atlantic	Western Atlantic
Spring	Small	Morocco; Bay of Biscay	Off edge of Cont. Shelf (N.E., U.S.)
	Medium	Ibero-Moroccan Bay, Medit.?	Gulf Stream-Edge of Cont. Shelf
	Large	Ibero-Moroccan Bay, Medit.?	Bahamas-Gulf of Mexico
Early Summer	Small	Bay of Biscay; Morocco	Middle Atlantic Bight
	Medium	Ibero-Moroccan Bay, Medit.?	Middle Atlantic Bight; Gulf of Maine
	Large	Ibero-Moroccan Bay, Medit.? Norway	Cape Cod-Newfoundland
Mid-Summer-Early Fall	Small	Bay of Biscay; Morocco	Middle Atlantic Bight
	Medium	Scandinavia, Bay of Biscay	Middle Atlantic Bight; Gulf of Maine
	Large	Scandinavia, North Sea	Cape Cod-Newfoundland
Late Fall-Winter-Early Spring	Small	Morocco-Canary I. +?	
	Medium	Morocco-Canary I. +?	N. edge Gulf Stream N of 35°N
	Large	N.E. Atl.-Canary I.-Morocco	Gulf of Mex. W. Indies, Atlantic from 35°N to 10°S (or farther) and from the American coasts to about 40°W.

winter and summer habitats. Major departures from the ocean into relatively land-locked spawning areas, and returns to the ocean, take place on both sides of the Atlantic.

The patterns may be compared to gyres which are greatly elongated in the north-south direction and distorted by the contours of the land masses and by detours into and out of the European and American Mediterranean, where important spawning occurs. They are also influenced by hydrological conditions and coincide with favorable currents for much of their extent, particularly in the western Atlantic. The southward migrations are probably more diffuse than the northward ones, and extend much farther into the middle of the ocean, affording considerable opportunities for mixing. The movements in the eastern Atlantic gyre are generally counterclockwise, while those in the western Atlantic gyre are generally clockwise. Thus, one pattern is roughly a mirror image of the other.

The medium and smaller fish on both sides of the Atlantic move within these same patterns but to a much lesser extent in the north-south direction. For both groups migration appears to be

much simpler in the western than in the eastern Atlantic. The range of the fish tends to increase somewhat with each year of growth.

D. IDENTIFICATION OF STOCKS

Much important information obtained recently supports the tentative identifications of Atlantic-Mediterranean bluefin tuna stocks by Mather et al. (1974). These authors noted that an infinite number of combinations of stocks, and degrees of mixing between them, might theoretically exist in the Atlantic and connected seas, but considered the following basic combinations only:

1. A unit stock in the Atlantic and connected seas.
2. One stock in the Atlantic system and another in the Mediterranean system.
3. One stock in the eastern Atlantic and the Mediterranean, and another in the western Atlantic.
4. One stock in the Mediterranean, a second in the eastern Atlantic and a third in the western Atlantic.

They found no reason to believe that one or more separate stocks existed in the South Atlantic.

As they noted, varying degrees of mixing, or none, might occur between the components of dual- or multi-stock combinations. Tag return data for bluefin tuna, however, indicated that mixing tendencies may be strong. This was especially true of the large fish.

Mather et al. (1974) concentrated most of their discussion on two questions which still appear to be of paramount importance:

1. The identification of the stock or stocks of bluefin tuna in the Mediterranean and the eastern Atlantic.
2. The identification of the stock or stocks of bluefin tuna in the Atlantic Ocean.

They briefly reviewed the historical opinions and developments in research on the relationships between the Mediterranean and Atlantic bluefin tuna. They then discussed Sará's (1964, 1973) hypothetical migratory model for the migrations of bluefin tuna in the Mediterranean, which has also been described in the present work, and some of the evidence supporting this theory.

They also noted the findings of Hamre et al. (1966, 1968, 1971) which showed that there were considerable differences, in both the trends of the catches and their size composition, between the fisheries for large bluefin in the eastern Atlantic and those in the Mediterranean. These authors concluded tentatively that the respective fisheries were supported by different stocks. Mather et al. (1974) noted, however, that the catches of many Mediterranean trap fisheries had recently declined drastically, and the sizes of the fish taken had increased markedly. Thus, after a considerable lag, they appeared to have followed the trends of the northeastern Atlantic large fish fisheries.

Mather et al. (1974) generally supported Sarà's hypothesis, but also postulated a migration of newborn fish from the western Mediterranean to the Atlantic coast of Morocco in October and November. They pointed out that this was the most plausible explanation available for the continued productivity of the fisheries for small bluefin off the coast of Morocco and in the Bay of Biscay, and cited evidence that such a migration actually occurred. They also recommended the tagging of very small bluefin in the western Mediterranean and off the Atlantic coast of Morocco in order to test this hypothesis and determine the sources of recruitment to the major eastern Atlantic fishery for small bluefin in the Bay of Biscay. The Mediterranean phase of this recommendation has not been attempted, but a small-scale tagging operation was carried out most successfully off the Atlantic coast of Morocco in 1972 and 1973. This showed that at least some of the recruitment to the Bay of Biscay fishery was indeed drawn from the Moroccan coast (Lamboeuf 1975). This important and relatively inexpensive achievement further emphasizes the desirability of conducting similar experiments in the western Mediterranean. Results which would be of great importance in identifying the bluefin stocks in this critical area should be obtained quickly and at modest cost.

Important new information on the question of the eastern Atlantic-Mediterranean bluefin stocks has become available recently. The progression of Japanese longline catch rates in the area and season of the "arrival" and "re-

turn" runs and the overall estimate of the sizes of the fish taken (Shingu et al. 1974) strongly support Sarà's (1973) migratory theory.

The failure of the expedition "Moroc-Iberia I" to find early stages of bluefin in the Ibero-Moroccan Bay (Rodriguez-Roda 1975) and the discovery of new spawning areas in the Mediterranean (Duclerc et al. 1973, Scaccini et al. 1975, Piccinetti et al. 1976) emphasize the probable dependence of the eastern Atlantic fisheries on recruitment from the Mediterranean. We therefore now attach even greater importance to the spawning migration of large and some medium (as indicated by tag returns in Rodriguez-Roda 1969a) bluefin from the eastern Atlantic into the Mediterranean, and the recruitment of newborn fish from the Mediterranean to the eastern Atlantic fisheries. We conclude that the eastern Atlantic and Mediterranean bluefin constitute a stock which tends to separate into two components, one in each water mass, in its years of immaturity and its earlier ones of maturity, and to spawn in the Mediterranean and spend the rest of the year in the Atlantic when the fish exceed about 9 years in age and 100 kg to 150 kg in weight.

The status of the relatively small groups of large bluefin which occupy the Mediterranean throughout the year is unclear. Those in the western Mediterranean could well be contingents of fish which have chanced upon a good feeding area and dropped out of the normal migratory pattern. The group of large bluefin which reproduces in the Black Sea and winters in the Sea of Marmara is more likely, in our opinion, to be the nucleus of a separate population.

Mather et al. (1974) noted that the situation with regard to bluefin tuna in the Atlantic and connected seas other than the Mediterranean (North Sea, and the Baltic and its approaches, the Caribbean, and the Gulf of Mexico) was also extremely complex. They stated some arguments for a single stock occupying the entire ocean, and others for two stocks, with spawning areas on the east and west sides of the Atlantic.

The arguments for a single stock were as follows:

Fluctuations in catches, and trends in their size composition, appear to be

rather similar throughout the ocean. A correlation analysis, based on the dubious assumption that the sizes of the fish caught in the two fisheries were the same, showed a positive correlation in the catch per unit of effort between the small fish fisheries in the northwestern Atlantic and in the Bay of Biscay (Sakagawa and Coan 1974).

Tag returns have traced several transatlantic migrations of small and large bluefin tuna, as well as several other migrations between widely separated localities in the Atlantic.

Studies of heart muscle protein from bluefin tuna collected on opposite sides of the Atlantic showed no differences in the characteristics which were studied. The growth rates for bluefin tuna in the Mediterranean, the eastern Atlantic, and the western Atlantic appear to be similar.

The arguments for separate eastern and western Atlantic stocks were as follows:

Bluefin of all sizes are found on both sides of the ocean, with the exception that very few larvae or small (less than 10 cm) juveniles have been found in the eastern Atlantic.

Bluefin spawn on both sides of the Atlantic (whether the bluefin which arrive in the Ibero-Moroccan Gulf with ripening gonads and depart with spent gonads actually spawn in that area or in the Mediterranean seems irrelevant in this context). There is no evidence of extensive spawning in mid-Atlantic waters. Spawning in the eastern Atlantic (and/or the Mediterranean) is later than spawning in the western Atlantic.

There is no correlation between trap catches in the eastern Atlantic and Japanese longline catches in the western Atlantic (Sakagawa and Coan 1974).

The patterns of spring and summer-early fall distribution of bluefin tuna on the two sides of the Atlantic are quite similar.

The principal exceptions were attributed to different spawning habits. Spawning occurs later in the eastern Atlantic (Ibero-Moroccan Bay and/or Mediterranean) (about the end of June) than in the corresponding western Atlantic spawning area (Bahamas, Gulf of Mexico) (May, early June). The "return" (spent fish) run in the Straits of Florida occurs in May-June, whereas

the "return" run off southern Spain and Portugal occurs in July-August. This accounts for the later arrival in northern summering areas of the medium and large bluefin in the eastern Atlantic, as against the western Atlantic.

Also, the spawners in the Ibero-Moroccan Bay and in the Mediterranean, although predominantly large, include medium-sized and reportedly, even small fish, whereas all of those which spawn in the Bahamas-Gulf of Mexico area are giant fish (over 122 kg).

Tag return data indicated that west to east transatlantic migrations of small bluefin tuna are the exception rather than the rule. As of the end of 1972, about 9,700 small bluefin had been tagged in the Middle Atlantic Bight. Disregarding 1,112 local recaptures within less than six months of release, 1,201 returns were from the release area as against 40 from the eastern Atlantic.

Recoveries from large bluefin tuna tagged off the Bahamas were more numerous in the eastern Atlantic (8) than in the western Atlantic (5), but, with the collapse of the eastern Atlantic fisheries and increased effort in the western North Atlantic, the trend in recoveries has reversed itself. As with the transatlantic migrations of small bluefin, those of large bluefin appear to be important in some years and negligible in others. There have been no transatlantic returns from numerous taggings of large bluefin off New England, Canada, Norway, and Spain.

Preliminary comparisons of extensive data on the external morphology of bluefin tuna from the eastern and western Atlantic indicate that there are slight morphometric and meristic differences between fish from the respective areas.

There is little evidence for a separate stock of bluefin tuna in the South Atlantic. The oceanic distribution of the species appears to be continuous from off eastern Brazil to off New England and eastern Canada.

Also, the more significant Japanese longline catches of bluefin tuna appeared to progress seasonally from off eastern Brazil in March and April to off Cape Hatteras by the end of June. Furthermore, two bluefin tuna tagged in the Straits of Florida have been re-

captured in the western South Atlantic, one off easternmost Brazil, and the other off Argentina. No evidence that bluefin spawn in the South Atlantic has come to our attention.

Mather et al. (1974) concluded from the above information that the evidence was insufficient to permit clear cut conclusions, but believed that the most probable combinations were:

1. A single Atlantic or Atlantic-Mediterranean stock and one or more essentially Mediterranean stocks.

2. Two Atlantic spawning stocks, one spawning in the western Atlantic and the other spawning in the eastern Atlantic and/or the Mediterranean, with one or more essentially Mediterranean stocks.

They believed that the greatest weight of evidence appeared to favor the second arrangement. They noted, however, that for management purposes it must be recognized that important interchanges between the two proposed Atlantic stocks occur on an apparently erratic and unpredictable basis.

They noted that the problem of the stock structure of Atlantic bluefin is one of enormous complexity. With the existing depressed state of most of the fisheries, and the consequent diminution or termination of research on the species in several nations, there was no prospect that it could be solved definitively in the foreseeable future. They concluded that management of the species should be undertaken on the basis of the best information now available, if its commercial extinction was to be avoided.

Conservation measures for Atlantic bluefin were finally enacted by ICCAT in 1975. Also, under the stimulus of this organization, research on bluefin tuna in several nations has actually increased. Unfortunately, however, the failure of the fisheries in the Federal Republic of Germany, Norway and Portugal has forced some of the most competent experts on the bluefin into other fields.

Continued tagging in the western Atlantic by the Woods Hole Oceanographic Institution has yielded results of great value in determining the migratory patterns of the bluefin in that area. Recent tag returns have finally and definitely connected the spawning occurrence of giant bluefin in the Gulf

of Mexico with the migratory passage of similar fish through the Straits of Florida and their summer feeding occurrence in New England and Canadian waters. All of these migrations were recorded through taggings of giant fish. An even more significant return connected the Cape Hatteras-Cape Cod area, the only known nursery ground for young bluefin in the western Atlantic with the region's most important known spawning ground in the Gulf of Mexico. Another important group of recent returns connected the Cape Hatteras-Cape Cod summer concentration of small fish with their previously unknown wintering area in oceanic waters near the edge of the continental shelf east of this summer habitat. Previous returns had connected the nursery area south of Cape Cod with the summer habitat of larger bluefin north of this cape, and the offshore winter and spring habitat of the medium bluefin with their warm season feeding grounds north and south of Cape Cod. These returns collectively indicate a cohesive and self-sufficient western Atlantic bluefin population. The most important remaining link to be established among the occurrences of bluefin in the western North Atlantic would be the migration of newborn bluefin from the Gulf of Mexico to the Cape Hatteras-Cape Cod area. It would be well worth the effort to tag some age 0 fish in the Gulf, or in the Straits of Florida. Other important but more difficult objectives of tagging western Atlantic bluefin are to learn more about the extent of their normal oceanic distributions, and to estimate the frequency and importance of their transatlantic migrations.

In regard to the latter, the infrequency of west to east transatlantic migrations of small bluefin has become increasingly apparent. The last tag return revealing such a migration was from a fish tagged in 1967 and recaptured in 1968. More than 4,400 small bluefin have been marked in the western North Atlantic in the years 1968-1975. Not one of these tags has been returned from the eastern Atlantic, although 935 have been recovered in the western part of the ocean in the years 1969-1976. Transatlantic migrations of small bluefin, at least in the west to east direction, have become increasingly

poor evidence for a single Atlantic stock.

On the other hand, giant bluefin marked off the Bahamas continue to be recaptured occasionally off Norway. Since 1969, however, more of these fish have been recaptured in the western Atlantic than in its eastern waters. Unfortunately, no estimates of the recruitment of western Atlantic tuna to the northern European fisheries more recent than those of Tiews (1964) for the 1954-1962 season have come to our attention. These estimates were based on the body condition of the fish landed during the late part of the season.

It is very puzzling that 11 of the 15 returns from the 1,100 releases off the Bahamas have been from outside the western North Atlantic, whereas all of the 50 returns from 1,662 releases of large bluefin in New England and Canadian waters have been from within the western North Atlantic. Furthermore, not one of more than 450 medium bluefin tagged in offshore western Atlantic waters has been recaptured elsewhere. This might be explained on the basis that fish from the eastern Atlantic spawned in the Gulf of Mexico. The same arguments against the Bahamas-Norway migration being a part of the regular migratory pattern of the western Atlantic fish, however, could be used against its being part of the regular migratory pattern of the eastern Atlantic fish. Also, not one of the large and medium bluefin tagged off Norway and Spain has been captured west of longitude 10°W. The most probable explanation of this phenomenon is that the strong flow of the Gulf Stream system, especially when the relatively slow North Atlantic Current is fortified by exceptionally strong westerly winds, and the tendency of the tuna to swim in favoring currents overrides all other stimuli. Consequently, the fish do not leave the current when they normally would to reach their American feeding grounds, and continue across the ocean.

Other recent indications of the separation of stocks include the discovery of the major spawning grounds of giant bluefin in the Gulf of Mexico. The failure to find early stages of bluefin in the Ibero-Moroccan Bay and adjacent Atlantic and Mediterranean waters reinforces the view that the central

Mediterranean is the prime reproductive area for eastern Atlantic Mediterranean bluefin. Thus the major spawning grounds of the two proposed stocks are almost as far apart as they could be, in an east-west direction, in the Atlantic-Mediterranean system. As noted previously, specific size composition data on oceanic longline catches are meager. Shingu et al. (1974), however, presented some very useful data on the sizes and abundance of bluefin usually encountered in large areas of the Atlantic and Mediterranean. The area of minimum catches in the Atlantic north of latitude 15°N is between longitudes 20°W and 40°W. The catches there consist mainly of large fish. This might be the area where the proposed western and eastern Atlantic stocks meet. The catches in the equatorial region between latitudes 15°N and 10°S consist mainly of large fish, with a few mediums. South of latitude 10°S, catches of Atlantic bluefin are rare, and consist mainly of large fish. These data suggest that the South Atlantic is a marginal area for bluefin from the North Atlantic, rather than the habitat of a separate stock. The groups of bluefin which remain in equatorial waters during the northern warm season have probably found good feeding areas in the frontal areas of the currents, and remained in them instead of migrating northward to coastal feeding areas. Concentrations of feeding tunas of other species in frontal areas of the Pacific equatorial currents have been reported (Blackburn 1965, Laurs and Lynn 1977, Murphy and Shomura 1972).

Sorting out the populations of larger tuna in mid-ocean by conventional tagging seems an almost hopeless task. Possibly some of the more advanced biochemical methods will be more successful.

We conclude from the material considered that the following stocks constitute the most probable arrangement:

a) A western Atlantic spawning stock which is generally self sufficient and relatively uncomplicated. The chief problems remaining are to define its wintering and spawning areas completely. Contingents of large fish from this stock emigrate to the eastern Atlantic fairly frequently. Contingents of small fish do so only rarely.

b) A more complex stock which might be subdivided into eastern Atlantic and Mediterranean sub-stocks until the fish are about 9 years old. The eastern Atlantic substock probably recruits much of its strength from the Mediterranean substock. The fish over 9 years old constitute an eastern Atlantic Mediterranean spawning stock.

c) Possibly one or more localized Mediterranean stocks. The most probable separate stock would be the one which feeds and winters in the Sea of Marmara and spawns in the Black Sea.

E. RECOMMENDATIONS

It is clear that there are many unanswered questions relating to the stock or stocks of bluefin tuna in the Atlantic-Mediterranean system. As more data become available, many of these questions are beginning to be answered or at least indications of one choice are becoming clearer. There are some aspects of the bluefin's life history which we feel call for additional studies to more readily solve some of the gaps in the data. Perhaps one of the most important in terms of stock structure is one we have mentioned, to determine what percentage of the "arrival" fish which enter the Ibero-Moroccan Bay spawn there and what percentage spawns in the Mediterranean. Some type of a sonar scanning program might be established in the Strait of Gibraltar along with a tagging program (sonic if possible) of some of the fish taken in the "arrival" run in the Bay. Environmental conditions must be examined to determine what effect they have.

Knowledge of the distributive patterns of the bluefin could be greatly increased by more comprehensive sampling of the sizes of the catches, particularly in the oceanic longline fisheries. More attention should also be given to recording occurrences of age 0 bluefin. In the western Atlantic, at least, many fishermen apparently do not distinguish very small *Thynnus thynnus* from other small tuna-like fishes. Simple and clear identification keys should be distributed to individuals who handle large numbers of fish, including dockmasters, fish handlers and taxidermists, as well as fishermen.

Tagging of age 0 bluefin in key areas, such as the western Mediterra-

nean and the Straits of Florida should produce important results. Tagging of giant tuna under present conditions is difficult but is still producing good results. The use of sonic tags in key areas, such as the Windward Passage and the channels north of Cuba and around the Cay Sal Banks and the Straits of

Gibraltar, Messina, and Bosphorus, would be an efficient and positive way to obtain important information.

Present studies must be continued, as the data generated by them have helped immensely in recent years. We feel, however, that the above efforts will provide the most suitable informa-

tion to complete the picture of the life history of this species in the shortest period of time. This will allow fishery scientists and managers to proceed with the preservation and rebuilding, where necessary, of this valuable resource with the best understanding possible.

VIII. BIBLIOGRAPHY

A. INTRODUCTORY NOTES

The following list of references contains many which have not been cited in the text. These may be of interest to readers who wish to study the matters discussed in this work more closely or are interested in aspects of the subject which have not been considered here. It is not, however, a complete bibliography of the bluefin tuna. Additional references may be found in FAO Fisheries Reports No. 6, Vol. 4 (1964), and in the standard biological and zoological abstracts and records.

Much information on the species has been consolidated by some authors and organizations. Parona (1919), de Buen, F. (1925) and others have summarized many of the pre-twentieth century works. In a series of reports, Heldt reviewed most of the pertinent material which appeared in the years 1924-1937, as well as some of earlier dates, and provided extensive bibliographies. More recently, the Working Groups on Bluefin Tuna of the International Council for the Exploration of the Sea have been reporting annually on the trends in bluefin tuna catches. Finally, a great deal of timely information is appearing in the working documents, reports and publications of the International Commission for the Conservation of Atlantic Tunas.

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