LIFE HISTORY AND ECOLOGY
OF THE GRAY WHALE
(*Eschrichtius robustus*)

RICE AND WOLMAN

Ma-R495

HARVARD UNIVERSITY

LIBRARY

OF THE

Museum of Comparative Zoology

MUS. COMP. ZOOL.
LIBRARY

OCT 26 1971

HARVARD
UNIVERSITY

**THE LIFE HISTORY AND ECOLOGY
OF THE GRAY WHALE
(*ESCHRICHTIUS ROBUSTUS*)**

SPECIAL PUBLICATIONS

This series, published by the American Society of Mammalogists, has been established for papers of monographic scope concerned with some aspect of the biology of mammals.

Correspondence concerning manuscripts to be submitted for publication in the series should be addressed to the Editor for Special Publications, James N. Layne (address below).

Copies of special publications may be ordered from the Secretary-treasurer of the Society, Dr. Bryan P. Glass, Department of Zoology, Oklahoma State University, Stillwater, Oklahoma 74074.

Price of this issue \$5.00

COMMITTEE ON SPECIAL PUBLICATIONS

JAMES N. LAYNE, *Editor*

Archbold Biological Station,
Route 2, Box 380,
Lake Placid, Florida 33852.

J. KNOX JONES, JR., *Managing Editor*

Museum of Natural History,
University of Kansas,
Lawrence, Kansas 66044.

CONSULTING EDITORS FOR THIS ISSUE

ROBERT T. ORR

WILLIAM E. SCHEVILL

Special Publication No. 3 was financed in part by contributions in memory of Paul Martin, Olympia, Washington

THE LIFE HISTORY AND ECOLOGY
OF THE GRAY WHALE
(*ESCHRICHTIUS ROBUSTUS*)

By

DALE W. RICE

AND

ALLEN A. WOLMAN

U. S. FISH AND WILDLIFE SERVICE

BUREAU OF COMMERCIAL FISHERIES

MARINE MAMMAL BIOLOGICAL LABORATORY

SEATTLE, WASHINGTON

SPECIAL PUBLICATION NO. 3

THE AMERICAN SOCIETY OF MAMMALOGISTS

PUBLISHED 30 APRIL 1971

Ma-R495

MUS. COMP. ZOOL.
LIBRARY

OCT 26 1971

HARVARD
UNIVERSITY.

\$5.00

Library of Congress Catalog Card No. 79-159963
© 1971 by The American Society of Mammalogists

FOREWORD

WHALES long remained among the world's least known mammals because their large size and oceanic habitat make them difficult to observe and collect. Individual whales cannot be observed repeatedly, therefore knowledge of most aspects of their life history must be deduced from data provided by examining large series of specimens. In the early decades of this century the expansion of the modern whaling industry with its efficient catcher boats and its mechanized shore stations and floating factory ships finally provided biologists the opportunity to undertake large-scale studies of whales. Concern for the future of whale stocks provided an incentive for government support of whale research. As a result, we have now learned more about the biology of the rorquals and the sperm whale than of most other species of wild mammals. Gray whale populations, however, had been depleted before this opportunity for research arose. Although field observations had provided a fairly detailed picture of the distribution, migration, and behavior of the gray whale, many important aspects of the species' biology—such as age and growth, reproduction, parasites, pathology, and population dynamics—remained virtually unknown.

Under the protection afforded by the 1946 International Convention for the Regulation of Whaling, the California gray whale stock has increased so much that a resumption of commercial exploitation has been considered. As the dearth of basic data on the biology of the species would handicap any efforts at rational regulation of the harvest, the Bureau of Commercial Fisheries in 1959 initiated a research program that included collecting small series of gray whales under Special Scientific Permits. Beginning in 1966, the number of animals taken annually was increased upon recommendation of the Scientific Committee of the International Whaling Commission, which has reviewed the work each year and provided much encouragement and advice. The data now available reveal the basic features of the ecology of the gray whale and provide a foundation for further studies on its population dynamics.

This study would not have been possible without the cooperation of the Del Monte Fishing Company and the Golden Gate Fishing Company of Richmond, California. John Caito and Charles Caito of Del Monte, and Robert Casebeer of Golden Gate placed the

facilities and crews of their whaling stations and catcher boats at our disposal for collecting and examining specimens. Kenneth C. Balcomb III, James Ekberg, Bernard Lenheim, and Toshio Kasuya (Ocean Research Institute, University of Tokyo), assisted in the examination of whales at the whaling stations. Margaret Anderson, Lawrence Dickson, Susan D'Vincent, Ekberg, James Houk, Hiroshi Kajimura, Lenheim, Donald Ramsey, Jeffrey Rochin, James Rote, Catherine Short, and Robert Strawn manned the counting stations. Lenheim, Ramsey, and Ancel M. Johnson conducted the transect cruises of the catcher-boat *Allen Cody*. Balcomb, Kasuya, Thomas J. McIntyre, Masaharu Nishiwaki (Ocean Research Institute), Daniel Lluich B., and Joaquin Arvizu M. (both with the Instituto Nacional de Investigaciones Biologico Pesqueras, Mexico) assisted in the whale-marking cruises. Ford Wilke, Johnson, and Lenheim assisted in the aerial surveys. Francis H. Fay, Arctic Health Research Laboratory, U. S. Public Health Service, provided a sample of the stomach contents of a gray whale killed near St. Lawrence Island, Alaska. Earl L. Bousfield, National Museum of Canada, identified the amphipods, provided information on the habits of benthic invertebrates, and made suggestions concerning the feeding behavior of gray whales. The following individuals identified other stomach contents or parasites: Martin W. Johnson and Margaret D. Knight, Scripps Institution of Oceanography (crab larvae); Josephine F. L. Hart, British Columbia Provincial Museum (cumaceans); Frank Bernard (ascidians and holothurians) and Cyril Berkeley (polychaetes and salps), Pacific Biological Station, Fisheries Research Board of Canada; Yuk-maan Leung and John L. Mohr, University of Southern California (cyamids); Kenneth M. Neiland, Alaska Department of Fish and Game (acanthocephalans and campulid trematodes); Robert L. Rausch, Arctic Health Research Laboratory (cestodes and notocotylid trematodes); John T. Davey, Commonwealth Bureau of Helminthology (nematodes). Daniel F. Cowan, Michigan State University, examined a pathological liver specimen. The late Gordon C. Pike, Arctic Biological Station, Fisheries Research Board of Canada, made the baleen tracings and allowed us to see his unpublished manuscript on gray whales taken off British Columbia. Unless otherwise noted, individuals mentioned above are present or former employees of the Marine Mammal Biological Laboratory, Bureau of Commercial Fisheries.

CONTENTS

Introduction	1
Nomenclature	5
Field and Laboratory Procedures	7
Collection of Specimens	7
Field Observations	9
Seasonal Migratory Cycle	11
California Stock	11
Korean Stock	19
Atlantic Stocks	20
Discussion and Conclusions	21
Food and Feeding	23
Stomach Contents	23
Seasonal Changes in Nutritive Condition	27
Discussion and Conclusions	36
Age and Growth	38
Age Determination	38
Growth	43
Puberty and Sexual Maturity	46
Physical Maturity	49
Discussion and Conclusions	50
Female Reproductive Cycle	52
Ovarian Cycle	52
Pregnancy	72
Lactation	86
Anestrus	90
Discussion and Conclusions	90
Male Reproductive Cycle	92
Testes	92
Penis	94
Discussion and Conclusions	95

Predators	98
Parasites and Epizoites	100
Ectoparasites and Epizoites	100
Endoparasites	104
Discussion and Conclusions	108
Population	109
Present Numbers	109
Population Trends	112
Density and Biomass	114
Population Structure	115
Population Dynamics	117
Discussion and Conclusions	118
Exploitation	120
Aboriginal Whaling	120
Commercial Whaling	121
Summary	127
Literature Cited	132
Index	141

INTRODUCTION

IN February each year, pod after pod of gray whales departs from the tropical mangrove-fringed lagoons bordering Bahia Magdalena, from Laguna Ojo de Liebre in the heart of the Vizcaino Desert, and from other lagoons on the west coast of Baja California. Swimming slowly but steadily, they move northward along the coast; four months later the same whales may be surfacing and blowing among the ice floes of the Chukchi Sea. This migration is the longest performed by any mammal.

The gray whale, *Eschrichtius robustus* (Lilljeborg, 1861), is unique in other ways. It is the sole member of the family Eschrichtiidae and the most primitive surviving baleen whale. In structure it is remarkably similar to the extinct cetotheres, which were ancestral to all living baleen whales. The gray whale became extinct in the North Atlantic only a few centuries ago and is now a relict species confined to neritic waters of the North Pacific Ocean and adjacent waters of the Arctic Ocean (Fig. 1).

Because gray whales swim slowly and congregate in near-shore waters, they were easy prey to whalers. By the turn of the century, the species was almost extinct. Since 1946, the eastern Pacific stock has increased under the legal protection afforded by the International Convention for the Regulation of Whaling to the point that commercial utilization may again be advocated.

Gray whales are the only large whales that can regularly be observed in large numbers from shore. Their annual passage along the coast of California is one of the world's outstanding wildlife spectacles. Public interest in gray whales is increasing, and they have become an important tourist attraction in southern California. More than a million people visit Cabrillo National Monument on Point Loma, San Diego, each year to watch the migrating whales, and several sport-fishing companies in San Diego and San Pedro profitably operate "whale watching" cruises (Rice, 1961).

The abundance and accessibility of gray whales in their calving lagoons and along the coast is also attracting a growing number of experimental biologists, and there is cause for concern that, especially on the calving grounds, repeated harassment of gray whales

FIG. 1. Distribution of the gray whale. A few gray whales spend the summer in the migration area, especially along the coast of Washington and Oregon.

by investigators using small boats or aircraft in attempts to implant telemetering and tracking devices or drug darts may deleteriously affect reproduction (Schevill *et al.*, 1967; American Society of Mammalogists, 1967). Another threat to the survival of the gray whale is increasing industrial development and boat and ship traffic in the remaining calving lagoons (Marx, 1966). The species has long since been driven from San Diego Bay.

The gray whale is clearly an important species from the standpoint of basic scientific interest, esthetic appeal, and economic significance. If commercial exploitation is resumed it should be limited to the sustainable yield so that the scientific and esthetic values of the population may be preserved. A wise management program must be based on a sound knowledge of the biology of the species.

Beginning with Scammon's (1874) classic account, the gray whale has been the subject of many field observations (for example, Gilmore, 1960*a*, 1960*b*; Hubbs, 1959; Hubbs and Hubbs, 1967; Pike, 1962*a*). As a result, certain facets of its life history and ecology, such as distribution, migrations, and behavior, are better known than for other baleen whales.

Only five biologists have had the opportunity to examine series of gray whales. Andrews (1914) studied 23 specimens taken during southward migration and brought into the shore station at Ulsan, Korea, in January and February 1912. In his monograph he presented a historical review of earlier research on the species. Zenkovich (1934*a*, 1934*b*, 1937*a*, 1937*b*, 1937*c*) examined 104 gray whales aboard the Soviet floating factory *Aleut* during the summers of 1933 through 1936. Tomilin (1937) examined 54 specimens aboard the *Aleut* in August and September 1934. Unfortunately, neither Andrews, Zenkovich, nor Tomilin recorded reproductive information other than measurements of fetuses and condition of mammary glands. Pike (1962*a* and unpublished data) examined 10 northward migrating gray whales killed under a special scientific permit and brought into the shore station at Coal Harbour, British Columbia, during the first week of April 1953. Zimushko (1969*a*, 1969*b*) reported on 63 gray whales collected off the Chukotsky Peninsula in the summer and autumn of 1965 and 1966.

Few other original data based upon examination of dead gray whales have been published. Gilmore (1960*a*) and Eberhardt and Norris (1964) examined a number of dead calves at Laguna Ojo de Liebre, Baja California, and Maher (1960) reported on several whales killed by Eskimos at Barrow, Alaska.

Statistical data from commercial catches of gray whales in Baja California and in the Bering Sea were analyzed by Risting (1928). Unfortunately, his data are unreliable, because body lengths were estimated rather than measured (see Mackintosh and Wheeler, 1929, p. 273), and therefore the conclusions concerning fetal growth and size at sexual maturity are not valid. Mizue (1951) presented statistical data from gray whale catches in Korea.

The Bureau of Commercial Fisheries began a program of research on the species in 1952 under the leadership of Raymond M. Gilmore. During the first five years, the work consisted of field observations

and censuses designed primarily to determine the extent of the calving grounds and to document fluctuations in population size (Gilmore, 1960*a*, 1960*b*).

In 1958, responsibility for whale research was transferred to the Marine Mammal Biological Laboratory in Seattle, Washington, under the direction of the senior author. Beginning in 1959, small series of gray whales have been periodically collected to obtain basic data on all aspects of the life history and ecology of the species. Particular emphasis has been given to reproduction, growth, age, and population structure. As collections and observations had to be made incidentally to studies on rorquals and sperm whales, they have been mostly confined to the periods when the gray whales were on migration along the coast of California. This report presents the results of the study from 1959 through February 1970.

NOMENCLATURE

THERE has long been a controversy over the correct scientific name of the gray whale. *Eschrichtius robustus* (Lilljeborg, 1861) is used here for the extinct Atlantic and the living Pacific populations of gray whales following Cederlund (1939). As the data and conclusions of this author have been mostly ignored by subsequent workers, none of whom has contributed new evidence to refute his conclusions, it seems desirable to briefly review the nomenclature of the gray whale.

The generic name *Eschrichtius* Gray (1864) is now used by virtually all taxonomists. There are three available species-group names (Herschkovitz, 1966) that require consideration. These are, in order of priority: (1) *Balaena gibbosa* Erxleben (1777), based on the New England "scrag whale" described by Dudley (1725); (2) *Balaenoptera robusta* Lilljeborg (1861), based on subfossil skeletal remains from Gräsö, Sweden; and (3) *Agaphelus glaucus* Cope (1868), based on gray whales from the coast of California. Two questions must be resolved: (1) which of the first two names should be used for the Atlantic population, and (2) is the Pacific population taxonomically distinct from the Atlantic population?

The applicability of Erxleben's name *gibbosa* to the gray whale depends upon the identity of Dudley's "scrag whale." Dudley's (1725) brief description reads as follows: "The Scrag Whale is near a-kin to the Fin-back, but, instead of a Fin upon his Back, the Ridge of the Afterpart of his Back is scragged with half a Dozen Knobs or Nuckles; he is nearest the right Whale in Figure and for Quantity of Oil; his Bone is white, but won't split." The lack of a dorsal fin, knobs on the back, and white baleen are diagnostic of the gray whale. It seems improbable that Dudley's description of the scrag whale is inaccurate because all other large whales described by him are readily recognizable. On the other hand, there are minor discrepancies between Dudley's description of the scrag whale and the gray whale. For one thing, the oil yield is too high; Scammon (1874) stated that right whales yielded an average of 60 barrels, but that gray whales produced only 20 with a maximum of 60 or 70. For another, the number of knobs on the back is too few; gray

whales have nine to 14 knobs behind the dorsal hump, although the posterior knobs are weakly defined. These discrepancies might seem minor were it not for the fact that no other account of early whaling gives any indication of the occurrence of *Eschrichtius* in the North Atlantic (True, 1904) and the fact that the term "scrag" or "scragg" was applied to different kinds of whales, particularly small, lean, right whales (Allen, 1916; Eschricht and Reinhardt, 1866). As the identity of Dudley's scrag whale can never be unequivocally determined, we agree with Cederlund (1939) and Schevill (1952) that Lilljeborg's specific name should be used for the Atlantic gray whales.

The question of the taxonomic relationship of the Pacific and Atlantic gray whale stocks has been investigated by van Deinse and Junge (1937) and Cederlund (1939), who compared the sub-fossil skeletal material from the Atlantic with skeletons and published data and photographs of Pacific gray whales. These authors found no consistent differences between the Atlantic and Pacific specimens and concluded that these populations were conspecific.

FIELD AND LABORATORY PROCEDURES

Collection of Specimens

A total of 316 gray whales was examined. These were collected by the whale catcher boats of the Del Monte and the Golden Gate Fishing Companies, Richmond, California, under special scientific permits issued to the Marine Mammal Biological Laboratory. The whales were taken along the coast of central California between Half Moon Bay ($37^{\circ}30'$ N lat.) and Point Reyes ($38^{\circ}00'$ N lat.).

The collections were scheduled to provide representative samples for the periods of the southward (December to January) and northward (February to April) migrations. The total sample included 180 southbound migrants (85 males, 95 females) and 136 northbound migrants (81 males, 55 females). Dates of collection, numbers of specimens (in parentheses), and persons who made the examinations and measurements are as follows: 23 to 26 February 1959 (two) Rice; 27 to 30 March 1962 (four) Rice; 14 to 25 March 1964 (20) Rice; 22 to 29 March 1966 (26) Rice, Wolman, Balcomb; 14 December 1966 to 19 January 1967 (95) Rice, Wolman, Ekberg, Kasuya; 21 February to 9 March 1967 (30) Wolman, Ekberg; 14 to 25 January 1968 (35) Rice, Wolman; 26 February to 11 March 1968 (24) Wolman, Lenheim; 2 to 11 April 1968 (seven) Rice, Wolman; 20 December 1968 to 9 January 1969 (50) Rice, Lenheim; 2 to 16 March 1969 (23) Wolman, Lenheim.

Whales were delivered to the shore stations of the Del Monte and Golden Gate Fishing Companies at Point San Pablo, Richmond, California, where the following data were recorded.

MEASUREMENTS AND COUNTS.—Twenty-two standard external body measurements of the first 177 whales collected were made with a steel tape graduated in centimeters. A preliminary analysis revealed that many of these measurements were redundant, imprecise, or useless. Consequently, only nine measurements were made on the last 139 specimens. These were: total length (straight line from tip of snout to notch of flukes); head length (from tip of snout to occipital condyles); tail length (from notch of flukes to anus); maximum girth of body

(determined by measuring from the mid-dorsal line to the mid-ventral line on the side of the whale that was uppermost as the animal lay on the flensing deck and multiplying by two); span of flukes; breadth of flukes (from notch to nearest point on leading edge); anterior length of flipper; posterior length of flipper; and maximum width of flipper. Sixteen skulls and one complete skeleton were collected for cranial measurements. Throat grooves, baleen plates, and knobs on the dorsal ridge of the caudal peduncle were counted on most specimens.

BODY WEIGHTS.—Weights of six whales were determined by summing the weight of the meat produced after it had been packaged in 50-pound (22.7 kilogram) bags and the weights of the blubber, viscera, and bones, which were determined by weighing each truckload of raw material on commercial truck scales. One near-term fetus was weighed in pieces.

ECTOPARASITES AND EPIZOITES.—Abundance, position, and sizes of ectoparasites and epizotes on the body surface and baleen plates were recorded, and a series of each species was collected for identification.

SCARS.—The nature and position of any scars and wounds were noted.

BLUBBER THICKNESS.—Thickness of the blubber was measured (to the nearest half centimeter) at a mid-lateral point on the body opposite the dorsal hump.

MAMMARY GLANDS.—Development of the mammary glands and presence or absence of secretory activity was noted. Maximum thickness of the glands, as determined by inspection, was measured to the nearest half centimeter. A small portion of mammary gland tissue was fixed in 10 per cent formalin or FAA (10 parts formalin, 30 parts isopropanol, 5 parts acetic acid, 55 parts water), sectioned at 10 microns, and stained with hematoxylin and eosin. The development of glandular tissue subsequently was determined by projecting a randomly selected section about one-quarter of a square centimeter onto a sheet of paper on which 100 dots were arranged in a regular 10 by 10 grid; the number of dots falling within glandular areas was used as an index of the proportion of glandular tissue.

OVARIES.—The ovaries of each female were collected and fixed in 10 per cent formalin. The preserved ovaries were weighed to the nearest hundredth of a kilogram and serially sectioned at half a centimeter on a mechanical meat slicer. Each corpus luteum and corpus albicans revealed through sectioning was measured, to the nearest millimeter, across its greatest diameter and across its maximum diameter at right angles to the greatest diameter; and the two measurements were averaged. The maximum diameter of the largest Graafian follicle also was measured to the nearest millimeter.

UTERUS.—The diameter of each uterine horn at approximately the middle was measured to the nearest half a centimeter. A sample of the uterine wall was fixed in 10 per cent formalin or FAA, sectioned at 10 microns, and stained with hematoxylin and eosin for histological study. In specimens in which a corpus luteum or recently ovulated follicle was present in either ovary, but there was no obvious indication of pregnancy, the entire uterus was removed from the carcass, each uterine horn slit open along its entire length, and the

surface of the endometrium carefully searched. Embryos and small fetuses were preserved in 10 per cent formalin and their length (crown to tip of tail, with body straightened) and sex recorded. Standard body measurements were made on near-term fetuses and the sex was noted.

TESTES.—Each testis was weighed to the nearest tenth of a kilogram at the whaling station. A small sample (1 to 2 cubic centimeters) of the largest testis of each whale was taken for microscopic examination from the middle of the gonad about halfway between the surface and center and fixed in FAA, 10 per cent formalin, or Bouin's solution. Specimens were sectioned at seven microns and stained with hematoxylin and eosin. Mean diameter of the seminiferous tubules was calculated from measurements with an ocular micrometer of the greatest diameter and maximum diameter at right angles to the greatest diameter of 20 tubules cut in cross section. The presence or absence of fluid in the epididymides and deferent ducts was noted.

PENIS.—The length of the extruded penis from the base on the ventral surface to the tip and the circumference at the base were measured to the nearest centimeter. These measurements could not be made on some males, especially immature individuals, because the penis was not completely extruded.

STOMACH CONTENTS.—The quantity of any food remains in the stomach was estimated and a sample preserved for identification.

ENDOPARASITES.—The stomach, intestine, liver, kidneys, lungs, peribullary sinuses, and blubber were examined for endoparasites. The intestine was slit open at three or more randomly selected points, and in the years 1967, 1968, and 1969 the rectum also was opened for inspection. The tips of the liver lobes were examined for evidence of cirrhosis and were sliced to reveal the bile ducts. The kidneys were slit to expose the main urinary duct.

VERTEBRAL EPIPHYSES.—The degree of fusion of the epiphyses of the anterior thoracic vertebrae to their centra was determined by chopping into the ends of the vertebrae with a hatchet to a depth of several centimeters.

EAR PLUGS.—An attempt was made to collect at least one ear plug from each whale. In a few animals, however, the plug was so soft that it could not be successfully removed. Ear plugs were preserved in 10 per cent formalin. They were bisected longitudinally and gently polished on a whetstone, so that the growth layers could be counted.

BALEEN PLATES.—Several of the longest baleen plates were collected from each whale. Variations in thickness of the plates were recorded graphically by means of an apparatus similar to that used by Ruud (1940).

Field Observations

Observations on living gray whales were made from coastal look-out points, chartered whale catcher boats, and light aircraft.

COASTAL STATIONS.—During the southward migration in 1967–68, 1968–69, and 1969–70, coastal lookout stations were established to count migrating whales. One was on Point Loma at San Diego, California ($32^{\circ}40'$ N lat.), 130 meters above sea level (Rice, 1961) and is the site where previous counts were made (Gilmore, 1960a, 1960b; Rice, 1961). This station was manned for 52 days (27 December to 16 February) in 1967–68 and for 57 days (20 December to 14 February) in 1968–69. The second station was 2 km. S Yankee Point, Monterey Co., California ($36^{\circ}29'$ N lat.), 23 meters above sea level and about 100 meters back from the shoreline. This was near the site where a partial count of migrating gray whales was made in 1966–67 (Adams, 1968). We manned this station for 49 days (18 December to 4 February) in 1967–68, 60 days (10 December to 7 February) in 1968–69, and 64 days (8 December to 9 February) in 1969–70.

Observations were made continuously from 0700 to 1700 hours (essentially sunrise to sunset) each day. At each station, two observers each worked a 5-hour shift; morning and afternoon shifts were alternated between the two observers. The number of whales, time of passage, estimated distance from shore, and direction of travel were recorded for each group sighted. Wind direction and force, cloud cover, precipitation, and fog were logged throughout the day.

VESSELS.—Between 25 January and 9 February 1968, we ran a series of transect cruises between Point Loma and a position west of Tanner and Cortez Banks. A similar transect was run off Yankee Point on 18 January 1968. While the vessel was underway, a constant watch for gray whales and other marine mammals was maintained on the bridge. All whales sighted were approached closely enough to ensure positive identification and the number of whales in each pod, the direction of travel, and the position and time of sighting recorded.

Observations on gray whales also were made during many cruises conducted for marking rorquals (Balaenopteridae) and sperm whales (*Physeter catodon*). The area covered included the waters along the coast from Point Reyes, California (38° N lat.), south to Isla Clarion off Colima, Mexico (18° N lat.). The cruises, totaling 15 months, were made mostly between December and April from 1962 to 1969. The calving grounds in Laguna Ojo de Liebre, Laguna Guerrero Negro, Laguna San Ignacio, and Bahia Magdalena, Baja California, were briefly visited. Gray whales were sighted on 304 occasions, and a total of 1045 individuals was recorded.

AIRCRAFT.—On 25 and 26 March 1969, an aerial survey was made in both directions along the entire coast between San Francisco, California (38° N lat.), and Cape Flattery, Washington (48° N lat.). Two aircraft (a Cessna 177 and a Cessna 185) were used, each with two observers in addition to the pilot. The flight path was 0.3 to 2.0 kilometers offshore at an average altitude of 230 meters and air speed of 200 kilometers per hour. When pods of whales were sighted they were often circled at a lower altitude. Data were recorded on a tape recorder. Sighting conditions were optimum, with calm seas and clear skies, throughout the period of the survey.

SEASONAL MIGRATORY CYCLE

GRAY whales now occur only in the North Pacific Ocean and adjacent waters of the Arctic Ocean. The species also existed in the North Atlantic until a few centuries ago. There are presently two geographically isolated stocks (Fig. 1): an eastern Pacific stock, which migrates between Baja California and the Bering and Chukchi seas, and a western Pacific stock, which migrates between South Korea and the Okhotsk Sea. These may be designated the California stock and the Korean stock, respectively, on the basis of their breeding grounds.

California Stock

SUMMER GROUNDS.—From late May through October, gray whales occupy the shallow waters of the northern and western Bering Sea, the Chukchi Sea, and the western Beaufort Sea. They are common along the Koryak coast of Siberia from Cape Navarin to Glubokoi Inlet (Berzin and Rovnin, 1966). Farther to the southwest they are rare; a few have been seen as far as Kronotskiy Bay on the Kamchatka Peninsula (Tomilin, 1957) and the Kommandorskiye Islands (Barabash-Nikiforov, 1938; Grebnitskii, 1902). In the Gulf of Anadyr, these whales are abundant along the southwest shore from Cape Navarin to Tymna Lagoon; they have not been seen in the northwestern part of the gulf from the Anadyr Estuary to Cape Kresta (Berzin and Rovnin, 1966). Gray whales are also common along the northeastern shore of the Gulf of Anadyr, from Cape Retkon to Cape Chaplino (Berzin and Rovnin, 1966), around St. Lawrence Island (Ichihara, 1958), around the shores of the Chukotskiy Peninsula as far northwest as Cape Serdtse Kamen' (Nikulin, 1946), in Kotzebue Sound (Wilke and Fiscus, 1961), and in the Chukchi Sea (north as far as 69° N lat.—Nasu, 1960). A few go westward along the coast as far as Tynkurginpil'gyn Lagoon (Berzin and Rovnin, 1966), and northwestward through the pack ice as far as Wrangel Island (Sleptsov, 1955).

Along the Arctic coast of Alaska they are found regularly from Cape Thompson (Pike, 1962a) east to Point Barrow, and a few have

been reported by Eskimos along the shores of the Beaufort Sea as far east as Barter Island (Maher, 1960). To the southeast, there are few records of gray whales. One was found stranded at Scammon Bay, south of the Yukon Delta, in September (Fay, *in* Pike, 1962*a*). There is only one published record of gray whales from the Pribilof Islands (Gilmore, 1960*b*), but several were seen around St. George Island in the summers of 1965 and 1968 by C. H. Fiscus, A. M. Johnson, and V. B. Scheffer (personal communication). Gray whale remains have been found on St. Matthew Island (Pike, 1962*a*), and C. H. Fiscus (personal communication) saw four gray whales in Sarichef Strait between St. Matthew Island and Hall Island on 3 August 1960.

Not all gray whales migrate to the Arctic in the summer. A few remain scattered along the west coast of North America. Pike and MacAskie (1969) reported several near Langara, Queen Charlotte Islands, British Columbia, in late August and early September of 1959 and 1960, and a young male stranded near Ucluelet, Vancouver Island, on 16 August 1966. Some were seen near Lapush, Washington, in June and July 1961 by C. Munsen (personal communication) and in July 1967 by the junior author. A few were seen near Kalaloch, Washington, in July 1968, by A. M. Johnson (personal communication). Fiscus (personal communication) saw one near Cannon Beach, Oregon, in July 1969. Gilmore (1960*a*) reported that a few regularly spend the summer in the vicinity of St. George Reef and Pelican Bay in northern California and southern Oregon. Whalers working off San Francisco occasionally see gray whales during the summer. L. Newton (personal communication), captain of the catcher boat "Lynnann," saw a few near the Farallon Islands, California, throughout the summer of 1964; they remained until late September or early October. K. C. Balcomb saw a small gray whale in Bahia Magdalena, Baja California, on 11 June 1965, during one of our whale marking cruises aboard the catcher boat "Sioux City."

The northern boundary of the known summer range of the gray whale corresponds closely with the southern edge of the zone of close pack ice during the period 1 to 15 September (U. S. Navy Hydrographic Office, 1958). Close pack ice may limit their movements. Scammon (1874) and Sleptsov (1955) have reported seeing

gray whales in broken pack ice. Gray whales do not arrive at Point Hope or at Barrow, Alaska, until most of the ice has gone out, long after the bowhead whales have arrived. As few observers experienced in identifying whales enter the close pack ice in ships or fly over it in the summer, the extent to which gray whales penetrate the pack ice is unknown. In the western Bering Sea, gray whales are confined to coastal waters, their seaward range being delimited by the edge of the Continental Shelf. They have never been found in the deep waters of the southwestern Bering Sea. Their feeding habits (see section on food and feeding) apparently restrict them to shallow water. Although most of the eastern Bering Sea is shallow, the scarcity of gray whales there is believed to be the result of a low biomass of benthos, 55 grams per square meter, compared with 200 to 900 grams per square meter in the northwestern region (Berzin and Rovnin, 1966; Neiman, 1963). ✓

MIGRATIONS.—Pike (1962*a*) summarized all published information on the migration route of the California population and presented significant new data. There are few observations on southward-migrating whales in the northern part of their range. From October through January, they probably move down the eastern side of the Bering Sea, go through Unimak Pass, and then follow the coast to Baja California. A few go around Cabo San Lucas and cross to the eastern side of the Gulf of California. From late February to June, the northward migration of males and females without calves, which is much better documented, follows the reverse route.

Our observations during whale marking cruises off California and Baja California show that the majority of gray whales migrate within a few kilometers of shore when passing points, headlands, and sectors of coastline where the Continental Shelf is narrow and there are no off-lying islands. Many tend to take the most direct route, however, when crossing bights and indentations of the coastline. For example, many southbound whales, after passing Point Conception ($34^{\circ}27'$ N lat.), head southeast through the Channel Islands, passing as much as 200 kilometers offshore from the mainland of southern California (Rice, 1965). Some gray whales make a similar offshore passage from about Punta Baja ($29^{\circ}57'$ N lat.). ✓

to Isla Cedros ($28^{\circ}22'$ N lat.), Baja California, thus avoiding the long journey around the shores of Bahia Sebastian Vizcaino. Quantitative data on offshore migration are presented in the chapter on populations.

The route taken by females with calves during the spring migration is unknown. During this study, the catcher-boat crews saw only one female with a calf—near Point Reyes on 15 March 1969. From 1959 through 1967, we collected no gray whales later than 30 March, and during that time we thought females with calves moved north later in the season. Therefore, in 1968 we hunted gray whales until 25 April, 14 days after the last whale was taken, and had one boat searching exclusively for females with calves from 2 to 25 April. Each year from 1956 through 1968, the regular sperm whaling season opened on 1 April and the baleen whaling season opened on 1 May (1956–59) or 16 April (1960–68). During these years, the whalers never saw a gray whale accompanied by a calf. Shore-based whalers working from San Simeon, California, in the 1880's likewise told Townsend (1887) that they never encountered females with calves.

On whale marking cruises in 1965, 1966, 1967, and 1969, we traveled north during late February, March, and early April, by which time most females with calves had already left the calving lagoons. We put in at many points along the coast between Cabo San Lucas (23° N lat.), Baja California, and San Francisco (38° N lat.), California, but never encountered a female accompanied by a calf, although we saw many northward-migrating gray whales. During the transect cruises, we saw two females with calves on 10 February 1968 (at $32^{\circ}48'$ N and $118^{\circ}08'$ W, heading west-northwest near San Clemente Island). During the aerial surveys between San Francisco, California, and Cape Flattery, Washington, on 25 and 26 March 1969, no females with calves were identified among 816 gray whales sighted. Morejohn (1968) reported a female with a calf at Moss Landing, northeast of Monterey, California, on 2 May 1967.

Gray whales observed on migration are usually swimming steadily and continuously in a constant direction on a course parallel to the shore. They surface regularly about every 3 to 5 minutes to blow three to five times. When out of sight of land,

they usually travel in a straight line. General observations indicate that the usual swimming speed is about 7 to 9 kilometers per hour (4 to 5 knots). Wyrick (1954) followed four separate gray whales migrating south past San Diego, California, for a total of more than 5 hours; their average speed was 8.5 kilometers per hour (4.6 knots). Cummings *et al.* (1968) tracked nine lone whales (some in daytime, others at night), over distances less than 1.7 kilometers and found the average speed to be 10.2 kilometers per hour (5.5 knots).

There was no consistent hourly variation in the number of gray whales migrating south past the counting stations, contrary to the opinion of Ramsey (1968). This lack of variation indicates that gray whales, on the average, maintain a constant speed throughout daylight hours.

There are few observations to show how fast gray whales travel at night. Unlike sperm whales, baleen whales are rarely, if ever, seen resting at the surface. Since they must rise to the surface regularly every few minutes to breathe, they must continue to swim at least slowly during hours of darkness. In polar regions during the summer when daylight is continuous, baleen whales appear to remain active continuously. ✓

Cummings *et al.* (1968) used an array of hydrophones mounted on the sea bottom off San Diego to track migrating gray whales. They reported the following: "Gray whales were soniferous day and night. One hundred twenty-four signals were recorded from at least 61 whales between 1800 and 0600 h, compared with 107 signals recorded from at least 157 whales between 0600 and 1800 h. All whales seen or heard at night apparently were migrating southward, and there was no evidence of the popular notion that gray whales characteristically stopped migrating at night to rest or to sleep." ✓

The average speed of gray whales along their entire migration route, calculated from dates of peak passage at various points along the coast, is about 185 kilometers per day, or 7.7 kilometers per hour, on the southward migration and half as fast on the northward migration (Pike, 1962a). If their average speed during the 10 hours of daylight is 8.5 kilometers per hour, they cover 85 kilometers; to travel the remaining 100 kilometers during the 14

FIG. 2. Collection dates of gray whales, according to sex, age, and reproductive status. Each square represents one animal.

hours of darkness, they must average 7.1 kilometers per hour, or 92 per cent of their speed during daylight.

During migration, there is a partial temporal segregation of gray whales according to sex, age, and reproductive status. This is evident from Fig. 2 in which the collection date of each whale is plotted according to sex, maturity, and reproductive status. These data cannot be regarded as strictly representative, however, because the collecting effort was not the same throughout the season. It must be kept in mind also that the gunners doubtless tended to select the larger animals, even though we imposed no size limitations. This tends to bias the sample in favor of mature animals and females, especially those in late pregnancy. The mean and extreme dates of passage for each class (Table 1), however, should be fairly reliable.

In general, in both the southward and the northward migration, females migrate earlier than males and adults migrate earlier than sexually immature animals. The vanguard of the southward migration from mid-December to the first of January is composed predominantly of females carrying near-term fetuses. The late-pregnant females are followed by adult females that have recently

TABLE 1

MEAN PASSAGE DATES OF MIGRATING GRAY WHALES OFF CENTRAL CALIFORNIA
(38° N LAT.) CLASSIFIED ACCORDING TO SEX, AGE, AND REPRODUCTIVE STATUS.

Category	Mean passage date		Days elapsed
	Southbound	Northbound	
Late pregnant (southbound); postpartum females (northbound)	31 December	26 March	85
Recently ovulated (southbound); early pregnant females (northbound)	5 January	28 February	54
Recently ovulated (southbound); metestrous and anestrus females (northbound)	5 January	14 March	68
Immature females	11 January	21 March	69
Adult males	9 January	12 March	62
Immature males	15 January	23 March	67

ovulated but have no macroscopically visible conceptus in the uterus; most of these females presumably weaned a calf a few months previously. The number of females in this class that were collected was fewer than expected. This probably resulted from gunner selection, although there also is a possibility that such females travel farther offshore. Next to pass are the immature females and, at about the same time, the adult males. Last to pass are the immature males.

During the northward migration, the first to pass are the newly pregnant females, which comprised the recently ovulated class of the preceding southward migration. Most of them pass within a limited period of about 15 days. We took them only between 21 February and 7 March in 1967, and between 26 February and 10 March in 1968. None was taken in 1969, when collecting did not commence until 2 March. The peak passage of adult males occurs more than 2 weeks later than that of the pregnant females. Adult males are followed by a few anestrus females that have failed to conceive. Immature whales of both sexes are the last to pass. Only two postpartum females were collected, both in late March. Neither was lactating; obviously their calves were stillborn or were lost shortly after birth.

Migrating gray whales travel singly or in pods of up to 16 individuals. In the course of the southward migration past Cali-

FIG. 3. Frequency distribution of group size of gray whales passing Yankee Point and Point Loma, by 10-day periods, during the southward migrations of 1967-68 and 1968-69. Solid bars indicate the number of groups, open bars the number of whales.

fornia, there are marked changes in the sizes of the groups (Fig. 3). During the early part of the migration, single whales (presumably mostly females carrying near-term fetuses) predominate, and almost no whales are in groups of more than six. During the

remainder of the migration, groups of two predominate. Most of the larger groups pass in the middle of the season, and towards the end of the season no groups contain more than five whales.

WINTER GROUNDS.—In January and February most gray whales of the eastern Pacific population are in warm temperate or tropical waters on the west coast of Baja California and the southern Gulf of California. Our southernmost sighting was at Punta Mita, Bahia de Banderas, Jalisco ($20^{\circ}45' \text{ N}$, $105^{\circ}34' \text{ W}$) on 17 February 1965. Gilmore (1960a) reported alleged sightings of gray whales at Isla Guadalupe and at Isla Clarion; we have seen none there nor anywhere else far off the coast of Mexico.

Most calves, as far as is known, are born in certain shallow lagoons. The six known calving areas, charted in detail by Gilmore (1960a), are as follows: *California and west coast of Baja California*—San Diego Bay (no longer occupied), Laguna Ojo de Liebre ("Scammon's Lagoon") and the adjacent Laguna Guerrero Negro, Laguna San Ignacio, and Bahia Magdalena and adjacent waters (including Bahia Almejas, Canal San Carlos, Estero Soledad, Estero Santo Domingo, Estero Las Animas); *eastern shore of Gulf of California*—open coast south of Yavaros, Sonora (see Gilmore *et al.*, 1967), and Bahia Reforma, Sinaloa.

Korean Stock

There is little information on the distribution of the Korean stock. No gray whales have been reported in recent years in either the Okhotsk Sea or the Sea of Japan, according to (personal communications) V. A. Arseniev and M. V. Ivashin of the All-Union Research Institute for Marine Fisheries and Oceanography, Moscow; H. Omura of the Whales Research Institute, Tokyo; and M. Nishiwaki of the Ocean Research Institute, Tokyo.

SUMMER GROUNDS.—Gray whales occupy, or at least formerly occupied, the northern Okhotsk Sea. They penetrated as far north as Penzhinskaya Bay (Krasheninnikov, 1755), and ranged southward as far as Akademii and Sakhalinskiy gulfs on the west (Sleptsov, 1955), and the mouth of the Kikhchik River on the east (Ditmar, 1890).

MIGRATIONS.—The migration route of the Korean stock of gray whales lay along the mainland coast of eastern Asia from Tatarskiy Strait to South Korea. Southbound whales passed Ulsan, South Korea, from late November to late January, and northbound whales passed there from the middle of March to the middle of May (Andrews, 1914). All the whales apparently passed through Tatarskiy Strait, as none was ever seen in La Perouse Strait between northern Hokkaido and southern Sakhalin (Mizue, 1951).

WINTER GROUNDS.—The channels, inlets, and bays along the southern coast of South Korea are believed to have been the winter calving grounds of the western Pacific gray whales. According to Andrews (1914): "In November and December, when the females are taken, almost every individual will be found to be carrying young nearly ready for birth. As these would necessarily be delivered within two or three weeks after passing Ulsan, the birth must occur in the bays among the numerous islands at the extreme southern end of the peninsula. Indeed Captain H. G. Melsom, who has hunted gray whales for 15 years along the Korea coast, has often observed them in this vicinity, but because of the abundance of other and more valuable species, they are not killed at this time by the Japanese."

Atlantic Stocks

Subfossil gray whale bones have been found at five localities along the coast of northwestern Europe: Pentuan, Cornwall, and Torquay, Devonshire, England, on the English Channel; IJmuiden and Wieringermeer Polder in the Netherlands; and on the Island of Gräsö, Sweden, in the northern Baltic (van Deinse and Junge, 1937). The most recent bones are those from IJmuiden, which date from about A.D. 500. There are no historical records of gray whales in the eastern North Atlantic. The summer grounds of the eastern Atlantic gray whales probably were in the Baltic Sea, where *Ampelisca macrocephala* (the predominant food of the California stock in the Bering Sea) is abundant (Kannevorff, 1965). Their winter grounds were perhaps along the Atlantic or Mediterranean coasts of southwestern Europe or northwestern Africa.

Discussion and Conclusions

In their annual migrations between summer feeding grounds in Arctic waters and winter breeding grounds in subtropical waters, gray whales may travel more than 18,000 kilometers each year, a distance exceeding that traveled by any other baleen whale. This extensive migration, spanning 50 degrees of latitude, exposes them to a broad range of environmental conditions. Sea surface temperatures on the summer grounds range from about 8° centigrade down to 0° or slightly less in the pack ice. On the winter grounds, temperatures range from about 18° centigrade at the latitude of Laguna Ojo de Liebre to 22° off Cabo San Lucas. In mid-summer most gray whales experience more than 22 hours of light each day, and those north of the Arctic Circle experience continuous daylight for several weeks. As the whales migrate southward, they are subjected to a rapidly decreasing photoperiod, which reaches a minimum of less than 8 hours in early December. Day length increases slowly during the remainder of the southward migration and while the whales are on the winter grounds, and then increases rapidly as the animals move north in the spring. The variable photoperiods to which the species is exposed may be an important proximate factor in regulating gonadal development.

There is no evidence to suggest that gray whales slow down at night while migrating southward. The length of their migration route, and their relatively slow swimming speed, makes it necessary for them to travel almost continuously at night as well as day.

The reasons for this long migration become apparent when the food habits of the gray whale are considered. In summer, the species requires areas of shallow water with an abundant benthos. In the North Pacific, large areas with such conditions are found only in parts of the Bering Sea and adjacent waters of the Arctic Ocean, and in the northern Okhotsk Sea. For almost half the year, the ice cover on these summer grounds cuts off the whales' major food supply and forces them to migrate.

Because they cannot feed much during the winter, it is necessary that they seek warmer waters to minimize energy requirements, particularly for the newborn calves. During the winter, the eastern North Pacific from California north is cold (less than 15° centigrade) and is subject to frequent storms with northwest winds that cause

heavy surf along the coast. The lagoons of Baja California are the nearest areas of warm, shallow, protected waters suitable for calving.

Females ready to bear a calf arrive on the winter grounds earlier and spend more time there than females that have recently mated. Apparently, calves must remain in warm protected waters until they have grown sufficiently to face the rigors of the long northward migration. The movements of females with calves after they leave the breeding lagoons are unknown. Unlike the other members of the population, they must travel farther offshore.

Pregnant females apparently are the first to arrive on the summer feeding grounds and spend more time there than lactating females. This is also true of fin whales, *Balaenoptera physalus* (Mackintosh, 1965), and humpback whales, *Megaptera novaeangliae* (Dawbin, 1966), and is no doubt related to the need of pregnant females to acquire more fat reserves (see discussion beyond of seasonal changes in nutritive condition).

FOOD AND FEEDING

Stomach Contents

SUMMER.—Few data are available on the stomach contents of gray whales killed on the summer grounds. Zenkovich (1934a, 1934b, 1937c) and Tomilin (1937) examined 104 and 54 stomachs, respectively, of whales taken in the Bering and Chukchi Seas from August to October. They did not publish quantitative data, but reported finding mostly gammaridean amphipods, of which were listed the following forms: Family Ampeliscidae—*Ampelisca macrocephala*; family Aoridae—*Lembos arcticus*; family Lysianassidae—*Anonyx nugax* and an unidentified species; family Haustoriidae—*Pontoporeia femorata*; family Eusiridae—*Eusirus* sp.; family Atylidae—*Atylus* sp.; family Gammaridae—unidentified species.

Ampelisca macrocephala predominated in the stomachs of whales killed in the Chukchi Sea and northern Bering Sea, whereas a species of Atylidae, apparently *Atylus carinatus*, predominated in those from along the coast between Natal'inskiy Bay and Cape Navarin. In addition to amphipods, several stomachs contained a few bottom-dwelling isopods, mysids (*Mysis oculata*), mollusks (*Buccinum* sp.), polychaetes (*Travisia forbesi*), and hydroids (Sertulariidae).

Pike (1962a) examined samples of the stomach contents of two gray whales killed by Eskimos off St. Lawrence Island in May and June. He found mostly the amphipods *Ampelisca macrocephala* and *A. eschrichti*, and a few *Anonyx nugax*; other items recorded were decapod crustaceans (including *Chionoecetes bairdi*, *Hyas coarcticus*, and *Liocyma fluctuosa*), cumaceans, polychaete (*Pectinaria* sp.) tubes, gastropods, and ascidians.

We examined a sample (collected by F. H. Fay) of the stomach contents of an immature female gray whale killed by Eskimos about 9 kilometers southwest of the village of Gambell, St. Lawrence Island, Alaska, in water about 30 meters deep. The sample of about 1 liter was a composite of random samples from several parts of the total contents of the stomach. More than 95 per cent of the sample consisted of gammaridean amphipods, ranging from less

than 6 to more than 25 millimeters in length. A few other invertebrates were present. Following is a complete list of the species identified. Classification of amphipods at the level of family and genus follows Barnard (1969). The numbers of each species of amphipod identified are given in parentheses, but they do not necessarily represent the proportion of each species in the total sample.

CLASS CRUSTACEA

Order AMPHIPODA

Family Lysianassidae

Anonyx sp. (16)*Hippomedon* ?*minusculus* (1)*Hippomedon* cf. *abyssi* (4)*Orchomene minuta* (12)

Family Phoxocephalidae

Paraphoxus ?*milleri* (3)

Family Ampeliscidae

Ampelisca macrocephala (ca. 85)*Ampelisca* sp. (fragments)

Family Pleustidae

Pleustes sp. (2)

Family Oedicerotidae

Acanthostpheia malmgreni (6)

Family Atylidae

Atylus bruggeni (1)

Family Isaeidae

Protomedeia grandimana (1)

Family Ischyroceridae

Ischyrocerus latipes (1)

Family Podoceridae

Dulichia cf. *knipowitschi* (1)

Order CUMACEA

Diastylis bidentata

CLASS POLYCHAETA

Unidentified tube

CLASS HOLOTHUROIDEA

Unidentified holothurian

CLASS TUNICATA

Order ASCIDIACEA

? *Phallusia* sp.

Order THALIACEA

? Salps (attached to polychaete tube)

All of the organisms found in the stomachs of gray whales killed on the Arctic summer grounds are typically infaunal benthic species, that is, they burrow or live buried in the bottom sediments. *Ampelisca macrocephala*, the species most commonly eaten, is a large amphipod about 25 millimeters long. A study of its life history has been published by Kanneworff (1965). In the Bering and Chukchi Seas, *A. macrocephala* occurs mainly on sandy bottoms at depths of 5 to 300 meters (Gur'yanova, 1955).

Most of the amphipods in our sample were adult females, which are rarely found above the substratum during the day, although they form an appreciable part of the planktonic population at night; males alone tend to be pelagic during the day (E. L. Bousfield, personal communication).

In addition to food items, there was a considerable amount of fine gray sand or silt mixed with the stomach contents of the whale from St. Lawrence Island that we examined. Such extraneous material has also been recorded by other authors. Pike (1962a) found sand, silt, and bits of wood in the two samples he examined, and Zenkovich (1937a) found quantities of pebbles, as much as "2-3 pails," in many stomachs. Tomilin (1937) also reported finding silt, pebbles, and a large cobblestone, in addition to kelp leaves.

In northern California, Howell and Huey (1930) found a quantity of *Euphausia pacifica* in the baleen of a gray whale killed on 21 July 1926; they did not examine the stomach. This euphausiid is the chief food of rorquals in the waters off California.

The occasional infestation of gray whales with parasites that probably require fishes as intermediate hosts (see discussion of parasites in a later chapter) suggests that they sometimes eat fish.

DURING MIGRATION.—Our data confirm the reports by other authors (Andrews, 1914; Pike, 1962a; Scammon, 1874) that the stomachs of migrating gray whales are almost invariably empty. Stomachs of all 180 southbound migrants and those of 134 of the 136 northbound migrants examined contained no traces of food, and the intestines contained only small amounts of a thick greenish fluid, apparently bile and mucosal secretions. One of the two specimens containing food was an anestrus female taken on 20 March 1964. Its stomach contained about 20 liters of the zoea stage larvae of the littoral crab *Pachycheles rudis* (Anomura,

Porcellanidae) and a few brachyuran zoeae, probably of the genus *Fabia* (Brachyura, Pinnotheridae). The other animal was an immature female taken on 11 April 1968. Its stomach contained about 50 liters of the zoea stage larvae of a pinnotherid crab, probably the same species found in the preceding specimen, and a few scattered porcellanid zoeae, which were in too poor condition to identify further.

Migrating whales sometimes have gravel and other miscellaneous items in their stomachs. We found almost a kilogram of gravel in the stomach of one southbound, recently-ovulated female; mixed with the gravel were numerous ascidian tunics, fragments of hydroid stems and polychaete worm tubes, a few gastropod opercula, one pelecypod shell, and two tiny fragments of waterlogged wood. A late pregnant female had several liters of hydroid stems and a few polychaete tubes in her stomach, but no gravel or sand. The stomachs of two immature males collected during the northward migration each contained about 10 kilograms of gravel. The stomach of an early pregnant female contained about 100 kilograms of gravel in which were a few polychaete tubes, hydroid stems, and a small bit of waterlogged wood. A northbound immature female contained about 50 kilograms of sand and silt. The stomachs of several other animals contained traces of sand and gravel. Andrews (1914) found pebbles in the stomachs of two southbound migrants taken off Korea. Gravel and sand are probably ingested accidentally while the whale is feeding.

WINTER.—Scammon (1874) appears to have been the only person to examine the stomachs of animals taken in the calving lagoons. He examined "several" and found no food—only a small quantity of vegetable matter that was no doubt accidentally ingested.

According to Matthews (1932), Norwegian whalers found gray whales feeding on the "red crab," *Pleuroncodes planipes* (Anomura, Galatheidae), at Bahia Magdalena, Baja California, in 1926. He did not indicate whether this was ascertained by actual examination of stomachs. The red crab exists in both a benthic and pelagic phase (Boyd, 1967) and at times is extremely abundant off the western coast of central and southern Baja California. We found red crabs so abundant in Bahia Magdalena on the night of 6 February 1965 that they formed a continuous, tightly packed layer

on the surface, evidently attracted by the lights of our anchored vessel. On 1 March 1967, we passed through many dense shoals of these crabs, each a few meters wide and up to half a kilometer long or longer, just inside the 180-meter isobath about 45 km. SW Punta Abreojos. However, we never saw gray whales that appeared to be feeding on red crabs. *Pleuroncodes* apparently does not occur in Laguna Ojo de Liebre. According to Matthews (1932), Norwegian whalers noticed that the blubber oil obtained from "sei" whales (*Balaenoptera borealis* or *B. edeni*) on the Mexican coast was yellowish; he suggested that this was due to their feeding on *Pleuroncodes*. We have found that the blubber of gray whales is often yellow or orange during both the southward and northward migrations. A similar variation in blubber color was noted by Andrews (1914) in northbound Korean whales and by Zenkovich (1934a) in summer-taken specimens from the Bering Sea.

There is only one report on the stomach contents of gray whales on or near the wintering grounds in the western Pacific (Mizue, 1951). Two individuals killed in the northern waters of the Yellow Sea in May 1922 contained *Nephrops thomsoni*, a small benthic anomuran decapod similar to *Pleuroncodes*. These whales were taken unusually late in the spring and probably somewhat outside the normal range.

Seasonal Changes in Nutritive Condition

During southward migration, gray whales are fat, whereas during northward migration they are much thinner. Quantitative information on nutritive condition is provided by body weight, blubber thickness, and oil yield.

BODY WEIGHT.—We calculated and compared body weights of gray whales on southward and northward migrations, and attempted to estimate metabolic rate to determine if the difference between the two periods is sufficient to account for energy requirements in winter.

Weights and lengths of nine gray whales are given in Table 2. To calculate weights of other whales that could not be weighed, we used the formula $W = aLG^2$, where W = weight in kilograms, L = length in meters, and G = maximum girth in meters. The

FIG. 4. Comparison of calculated weights of immature male gray whales during the southward and northward migrations. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

value of a was derived from the seven gray whales of known weight, length, and girth (Table 2); this ranged from 32 to 44. The limited data suggest that a and body length are not correlated. This lack of correlation is not unexpected, as there is virtually no change

FIG. 5. Comparison of calculated weights of adult male gray whales during the southward and northward migrations. Solid circles and unbroken line represent southbound migrants; open circles and broken line represent northbound migrants.

TABLE 2
WEIGHTS AND MEASUREMENTS OF NINE GRAY WHALES. UNLESS OTHERWISE NOTED SPECIMENS WERE COLLECTED IN PRESENT STUDY.

Sex	Age	Date	Body length (meters)	Girth (meters)	Weight ¹		Value of a^2
					Kilograms	Pounds	
♀	Fetus	20 January 1968	4.75	2.15	(409)	901	41
♀ ²	Immature	10 January 1961	8.53	—	(6,632)	14,620	—
♂	Immature	30 March 1962	9.65	5.00	(8,808)	19,400	36
♂	Immature	28 March 1962	9.90	4.80	(8,876)	19,550	39
♂	Adult	29 March 1962	11.72	6.00	(15,686)	34,550	37
♂	Adult	27 March 1962	12.40	5.50	(16,594)	36,550	44
♀	Adult (pregnant)	23 February 1959	12.70	—	(16,360)	36,000	—
♀ ³	Adult (pregnant)	19 August 1936	13.35	8.48 ⁴	31,466	(69,380)	33
♀	Adult (pregnant)	14 December 1966	13.55	8.80	(33,846)	74,550	32

¹ Converted values in parentheses.

² Data from Gilmore (1961); originally recorded as 28 feet.

³ Data from Zenkovich (1937b).

⁴ Greatest height given as 270 centimeters; girth estimated as $\pi \times 2.70$ meters.

⁵ See text for explanation.

FIG. 6. Comparison of calculated weights of immature female gray whales during the southward and northward migrations. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

FIG. 7. Comparison of calculated weights of recently ovulated female gray whales during the southward migration and early pregnant and anestrous females during the northward migration. Symbols are as follows: solid circles and unbroken line, southbound migrants; open circles and long-dashed line, early pregnant northbound migrants; triangles and short-dashed line, anestrous northbound migrants.

FIG. 8. Comparison of calculated weights of late pregnant female gray whales during the southward migration and postpartum females during the northward migration. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

in body proportions with increasing length. We have used the mean value of 38. Estimates of percentage weight loss are independent of the value of a used.

The calculated weights of all whales (except for seven for which there were no comparable girth measurements) classified according to sex, age, and reproductive status, are plotted against body length in Figs. 4 to 8. Each class of southbound migrants is compared with the corresponding class of northbound migrants. Within each class, weight was closely correlated with length to the third power (in other words, there was no change in relative girth with increase in length), so we calculated mean weight-length curves for each

class with the equation $W = bL^3$. The value of b was calculated from the formula

$$b = \frac{\Sigma(G/L)^2}{N} a.$$

The mean absolute weights of whales of any given length during their southward and northward migrations may thus be compared. Their relative weights are simply a function of G^2 .

The total weight loss of gray whales between the southward and northward migrations varied from 11 to 29 per cent and was correlated with elapsed time (Table 3). Weight loss per day varied from 0.21 to 0.37 per cent. Weight lost by postpartum females is, of course, not entirely attributable to metabolism. The fetus and fetal membranes and fluids probably account for about 2000 kilograms. The nutritive condition and energy requirements of pregnant and postpartum females are discussed beyond.

To determine if the observed weight loss is sufficient to account for energy requirements during the 54 to 85 days elapsing between the southward and northward migrations past San Francisco, it was necessary to estimate the metabolic rate. For simplicity, we have estimated the metabolic rate of a near-average gray whale weighing 20 metric tons on the basis of oxygen consumption and have assumed that the number of kilocalories per day per kilogram of body weight expended is the same for all whales regardless of body length. This assumption is open to question, but more data are required before more refined estimates of metabolic rate can be made.

No data are available on the lung volume of gray whales. As the relative size and shape of the lungs are similar to those of fin whales, we have used Scholander's (1940) measurements of 800, 1500, and 2000 liters for the lung capacity of three fin whales 15.2, 20.7, and 22.0 meters long, respectively, as a basis for estimating a value for the gray whale. His estimates of the body weights of these whales were too high, so we used Ash's (1952) formula to recalculate the weights as 20, 49, and 58 metric tons, respectively. The mean lung capacity in liters is thus equal to 3.5 per cent of the body weight in kilograms. A 20-ton whale would, therefore, have a lung capacity of 20,000 by 0.035, or 700 liters. The volume

TABLE 3
WEIGHT LOSS OF GRAY WHALES BETWEEN SOUTHWARD MIGRATION (SM) AND NORTHWARD MIGRATION (NM).

Age, sex, and reproductive status	Number		Value of b^1 (mean $\pm$ SE)		Total weight loss (per cent)	Mean number of days elapsed	Mean weight loss per day (per cent)
	SM	NM	SM	NM			
Immature (males)	18	25	11.84 $\pm$ 0.26	9.47 $\pm$ 0.23	20.0	67	0.30
Adult (males)	63	54	11.83 $\pm$ 0.17	9.51 $\pm$ 0.11	19.6	62	0.32
Immature (females)	11	23	12.09 $\pm$ 0.57	9.03 $\pm$ 0.29	25.3	69	0.37
Adult (females)							
Recently ovulated (SM); early pregnant (NM)	27	22	12.43 $\pm$ 0.30	11.01 $\pm$ 0.42	11.4	54	0.21
Recently ovulated (SM); anestrous (NM)	27	8	12.43 $\pm$ 0.30	9.44 $\pm$ 0.40	24.1	68	0.35
Late pregnant (SM); postpartum (NM)	54	2	16.80 $\pm$ 0.27	11.95 $\pm$ 1.25	28.9	85	0.34

¹ See text for explanation.

of tidal air may be estimated at 80 per cent, as Irving *et al.* (1941) found in *Tursiops truncatus*, giving an estimate of 560 liters per breath. Oxygen utilization may be estimated at 10 per cent of tidal volume, based on *Tursiops* (Irving *et al.*, 1941), giving an estimate of 56 liters of oxygen per breath. As a gray whale breathes about once a minute, it uses an estimated 80,640 liters of oxygen per day, or 0.17 cubic centimeters per gram per hour. Since 1.99 liters of oxygen are required to oxidize 1 gram of fat (Bishop, 1950), 80,640 liters is sufficient to oxidize 41 kilograms or 0.20 per cent of the animal's body weight per day.

Oxidation of 1 gram of fat produces 9.54 kilocalories (Bishop, 1950), so the whale will produce about 3.8 by 10^5 kilocalories per day or 19 kilocalories per kilogram per day. This estimate of the metabolic rate is lower, on the basis of kilocalories per kilogram of body weight, than that of smaller mammals, but lies above Benedict's (1938) "mouse-to-elephant" curve. His curve gives a value of 70 times $20,000^{0.75}$, or about 1.2 times 10^5 kilocalories per day for a 20-ton animal. It should be noted, however, that our estimate cannot be considered a basal rate, because it is based on the respiration rate of an actively swimming animal. In some other mammals, the energy expended over a 24-hour period ranges between 1.3 and 4.0 times the basal rate, and for animals performing a moderate amount of work the average is approximately three times the basal rate (Brody, 1945). On this basis, the metabolic rates of large whales do not appear to be far above the "mouse-to-elephant" curve (see Kanwisher and Sundnes, 1966).

BLUBBER THICKNESS.—The thickness of the blubber has long been about the only measurement that has been used as an indicator of the nutritive condition of large whales (Slijper, 1954). Blubber thickness of gray whales was not correlated with body length, so we have used absolute measurements in our analysis. All sex and age classes of gray whales showed a slight decrease in blubber thickness between the southward and northward migration (Table 4), but this decrease was not statistically significant ($P > .05$) for any class.

Blubber thickness is less sensitive than girth as an indicator of the nutritive condition of gray whales. The reduction of girth reduces body surface area, and thus tends to make the blubber

TABLE 4

COMPARISONS OF BLUBBER THICKNESS OF GRAY WHALES DURING MIGRATION PERIODS.

Age, sex, and reproductive status	Number	Blubber thickness (cm)	
		Mean $\pm$ SE	Range
Immature males			
Southward	17	12.8 $\pm$ 0.3	10.5-15.0
Northward	25	12.6 $\pm$ 0.3	9.5-16.0
Adult males			
Southward	66	13.5 $\pm$ 0.2	9.5-17.5
Northward	44	12.8 $\pm$ 0.2	10.5-16.0
Immature females			
Southward	11	14.4 $\pm$ 0.4	12.5-16.5
Northward	23	12.8 $\pm$ 0.4	8.0-17.0
Adult females			
Southward (recently ovulated)	27	15.7 $\pm$ 0.4	10.5-20.0
Northward (early pregnant)	22	15.2 $\pm$ 0.4	10.0-18.5
Northward (anestrous)	8	13.3 $\pm$ 1.1	9.5-19.0
Southward (late pregnant)	53	15.7 $\pm$ 0.2	12.5-19.0
Northward (postpartum)	2	14.5	10.0-19.0

thicker. It was apparent to us while examining the viscera of southbound and northbound migrants that weight loss is due more to utilization of body fat than to utilization of blubber.

OIL YIELD.—The oil yield of the carcass is probably the most reliable indicator of nutritive condition, but such data are not available for individual gray whales. The mean estimated body weight and mean yields of oil, meal, and meat from southbound whales were two and one-half to three times those of northbound animals (Table 5). The southbound sample consisted mostly of adult females carrying near-term fetuses; the northbound sample consisted mostly of males, and included many immature animals. The cubic mean length of the southbound whales was 12.62 meters, whereas that of the northbound animals was 11.23 meters. Quantities of each product were also affected by the relative amount of meat salvaged from each carcass. The remainder of each carcass was rendered for oil and meal. The difference between calculated body weight and total weight of oil, meal, and meat may be attributed to water loss during rendering of the oil and drying of the meal. Inasmuch as the samples are heterogeneous as regards

TABLE 5

MEAN WEIGHTS OF OIL, MEAL, AND MEAT PRODUCED FROM GRAY WHALES TAKEN IN SOUTHWARD AND NORTHWARD MIGRATIONS. MEAN CALCULATED BODY WEIGHT OF 26 SOUTHBOUND WHALES WAS 31,662 KILOGRAMS AND THAT OF THE 26 NORTHBOUND WHALES WAS 12,861 KILOGRAMS.

Products	Southward migration		Northward migration	
	Kilograms	Per cent	Kilograms	Per cent
Oil	7,559	39.6	2,496	38.1
Meal	6,834	35.8	2,520	38.5
Meat	4,689	24.6	1,533	23.4
Total	19,082	100.0	6,549	100.0

sex, age, and reproductive status, they are not directly comparable, but they do show the great difference in body weight between southbound and northbound migrants. The ratio of oil to meal also indicates a moderate decrease in relative oil yield between the southward and northward migrations.

Discussion and Conclusions

The predominance of gammaridean amphipods, especially *Ampelisca macrocephala*, among stomach contents indicates that gray whales, unlike other baleen whales, are primarily, if not exclusively, bottom feeders. The poor representation of polychaete worms and mollusks, which are usually dominant in the infauna, suggests that gray whales are selective feeders. Perhaps they stir up the bottom sediments with their snouts, then filter the turbid water immediately above the bottom from which the heavier mollusks have settled out. The worms presumably retreat deep into their tubes and burrows, whereas the amphipods, freely swimming, are trapped in the baleen plates. The occurrence of sand, silt, and gravel in the stomachs provides further evidence that gray whales feed on the bottom. In the Chukchi Sea, several observers (Pike, 1962a; Scammon, 1874; Wilke and Fiscus, 1961) have reported seeing gray whales, presumably feeding, surfacing with muddy snouts. Greater wear of the baleen on the right side suggests that gray whales swim on their right side while feeding (Kasuya and Rice, 1970). Fin whales (Gunther, 1949), Bryde's whales, *Balaenoptera edeni* (Rice, field notes), and humpback whales (Andrews, 1909)

swim on their sides when feeding near the surface. Swimming on their side permits whales to turn more easily in the horizontal plane.

While migrating, gray whales apparently rarely attempt to feed, at least along the southern sector of their migration route. What little evidence is available also indicates that gray whales seldom, if ever, feed while on the winter grounds. A calculated weight loss of 0.21 to 0.37 per cent of body weight per day between the southward and northward migration past San Francisco exceeds the hypothetical value of 0.20 per cent per day based upon their estimated metabolic requirements. Thus, there is no reason to assume that gray whales must feed while on the winter grounds. This conclusion may not apply to females with calves, however, as we have no data for them.

AGE AND GROWTH

Age Determination

No gray whales of known age have been studied. Age must be deduced from indirect evidence and by analogy with other species of baleen whales. Jonsgård (1969) reviewed methods of determining the ages of cetaceans. Three criteria appeared promising for determination of age in gray whales. These are the number of growth layers in the ear plugs, corpora albicantia in the ovaries, and growth zones in the baleen plates.

EAR PLUGS.—In balaenopterid whales, the number of growth layers in the ear plug is generally considered to be the most useful indicator of age (Purves, 1955; Laws and Purves, 1956). Each layer consists of one light and one dark lamina. There has been controversy, however, over the correlation between number of growth layers and absolute age. Data on ear plugs collected from fin whales marked more than 25 years previously, and several independent lines of indirect evidence, support the hypothesis that only about one growth layer is formed each year, at least in sexually mature fin whales (Ohsumi, 1964a). Ichihara (1966) provided evidence suggesting that in immature fin whales the rate of accumulation of ear plug laminae is irregular, varying from one to two annually, with a mean of one and one-half. Roe (1967a, 1967b), however, on the basis of histological examination of the ear plugs of fin whales collected in all months of the year, concluded that one growth layer is produced each year in both immature and adult whales of both sexes. He found that the light laminae are formed in summer and the dark laminae in winter. He also noted that the ear plugs of immature whales usually have minor laminae similar to but much thinner than the normal laminae; their significance is obscure, but he concluded that they should not be included in lamina counts for age determination.

Ear plugs of gray whales (Figs. 9–11) are soft, especially in the smaller animals, and difficult to remove without distortion or breakage. Some of the plugs have a fibrous, columnar, or amorphous

FIG. 9. Ear plugs of immature gray whales bisected longitudinally. A, 9.8-meter male, estimated age one year (attached to the "glove finger" of the tympanic membrane); B, 8.6-meter female, estimated age one year (attached to "glove finger"); C, 10.1-meter male with three growth layers; D, 11.3-meter female with six growth layers. All plugs are to same scale.

structure in which no laminae can be discerned. In the remaining plugs, laminae are vaguely to moderately well defined. Readable ear plugs were obtained from only 100 (60 per cent) of 166 males and 68 (45 per cent) of 150 females. On the better plugs, repeated counts of the laminae were consistent to within plus or minus 10 per cent of the total count. Males more often show regular laminae than do females, presumably because the annual physiological rhythm of females is modified by their longer and more irregular reproductive cycle.

The ear plug laminae are broad and poorly defined in immature whales but narrow and more sharply defined in adults. In many plugs from mature gray whales, the laminae are clear in the basal portion but indistinct or absent in the distal portion. This dif-

FIG. 10. Ear plugs of adult gray whales bisected longitudinally. A, 11.7-meter male with 11 growth layers; B, 11.4-meter female with 14 growth layers; C, 12.8-meter female with 18 growth layers; D, 12.3-meter male with 21 growth layers. All plugs are to same scale.

ference in the two regions suggests that the laminae laid down during immaturity may disappear as the plug grows. Another possible explanation—that some animals do not begin to produce clear laminae until they attain sexual maturity—appears unlikely, because the proportion of readable plugs was higher in immature than in mature whales (65 compared to 59 per cent in males and 56 compared to 42 per cent in females).

We found no ear plugs in several near-term fetuses that we dissected, and found no individuals with only one growth layer in the ear plugs. The smallest animals collected, 8.63 to 10.34 meters long, had two growth layers. We assumed that most of these animals were yearlings, and that the first layer forms during the nursing period and the second in late summer after weaning. As a working hypothesis, we assumed that each subsequent growth layer represented one year of growth in both immature and mature whales

FIG. 11. Ear plugs of adult gray whales. A, 11.7-meter male with 23 growth layers; B, 12.5-meter female with 24 growth layers; C, 12.5-meter male with 40 growth layers; D, 11.7-meter male with amorphous plug showing no growth layers. All plugs are to same scale.

This interpretation is consistent with our estimate of the rate of accumulation of corpora albicantia in the ovaries (see discussion of reproductive cycle beyond). As it appears that two layers are formed the first year, the age of a whale in years should be one less than the number of growth layers in its ear plug. If, as suggested above, the earlier layers disappear in older animals, the count of growth layers provides only a minimum estimate of age.

OVARIES.—As the ovulation rate appears to be regular at about 0.50 per year, and the corpora albicantia remain permanently visible in the ovaries, the number of corpora in the ovaries provides a reliable estimate of the number of years elapsed since a female attained puberty. The mean age at puberty appears to be about 8 years (see below). Therefore, the age of a recently ovulated or early pregnant female is about twice the number of corpora (including

FIG. 12. Body length in relation to number of growth layers in ear plugs of female gray whales (open circles, immature females; solid circles, adult females; line, von Bertalanffy growth curve).

the corpus luteum) in her ovaries plus 6 years, and that of a late pregnant or postpartum female twice the number of corpora plus 7 years.

BALEEN PLATES.—Ruud (1940, 1945) found that the growth of baleen plates of blue (*Balaenoptera musculus*), sei (*B. borealis*), and fin whales is characterized by seasonal changes in thickness and that the pattern of variation in thickness can be used to estimate the age of the whales (see van Utrecht-Cock, 1965). Because of constant wear, there is rarely more than 5 or 6 years of growth present in a baleen plate. Thus this method is useful only for young whales.

Baleen plates of most gray whales show moderately well-defined "steps," or growth zones, each of which presumably represents one year of growth. None of the baleen plates we examined showed more than four growth zones, regardless of the age of the whale as estimated from the ear plugs. The number of growth zones in the baleen plates of most whales was less than the number of growth layers in the ear plug, and in no specimen was it greater. It thus appears that wear on the baleen plates of the gray whale is more rapid than in other baleen whales, probably because of greater abrasion resulting from bottom-feeding habits.

FIG. 13. Body length in relation to number of growth layers in ear plugs of male gray whales (open circles, immature males; solid circles, adult males; line, von Bertalanffy growth curve).

Growth

The external morphology and osteology of the gray whale have been described in detail by Andrews (1914), Zenkovich (1934a), and Tomilin (1957). Further data on growth in length, ontogenetic changes in body proportions, and sexual dimorphism were obtained in this study.

LENGTH.—Body lengths of males and females one year old and older have been plotted against the number of growth layers in the ear plugs in Figs. 12 and 13. Growth curves for each sex were calculated by using the von Bertalanffy equation (von Bertalanffy, 1938; Beverton and Holt, 1957) as follows: $l_t = L_\infty [1 - e^{-K(t-t_0)}]$, where l = body length in meters, L_∞ = asymptotic body length, K = rate at which length approaches the asymptote, and t = time in years. The results are given below (mean and standard deviation).

Females	Males
$L_\infty = 12.97 \pm 0.11$	$L_\infty = 12.43 \pm 0.12$
$K = 0.246 \pm 0.035$	$K = 0.141 \pm 0.021$
$t_0 = -2.842 \pm 0.772$	$t_0 = -8.346 \pm 1.721$

It should be emphasized that because of the small sample sizes and the difficulty of reading ear plugs these curves are not com-

FIG. 14. Body length in relation to number of corpora albicantia and corpora lutea in ovaries of adult female gray whales. Crosses are running means of two; growth curve fitted by eye to mean values.

pletely reliable. The samples of the younger age groups are biased in favor of the larger individuals. Furthermore, possible disappearance of some ear plug laminae in older animals may have resulted in the estimated mean length at any given age being greater than the true mean.

In Fig. 14, the body length of adult females has been plotted against the number of corpora in the ovaries and a curve fitted by eye to the running means of two. This curve is probably a more accurate representation of the growth characteristics of adult females than the von Bertalanffy curve.

From a mean length at birth in January of about 4.9 meters, calves grow to a mean length of about 8.5 meters at weaning in August and to 9.3 meters by the following winter. With this first annual increment of 90 per cent of neonatal size, the females attain 66 per cent of their ultimate body length and the males 72 per cent. The growth rate drops to 7 per cent during the second year and continues to decline in subsequent years, but growth continues until at least about 30 years of age.

TABLE 6

BODY PROPORTIONS (EXPRESSED AS PERCENTAGE OF TOTAL BODY LENGTH) OF NEAR-TERM FETUSES AND POSTNATAL GRAY WHALES. SEE TEXT FOR DESCRIPTION OF MEASUREMENTS.

Measurement	Females				Males			
	Fetuses		Postnatals		Fetuses		Postnatals	
	N	Mean $\pm$ SD	N	Mean $\pm$ SD	N	Mean $\pm$ SD	N	Mean $\pm$ SD
Head length	17	22.4 $\pm$ 1.1	136	23.2 $\pm$ 1.0	25	22.5 $\pm$ 1.3	155	23.3 $\pm$ 0.9
Tail length	25	28.4 $\pm$ 2.4	147	30.3 $\pm$ 1.6	30	28.2 $\pm$ 2.6	167	29.7 $\pm$ 1.3
Fluke span	25	22.8 $\pm$ 1.8	120	24.3 $\pm$ 1.8	30	22.6 $\pm$ 1.8	138	24.9 $\pm$ 1.6
Fluke breadth	25	7.6 $\pm$ 0.6	141	7.3 $\pm$ 0.5	30	7.3 $\pm$ 0.6	152	7.3 $\pm$ 0.6
Flipper length	25	19.6 $\pm$ 1.0	147	17.3 $\pm$ 1.1	29	19.9 $\pm$ 0.8	166	17.8 $\pm$ 1.2
Flipper width	25	6.8 $\pm$ 0.5	144	6.5 $\pm$ 0.5	29	7.0 $\pm$ 0.4	166	6.7 $\pm$ 0.6

PROPORTIONS.—We have analyzed the following six body measurements to determine if body proportions change with age: (1) head length, (2) tail length, (3) span of flukes, (4) breadth of flukes, (5) length of flippers, and (6) width of flippers.

A comparison of these measurements (expressed as a percentage of body length) of near-term fetuses with those of postnatal whales (Table 6) shows that mean tail length increases from 28.2 to 29.7 per cent in males ($P < .05$) and from 28.4 to 30.3 per cent in females ($P < .001$). Relative flipper length decreases from 19.9 to 17.8 per cent ($P < .001$) in males and from 19.6 to 17.3 per cent ($P < .001$) in females. Fluke span increases from 22.6 to 24.9 per cent ($P < .005$) in males and from 22.8 to 24.3 per cent ($P < .01$) in females. Examination of near-term fetuses suggests that the apparent increase in relative fluke span does not represent differential growth, but instead is simply the result of postnatal abduction of the flukes in the horizontal plane from the adducted and folded position *in utero*. There are no significant age differences in relative head length, fluke breadth, or flipper width.

The magnitude of changes in body proportions of gray whales from one year of age to physical maturity also was examined. All postnatal animals of each sex were grouped into one-meter length classes. The mean and standard deviation of each measurement for each length class were calculated and the mean expressed as a percentage of total body length (Table 7). Only specimens for which

all six measurements were available were included. For each series of measurements, we calculated the allometric equation $Y = bX^d$, where X = body length and Y = measurement being compared with X . The constant of allometry, d , does not differ significantly ($P > .05$) from unity for any of the series of measurements for either sex, indicating that body proportions change little after one year of age.

SEXUAL DIMORPHISM.—There was no significant difference between the sexes in body length of near-term fetuses. As noted above, females grow more rapidly after birth and average larger than males at any given age, as is true for all other species of baleen whales.

The data in Tables 6 and 7 reveal small but statistically significant postnatal differences between the sexes in some body proportions. Thus, males have longer flippers ($P < .01$) and shorter tails ($P < .01$) than females. There is no sexual dimorphism in number of throat grooves, baleen plates, or crenulations on the dorsal ridge of the caudal peduncle.

Puberty and Sexual Maturity

As ordinarily used by cetologists, puberty refers to the age at which gametes are first produced, and sexual maturity is the age at which the animal reaches its full reproductive power. For purposes of this study, any animal that had attained puberty is referred to as an adult.

Puberty in the female is indicated by the presence of a corpus luteum or at least one corpus albicans in the ovaries. Females are considered to be sexually mature at the onset of the first pregnancy. Evidence of sexual maturity thus is pregnancy, lactation, or the presence of mature but involuted mammary glands and a parous type uterus. In the female gray whale, attainment of puberty and sexual maturity usually coincide, but in five of 15 nulliparous and primiparous females, the presence of a corpus albicans (in one case, three corpora), in addition to a corpus luteum or recently ovulated follicle, indicated that they had attained puberty but had not conceived at least a year before their most recent estrous cycle.

Males are considered to be sexually mature when first capable of successfully impregnating females. It is impossible to make a distinction between puberty and sexual maturity in the male on

TABLE 7
MEASUREMENTS (IN METERS) AND RELATIVE SIZE (AS PERCENTAGE OF BODY LENGTH) OF VARIOUS BODY PARTS OF GRAY WHALES.

Class range of body length	N	Head length		Tail length		Fluke span		Fluke breadth		Flipper length		Flipper width			
		Mean body length	Per cent	Mean $\pm$ SD	Per cent	Mean $\pm$ SD	Per cent	Mean $\pm$ SD	Per cent	Mean $\pm$ SD	Per cent	Mean $\pm$ SD	Per cent		
Females															
Near-term fetuses	17	4.69		1.05 $\pm$ 0.09	22	1.33 $\pm$ 0.14	28	1.08 $\pm$ 0.12	23	0.36 $\pm$ 0.04	7.7	0.92 $\pm$ 0.08	20	0.32 $\pm$ 0.03	6.8
8.01-9.00	3	8.69		1.92 $\pm$ 0.03	22	2.77 $\pm$ 0.02	32	2.12 $\pm$ 0.11	24	0.65 $\pm$ 0.02	7.5	1.46 $\pm$ 0.07	17	0.54 $\pm$ 0.03	6.2
9.01-10.00	5	9.58		2.21 $\pm$ 0.13	23	3.05 $\pm$ 0.15	32	2.38 $\pm$ 0.16	25	0.70 $\pm$ 0.06	7.3	1.67 $\pm$ 0.13	17	0.63 $\pm$ 0.03	6.6
10.01-11.00	8	10.49		2.43 $\pm$ 0.19	23	3.26 $\pm$ 0.15	31	2.46 $\pm$ 0.27	23	0.76 $\pm$ 0.06	7.2	1.80 $\pm$ 0.19	17	0.68 $\pm$ 0.04	6.5
11.01-12.00	23	11.68		2.75 $\pm$ 0.10	24	3.64 $\pm$ 0.10	31	2.90 $\pm$ 0.13	25	0.88 $\pm$ 0.04	7.5	1.99 $\pm$ 0.11	17	0.76 $\pm$ 0.05	6.5
12.01-13.00	42	12.52		2.90 $\pm$ 0.10	23	3.78 $\pm$ 0.23	30	3.07 $\pm$ 0.22	25	0.91 $\pm$ 0.05	7.3	2.16 $\pm$ 0.14	17	0.81 $\pm$ 0.04	6.5
13.01-14.00	22	13.33		3.05 $\pm$ 0.11	23	3.96 $\pm$ 0.15	30	3.16 $\pm$ 0.24	24	0.93 $\pm$ 0.06	7.0	2.35 $\pm$ 0.23	18	0.87 $\pm$ 0.05	6.5
14.01-15.00	1	14.20		3.20	23	4.20	30	3.24	23	0.95	6.7	2.60	18	0.94	6.6
Males															
Near-term fetuses	24	4.56		1.02 $\pm$ 0.07	22	1.29 $\pm$ 0.13	28	1.02 $\pm$ 0.11	22	0.34 $\pm$ 0.03	7.5	0.92 $\pm$ 0.07	20	0.32 $\pm$ 0.02	7.0
9.01-10.00	9	9.81		2.26 $\pm$ 0.08	23	3.06 $\pm$ 0.12	31	2.48 $\pm$ 0.10	25	0.71 $\pm$ 0.05	7.2	1.71 $\pm$ 0.10	17	0.65 $\pm$ 0.03	6.6
10.01-11.00	27	10.62		2.51 $\pm$ 0.13	24	3.20 $\pm$ 0.19	30	2.68 $\pm$ 0.21	25	0.76 $\pm$ 0.04	7.2	1.91 $\pm$ 0.13	18	0.71 $\pm$ 0.05	6.7
11.01-12.00	56	11.62		2.73 $\pm$ 0.12	23	3.42 $\pm$ 0.15	29	2.87 $\pm$ 0.22	25	0.84 $\pm$ 0.06	7.2	2.05 $\pm$ 0.16	18	0.77 $\pm$ 0.05	6.6
12.01-13.00	33	12.36		2.23 $\pm$ 0.09	23	3.66 $\pm$ 0.14	30	3.05 $\pm$ 0.16	25	0.89 $\pm$ 0.03	7.2	2.18 $\pm$ 0.15	18	0.84 $\pm$ 0.04	6.8
13.01-14.00	3	13.21		2.90 $\pm$ 0.21	22	3.91 $\pm$ 0.07	30	3.27 $\pm$ 0.13	25	0.91 $\pm$ 0.05	6.9	2.33 $\pm$ 0.10	18	0.86 $\pm$ 0.04	6.6

FIG. 15. Percentage of adult gray whales according to body length (grouped by 0.3-meter length classes). Open circles and broken lines represent males; solid circles and unbroken lines represent females.

the basis of our data. We determined the attainment of puberty by histological examination of the testes and regarded as adult all males whose testes showed evidence of spermatogenesis.

Fig. 15 shows that 50 per cent of the females have attained puberty by the time they reach a length of about 11.7 meters. The two smallest females that had reached puberty were 10.92 meters and 11.20 meters long; both were nulliparous and had recently ovulated for the first time. The smallest parous female was 11.24 meters long, whereas the largest immature female was 12.92 meters in length.

Fifty per cent of the males had attained puberty at a length of 11.1 meters (Fig. 15). The smallest male showing spermatogenic activity was 10.56 meters long, and the largest immature male was 11.75 meters long.

The age at puberty was estimated by plotting the percentage of animals that had attained puberty against the number of growth layers in the ear plug (Fig. 16). The mean number of growth layers at puberty was nine, giving an estimated age of 8 years. In both males and females, the fewest growth layers found in the ear plug

FIG. 16. Percentage of adult gray whales in relation to number of growth layers in ear plugs. Open circles represent males and solid circles represent females; line connects running means of three for both sexes combined.

of an adult animal was six, whereas the highest number in an immature animal was 11 (excepting one female with 13). On this basis, age at puberty is estimated to range from 5 to at least 11 years. Because of the difficulty of counting growth layers in ear plugs of immature animals, these figures may not be entirely reliable.

Physical Maturity

We collected few physically mature animals, as determined by the complete fusion of the vertebral epiphyses with the centra. Only two of the females examined fell in this class. They were 13.98 and 14.20 meters long. The smaller had 35 corpora in the ovaries and about 41 growth layers in the ear plugs, whereas the larger had 22 corpora and 43 laminae in the ear plugs. Physically immature females had 20 or fewer corpora and as many as 40 growth layers. Except for one individual with unreadable ear plugs that was 14.05 meters long, physically immature females were 13.75 meters or less in length.

Five males were regarded as physically mature. They ranged from 12.75 to 13.30 meters in length. The smallest had only 21 growth layers in the ear plug, whereas the others had 38 to 70 (the plugs of one were unreadable). Physically immature males did not exceed a length of 12.80 meters, except for one with 23 growth layers that was 13.23 meters long.

The largest reliably measured gray whales on record are males 14.3 meters long and a female 15.0 meters in length (Zenkovich, 1937a).

Discussion and Conclusions

Growth layers in the ear plugs have limited use for age determination in the gray whale because of uncertainty in counting them and because not all individuals have readable plugs. They provide a minimum estimate of age because laminae produced early in life may disappear in older whales. The number of corpora in the ovaries appears to be a more reliable method for age determination in adult females. Growth zones in the baleen plates are of little use for age determination because of the rapid wear of the plates.

Gray whales grow rapidly during their first year. Rapid initial growth is essential in large aquatic mammals that depend primarily on size for thermoregulation and protection from predators.

Between late fetal life and one year of age, relative length of the flipper decreases slightly and relative length of the tail increases slightly. There are no appreciable changes in body proportions from one year to physical maturity. The latter conclusion is contrary to the findings for blue whales and fin whales (Mackintosh and Wheeler, 1929; Ohsumi, 1960), sei whales (Matthews, 1938), humpback whales (Matthews, 1937), right whales, *Balaena glacialis* (Omura *et al.*, 1969), and bowhead whales, *Balaena mysticetus* (Eschricht and Reinhardt, 1866). In most of these species, as body length increases the head becomes relatively longer, the tail relatively shorter, and the flippers and flukes relatively shorter and narrower.

Sexual maturity is attained in both sexes at a mean age of 8 years (range, 5 to 11), at a mean length of 11.1 meters in males and 11.7 meters in females. This estimate of age at sexual maturity is

in general agreement with estimates for fin whales (Nishiwaki *et al.*, 1958) and humpback whales (Chittleborough, 1959) that were based on counts of growth layers in the ear plugs. Physical maturity is attained at a mean length of about 13.0 meters in males and 14.1 meters in females, at a mean age of about 40 years. As in other baleen whales, females are larger than males. Sexual dimorphism in body proportions is slight, but males have slightly larger flippers and shorter tails than females.

FEMALE REPRODUCTIVE CYCLE

REPRODUCTION in cetaceans has been reviewed by Harrison (1969), Rice (1967), and Slijper (1956, 1963). Our collection of 116 adult females included animals in four stages of the reproductive cycle (sample sizes in parentheses): southbound females that had recently ovulated (28); northbound females in early pregnancy (22); southbound females in late pregnancy (56, including one recently aborted individual); and northbound postpartum females (two, neither of which was lactating, apparently having lost their calves). In addition, eight northbound metestrous and anestrous females, which had failed to conceive, were included in the sample. Some anestrous females would also be expected on the southward migration, but none was collected in this study.

Where appropriate, the data on the 15 females undergoing their first reproductive cycle were analyzed separately from the data on the 101 females that had previously experienced one or more cycles. We defined a female as *nulliparous* if she has never given birth (or aborted) and was not visibly pregnant (although she may contain a macroscopically undetectable conceptus), as *primiparous* if she was in her first pregnancy or had given birth (or aborted) only once, and as *multiparous* if she had given birth (or aborted) at least twice or had given birth (or aborted) only once and was currently pregnant; *parous* refers to any female that had conceived at least once (North Pacific Fur Seal Commission, 1963). Nulliparous females and primiparous females in early pregnancy were recognized by the condition of the mammary glands and uterus as described below. Females in late pregnancy and postpartum females with a single corpus luteum and no corpora albicantia were obviously primiparous, and those with at least one corpus albicans in addition to the corpus luteum were regarded as multiparous.

Ovarian Cycle

The ovaries of the gray whale are morphologically similar to those of the fin whale (Laws, 1961; Mackintosh and Wheeler, 1929; Ommanney, 1932), and the humpback whale (Dempsey and Wislocki,

FIG. 17. Ovaries of gray whales showing various stages of ovarian cycle. A, 8.6-meter immature female with no large Graafian follicles; B, 11.2-meter immature female with enlarged Graafian follicles; C, southbound female with recently ruptured Graafian follicle in right ovary and corpus luteum of ovulation in left ovary; D, southbound, recently ovulated female with developing corpus luteum in left ovary. All ovaries are to same scale.

1941). They are elongate, flattened, and oval, with the anterior end slightly larger than the posterior end. Some are exceptionally long and narrow, being almost strap-shaped. The larger Graafian follicles and corpora albicantia protrude from the surface. Ovaries

FIG. 18. Transverse sections of ovaries shown in Fig. 17. Sections shown in C and D transect the most recent corpora. All sections are to same scale.

representative of various stages of the reproductive cycle are shown in Figs. 17 to 20.

OVARY WEIGHTS.—There is no marked or consistent difference in weight between left and right ovaries. The mean weight of both ovaries of sexually immature females is plotted against body length in Fig. 21. In the smaller individuals, ovary weights range from 70 to 250 grams, with a mean of 136. At a body length of 11.2 to 11.4 meters, corresponding to an estimated age of about 5 years,

FIG. 19. Ovaries of gray whales showing various stages of the ovarian cycle. A, northbound, early pregnant female (90-millimeter fetus) with corpus luteum in left ovary; B, southbound late pregnant female (4.86-meter fetus) with corpus luteum in right ovary; C, northbound postpartum female (that had lost her calf) with regressing corpus luteum in left ovary; D, northbound anestrous female with large corpus albicans derived from the most recent corpus luteum in right ovary. All ovaries are to same scale.

ovarian weight increases abruptly to 250 to 550 grams (mean, 312), approximating that of younger sexually mature females.

The weight of the ovaries of sexually mature females is greatly increased when a corpus luteum is present. As most mature females

FIG. 20. Transverse sections through the most recent corpus in each pair of ovaries shown in Fig. 19. All sections are to same scale.

FIG. 21. Ovary weights of immature female gray whales plotted against body length. Line connects mean weights at one-meter length intervals.

FIG. 22. Ovary weights of adult female gray whales plotted against number of corpora in ovaries.

FIG. 23. Diameter of largest Graafian follicle versus body length of immature female gray whales. Solid circles indicate southbound migrants; open circles indicate northbound migrants.

had a corpus luteum in one ovary, we have used only the weight of the other ovary in making comparisons. For females without a corpus luteum, we have used the mean weight of the two ovaries. In Fig. 22, these weights are plotted against the number of corpora in both ovaries.

The weights of mature ovaries without a corpus luteum vary from 170 to 1270 grams. The regression of ovary weight on number of corpora is $Y = 316 + 15X$, where Y = ovary weight in grams and X = number of corpora. As the slope of this line differs significantly from zero ($P < .001$), ovarian weight apparently increases with age from a mean of 331 grams at puberty to 646 grams at an age of 50 years.

FOLLICLES.—None of the follicles in the ovaries of immature females up to 9.6 meters long exceeded 7 millimeters in diameter; in all immature females longer than 10.2 meters, the largest follicle

FIG. 24. Frequency distribution of diameter of largest Graafian follicle in ovaries of adult female gray whales in different phases of the reproductive cycle (N, northbound migrants; S, southbound migrants).

in either ovary exceeded 14 millimeters (Fig. 23). In the latter animals the largest follicles ranged from 18 to 34 millimeters (mean, 27) in southbound animals and from 14 to 28 millimeters (mean, 21) in northbound animals. These data suggest that females first begin to undergo a seasonal cycle of follicle-stimulating hormone secretion when they reach a length of between 9.6 and 10.2 meters at an estimated age of 2 or 3 years. Laws (1961) found a seasonal follicular cycle in immature fin whales. It should be noted that the follicles in these older immature females are significantly larger than those of late pregnant or postpartum females and slightly larger than those of northbound anestrus females. It is probable that the southbound immature females with follicles about 30 millimeters in diameter or larger (see below) are destined to ovulate for the first time later in the same season.

The size of the largest follicle in either ovary of adult females differs markedly in various phases of the reproductive cycle (Fig. 24). All southbound females not carrying near-term fetuses had recently ovulated. The largest follicle in these specimens ranged

from 18 to 40 millimeters (mean, 28) in diameter (except for one nulliparous animal in which maximum follicle diameter was only 6 millimeters). Assuming that the largest follicle had ovulated, the biggest remaining follicle in these females would have been the second largest follicle just before ovulation. It thus appears that in gray whales the follicle exceeds 30 millimeters and may reach 40 before rupturing. Chittleborough (1954) found that the follicles of humpback whales exceed 30 millimeters before ovulation.

In the northbound early-pregnant females, the diameter of the largest follicles average less than two months earlier, ranging from 16 to 33 millimeters, with a mean of 22.

In strong contrast to females that had recently ovulated, southbound pregnant females carrying near-term fetuses had no greatly enlarged follicles. The largest follicle varied from 3 to 16 millimeters, with a mean of only 6. A female taken on 8 January that had apparently aborted recently likewise had no follicles larger than 6 millimeters. Such follicles are significantly smaller than those of anestrus females. The small size of follicles in late-pregnant females suggests that the progesterone secreted by the corpus luteum suppresses follicular maturation. Chittleborough (1954) found that the follicles of humpback whales in late pregnancy were smaller than those in anestrus animals. No such marked reduction has been found in blue whales and fin whales examined mostly during midpregnancy (Laws, 1961; Mackintosh and Wheeler, 1929; Nishiwaki and Oye, 1951).

In the two northbound females examined that were nonlactating and postpartum, the largest follicles were 24 and 29 millimeters in diameter. Their size suggests a resumption of follicular maturation after regression of the corpus luteum.

Northbound females that were neither pregnant nor postpartum had follicles ranging from 1 to 37 millimeters (mean, 18) in diameter. In three of these females that had recently ovulated, the largest follicles ranged from 14 to 37 millimeters, with a mean of 24. These approximate maximum follicle sizes of southbound females that had recently ovulated and were presumably pregnant. These three females probably should be regarded as being in metestrus. Five anestrus females that had not ovulated recently had follicles with maximum diameters of 1 to 25 millimeters, with a mean of 14.

This size range is probably closest to that of follicles of fully anestrus females.

Nine pairs of ovaries contained one to several thin-walled, fluid-filled cysts up to about 8 centimeters in diameter. Presumably, these are cystic follicles.

FREQUENCY OF OVULATION.—Nonpregnant adult females regularly ovulate in late November and early December (see discussion of gestation period and fetal growth beyond), while still north of central California on the southward migration. All of the adult females collected in southward migration that were not carrying near-term fetuses had recently ovulated, as revealed by the presence of recently ruptured follicles or developing corpora lutea. The mean number of recent ovulations in these females was 1.14 for nulliparous animals and 1.10 for parous animals (Table 8). It is possible that some of these whales would have ovulated again later if their most recent ovulation did not result in conception.

The mean number of recent ovulations in northbound females (excluding postpartum animals) was 1.33 in the nulliparous and the primiparous pregnant females and 0.85 in the parous nonpregnant and the multiparous pregnant females. The diameter of the largest corpus albicans in the ovaries of each metestrous and anestrus female suggests, however, that some of these may have been fairly recently formed corpora whose recent origin was no longer apparent. These corpora ranged from 24 to 39 millimeters in diameter, with a mean and standard error of 32.3 ± 3.0 , whereas the largest corpus albicans in each early pregnant female ranged from 18 to 42 millimeters, with a mean and standard error of 27.4 ± 1.6 . The latter presumably were the corpora lutea of the previous pregnancy that had regressed after the end of lactation several months earlier.

The mean ovulation rate estimated for females during their regular biennial breeding season was 1.20 for nulliparous females, 0.96 for parous females, and 1.00 for all females (Table 8). For reasons stated above, these estimates may be slightly low.

Each of two females taken on 16 and 18 January had both recently ruptured follicles and a corpus luteum of ovulation. This observation suggests that about 40 days intervene between successive ovulations during one breeding season.

TABLE 8
NUMBER OF RECENT OVULATIONS IN ADULT FEMALE GRAY WHALES, EXCLUDING
LATE PREGNANT AND POSTPARTUM FEMALES.

Direction of migration and reproductive status	Number of whales	Number of recent ovulations ¹				Total recent ovula- tions	Ovula- tion rate
		0	1	2	3		
<i>Southbound</i>							
Nulliparous	7	0	6	1	0	8	1.14
Parous	21	0	20	0	1	23	1.10
Total	28	0	26	1	1	31	1.11
<i>Northbound</i>							
Nulliparous or primiparous							
Nonpregnant	1	0	0	1	0	2	2.00
Pregnant	2	0	2	0	0	2	1.00
Subtotal	3	0	2	1	0	4	1.33
Parous or multiparous							
Nonpregnant	7	5	2	0	0	2	0.29
Pregnant	20	0	19	1	0	21	1.05
Subtotal	27	5	21	1	0	23	0.85
Combined northbound sample							
Nonpregnant	8	5	2	1	0	4	0.50
Pregnant	22	0	21	1	0	23	1.05
Total	30	5	23	2	0	27	0.90
<i>All specimens</i>							
Nulliparous or primiparous	10	0	8	2	0	12	1.20
Parous or multiparous	48	5	41	1	1	46	0.96
Grand total	58	5	49	3	1	58	1.00

¹ Figures in body of table indicate the number of whales that had the number of recent ovulations shown at the top of each column.

The only evidence for multiple (simultaneous) ovulation was one female with two recently ruptured follicles of the same size.

The nature of the estrous cycle in baleen whales has been the subject of controversy, because few specimens taken during the breeding season have been available for study, and conclusions have had to be drawn mostly from indirect evidence. Harvey (1963) reviewed the relevant literature and concluded that balaenopterid whales are monestrous. Chittleborough (1965), however, presented direct evidence that female humpback whales, although they usually conceive after ovulating only once, may undergo two or three estrous

cycles if pregnancy does not intervene. Gambell's (1968) data strongly suggest a similar condition in sei whales. Potential polyestry would be of considerable selective advantage in a species that can produce no more than one offspring every 2 years, that does not form permanent pair bonds, and that may be so widely dispersed that a male might not be available when the female first comes into estrus.

As southbound female gray whales carrying near-term fetuses had no enlarged follicles, it may be concluded that there is usually no postpartum estrus in this species. However, postpartum estrus sometimes occurs in other whale species. A postpartum estrus resulting in pregnancy almost invariably occurs in the minke whale, *Balaenoptera acutorostrata* (Jonsgård, 1951; Omura and Sakiura, 1956). Postpartum estrus in a high proportion of Southern Hemisphere humpback whales also is indicated by the fact that eight (44 per cent) of 19 lactating animals examined in one study were simultaneously pregnant (Chittleborough, 1958). Likewise, 15 (12 per cent) of 129 lactating Southern Hemisphere fin whales also were pregnant (Laws, 1961). According to Gambell (1968) an estimated 11 per cent of female Southern Hemisphere sei whales experienced postpartum estrus.

The two nonlactating postpartum females examined had not recently ovulated, but the fact that they had follicles (24 and 29 millimeters) much larger than any late pregnant female and larger than the average for anestrus females indicates a resumption of follicular maturation after the corpus luteum starts to regress and progesterone secretion is reduced. It is possible that such follicles may develop sufficiently to undergo ovulation. Chittleborough (1958) has shown that humpback whales usually recommence estrous cycles immediately after stillbirth or early loss of the calf. Ovulation following stillbirth or loss of a calf would be so infrequent that it would not significantly affect the mean ovulation rate.

The possibility of postlactation ovulation, or ovulation by any nonpregnant females during the summer, remains to be considered. The southbound females that had recently ovulated, most of which presumably had ceased lactating about 5 months previously, gave no evidence of having ovulated more than once since that time.

In each, the largest corpus albicans was 22 to 38 millimeters in diameter (mean, 29); this was no doubt the regressing corpus luteum of lactation. Only data from females collected on the summer grounds can provide direct evidence on this point. There is evidence that a considerable proportion of Southern Hemisphere fin whales experience a postlactation ovulation (Laws, 1961), and about 12.5 per cent of the female Southern Hemisphere sei whales ovulate in the summer (Gambell, 1968). These summer ovulations almost never result in pregnancy. In humpback whales, which lactate for approximately 10½ months, an estrous cycle usually commences immediately following the end of lactation; this cycle corresponds with the normal winter breeding season and usually results in pregnancy (Chittleborough, 1958).

The two oldest females studied, with 19 and 34 corpora albicantia, were pregnant, so there is no indication of cessation of breeding in old females.

In summary, female gray whales normally experience one estrous cycle every 2 years, although rarely they may ovulate twice or perhaps three times during one breeding season. The mean ovulation rate for parous females is 0.96 per breeding season. A female that fails to conceive during one breeding season probably undergoes an estrous cycle again the following year. As the pregnancy rate is 0.46 (see below), the mean ovulation rate per year of parous females is 0.52 ($[1.00 - 0.46] \times 0.96$).

CORPORA LUTEA.—Our material included three ovaries with recently ruptured Graafian follicles that provided data on early development of the corpus luteum. In one case the rupture site was still open (Figs. 17 and 18), and in the other two the rupture sites were still obvious as dark spots, although no actual openings were visible. These follicles, 24, 25, and 25 millimeters in diameter, were smaller than mature unruptured follicles. Loss of fluid presumably causes the follicle to collapse immediately after rupture. There is a marked infolding of the walls and a proliferation of luteal tissue from the membrana granulosa. The luteal tissue fills almost the entire antrum. One corpus contained a small amount of liquor folliculi in the central cavity. Subsequent development of the corpus luteum depends upon whether or not pregnancy ensues.

It is difficult to distinguish corpora lutea of ovulation from corpora lutea of pregnancy, because failure to find a visible conceptus in the uterus is not proof that an animal has not conceived. Only in the four females that had recently undergone more than one estrous cycle was it certain that corpora lutea of ovulation were present (Figs. 17 and 18). In these animals the penultimate corpora were 13, 15, 21, and 25 millimeters in diameter. Because of their small size, they did not greatly protrude from the surface of the ovaries. In cross section, the corpora were somewhat irregular or stellate in outline. The layer of luteal tissue was thin and greatly plicated, and no cavity remained. The luteal tissue was pale yellow, as in corpora lutea of pregnancy, in the larger two of the four corpora and more orange-yellow in the two smaller corpora.

Three northbound females had corpora lutea 22, 81, and 102 millimeters in diameter but showed no macroscopic evidence of pregnancy. The two larger corpora in this series were indistinguishable from corpora lutea of pregnancy.

The above data indicate that corpora lutea of ovulation do not attain a size greater than about 25 millimeters and rapidly regress if the female comes into estrus again after a brief diestrous period. The fate of the corpus luteum when the female does not become pregnant or undergo another estrous cycle requires further study.

Corpora lutea of pregnancy in the gray whale (Figs. 17 and 20) are similar to those of the fin whale (Laws, 1961) and humpback whale (Chittleborough, 1954). They protrude from the body of the ovary, from which they are separated by a constricted neck.

In most of the southbound females that had recently ovulated but were not yet visibly pregnant, the corpora lutea ranged from 37 to 87 millimeters (mean, 56; standard deviation, 16). Females with small fetuses collected two months later during northward migration had corpora lutea ranging from 61 to 100 millimeters in diameter (mean, 82; standard deviation, 11). In these animals, the size of the corpus luteum was correlated with the length of the fetus. The female carrying the smallest fetus (25 millimeters long) had a corpus luteum only 63 millimeters in diameter. In females with fetuses 120 to 140 millimeters in length (estimated age 87 to 89 days), the average diameter of the corpus luteum was 84 millimeters, which is not significantly different from that in late pregnant females.

Chittleborough (1954) has shown that it takes nearly three months for the corpus luteum of the humpback whale to reach maximum size. In southbound female gray whales with near-term fetuses, the corpora lutea varied from 61 to 115 millimeters in diameter (mean, 87; standard deviation, 12). No data were obtained on the condition of the corpora lutea in lactating females.

Twenty-one per cent of the corpora lutea of pregnancy contained central vesicles filled with liquor folliculi. Thus, in this species the presence or absence of a central vesicle is of no use in distinguishing corpora lutea of ovulation from those of pregnancy. Laws (1961) has refuted the contention of some authors (for example, Robins, 1954) that the absence of a central vesicle is diagnostic of corpora lutea of ovulation in balaenopterid whales. The largest vesicle in our animals was 54 millimeters in diameter. A few were irregularly shaped or eccentrically located. Some corpora lutea had gel-filled cavities up to 24 millimeters in diameter located around their periphery or at the base (Fig. 20). Although these structures resemble large, flattened follicles, their close association with the corpus luteum suggests that they are part of it.

Only one whale, a primiparous late pregnant female, had an accessory corpus luteum (in the opposite ovary from the primary corpus luteum). It was 14 millimeters in diameter and lacked a stigma, suggesting that it must have developed from an unruptured follicle.

CORPORA ALBICANTIA.—The corpora albicantia (Fig. 20F) of gray whales are morphologically similar to those of balaenopterid whales, and the sequence of changes during regression is essentially the same as described by Laws (1961) and van Lennep (1950) for the fin whale.

The earliest stages of regression were seen in the two postpartum females that had recently lost their calves (Figs. 19, 20). The corpora lutea in these individuals were 53 and 60 millimeters in diameter. The connective tissue septa characteristic of corpora albicantia were already obvious, and the color of the luteal tissue was more orange than is typical of the corpus luteum of pregnancy.

As the corpus albicans continues to shrink, it recedes below the surface of the ovary. The color changes to brown as collagen

TABLE 9
DIAMETER (mm) OF CORPORA ALBICANTIA IN OVARIES OF GRAY WHALES AT DIFFERENT STAGES OF THE REPRODUCTIVE CYCLE.
SEE TEXT FOR EXPLANATION OF SIZE CLASS.

Size class of corpora albicantia	Recently ovulated			Early pregnant			Late pregnant			Postpartum		
	N	Mean $\pm$ SE	Range	N	Mean $\pm$ SE	Range	N	Mean $\pm$ SE	Range	N	Mean	Range
1	20	20.1 $\pm$ 0.9	22-38	20	27.4 $\pm$ 1.6	18-42	50	24.8 $\pm$ 0.7	17-35	2	26.5	26-27
2	18	22.0 $\pm$ 0.8	14-31	20	21.8 $\pm$ 0.7	17-30	43	20.5 $\pm$ 0.5	14-29	2	24.5	24-25
3	16	19.7 $\pm$ 0.7	14-26	16	20.4 $\pm$ 0.7	17-28	38	19.3 $\pm$ 0.6	12-29	1	23	
4	14	19.4 $\pm$ 0.7	16-26	15	18.4 $\pm$ 0.9	12-23	31	18.7 $\pm$ 0.6	10-28	1	22	
5	12	17.7 $\pm$ 0.9	12-23	11	18.0 $\pm$ 0.9	14-22	27	17.9 $\pm$ 0.5	14-24	1	20	
6	11	16.5 $\pm$ 0.8	12-21	6	17.5 $\pm$ 1.3	13-21	25	16.8 $\pm$ 0.5	12-24	1	18	
7	8	17.1 $\pm$ 0.6	15-20	3	18.0 $\pm$ 1.5	15-20	22	15.6 $\pm$ 0.6	11-23	1	16	
8	6	16.2 $\pm$ 0.5	15-18	3	17.7 $\pm$ 1.9	14-20	19	15.3 $\pm$ 0.7	10-23	1	16	
9	5	15.4 $\pm$ 0.8	13-17	33	17.0 $\pm$ 1.5	14-19	12	15.2 $\pm$ 0.6	13-20	1	15	
10	5	15.0 $\pm$ 0.9	12-17	2	17.5	16-19	9	14.9 $\pm$ 1.0	13-19			
11	4	15.0 $\pm$ 0.6	14-16	2	16.0	13-19	7	14.1 $\pm$ 1.3	8-19			
12	4	14.2 $\pm$ 0.6	13-16	2	15.5	12-19	3	16.0 $\pm$ 1.5	14-19			
13	3	13.7 $\pm$ 0.9	12-15	1	18		3	15.7 $\pm$ 1.7	14-19			
14	2	14.0	13-15	1	18		2	13.5	12-14			
15	1	15		1	18		1	13				
16	1	15		1	18		1	13				
17	1	15		1	18		1	12				
18	1	14		1	18		1	12				
19	1	14		1	18		1	10				
20	1	14		1	18							
21	1	12		1	17							
22-34				1	17-6							

replaces the luteal cells, and the proportion of connective tissue increases. Some of the smaller corpora albicantia consist almost entirely of unpigmented connective tissue.

The corpora albicantia persist throughout life in the ovaries of fin whales (Laws, 1961) and this probably applies to all large balaenopterids. This also occurs in sperm whales (Best, 1967), but not in at least some of the smaller odontocetes, such as the pilot whale, *Globicephala melaena* (Harrison, 1949; Sergeant, 1962).

The corpora persist as permanently recognizable structures in the ovaries of gray whales. The corpora albicantia of each female (excluding nulliparous and primiparous ones) were classified according to relative size in the following manner: class 1, the largest corpus in each whale; class 2, the second largest, and so on. The mean, standard error, and range for each of these classes in females in each phase of the reproductive cycle are presented in Table 9. It is apparent from the size distribution that after an initial phase of rapid regression, there is little further decrease in size of the corpora albicantia. Few were less than 12 millimeters in diameter.

In the discussion of time and frequency of ovulation, it was concluded that females usually ovulate only once every 2 years. If this is true, and the corpora albicantia persist for life, the rate of accumulation of corpora albicantia would be close to 0.5 per year. We examined two other lines of evidence bearing on this question: the size frequency distribution of the corpora albicantia and the correlation between number of corpora albicantia and number of growth layers in the ear plug.

The means, standard errors, and ranges of the diameters of the corpora lutea and two largest corpora albicantia of females in each stage of the reproductive cycle are shown in Fig. 25. We assumed that each female ovulates only once every 2 years, and adjusted the horizontal time scale accordingly. The smooth line shows the presumed rate of regression in size of the corpus albicans during the first 4 years. If the smaller corpora albicantia (Table 9) were similarly plotted, the line would gradually approach the horizontal at about 14 millimeters beyond 20 years. It is apparent from Fig. 25 that a presumed accumulation rate of one corpus albicans every 2 years is consistent with the observed size-frequency distribution of

FIG. 25. Diameter of corpus luteum and two largest corpora albicantia in ovaries of gray whales in different stages of the reproductive cycle. The horizontal scale represents the age of each corpus, assuming one ovulation every two years. RO, recently ovulated females; EP, early pregnant females; LP, late pregnant females; PP, postpartum females. The two postpartum females had lost their calves, thus their corpora lutea were smaller than in lactating animals. Horizontal dashes, mean; vertical bars, two standard errors on either side of mean; vertical lines, range. Curve fitted by eye to mean diameters of corpora.

corpora. If the ovulation rate were significantly greater, the size-frequency data would not show such a regular decline. The data on ovulation further indicate that the rate cannot be less than about 0.5 per year.

The relationship between number of corpora albicantia and the number of growth layers in the ear plug is presented in Fig. 26. The solid line ($Y = 0.5X - 3.5$) represents the expected correlation between number of corpora and number of growth layers under the assumptions that two growth layers are formed the first year

FIG. 26. Number of corpora in the ovaries versus the number of growth layers in the ear plugs of adult female gray whales. The hypothetical correlation is represented by the unbroken line (mean) and the broken lines (range).

and one each year thereafter, and that one corpus is formed every 2 years beginning at 8 years of age (mean age at sexual maturity). The two broken lines ($Y = 0.5X - 2.0$ and $Y = 0.5X - 5.0$) represent the lower and upper limits, respectively, of variation expected because of the variation in the age at sexual maturity of from 5 to 11 years. Deviations from the hypothetical mean number of growth layers are markedly skewed. The mode falls on the lower limit (-3); 41 per cent of the specimens fall within the expected limits (-3 to +3). Only one whale falls above the expected limits (+7); 57 per cent fall below the lower limit (-3 to -37), with 33 per cent falling between -3 and -7. These data are thus consistent with the conclusions that corpora accumulate at a rate of 0.5 per year and growth layers in the ear plug accumulate at a rate of one per year, although the earlier layers may not be discernible.

The only corpora albicantia that are unquestionably derived from corpora lutea of ovulation are those in nulliparous and

primiparous females. These corpora do not differ in size or other respects from those representing corpora lutea of pregnancy. In three recently ovulated nulliparous females, the largest corpora albicantia were 23, 30, and 34 millimeters in diameter, and in two primiparous females in early pregnancy they were 13 and 29 millimeters in diameter. All except the smallest of these were within the size range of the largest corpora albicantia in multiparous females in corresponding phases of the reproductive cycle (Table 9).

In addition to normal corpora albicantia, the ovaries of 13 females each contained one to three small orange bodies 4 to 9 millimeters in diameter and which were either compressed and elongate, or stellate, in cross section. The total number of these structures in the 13 animals was 17, which was 2 per cent of the corpora albicantia present in all the females. They are similar to the corpora atretica described by Laws (1961) for the fin whale and presumably originate by atresia of follicles that have not ovulated. This assumption is supported by the finding of a few unruptured follicles with a partial lining of yellow-orange colored tissue. These corpora apparently do not represent ovulations and they were not included in counts of corpora albicantia.

FUNCTIONAL SYMMETRY AND POLARITY OF OVARIES.—Of the total of 756 corpora, 418 (55.3 per cent) were in the left ovary and 338 (44.7 per cent) in the right ovary. The probability of this ratio occurring in a random distribution is less than .05, suggesting that the observed dominance of the left ovary may be real. Laws (1961) found a slight but statistically insignificant dominance of the right ovary in fin and blue whales. In many odontocetes, most ovulations occur in the left ovary (Ohsumi, 1964b).

The position of each of 179 corpora in the anterior, second, third, or posterior quarter (measured linearly) of 52 mature ovaries was recorded. There was a significant ($P < .005$) preponderance of corpora toward the anterior pole. The numbers of corpora in each quarter, from anterior to posterior, were: 61 (34 per cent), 48 (27 per cent), 45 (25 per cent), and 25 (14 per cent). A preponderance of ovulations from the anterior pole of the ovary was also found in fin and sei whales (Laws, 1957) and in the sperm whale (Best, 1968), but not in the pilot whale (Harrison, 1949; Sergeant, 1962) or false killer whale, *Pseudorca crassidens* (Comrie and Adam, 1938).

Pregnancy

PREGNANCY RATE.—The pregnancy rate is difficult to determine directly because of bias introduced into the sample by the temporal and spatial differences in migration patterns between females in different phases of the reproductive cycle and by gunner selection for the larger animals. In the series of 84 southbound migrants examined, the ratio of late pregnant females to other mature females was two to one, whereas the actual ratio in the population must be less than one to one. The sample of northbound adult females consisted of 22 early pregnant females and eight anestrus females, but only two postpartum females. As it is logical to assume that the number of postpartum females in the spring population should be nearly equal to the number of pregnant females, the sample was obviously biased.

Because the proportion of late pregnant and postpartum females in the samples was biased, these animals were excluded from calculations of the pregnancy rate and appropriate corrections made to determine the overall pregnancy rate in the adult female segment of the population.

The pregnancy rate of females that had already undergone at least one pregnancy will be considered first. During the southward migration, all females that were not carrying near-term fetuses had a developing corpus luteum. If we assume that all of them had conceived, their pregnancy rate would be 1.00. As a few may not have conceived, this figure may be a slight overestimate. During northward migration, 20 of 27 females (exclusive of postpartum females) were pregnant, giving a pregnancy rate of 0.74. Two of the females that were not visibly pregnant each had a corpus luteum that we assumed to be a corpus luteum of ovulation. Although it is possible that they had recently conceived and were carrying a conceptus too small to detect, we think this is unlikely so late in the season. Considering both the northbound and southbound migrants, 41 of the 48 were pregnant or could reasonably be assumed to have already conceived. This gives a pregnancy rate of 0.85 per breeding season.

Considering females that had not undergone a previous pregnancy, all seven taken on the southward migration had recently

ovulated. Each of five animals had a single corpus luteum 19 to 62 millimeters in diameter and were assumed to have already conceived. One with a recently ruptured follicle and a corpus luteum of ovulation (25 millimeters in diameter) possibly had done so. The last had what appeared to be a corpus luteum of ovulation (27 millimeters in diameter) and Graafian follicles up to 35 millimeters in diameter, so it might have ovulated again later and then conceived. Of the three northbound animals examined, two were pregnant. The third had two fairly recent corpora lutea (22 and 13 millimeters in diameter) and was probably not pregnant. Thus, of 10 females that had not previously been pregnant, seven were pregnant, two were not pregnant but probably would have conceived later, and one probably would not have conceived that season. These data indicate a probable pregnancy rate of 0.90 per breeding season, but further data are needed to determine whether newly mature females are as fertile as older individuals.

The combined pregnancy rate for nulliparous and parous females, exclusive of late pregnant and postpartum animals, is 0.86. To determine the overall pregnancy rate for all adult females in the population, we made a correction for the biased representation of late pregnant and postpartum females in the sample. If the pregnancy rate remains constant from year to year, or if the sample was taken over a period of several years, the overall pregnancy rate may be calculated as $0.86/1.86$, or 0.46 per year.

Zenkovich (1937a) examined a large series of gray whales taken in the Bering Sea between August and October from 1933 to 1936. Assuming that all females 12.0 meters or more in length were sexually mature, there were 57 mature females in his sample. Of these, only 16 were pregnant, giving a calculated pregnancy rate of only 0.28. G. C. Pike (unpublished data) reported that only one of three adult females he examined off British Columbia in April was pregnant.

Of the seven northbound adult females (exclusive of postpartum individuals) that were not pregnant, only three had recently ovulated, indicating that missed pregnancies may result from either failure to ovulate or failure to conceive following ovulation.

BREEDING SEASON.—Almost all of the adult females (except those carrying near-term fetuses) taken during southward migration

TABLE 10
BODY LENGTH OF GRAY WHALE EMBRYOS AND EARLY FETUSES (CROWN-RUMP
LENGTH OF EMBRYOS IN PARENTHESES).

Date of collection	Length (mm)	
	Males	Females
21 February	80	90
22 February	120	
23 February	59 (40), 85	
24 February	110	90, 110
26 February		80
28 February	85	90
1 March	75, 120	140
2 March	39 (16)	25 (10), 105
6 March		120, 120
7 March		110
8 March		135
10 March		120

probably had already conceived, although none was visibly pregnant. The mean conception date calculated from the fetal growth curve (see below) is 5 December. We calculated the duration of the breeding season by estimating the ages of the 22 embryos and early fetuses collected. The estimated ages were based on certain assumptions about early fetal growth discussed below. The calculated conception dates fall between 27 November and 13 December, except for one on 22 December and one on 5 January. The female that conceived about 22 December was multiparous and showed evidence of two recent ovulations, indicating that she had failed to conceive following her first ovulation that season. The female that conceived about 5 January was primiparous; Laws (1961) found that newly mature female fin whales conceive, on the average, later than multiparous females.

The duration of the breeding season also was estimated on the basis of length measurements for 16 fetuses collected in late summer by Zenkovich (1937*a*). The estimated conception dates of 12 (75 per cent) of these fetuses fall between 23 November and 14 December, and all fall between 13 November and 10 January. Individual variations in growth rate will give a spurious spread to the calculated range, so that the actual breeding season is doubtless even shorter than these data indicate. For the same reason, the

FIG. 27. Embryos and early fetuses of gray whales. A, 25-millimeter (10 millimeters crown-rump) female embryo, estimated age 55 days; B, 39-millimeter (16 millimeters crown-rump) male embryo, estimated age 70 days (note hind limb buds); C, 120-millimeter male fetus, estimated age 87 days (note size and position of penis); D, 110-millimeter female fetus, estimated age 86 days (note size and position of clitoris).

data from near-term fetuses are even less useful for calculating conception dates.

GESTATION PERIOD AND FETAL GROWTH.—Available measurements of fetuses are limited to the periods of early and late pregnancy.

A total of 22 embryos and early fetuses was collected between 21 February and 10 March (Table 10, Fig. 27). Body length, measured from the crown to the tip of the straightened tail varied between 25 and 140 millimeters (mean, 96; standard error, 6).

Additional data on fetal sizes in the gray whale are contained in a number of reports. Scammon (1874) examined five embryos taken on the California coast, but gave no measurements or dates. Andrews (1914) reported fetuses 180 and 250 millimeters long taken on 13 and 14 March 1912, on the coast of Korea. Pike (unpublished data) found a 250-millimeter fetus the first week of April from the coast of Vancouver Island, British Columbia. Zenkovich (1937a) published data for 16 fetuses collected in the Bering Sea between 8 August and 24 September. Their lengths ranged from 1.70 to 2.64 meters, with a mean and standard error of 2.05 ± 0.06 . Townsend (1887) examined four fetuses taken in December 1885 at San Simeon, California, and stated: "Their average length was about 12 feet [3.66 meters]; the longest . . . 17 feet [5.18 meters] long." Andrews (1914) inconsistently reported one fetus taken at Ulsan, Korea, on 8 January 1912, as 4.35 and 4.76 meters long.

We measured 55 near-term fetuses (30 males, 25 females) collected during a 38-day period from 14 December to 20 January. The length varied between 3.60 and 5.31 meters, with a mean and standard error of 4.62 ± 0.05 (Table 11, Fig. 28). The average length of females (4.65 ± 0.06 meters) was slightly greater than that of males (4.60 ± 0.08), but the difference was not statistically significant ($P > .10$). If these measurements are grouped by shorter time periods, they show no change in mean length from mid-December until late January. This suggests that the timing of migration of a pregnant female depends upon how advanced her pregnancy is.

The statistics for Norwegian factory ship operations near the calving grounds on the west coast of Baja California from 1924 to 1927 (published in part by Risting, 1928) list 20 fetuses taken from 29 December to 16 February with estimated (not actually

TABLE 11
BODY LENGTH OF NEAR-TERM FETUSES OF GRAY WHALES.

Date of collection	Length (meters)	
	Males	Females
14 December	4.86	
15 December		4.58
16 December	4.53, 4.65, 4.67	
18 December		4.50
19 December	4.15	
20 December	4.07, 4.54, 4.84	4.55, 4.78, 5.12
21 December	3.85, 4.62, 4.63	5.08
22 December	4.62, 4.79	
27 December	4.22, 4.89	3.60
28 December	4.52, 4.81	4.32
29 December	4.70	5.12, 5.12
30 December		5.24
2 January	4.72	4.58
3 January	4.77, 5.31	4.42, 4.44, 4.93
4 January		4.54, 4.92
5 January	4.72	4.24
7 January	4.52, 5.24	4.43
8 January		4.11, 4.73
11 January		4.33, 5.11
12 January	4.59	
13 January	4.41, 4.48	
15 January	4.26	
16 January	4.53	
18 January		4.80
19 January	4.39	
20 January		4.75

measured) lengths ranging from 6 to 18 Norwegian feet (1.90 to 4.71 meters).

Measurements of six recently born calves found dead at Laguna Ojo de Liebre, Baja California, in late January and early February, are given by Eberhardt and Norris (1964). These ranged from 3.95 to 5.40 meters (mean, 4.68; standard error, 0.245). Gilmore (1960a) also listed measurements of seven recently born calves found in the same lagoon. The total lengths given for these calves (3.54 to 4.51 meters, mean, 4.05) are well below those presented by Eberhardt and Norris and even average less than our December fetuses. Therefore, we can only conclude that Gilmore made his measurements differently or that the published figures are in error.

FIG. 28. Near-term gray whale fetus 4.54 meters long. Note color pattern of whitish rings and blotches (the other marks are postmortem abrasions).

Only three of the series of measurements presently available are large enough to provide statistically reliable data for use in constructing a fetal growth curve for the gray whale. These include our series of early embryos and fetuses, Zenkovich's series taken in late summer, and our series of near-term fetuses. The means for these three sets of measurements have been plotted in Fig. 29. It is apparent that the points do not fall on a straight line. Laws (1959) found that in balaenopterid whales, excepting the earliest

FIG. 29. Estimated prenatal growth curve based on measurements of 22 embryos and early fetuses collected in February and March, Zenkovich's (1937a) 16 mid-term fetuses collected in August and September, and 55 near-term fetuses collected in December and January. Horizontal dashes indicate means; vertical bars represent two standard errors on either side of mean, and vertical lines represent the range. For estimation of t_0 see text.

part of pregnancy, the length of the fetus increases linearly during the first half of pregnancy and logarithmically during the last half. A similar curve fits the present data (Fig. 29). From the slope of the lower portion of this curve, we estimated the "specific fetal growth velocity," or a of Huggett and Widdas (1951), as 0.95.

To determine the total gestation period, it is necessary to estimate the length of the gestation period before the beginning of the linear growth phase, termed t_0 by Huggett and Widdas (1951). J. G. Sinclair, who is studying the anatomy of two early fetuses (25 and 39 millimeters long from crown to tip of tail, and 10 and 16 millimeters in crown-rump length), has, on the basis of their stage of development, estimated their ages at about 55 and 70 days. According to Sinclair, the rapid linear growth phase starts when ossification begins, at a crown-rump length of about 35 millimeters; this is equivalent to a length of about 55 from crown to tip of tail. Judging from the estimated ages of the two early embryos, this length would be reached at an age of at least 80 days, or perhaps slightly more. An estimate of t_0 will therefore be $80 - (5.5 \times 0.95)$, or about 75 days. The growth curve, extrapolated backwards, intercepts the abscissa on 18 February (Fig. 29). Adding to this the estimate of t_0 , the calculated mean conception date falls on 5 December.

If the growth curve is projected forward, it intercepts the mean length of the six newborn calves observed by Eberhardt and Norris (1964) on 2 January, only 2 days later than the mean date of passage of pregnant females past San Francisco. Considering the speed of migration, it would take the whales at least 9 to 12 days to travel from San Francisco to the major calving grounds at Laguna Ojo de Liebre, Laguna San Ignacio, and Bahia Magdalena. Therefore, the mean birth date would be about 10 January, when the projected growth curve reaches 4.90 meters. This estimate of length at birth falls within one standard error of the mean of newly born calves, so the agreement is close.

Based upon the calculated mean dates of conception and parturition, the mean length of the gestation period is estimated to be slightly more than 13 months, or about 400 days.

Applying Laws (1959) method of estimating t_0 for baleen whales to the data of this study yields values of only 31 days for t_0 and

FIG. 30. Diameter of the uterine cornua of gray whales in different stages of the reproductive cycle. For pregnant and postpartum females, measurements of the horn in which implantation occurred are plotted above the base line and those for the other horn below. Symbols are as follows: horizontal dashes, mean; vertical bars, one standard deviation on either side of the mean; vertical lines, range; S, southbound migrants; N, northbound migrants.

no more than one year for total gestation period, which are not consistent with the actual data. The discrepancy results from the way in which Laws interpreted data for several species of terrestrial mammals given by Huggett and Widdas (1951) in estimating the length of t_0 for three species of odontocetes in which fetal growth is linear until the end of pregnancy. His estimates showed an *inverse* relationship between t_0 and length of gestation period (and also a). Huggett and Widdas' data show, however, that " t_0 increases as gestation times lengthen but forms a decreasing fraction of total gestation time" (*italics added*). There are no data to justify Laws' conclusions; his error appears to be the result of using imprecise, arbitrary percentage values for t_0 . Laws then estimated the length of t_0 in the humpback whale as 38 days on the basis of published fetal length data and Chittleborough's (1954, 1958) data on the mating and calving seasons. Chittleborough's data suggest, however, a peak conception date in late July, not early August as stated by Laws, so Laws' estimate of t_0 is doubtless too short. Since his four estimates of t_0 , for three species of odontocetes and one

mysticete, showed an apparently consistent inverse relationship between t_0 and a , he extrapolated these results to other species of baleen whales. This resulted in his inexplicable and anomalous conclusion that the larger species of balaenopterid whales have shorter gestation periods than the smaller ones. Any logical extrapolation of the data presented by Huggett and Widdas would result in an estimate of at least 50 or 60 days for the duration of t_0 in larger cetaceans. In any event, it is dangerous to extrapolate from small terrestrial mammals to large cetaceans.

We suspect that when more direct evidence is available on early embryonic growth, most large mysticetes will be found to have a gestation period of about a year or somewhat longer. It is certainly approximately 13 months in the gray whale, and probably more than a year in the humpback whale. A gestation period longer than one year would not preclude an occasional pregnancy resulting from a postpartum ovulation, as has been reported in fin whales (Laws, 1961) and humpback whales (Chittleborough, 1958), but it does indicate that such pregnancies cannot occur regularly if a marked seasonality of breeding is to be maintained.

CALVING SEASON.—The mean calving date, as indicated above, is estimated to be about 10 January. The duration of the calving season should be generally similar to that of the breeding season, but slightly more prolonged because of individual variation in the length of the gestation period. As noted above, the timing of the southward migration of pregnant females depends on the stage of gestation. Because late pregnant females pass San Francisco for at least 38 days, we may assume that the calving season lasts about that many days. Therefore, we estimate that calving occupies a period of 5 or 6 weeks from late December to early February. This is corroborated by field observations of recently born calves (Eberhardt and Norris, 1964; Gilmore, 1960*a*, 1960*b*; Gilmore and Ewing, 1954; Hubbs and Hubbs, 1967).

CYCLIC CHANGES IN THE UTERUS.—Gray whales have a bipartite uterus similar to that of other baleen whales (Mackintosh and Wheeler, 1929; Matthews, 1948). The placenta is of the diffuse, nondeciduate, epitheliochorial type. Measurements of the diameter of the uterine cornua of specimens examined in this study are presented in Fig. 30. Histological characteristics of the endometrium

FIG. 31. Photomicrographs of sections of the endometrium of gray whales in different stages of the reproductive cycle. A, immature female; B, northbound anestrous female; C, southbound recently ovulated female; D, northbound early pregnant female (110-millimeter fetus); E, southbound late pregnant female (3.60-meter fetus); F, northbound postpartum female. All sections are to same scale.

TABLE 12
CONDITION OF THE UTERUS OF GRAY WHALES IN VARIOUS STAGES OF THE REPRODUCTIVE CYCLE.

Direction of migration and reproductive status ¹	Number	Thickness of wall (mm)		Height of folds (mm)		Endometrium thickness			Endometrial glands		
		Mean $\pm$ SD	Range	Mean $\pm$ SD	Range	Total (mm)	Stratum compactum (microns)		Mean $\pm$ SD	Range	Diameter (microns)
							Mean $\pm$ SD	Range			
Immature (S)	10	10.4 $\pm$ 3.6	4-16	8.2 $\pm$ 3.3	3-12	2.9 $\pm$ 1.5	63 $\pm$ 15.4	30-90	50 $\pm$ 12.5	30-70	Wide
Immature (N)	23	9.1 $\pm$ 3.7	4-18	10.2 $\pm$ 4.3	4-20	1.6 $\pm$ 0.8	81 $\pm$ 28.3	35-150	42 $\pm$ 8.0	35-70	Wide
Anestrus											
(nulliparous) (N)	1	18		11		2.5	65		50		Close
Recently ovulated											
(multiparous) (S)	7	16.3 $\pm$ 4.1	11-23	10.0 $\pm$ 5.0	5-20	2.9 $\pm$ 0.9	109 $\pm$ 40.3	75-175	70 $\pm$ 18.8	55-65	Close
Early pregnant											
(primiparous) (N)	2	17.5	17-18	9.5	9-10	4.3	165	155-175	68	60-75	Close
Late pregnant											
(primiparous) (S)	5	13.6 $\pm$ 4.2	7-18	3.2 $\pm$ 2.5	1-7	3.1 $\pm$ 0.4	556 $\pm$ 360.6	315-1150	102 $\pm$ 22.1	95-145	Close
Anestrus (parous) (N)	7	18.6 $\pm$ 5.8	9-26	15.1 $\pm$ 5.2	4-20	1.8 $\pm$ 1.4	96 $\pm$ 32.9	70-360	39 $\pm$ 9.9	30-60	Close
Recently ovulated											
(parous) (S)	21	23.0 $\pm$ 6.5	11-35	9.9 $\pm$ 7.5	0-25	3.3 $\pm$ 2.6	135 $\pm$ 54.7	75-250	61 $\pm$ 14.1	45-75	Close
Early pregnant											
(multiparous) (N)	17 ²	18.4 $\pm$ 5.0	8-29	9.3 $\pm$ 5.4	2-20	3.4 $\pm$ 0.9	153 $\pm$ 30.9	95-200	57 $\pm$ 10.4	45-80	Close
Late pregnant											
(multiparous) (S)	48 ³	24.4 $\pm$ 7.5	12-45	4.9 $\pm$ 2.7	0-21	3.9 $\pm$ 1.5	724 $\pm$ 400	190-2400	128 $\pm$ 17.9	90-170	Close
Postpartum											
(multiparous) (N)	2	22.5	21-24	19.5	14-25	1.6	75	70-80	40	30-50	Close

¹ (S) = southbound migrants, (N) = northbound migrants.

² N = 18 for wall thickness; N = 14 for stratum compactum thickness.

³ N = 45 for stratum compactum thickness.

are illustrated in Fig. 31 and endometrial measurements are presented in Table 12. There was no endometrial epithelium in any of our specimens, probably because of postmortem changes.

In immature whales (Fig. 31A), the diameter of the uterine cornua ranges from 3.5 to 12.0 centimeters. The average thickness of the wall is 9 millimeters and the mean height of cornual folds is 10 millimeters. The average thickness of the endometrium is 2.9 millimeters in southbound animals and 1.6 in northbound animals. The surface of the endometrium is fairly smooth, with only a few small furrows, and it has few glandular ducts that have a mean diameter of 44 microns. The lumina of the glands are either small or not visible. Capillaries are scattered but fairly numerous.

At any stage of the reproductive cycle the uterine cornua of primiparous females average smaller than the cornua of females that have undergone a previous pregnancy, but they cannot be distinguished on the basis of histological criteria.

The cornua of northbound, sexually mature, anestrus females (Fig. 31B) are in the fully involuted condition. They range from 11 to 26 centimeters in diameter and 19 millimeters in thickness, and the folds are high, averaging 15 millimeters. The mean thickness of the endometrium is 1.8 millimeters, of which the stratum compactum comprises 96 microns. The area of division between the stratum compactum and the stratum spongiosum is poorly defined. The glands are small, with a mean diameter of 39 microns, and are more closely spaced than in immature females.

The cornua of southbound whales that have recently ovulated (Fig. 31C) are slightly larger than those of anestrus females. They range from 15 to 28 centimeters in diameter. Mean fold height has decreased to 10 millimeters, and the mean thickness of the endometrium and stratum compactum have increased to 3.3 millimeters and 135 microns, respectively. The inner surface of the uterus is more uneven than in immature individuals, with deeper furrows and a greater number of glandular openings. The average diameter of the glands has increased to 61 microns, and the lumina are mostly open. These data on gray whales differ from Matthew's (1948) observation (based on one specimen) that in fin whales there is a marked temporary increase in endometrial thickness and gland diameter at the time of ovulation.

In early pregnancy (Fig. 31D), the cornua range from 12 to 34 centimeters in diameter, the difference between gravid and non-gravid cornua not being statistically significant. Mean fold height is 10 millimeters. The endometrium (mean, 3.4 millimeters) and the stratum compactum (mean, 153 microns) are slightly thicker than in recently ovulated animals, and there are many large vessels visible in the stratum spongiosum. The glands have a mean diameter of 57 microns, slightly less than in females that have recently ovulated. No dendritic structures are visible yet, though the surface is quite uneven and numerous crypts are visible in the stratum compactum.

Whales in advanced pregnancy (Fig. 31E) have wide cornua, ranging from 76 to 120 centimeters in diameter in the horn carrying the fetus and from 40 to 105 in the other horn. The nongravid horn contains part of the placental membranes of the fetus and is filled with fluid. The uterine wall is greatly thickened, mostly as a result of an increase in the thickness of the inner layer of circular muscles. The folds have almost disappeared, contrary to the condition reported in blue and fin whales by Slijper (1956). Their disappearance seems to be a direct result of the distension of the uterine wall, and they tend to reappear when samples of the wall contract in fixatives. The endometrium is relatively thick (mean, 3.9 millimeters) because of highly developed dendritic structures, which average 724 microns in height. One female with a length of 12.98 meters had a maximum stratum compactum thickness of 3600 microns. This is markedly thicker than that of the fin and blue whales in late pregnancy which Matthews (1948) examined, the thickest of which was 200 to 1000 microns. Vessels in the stratum spongiosum are large and many are filled with blood cells. The mean diameter of the glands has increased to 128 microns.

In the two postpartum whales examined (Fig. 31F), the cornua that had contained the fetus were 34 and 70 centimeters wide, whereas the others were 16 and 34. The uterine folds were 14 and 25 millimeters high. The thickness of the endometrium had decreased to 1.0 to 2.1 millimeters and the stratum compactum to 70 to 80 microns. Dendritic structures were absent, and blood vessels were fewer and smaller. Gland diameters also had decreased to 30 to 50 microns.

POSITION OF THE FETUS.—All near-term fetuses were positioned in the uterus with the tail towards the cervix; this would ensure caudal presentation at birth, as is usual in cetaceans (Slijper, 1956). Inasmuch as the uterine horns are curved during advanced pregnancy, the head of the fetus is actually oriented towards the tail of the mother.

There was no evidence of differential tendency for implantation to occur in the right or left uterine horns. In 76 pregnant females, the fetus was in the left cornu in 37 and in the right in 39. In three cases, the fetus was in the cornu on the side opposite the ovary containing the corpus luteum, indicating transuterine migration of the ovum.

WEIGHT GAIN DURING PREGNANCY.—During the southward migration, females carrying near-term fetuses averaged 35 per cent heavier than those that had recently ovulated and most of which had presumably weaned a calf a few months previously (Table 3; Figs. 7–8). About 1000 to 2000 kilograms of this difference can be attributed to the fetus and fetal membranes and fluids, so that the gain in body weight attributable to fat stores is about 25 to 30 per cent. As there is no difference in blubber thickness between these two classes of females, most of the weight increase may be attributed to increased body fat stores.

Extra energy stores are necessary in late pregnant females to sustain rapid fetal growth and maintain the newborn calf, as well as provide for their own needs during the southward migration, the winter, and the northward migration. Acquisition of extra fat stores during pregnancy is characteristic of some other marine mammals that fast throughout the entire lactation period (Kenyon and Rice, 1959; Rice, 1960).

Lactation

LACTATION PERIOD.—According to Tomilin (1957), juvenile gray whales taken during August, September, and October in the Bering and Chukchi seas had already been weaned. He assumed that animals 8.5 to 9.5 meters long were calves of the year, an assumption supported by our data (see section on growth). None had milk in its stomach and even the smallest had been feeding on crustaceans,

although many still accompanied their mothers (Zenkovich, 1937a). These Russian workers examined 57 sexually mature females (we are assuming that females 12.0 meters or more in length were sexually mature); of these, 16 were pregnant. Of the remaining 41, only three were still lactating, including one collected on 21 August and another on 1 September. The collection date for the third is not given.

Maher (1960) reported the capture of two lactating females accompanied by calves at Barrow, Alaska, on 19 July and 13 September. The calf of the specimen taken in July had an estimated length of 25 to 28 feet (7.6 to 8.5 meters) and the young of the other was also about 25 feet. On 10 August a 25-foot calf associating with an adult was killed in the same area.

Tomilin and Zenkovich estimated 6 months as the mean length of the lactation period. They believed that most calves were born in February. As the present data indicate mid-January as the peak of the calving season, 7 months seems a more reasonable estimate of the mean duration of lactation. However, more data are needed. As with other cetaceans, weaning is probably gradual and prolonged.

CYCLIC CHANGES IN THE MAMMARY GLANDS.—In gross anatomy, position, and relative size, the mammary glands of gray whales are similar to those of other baleen whales. Changes in thickness of the gland at different phases of the reproductive cycle are shown in Fig. 32. The histological specimens were not fresh enough at time of fixation to allow study of cellular details.

The mammary glands of one 11.8-meter, sexually immature female were 77 centimeters long and 17 wide. The maximum thickness of the glands of immature females was 1.0 to 6.5 centimeters. The fresh tissue of mammary glands of virgin females is pinkish in color. The glands consist mostly of stroma. The lacteal ducts are small, widely spaced, and surrounded by only a thin layer of glandular tissue.

The mammary glands of nulliparous females at puberty and females early in their first pregnancy resemble those of virgin females in their histology, but they may be slightly thicker (up to 9.0 centimeters). The mammary glands of primiparous females in late pregnancy consist of 66 to 91 per cent (mean, 81) glandular

FIG. 32. Thickness of mammary glands of gray whales in different stages of the reproductive cycle. Symbols are as follows: horizontal dashes, mean; vertical bars, one standard deviation on either side of mean; vertical lines, range; S, southbound migrants; N, northbound migrants. Values plotted for post-partum females were from nonlactating individuals.

tissue and are grossly and histologically indistinguishable from those of multiparous females.

The involuted glands of parous animals in anestrus taken during the spring migration are larger than those of virgin individuals. One female 13.3-meters long had mammary glands 145 centimeters long and 32 wide. The mammary tissue varies from 3.5 to 10.0 centimeters (mean, 7.8) in thickness and is pale yellowish-brown in color. Histologically, the glands consist of 37 to 66 per cent (mean, 56) glandular tissue separated by a moderate amount of stroma. They show an extensive system of secretory lobules, which in section are somewhat polygonal and flattened. No secretory activity is apparent.

All females collected during southward migration that had recently ovulated, the majority of which had presumably ceased lactating about the previous July, had nearly or completely involuted glands 5.0 to 9.5 centimeters in thickness. They consisted of 41 to 65 per cent (mean, 53) glandular tissue, and were not distinguishable histologically from the glands of the anestrous females taken in spring. No secretory activity was noted.

The mammary glands of northbound females in early pregnancy also were grossly and histologically indistinguishable from the involuted glands of anestrous females. They consisted of 24 to 63 per cent (mean, 43) glandular tissue.

The mean depth of the lacteal tissue of females in advanced pregnancy was 13.0 centimeters. The mammary tissue is pink and softer than that of involuted glands, and histologically it shows extensive proliferation of the lobule-alveolar system. In section the lobules are large and round, comprising 67 to 91 per cent (mean, 80) of the gland, with relatively little stroma. In a few of the glands examined at this stage, no secretory activity was noticeable, but most already showed a considerable amount of secretory activity. Some had only a small amount of translucent, yellowish fluid in the ducts, others contained so much fluid (colostrum?) that it spurted from the teats when the animals were hauled onto the flensing deck. One female that apparently had recently aborted (or was immediately postpartum), killed on 8 January, had the thickest glands (21.0 centimeters) of any examined and was secreting colostrum copiously.

Unfortunately, we collected no actively lactating animals. The glands of the two nonlactating, postpartum females were grossly and histologically indistinguishable from those of females in late pregnancy. Their thickness was slightly reduced; they consisted of 56 to 72 per cent (mean, 64) glandular tissue and were secreting yellowish, translucent fluid.

Zenkovich (1938) reported that the milk of gray whales taken in August near the end of the lactation period consisted of 53.04 per cent fat, 6.38 per cent dry residue, and 40.58 per cent water. The fat content is greater than has been reported for any other species of cetacean.

Anestrus

Females are probably in anestrus for 3 to 4 months from the end of lactation about August until the onset of the next estrous period in late November or December. As noted earlier, a few females fail to come into estrus at this time and presumably would not do so again until at least a year later; they would thus undergo an anestrus period of 16 months or longer. Other females come into estrus but fail to conceive and return to the anestrus state, probably nearly a year in duration.

Discussion and Conclusions

The complete reproductive cycle of the female gray whale occupies 2 years. Females come into estrus during about a 3-week period in late November and early December. They usually conceive following their first ovulation, but if they fail to do so, they may undergo another estrous cycle about 40 days later. Pregnancy lasts for about 13 months (400 days). Parturition occurs within a period of 5 to 6 weeks from late December to early February. The calf is nursed for about 7 months. After weaning their calf about August, females are in anestrus for 3 or 4 months until November or December, when most of them go into estrus and commence a new pregnancy. A few either fail to ovulate, or ovulate but fail to conceive, and are in anestrus for another year. There is no evidence for postpartum or postlactation ovulation. Evidence for the possible occurrence of ovulation following stillbirth or early loss of the calf is suggestive but inconclusive.

The reproductive cycle of the female gray whale is basically similar to that of the larger rorquals. One important difference is that the extremely long migration route and restricted calving grounds of the gray whale impose a much stricter annual schedule. For example, the majority of gray whale calves are born during a period of 5 to 6 weeks, as contrasted with about 5 months in the rorquals.

The gray whale's ovulation rate of about 0.50 per year is less than that reported by some authors for rorquals. The ovulation rate of the fin whale was estimated as 1.40 per year by Laws (1961) and 1.25 per year by van Utrecht-Cock (1965). Laws, however, admitted

that the rate may be only half his estimate. Nishiwaki *et al.* (1958) estimated the ovulation rate of southern fin whales as 0.90 per year and that of North Pacific fin whales as 0.80 per year. Chittleborough (1959) estimated the ovulation rate of humpback whales at 1.10 per year. Nishiwaki *et al.* and Chittleborough assumed that two growth layers were formed in the ear plug each year, so the true ovulation rates are probably nearer 0.40 to 0.45 per year for fin whales and 0.55 per year for humpback whales. The annual ovulation rate of Southern Hemisphere sei whales is 0.69 (Gambell, 1968). Rorquals, apparently unlike gray whales, sometimes experience postpartum and postlactation or summer ovulations.

When comparing ovulation and pregnancy rates of different species and stocks of whales, it must be borne in mind that the reproductive performances of mammals—even large, late maturing and slow breeding species—are quite labile in response to population density in relation to carrying capacity of the range. Laws (1962) and S. Ohsumi and Y. Shimadzu (personal communication) have shown a reduction in age at sexual maturity and an increase in the pregnancy rate of Southern Hemisphere fin whales in response to excessive exploitation. Among large terrestrial mammals, Buss and Smith (1966) have shown a marked decrease in pregnancy rate in a population of African elephants, *Loxodonta africana*, brought about by an increase in population density and resultant deterioration of the habitat.

Presumably population density influences reproduction through nutrition or through ethological factors. In the gray whale, nutrition could be of critical importance, because the pregnant female must accumulate enough energy stores during the summer to support herself and her fetus through a long migration, to support herself and the newborn calf for a month or more on the wintering grounds, and to sustain both herself and the rapidly growing calf during the long return migration to the summer feeding grounds. Under such conditions, selective pressure for suppression of ovulation at times when the female is not physiologically capable of carrying a new pregnancy to term might be expected. Thus it may be that in the gray whale the potentiality for a postpartum estrous cycle is being or has been genetically eliminated from the population.

MALE REPRODUCTIVE CYCLE

DATA on the reproductive biology of the male gray whale were obtained from a sample of 166 animals. Of this number, 123 had attained puberty, including 67 southbound and 56 northbound migrants.

Testes

The testes of gray whales are cylindrical, moderately elongate, and generally similar to those of rorquals.

WEIGHTS.—No significant or consistent difference in weight between left and right testes was found.

In all sexually immature males examined, both testes weighed less than 8.2 kilograms and, in all individuals except three, the combined weight of the testes was less than 5.0 kilograms (Fig. 33). With one exception, the testes of mature males weighed more than 5.7 kilograms and few had testes lighter than 17.0 kilograms. The exception was a mature northbound animal with unusually small testes that weighed only 0.8 kilogram. Following the abrupt increase in testis weight immediately after puberty, the rate of increase rapidly declines with increasing body length.

The paired testes of the southward migrating adult males taken in December and January ranged from 7.9 to 67.5 kilograms, with a mean and standard error of 38.4 ± 1.4 . Mean testis weights for 10-day intervals throughout the southward migration period show no significant changes (Table 13). In northbound adults, the testes were much lighter, ranging from 5.7 to 44.8 kilograms with a mean and standard error of 22.5 ± 0.9 . Mean testis weights decreased from 24.8 kilograms in late February to 18.0 kilograms by the end of March. Zimushko (1969*b*) found that the testes of 25 adults taken from July through October ranged from 14 to 27 kilograms (mean, 23).

HISTOLOGY.—Because of the rapidity of postmortem degeneration of testis tissue, detailed cytological study of our material was not possible. Representative histological sections are shown in Fig. 34.

FIG. 33. Testes weights of gray whales in relation to body length. Symbols are as follows: solid triangles, southbound immature males; solid circles, southbound adult males; open triangles, northbound immature males; open circles, northbound adult males. Unbroken line connects means of 0.3-meter length groups of southbound males; broken line connects means of 0.3-meter length groups of northbound males.

In immature testes, the seminiferous tubules were closed and small, their average diameters ranging from 45 to 102 microns (mean, 75). In mature testes, the tubules had open lumina and average diameters ranging from 104 to 214 microns. In males that have reached puberty, there is a significant ($P < .001$) positive correlation between tubule diameter and testis weight (Fig. 35). This correlation is expressed by the formula $Y = 120 + 1.3X$, where Y = tubule diameter in microns and X = testis weight in kilograms.

Mean tubule diameters of the testes of southbound migrants ranged from 114 to 214 microns (mean, 177; standard error, 2). Mean tubule diameter of northbound migrants was significantly smaller, ranging from 104 to 186 microns, with a mean of 148 and a standard error of .3). Mean tubule diameters for each 10-day

TABLE 13

TESTIS WEIGHTS AND SIZE OF SEMINIFEROUS TUBULES OF ADULT MALE GRAY WHALES AT 10-DAY INTERVALS DURING MIGRATION.

Period	Testis weight (kg)			Tubule diameter (microns)		
	N	Mean $\pm$ SE	Range	N	Mean $\pm$ SE	Range
<i>Southward migration</i>						
12-21 December	4	41.3 $\pm$ 3.7	33.1-47.6	4	184 $\pm$ 3	177-189
22-31 December	6	36.9 $\pm$ 6.3	23.5-66.5	6	176 $\pm$ 6	154-193
1-10 January	30	36.0 $\pm$ 2.3	7.9-63.3	29	171 $\pm$ 4	114-206
11-20 January	20	40.4 $\pm$ 1.9	26.5-53.2	20	183 $\pm$ 4	153-214
21-30 January	7	43.1 $\pm$ 5.4	26.1-67.5	7	184 $\pm$ 5	161-198
<i>Northward migration</i>						
20 February-1 March ¹	7 ¹	24.8 $\pm$ 2.6	17.9-34.5	8	147 $\pm$ 8	111-179
2-11 March	24	24.0 $\pm$ 1.4	11.5-44.8	24	148 $\pm$ 4	104-176
12-21 March	15	21.8 $\pm$ 1.6	5.7-31.5	14	143 $\pm$ 6	107-186
22-31 March	9	18.0 $\pm$ 1.4	11.7-23.3	9	156 $\pm$ 4	142-186

¹ One male with abnormally small testes weighing 0.8 kg omitted.

interval do not reveal any significant increase or decrease within either migration period (Table 13).

The seminiferous tubules of almost all adult males appeared to be undergoing spermatogenesis, but it was difficult or impossible to ascertain the precise stages. The vasa deferentia and epididymides of all postpubertal males that were examined contained abundant fluid. Because of the long postmortem time, we did not attempt to collect vas deferens fluid for counts of sperm density.

Penis

The penis of the gray whale is an elongate, evenly tapering, conical, flesh-colored organ similar to that of the rorquals, and unlike the slender cylindrical black organ of right whales.

The length of the penis ranged from 55 to 145 centimeters in immature males and from 100 to 170 in adults. There is a significant ($P < .001$) positive correlation between penis length and body length (Fig. 36). This correlation is expressed by the formula $Y = 0.21X - 1.14$, where Y = penis length in meters and X = body length in meters. On the basis of this formula, at a body length of 11.1 meters, which is the average length at puberty, mean penis length is 1.08 meters. A penis length of 114 centimeters correctly separates 79 per cent of our specimens into immature and adult categories.

FIG. 34. Photomicrographs of sections of testes of gray whales in different stages of the reproductive cycle. A, immature male; B, pubertal male with both closed and open seminiferous tubules; C, adult southbound male; D, adult northbound male. All sections are to same scale.

Discussion and Conclusions

Testes weighing more than 5.0 kilograms are a reliable indication of maturity in male gray whales. A penis length greater than 1.1 meters also separates most mature animals from those that are sexually immature.

The much heavier testes and larger seminiferous tubules of males taken during southward migration compared with those of males collected during northward migration and on the summer grounds indicate that male gray whales have a marked seasonal sexual

FIG. 35. Relation between size of seminiferous tubules and weight of testes of gray whales. Symbols are as follows: solid triangles, southbound immature males; solid circles, southbound adult males; open triangles, northbound immature males; open circles, northbound adult males. Regression of tubule diameter on testis weight based on adult males.

FIG. 36. Relation between penis length and body length of gray whales. Open circles represent immature males and closed circles represent adult males.

cycle, with a peak of spermatogenetic activity in late autumn or early winter. This period correlates closely with the time females come into estrus. Although there are no reported field observations of copulation at this time, biologists have not studied the behavior of gray whales in southward migration north of San Francisco. Courting and copulating gray whales often are seen on and near the calving grounds in Baja California in January (Gilmore, 1960a); this period coincides with the second estrous cycle of those few females that are not impregnated during their first cycle. Apparent courtship behavior, including males with an erect penis, has been observed during northward migration on the coast of California in March (Houck, 1962) and on the coast of Washington as late as April (C. E. Munsen, personal communication). Courtship behavior and apparent copulation also have been observed in the Bering Sea in June, July, August, and September (Sauer, 1963; Fay, 1963; Tomilin, 1937). Its significance at these times is unknown; certainly it never results in successful conception. In the bottlenose dolphin (*Tursiops truncatus*), copulation behavior does not necessarily indicate sexual fertility in males, as males born in captivity may begin to copulate frequently when only a few days old (Caldwell and Caldwell, 1968).

The existence of a male reproductive cycle in other mysticetes appears to be variable. Male humpback whales show a marked seasonal variation in weight of the testes and spermatogenetic activity (Chittleborough, 1955; Nishiwaki, 1959; Omura, 1953; Symons and Weston, 1958). In blue and fin whales there is a less well-marked seasonal cycle in spermatogenetic activity, although available data do not clearly demonstrate an associated cycle in testis weight (Laws, 1961; Mackintosh and Wheeler, 1929). In sei whales there is no seasonal variation in either weight or histology of the testes (Gambell, 1968).

PREDATORS

KILLER whales, *Orcinus orca*, are the only known predators of baleen whales (Nishiwaki and Handa, 1958). Killer whales rarely have been observed attacking gray whales. However, Scammon (1874) saw three killer whales attack and kill a gray whale calf accompanied by its mother in a lagoon in Baja California. Gilmore (1961) reported an unsuccessful attack by six killer whales on two gray whales at La Jolla, California. Morejohn (1968) observed an unsuccessful attack by seven killer whales on three gray whales, including a female with a calf, at Moss Landing, California. V. B. Scheffer (personal communication) saw six killer whales unsuccessfully attack a gray whale in Monterey Bay, California, on 9 March 1952. Burrage (1964) observed avoidance behavior of a pod of six gray whales on the approach of five killer whales at La Jolla. Pike and MacAskie (1969) reported killer whales attacking a pair of gray whales off the Queen Charlotte Islands. Andrews (1914) recounted descriptions by whalers of the reaction of gray whales to the approach of killer whales in Korean waters and reported killers feeding on the carcasses of gray whales being towed by catcher boats.

We found healed parallel scars that were obviously the tooth marks of killer whales on 57 (18 per cent) of the gray whales that we examined. Other whales doubtless bore unrecognizable killer whale tooth scars. Fifty-two of the whales had scars on the flukes, and 15 animals had scars on one or both flippers. Eight other whales had scars elsewhere on the body, as follows (number of individuals in parentheses): flanks (four), caudal peduncle (one), anal region (one), dorsal hump (one), throat (one), and snout (one). The predominance of scars on the flukes and flippers suggests that killer whales usually attempt to kill gray whales by seizing their flukes and flippers so as to immobilize and drown them. The number of scarred animals indicates a fairly high frequency of unsuccessful attacks on gray whales by killer whales. The proportion of successful attacks is unknown. Like other predators such as the wolf, *Canis-lupus*, killer whales probably succeed

in killing only a small proportion of the large prey that they attack (Mech, 1966). Jonsgård (1968) has pointed out that there is no incontrovertible proof that killer whales are capable of killing baleen whales that are not incapacitated or otherwise at a disadvantage.

We found no gray whale remains in the stomachs of 10 killer whales taken in the eastern North Pacific, although five of the killer whales were collected at a time when gray whales were present in the vicinity (Rice, 1968).

PARASITES AND EPIZOITES

Ectoparasites and Epizoites

ALL gray whales examined were heavily infested with ectoparasites and epizoites, including three species of cyamids and one species of barnacle. Zenkovich (1937a) reported that a few gray whales, which had presumably just emerged from brackish lagoons bordering the Bering Sea, carried no cyamids and no live barnacles. He experimentally showed that brief immersion in fresh or brackish waters kills these parasites. We found small patches of an olive-colored skin film on a few whales, but were unable to find any diatoms in scrapings from such areas. Hubbs' (1959) report of kelp growing on gray whales probably was based on observation of whales that had temporarily picked up strands of kelp while swimming through kelp beds. The baleen plates of the whales examined in this study were generally clean and carried no film of microorganisms.

BARNACLES.—*Cryptolepas rhachianecti* Dall, 1872 (Fig. 37), is the only barnacle found on gray whales, to which it is host-specific. This sessile species is closely related to the genus *Coronula*, which occurs regularly on humpback whales but rarely on other species. Its mode of attachment to the skin appears to be similar to that of *Coronula* (Darwin, 1854).

These barnacles were present on every whale examined, which has been the experience of other workers who have studied gray whales. They may occur in small clusters almost anywhere on the trunk or on the surfaces of the flukes and flippers, but are most abundant on areas that are exposed to the air when the whale surfaces. They often form a continuous mass on the dorsal aspect of the rostrum and the most anterior part of the back. These areas also are those most directly exposed to food-carrying water currents as the whale stirs up the bottom sediments. The barnacles are oriented with their cirri generally directed towards the anterior end of the whale (Kasuya and Rice, 1970).

Virtually all barnacles on whales taken during the southbound migration are large (20 to 40 millimeters in diameter). Only one

FIG. 37. Barnacles *Cryptolepas rhachianecti* on skin of gray whales. A, south-bound whale with large barnacles only; B, northbound whale with many small as well as large barnacles. The anterior end of each whale is to the left. Note the many *Cyamus scammoni* on the barnacle clusters and a few *C. ceti* mostly around the periphery of the clusters.

southbound whale, a pregnant female taken on 27 December 1968, bore small barnacles (3 to 5 millimeters in diameter). Northbound whales carry two discrete size groups of barnacles. Besides the large individuals that are 20 to 40 millimeters in diameter, there are usually large numbers of small individuals that range from 2 to 5 millimeters in diameter. Thus it is apparent that barnacles spawn while the whales are concentrated on their winter grounds and when the cypris larvae of the barnacles have the greatest opportunity for finding a new host. The small barnacles often are located close together, so there must be much mortality due to crowding as they grow.

CYAMIDS.—Gray whales are host to three species of cyamids (Fig. 37). Most previous workers have reported only one species, the unique and easily recognized *Cyamus scammoni*, but they doubtless overlooked the other species. Hurley and Mohr (1957) were the first to report the other two, *Cyamus ceti* and *C. kessleri*. Few cetaceans are host to more than one species of cyamid. The only other cetaceans on which three species have been found are the right whale and the sperm whale (Leung, 1967), but it is not known how frequently three species of cyamids may occur on a single individual of these host species. All except one of our gray whales were lightly to heavily infested with cyamids, and the three species occurred together on 310 (98.1 per cent) of the 316 examined. However, they tended to segregate on different parts of the body as described below.

Cyamus scammoni Dall, 1872, is invariably the most abundant cyamid on the gray whale and is restricted to this host. We found it on 315 (99.7 per cent) of the 316 whales examined. It is found mostly around clusters of barnacles. A few individuals may be scattered elsewhere on the body, most often in the fold at the axilla of the flippers, in the notch of the flukes, in the umbilicus, and sometimes in the genital groove. We found no trace of the cornified area on the dorsal surface of the rostrum reported by Andrews (1914) and supposed by him to be produced by the action of cyamids. On several whales, we found large numbers of *C. scammoni* in fairly fresh wounds. The two most notable cases were a large adult male taken on 25 March 1964 with a deep wound 1.40 meters long and 0.35 of a meter wide in the blubber of the back slightly to the right

of the middorsal line opposite the flipper; and a female taken on 20 December 1968 with a wound 0.85 by 0.85 meters and 14 centimeters deep on the back about 2 meters anterior to the dorsal hump. In both specimens, the wounds were completely filled with tightly packed masses of cyamids, mostly, if not entirely, *C. scammoni*. More than 100,000 were collected from the male (Leung, 1965). Many of the individuals were exceptionally large.

Cyamus ceti Linnaeus, 1758, was originally described from the bowhead whale from the Atlantic sector of the Arctic Ocean. Hurley and Mohr (1957) first found it on the gray whale at Barrow, Alaska. They reported that their specimens agreed closely with descriptions of this species and with specimens taken from bowhead whales captured at Barrow. L. Margolis (letter, July 1959), however, is somewhat doubtful about the identification of specimens from gray whales as *C. ceti*, because he has found minor differences between specimens from gray whales and those from Atlantic-Arctic bowheads. As most cyamids are host-specific, it would be most unusual for one species to infest hosts belonging to different families. This specificity is, no doubt, primarily a result of cyamids spending their entire life upon the host, so that transference can rarely occur except between members of a pair during copulation or between mother and calf during birth or suckling. This species is much less numerous than *C. scammoni*, but usually more frequent than *C. kessleri*. We recorded it on 314 (99.4 per cent) of 316 whales. It most commonly lives in grooves and skin folds on the body as follows: around the blowholes; in the angle of the gape; in the throat grooves; around the eyes; at the bases of the flippers; on the umbilicus; in the mammary slits; and, rarely, in the genital and anal grooves. Small patches of them are sometimes found elsewhere on bare skin. A few may be found adjacent to *C. scammoni* around the edges of clusters of barnacles, but competition with the larger species appears largely to exclude *C. ceti* from barnacle clusters.

Cyamus kessleri Brandt, 1872, was first described from an unidentified species of whale from the Bering Sea. Hurley and Mohr (1957) rediscovered it on a gray whale killed at Barrow, Alaska. It has subsequently been found only on gray whales. This is usually the least abundant species of cyamid on the gray whale. We found it on 310 (98.1 per cent) of 316 whales. It occurred almost exclusively

around the anus and in the genital grooves. A few were occasionally located in the mammary slits and elsewhere on the body.

Endoparasites

Before these studies, no endoparasites had been identified from the gray whale, although an unidentified cestode was reported by Tomilin (1937) from individuals of this species in the Chukchi Sea. We found eight species of endoparasites in the digestive system, including three trematodes, two cestodes, one nematode, and two acanthocephalans. Some of these seem to represent undescribed species. The taxonomy of the cestodes is being studied by R. Rausch and that of the acanthocephalans by K. Neiland. We found no parasites in the kidneys, lungs, peribullary air sinuses, or blubber. Treshchev *et al.* (1969) have published an abstract of recent studies on the helminthofauna of gray whales in the Bering and Chukchi seas.

TREMATODES.—*Lecithodesmus goliath* van Beneden, 1959, was found in only two gray whales. These large flukes live in the bile ducts of the liver. Specimens from gray whales range from 35 to 54 millimeters (mean, 45) in length and 10 to 14 millimeters (mean, 12) in width. This species differs from *L. spinosus* Margolis, 1955, in its incompletely spined cuticle. *L. goliath* has been reported from many species of baleen whales (Delyamure, 1955). Two flukes were found in an immature female whale taken on 16 March 1969; no pathological conditions were grossly visible in the liver. Forty-seven flukes were recovered from a mature male whale taken on 13 March 1969, and many others were doubtless present. The bile ducts of this whale had distorted, inflamed biliary epithelium and were rimmed with thick walls of dense scar tissue. We have never observed such marked pathogenic effects associated with heavy infestations of *Lecithodesmus* in sei whales, which suggests that the gray whale is not a normal host for these flukes.

Orthosplanchnus pygmaeus was described by Yurakhno (1967) from the intestine of a gray whale taken off the Chukotskiy Peninsula. Other members of this genus infest the bile ducts and gall bladder of Arctic pinnipeds.

Ogmogaster pentalineatus Rausch and Fay, 1966, was described as a new species on the basis of our specimens and the type series

collected by Fay from a gray whale at St. Lawrence Island, Alaska. The name *Ogmogaster delamurei* Treshchev (1966a), based upon specimens found in gray whales taken in the Chukchi Sea near Enurmino on the Chukotskiy Peninsula, is a junior synonym of *O. pentalineatus* (Skriabin, 1969). *O. pentalineatus* has been found only in gray whales. Entire specimens are easily recognized by the smoothly rounded or weakly undulate edge of the body and by the five ridges on the ventral surface. The species usually does not attain a length greater than about 3.5 millimeters, although one specimen measured 5.6 millimeters.

Field inspection of the surface of the mucosa of the small intestine at several randomly selected points revealed *O. pentalineatus* in only eight (2.5 per cent) whales. A more careful search of a section of the small intestine in a tray of water sometimes showed these flukes to be present in whales in which our spot-check had revealed none. The type series of more than 200 individuals was found in the small intestine (Rausch and Fay, 1966). In 1967, large numbers of this species were discovered in the rectum of one whale, so in 1968 and 1969 that portion of the rectum exposed on the inner side of the blubber after the blubber had been flensed from the whale was routinely examined. *O. pentalineatus* was recorded from 31 (22 per cent) of 139 whales examined in this manner. In all except seven cases, this species was living alongside *O. antarcticus*, although usually in lesser numbers. Of 1280 *Ogmogaster* collected from the rectum of 53 whales, only 227 (18 per cent) were *O. pentalineatus*. Usually fewer than 20 individuals of the latter species were present, but one whale contained well over 100.

Ogmogaster antarcticus Johnston, 1931, occurred in 46 (33 per cent) of 139 whales examined in 1968 and 1969. This species is distinguished from *O. pentalineatus* by the greater number of ridges (12 to 15) on the ventral surface, the 15 to 20 conspicuous marginal crenulations on each side of the body, and the four or five lateral loops in each intestinal caecum. It also typically attains larger size, reaching 6.0 millimeters in length. In rorquals (*Balaenoptera* species), this species has a maximum length of 10 millimeters (Rausch and Fay, 1966). Our specimens agree well with the descriptions of *O. antarcticus* as diagnosed by Delyamure (1955) and Rausch and Fay (1966). *O. antarcticus* has been reported previously from the intestines of Antarctic seals (tribe Lobodontini) and from

the intestines of rorquals in the North Pacific and North Atlantic as well as the Southern Hemisphere. In this study *O. antarcticus* was found only in the rectum. The maximum number recovered from one whale was 199. In 24 of the 139 whales examined it was associated with lesser numbers of *O. pentalineatus*. Treshchev *et al.* (1969), strangely enough, did not find this species in gray whales collected on the summer grounds.

Ogmogaster plicatus Creplin, 1829, was reported in a gray whale obtained off the Chukotskiy Peninsula (Treshchev *et al.*, 1969). Otherwise the species has been found only in the intestines of rorquals in the North Pacific and North Atlantic; we have found it in fin whales collected off San Francisco. This species differs from *O. antarcticus* in having more ventral ridges (19 to 28), more than 20 marginal crenulations on each side of the body, and larger size (maximum length 14 millimeters).

The life histories of the species of *Ogmogaster* are unknown. The food habits of their definitive hosts suggest that their second intermediate hosts are crustaceans.

CESTODES.—The genus *Priapocephalus* includes cestodes characterized by a bulbous scolex that lacks suckers and has a basal collar. *P. eschrichtii* recently has been described by Murav'eva and Treshchev (1970) from gray whales in the Chukchi Sea. The other two described species are *P. grandis* Nybelin, 1922, from rorquals (*Balaenoptera* species) and right whales in the Southern Hemisphere, and *P. minor* Nybelin, 1928, from rorquals in the North Atlantic and North Pacific (Baer, 1954; Delyamure, 1955; Markowski, 1955). The larval host of *Priapocephalus* is unknown. We collected two kinds, apparently different species, from the gray whale.

The commonest species has a narrow (less than 1 millimeter wide) strobila that is of uniform width throughout. It is difficult to collect complete strobilae, but they attain a length of at least 25 centimeters. The proglottids are about 0.3 to 0.4 of a millimeter long, and the scolex is about 3 millimeters in diameter. This species was found in the small intestine of 94 (30 per cent) of the 316 whales. Usually infestations were light and rather local, although a few whales were heavily infested.

The second species differs from the previous species in that its strobila is much wider—2 to 4 millimeters. Although the proglottids

adjacent to the scolex are as narrow as those of the previous species, they rapidly become wider distally. The proglottids are about 0.5 to 0.8 of a millimeter long. The scolex is similar to that of the previous species. This cestode was found in the large intestine of an immature female whale taken on 11 April 1968. The whale was heavily infested with this parasite, and no other species of cestode was present.

Tomilin (1937) reported an unidentified cestode from the gray whale. He stated (translation): "In 1934, internal parasites (tapeworms) Cestoda Ord. Pseudophaliidae [sic] (species not determined) 40 meters in length (deposited in parasitological laboratory of the Institute of Zoology, MGU) were found in the intestines of two gray whales. Their segments attained a width of 2 centimeters. The worms equaled about 48 liters in volume, in each animal." From their size, we would guess that these must be *Diplogonoporus balaenopterae* Lönnberg, 1891, a species frequently found in rorquals (*Balaenoptera* and *Megaptera*). The life cycle of *Diplogonoporus* is unknown, but the plerocercoids can be expected to occur in fishes (Rausch, 1964).

NEMATODES.—*Anisakis simplex* Rudolphi, 1809, was found in only one gray whale. There were many immature individuals, 20 to 35 millimeters long, of this species in the first and second chambers of the stomach of an immature male killed on 3 April 1968. They were not attached to the mucosa. In a recent revision of this genus, J. T. Davey (personal communication) recognized only three species. Our specimens differ from *A. physeteris* Baylis, 1923, in the possession of a sigmoid esophagus. Only mature males of *A. simplex* can be distinguished from *A. typica* Diesing, 1860. *A. simplex* occurs in all species of balaenopterid whales as well as many other species of marine mammals from all over the world, especially from colder seas, whereas *A. typica* is known only from delphinids from warmer seas. Therefore Davey (personal communication) had little hesitation in assigning our specimens to *A. simplex*. The life cycle of *Anisakis* is unknown, but it is probable that two intermediate hosts are needed (Berland, 1961). Fishes are the usual source of infestations in marine mammals (van Thiel, 1966), in which these worms reach maturity.

ACANTHOCEPHALANS.—*Corynosoma* sp. was found in 18 (5.7 per cent) of the 316 gray whales studied. They were rather loosely attached to the mucosa of the small intestine. Most infestations were light, the heaviest being a whale that had 60 individuals within a 0.3-meter section of intestine. Specimens from gray whales are 4 to 5 millimeters long; the anterior half of the trunk is bulbous, the posterior half elongate and tapering. Treshchev (1966*b*) described a new species, *C. septentrionalis*, and reported (Treshchev *et al.*, 1969) *C. semerme* Forssell, 1904, *C. strumosum* Rudolphi, 1802, and *C. validum* Van Cleave, 1953, from gray whales collected off the Chukotskiy Peninsula. The life cycles of a few species of *Corynosoma* are known. All these involve crustaceans as first intermediate hosts, and fishes as second intermediate hosts (Golvan, 1959). Seals and aquatic birds are the definitive hosts of most species of this genus; a few species parasitize toothed whales (Delyamure, 1955; Golvan, 1959). The discovery of species of this genus in gray whales is the first known occurrence in a baleen whale, although we recently have found *Corynosoma* in fin whales.

Bolbosoma sp. was present in the small intestine of an immature male whale captured on 3 April 1968. The two specimens found were white and about 30 millimeters long. The trunk (when turgid after being placed in fresh water) was slightly more than a millimeter in diameter. One was loosely attached to the mucosa; the head of the other was imbedded in a small, thick-walled, pus-filled cyst in the mucosa. The life cycles of species of *Bolbosoma* are unknown.

Discussion and Conclusions

The gray whale is more heavily infested with a greater variety of ectoparasites and epizootes than any other species of cetacean. This may be at least partly due to the fact that they swim slowly and live throughout the year in shallow coastal waters rich in nutrients. In contrast, they are infrequently infested with endoparasites. Their long period of fasting each year may inhibit the survival of parasites in the digestive tract. Except for liver flukes, none of the ectoparasites or endoparasites appears to have any significant pathogenic effects.

POPULATION

ALTHOUGH a reasonably complete understanding of the population dynamics of the California stock of gray whales will require further investigation, data obtained in the present study provide a basis for some tentative conclusions.

Present Numbers

Because gray whales migrate close to the coast, a large proportion of the population may be counted from vantage points on shore, providing an index of population size. Between the migration seasons of 1952-53 and 1960-61, four essentially full-time counts were made at the Point Loma coastal station (Gilmore, 1960a, 1960b; Rice, 1961). In the course of offshore cruises for marking whales of other species, beginning in 1964, we found unexpectedly large numbers of southbound gray whales passing the coast of southern California far offshore (Rice, 1965; unpublished data). However, in the area of the counting station south of Yankee Point, observations during whale marking cruises indicated that few gray whales pass so far offshore that they cannot be seen from land.

Daily counts of southbound whales migrating past these two points are shown in Fig. 38. In 1967-68, 3120 whales were counted at Yankee Point and 1324 at Point Loma. In 1968-69, 3280 were counted at Yankee Point and 1154 at Point Loma. Thus, of the number of whales that passed Yankee Point only 35 to 42 per cent were seen passing Point Loma. In 1969-70, 3345 were counted at Yankee Point, and no count was made at Point Loma.

To calculate total population size from these counts, we must estimate the number of whales that were missed because of poor visibility, the whales that passed too far offshore to be seen, and the whales that passed at night. We estimated the number of whales missed because of poor visibility by considering only the counts made during days when visibility was good. As visibility is limited most by fog, drizzle, or rain, and by winds strong enough to create whitecaps, we considered only the days when there was no precipitation or fog and winds were below 19 kilometers per

FIG. 38. Daily counts of gray whales passing Yankee Point and Point Loma, California, during the southward migrations of 1967-68 and 1968-69.

hour (10 knots). Days with good visibility and days with poor visibility were interspersed at random throughout each census period, so we extrapolated the counts made during the days with good visibility to include the entire period of each census. Some whales were doubtless missed even during days with good visibility, and, of course, a few passed early in the season before the counts began and late in the season after the counts ended.

To determine the number of whales passing too far offshore to be seen, we ran transect cruises from Yankee Point and Point Loma across the migration path of the whales. In a transect from Yankee Point on 18 January 1968, extending 37 kilometers offshore, no gray whales were seen farther from shore than 6 kilometers, and only nine of the 33 whales sighted were beyond 4.5 kilometers from shore. The remaining 24 were within 1.5 kilometers of land. Under conditions of good visibility, observers on shore could detect whales at an estimated distance of 7.4 kilometers, but 95 per cent of the whales were estimated to be within 1.9 kilometers of shore. Therefore, we conclude that the number of whales passing too far off-

shore from Yankee Point to be seen by the observers during periods of good visibility was insignificant.

Between 25 January and 9 February 1968, we ran seven transects totaling 1572 kilometers between Point Loma and longitude $119^{\circ}20'$ W, just beyond Tanner and Cortez Banks. During 100 kilometers of cruising within 9.3 kilometers of shore, 37 gray whales were seen, an average of 0.37 per kilometer cruised. During 1472 kilometers of cruising beyond 9.3 kilometers from shore, 40 gray whales were sighted, an average of 0.027 per kilometer. The width of the migration path at this latitude is at least 194.5 kilometers, of which 9.3 kilometers is within sight from Point Loma. The ratio of whales passing offshore to those passing within sight of land is thus $(185.2 \times 0.027) : (9.30 \times 0.37) = 5.00 : 3.44$. This ratio indicates that only 41 per cent of the whales migrating south past southern California passed within sight of Point Loma. This agrees with our estimates of 35 to 42 per cent based upon a comparison of the Point Loma and Yankee Point counts. Therefore, we have multiplied the Point Loma counts by 2.44 (100/41), to estimate the total number of whales moving past the latitude of Point Loma during daylight hours.

Because there is no evidence that migrating gray whales slow down at night, we have multiplied the estimated number of whales passing during the 10 hours of daylight during which counts were made by 2.4 to estimate the total number of whales passing each counting station during each of the two seasons.

Estimates of total population size, based on the foregoing corrections, are shown in Table 14. The Yankee Point estimates are probably more accurate than the Point Loma estimates, because of the greater possibility of error in adjusting for offshore migration at Point Loma. The 1968-69 and 1969-70 estimates are probably more accurate than those for 1967-68 because the counts started earlier in the season. The best estimate of the present population size of the California gray whale stock is approximately 11,000.

The reliability of this estimate is difficult to assess. A probable lower limit may be estimated by multiplying the actual counts at Yankee Point by 2.4 to allow for the whales passing at night, which gives figures of about 7500 for all three seasons. An upper

TABLE 14

COUNTS OF SOUTHWARD MIGRATING GRAY WHALES AND ADJUSTED ESTIMATES OF TOTAL GRAY WHALE POPULATION SIZE, 1967-68 TO 1969-70.

Season	Locality	Entire period		Days with good visibility		Whales per day	Estimate of whales passing during daylight	Adjusted for offshore migration	Adjusted for night migration
		No. of days	No. of whales	No. of days	No. of whales				
1967-68	Yankee Point	49 ¹	3,120	32	2,430	76	3,724		8,938
	Point Loma	52	1,324	29	879	30	1,560	3,806	9,134
1968-69	Yankee Point	60	3,280	29	2,174	75	4,500		10,800
	Point Loma	57	1,154	26	758	29	1,653	4,033	9,679
1969-70	Yankee Point	64	3,345	32	2,257	71	4,544		10,906

¹ No count made on two of these days.

limit was estimated by drawing a line connecting the highest daily counts at Yankee Point and measuring the area under the line to estimate the number of whales passing during daylight. The total was then calculated by multiplying this value by 2.4 to compensate for night migration. The resulting estimates of the upper limit were about 13,000 in 1967-68, and 12,000 in 1968-69 and 1969-70.

Population Trends

In the decades prior to 1947, before legal protection was afforded by the International Convention for the Regulation of Whaling, the gray whale population is believed to have been considerably lower than it is now, but there are no quantitative data available upon which to base an estimate of its size during this period.

The estimated population size based upon four complete counts made at Point Loma from 1952-53 to 1959-60 (Gilmore, 1960a; Rice, 1961) showed a rather consistent increase of about 11 per cent per year. A regression analysis of the logarithms of these counts gives an estimate of the rate of population change as +12.2 per cent per year, with a 95 per cent confidence interval of -4.0 to +31.2 per cent. This study, however, has thrown doubt on the reliability of estimates of absolute population size based upon these counts.

The most questionable factor is the estimate of the extent of offshore movement, which Gilmore arbitrarily estimated at 5 per cent of the inshore movement. In contrast, present evidence indicates that offshore movement is about 144 per cent of the inshore movement along this stretch of coast.

The 1967-68 and 1968-69 counts at Point Loma were 44 and 51 per cent, respectively, below the 1959-60 count of 2344. Either some factor such as increase in small boat traffic has caused a larger proportion of the population to pass farther offshore at Point Loma, or the population in 1959-60 actually was much higher than estimated and has since decreased.

Hubbs and Hubbs (1967) made aerial surveys of the gray whale wintering grounds in Baja California between late January and early March in most years from 1952 to 1964. They suggested that the population increased from 1952 to 1954 and thereafter remained constant at about 3000. A regression analysis of the logarithms of their five complete counts from 1954 to 1964 gives an estimated rate of population change of +0.8 per cent per year, with a 95 per cent confidence interval of -4.5 to +6.4 per cent. Their estimate of absolute population size was based on an "admittedly rather intuitive estimate that about half of the population was observed on the flights." Between soundings, gray whales are at the surface or sufficiently near it to be visible for only about 1 out of every 5 minutes. Therefore, applying this correction to the data of Hubbs and Hubbs would give an estimate of about 7500 animals. Gilmore (1960a), who participated in some of these aerial counts, came to a similar conclusion.

In 1966-67, Adams (1968) made a partial count during the southward migration at Yankee Point. His counts were conducted only during periods of optimum visibility and included only 9.16 per cent of the daylight hours during the migration period. The number of whales actually counted was 1084. This count was adjusted to cover all daylight hours, increased by 5 per cent to account for offshore migration and 70 per cent for night migration, to yield a total estimate of 18,300. This estimate is probably too high because the counts were made only during limited periods when the most whales could be seen. Adams reported an average of up to 55 whales passing per hour, which extrapolates to a rate

of 550 per 10-hour day; we never counted more than 46 whales in one hour nor more than 197 per day during our full-time counts from 1967-68 to 1969-70.

Our counts at Yankee Point suggest that the population remained essentially stable from 1967-68 to the 1969-70 season.

Density and Biomass

Population density is ecologically most significant in relation to the feeding grounds. The summer range of the gray whale in the Bering and Chukchi seas occupies about 1,000,000 square kilometers. With a population of about 10,000, the average density is approximately one whale per 100 square kilometers. Density, of course, may vary markedly between different portions of the summer grounds (Berzin and Rovnin, 1966).

The total biomass of the gray whale population based on estimated numbers, sex and age structure, and mean body weights of each sex, age, and reproductive category is estimated at approximately 1.4×10^5 metric tons. The weight of an average gray whale is thus about 14 metric tons. The mean biomass on the summer grounds would thus be about 14 metric tons per 100 square kilometers, or 140 kilograms per square kilometer.

As a gray whale requires an estimated 19 kilocalories per kilogram per day, a 14-ton individual will require about 2.7×10^5 kilocalories per day, or 9.7×10^7 kilocalories per year. Inasmuch as gray whales must consume enough food during about half the year to sustain them the entire year, their daily energy requirements on the summer grounds would be about 5.3×10^5 kilocalories. Thus, if one kilogram of amphipods supplies 500 kilocalories, a gray whale weighing 14 tons must consume about a ton, or approximately 7 per cent of its weight, of amphipods per day.

The gray whale population consumes about 10 kilograms of food per day, or nearly 2 tons a year, per square kilometer. This quantity represents about 0.2 to 1.0 per cent of the standing crop of benthos (Neiman, 1963). Energy exchange amounts to 5.3×10^3 kilocalories per day. Although these figures are rough approximations, they provide some indication of the magnitude of the ecological role of the gray whale in the shallow waters of the Bering and Chukchi seas.

TABLE 15
SEX RATIOS OF GRAY WHALE AGE GROUPS.

Age group	No. males	No. females	Per cent males
Early fetuses	9	13	41
Near-term fetuses	30	25	55
Immatures	43	34	56
Adults	123	116	51
Combined total	205	188	52

Population Structure

SEX RATIO.—The combined sex ratio of fetal, immature, and adult gray whales was 52 per cent males to 48 per cent females (Table 15). In none of the age classes does the ratio differ significantly from one to one. The observed slight preponderance of males is probably not real, especially in view of the fact that lactating females were not represented in the sample.

TABLE 16
AGE COMPOSITION OF ADULT FEMALE COMPONENT OF SAMPLE BASED ON COUNTS OF CORPORA IN OVARIES.

Number of corpora	Estimated age (years)	Number of individuals
1	8-9	8
2	10-11	15
3	12-13	12
4	14-15	11
5	16-17	9
6	18-19	11
7	20-21	11
8	22-23	6
9	24-25	8
10	26-27	5
11	28-29	3
12	30-31	5
13	32-33	4
14	34-35	2
15	36-37	2
20	46-47	1
22	50-51	1
35	76-77	1

TABLE 17
AGE COMPOSITION OF GRAY WHALE SAMPLE BASED ON COUNTS OF GROWTH
LAYERS IN EAR PLUGS.

No. of growth layers	Estimated age (years)	Number of individuals		
		Males	Females	Total
2	1	3	5	8
3	2	5	2	7
4	3	2	1	3
5	4	4	2	6
6	5	3	4	7
7	6	5		5
8	7	7	5	12
9	8	3	3	6
10	9	5	3	8
11	10	6	3	9
12	11	3	5	8
13	12	6	4	10
14	13	6	1	7
15	14	2	1	3
16	15		3	3
17	16	4	2	6
18	17	3	1	4
19	18	3	3	6
20	19	3	5	8
21	20	6	1	7
22	21	4	1	5
23	22	2		2
24	23	1	4	5
25	24	1		1
26	25		1	1
27	26		1	1
28	27	1	2	3
29	28	2		2
30	29		2	2
33	32	1		1
35	34	1		1
38	37	1		1
40	39	4	1	5
41	40		1	1
47	46	1		1
48	47		1	1
58	57	1		1
70	69	1		1

AGE COMPOSITION.—Age composition of our sample, based on counts of corpora in the ovaries of adult females and counts of growth layers in the ear plugs of both sexes, is given in Tables 16 and 17. Although corpora counts are believed to be more

reliable than the data from ear plugs, the latter are useful because they are the only known means of determining the ages of males and of immature whales, and they permit a comparison between the sexes.

Immature whales comprised 24 per cent of the sample (26 per cent males, 23 per cent females). The data for this age class are biased because gunners select against smaller animals and because a larger proportion of immature whales have "readable" ear plugs. The proportion of immature whales in the population is certainly higher than indicated by our sample. If the apparent annual survival rate (S) of immature whales were the same as that of adults (0.92—see below) and sexual maturity were attained at 8 years of age, the proportion of immature whales 1 to 7 years old in the population would equal $1-S^7$, or 44 per cent. This is probably an underestimate, as the mortality of immatures is more likely to be greater than that of adults.

Another method of estimating the proportion of immature whales in the population based on the birth rate is applicable only if the population is stable. The birth rate is about 0.23 of the adult stock (see below). Since births must balance deaths in a stable population, the birth rate would be $(1-S)/S$, or 0.09 of the total stock alive at the beginning of the calving season. With a birth rate of 0.23 of the adult stock, the proportion of immature whales in the population would be $(0.23 - 0.09)/0.23$, or 61 per cent.

Population Dynamics

NATALITY.—On the basis of our estimate of a pregnancy rate in adult females of 0.46 per year and an assumption of an equal sex ratio, the birth rate in the California gray whale population is about 0.23 of the adult stock. As the present data indicate that adults constitute no more than 56 per cent of the population, the overall birth rate would not exceed 0.13. The approximate potential maximum rate of increase would approach this value.

MORTALITY.—The mean annual mortality rate of the adult female component of the sample, based on ages estimated from corpora counts, was calculated using Chapman and Robson's (1960) formula $M = 1 - (T/[N + T - 1])$, where M = annual mortality

rate and $T = \Sigma(\text{age}-8)$ (frequency). The resulting estimate of the mortality rate is 0.082.

The mortality rate for each sex was also calculated from the ear-plug data. As the proportion of immature whales in the sample is apparently biased, only whales of estimated ages of 8 years or older were used in the analysis, thus making the estimates directly comparable with those based on ovarian data. The resultant mortality values are 0.081 for males and 0.095 for females, which agree well with the estimates based on ovary analysis. They also indicate that there is probably little sex difference in mortality rate, a conclusion further supported by the essentially equal sex ratio at all ages.

Discussion and Conclusions

The California gray whale population was probably at least 8000 but less than 13,000 during the southward migration in 1969-70, with 11,000 being the most reasonable estimate.

Estimates of population size in earlier years based on shore counts at Point Loma (Gilmore, 1960*a*, 1960*b*; Rice, 1961) and aerial censuses in Baja California (Hubbs and Hubbs, 1967) are probably too low. However, they suggest that the population increased moderately from the early 1950's to 1960. The evidence for population trends from 1960 to 1967 is equivocal. The counts at Yankee Point suggest that the population has remained essentially stable from 1967-68 to 1969-70.

The sex ratio is about one to one at all ages. Probably at least 44 per cent of the population is sexually immature. The birth rate is 0.13 or slightly less. The age structure of the population suggests that the mortality rate has been 0.08. The size of any age class at a given time depends on its initial size and on its mortality rate. Therefore, the mortality rate calculated from the age composition represents the true mortality rate only if the initial size of each age class was the same, a situation likely to exist only in a stable population with a constant birth rate. In an increasing population with a constant birth rate, the initial size of each succeeding age class is greater. If the gray whale population was increasing at a rate of about 0.12 per year between 1952-53 and 1959-60, as the

counts from Point Loma suggest, mortality would have to have been almost zero to produce the observed age structure. A low mortality rate would be expected in an initially small, rapidly increasing population comprised predominantly of younger animals. Inasmuch as the population has been stable since 1967, the mortality rate must have increased to equal the birth rate, but this change would have been too recent to have had a noticeable effect on the age structure of the population. However, additional data are needed, particularly on the actual age structure of the immature segment of the population and on population trends, before recruitment and mortality can be more accurately estimated.

EXPLOITATION

Aboriginal Whaling

The Nootka, Makah, Quillayute, and Quinault Indians, the renowned aboriginal whalers living on the west coast of Vancouver Island and the State of Washington, regularly hunted gray whales since prehistoric times. Gray whale bones have been found in ancient middens near Lapush, Washington (Reagan, 1917). Indians chased whales in dugout canoes and struck them with harpoons attached to a line and float (Swan, 1870; Swanson, 1956; Waterman, 1920). Aboriginal whaling survived until 1928 on the coast of Washington (Anonymous, 1949).

Indians of the Kodiak Island and eastern Aleutian area killed whales with aconite-poisoned lances, a method also used by the Kamchadal in Kamchatka (Heizer, 1943). It is not known to what extent these people captured gray whales; their usual quarry was probably the right whale or the humpback whale.

The Koryaks who lived on the shores of Olyutorskiy Gulf north of the Kamchatka Peninsula in the 18th century regularly caught gray whales in large nets made of strips of walrus skin, which they set at the mouths of inlets (Krasheninnikov, 1755; Steller, 1774). Gray whales still are occasionally caught in this manner (Tomilin, 1957).

The Eskimos of Arctic Alaska and the Chukchi of eastern Siberia have for thousands of years hunted the bowhead whale and the gray whale from skin-covered "umiaks." In aboriginal times they used hand harpoons. After contact with American whalers in the late 19th century, they adopted the darting-gun and bomb-lance (Rainey, 1947). Whaling is still regularly practiced by the Eskimos of the villages of Barrow, Wainwright, and Point Hope on the Arctic coast of Alaska. In this area the catch is mostly bowhead whales. From 1954 through 1959, only nine gray whales were killed at Barrow and one at Wainwright (Maher, 1960). The natives of the village of Gambell on St. Lawrence Island (Francis H. Fay, personal communication) and the villages of Sireniki, Imtuk, Chaplino, Naukan, Uelen, and Enurmino on the Chukotskiy Peninsula

(Tomilin, 1957; Treshchev, 1966a) also still hunt whales. The catch in these areas is almost entirely gray whales. One hundred fourteen were killed in 1965 and 53 in 1966 off the Chukotskiy Peninsula (Zimushko, 1969a).

Commercial Whaling

Whaling in Japan dates back more than a thousand years, but it was not until about 1606 that commercial whaling was established. From the town of Taiji, the industry spread rapidly throughout the islands. At first, hand harpoons were used, but in 1674 the use of nets was introduced and widely adopted. Early 19th century Japanese illustrations show that gray whales were hunted in addition to the commonly taken right and humpback whales (Fraser, 1937; Japanese Fisheries Agency, 1954; Omura *et al.*, 1953).

The possibility that gray whales survived in the North Atlantic until the early 18th century and were pursued by New England whalers is suggested by Dudley's (1725) account of the enigmatic "scrag whale" mentioned earlier.

During the late 18th and 19th centuries the American high-seas, open-boat whale fishery developed and gradually spread to all oceans. In 1846, the whalers discovered the winter grounds of the Pacific gray whale along the west coast of Baja California. Scammon (1874) estimated the gray whale population as "probably not over 30,000" between 1853 and 1856. The annual congregations of gray whales in the lagoons attracted the American whalers, and by the winter of 1860-61 about 60 whaling vessels were engaged in lagoon whaling in Baja California (Starks, 1922). The first shore whaling station was established in 1854 (Starks, 1922), and by 1874, 11 shore stations were operating along the coast of California and Baja California (Scammon, 1874; Jordan, *in* Clark, 1887). Scammon estimated that about 10,800 gray whales were killed there between 1846 and 1874. Others were killed in the Bering Sea and Arctic Ocean. Scammon estimated the population of gray whales as 8000 to 10,000 in 1874. By 1886 only five shore whaling stations remained; they took 58 gray whales in 1883-84, 68 in 1884-85, and 41 in 1885-86 (Townsend, 1887). During the latter season, Townsend estimated that only 160 southbound gray whales passed

San Simeon, California, in December and January. Regular shore whaling ceased about 1900 (Starks, 1922).

During the early 20th century there was little exploitation of gray whales, although American whaling ships doubtless took a few; 31 were taken in waters off Mexico and California, and one off Alaska, by the whaling schooner "Carolyn Frances" as late as 1921 (Starks, 1922; Bower, 1923). During this period the stock probably increased.

The perfection of the modern harpoon gun in 1864 by the Norwegian whaler Svend Foyn ushered in the era of modern whaling. Captain H. G. Melsom of the Toyo Hogeï Kabushiki Kaisha [Oriental Whaling Co., Ltd.] of Osaka, Japan, inaugurated a winter fishery for the gray whale at a shore station at Ulsan on the east coast of Korea, about 1899 (Andrews, 1914). A total of 1474 gray whales was killed off Korea from 1910 to 1933. Catches were declining by the 1920's, and whaling ceased after 1933, when only two gray whales were taken. This rapid decline suggests that the Korean stock numbered only some 1000 to 1500 whales in 1910, and was virtually extinct by 1933.

Exploitation of the California stock of gray whales by modern methods began with the establishment of several shore whaling stations along the west coast of North America, the first in 1905. Few gray whales were killed, however, because they were rare and could be taken only during the winter and early spring when the weather was bad. The few taken were brought into the stations at Port Hobron on Sitkalidak Island and Port Armstrong on Baranof Island, Alaska, Bay City, Washington, and Trinidad and Moss Landing, California.

The introduction of floating factory ships gave modern whalers a mobility that greatly increased their efficiency. Because whales were flensed while floating alongside the ship, these early floating factories could operate only in sheltered anchorages. A Norwegian factory ship, "Capella I," took 19 gray whales off Baja California in the spring of 1914. From 1924-25 until 1928-29, Norwegian whaling interests operated factory ships each winter and spring at Bahia Magdalena and other points along the coast of Baja California. Catches of gray whales steadily declined from 100 in 1924-25 to two in 1928-29 as the whalers turned their attention

TABLE 18
RECORDED CATCH OF GRAY WHALES BY MODERN STYLE WHALING FROM 1910 TO
1946. SEE TEXT FOR SOURCES OF DATA.

Year	California stock												Korean ¹ stock	
	Baja California		California		Wash- ington	Alaska		Bering and Chukchi seas		Total				
	Fl. F. <i>Capella I</i>	Fl. F. <i>Kommandören I</i>	Fl. F. <i>Mexico</i>	Fl. F. <i>Esperanza</i>	Sh. St. Moss Landing	Sh. St. Trinidad	Fl. F. <i>Lansing</i>	Sh. St. Bay City	Sh. St. Port Armstrong	Sh. St. Port Hobron	Fl. F. <i>Kommandören I</i>	Fl. F. <i>Aleut</i>		Fl. F. <i>Tonan Maru</i>
1910														6
1911														121
1912														193
1913									1			1		131
1914	19											19		155
1915														139
1916														178
1917														69
1918														104
1919														46
1920					2							2		68
1921					1							1		78
1922					5							5		40
1923														27
1924								1				1		17
1925		82	18								33	133		10
1926		36	5			1						42		11
1927		16		13			3					32		10
1928				9			1			2		12		9
1929				2								2		12
1930														30
1931														11
1932														7
1933										2	2	4		2
1934											54	54		
1935											34	34		
1936											102	102		
1937											14	14		
1938											54	54		
1939											29	29		
1940											47	58	105	
1941											57	57		
1942											101	101		1
1943											77	77		
1944														
1945											30	30		
1946											22	22		

¹ Catch by shore stations, almost all in Korea; for particulars see Mizue (1951). The whale taken in 1942 was killed in the Kuril Islands.

to the abundant and more profitable blue and humpback whales. A total of 181 gray whales was killed during these five seasons. One of these Norwegian factory ships, the "Kommandören I," took 33 gray whales in Natal'inskiy Bay, northeastern Kamchatka, in the summer of 1925. An American floating factory, the "Lansing," began operating in California in 1927. In 1932 she was replaced by the "California," which operated until 1937.

The invention of the stern slipway in 1925 made it possible to haul whales aboard the factory ship, thus permitting whalers to operate on the high seas and freeing them from regulation by national governments. The Soviet floating factory "Aleut" began operating in the western Bering Sea in 1933. Gray whales were an important part of her catch. The Japanese floating factory "Tonan Maru" took 58 gray whales in the Chukchi Sea in 1940, and the "Aleut" continued to take gray whales until 1946. From 1933 to 1946, a total of 681 gray whales was killed in the Bering and Chukchi seas. Annual catches provide no clear evidence of any changes in population size during this period.

The 1937 International Agreement for the Regulation of Whaling, which forbade the killing of gray whales, was adhered to by the governments of many whaling nations, including the United States, Canada, and Mexico, but not Japan or the Soviet Union. The 1946 International Convention for the Regulation of Whaling was ratified by the Governments of 17 nations, including Canada, Japan, Mexico, the Soviet Union, and the United States. This convention forbids the killing of gray whales, except by aborigines or a contracting government on behalf of aborigines and only when the meat and products are to be used exclusively for local consumption by the aborigines. Contracting governments may also grant special permits authorizing the collecting of gray whales for scientific research.

Statistics on catches of gray whales by modern style whaling as published in the International Whaling Statistics (IWS) are incomplete and in some instances erroneous; many data from prior to 1937 are combined under the category "North Pacific." We have attempted to compile a complete record of all gray whales killed from 1910 to 1946 (Table 18). No data are available on Korean catches before 1910. Although modern style whaling began on the

west coast of North America in 1905, no gray whales were killed until 1913. No gray whales have been taken commercially since the International Convention for the Regulation of Whaling went into effect in 1947, except for one taken in error by the shore station at Coal Harbour, British Columbia, in 1951. In 1953, 10 specimens were taken under a special scientific permit at Coal Harbour. As far as we can ascertain, these statistics are complete except for possible catches off California during the years 1930 and 1932-36, as noted below, and for any that might be included under a few unspecified whales taken in California, British Columbia, and Alaska. The sources of our data for each area in which modern whaling has been conducted are given below.

Baja California.—Data on the 1914 catch of the floating factory "Capella I" are from Tønnessen (1967). Catch figures for 1924-25 through 1929 and for 1935 are from original daily catch records submitted by whaling companies to the Bureau of International Whaling Statistics and kindly made available by Einar Vangstein.

California.—Data from 1918 through 1929 are from Starks (1922), Radcliffe (1933), and Kellogg (1931). Catch statistics by species are not available for the floating factory "Lansing" in 1930 or the floating factory "California" from 1932 through 1936 (total catches for all species are listed in the annual statistical issues of "Pacific Fisherman"). No whaling was conducted in 1931. Catch statistics subsequent to 1936 are from files of the U. S. Bureau of Commercial Fisheries.

Washington.—Catch statistics of the shore station at Bay City, Washington, from 1911 to 1925, as compiled by Scheffer and Slipp (1948).

British Columbia.—Catch statistics for 1905 through 1946, compiled by Gordon Pike (1962*b*) from Annual Reports of the Canadian Department of Fisheries, list no gray whales.

Alaska.—Catch statistics are on file with the U. S. Bureau of Commercial Fisheries.

Bering and Chukchi seas.—Catch statistics for the Norwegian floating factory "Kommandören I" are from IWS, those for the Soviet floating factory "Aleut" are from Sleptsov (1955), and those

for the Japanese floating factory "Tonan Maru" are from Sakiura *et al.* (1953).

Korea.—Catches by Korean shore stations are from Mizue (1951) and IWS. Their figures for the period 1920 to 1930 are erroneous; correct figures were published by Tønnessen (1967) and in Norsk Hvalfangst-Tidende, 16:13 (1927), 19:161 (1930), and 20:142 (1931).

Kuril Islands.—Mizue (1951) recorded one gray whale taken by a shore station at Otomae (on Shiashkotan Island), in the northern Kuril Islands, in 1942; this locality is outside the normal range of the species.

SUMMARY

1. This study is based on data obtained from 316 gray whales collected off the coast of central California between 1959 and 1969 and on field observations. The latter included counts of southward migrating whales from shore stations during the winters of 1967-68 to 1969-70, observations made during cruises off California and Mexico from 1962 to 1969, and aerial observations along the coast of Washington, Oregon, and California in 1969. In addition, the stomach contents of a gray whale killed by Eskimos at St. Lawrence Island, Alaska, were analyzed.

2. Gray whales usually travel within a few kilometers of shore while migrating from their summer grounds in the Bering and Chukchi seas to their winter grounds along the coast of Baja California, but off southern California the majority take a more direct offshore route from Point Conception to northern Baja California. The northward migration follows the same route, except that females with calves apparently travel offshore. Migrating gray whales swim at about 8.5 kilometers per hour; on the southward migration they travel about 185 kilometers per day. There is no evidence that the whales travel slower at night than during daylight. Migrating gray whales are temporally segregated according to sex, age, and reproductive status. During southward migration, the sequence of passage is as follows: females in late pregnancy, females that have recently ovulated, adult males, immature females, and immature males. During northward migration, the sequence is as follows: newly pregnant females, anestrus females, adult males, immature females, immature males, and postpartum females. The earliest southbound migrants (mostly late pregnant females) usually travel singly, whereas later migrants usually are in pods of two or more.

3. Food of gray whales on their summer grounds in the northern Bering and Chukchi seas includes at least 17 species of benthic gammaridean amphipods, among which *Ampelisca macrocephala* predominates. The nature of the food indicates that gray whales are bottom feeders. Virtually no food is consumed during migration,

although rarely small quantities of decapod nauplii (*Pachycheles rudis* and ?*Fabia* sp.) are eaten. There is little evidence that gray whales feed on their winter grounds off Baja California. In the interval between their southward and northward migration past San Francisco, the whales lose from 0.21 to 0.37 per cent of their body weight per day. This weight reduction is sufficient to account for the estimated energy expenditure during the winter. Blubber thickness and oil yield also decrease during winter.

4. Age may be estimated from the number of growth layers in the ear plug, indirect evidence suggesting that two layers are formed the first year and one each year thereafter. However, the value of ear plugs for age determination is limited because many plugs do not have clear laminations, and earlier laminations may disappear in older animals. The number of corpora albicantia in the ovaries provides a more reliable estimate of the age of adult females. Growth zones in the baleen plates are of little use for age determination because of rapid wear.

5. Mean body length at birth is about 4.9 meters. Mean length at weaning at an age of 7 months is about 8.5 meters. Puberty is attained at an estimated mean age of 8 years (range, 5 to 11 years) and a mean body length of about 11.1 meters in males and 11.7 meters in females. Physical maturity is attained at about 40 years at a mean body length of about 13.0 meters in males and 14.1 meters in females.

6. Ontogenetic changes in body proportions are slight. From late fetal life to a year of age, relative length of the flippers decreases and relative length of the tail increases. There are no significant changes in body proportions between the end of the first year and physical maturity. Females have slightly shorter flippers and longer tails than do males.

7. In immature females, seasonal enlargement of the follicles begins at a body length of about 9.9 meters and an age of 2 or 3 years. Mean weight of individual ovaries increases rapidly from about 140 to 300 grams when body length reaches about 11.3 meters at about 5 years of age. The ovaries weigh about 340 grams at sexual maturity and continue to increase slowly throughout life,

reaching about 646 grams at 50 years of age. The uterine cornua are 3.5 to 12.0 centimeters in diameter in immature females and more than 11.0 centimeters in adult females. The mammary glands do not develop until the female is well into her first pregnancy.

8. Female gray whales normally come into estrus biennially in late November and early December. Most individuals ovulate only once each season, although whales failing to conceive after their first ovulation may experience a second estrous cycle the same season. Multiple ovulations are extremely rare. Mean ovulation rates are 1.20 per breeding season for nulliparous females and 0.96 per breeding season (0.52 per year) for parous females. There is no evidence for postpartum ovulation or for ovulation at any other time of year. However, increase in follicle size following stillbirth or early loss of the calf suggests that females might ovulate following such an event. Females continue to breed at an advanced age. Corpora lutea of pregnancy average 8.7 centimeters in diameter, whereas corpora lutea of ovulation do not exceed 2.5 centimeters (at least if another estrous cycle soon follows). Corpora albicantia derived from corpora lutea of ovulation are indistinguishable from those derived from corpora lutea of pregnancy. Corpora albicantia persist in the ovaries throughout life. About 55 per cent of ovulations occur in the left ovary and 61 per cent occur in the anterior half of the ovaries.

9. Most conceptions occur within a 3-week period during southward migration, with a peak about 5 December. The pregnancy rate is 0.86 per breeding season (0.46 per year). The gestation period is about 13 months, and fetal growth is accelerated during the last half of pregnancy. During southward migration, late pregnant females (exclusive of their conceptus) average 25 to 30 per cent heavier than the other adult females. Births occur within a period of 5 to 6 weeks, with a peak occurring about 10 January. Caudal presentation at birth is normal.

10. Lactation lasts an average of about 7 months, ending in August.

11. Females are usually in anestrus from August to November or December. However, females that fail to ovulate or conceive

during the winter are probably in anestrus for the following 12 months.

12. In immature males, the weight of both testes is usually less than 5 kilograms, and the seminiferous tubules average 45 to 102 microns in diameter. Testis weight of sexually mature males is more than 5 kilograms, and the average diameter of the seminiferous tubules exceeds 104 microns. Penis length is correlated with body length and is usually less than 1.1 meters in immature males.

13. The average weight of the testes of adult males during southward migration in December and January is 38 kilograms, and the mean diameter of the seminiferous tubules is 177 microns. During northward migration in February and March, mean testes weight and tubule diameter are 22 kilograms and 148 microns, respectively. From July through October, the testes average 23 kilograms. These differences suggest a marked seasonal sexual cycle in the male, with a peak of spermatogenetic activity in autumn or early winter.

14. The killer whale, *Orcinus orca*, appears to be the only predator on gray whales. The mortality rate from killer whale attacks is unknown. However, frequency of tooth scars indicate that killer whale attacks on gray whales are often unsuccessful.

15. Epizoots of gray whales include the following (percentage of occurrence in parentheses): the barnacle *Cryptolepas rhachianecti* (100) and the cyamids *Cyamus scammoni* (99.7), *C. ceti* (99.4), and *C. kessleri* (98.1). Endoparasites collected include the trematodes *Lecithodesmus goliath* (0.6), *Ogmogaster pentalineatus* (more than 22), and *O. antarcticus* (33); two apparently undescribed species of the cestode *Priapocephalus*, one in the small intestine (30) and the other in the large intestine (0.3); the nematode *Anisakis simplex* (0.3); and two acanthocephalans, *Corynosoma* sp. (5.7) and *Bolbosoma* sp. (0.3). Obvious pathogenic effects were noted only for the liver fluke, *Lecithodesmus goliath*.

16. Population size of the California stock during the southward migration of 1969-70 was estimated to be about 11,000. Although previously published estimates of numbers of the California stock are questionable, the population appears to have increased from

1947 to 1960. Trends from 1960 to 1967 are uncertain. Since 1967, population size has remained essentially stable.

17. The sex ratio is essentially equal in all age groups. The birth rate does not exceed 0.13. The calculated annual death rate of adults is 0.08. This is probably an overestimate, although, if the population is now stable, the death rate must have recently increased to near the birth rate.

18. The California gray whale stock was severely overexploited between 1846 and 1900. During the present century this population has been only lightly exploited. Factory ships took an average of 36 gray whales per year in Mexico from 1924-25 to 1928-29 and an average of 48 per year in the Bering Sea from 1933 to 1946. Since then the species has been protected from commercial whaling by the International Convention for the Regulation of Whaling. The Korean stock was virtually exterminated between 1899 and 1933.

LITERATURE CITED

- ADAMS, L. 1968. Census of the gray whale, 1966-67. Norsk Hvalfangst-Tidende, 57:41-43.
- ALLEN, G. M. 1916. The whalebone whales of New England. Mem. Boston Soc. Nat. Hist., 8:105-322.
- AMERICAN SOCIETY OF MAMMALOGISTS. 1967. [Resolutions adopted at 47th annual meeting]. J. Mamm., 48:714-715.
- ANDREWS, R. C. 1909. Observations on the habits of the finback and humpback whales of the eastern North Pacific. Bull. Amer. Mus. Nat. Hist., 26:213-226.
- . 1914. Monographs of the Pacific Cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). Mem. Amer. Mus. Nat. Hist. (New Ser.), 1:227-287.
- ANONYMOUS. 1949. Whaling—as the Quinault Indians used to harpoon 'em. Internat. Fisherman and Allied Worker, Sept., p. 6.
- ASH, C. E. 1952. The body weights of whales. Norsk Hvalfangst-Tidende, 41:364-374.
- BAER, J. G. 1954. Revision taxonomique et étude biologique des Cestodes de la famille des Tetrabothriidae. Mém. Univ. Neuchatel, 121 pp.
- BARABASH-NIKIFOROV, I. 1938. Mammals of the Commander Islands and the surrounding sea. J. Mamm., 19:423-429.
- BARNARD, J. L. 1969. The families and genera of marine gammaridean Amphipoda. Bull. U.S. Nat. Mus., 271:1-535.
- BENEDICT, F. G. 1938. Vital energetics. Carnegie Inst. Washington, Publ. 503, 215 pp.
- BERLAND, B. 1961. Nematodes from some Norwegian marine fishes. Sarsia, 2:1-50.
- BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth. Human Biol., 10:181-213.
- BERZIN, A. A., AND A. A. ROVNIN. 1966. Raspredelenie i migratsii kitov v severo-vostochnoi chasti Tikhogo Okeana, v Beringovom i Chukotskom Moryakh [Distribution and migrations of whales in the north-east part of the Pacific Ocean, Bering and Chukchi seas]. Izv. TINRO, 58:179-207 (in Russian).
- BEST, P. B. 1967. The sperm whale (*Physeter catodon*) off the west coast of South Africa. I. Ovarian changes and their significance. Invest. Rep. Div. Sea Fish. South Africa, 61:1-27.
- . 1968. The polarity of sperm whale ovaries. Norsk Hvalfangst-Tidende, 57:43-45.
- BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Min. Agr., Fish. and Food, Fish. Invest., Ser. 2, 19:1-533.
- BISHOP, D. W. 1950. Respiration and metabolism. Pp. 209-289, in Comparative animal physiology (C. L. Prosser, ed.), W. B. Saunders Co., Philadelphia.
- BOWER, W. T. 1923. Alaska fishery and fur-seal industries in 1921. Rep. U. S. Comm. Fish. for 1922, Appendix 10, 85 pp.
- BOYD, C. M. 1967. The benthic and pelagic habits of the red crab, *Pleuroncodes planipes*. Pacific Sci., 21:394-403.

- BRODY, S. 1945. Bioenergetics and growth. Reinhold Publ. Corp., New York, 1023 pp.
- BURRAGE, B. R. 1964. An observation regarding gray whales and killer whales. Trans. Kansas Acad. Sci., 67:550-551.
- BUSS, I. O., AND N. S. SMITH. 1966. Observations on reproduction and breeding behavior of the African elephant. J. Wildlife Mgt., 30:375-388.
- CALDWELL, D. K., AND M. C. CALDWELL. 1968. The dolphin observed. Nat. Hist., 77(8):58-65.
- CEDERLUND, B. A. 1939. A subfossil gray whale discovered in Sweden in 1859. Zool. Bidr. Uppsala, 18:269-285.
- CHAPMAN, D. G., AND D. S. ROBSON. 1960. The analysis of a catch curve. Biometrika, 16:354-368.
- CHITTLEBOROUGH, R. G. 1954. Studies on the ovaries of the humpback whale, *Megaptera nodosa* (Bonnaterre), on the western Australian coast. Australian J. Marine Freshwater Res., 5:35-63.
- . 1955. Aspects of reproduction in the male humpback whale, *Megaptera nodosa* (Bonnaterre). Australian J. Marine Freshwater Res., 6: 1-29.
- . 1958. The breeding cycle of the female humpback whale, *Megaptera nodosa* (Bonnaterre). Australian J. Marine Freshwater Res., 9:1-18.
- . 1959. Determination of age in the humpback whale, *Megaptera nodosa* (Bonnaterre). Australian J. Marine Freshwater Res., 10:125-143.
- . 1965. Dynamics of two populations of the humpback whale. Australian J. Marine Freshwater Res., 16:33-128.
- CLARK, A. H. 1887. The whale fishery. 1. History and present condition of the fishery. The fisheries and fishery industries of the United States (G. B. Goode, ed.), U. S. Govt. Printing Office, Washington, D. C., Sec. 5, 2:3-218.
- COMRIE, L. C., AND A. B. ADAM. 1938. The female reproductive system and corpora lutea of the false killer whale, *Pseudorca crassidens* Owen. Trans. Royal Soc. Edinburgh, 59:521-531.
- COPE, E. D. 1868. On *Agaphelus*, a genus of toothless Cetacea. Proc. Acad. Nat. Sci. Philadelphia, 20:225.
- CUMMINGS, W. C., P. O. THOMPSON, AND R. COOK. 1968. Underwater sounds of migrating gray whales, *Eschrichtius glaucus* (Cope). J. Acoust. Soc. Amer., 44:1278-1281.
- DARWIN, C. 1854. A monograph on the sub-class Cirripedia . . . the Balanidae (or sessile cirripedes) . . . Ray Soc., London, 8 + 684 pp.
- DAWBIN, W. H. 1966. The seasonal migratory cycle of humpback whales. Pp. 145-170, in Whales, dolphins, and porpoises (K. S. Norris, ed.), Univ. California Press, Berkeley and Los Angeles.
- DEINSE, A. B. VAN, AND G. C. A. JUNGE. 1937. Recent and older finds of the California gray whale in the Atlantic. Temminckia, 2:161-188.
- DELYAMURE, S. L. 1955. Gel'mintofauna morskikh mlekopitayushchikh v svete ikh ekologii i filogenii [Helminthofauna of marine mammals—ecology and phylogeny]. Akad. Nauk SSSR, Moscow, 517 pp. [Translated by the Israel Program for Scientific Translations, Jerusalem, 1968, 522 pp.]
- DEMPSEY, E. W., AND G. B. WISLOCKI. 1941. The structure of the ovary of the humpback whale (*Megaptera nodosa*). Anat. Rec., 80:243-257.

- DITMAR, K. VON. 1890-1900. Reisen und Aufenthalt in Kamchatka in den Jahren 1851-1855. Akad. Nauk, St. Petersburg. 2 vols., 865 + 273 pp. [Not seen; cited from Tomilin, 1957.]
- DUDLEY, P. 1725. An essay upon the natural history of whales. Phil. Trans. Royal Soc. London, 33:256-269.
- EBERHARDT, R. L., AND K. S. NORRIS. 1964. Observations of newborn Pacific gray whales on Mexican calving grounds. J. Mamm., 45:88-95.
- ERXLEBEN, J. C. P. 1777. Systema regni animalis . . . Classis I. Mammalia. Lipsiae, 48 + 636 + 64 pp.
- ESCHRICHT, D. F., AND J. REINHARDT. 1866. On the Greenland right whale (*Balaena mysticetus*, Linn.). Ray Soc., London, 150 pp.
- FAY, F. H. 1963. Unusual behavior of gray whales in summer. Psychol. Forsch., 27:175-176.
- FRASER, F. C. 1937. Early Japanese whaling. Proc. Linn. Soc., London, 150: 19-20.
- GAMBELL, R. 1968. Seasonal cycles and reproduction in sei whales of the southern hemisphere. Discovery Rep., 35:31-134.
- GILMORE, R. M. 1960a. A census of the California gray whale. U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 342, 30 pp.
- . 1960b. Census and migration of the California gray whale. Norsk Hvalfangst-Tidende, 49:409-431.
- . 1961. The story of the gray whale. Privately published, San Diego, 2d ed., 16 pp.
- GILMORE, R. M., R. L. BROWNELL, JR., J. G. MILLS, AND A. HARRISON. 1967. Gray whales near Yavaros, southern Sonora, Golfo de California, Mexico. Trans. San Diego Soc. Nat. Hist., 14:198-203.
- GILMORE, R. M., AND G. EWING. 1954. Calving of the California grays. Pacific Discovery, 7(3):13-15.
- GOLVAN, Y. J. 1959. Acanthocephales du genre *Corynosoma* Lühe 1904, parasites de mammifères d'Alaska et de Midway. Ann. Parasitol. Hum. Comp., 34:288-321.
- GRAY, J. E. 1864. Notes on the whalebone-whales; with a synopsis of the species. Ann. Mag. Nat. Hist., ser. 3, 14:345-353.
- GREBNITSKII, N. A. 1902. Komandorskie Ostrova [The Commander Islands]. Izd. Dep. Zemled., St. Petersburg. [Not seen; cited from Tomilin, 1957.]
- GUNTHER, E. R. 1949. The habits of fin whales. Discovery Rep., 25:113-142.
- GUR'YANOVA, E. F. 1955. Amphipoda. Pp. 132-144, in Atlas bespozvonochnykh dal'nevostochnykh morei SSSR (E. N. Pavlovskii, ed.), Akad. Nauk SSSR, Moscow and Leningrad. [Amphipoda. Pp. 180-196, in Atlas of the invertebrates of the far eastern seas of the USSR. Translated by the Israel Program for Scientific Translations, Jerusalem, 1966.]
- HARRISON, R. J. 1949. Observations on the female reproductive organs of the ca'ing whale *Globicephala melaena* Traill. J. Anat., 83:238-253.
- . 1969. Reproduction and reproductive organs. Pp. 253-348, in The biology of marine mammals (H. T. Andersen, ed.), Academic Press, New York and London.
- HARVEY, L. A. 1963. Whale biology: exercises in deduction and extrapolation. Sci. Progr., 51:105-113.
- HEIZER, R. F. 1943. Aconite poison whaling in Asia and America: an Aleutian transfer to the New World. Bull. Bur. Amer. Ethnol., 133:415-468.

- HERSHKOVITZ, P. 1966. Catalog of living whales. Bull. U. S. Nat. Mus., 246: 1-259.
- HOUCK, W. J. 1962. Possible mating of grey whales on the northern California coast. Murrelet, 43:54.
- HOWELL, A. B., AND L. M. HUEY. 1930. Food of the gray and other whales. J. Mamm., 11:321-322.
- HUBBS, C. L. 1959. Natural history of the gray whale. Proc. XVth Internat. Congress Zool., pp. 313-316.
- HUBBS, C. L., AND L. C. HUBBS. 1967. Gray whale censuses by airplane in Mexico. California Fish and Game, 53:23-27.
- HUGGETT, A. ST. G., AND W. F. WIDDAS. 1951. The relationship between mammalian foetal weight and conception age. J. Physiol., 114:306-317.
- HURLEY, D. E., AND J. L. MOHR. 1957. On whale-lice (Amphipoda: Cyamidae) from the California gray whale, *Eschrichtius glaucus*. J. Parasitol., 43:352-357.
- ICHIHARA, T. 1958. Gray whale observed in the Bering Sea. Sci. Rep. Whales Res. Inst., 13:201-206.
- . 1966. Criterion for determining age of fin whale with reference to ear plug and baleen plate. Sci. Rep. Whales Res. Inst., 20:17-82.
- IRVING, L., P. F. SCHOLANDER, AND S. W. GRINNELL. 1941. The respiration of the porpoise, *Tursiops truncatus*. J. Cell. Comp. Physiol., 17:145-168.
- JAPANESE FISHERIES AGENCY. 1954. Japanese whaling industry. Japan Whaling Assoc., Tokyo, 50 pp.
- JONSGÅRD, A. 1951. Studies on the little piked whale or minke whale (*Balaenoptera acuto-rostrata* Lacépède); report on Norwegian investigations carried out in the years 1943-1950. Norsk Hvalfangst-Tidende, 40: 209-232.
- . 1968. A note on the attacking behaviour of the killer whale (*Orcinus orca*). Norsk Hvalfangst-Tidende, 57:84-85.
- . 1969. Age determination of marine mammals. Pp. 1-30, in The biology of marine mammals (H. T. Andersen, ed.), Academic Press, New York and London.
- KANNEWORFF, E. 1965. Life cycle, food, and growth of the amphipod *Ampelisca macrocephala* Liljeborg from the Øresund. Ophelia, 2:305-318.
- KANWISHER, J., AND G. SUNDNES. 1966. Thermal regulation in cetaceans. Pp. 397-409, in Whales, dolphins, and porpoises (K. S. Norris, ed.), Univ. California Press, Berkeley and Los Angeles.
- KASUYA, T., AND D. W. RICE. 1970. Notes on baleen plates and on arrangement of parasitic barnacles of gray whale. Sci. Rep. Whales Res. Inst., 22: 39-43.
- KELLOGG, R. 1931. Whaling statistics for the Pacific Coast of North America. J. Mamm., 12:73-77.
- KENYON, K. W., AND D. W. RICE. 1959. Life history of the Hawaiian monk seal. Pacific Sci., 13:215-252.
- KRASHENINNIKOV, S. P. 1755. Opisanie zemli Kaïchatki [Description of the land Kamchatka]. Imper. Akad. Nauk, St. Petersburg, 2 vols., 438 + 319 pp.
- LAWS, R. M. 1957. Polarity of whale ovaries. Nature, 179:1011-1012.
- . 1959. The foetal growth rates of whales, with special reference to the fin whale, *Balaenoptera physalus* Linn. Discovery Rep., 29: 281-308.

- . 1961. Reproduction, growth and age of southern fin whales. *Discovery Rep.*, 31:327-486.
- . 1962. Some effects of whaling on the southern stocks of baleen whales. Pp. 137-158, in *The exploitation of natural animal populations* (R. F. LeCren and M. W. Holdgate, eds.), John Wiley & Sons, Inc., New York.
- LAW, R. M., AND P. E. PURVES. 1956. The ear plug of the Mysticeti as an indication of age with special reference to the North Atlantic fin whale (*Balaenoptera physalus* Linn.). *Norsk Hvalfangst-Tidende*, 45: 413-425.
- LENNEP, E. W. VAN. 1950. Histology of the corpora lutea in blue and fin whale ovaries. *Proc. Kon. Ned. Akad. Wet.*, 53:593-599.
- LEUNG, Y. M. 1965. A collection of whale-lice (Cyamidae: Amphipoda). *Bull. S. California Acad. Sci.*, 64:132-143.
- . 1967. An illustrated key to the species of whale-lice (Amphipoda, Cyamidae), ectoparasites of Cetacea, with a guide to the literature. *Crustaceana*, 12:278-291.
- LILLJEBORG, W. 1861. Hvalben funna i jorden på Gräsön i Roslagen i Sverige. *Forhandl. Skand. Naturf.*, 8 de Møde, Kjöbenhavn, 1860:599-616.
- MACKINTOSH, N. A. 1965. The stocks of whales. *Fishing News (Books) Ltd.*, London, 232 pp.
- MACKINTOSH, N. A., AND J. F. G. WHEELER. 1929. Southern blue and fin whales. *Discovery Rep.*, 1:257-539.
- MAHER, W. J. 1960. Recent records of the California gray whale (*Eschrichtius glaucus*) along the north coast of Alaska. *Arctic*, 13:257-265.
- MARKOWSKI, S. 1955. Cestodes of whales and dolphins from the Discovery collections. *Discovery Rep.*, 27:377-395.
- MARX, W. 1966. An eviction of whales. *Atlantic*, 217(4):91-95.
- MATTHEWS, L. H. 1932. Lobster-krill, anomuran crustacea that are the food of whales. *Discovery Rep.*, 5:467-484.
- . 1937. The humpback whale, *Megaptera nodosa*. *Discovery Rep.*, 17:7-92.
- . 1938. The sei whale, *Balaenoptera borealis*. *Discovery Rep.*, 17: 183-290.
- . 1948. Cyclic changes in the uterine mucosa of balaenopterid whales. *J. Anat.*, 82:207-232.
- MECH, L. D. 1966. The wolves of Isle Royale. *U. S. Nat. Park Serv., Fauna Ser.*, 7:1-210.
- MIZUE, K. 1951. Gray whales in the east sea area of Korea. *Sci. Rep. Whales Res. Inst.*, 5:71-79.
- MOREJOHN, G. V. 1968. A killer whale—gray whale encounter. *J. Mamm.*, 49:327-328.
- MURAV'eva, S. I., AND V. V. TRESHCHEV. 1970. Novaya tsestoda—*Priapocephalus eschrichtii* sp. n. (Cestode, Tetrabothriidae)—parazit serogo kita iz Chukotskogo Morya [New cestoda—*Priapocephalus eschrichtii* sp. n. (Tetrabothriidae)—a parasite of grey whale (*Eschrichtius gibbosus* Erxleben, 1777) from the Chukotsk Sea]. *Vestnik Zool., Akad. Nauk Ukr. SSR*, 1970:84-86 (Russian with English summary).
- NASU, K. 1960. Oceanographic investigation in the Chukchi Sea during the summer of 1958. *Sci. Rep. Whales Res. Inst.*, 15:143-157.

- NEIMAN, A. A. 1963. Kolichestvennoe raspredelenie bentosa i kormovaya baza donnykh ryb v vostochnoi chasti Beringova morya [Quantitative distribution of benthos and the food supply of benthic fish in the eastern Bering Sea]. Trudy VNIRO, 48:145-205.
- NIKULIN, P. G. 1946. O raspredelenii kitoobraznykh v moryakh omyvayushchikh Chukotskii Poluostrov [Concerning the distribution of whales in seas adjacent to the Chukotskiy Peninsula]. Izv. TINRO, 22: 255-257.
- NISHIWAKI, M. 1959. Humpback whales in Ryukyuan waters. Sci. Rep. Whales Res. Inst., 14:49-87.
- NISHIWAKI, M., AND C. HANDA. 1958. Killer whales caught in the coastal waters off Japan for recent 10 years. Sci. Rep. Whales Res. Inst., 13:85-96.
- NISHIWAKI, M., T. ICHIHARA, AND S. OHSUMI. 1958. Age studies of fin whales based on ear plug. Sci. Rep. Whales Res. Inst., 13:155-169.
- NISHIWAKI, M., AND T. OYE. 1951. Biological investigation on blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) caught by the Japanese Antarctic whaling fleets. Sci. Rep. Whales Res. Inst., 5:91-167.
- NORTH PACIFIC FUR SEAL COMMISSION. 1963. Glossary of terms used in fur seal management. U. S. Fish Wildl. Serv., Fish. Leaflet 546, 9 pp.
- OHSUMI, S. 1960. Relative growth of the fin whale *Balaenoptera physalus* (Linn.). Sci. Rep. Whales Res. Inst., 15:17-84.
- . 1964a. Examination on age determination of the fin whale. Sci. Rep. Whales Res. Inst., 18:49-88.
- . 1964b. Comparison of maturity and accumulation rate of corpora albicantia between left and right ovaries in Cetacea. Sci. Rep. Whales Res. Inst., 18:123-148.
- OMMANNEY, F. D. 1932. The urino-genital system of the fin whale (*Balaenoptera physalus*). Discovery Rep., 5:363-466.
- OMURA, H. 1953. Biological study on humpback whales in the Antarctic whaling areas IV and V. Sci. Rep. Whales Res. Inst., 8:81-102.
- OMURA, H., K. MAEDA, AND I. MIYAZAKI. 1953. Whaling in the adjacent waters of Japan. Norsk Hvalfangst-Tidende, 42:199-212.
- OMURA, H., S. OHSUMI, T. NEMOTO, K. NASU, AND T. KASUYA. 1969. Black right whales in the North Pacific. Sci. Rep. Whales Res. Inst., 21:1-78.
- OMURA, H., AND H. SAKIURA. 1956. Studies on the little piked whale from the coast of Japan. Sci. Rep. Whales Res. Inst., 11:1-37.
- PIKE, G. C. 1962a. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). J. Fish. Res. Bd. Canada, 19:815-838.
- . 1962b. Canadian whaling off British Columbia, and progress of research, 1948-1959. Fish. Res. Bd. Canada, Nanaimo, 41 pp. (Mimeographed).
- PIKE, G. C., AND I. B. MACASKIE. 1969. Marine mammals of British Columbia. Bull. Fish. Res. Bd. Canada, 171:1-54.
- PURVES, P. E. 1955. The wax plug in the external auditory meatus of the Mysticeti. Discovery Rep., 27:293-302.
- RADCLIFFE, L. 1933. Economics of the whaling industry with relationship to the convention for the regulation of whaling. 73d Congr., 2d Session, Senate Comm., U. S. Govt. Print. Office, Washington, D. C., 79 pp.
- RAINEY, F. G. 1947. The whale hunters of Tigara. Anthropol. Papers Amer. Mus. Nat. Hist., 41:229-283.

- RAMSEY, D. H. 1968. Diurnal fluctuations in censuses of migrating California gray whales. *Norsk Hvalfangst-Tidende*, 57:101-105.
- RAUSCH, R. L. 1964. Studies on the helminth fauna of Alaska. XLI. Observations on cestodes of the genus *Diplogonoporus* Lönnberg, 1892 (Diphylobothriidae). *Canadian J. Zool.*, 42:1049-1069.
- RAUSCH, R. L., AND F. H. FAY. 1966. Studies on the helminth fauna of Alaska. XLIV. Revision of *Ogmogaster* Jägerskiöld, 1891, with a description of *O. pentalineatus* sp. n. (Trematoda: Notocotylidae). *J. Parasitol.*, 52:26-38.
- REAGAN, A. B. 1917. Archaeological notes on western Washington and adjacent British Columbia. *Proc. California Acad. Sci.*, Fourth ser., 7:1-31.
- RICE, D. W. 1960. Population dynamics of the Hawaiian monk seal. *J. Mamm.*, 41:376-385.
- . 1961. Census of the California gray whale. *Norsk Hvalfangst-Tidende*, 50:219-225.
- . 1965. Offshore southward migration of gray whales off southern California. *J. Mamm.*, 46:504-505.
- . 1967. Cetaceans. Pp. 291-324, in *Recent mammals of the world* (S. Anderson and J. K. Jones, Jr., eds.), Ronald Press, New York.
- . 1968. Stomach contents and feeding behavior of killer whales in the eastern North Pacific. *Norsk Hvalfangst-Tidende*, 57:35-38.
- RISTING, S. 1928. Whales and whale fetuses. *Cons. Perm. Internat. Explor. Mer, Rapp. Proc. Verb. Reun.*, 50:1-122.
- ROBINS, J. P. 1954. Ovulation and pregnancy corpora lutea in the ovaries of the humpback whale. *Nature*, 173:201-203.
- ROE, H. S. J. 1967a. Rate of lamina formation in the ear plug of the fin whale. *Norsk Hvalfangst-Tidende*, 56:41-45.
- . 1967b. The seasonal formation of laminae in the ear plug of the fin whale. *Discovery Rep.*, 35:1-30.
- RUUD, J. T. 1940. The surface structure of the baleen plates as a possible clue to age in whales. *Hvalråd. Skr.*, 23:1-24.
- . 1945. Further studies on the structure of the baleen plates and their application to age determination. *Hvalråd. Skr.*, 29:1-69.
- SAKIURA, H., K. OZAKI, AND H. FUJINO. 1953. Biological investigation of the northern Pacific baleen whales caught by the Japanese whaling fleet in 1952. Fisheries Agency of Japanese Government, Tokyo, 64 pp.
- SAUER, E. G. F. 1963. Courtship and copulation of the gray whale in the Bering Sea at St. Lawrence Island, Alaska. *Psychol. Forsch.*, 27:157-174.
- SCAMMON, C. M. 1874. The marine mammals of the northwestern coast of North America. John H. Carmany & Co., San Francisco, 319 pp.
- SCHEFFER, V. B., AND J. W. SLIPP. 1948. The whales and dolphins of Washington State with a key to the cetaceans of the west coast of North America. *Amer. Midland Nat.*, 39:257-337.
- SCHEVILL, W. E. 1952. On the nomenclature of the Pacific gray whale. *Breviora*, 7:1-3.
- SCHEVILL, W. E., C. RAY, K. W. KENYON, R. T. ORR, AND R. G. VAN GELDER. 1967. Immobilizing drugs lethal to swimming mammals. *Science*, 157:630-631.
- SCHOLANDER, P. F. 1940. Experimental investigations on the respiratory function in diving mammals and birds. *Hvalråd. Skr.*, 22:1-131.

- SERGEANT, D. E. 1962. The biology of the pilot or pothead whale *Globicephala melaena* (Traill) in Newfoundland waters. Bull. Fish. Res. Bd. Canada, 132:1-84.
- SKRIABIN, A. S. 1969. Novyi vid trematod roda *Ogmogaster* (Notocotylidae)—parazit usatykh kitov [A new species of trematode of the genus *Ogmogaster* (Notocotylidae)—parasite of baleen whales]. Zool. Zhur. 48:1882-1885.
- SLEPTSOV, M. M. 1955. Kitoobraznye dal'nevostochnykh morei [Cetaceans of Far Eastern Seas]. Primorskoe Knizhnoe Izdatel'stvo, Vladivostok, 2d ed., 161 pp.
- SLIJPER, E. J. 1954. On the importance of measuring the thickness of the layer of blubber in whales. Norsk Hvalfangst-Tidende, 43:510-516.
- . 1956. Some remarks on gestation and birth in Cetacea and other aquatic mammals. Hvalråd. Skr., 41:1-62.
- . 1963. Functional morphology of the reproductive system in Cetacea. Pp. 277-319, in Whales, dolphins, and porpoises (K. S. Norris, ed.), Univ. California Press, Berkeley and Los Angeles.
- STARKS, E. C. 1922. A history of California shore whaling. California State Fish and Game Comm., Fish. Bull., 6:1-38.
- STELLER, G. W. 1774. Beschreibung von dem Lande Kamtschatka . . . J. G. Fleischer, Frankfurt and Leipzig, 384 pp.
- SWAN, J. G. 1870. The Indians of Cape Flattery at the entrance to the Strait of Fuca, Washington Territory. Smithsonian Contrib. Knowl., 16 (8): 1-108.
- SWANSON, E. A. 1956. Nootka and the California gray whale. Pacific Northwest Quart., 47:52-55.
- SYMONS, H. W., AND R. D. WESTON. 1958. Studies on the humpback whale (*Megaptera nodosa*) in the Bellinghausen Sea. Norsk Hvalfangst-Tidende, 47:53-81.
- THIEL, P. H. VAN. 1966. The final hosts of the herringworm *Anisakis marina*. Trop. Geogr. Med., 18:310-328.
- TOMILIN, A. G. 1937. Kity Dal'nego Vostoka [The whales of the Far East]. Uchenye Zapiski Moskovskogo Gosudarstvennogo Universiteta, Ser. Biol. Nauk, 12:119-167 (Russian with English summary).
- . 1957. Zveri SSSR i prilozhashchikh stran. Tom IX. Kitoobraznye [Mammals of the U.S.S.R. and adjacent countries. Vol. 9. Cetacea]. Akad. Nauk SSSR, Moscow, 756 pp. (Translated by the Israel Program for Scientific Translations, Jerusalem, 1967, 717 pp.)
- TOWNSEND, C. H. 1887. Present condition of the California gray whale fishery. Bull. U. S. Fish Comm., 6:340-350.
- TRESHCHEV, V. V. 1966a. Novyi vid roda *Ogmogaster* Jägerskiöld, 1891 (*Ogmogaster delamurei* n. sp.) [A new species of the genus *Ogmogaster* Jägerskiöld, 1891 (*Ogmogaster delamurei* n. sp.)]. Pp. 22-25, in Parazity, promezhutochnye khoziaeva i perenoschiki. Akad. Nauk Ukr. SSR, Kiev (Russian with English summary).
- . 1966b. Novyi vid skrebnaya ot kita Chukotskogo Morya [A new species of Acanthocephala from the Chukotsk Sea]. Trudy Ukr. Respubl. Nauch. Obshch. Parazit., 5:112-115 (Russian with English summary).
- TRESHCHEV, V. V., M. V. YURAKHNO, AND V. V. ZIMUSHKO. 1969. O gel'minto-faune serogo kita Beringova i Chutotskogo morei [The helminthofauna

- of the gray whale of the Bering and Chukchi seas]. Pp. 130-131, in *Voprosy morskoi biologii* (V. A. Vodianitskii, ed.), Akad. Nauk Ukr. SSR, Kiev.
- TRUE, F. W. 1904. The whalebone whales of the western North Atlantic. *Smithsonian Contrib. Knowl.*, 33:1-332.
- TØNNESSEN, J. N. 1967. Den moderne hvalfangst historie. Norges Hvalfangstforbund, Sandefjord, vol. 2, 620 pp.
- U. S. NAVY HYDROGRAPHIC OFFICE. 1958. Oceanographic atlas of the polar seas. Part II, Arctic, H. O. Publ. no. 705, part II, 149 pp.
- UTRECHT-COCK, C. N. VAN. 1965. Age determination and reproduction of female fin whales, *Balaenoptera physalus* (Linnaeus, 1758) with special regard to baleen plates and ovaries. *Bijdr. Dierk.*, 35:39-100.
- WATERMAN, T. T. 1920. The whaling equipment of the Makah Indians. *Univ. Washington Publ. Anthropol.*, 1:1-67.
- WILKE, F., AND C. H. FISCUS. 1961. Gray whale observations. *J. Mamm.*, 42: 108-109.
- WYRICK, R. F. 1954. Observations on the movements of the Pacific gray whale *Eschrichtius glaucus* Cope. *J. Mamm.*, 35:596-598.
- YURAKHNO, M. V. 1967. Novyi vid roda ortosplanukhnus—*Orthosplanchnus pygmaeus* (Trematoda, Campulidae)—parazit kita [*Orthosplanchnus pygmaeus* sp. n. (Trematoda, Campulidae): a parasite of the whale]. *Vestnik Zool.*, Akad. Nauk Ukr. SSR, 1967:79-82 (Russian with English summary).
- ZENKOVICH, B. A. 1934a. Materialy k poznaniyu kitoobraznykh dal'nevostochnykh morei (Seryi Kaliforniiskii kit—*Rhachianectes glaucus* Cope) [Research data on Cetacea of far eastern seas (the gray California whale—*Rhachianectes glaucus* Cope)]. *Vestnik Akad. Nauk SSSR, Dal'nevostochnyi Fil.*, 10:9-25.
- . 1934b. Nekotorye nablyudeniya nad kitami Dal'nego Vostoka [Some data on whales of the Far East]. *C. R. (Doklady) Acad. Sci. URSS*, 2(6):388-392 (Russian and English).
- . 1937a. Esche o serom kaliforniiskom kite (*Rhachianectes glaucus* Cope, 1864) [More on the gray California whale (*Rhachianectes glaucus* Cope, 1864)]. *Vestnik Akad. Nauk SSSR, Dal'nevostochnyi Fil.*, 23:91-103.
- . 1937b. Weighing of whales. *C. R. (Doklady) Acad. Sci. URSS*, 16: 177-182.
- . 1937c. The food of far-eastern whales. *C. R. (Doklady) Acad. Sci. URSS*, 16:231-234.
- . 1938. Milk of large-sized cetaceans. *C. R. (Doklady) Acad. Sci. URSS*, 20:203-205.
- ZIMUSHKO, V. V. 1969a. Nekotorye dannye po biologii serogo kita [Some data on the biology of the gray whale]. Pp. 93-97, in *Morskie mlekopitayushchie* (V. A. Arseniev, B. A. Zenkovich, and K. K. Chapskii, eds.), Akad. Nauk USSR, Moscow.
- . 1969b. Materialy po razmnzheniyu serykh kitov [Data on reproduction of the gray whale]. Pp. 24-28, in *Chetvertoe vsesoyuznoe Soveschaniye po izucheniyu morskikh mlekopitayushchikh*, Akad. Nauk USSR.

INDEX

- Acanthocephalans, 108
Age composition, 116
Amphipods, 23–24
Ascidians, 23–24
- Balaena*:
 glacialis, see right whale
 mysticetus, see bowhead whale
Balaenoptera:
 acutorostrata, see minke whale
 borealis, see sei whale
 edeni, see Bryde's whale
 musculus, see blue whale
 physalus, see fin whale
Balaenopteridae, see rorquals
Baleen plates, 9, 42
Barnacles, 100
Biomass, 114
Blubber, 8, 34
Blue whale, 42, 50, 71, 85, 97, 124
Body length, 43
Body measurements, 7
Body proportions, 45
Body weights, 8, 27, 86
Bottlenose dolphin, 34, 97
Bowhead whale, 13, 50, 103, 120
Breeding season, 73
Bryde's whale, 36
- Calving season, 81
Cestodes, 106
Copulation, 97
Corpora albicantia, 8, 41, 66
 accumulation rate, 69
 persistence, 68
 regression, 66
Corpora atretica, 71
Corpora lutea, 8, 64
 accessory, 66
 of ovulation, 65
 of pregnancy, 65
- Crabs, see decapods
Cumaceans, 23, 24
Cyamids, 102
- Decapods, 23, 25–27
Distribution, 1, 2, 11
- Ear plugs, 9, 38
Ectoparasites, 8, 100
Endoparasites, 9, 104
Epizoites, 8, 100
Eschrichtius robustus, 5
Euphausiids, 25
- False killer whale, 71
Fetal growth, 76
Fin whale, 22, 32, 36, 38, 42, 50, 52,
 63–66, 68, 71, 84–85, 90–91, 97,
 106, 108
Follicles (Graafian), 58
 cystic, 61
- Gastropods, 23
Gestation period, 76
Globicephala, see pilot whale
Group size, 17
- Holothurians, 24
Humpback whale, 22, 36, 50, 52, 62–
 66, 80, 91, 97, 100, 120–121, 124
Hydroids, 23
- Isopods, 23
- Killer whale, 98–99
- Lactation period, 86
- Mammary glands, 8, 87–89
Megaptera, see humpback whale
Metabolic rate, 32, 114

Migrations:

- California stock, 13
- Korean stock, 20
- night, 15, 21, 111
- offshore, 13, 109, 110
- segregation during, 16
- speed of, 15-16

Milk, 89

Minke whale, 63

Mortality, 117

Mysids, 23

Natality, 117

Nematodes, 107

Nomenclature, 5

Oil yield, 35

Orcinus, see killer whale

Ovaries, 8, 52-71

- as age criterion, 41
- functional symmetry, 71
- polarity, 71
- weights, 54

Ovulation:

- frequency, 61, 90
- multiple, 62

Pack ice, 12, 21

Penis, 9, 94

Photoperiod, 21

Physeter, see sperm whale

Pilot whale, 68, 71

Polychaetes, 23-24

Population:

- density, 114
- dynamics, 117
- size, 109
- structure, 115
- trends, 112

Pregnancy rate, 72

Pseudorca, see false killer whale

Right whale, 5-6, 50, 102, 106, 120-121

Rorquals, 10, 25, 38, 62, 66, 81, 90-92, 105-107

Salps, 24

Scars, 8, 98

Scrag whale, 5, 121

Segregation, 16

Sei whale, 27, 42, 50, 63, 64, 71, 91, 97, 104

Sex ratio, 115

Sexual dimorphism, 46

Sperm whale, 10, 15, 68, 71, 102

Stomach contents, 9

- during migration, 25
- summer, 23
- winter, 26

Summer grounds:

- Atlantic stocks, 20
- California stock, 11
- Korean stock, 19

Swimming speed, 15

Taxonomy, 1, 6

Testes, 9, 92-97

- histology, 9, 92
- weights, 9, 92-94

Trematodes, 104

Tursiops, see bottlenose dolphin

Uterus, 8, 81-85

Vertebral epiphyses, 9, 49

Winter grounds:

- Atlantic stocks, 20
- California stock, 19
- Korean stock, 20

3 2044 114 193 295

Date Due

~~MAR 7 1974~~~~DEC 19 1974~~~~NOV 28 1975~~~~DEC 15 1975~~~~DEC 31 1975~~~~JAN 20 1976~~~~MAR 23 1976~~~~DEC 30 1977~~

~~C.L.L. to KSL,
Yale. sent
9 Jan 78, due
after 2 weeks' use~~

~~DEC 24 1985~~