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MODERN POPULATIONS, **MIGRATIONS**, DEMOGRAPHY, **TROPHICS**,
AND HISTORICAL STATUS OF THE PACIFIC WALRUS

by

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with

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ABSTRACT

The Pacific walrus population probably was not greatly affected by the incursions of the Russian merchant companies in the 18th and early 19th centuries, because their catches were mostly small and mainly of adult males. But it was severely depleted at least three times after the purchase of Alaska from Russia, first by the Yankee whalers between 1868 and 1880, when they took at least 130,000 animals, mainly adult females. The second depletion was by the American "arctic traders" in the beginning of the 20th century, when they extirpated most of the herds summering in the Bering Sea and greatly reduced those in the **Chukchi**, as well. The third depletion was by Soviet sealers in the **1930's** to 50's, when they took at least 140,000 animals and again brought the population to a low level. The depletion by the Yankee whalers was perhaps the most devastating of the three, because it struck quickly and intensively at a stationary population, made up mainly of old, unproductive animals. It had recovered only partially by the time the traders began their taking, but by then it was broadly based in young, productive animals, hence more adaptive and resilient than before. Following the traders, it probably nearly recovered to its 18th century size before the Soviets began their intensive catching. Although they removed nearly as large a number of animals as the whalers had, the youthful, resilient population was better able to withstand and compensate for the increased mortality. Recovery from that third depletion took about 25 years, and the population apparently reached its new maximum in the late **1970's**. It now contains a large proportion of old animals, whose productivity is low and has been lowered still further by a high rate of fetal abortion, possibly attributable to malnutrition, an infectious agent, or a combination of those factors. Its recruitment has been very poor in recent years, due to high postnatal mortality of calves. With such low recruitment and with steeply rising catches in both Alaska and **Chukotka**, the population probably is in a decline again at present.

Pacific walruses currently inhabit nearly all of their pre-19th century range. Apparently, nearly all of the adult males now summer in the Bering Sea, **while** all of the females and young summer in the **Chukchi**. In autumn, the males and females evidently meet in the Bering Strait region, before moving into their wintering-breeding areas in the Bering Sea. In the breeding areas, the adult males evidently eat little or no food during the rut. The adult females apparently eat little during the summer, possible associated with their annual molt. Animals in the western **Chukchi** Sea in summer appear to be as dependent on **polychaetes** and ringed seals as they are on mollusks.

Walruses are more easily disturbed by odors than by sight or sound of man and his machinery. Herds of females and young **in** the eastern **Chukchi** Sea in summer are likely to be affected by man-made disturbance, mainly through separation of calves from their mothers.

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INTRODUCTION

General Nature and Scope of Study

The Pacific walrus population inhabits the waters over the entire continental shelf of the Bering and **Chukchi** seas. That population is a natural resource of paramount economic importance to coastal people of both **Chukotka** and Alaska, and for that reason, it has been under intensive study by management biologists of the Soviet Union and the United States for more than 50 years. Much has been learned about walruses in that time, but many important problems still remain unsolved.

The goal of this project has been to contribute further information on the subjects of (1) dynamics of the Pacific walrus population, especially from an historical aspect, (2) the current seasonal distribution and movements of the various parts of that population, (3) the principal kinds of foods eaten by the animals in different parts of their range and in different seasons of the year, and (4) the reactions of walruses to man-made disturbances. Those topics were selected as most relevant and most likely to yield information that would meet the needs of agencies and organizations concerned with potential effects of offshore oil and gas development on the walruses of the **Bering-Chukchi** region. Our general approach to each of those topics was as follows:

Population Dynamics

The Pacific walrus population has a long history of fluctuations in numbers at the hands of man. That history is moderately well documented but in a widely scattered scientific and **semipopular** literature, as well as in unpublished reports, government files, private journals, and field notes. We contributed some new information to that and undertook a compilation and synthesis of the earlier information, feeling that a better understanding of the status of the population in the past would help to develop a clearer perspective of the present and future. The lessons of history appeared to be particularly valuable as contributions to the basis for predicting the course ahead and for identifying convenient means for monitoring the population along that course.

Distribution and Movements

The overall distribution of the Pacific walrus, as currently understood (Fay, 1982; Fedoseev, 1982), indicates that virtually the entire population resides in the Bering Sea in winter, principally in a large **ice-generating** area to the south of the **Chukchi** Peninsula and St. Lawrence Island, and in another such area that extends from south of Nunivak Island into Bristol Bay. In spring, all of the females and young migrate northward, into the **Chukchi** Sea, leaving most of the adult males behind in the

Bering Sea, where they spend the summer. The locations of most of the major concentrations of walrus in each month from March to September have been delineated, but the distribution during November and December, when the most intensive feeding may take place, and in January and February, during the mating season, have not been documented adequately. The fall migration corridors are virtually unknown; even the spring migration corridors are poorly known except in the Bering Strait region, and for that reason, the principal calving areas have not been defined. Our thrust has been to contribute to filling as many of those gaps as possible and to encourage the governmental agencies on both sides of the International Date Line to contribute, as well.

Complementary to description of the distribution and main migration routes is the need to determine the sex and age composition of the animals inhabiting each area in each season. That information will indicate which segments of the population are likely to be impacted the most. It also could be useful in contributing to knowledge of the composition of the population at large and its natural mortality and productivity.

Feeding

The feeding habits of walrus in the **Bering-Chukchi** region had been documented principally from stomach contents of animals taken in the spring in the area from St. Lawrence Island to Bering Strait (Fay et al., 1977; Lowry and Frost, 1981). Only fragmentary data, most of them qualitative, were available from other seasons and other areas (Nikulin, 1941; Brooks, 1954; Tikhomirov, 1964b; Krylov, 1971). The implication of those qualitative reports was that the diet varies greatly in relation to season, region, sex, and age (Fay, 1982).

In general, walrus appear to feed mainly on mollusks, some of which could be severely impacted by environmental pollution (Kelly, 1980). A growing body of evidence suggests that other kinds of invertebrates may be at least equally important as food in some parts of the walrus' range or important as alternate prey when mollusks are unavailable. We sought to obtain more substantive information on those points by investigating the feeding habits of Pacific walrus in as many seasons and different parts of their range as feasible. The risk of impact of offshore oil development on their food supply will remain inadequately known until such information is available.

Response to Disturbance

The reaction of walrus to man and his machines can be described generally as "escape response" and attributed to visual, auditory, and olfactory cues (Loughrey, 1959). The severity of the effects, as we perceive them, range from no reaction at all, to fright, flight, or at worst,

death, depending on the circumstances. All walrus do not respond in the same way, and the responses of an individual may vary in different times and places. In some instances, the animals may even be attracted, rather than repelled by human presence. Many factors appear to play a part in the severity of the response, including sex and age of the animals, the size and location of the group (on ice, in water, on land), their distance from the disturbance, and the kind and intensity of the disturbing factor. The reactions of walrus to disturbance by man have not been well documented; even uncritical anecdotal accounts are scarce. We strove to obtain a better understanding of the immediate effects of disturbance and to search for evidence to confirm or deny the suspicions of potential long-term impacts from chronic disturbance.

Relevance to Problems of Petroleum Development

All of the proposed OCS oil lease areas on the **Bering-Chukchi** shelf lie within the known range of the Pacific walrus population (Fig. 1). Development of some of those may impinge on major mating areas in winter, migration corridors and calving areas in spring, nursery areas in summer, and migration and feeding areas in autumn. Oil transport routes could impinge on all of those habitats, year-round. Because the population is large at present, concern for its preservation is minimal, even though the animals are practically confined to the shelf and wholly dependent on its **benthic** resources. We expect that some impact on the population by oil development is inevitable. To judge the probability and potential for that impact and devise the means to mitigate it, better understanding of the population and its habitat requirements is needed.

Objectives

Our specific objectives in this project have been to contribute to better understanding of:

- 1) the history of the population, especially as regards its fluctuations in size and structure and the attendant circumstances at the time of those fluctuations,
- 2) the current seasonal distribution of the population, ideally in terms of sex/age composition, with emphasis on identifying the principal times and places in which mating, birth, and feeding take place,
- 3) the seasonal and regional feeding habits of the animals, and
- 4) the effects on walrus of disturbance by man.

For various reasons, we could not address all of those objectives as **fully** as we desired in this project, but we did obtain much of the informa-



Figure 1. The range of the Pacific walrus population (\\) relative to actual and proposed oil lease areas (////) on the western Alaskan outer continental shelf.

tion that we sought, through it and a series of complimentary projects that were funded by other agencies and organizations. This report is a synopsis of the current state of knowledge, based on the results from all of those, as well as on previous work by us and others.

STUDY AREA

The study area was the entire range of the Pacific walrus population on the continental shelf of **the** Bering and **Chukchi** seas, within the 100-m isobath (Fay, 1982). In this and associated projects, we sampled in the pack ice of the Bering and **Chukchi** seas (Navarin, St. Matthew, Norton, and Hope basins) in May and June 1980 via the CGC POLAR STAR, in the southeastern Bering Sea (St. George and North Aleutian Shelf lease areas) in February and March of 1981 via the Soviet vessel ZRS ZVYAGINO, in Bristol Bay (North Aleutian Shelf) in April to November 1980 and January to May 1981 via chartered aircraft and the State of Alaska's R/V RESOLUTION, in the eastern **Chukchi** Sea (Barrow Arch lease area) in July and September of 1981 via the CGC POLAR STAR and N/S OCEANOGRAPHER, respectively, and in the eastern and western Chukchi Sea in July and August of 1982 via the Soviet vessel K/S ENTUZIAST. We also sampled on the Penuk Islands, Bering Sea (Norton lease area) during the autumn of 1981 and summer of 1982, and in the central and western **Chukchi** Sea, adjacent to the Barrow Arch lease area, in the summer of 1983 via the Soviet vessel ZRS ZYKOV. We also obtained information for this project from study of walruses in captivity at Marineland, California, during 1981 and 1982, and in conjunction with the Alaskan Eskimo Walrus Commission's and U. S. Fish and Wildlife Service's joint program of harvest monitoring in 1980 and 1982.

SOURCES, METHODS, AND RATIONALE OF DATA COLLECTION

History of the Population

Historical information from the 18th, 19th, and first half of the 20th century was extracted mainly from published sources in both Russian and American literature and from some unpublished reviews of those sources. In addition, distributional **data** from the ships' logs of the 19th-century Yankee whalers were provided by J. R. **Bockstoe** and D. B. **Botkin**. Much of the more recent information, from 1950 to 1983, also was extracted from publications and unpublished reports; a large part of it was derived from files of the Alaska Department of Fish and Game (**ADF&G**) and the **P.I.'s** files from previous work for **the** Arctic Institute of North America, the U. S. Public Health Service, the Alaska Sea Grant Program, the U. S. Fish and Wildlife Service (**USFWS**), the U. S. Marine Mammal Commission, and University of Alaska-Fairbanks. Results from aerial censuses of the walrus population from 1960 to 1980 were from unpublished reports provided by the USFWS and from published and unpublished accounts from the Magadan Section, Pacific Research Institute of Fisheries and Oceanography (**MoTINRO**), in the

Soviet Union. The methods employed in the harvest sampling and censuses already have been described in detail by Fay (1955, 1958), Kenyon (1960a, 1972), Harbo (1961), Fedoseev (1962), Burns (1965), Gol'tsev (1972, 1975a), Fay et al. (1977), Estes and Gilbert (1978), Fay and Lowry (1981), Fedoseev (1981), Fay and Stoker (1982a,b), and Johnson et al. (1982).

Distribution **and** Composition

Distributional information, new since Fay's (1982) compilation, was acquired partly from other OCSEAP and MMS investigators and partly by personnel of this and related projects during observation from ships and aircraft. For the most part, that information consisted of sightings along the flight or cruise tracks, with notation of time (for estimation of position), group size and location (i.e., on ice, on shore, in water), and when feasible, composition of the group by sex and approximate age. Animals were regarded as being in a "group" when they were separated from others by at least one body length (after Estes and Gilbert, 1978). Behavioral information about mating, calving, feeding, and responses to disturbance often was obtained in conjunction with those sightings. Since we operated in this project mainly from ships of opportunity, we usually had no control over timing and little control over location of the cruise tracks.

Specific efforts to obtain compositional data from the present population were conducted during five cruises in the Chukchi Sea in 1981 to 1983. The first compositional survey, in July 1981 via the icebreaker CGC POLAR STAR, was designed to cover a 65-km-wide band along the southern part of the pack ice between Point Barrow, Alaska and 169°W longitude. That coverage included about 90 percent of the walrus habitat in the eastern Chukchi Sea identified by Estes and Gilbert (1978) and by Johnson et al. (1982) from aerial surveys of the region. In the first week of the 2-week cruise, we explored as much of that band as possible from east to west, via ship and helicopter, to locate the main concentrations of walruses and to determine whether there was any geographical segregation by sex. On our return eastward in the second week of the cruise, we allocated most of our time to compositional sampling in the areas where the animals had been found to be concentrated. This was followed 2 months later by the second compositional survey in the same area, via the N/S OCEANOGRAPHER. That survey was done as an adjunct to other projects and only in the ice edge, since the ship is not an icebreaker.

The third and fourth compositional surveys were conducted in July and August 1982 via the Soviet vessel K/S ENTUZIAST. Again, because the ship was not an icebreaker, it was limited to working in the edge of the pack. The ship's mission was primarily to search for whales, but we were permitted to survey for walruses, as well, along the entire ice edge from Cape

Schmidt, **Chukotka** to Barrow, Alaska. We did that twice, each time with a different set of observers. The fifth survey was conducted in August 1983 via the Soviet ship ZRS **ZYKOV**. This also was in the edge of the pack but covered only a small part of the distributional area in the western **Chukchi** Sea, near Cape Schmidt.

On each of those surveys, most of the groups of walrus were observed from the ship; during the first survey, a few were observed from **small** boats. Once located, each group of walrus generally was approached by the ship upwind at speeds of 2 to 3 kt, to a minimal distance of **about** 100 to 200 m. During the approach, one observer using a 16-36x "zoom" spotting scope identified the sex and age of each of the animals in the group. A second observer, who was the recorder, counted the number of animals in the group and, when possible, assisted the first observer with the classifications. In some instances, a third observer took photographs of each group, using a 35-mm SLR camera, equipped usually with a 70- to 200-mm zoom telescopic lens. Our rationale in combining visual and photographic methods was that the photos would provide back-up documentation and would allow us to examine the feasibility of using photography alone for future compositional surveys.

Our classification of individuals to age was based on size and shape of the tusks, relative to breadth and depth of the snout. The classes were defined by a set of outline drawings that were traced from photographs depicting front and side views of the head. The scale of those sketches was based on the tusk length data obtained by Fay (1982) and on data gathered more recently by us concerning the length of the tusks and the width and depth of the snout (Table 1). For the classes that lacked data on snout dimensions, we simply estimated by extrapolation from the available data in the other classes, as well as by comparing dimensions among animals shown in the photos. Obviously, the data base of snout dimensions for most of the age classes still is deficient.

The outline drawings (Fig. 2) show males and females of average dimensions at 0 (calf of the year), 1, 2, 3, 4 to 5, 6 to 9, 10 to 15, and >15 years of age. Recognizing that the variation in size among members of each class is wide (about ± 20 to 50%), and that the overlap between classes is extensive (e.g., see Fay, 1982, fig. 81), we accepted the **fact** that some subjectivity would enter into the classification of "borderline" cases, and that some of the individuals placed in each class actually would belong in the preceding and some in the succeeding class. We believe those kinds of errors will tend to be uniformly present in all samples and will not affect the validity of comparisons among samples. Accuracy in aging is not a requirement in this sampling scheme; the requirement is for precision in classifying the animals into groups that are morphologically alike.

Table 1. Average dimensions of tusks¹ and snout² of Pacific walruses in each age class.

Age class (yrs)	Males					Females			
	Tusk length (cm)	N	Snout dimensions		Tusk length (cm)	N	Snout dimensions		
			Width M ± SD	Depth M ± SD			Width M ± SD	Depth M ± SD	
0	0	2	17.0±1.41	7.8±1.06	0	1	16.0	11.0	
1	2	2	20.0±2.83	11.5±0.71	2	0			
2	7	0			5	0			
3	11	3	25.2±1.23	13.5±1.80	8.5	1	24.0	11.0	
4-5	16	2	24.5±0.71	14.5±2.12	12.5	4	22.5±0.58	12.4±2.75	
6-9	24	4	31.2±3.20	17.0±1.41	20	5	25.3±2.59	14.7±1.92	
10-15	36	4	31.8±1.50	17.8±1.50	33	8	26.6±3.07	14.9±2.40	
>15	52	12	35.6±2.64	18.7±2.20	44	15	27.2±3.76	16.0±2.09	

¹Length of tusk along anterior surface, from edge of gingiva to distal tip. Rounded estimate of mean, based on Fay (1982, fig. 81) and data gathered during this project. This is the length visible in anterior view only; in side view, about 2 to 1 cm of the base of the tusk is hidden by the upper lip.

²Mean ± one standard deviation of N measurements of greatest width and depth of snout on non-distorted, dead specimens.

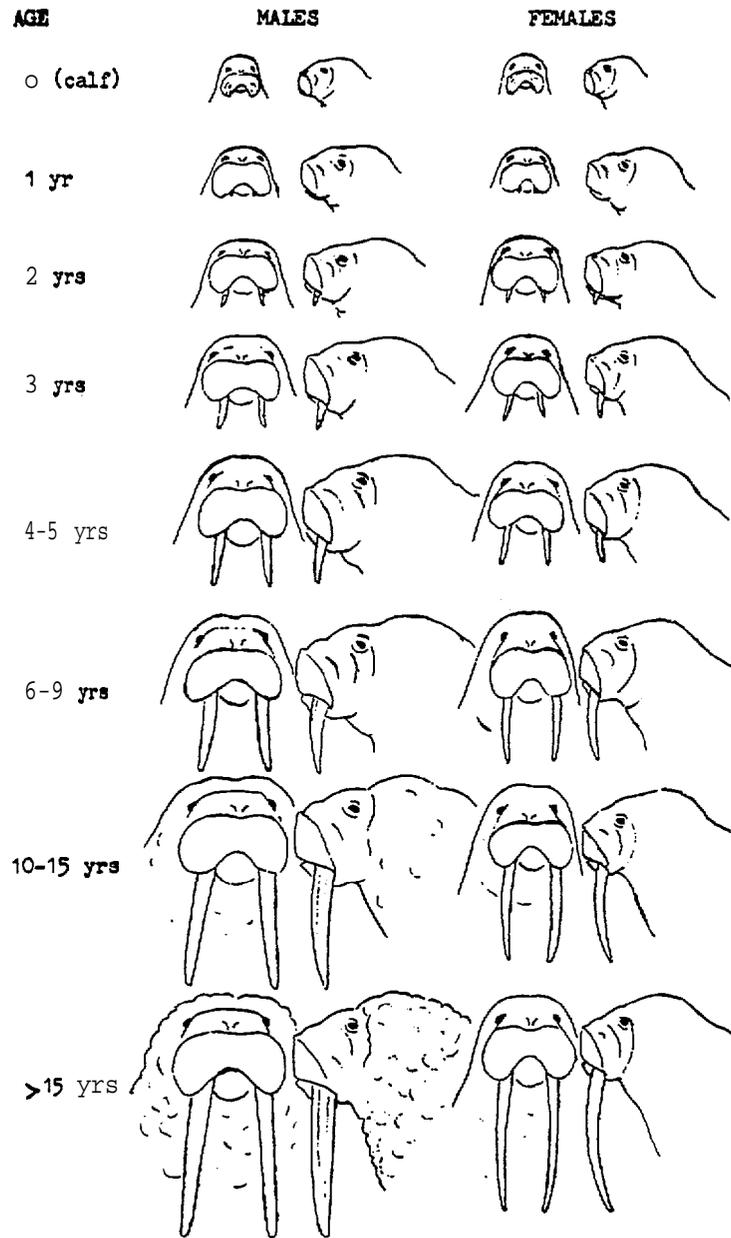


Figure 2. Facial outlines used for classification of walrus by age, during visual surveys of group composition. Age classification is based primarily on tusk size and shape, relative to depth and breadth of the snout.

For animals in the first five age classes, identification to sex was regarded as unimportant, since nearly all of those are sexually immature. Only the animals 6 years and older were identified to sex, based in part on facial and tusk characters and in part on shape and coloration of the body, texture of the **skin**, presence of urogenital **apertures**, and SUCH indicators as attendance of suckling young. Adult females often were classified only as "6+ years", since they usually were too numerous to classify further in the short time spent with each group. About two-thirds of the **6-yr-old** females are sexually mature; **nearly all** of the **older females** are mature (Fay, 1982). For the males, which were less numerous, hence more **easily** considered individually, we classified the animals 6 yrs and older as 6-9, 10-15, and >15 years. Males 6 to about 15 years old are subadults; nearly all of the males more than 15 years old are sexually and socially mature adults (Fay, 1982).

Feeding Habits

We obtained new information about the kinds of food eaten by walruses in their natural environment by examining the stomach contents of specimens collected at sea. Some of those specimens were from scientific samples taken during two Soviet-American research cruises; most of the rest were from the Eskimos' spring harvests in the eastern Bering Sea in 1980 and 1982.

For each specimen, the sex, date, and location, were recorded. Stomach contents were washed in sea water to remove the fine, particulate digesta and to separate the organic matter from the heavier inorganic sediments. Prey were identified by visual comparison of items in the stomachs with expertly identified whole specimens in the reference collections of the Institute of Marine Science, University of Alaska, Fairbanks. The identifiable prey were sorted into **taxonomic** groups to the lowest rank possible. Each group was weighed to the nearest gram and the number of individuals counted. Fragments not assignable to Genus or Species often were assignable to Class, Order, or Family. For those, the number of individuals could not be determined, but the weight was recorded. The weight of inorganic sediments was recorded separately.

The feeding habits from a temporal aspect, in relation to age, sex, and season of the year, were investigated on the basis of daily records of the food intake by two breeding pairs of walruses and their offspring that were reared in captivity at the **Marineland** aquarium in California (Gehrich, 1984). Those records consisted of the weights of foods consumed per day by each walrus from 1974 to 1982, as recorded by their keepers. The recorded intakes in pounds per day were converted to kilocalories (**kcal**) per day, based on their nutrient composition as given by Gerasi (1975) and the gross energy values provided by Pike and Brown (1975). Although the amount of food eaten by captive animals may not be precisely the same as

that eaten under natural conditions, the relative amounts should vary in a similar way with body size and with seasonal biological events, such as breeding, pregnancy, lactation, and the molt.

Effects of Disturbance

As opportunity permitted in the course of other field work in this and the related projects, we gathered data on the effects of man-made disturbance on walruses. This was entirely a passive effort; we did not attempt to experiment with or intentionally disturb the animals.

In many instances, we were able to record the flight-distance in relation to wind direction and source of disturbance. We also obtained some data on who (sex/age class) was last to leave the ice, and how often calves were abandoned by the adults when disturbed.

Thus, this study had many facets, most of which were strongly reliant on specialized logistic support and exceptionally favorable weather. Because those two conditions coincided only once in while, and because we had only parts of 3 years in which to achieve our 4- or 5-year objectives, we did not solve all of the problems by any means, but we did contribute significantly to the solution of some of them. The following are the results of our work.

RESULTS

Historical Review

The recorded history of walruses in the Bering-Chukchi region begins with their first appearance there in the fossil record in late Sangamon (Pelukian) time, more than 52,000 but probably not more than 101,000 years ago. Skeletal remains known or presumed to be of that age have been recorded from marine deposits in the eastern Chukchi Sea near Barrow, Point Lay, Noorvik, and Cape Espenberg, Alaska, as well as in the northern Bering Sea near Nome, on St. Lawrence Island, and in the Dease Inlet-Dan Lake area of southeastern Bering Sea (Hopkins, 1967; Repenning and Tedford, 1977; C. A. Repenning, J. J. Burns, and F. H. Fay, unpublished). The implication of those records is that the distribution of walruses in the region, presumably not long after their arrival from the North Atlantic Ocean, may have been about as great in latitude as it is now.

With the subsequent climatic cooling, lowering of sea level, and exposure of the Bering "land-bridge," during the last (Wisconsin-Würm) glacial advance (Hopkins, 1972), the range of walruses apparently expanded

markedly to the south, along both sides of the North Pacific Ocean. A skull and skeleton found recently near Qualicum Beach, Vancouver Island were radiocarbon dated at 40,000 years B.P. (C. R. Harington, pers. commun.). Part of another skull (not dated) was dredged up from a submerged Pleistocene beach off central California, not far from a 19,000 year B.P. Steller sea cow (Harington, 1978; C. A. Repenning, pers. commun.). A fragment of a walrus tusk found on the Queen Charlotte Islands, British Columbia also may be of Wisconsin age (Harington, 1975).

Although walrus appear to have been widely distributed along the North American coast during the Wisconsin glaciation, they probably were not numerous there, even in the Bering Sea, for the narrow continental shelf would have offered them little area for feeding. They probably were more abundant on the Asian coast, where they had access to a much broader shelf in the Okhotsk Sea. Late Pleistocene finds from Sakhalin (Matsumoto, 1926) and from the adjacent Siberian mainland (Borisiak, 1930) attest to the former presence of walrus there at that time. In the Chukchi Sea, north of the land bridge, walrus probably were scarce or absent, for the continental shelf was dry land, and the adjacent Arctic Ocean was deep and at least as perpetually ice-bound as it is now (Herman et al., 1971; Herman, 1974).

For several thousand years in the end of the Pleistocene Epoch, as climatic warming and inundation of the Bering land bridge took place, walrus evidently re-occupied the Bering-Chukchi region and withdrew from most of their southern areas of expansion. They evidently continued to inhabit the Okhotsk Sea until rather recent time, however, as indicated by the presence of "blackened" (?semi-fossil) tusks at Kin'kil and Nagaev Bay on the coast of northwestern Kamchatka (Arsen'ev, 1927; Nikulin, 1941) and by remains associated with human habitation in several locations on southern Sakhalin (Voronov and Voronov, 1981). Blackened, semi-fossilized ivory and bones have been found also in several locations along the present Bering Sea coast of Alaska, for example on Cape Constantine (Bristol Bay), at St. Paul Island (Pribilofs), and on St. Lawrence and the Penuk islands, near Bering Strait (F. H. Fay, unpublished).

For the past two or three millennia, walrus probably were distributed about as widely in the Bering-Chukchi region as they are today, to judge from the occurrence of their ivory in Aleut and Eskimo archaeological sites. Although implements made from walrus ivory are common in Alaskan coastal sites from Bristol Bay to Barrow, they are scarce to absent in the Aleutian Islands and the Gulf of Alaska (De Laguna, 1934, 1956; Geist and Rainey, 1936; Collins, 1937; Oswalt, 1955; Heizer, 1956; Ford, 1959). On the Asian coast, walrus are said to have occurred in the Bering Sea as far south as eastern Kamchatka and the Commander Islands (Tikhomirov, 1964a; Chugunkov, 1970), and they apparently were present also about the Kuril Islands and throughout the Okhotsk Sea, as well (Voronov and Voronov,

1981). Far to the north, their limits in the pre-contact (by Russians) period have not been defined authoritatively in the literature but presumably were about the same as they are now. Their greatest concentration, apparently, was in the Bering Strait region, much as it is today (Rudenko, 1961; Arutiunov and Sergeev, 1968). They were abundant enough there to have had a major influence on the foundation and development of the **marine-oriented** Eskimo culture.

The Russian Expansion Period, 1648-1867

Quantities of walrus ivory were discovered at the mouth of the Anadyr River by Russian **cossacks** about 1648-49, when they first reached that area ostensibly from the north, via the **Kolyma** River and Bering Strait (Ray, 1975). The news of that discovery, however, did not reach the rest of the world until a century later, and in the meantime, Kamchatka was discovered and had been subjugated (Collins, 1937). By the time of Bering's second voyage in 1741, the walruses of the **Okhotsk** Sea no longer existed, but the **Bering-Chukchi** walrus population probably was in virtually primeval condition. Although it already had been cropped by aborigines for several thousand years, their catches probably were not large enough to have had any significant effect on the size or composition of the population. At that time, the 5,000 or so walrus-hunting natives of the region were centered principally in the northern Bering and southern **Chukchi** seas, as they are now. With their primitive weapons, they might have been able to take as many as 2 to 3 thousand walruses per year (but probably not more) to meet their material and nutritional needs. Hence, when the first boatloads of Russian hunters arrived in Alaska in the mid-18th century, they probably found walruses about as numerous and widespread as the carrying capacity of the environment would allow. Over the next 126 years, however, they considerably changed that status.

In the first 40 years of Russian expansion into the Bering Sea, the hunters ranged mainly along the Commander and Aleutian islands, from which they brought back ample cargos of skins from sea otters, fur seals, and foxes but very little walrus ivory (Table 2). Certainly, they were not unaware of the value of the ivory, for it had been an important commodity in their trade with the orient and middle-east for at least the previous 8 or 9 hundred years (Cammann, 1954). Apparently, the scarcity of ivory in the cargoes of vessels returning from the Commander and Aleutian islands was due to the walruses being as scarce there in the 18th century as they are today.

By the 1760's, the hunters were pressing farther eastward for their game, as the stocks of **furbearers** became depleted in the islands (Berkh, 1974). When they reached into Bristol Bay and northward to the **Pribilof** Islands in the 1780's and 90's, their cargos of ivory increased dramatically. An extreme example was recorded in the late 1780's, when a team of 20

Russian and 20 **Aleut** hunters at the **Pribilof** Islands took more than 16,500 kg of tusks in two years (Tikhmenev, 1979). Since the **Pribilofs** were used as a **haulout** area almost entirely by male walruses (**Tikhmenev**, 1978), and one tusk from an adult male averages about 2.54 kg (**S.D.** = 0.565, N = 83 : U.S. Fish and Wildlife Service data by A. Thayer, unpublished), that catch probably was of about 3,250 animals. Those animals probably were taken principally from the Northeast Point on St. Paul Island, since that apparently was the largest hauling ground. The hunters were so effective that, by 1805, walruses were "all gone" from St. Paul and St. George islands, according to Agent **Sarichev** (True, 1899), but they still "covered" nearby Walrus Island, and the hunters were sent there to harvest them about that time (Tikhmenev, 1979).

Table 2. Amounts of walrus ivory acquired by the Russian hunting companies in the Bering Sea, 1743 to 1860.

Years	Walrus ivory (kg)	
	Total	Average/year
1743 - 62 ¹	1,015	51
1763 - 82 ¹	6,186	309
1783 - 98 ¹	22,434	1,496
1798 - 1822 ¹	32,570	1,303
1821 - 4 ₂ ²	106,456	4,839
1842 - 60 ³	47,972	2,525

¹From **Berkh** (1974).

²From Tikhmenev (1978).

³From **Golovin** (1979).

The expansion of Russian influence in the Bering Sea took place in a disorderly fashion by individual fur-trading companies until 1797, but those companies were merged in that year into one company under government franchise (**Tikhmenev**, 1978). Thus, the Russian-American Company from its birth was well established in North America, and by 1820 it commanded 15 settlements that reached from the **Pribilof** Islands to central California. About that time, the Company was exporting nearly 5,000 kg of walrus ivory annually from Alaska, mainly to Turkey and Persia (**Okun**, 1951). That amount of ivory is equivalent to at least 1,000 male walruses or about twice as many females and young per year. Probably about half of those walruses were **taken** by the Russians; the other half were taken by the native inhabitants of the region. The catch of walruses by the Russian hunters was entirely for the ivory, as the Company had no markets for the thick, tough hides or for the meat or oil at that time. The natives' catch, conversely, was primarily for the meat, oil, and skins, so they usually had a surplus of ivory available for trade.

Acquisitions of walrus ivory by the Russian-American Company continued to rise for at least another 20 years, principally in connection with further expansion into the northern Bering Sea. Apparently, much of that increase in acquisitions was from trade with the Eskimos. In June 1830, for example, Captain **Etholen** sailed from Sitka to Norton Sound, where he found walruses present in "enormous number" around the shores of Sledge Island, near the present city of **Nome**. Presumably, his crew caught some of those, but he also found walrus ivory available in some quantities for trade at St. Lawrence Bay and in the five villages on St. Lawrence Island, whose primary industry was walrus hunting. He evidently stopped as well at St. Matthew and Hall islands, where he found walruses present (**Tikhmenev**, 1978) and may have taken some. Three years later, Captain **Teben'kov** acquired over 7,000 kg of walrus ivory in trade from the natives at **Mechigmen Bay, Chukotka** (Ibid.).

From 1842 to 1860, the Company's average annual export of walrus ivory was down nearly 50%, to about 2,500 kg per year. At least one-third of that was from barter with the natives, especially at the Company's station in Port **Moller**, Bristol Bay (Tikhmenev, 1978; **Golovin**, 1979), and ever greater reliance for ivory was being placed on the native catch in the northern Bering Sea. The decline in weight of ivory exported may have been caused in part by inclusion of more tusks from females and young, which are much smaller than those from **adult** males. The decreasing export also was caused in part by depletion of some of the most accessible herds, such as those on the **Pribilof** Islands.

Thus, from the time of **Vitus** Bering's historic voyage of discovery to southeastern Alaska, until the purchase of Alaska from imperial Russia by the United States, the record of the Pacific walrus population is mainly a record of human events. From it, we can surmise that the great herds of

bull walruses, which summered in Bristol Bay and about the **Pribilof** Islands were nearly extirpated by the mid-19th century, and we can guess that the same kind of damage probably was done on the other side, in the **Koryak-Kamchatka** region. Apparently, the herds in the pack ice to the north were little affected. Although there may have been some indirect impact, caused by development of ivory trade with the Eskimos, the amount of that impact probably was insignificant, compared with that of the Yankee whalers, who were next on the scene.

The Yankee Whaler Period, 1848-1914

While the Russian-American Company was still expanding its sphere of influence in western North America, the Yankee whalers entered the **Bering-Chukchi** region. At first, they conducted their whale-catching only in the vicinity of the Aleutian Islands, but by 1848 they reached northward to Bering Strait (**Bockstoce**, 1980). Their primary objective there was the taking of bowhead whales (**Balaena mysticetus**). They also began almost at once to take a few walruses, as well. At first, the walruses may have been taken "more out of curiosity than...for economic gain." By the late 1860's, however, when the bowhead population had been severely reduced and a strong market for walrus products developed, the "deliberate walrus hunt" was underway (**Bockstoce and Botkin**, 1982, p. 183).

The walrus population of the region evidently was still very large when the whalers began their harvesting. Even after the heavy toll taken earlier by the Russians, some animals still could be found in Karaginskii Gulf and Bristol Bay, as well as on the **Pribilof** and St. Matthew islands (Dan, 1870; **Scammon**, 1874; Elliott, 1875; Townsend, 1887; Arsen'ev, 1927; **Chugunkov**, 1970; Pinigin and Prianishnikov, 1975). Farther north, in the ice, the animals were abundant, having been hunted only by the natives, whose catches were mainly for their own subsistence. We have not been able to determine the size of those catches, for they apparently were not recorded and have never been estimated. We suspect that, even with a bit of excess for trading, the total native catch was no more than 2-3,000 walruses per year.

The whalers took only insignificant numbers of walruses up to the mid-1860's. And because they killed the animals by means of harpoon and lance, the number that escaped mortally wounded and the number killed and lost due to sinking probably were negligible. By 1869, however, their catch had risen steeply (Fig. 3), and their hunting methods had changed markedly, for they began to kill the animals by means of firearms. With that conversion to firearms, the number of animals wounded and the number lost due to sinking rose markedly. According to Nye (1879 in Allen, 1880) and Arsen'ev (1927), only about one-third of the animals **shot** was retrieved. Although those may have been overly pessimistic views, there are few data with which to confirm or deny them. The only recorded statistics known to us are

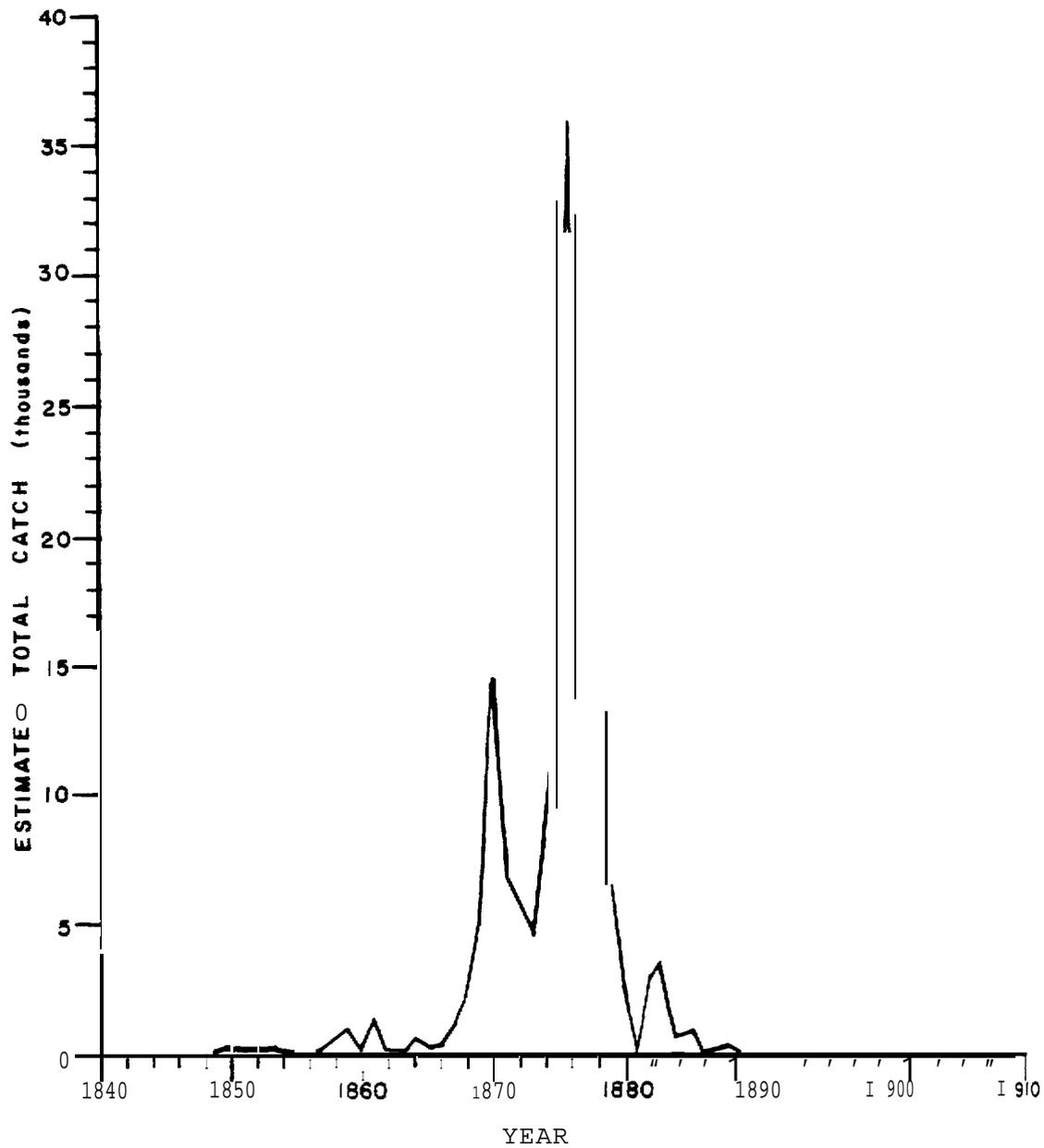


Figure 3. Estimated annual catch of Pacific walrus by the Yankee whalers in the **Bering-Chukchi** region, 1849-1910 (after **Bockstoce and Botkin, 1982**).

those extracted by **Bockstoce** from the whalers' logbooks (**Bockstoce** and **Botkin**, 1982). Expressed as number retrieved/number shot, those statistics were as follows: 59/82, 0/24, 118/130, and 18/40 or 50. Thus, the proportion retrieved ranged from 0 to 90% and, as a whole, suggested that the average proportion retrieved may have been about two-thirds of the number shot, as it has been in recent years (Buckley, 1958; **Krylov**, 1968).

The Yankee whalers directed their hunting mainly toward the walruses in the pack ice, north of Bering Strait. More than 90% of their catches were taken in the ice of the Chukchi Sea in late June, July, and August (**Bockstoce** and **Botkin**, 1982). The distribution of those catches and of their additional sightings of walruses corresponds well to present distribution of the animals in those months (Fig. 4). For that reason, we assume that the sex/age composition of the herds that they hunted also was comparable to the composition of herds found there at present. The walruses that summer in that region nowadays are mainly adult females with their young. Whereas the Russian-American Company's hunters had been taking mostly adult male walruses in the south, the Yankee whalers apparently were taking mostly females and young in the north. The latter was confirmed by Nye (1879 in Allen, 1880). Hence, the whalers' impact on the walrus population was **much** more depletive, for not only were they lowering the numbers, they were lowering the reproductive capacity of the population, as well. Additional mortality probably was caused by the whalers setting free the young calves, after their mothers were shot (Clark, 1887). Although a few calves may have been "adopted" by other females (e.g., see Burns, 1965; **Eley**, 1978; Fay, 1982), the rest of them probably died from starvation.

In the 12 years from 1869 to 1880, the catch of walruses by the Yankee whalers amounted to an estimated 130,000 walruses (**Bockstoce** and **Botkin**, 1982). More than half of those were taken within a 4-year period, from 1875 to 1878. The average annual catch by the whalers alone over the 12-year period was on the order of 11,000 walruses per year, and the losses from wounding, sinking, and abandoned calves probably were at least an additional 6-8,000 per year. Some additional number was taken by vessels of other nations, as well as by the native inhabitants of the region, who by this time also were using firearms (Ray, 1975; Fitzhugh and Kaplan, 1982). The overall result by 1880, according to Nelson and True (1887), was that the walrus population had been reduced to about half of its former size, and the native population that was dependent on it underwent a 33% reduction, due to starvation (Allen, 1895). In those villages where the dependence on walruses was greatest, because the economic base was narrow (i.e., on the Bering Sea islands), about half to two-thirds of the native residents died (Nelson and True, 1887; Muir, 1917).

The catching of walruses by the whalers continued at a reduced rate for about 35 years longer. By 1890 it was down to a few score per year, and from 1890 onward, it dwindled to insignificance. It ceased altogether

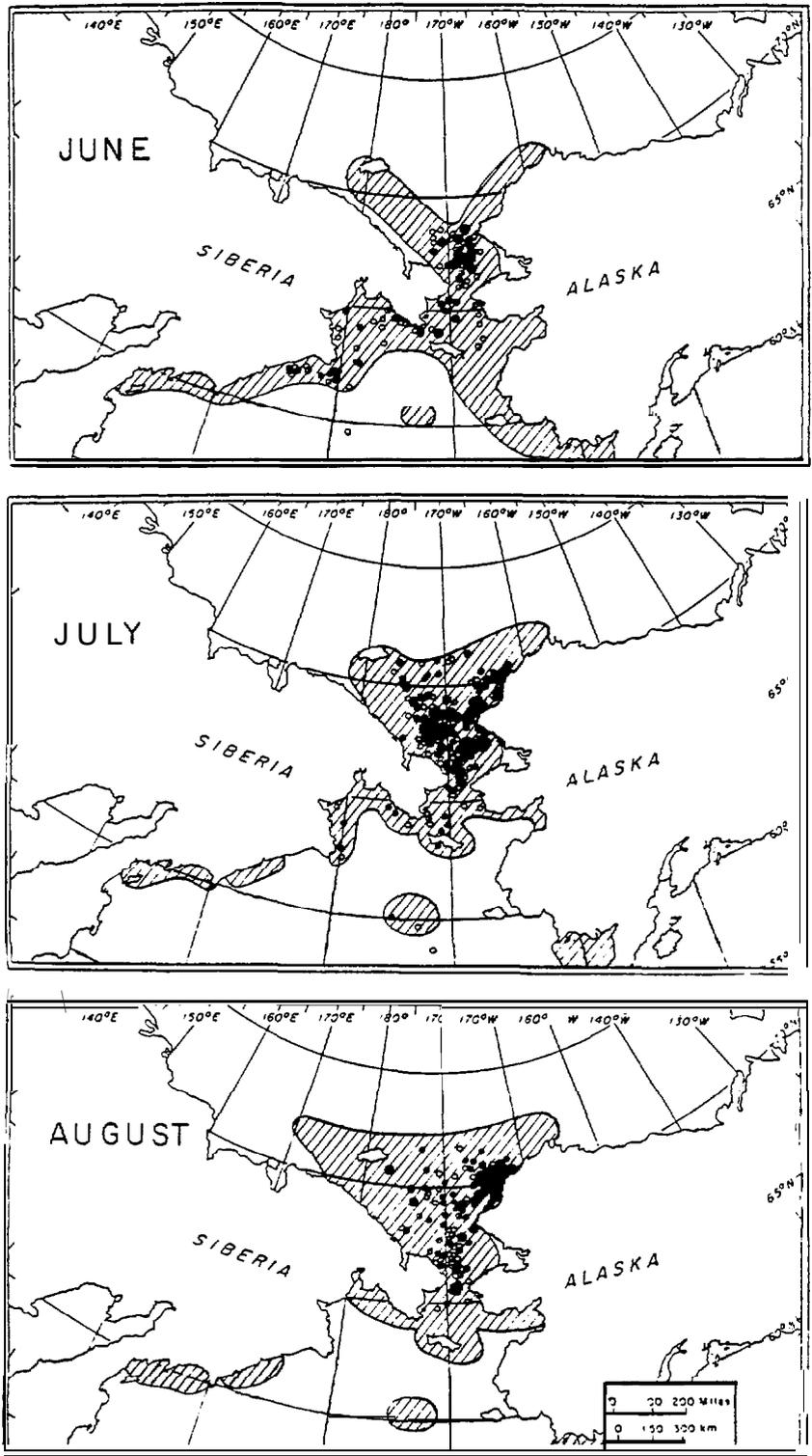


Figure 4. Distribution of sightings (circles) and catches (dots) of walrus by the Yankee whalers in June-August, during the first 20 years of their harvesting (J. R. Bockstoece and D. B. Botkin, pers. commun). Present range of the Pacific walrus (cross-hatched, after Fay, 1982) in those months is shown for comparison.

at the beginning of World War I, when, according to Madsen and Douglas (1957) and **Bockstoce** and **Botkin** (1982), the world market for walrus products collapsed. The size of the take by natives at that time is not completely known. Krupnik's (1977) **resumé** for 1895 (based on "Patkanov, 1912") indicates that at least 1,300 animals were taken per year in **Chukotka**. We assume that several hundred more were taken in Alaska.

From Depletion to Partial Recovery, 1900-1935

In the declining years of the Yankee whaling fleet, a new group of users of the Pacific walrus population arose. These were the "arctic traders," who dealt primarily in barter with the natives of the region for ivory and furs, and who partook in walrus hunting as a profitable sideline. Americans were the primary participants in that enterprise, according to **Arsen'ev** (1927) and **Nechiporenko** (1927), but they were not the only ones involved. Vessels of Canadian and Norwegian registries, at least, also participated in the venture.

Walruses apparently had reoccupied the eastern coast of Kamchatka, where they had been left virtually untouched by the whalers. They hauled out regularly on **Karaginskii** and **Verkhoturov** islands (Fig. 5), where they were hunted by the **Koryak** natives, and not infrequently, they occurred as far south as **Avacha Bay** (**Arsen'ev**, 1927; **Nikulin**, 1941; **Chugunkov**, 1970; **Pinigin** and **Prianishnikov**, 1975). In the end of the 19th century, however, three American schooners came to **Karaginskii** and **Verkhoturov** islands annually, and they quickly reduced the number of walruses there to zero (**Arsen'ev**, 1927). A government official at **Karaga** reported to **Niedieck** (1909) that the last walrus on **Karaginskii** Island was shot there about 1899 or 1900, and that none had been seen since. The skull of another, obtained in **Avacha Bay** in June 1900 by the U.S. Fish Commission vessel **ALBATROSS**, is in the Museum of Comparative Zoology at Harvard University (MCZ-10108). Apparently, only two other individuals were sighted in the entire region over the next two decades: one in **Morzhovoi Bay** in 1909 and one in **Shlyupochnoi Bay** in 1920 (**Arsen'ev**, 1927; **Nikulin**, 1941). Similarly, on the Alaskan side walruses were reported to have been numerous along the north side of **Unimak** Island until 1898 or 99, when a group of non-native hunters arrived and killed or drove away all of them (**Murie**, 1959). Only single animals and groups of "very limited number" were sighted in the **Bristol Bay** region for more than three decades thereafter, and even those were heavily hunted (**Osgood**, 1904; **Madsen** and **Douglas**, 1957; **Murie** 1959).

Thus, the traders apparently were responsible for extirpating walruses from the **Koryak-Kamchatka** region, and they probably had a similar effect along the north side of the **Alaska Peninsula** and in **Bristol Bay** by the early 1900's. The U. S. government placed a prohibition on the taking of walruses in Alaskan waters by non-natives in 1909 (**Madsen** and **Douglas**,

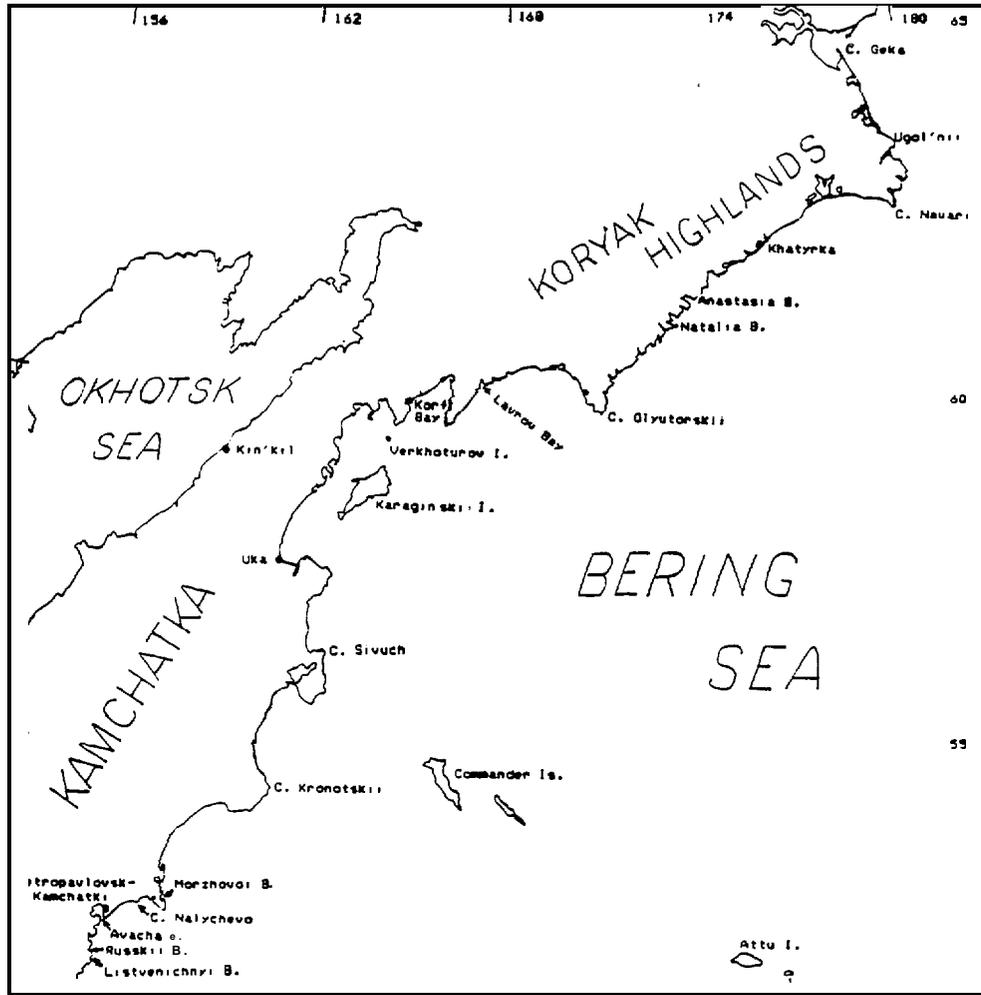


Figure 5. The Koryak-Kamchatka district of the Soviet Far-East, showing localities mentioned in the text.

1957), and on the taking of walrus for ivory alone by 1915 (Chandler, 1943). Having already depleted the more accessible herds on the Alaskan side anyway, the traders apparently were encouraged by those regulations to relocate all of their hunting to more northwestern waters. Their catches began to have a noticeably depleting effect in **Chukotka** by 1912, according to Nechiporenko (1927), and although they stopped for a time during World War I, they evidently resumed immediately after the war. Brooks (1954) stated that the hunting was *'heavy" at that time, and Burns (1965) speaks of one vessel in 1917 taking more than 1,300 animals near **Wrangel Island**.

Nechiporenko (1927) reported that the hunting by "foreign *predators'" declined along the Soviet coast after 1920. Nonetheless, Bernard (1925) indicated that it was still heavy on the Alaskan side, however, at least until 1923, when more than 1,000 carcasses washed ashore between **Cape Lisburne** and Barrow. During the 1920's, the Eskimos and coastal **Chukchi** of the Soviet Far East took between 1,300 and 3,000 walrus per year (Nechiporenko, 1927; Krupnik, 1980). The catches by Alaskan Eskimos in that period were not recorded, but a decade later they were estimated at 1,000 to 1,500 per year (Collins, 1940).

The combination of the continuing harvests by the natives and the additional take by the traders apparently was sufficient not only to prevent the recovery of the walrus population (after the whalers withdrew) but to reduce it even further. The elder Eskimos at Little Diomed Island whom Brooks (1954) queried in 1952-53, felt that the lowest ebb of the walrus population in the present century took place about 1920. On the Soviet coast, Nechiporenko (1927) reported that walrus were "very rare" south of **Kresta Bay** at that time. Arsen'ev (1927), citing "**Suvarov**," indicated that they occurred no farther south than **Cape Geka**, at the entrance to the **Anadyr estuary**.

A few groups of walrus began to reappear in the **Kamchatka district** in the late 1920's. In the winter of 1928-29, a group was seen near the village of **Uka**, southwest of **Karaginskii Island**, and in 1931, another group appeared farther north, in **Korf Bay** (**Nikulin**, 1941). Then, in 1935, about 500 were sighted in **Natalia Bay**, on the **Koryak coast**, and more than 1,000 were reported south of **Cape Navarin**. By 1939, individuals and small groups were reappearing at **Verkhoturov** and **Karaginskii Islands**, as well, where they had not been seen for 40 years (**Nikulin**, 1941; **Kosygin** and **Sobolevskii**, 1971; **Pinigin** and **Prianishnikov**, 1975). One wanderer even reached **Honshu, Japan** in 1937 (**Scheffer**, 1958).

To the north, herds were absent from former **haulouts** on parts of **St. Lawrence** and the **Punuk** islands in the 1920's, but they reappeared there in substantial numbers by the early to **mid-1930's** (**Murie**, 1936). A year or two of unusually high natural mortality of walrus on their autumn hauling grounds on the **Punuk Islands** also was reported at that time (**L. Kulukhon** in

Fay and Kelly, 1980). Similarly, on the Soviet side they had been absent in the 1920's from such major hauling grounds as Arakamchechen, Naukan, and Big Diomede (Fig. 6), but they reoccupied those haulouts in the 1930's (Arsen'ev, 1927; Ognev, 1935); Zenkovich, 1938; Belopol'skii, 1939). Of 38 hauling grounds recorded on the Soviet coast, the number in use rose from 17 in the 1920's to 19 in the 1930's, and the number in regular, annual use rose from 4 to 6 (Table 3). One of the former haulouts (Cape Geka), however, apparently was abandoned during the 1930's and has not been reoccupied since then. According to Soviet biologists queried by us, that abandonment was due to frequent disturbance by increased shipping and other traffic in the Anadyr estuary (G. A. Fedoseev, V. N. Gol'tsev, pers. commun.).

In the 1930's, F. A. Zeusler, captain of the U. S. Coast Guard ship that brought legal, medical, and dental aid to the Alaska coast each year, circulated 100 questionnaires to missionaries, teachers, and native residents of the villages from Mekoryuk to Barrow. He asked for their opinion about the current status of the walrus population. The response from the natives and missionaries, whose long term residence should have given the best perspective, was that the population was increasing. The response from the teachers, most of whom stayed in a village no more than 2 years and often found the walrus hunt repugnant, was that the population was decreasing. Thus, the real status of the population during this period is somewhat enigmatic. Our interpretation is that the traders' incursions virtually extirpated again the southern herds of summering males in the Bering Sea, and that their work in the pack ice continued to suppress but probably did not cause any major decrease in numbers there. We judge that because the population apparently began its recovery rather quickly, after the traders reduced their impact on it in the 1920's. But recovery was never completed, because another intensive harvesting program arose on the Soviet side very soon after the traders withdrew.

The Soviet Exploitation Period, 1931-1962

Up to the 1920's, the revolutionary government of the newly established Union of Soviet Socialist Republics paid little heed to its distant eastern border. The inhabitants of coastal Chukotka had more frequent and closer contact with American traders at that time than they did with their own officials. They even conducted their financial matters with American money and were reliant on goods brought to them from North America (Arsen'ev, 1927; Rozanov, 1931)). In an effort to bring those natives back into the Soviet sphere of influence and to dissolve their relationship with the Americans, the Soviet government sent its representatives into Chukotka in the 1920's to review the situation and make recommendations for improvement. Arsen'ev (1927), Netchiporenko (1927), and Rozanov (1931) were among those dispatched to Chukotka to review the means, amounts, and industrial

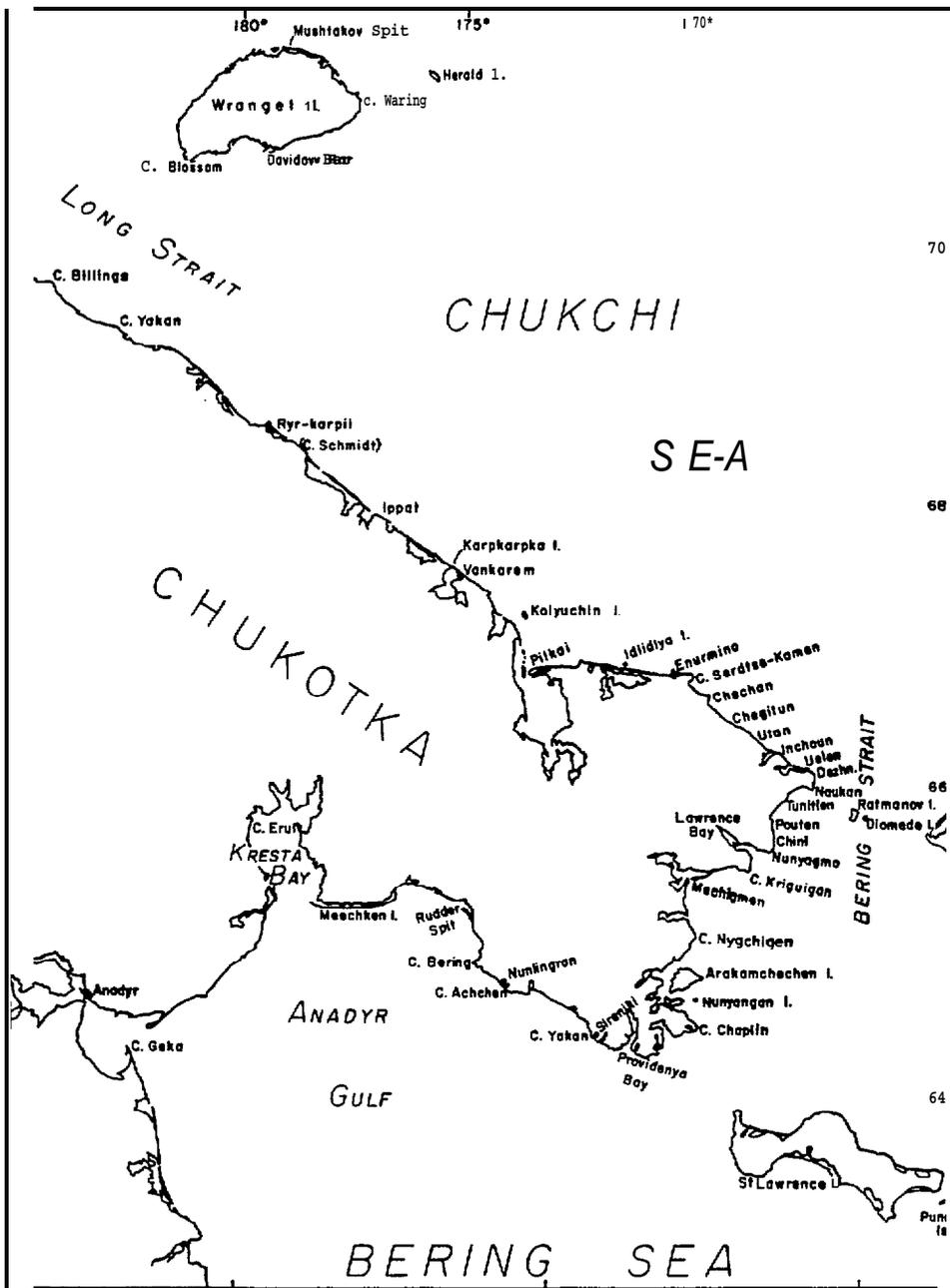


Figure 6. Eastern Chukotka, USSR, showing locations of walrus haulout sites listed in Table 2.

Table 3. Use by walruses of haulout areas on the coast of **Chukotka** per decade, 1920-1980, as reported in Soviet literature.¹

Haulout²	1920's	1930's	1950's	1960's	1970's
Cape Geka	Regular	None	None	None	None
Meechken	Regular	Regular	None	Regular	Regular
Cape Erulen	None	Irreg.	None	None	None
Cape Maska	None	Irreg.	None	None	None
Rudder	Regular	Regular	Regular	Regular	Regular
Cape Bering	None	Regular	None	None	None
Cape Chaplin	None	None	None	None	None
Nunyangan	None	None	None	None	Irreg.
Arakamchechen	None	Regular	Irreg.	Irreg.	Regular
C. Nygchigen	Irreg.	None	None	None	None
Mechigmen	Irreg.	None	None	None	None
Lawrence Bay	None	Irreg.	None	None	None
Nunyagmo-Chini	None	Irreg.	None	None	Irreg.
Tunitlen	None	Irreg.	None	None	None
Pouten	None	None	None	Irreg.	None
Naukan-Dezhnev	None	Irreg.	None	Irreg.	Irreg.
Big Diomede	None	Irreg.	None	Irreg.	Regular
Uelen	Irreg.	Irreg.	None	Irreg.	None
Inchoun	Irreg.	Regular	Irreg.	Irreg.	Regular
Utan	Irreg.	None	None	None	None
Chegitun	Irreg.	Irreg.	None	None	None

Table 3. Continued

Haulout ²	1920's	1930's	1950's	1960's	1970's
Chechan	None	Irreg.	None	None	Irreg.
Serditse-Kamen	Irreg.	Regular	None	Irreg.	Regular
Enurmino	None	None	None	Irreg.	None
Idlydlya	None	Irreg.	None	Irreg.	Irreg.
Pil'kai	Irreg.	None	None	None	None
Kolyuchin	Regular	Irreg.	None	Irreg.	None
Vankarem	Irreg.	Irreg.	None	None	None
Karpkarpka	None	None	None	Irreg.	None
Ippat	Irreg.	None	None	None	None
Ryr-karpii	Irreg.	None	None	None	None
Blossom	None	None	None	Irreg.	Irreg.
Davidov	None	None	None	Irreg.	Irreg.
Mushtakov	None	None	None	Irreg.	Irreg.
C. Waring	None	None	None	Irreg.	None
Herald 1.	None	None	None	Irreg.	Irreg.
Shelagskii	Irreg.	None	None	None	None
Prykadtagh	Irreg.	None	None	None	None

¹Data for 1920's from Arsen'ev (1927), Nechiporenko (1927), and Rozanov (1931); for 1930's from Ognev (1935), Zenkovich (1938), Belopol'skii (1939), and Nikulin (1941); for 1950's from Rass *et al.* (1955) and Geller (1957); for 1960's from Fedoseev (1966) and Gol'tsev (1968); and for 1970's from Gol'tsev (1975a), Fedoseev (1981, 1982), and Somov *et al.* (1982).

²"Regular" indicates annual use by one or more herds of 100 or more animals; "Irreg." indicates intermittent use by such herds; "None" means that the haulout was not used at all by such herds.

yields from the hunting of walruses, for the trade in walrus products was one of the strongest links with foreign sources. Finding the methods crude and the returns poor, they recommended that the productivity of the natives be increased by better mechanization of the hunting and rendering processes. They also recommended that the Soviet government offer higher prices and provide trade goods sufficient to replace those brought by the Americans. In response, the government began subsidizing their far-eastern natives, providing small vessels and new whaleboats to some communities and rendering plants to others (Rozanov, 1931; Krypton, 1956). At the same time, although the recommendations included prohibition of walrus hunting for "commercial gain" (Arsen'ev, 1927), the economics of the situation evidently required that the catch on the Soviet side be increased substantially by an additional take from government vessels, manned by non-native crews. The task of those crews was to harvest walruses mainly for ivory and hides, much as the American so-called "predators" had done before (Zenkovich, 1938). The American traders, meanwhile, also continued to take some walruses on the high seas (numbers unknown), and the Alaskan Eskimos continued to hunt for their own subsistence and to some extent for trade.

The walrus population, depressed for so long by the whalers' and traders' excessive catches, has been estimated to have recovered to more than 250,000 animals by 1931 (Kibal'chich and Borodin, 1982), based on a computer model using recent vital statistics and the record of catches since that time. A population of that size would have been sufficient to sustain a modest, well regulated fishery. But the Soviets evidently acted without sufficient time for reasoned judgement, for their catches of walruses rose markedly from a norm of 2-3,000 per year in the late 1920's to a high of at least 8,000 per year in the 1930's (Fig. 7). The general trend of the Soviet catch after 1938 was gradually downward until the early years of World War II; then it leveled off about 3-6,000 animals per year, during the 1940's and 1950's. That recorded catch apparently was the amount taken from the sealing vessels only, for the data presented by Krylov (1968), ostensibly for the total, do not jibe well with those compiled for the native catches by Krupnik (1980). That is, some additional amount apparently was taken by shore-based boats.

The average catch by Eskimos in Alaskan waters during the 1930's was estimated to have been between 1,000 and 1,500 animals per year (Collins, 1940; Brooks, 1954; Fay, 1955, 1958), but it evidently fluctuated widely. Missionaries B. LaFortune, T. Cunningham, and G. Carroll (unpubl. data), who resided on Little Diomed and King islands from 1929 to 1958, recorded wide variations in hunting success at those two localities; increase or decrease of the walrus population was not mentioned. Both Fay (1957, 1982) and Hughes (1960) reported some extremely low catches (30 to 70/village/year) at St. Lawrence Island in the 1940's and 50's, and A. Heinrich (in litt.) reported a low catch of only 20 at Little Diomed Island in

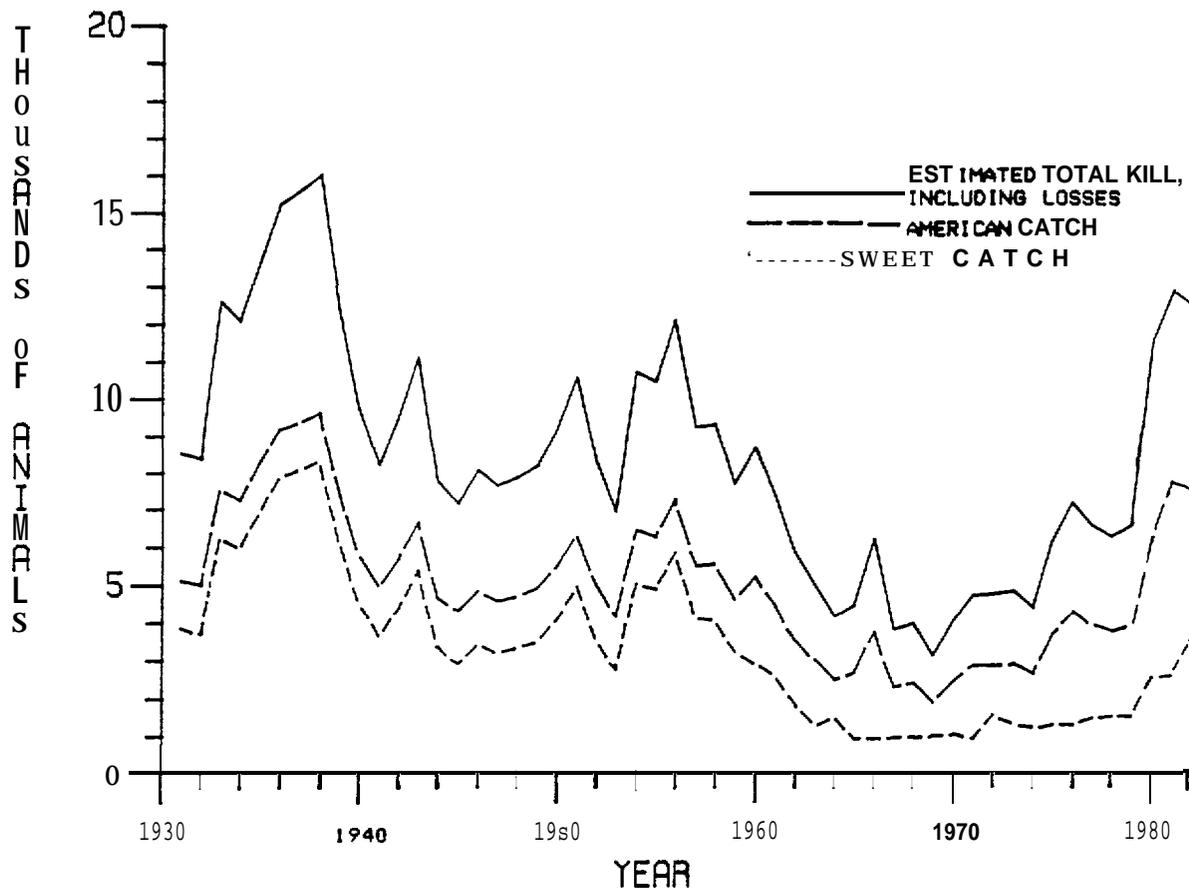


Figure 7. Reported annual catches of Pacific walrus, 1931-82. Curves based on reported data from **Chukotka** (lower, short dashes), plus the reported catches in Alaska (middle, longer dashes), to which has been added the best estimate of losses from sinking and wounding, to get the estimated total annual kill (upper, solid line).

1946, whereas catches of about 250 were not uncommon there about that time (Collins, 1939 in Brooks, 1954). The occurrence of those poor catches probably can **be attributed** in part to unfavorable ice conditions (Fay, 1982), but it also indicates extreme scarcity of walruses in areas where they usually had been most readily available. That is, the very large commercial catches by the Soviet Union apparently were having a telling effect. Commercial hunting of walruses by American traders was no longer a major factor in this decline, for the taking of walruses for any but subsistence purposes had been slowed by American federal regulation in the late 1930's and virtually stopped by the U. S. Walrus Act of 1941 (Ch. 368, 55 Stat. 632, 48 U.S.C. 248)

In both Chukotka and Alaska, the catches in this period were taken with high-powered rifles, but the rate of success in retrieval of the shot animals was not high. The catches amounted to about 60% of the numbers of animals shot; the remaining 40% were killed and lost due to sinking, or they escaped with mortal wounds (Zenkovich, 1938; Brooks, 1954; Buckley, 1958; Krylov, 1968). Thus, the overall kill in Chukotka and Alaska, including losses, probably went as high as 15-16,000 animals per year at the height of the Soviet harvests of the 1930's and probably did not dip below 7-8,000 per year in the rest of this 30-year period. The impact evidently was comparable to that of the Yankee whalers, 50-60 years earlier, although it was spread over a much longer period of time. During that period (1930's to 50's), Soviet reports of the walruses' use of traditional haul-out sites in Chukotka indicated a decline in the number of sites occupied from 19 in the 1930's to only 3 in the 1950's, and only one of those three was used on a regular, annual basis (Table 3). Large herds that had been hauling out on Big Diomedé (Ratmanov) Island during the autumn migration were absent or very small and irregular in occurrence after 1939 (N. Whitaker, A. Heinrich, J. J. Burns, pers. comm.). South of Anadyr Gulf, walruses became absent once again, except for one wanderer in the Okhotsk Sea in 1940 and another in 1957 (Rass et al., 1955; Kosygin and Sobolevskii, 1971). V. A. Arsen'ev (1976) has suggested that those two animals might have been brought southward from the Chukchi Sea by Soviet sealers and released in the Okhotsk area.

On the American side, as well, a great reduction in the use of coastal hauling grounds was evident. The small herds seen intermittently at Cape Lisburne in the 1930's and early 40's (L. S. Vincent, K. M. Kimble, unpubl. data) apparently were absent during the 1940's to 60's, judging from the lack of reports of their occurrence there; they reappeared there in the 1970's (A. Springer, D. Roseneau, pers. comm.). In Bristol Bay, the use of Amak Island by walrus herds was discontinued in the 1930's (F. A. Zeusler, unpubl. data) and apparently not resumed until the 1950's (K. W. Kenyon, pers. comm.).

Concern for the welfare of the walrus population and of the native

people who were dependent on it was expressed on the Soviet side by **Geller** (1957), **Kleinenberg** (1957), and **Sleptsov** (1961) and, simultaneously, on the American side by **Fay** (1957) and **Kenyon** (1960b). The awareness of the depleted state of the walrus had been derived independently on each side of the, then, "iron curtain", and the reactions that followed on each side also were unilateral, without any cross-communication. On the basis of recommendations from its scientists, the Soviet government in 1956 enacted a decree for "security of the animals of the Arctic" (**Kleinenberg et al.**, 1964) and conducted a considerable national campaign thereafter to make the need for protection widely known and understood (**Kosygin**, 1975). Gradually, the composition of the Soviet harvests was shifted from mixed sexes to males alone, killing of animals in the water and on the coastal hauling grounds was prohibited, and the vessel- and shore-based catches of walrus in the **Bering-Chukchi** region were reduced (**Tikhomirov**, 1964a). Finally, the government-operated catching from vessels was terminated in 1962 (**Gel'tsev**, 1975a), and a small quota of 1000 to 1500 animals was distributed among the native kolkhozes (**Tikhomirov**, 1964a). In Alaska, the walrus hunting had been limited earlier (1941) to that by natives for their own subsistence, and the newly formed State of Alaska implemented further protective measures to reduce the catch of adult females and prohibit taking on the principal hauling ground in Bristol Bay. These measures, on both sides, were intended to give the walrus population unprecedented protection and help it to restore itself.

The Protective Period, 1952-1982

The Soviet state walrus hunting industry, ostensibly based on sound biological data and internationally accepted wildlife management principles, had failed abysmally as a controlled cropping scheme by the mid-1950's, having depleted the very resource on which it was dependent. By then, the managers realized that not enough was known about the biology and ecology of walrus to manage them effectively on a sustained yield basis. The results also should have made clear the fact that neither country was capable of managing this common resource unilaterally, without even consulting the other.

In retrospect, the protective reactions that followed appear to have been over-reactions, but the information needed for conservation with a better foundation simply was not available. The greatest immediate value of the responses on both sides was that they drew attention to and support for further biological research. Those programs of research were justified on the grounds of dependence of the coastal natives of **Chukotka** and Alaska on the walrus as a major natural resource.

The importance of walrus to rural Alaskans had been made clear by the work of **Brooks** (1953, 1954), **Kenyon** (1960b), and others and was a major

point in the foundation of the research and management program of the new State of Alaska's Department of Fish and Game (ADF&G) in 1959. That program was developed at once and supplemented by occasional contributions from the research program of the U. S. Fish and Wildlife Service. Over the next two decades, it made significant advancements in knowledge about the walrus population.

Exchanges of information between American and Soviet biologists about walruses and hair seals also were begun in the late 1950's, at first through the North Pacific fur seal meetings, then through the Marine Mammal Project of the US-USSR Environmental Protection Agreement of 1972 (Miller and Zemskii, 1984). Since then, the information acquired by both sides, jointly and separately, concerning the Pacific walrus has provided one of the best documented records available of the natural and man-made dynamics of a pinniped population.

The following is a **resumé** of some of the principal findings from that work. In many instances, the data sets are not large, and the results derived from them, individually, are of little significance. Taken as a whole, however, they at least indicate the direction of change, if not the exact amount. Included is information on geographical distribution, size of the population, age composition, reproductive performance, feeding habits, physical condition, and natural mortality of the Pacific walrus population over the past 30 years.

Distribution---Soviet records of the use by walruses of summering areas along the **Koryak-Kamchatkan** shores of southwestern Bering Sea indicate that the animals began to re-appear there in the 1960's, after a 25- to 30-year absence, and that they subsequently became comparatively common again in all parts of the region (Chugunkov, 1970; Kosygin and Sobolevskii, 1971; Gol'tsev, 1975a; Pinigin and Prianishnikov, 1975). Since 1969-70, herds of 500 to 1,500 have been seen repeatedly in summer along the Koryak coast in the vicinity of Anastasia and Natalia bays. In the same period, herds at first of 25 to 200 and now of up to 1000 (G. A. Fedoseev, pers. **commun.**) have appeared in summer at Verkhoturov and Karaginskii Islands, as well. Nearly all of those have been males, as before; the record of one female with a calf in Lavrov Bay in the summer of 1970 was an unusual occurrence (Kosygin and Sobolevskii, 1971). More recently, herds of males have been seen along the Koryak coast, as far south as Olyutorskii Bay in late winter and spring (Kibal'chich, 1981; Calkins et al., 1981), and a few females with young have been sighted as far south as Khatyrka (G. A. Fedoseev, pers. **comm.**, 1980).

On the Alaskan side of the Bering Sea, south of the Yukon estuary, there are eight localities in which major hauling grounds are now or were formerly used on a regular, annual basis by large herds of walruses. Those are Amak Island, Port Moller, Cape Seniavin, Round Island, Big Twin Island,

Cape Newenham, Pribilof Islands, and St. Matthew Islands. More than 15 other sites have been used one or more times by herds of 20 or more animals, but not on a regular basis (Frost et al., 1982). The summering aggregation of bulls that hauls out on the Walrus Islands in northern Bristol Bay has grown from about 3000 in the late 1950's to about 12,000 in recent years (Kenyon, 1958; Taggart and Zabel, 1980; Frost et al., 1982). Walruses, probably from that same group, reappeared on Amak Island in 1962, after about a 30-year absence, and they seem to have reappeared in Port Moller about the same time. They recently have established themselves on another hauling ground at Cape Seniavin, but the history of that one is unknown (L. F. Lowry, C. Smith, pers. comm.).

Walruses apparently re-occupied the St. Matthew Islands in the fall of 1980 (R. D. Jones, pers. commun.), and they evidently began to reside there in summer, as well, by the following year (Frost et al., 1982; D. Irons, pers. commun.). To the best of our knowledge, the only previous records of their presence there were those by Etholin in 1830 (Tikhmenev, 1978) and by Hanna (1920) nearly a century later. We and several other observers have searched for walruses in that area numerous times in the 1960's and 70's, usually without sighting any or, at most, only one or two individuals. (D. R. Klein, R. L. Rausch, A. L. Sowls, A. DeGange, S. W. Stoker, and F. H. Fay, unpubl. data). That is, the recent re-occupation of the St. Matthew Islands appears to have been en masse, rather than by gradual increase. The hauling grounds on the Pribilof Islands, however, still remain unoccupied by any more than occasional individuals (Fay, 1982; Frost et al., 1982; F. H. Fay, K. W. Kenyon, and R. S. Peterson, unpubl. data). The recent use of Capes Pierce and Newenham probably also is not new but a re-occupation, though we have found no definite record of use of those sites before.

In the northern Bering and Chukchi seas, the walruses' use of haulouts on Chukotka showed a marked increase from a low of 3 sites in the 1950's to a high of 18 in use in the 1960's and 14 in the 1970's (Table 3). In those three decades, the number of hauling grounds in regular, annual use increased from 1 to 2 to 6, respectively. Of the latter, the Meechken and Rudder sites always were occupied principally in summer; the Arakamchechen, Big Diomedea, and Inchoun sites at first were occupied only during the autumn migration, then during the summer as well; the Serdtse-Kamen site always was used during only the autumn migration (Nikulin, 1947; Kleinenberg et al., 1964; Gol'tsev, 1968; Fedoseev, 1982). The Cape Chaplin haulout, which ostensibly was used often in the 19th century and earlier (Arsen'ev, 1927), has not yet been re-occupied in this century, for reasons unknown. Others, like those at Capes Geka in the Anadyr estuary, Erulen and Maska in Kresta Bay, Uelen at Bering Strait, and Vankarem and Ryr-karpi (Cape Schmidt) on the northern coast of Chukotka are now regarded as "extinct," inasmuch as walruses apparently are prevented or discouraged from hauling out there by continual human disturbances (construction,

shipping, etc.) (Fedoseev, 1982 and pers. **commun.**). None of the hauling grounds west of Cape Serdse-Kamen and on Wrangell and Herald Islands can be used on a regular basis, because they often are inaccessible due to heavy ice (Krylov et al., 1964; Gol'tsev, 1968; Tomilin and Kibal'chich, 1975).

On the Alaskan side north of the Yukon estuary, the number of regularly used haulouts apparently never was as large as on Chukotka (Table 4). Walrus began hauling out regularly in large numbers on the northwestern cape of St. Lawrence Island, near **Gambell**, in the fall of 1962, having been absent from that area for some 25 years (V. K. **Slwooko**, pers. **commun.**). Since then, the numbers hauling out and the duration of their stay have increased steadily (at least to 1978: T. **Antogham**, pers. **comm.**). They also hauled out in abundance on the northeastern end of that island in the fall of 1978, for the first time in at least 40 years (**Murie**, 1936; Fay and Kelly, 1980). At Kialegak Cape, on the southeastern part of the island, they reappeared in the fall of 1970, having been absent for several decades (V. K. **Slwooko**, pers. **commun.**), they hauled out there by the thousands in 1978 (Fay and Kelly, 1980).

On the Puduk Islands, just east of St. Lawrence Island, walrus have hauled out regularly during the fall migration for at least the past century, and the presence of a few there nearly every summer also was regarded as normal from about 1914 to 1945 (L. **Kulukhon**, pers. **commun.**). They were virtually absent there in summer for the next 25 years, with only one known exception (in 1956), but they have re-appeared there in summer on a regular basis since the 1970's (A. Akeya, T. Antogham, F. H. Fay, and B. P. Kelly, **unpubl.** data).

Farther north, in Bering Strait, walrus re-occupied Big Diomed Island in the fall of 1965, after about 30 years of absence or scarcity (J. J. Burns, pers. **comm.**). The numbers and duration of their stay there have increased steadily since that time (Frost et al., 1982). Nowadays, they occur not only during the fall migration but all summer, as well. Since the mid-1970's, some also have used Little Diomed and King islands intermittently, despite frequent harassment (E. Muktoyuk, J. J. Burns, pers. **commun.**).

In the eastern Chukchi Sea, the two haulouts at Cape Thompson and Point Hope saw irregular use in the past, during the fall migration. To the best of our knowledge, they have not been re-occupied. The haulout at Cape Lisburne, however, was re-established at least by 1975 (D. **Roseneau**, A. Springer, pers. **comm.**), after about 30 years of disuse. Farther north and east, walrus had not been seen in the Beaufort Sea for many years, but they began to reappear there in small numbers in the 1960's (Burns, 1965), and they now occur there more frequently.

Table 4. Use by walruses of haulout areas on Alaskan shores of the northern Bering Sea and Chukchi Sea in the present century.¹

Haulout	1920's	1930's	1940's	1950's	1960's	1970-80's
Egg I.	UNK	UNK	UNK	None	None	Irreg.
Besboro I.	UNK	UNK	UNK	None	Irreg.	Irreg.
Cape Darby	UN-K	UNK	UNK	UNK	None	Irreg.
Sledge I.	Irreg.	Irreg.	None	None	None	Irreg.
Punuk Is.						
(summer)	Irreg.	Irreg.	Irreg?	Irreg.	None	Reglr.
(fall)	None	Irreg.	Irreg?	Reglr.	Reglr.	Reglr.
St. Lawrence I.						
Kialegak Pt.	None	None	None	None	None	Irreg.
N. E. Cape	None	None	None	None	None	Irreg.
Salghat	Irreg.	Irreg.	None	None	None	Irreg.
C. Chibukak	Irreg.	Irreg.	None	Irreg.	Reglr.	Reglr.
King I.	UNK	UNK	UNK	None	None	Irreg.
Little Diomede	UNK	Irreg.	None	None	Reglr.	Reglr.
C. Thompson	UNK	Irreg.	UNK	None	None	None
Pt. Hope	UNK	Irreg.	UNK	None	None	None
C. Lisburne	UNK	Irreg.	Irreg.	None	None	Irreg.

¹From Hanna (1920, 1923), Murie (1936), Collins (1940), Brooks (1954), Frost *et al.* (1982, 1983), and unpublished notes from U. S. Fish and Wildlife Service and Alaska Department of Fish and Game files, as well as from A. Akeya, T. Antoghome, R. Baxter, J. J. Burns, A. DeGange, F. H. Fay, T. Gologergan, Jr., R. D. Guthrie, D. Irons, W. James, R. D. Jones, B. p. Kelly, K. W. Kenyon, D. L. Klein, L. Kulukhon, E. Muktoyuk, R. L. Rausch, D. Roseneau, V. K. Slwooko, T. Smith, A. Sowles, A. Springer, S. W. Stoker, R. Tremaine, and M. Ward.

Another indicator of change in the population is the frequency of occurrence of individual wanderers outside the usual limits of the range. In the 1950's, there were only three records of such wandering -- an animal sighted on Kodiak Island in 1954, one in Cook Inlet in 1955 (R. A. Ryder and L. Temple in **Fay**, 1982), and another in the Okhotsk Sea in 1957 (**Kosygin** and **Sobolevskii**, 1971). In the 1960's, four more were recorded: an individual was sighted in upper Cook Inlet in 1964 (**Fay**, 1982), and three were seen on the southeastern coast of **Kamchatka** in 1966 -- one individual at **Listvenichnyi** Bay, one in **Russkii** Bay, and the third was found dead at Cape **Nalychevo** in that year (**Chugunkov**, 1970).

On the Commander Islands, where only a few beach-cast carcasses had appeared in the 1950's and 60's (**Chugunkov**, 1970), two living walrus were seen in the early 1970's (**Pinigin** and **Prianishnikov**, 1975). Farther east, at least one animal was reported to have reached Atka Island in the central Aleutians in 1976 (K. W. **Kenyon**, pers. comm.), and two others were killed there about 1979 (**Fay**, unpubl. data). These were the first occurrences at Atka in 30 to 40 years, according to local residents. Still farther to the east, a group of about 20 made its way out through **Unimak** Pass and up along the southern coast of the Alaska Peninsula in the spring of 1979 (C. Smith, K. Pitcher, D. **Calkins**, pers. comm.). That group was gradually reduced in number as it moved eastward, through the **Shumagin** Islands, **Chignik** Bay, **Shelikof** Strait, and Cook Inlet; the last known survivor reached Yakutat Bay by mid-summer. In the 1980's, so far, the only report known to us has been of one walrus found dead in the northern **Kuril** Islands in 1983 (Yu. A. **Bukhtiyarov**, pers. comm.), the first known to have made its way that far south in about 45 years.

Population Size.—Estimation of the size of the Pacific walrus population by direct censuses began in the 1950's. Previous estimates were educated guesses, not based on actual census data. The first census estimate was based on counts along the cruise track of the American icebreaker **NORTHWIND**, which travelled widely in the pack ice of the Bering and **Chukchi** seas in May and June 1954. Assuming that the cruise track was made up of a series of random transects and that the observed number of animals per unit area could be extrapolated to the total range of the walrus population in that month, **Fay** (1957) estimated that the Pacific walrus population was made up of about 40 to 50 thousand animals. Although the method of census was primitive and the assumptions were not necessarily correct, the result, by chance, was very similar to some of those that followed.

An aerial survey conducted by P. G. **Nikulin** (in **Fedoseev**, 1962) on the Soviet side in the summer of 1958 yielded an estimate of about 40,000 animals there; the number on the American side at that time was unknown but believed to be very small. Another Soviet aerial census, this time using aerial photography of the herds on the coastal hauling grounds and visual

estimates of those on the ice, was conducted on the Soviet side in the autumn of 1960 by Fedoseev (1962). From it he estimated that there were about 46,000 animals west of the Date Line at that time, and he guessed that there were perhaps 4,000 more on the Alaskan side. In that same year, however, Kenyon (1960a) and co-workers had conducted two aerial censuses over the Bering Sea Pack ice, the first in late February to early March and the second in mid-April. The results from both of their surveys were very similar, with highest and lowest estimates ranging from 70 to 113 thousand animals and medians of about 85 to 95 thousand, respectively. These were nearly double the Soviet estimates, but the fact that they were different is not surprising, for they were based on surveys of nearly the entire population on its wintering range in the Bering Sea, whereas the Soviet survey had covered an unknown proportion of the population on the summering range in the western Chukchi Sea. In retrospect, we can see why the Soviets' results underestimated the whole population, because, as the latest censuses have shown, nearly half of the population probably was on the American side, out of range of the Soviets at the time.

Kenyon (unpublished data) conducted another census over the Bering Sea pack ice in March 1961 and, again, estimated the population between about 70 and 110 thousand (median, 85,000) animals. A third Soviet census in the autumn of 1964 by **Gol'tsev** (1968) yielded estimates of about 47 to 71 thousand (median, 59,000) animals for the portion of the population on the Soviet side. **Gol'tsev** did not make an estimate for Alaskan waters, apparently because he assumed that there was only an insignificant number of animals there. A fourth census by Kenyon and co-workers (unpublished data) in April 1968 again covered most of the population in the Bering Sea and yielded estimates ranging from 73 to 110 thousand animals.

The fourth Soviet census was conducted by **Gol'tsev** (1972) in the autumn of 1970, and from it he estimated about 101,000 animals in the whole population, apparently including a guess at the number in Alaskan waters. A fifth census by Kenyon (1972), conducted in April of 1972, yielded a similar median estimate of 123,000 for the whole population, with upper and lower limits of 85 to 162 thousand. This survey covered nearly the whole geographic range of the population in that month, hence was the best overall estimate to date.

Each of those censuses was done without benefit of communication between the Soviet and American biologists who conducted the surveys. Not until 1973 was that communication established, and it quickly led to discussion of past findings and plans for the future. The first cooperative census was conducted more or less concurrently on both sides of the International Date Line in September and October of 1975 (**Gel'tsev**, 1975a; **Estes and Gilbert** 1978), and it was followed by another in the same time period in 1980 (**Fedoseev**, 1981; **Johnson et al.**, 1982). In each of those, the Americans used strip sampling methods, involving visual counts along north-

south transects over the **Chukchi** pack ice, east of 174°W ; the Soviets made visual estimates from transects over the pack ice in the western **Chukchi** Sea, west of 174°W , and used direct counts from aerial photos of large herds on the ice and of all herds on the coastal hauling grounds. The results in 1975 indicated that there were about 120,000 animals in Soviet waters and about 112,000 in Alaska (Table 5). In 1980, the median estimates were again about 130,000 for Soviet waters and about 115,000 for Alaska. The estimates for the total population in those years, as we interpret them, were about 232,000 and 245,000, respectively, but these are not significantly different, because of the wide confidence limits.

The population estimates derived from all of those surveys probably were very conservative, because they could not take into account the effects of such factors as activity rhythms and animals out of sight underwater, which could exert very large influences on both the collection and the interpretation of the data. We assume that such errors tend to be relatively constant, and that the trend in numbers estimated, at least, was real. That trend was clearly upward in both the Soviet and the American results (Fig. 8), even though the timing and methods were quite different on each side, during most of that time. Because the Soviet census method remained basically the same from 1960 to 1980, the increase in population size indicated by their estimates cannot be ascribed to increased sophistication of methods or equipment. In each of their surveys, about 60% of the estimate was based on actual counts from photographs of the large herds on the ice as well as on each of the coastal hauling grounds; the rest of their estimate was based on strip sampling over the ice. The confidence limits on the results from the strip sampling are unknown to us but presumed to be wide, because the samples were small. Because the American estimates were based entirely on strip sampling and the confidence limits on the results are known to be extremely wide, we regard the American median estimates as less reliable than those from the Soviet side. Furthermore, the American surveys were done in different areas, at different times, with different equipment, and the analyses of the data were done by different methods, among years. Those conditions probably contributed further to making the American results incomparable from year to year.

The Soviets' results indicate that the proportion of the population that summers on their side tripled from 1958 to 1975 but leveled off in the late 1970's. Essentially the same is indicated by the estimates of the total population, as we interpret them. Although the implied magnitude of that change is questionable, because of the wide confidence limits on the estimates, we feel that the direction is believable because increase has been indicated also by the other indices of the population's status. Using a numerical model, DeMaster (1984) has shown that doubling of population might have been possible in the 20 years between 1955 and 1975, if (1) the initial population was at least 96,000 animals, (2) the adult survival rate

Table 5. Estimated size of the Pacific walrus population based on Soviet-American cooperative censuses in 1975 and 1980.¹

Date and location		Estimate
1975 Soviet side	5-6 Oct W. Chukchi ice	26,600
	18-21 Sep Chukotka haulouts	94,139
	4 Oct Koryak haulouts	220
	American side 8 Sep E. Chukchi ice - est. I	100,600 \pm 57,700
	- est. II	90,800 \pm 63,600
	Bristol Bay ²	6,500
1980 Soviet side	8 Oct W. Chukchi ice	55,000
	9 Oct Chukotka haulouts	69,400
	17 Oct Koryak haulouts	4,000
	27 Sep Kamchatka haulouts	1,500
	American side 15-20 Sep E. Chukchi ice - est. I	101,200 \pm 22,600
		- est. II
	Jul-Sep Bristol Bay ³	15,000

¹**Soviet** estimates based on data from **Gol'tsev** (1975a) and Fedoseev (1981), excluding any possible duplicate counts of the same animals. American estimates for 1975 based on Estes and Gilbert (1978), but only for North-South strips, comparable with the 1980 estimates by Johnson et al. (1982). The American estimates for both years were derived by two methods: I - from average numbers of individuals per unit area and II - from average groups per unit area. For each estimate, the mean and standard error are given.

²**From** an estimate of "5-8,000" on Round Island on 29 June to 4 July 1977 (**Arneson** and McDonald in Frost et al., 1982).

³From Taggart and **Zabel** (in Johnson et al., 1982).

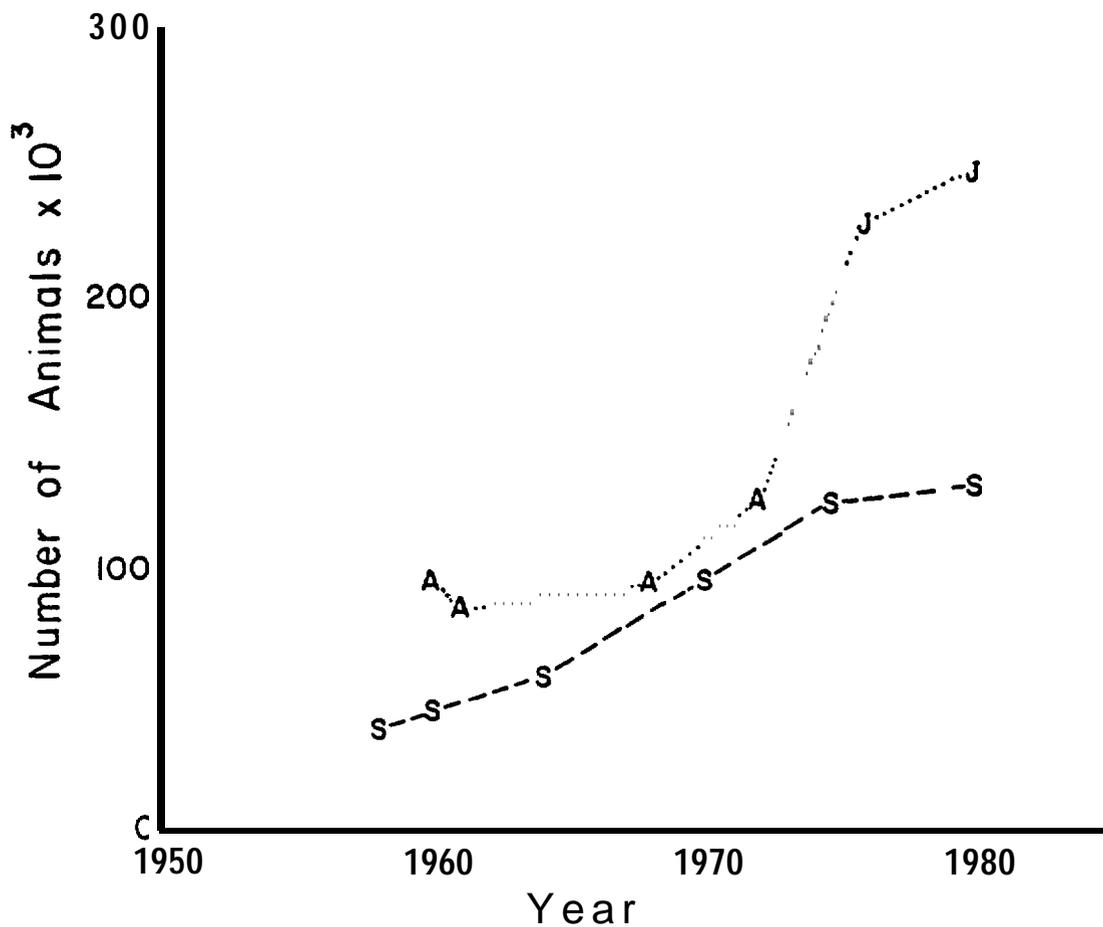


Figure 8. Estimates of the size of the Pacific walrus population, 1958-1980. Results from Soviet censuses of the number of animals west of the International Date Line in September-October (S) are compared with the results from American (A) and joint Soviet-American (J) mean estimates of the total population (data from Kenyon, 1960a, 1972, and unpublished; Fedoseev, 1962, 1981; Gol'tsev, 1968, 1972, 1975a; Estes and Gilbert, 1978; Johnson et al., 1982).

was at least **0.95**, (3) the sex ratio of adults was 1 male to 3 or more females, and (4) the productivity was at its maximum. We think that all of those provisions were met, hence that the population at least doubled between 1955 and 1975, and that it probably did not increase significantly since then.

Age Composition of Native Catch---Samples for analysis of the age/sex composition of the annual catch by Alaskan Eskimos were obtained intermittently over the past 30 years by Fay in 1952-59, by the Alaska Department of Fish and Game in 1960-79, and by the U.S. Fish and Wildlife Service and Eskimo Walrus Commission in 1980-84. Those samples were obtained principally in spring at the villages of **Gambell** and Savoonga on St. Lawrence Island and at **Ignaluk** on Little Diomedede Island. They represent about two-thirds of the annual catch in Alaska in those years (**Fay**, 1958; **Burns**, 1965, 1973).

The samples consisted of one or two cheek-teeth from nearly every animal taken (other than calves), during the spring hunt. Each tooth was sectioned longitudinally, and the age of the animal was determined by counting the annual layers of cementum (**Burns**, 1965; **Fay**, 1982). **All** of the age determinations reported here were done by J. J. **Burns** (Alaska Department of Fish and Game) and F. H. **Fay** (University of Alaska), who cross-checked their determinations repeatedly and found them comparable.

The samples were not collected every year or in any pre-arranged schedule but were obtained mainly as opportunity and funds permitted. The data from them have been treated as age-frequency tables, with sexes separated. Because the natives' catch tends to be biased toward adult animals, the immature age classes are very poorly represented. Hence, the age-class frequencies tend to be normally distributed on the x-axis (Fig. 9). This allows them to be compared by means of statistics of central tendency. The results of those comparisons are as follows:

Males: The mean age of males taken in the spring harvests at all three villages tended to be relatively constant at 13 to 15 years during the **1950's** and early **1960's** (Fig. 10). After the early **1960's**, however, the mean age of males rose steadily in each village's annual catch and was approaching 19 to 22 years in the most recent samples. This is a very significant increase. It was a gradual increase, and it took place without any change in the selective bias, according to the hunters that we have interviewed (**A. Akeya**, **T. Antoghame**, **M. Iya**, **L. Kulukhon**, **C. Pungowiyi**, pers. **commun.**). In all three villages, the hunters consistently selected for males with large tusks. In male walruses, tusk size increases with age, almost indefinitely (**Fay**, 1982).

The trend of increasing mean age of males in the catches since the early **1960's** has been produced by the taking of more old animals and fewer

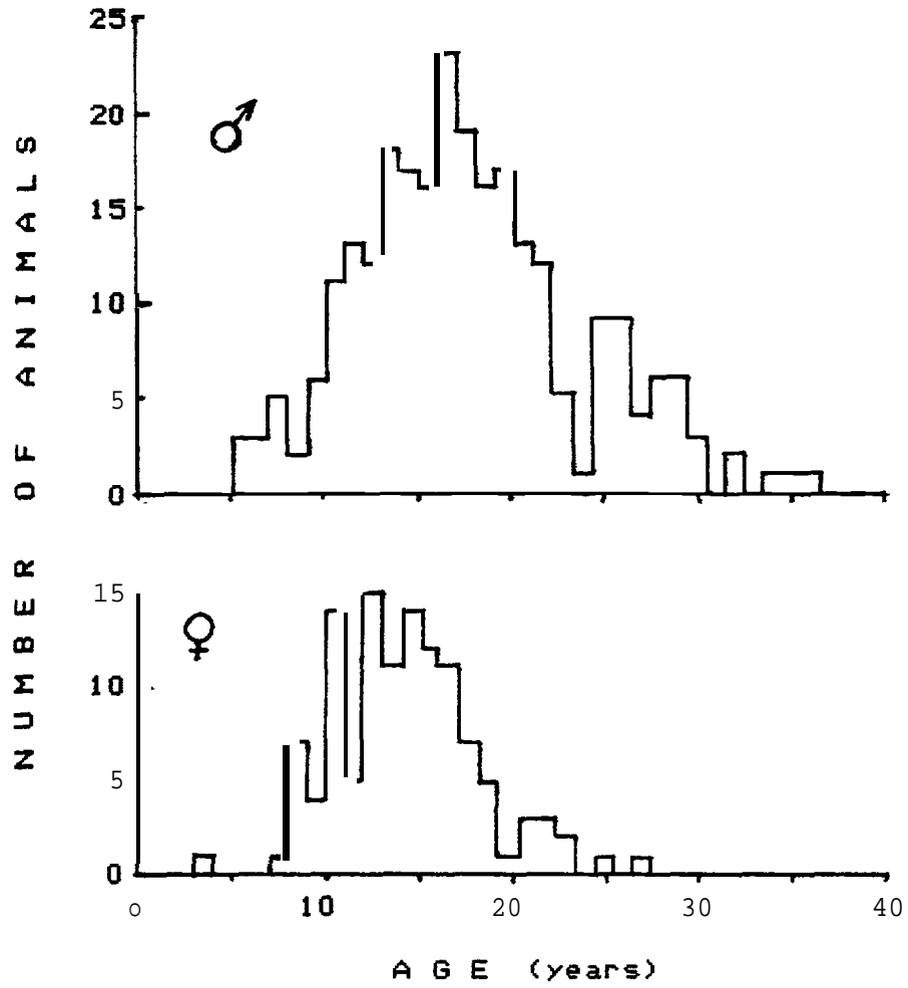


Figure 9. Age frequency histograms for male (upper) and female (lower) Pacific walrus taken at Little Diomedes Island in the spring of 1972 (Alaska Department of Fish and Game, unpubl. data).

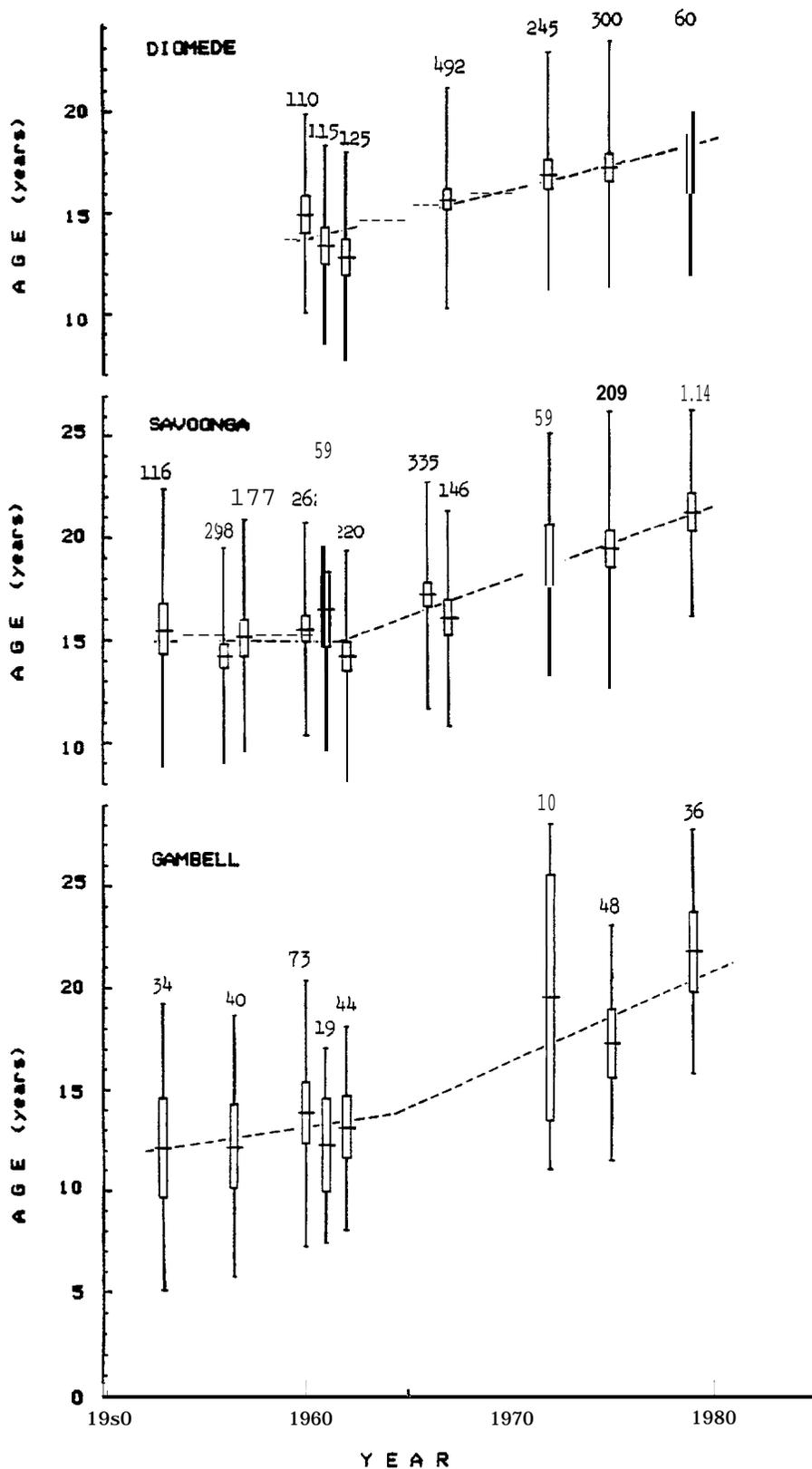


Figure 10. Change in mean age of the catches of male walruses, 1950-70's. Each bar represents one sample, of the size shown above it. Cross-bar is the mean; thin bars are ± 1 S.D.; open bar shows 95% confidence limits about the sample mean. Curves fitted by least squares.

young ones. The implication of this is that the old males have become more available and/or that the young males have become less available, over the past 20 years. Those conditions might be correlated with an increase in size of the walrus population, a shift in age composition to more old animals (brought on by either lowered recruitment or increased juvenile mortality), or a combination of those causes.

Females: The selective bias affecting the catch of females by the hunters at Little Diomedé is essentially the same as it is for the males. The hunters take primarily the larger, older animals, though about as much for the quality of the meat and hides as for the tusks. The meat of adult females is desired for human consumption, and the hides of the largest females are required for building and maintaining their "skin-boats" - (**umiaks**). The tusks of adult females also are preferred for carving, because the ivory is of a finer, more uniform quality than in the males. The ivory of the females is of optimal size and quality at ages between 15 and 25 years; after about 25 years, it tends to check increasingly and to diminish in length due to fracture and abrasion (**Fay, 1982**). Hence, where there is such selective bias and the availability is unlimited, the mean age of females in the catch should approach and level off about 17 to 20 years. The mean age of the females in the catches at Little **Diomedé**, like that of the males, was relatively stable during the population's recovery to rapid growth, in the late 1950's and early 1960's. Thereafter, it tended to rise steadily and was up to about 17 years by 1982 (Fig. 11).

At **Gambell** and Savoonga, the selective bias for females is different than it is for males and different than it is at **Diomedé**. Here, the hunters' search primarily for females with newborn calves, which are sought for their meat (dried for human consumption) and their skins (used for making rawhide ropes). Given the opportunity to choose from several females with calves, the hunters secondarily select for large body size and large tusks (**Fay, 1958**). As at **Diomedé**, the meat of the adult females is preferred over that of the males for human consumption, the female hides are needed for the **umiaks**, and the ivory of females is preferred for carving.

In the 1950's and 60's, the mean age of females taken at both **Gambell** and Savoonga tended to be constantly about the n-year level. This is a reflection of the fact that the age class of females with the highest probability of producing a calf was 11 years at that time (**Fay, 1982**). Then, in the 1970's and early 1980's, the mean age of females taken at both villages rose significantly. That increase might have been due in part to a change in age-relative fecundity and/or to an increase in average age of the females available. It apparently was not due to any change in the hunters' selection, for the hunters in both **Gambell** and Savoonga at that time were complaining about the scarcity of females with calves. That **is**, they still were seeking them preferentially but were having less success in

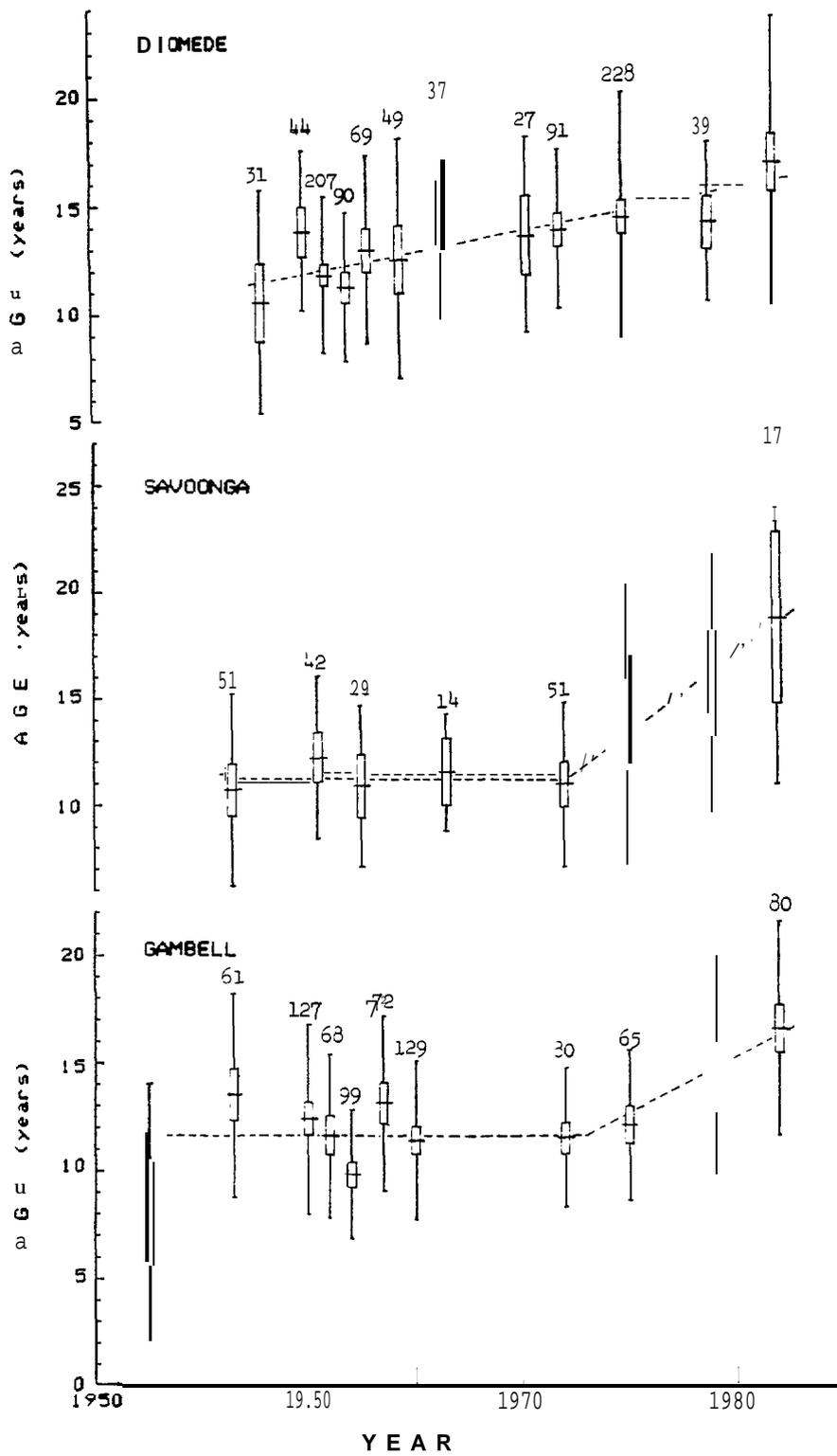


Figure 11. Change in mean age of the catches of female walrus, 1950-80's. Each bar represents one sample, of the size shown above it. Cross-bar is the mean; thin bars are ± 1 S.D.; open bar shows 95% confidence limits about the sample mean. Curves fitted by least squares.

finding them. **Some** of the hunters also remarked (to Fay) about an unusual abundance of females with stout, short, heavily abraded tusks. Such tusks are characteristic of very old animals, and fecundity decreases markedly in old age (**Fay**, 1982 and unpublished).

Another indication of increasing age of the females was the change in number of corpora counted in the ovaries (**Fay and Stoker, 1982a,b**). Because the corpora **albicantia** in the ovaries persist for many years, the number in each animal tends to increase with age (**Mansfield, 1958; Burns, 1965; Krylov, 1966**). The numbers of corpora per female in the catch samples at Diomedea appeared to increase continually from the 1950's to the 1980's. At **Gambell**, conversely, the number per female did not appear to change significantly up to the 1970's, but it did increase by the 1980's (**Fig. 12**). By comparing the cumulative relative frequencies of those samples, using the Kolmogorov-Smirnov Two Sample Test, the increases were found to be highly significant (**$P < 0.001$**). Those increases at both villages are directly attributable to increasing mean age of the animals in the catch.

Natural Mortality on the Punuk Islands.—During the southward migration each autumn, large numbers of walrus haul out on the **Punuk** Islands, apparently to rest briefly before continuing on their way to the wintering areas. During that pause, some of the animals die from natural causes (**Fay and Kelly, 1980**). The numbers of carcasses remaining in the following spring, after the autumn storms and winter ice have rearranged them, have varied from 0 to 466 per year over the past 35 years (**Fig. 13**). The trend in numbers per year, from the late 1940's to contemporary times was upward, possibly to a peak in 1978. That increase was highly significant, even when the unusually high mortality of 1978 was excluded (1948-65, $n = 8$ yrs, mean \pm se. = 35.3 \pm 7.6 carcasses/yr; 1968-81, $n = 6$ yrs, 87.8 \pm 13.7/yr; $t = 3.36$, **$P < 0.01$**). The mortality in the fall of 1982 apparently was very low, for only 18 carcasses remained in the spring (**A. Akeya, pers. comm.**).

A series of samples of the age composition of walrus that died on the **Punuk** Islands in several years was obtained by **the P.I.** and co-workers. Those samples consisted of one cheek tooth for age determination from each carcass. As in the foregoing, age was determined from counts of cementum layers in thin longitudinal sections of the teeth. Nearly all of the samples are very small, hence their variances are large. Nonetheless, they show an upward trend in both sexes, just as in the catch samples (**Fig. 14**).

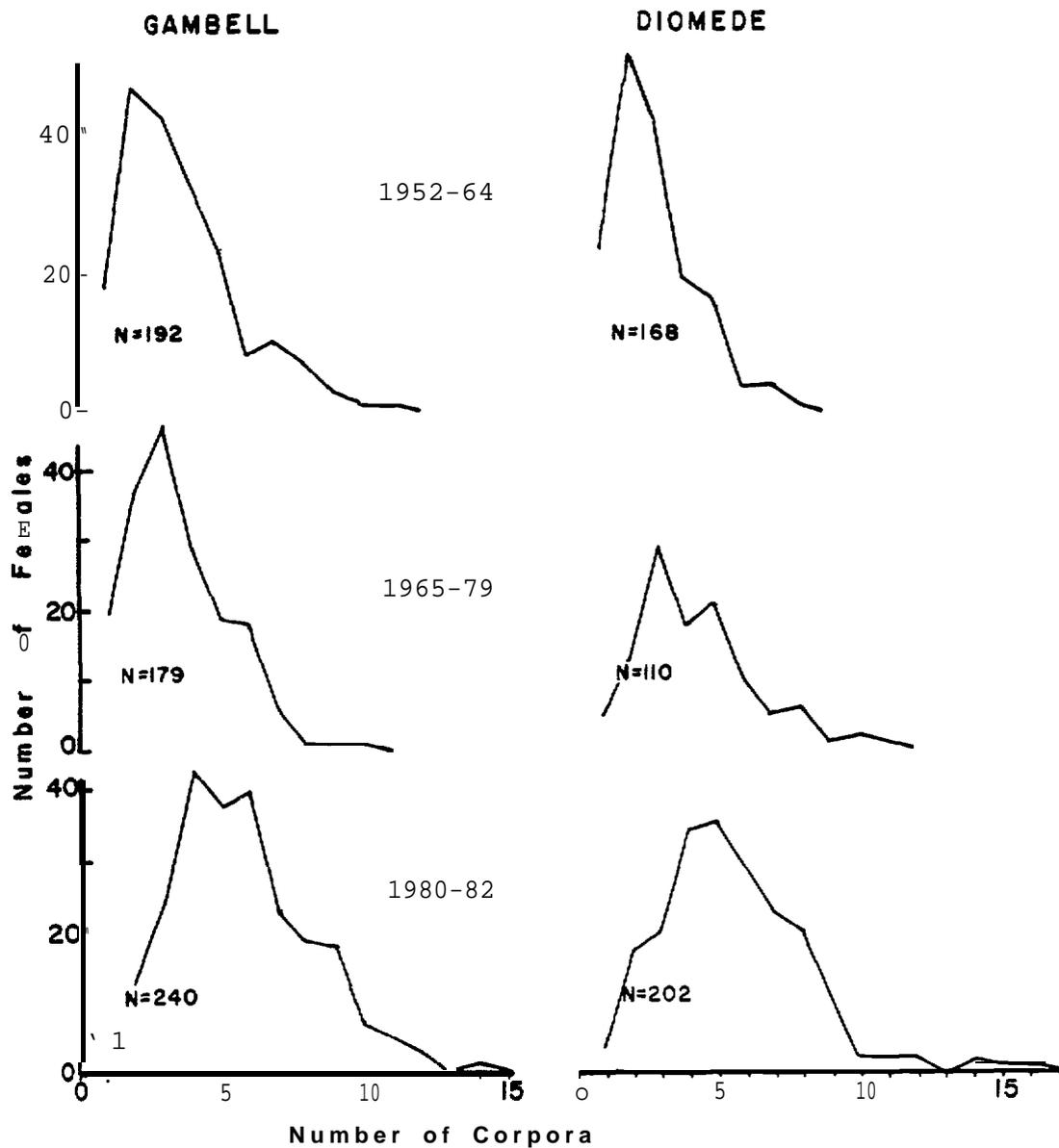


Figure 12. Comparative frequency of occurrence of numbers of corpora (lutea and *albicantia*, combined) in the ovaries of adult females from the spring catches at **Gambell** and Little Diomedede, 1952-82. Sample sizes (N) are shown for each curve (J. J. Burns and F. H. Fay, *unpubl.* data).

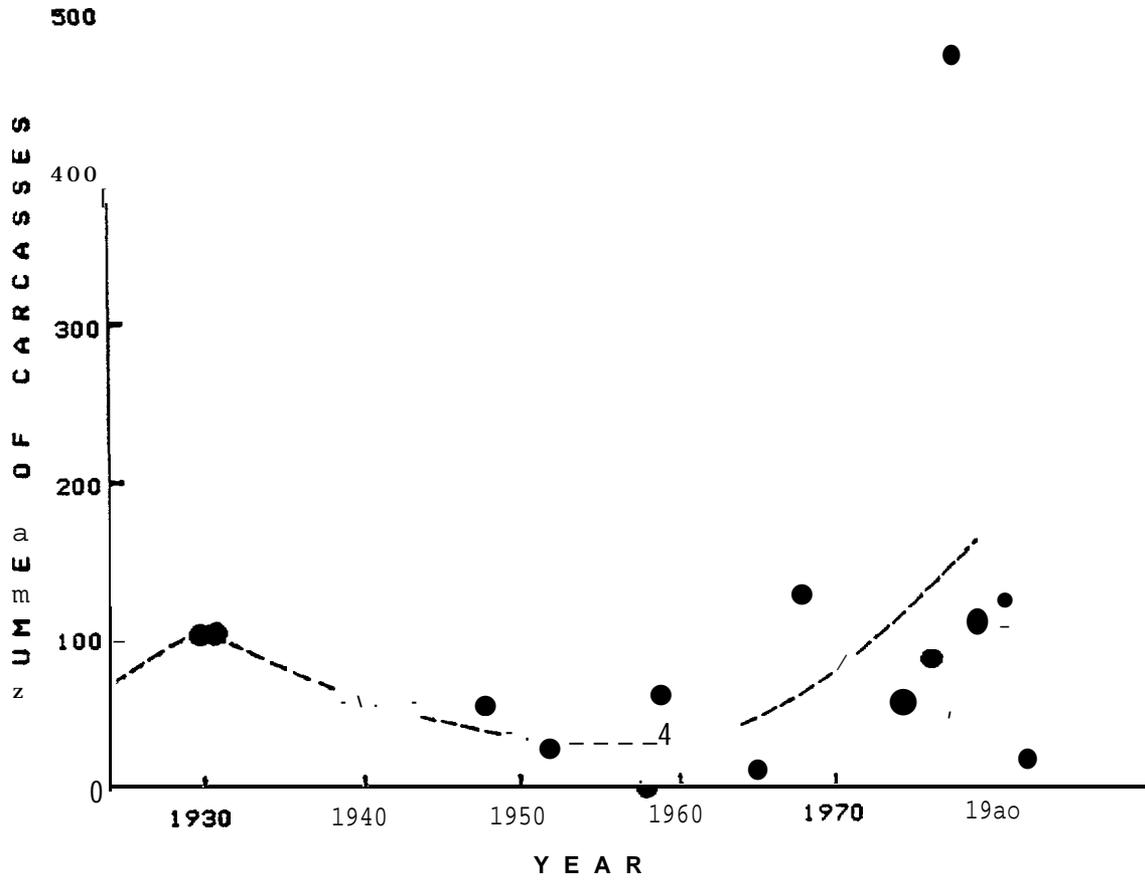


Figure 13. Natural mortality on the **Punuk** Islands during the autumn migration, 1930-82. Each dot represents the number of carcasses found there in the following spring. Dashed line is suggested trend (after Fay and Kelly, 1980 and **unpubl.** data).

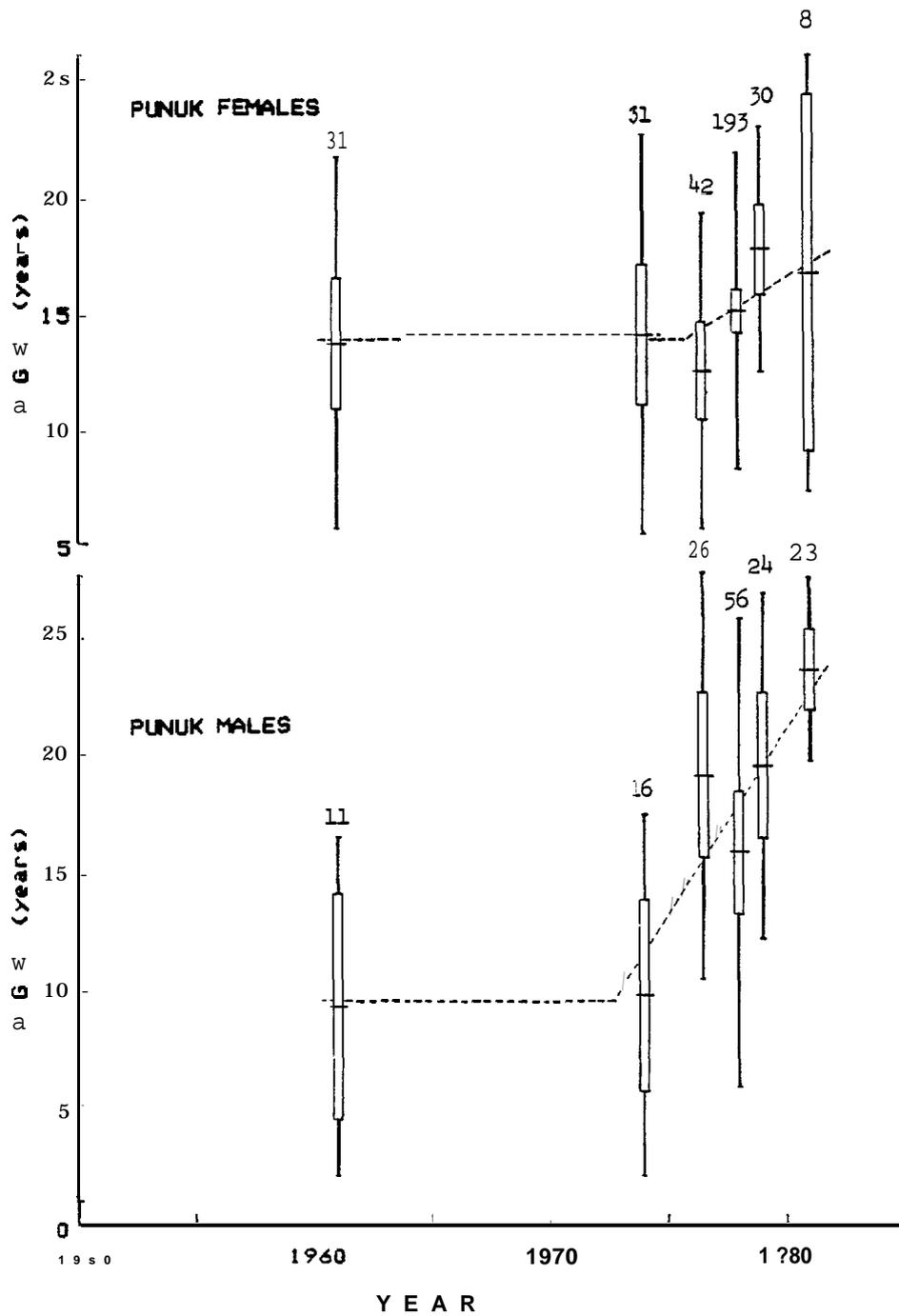


Figure 14. Change in mean age of walrus dying from natural causes on the **Punuk** Islands, 1961-81. Each bar represents one sample, of the size shown above it. Cross-bar is the mean; thin bars are + 1 S.D.; open bar shows 95% confidence limits about the sample mean. Curves fitted by method of least squares.

Reproduction.--Walrus give birth in the spring, mainly between mid-April and **mid-June**, during the northward migration from the Bering to the **Chukchi** Sea (**Fay**, 1982). Hence, the females taken at that time, in the spring catch, are readily classified as:

(1) immature, if they are not and never have been in estrus (i.e., have no corpora or ripe follicles in their ovaries),

(2) **newly** pregnant, if they show a new corpus **luteum** of pregnancy, whether or not an embryo can be seen in the uterus,

(3) **parturient**, if they are pregnant with a full-term fetus or have recently given birth to a new calf,

(4) barren, if they are none of the above but have experienced at least one **estrus**.

Although the samples from the catch are non-random, as noted above, hence not necessarily representative of a cross-section of the female population, those from any given locality are comparable from year to year, because they are affected by the same selective biases each year. The largest sets of those samples have been obtained at **Gambell** and Little Diomedé, beginning in 1952. From that time until the present, the most marked change indicated by them has been in the birth rate, as follows:

From the 1950's to the late 1970's, the frequency of occurrence of parturient females in the catches at both **Gambell** and Diomedé varied somewhat but appeared to be comparatively stable, year after year. In seven small samples from Little Diomedé in that period, the percentage of **parturient** animals per sample ranged from about 40 to 50%, which did not differ significantly from the expected values (Table 6). In 1980, however, the frequency was much lower than expected, and in 1982, it was somewhat higher than expected. At **Gambell**, in the 1950's to mid-60's, the observed frequency of occurrence tended to be higher than expected, because of the selection for cows with calves. That was followed by a period of little or no deviation from expected values in the late 1960's to late 70's, then by an extremely low frequency in 1980, and back to the higher than expected level again in 1982.

Because the age composition of the catches also changed significantly at both villages in that same 30-year period, we presumed that some of the deviations could have been attributable to age of the animals. To test for that, we compared the observed frequencies with expected values derived from mean ages of the catches and the age-relative fecundity as described by Fay (1982, tables 34, 35) and Fay and Stoker (1982b, table 4). The

Table 6. Chi-square goodness of fit test, comparing observed with expected frequencies of occurrence of **parturient** animals in samples of adult females from the spring catches of walrus at Little **Diomede** and **Gambell**, 1952-82. (Extracted from Appendix A)

DIOMEDE	Year of catch						
	1952-58	1962-64	1965	1966-68	1979	1980	1982
N	47	61	39	35	40	102	110
Ohs. f	22	31	16	17	16	15	57
Exp. f	19.33	25.09	16.04	14.40	16.45	41.55	41.14
Chi-Sq .	0.37	1.39	0.00	0.47	0.01	16.96	6.12

GAMBELL	Year of catch							
	1952-61	1962-64	1965	1966-68	1975	1979	1980	1982
N	93	109	114	11	43	29	163	87
Ohs. f	77	87	101	7	33	16	36	64
Exp. f	60.33	70.71	73.95	7.14	27.89	18.81	105.74	56.44
Chi-Sq .	4.61	3.75	9.89	0.00	0.94	0.42	45.99	1.01

results are shown in Table 7. For Diomedé, the frequency of occurrence of **parturient** females in the catches did not differ greatly from the expected frequencies, during 1952 to 1979, but in 1982, the frequency was much higher than expected. At **Gambell**, where there is strong selective bias for **parturient** females, the observed frequencies in the 1950's to mid-60's were consistently much higher than those predicted from age composition of the catches. But from the late 1960's to late 70's, at least, there was a tendency away from that pattern, with observed frequencies approaching the expected.

Table 7. Goodness of fit comparison of observed with expected frequencies of occurrence of parturient animals in samples of adult females from the spring catches of walrus at Little **Diomedé** and **Gambell**, 1952-58, using mean age of the catch and age-relative fecundity to generate expected values.¹

DIOMEDE	Year of catch					
	1952-58	1962-64	1965	1966-68	1979	1982
N	47	61	39	35	40	100
Ohs. f	22	31	16	17	16	57
Exp. f	22.86	26.40	15.58	10.36	13.36	23.79
Chi-Sq.	0.03	0.80	0.01	4.26	0.52	46.37

GAMBELL	Year of catch						
	1952-61	1962-64	1965	1966-68	1975	1979	1982
N	93	109	114	11	43	29	87
Ohs. f	77	87	101	7	33	16	64
Exp. f	38.79	50.78	52.13	3.32	18.36	9.40	21.21
Chi-Sq .	37.64	25.84	45.82	4.08	11.68	4.63	86.30

¹After Fay and Stoker (1982b, table 4).

Although the observed values at each village fluctuated from year to year during the 1950's and 60's, those fluctuations were not synchronous between the two villages. This indicated that the variation within each village's catches was not reflecting any population-wide changes but was attributable simply to variation in local hunting conditions and availability of animals, together with the normal variation among small samples. The coincidence of minor deviations, however, beginning in 1966-68, and of subsequent major deviations in 1980 and 82, suggested that the catches in both villages were being affected by changes in the population as a whole.

The ostensibly random samples taken by Soviet biologists in 1972-3 (Gel'tsev, 1975b) and during subsequent joint Soviet-American research cruises also suggested a trend of decrease in fecundity (Table 8). Some of that decrease may have been due to change in age; unfortunately, we do not yet have the age data from all of those samples, so cannot compare them with expected values. Certainly, the maximal decrease indicated in 1983 was not due to age alone, since that sample showed other, unique characters not related to age. In addition to having one of the lowest proportions of parturient females ever observed, it had the highest proportion of ovulations (72/120 = 60%) on record. Furthermore, nearly half of those ovula-

Table 8. Frequency of occurrence of **parturient**, pregnant, and barren **females in** non-selected samples of adult walrus taken during Soviet and joint Soviet-American research cruises, 1972-83.¹

		1972-3	1976	1981	1983
Sample N		201	34	73	120
Parturient	n	91	14	27	25
	(%)	(45.3)	(41.2)	(37.0)	(20.8)
Pregnant	n	87	15	26	33
	(%)	(43.3)	(44.1)	(35.6)	(27.5)
Barren	n	23	5	20	62
	(%)	(11.4)	(14.7)	(27.4)	(51.7)

¹From Gol'tsev (1975b), Fay (1982), and F. H. Fay and A. A. Kibal'chich, unpublished.

ting females had either rejected the **blastocyst** or failed to conceive (implant). That was the highest proportion of failures (44%) ever found in any sample. Of the females that had conceived successfully (**N=40**), 6 already in August had aborted their fetuses, and 1 other had a defective fetus that probably would have been aborted or born dead. That proportion of fetuses aborted also was extremely high (17.5%), similar to the proportion indicated in recent samples from the Alaskan Eskimos' catch (Fay and Stoker, **1982a,b**). Thus, only 33 (27.5%) of the 120 animals in the sample were newly pregnant with an apparently healthy fetus, and that, too, is a lower proportion of pregnancies than in any previous Soviet samples.

The proportion of newly pregnant animals in those non-selective samples also showed decline from 1972 to 1983 (Table 8). The frequency of occurrence of pregnancies in the catch samples, however, has been more difficult to trace, mainly because of small samples and selective bias, particularly at **Gambell**. The proportion of newly pregnant animals in the samples from both **Diomedede** and **Gambell** in the 1950's, 60's, and 70's were consistent with expected values (Table 9). But by the early 1980's,

Table 9. Frequency of occurrence of new pregnancies in the catch samples from **Diomedede** and **Gambell**, in relation to expected values, 1952-82. (Extracted from Appendix A)

DIOMEDE	1952-58	1962-64	1965	1966-68	1979	1980	1982
Sample N	47	61	39	35	40	102	100
Ohs. f	18	19	16	9	16	63	26
Exp. f	18.56	24.08	15.40	13.82	15.79	39.88	39.48
Chi-Sq.	0.02	1.07	0.02	1.68	0.00	13.41	4.60

GAMBELL	1952-61	1962-64	1965	1966-68	1975	1979	1980	1982
Sample N	93	109	114	11	43	29	163	87
Ohs. f	10	16	8	3	8	6	68	9
Exp. f	18.34	21.50	22.48	2.17	8.48	5.72	32.15	17.16
Chi-Sq.	3.79	1.41	9*33	0.32	0.03	0.01	39.98	3.88

the frequencies at both villages deviated significantly upward in 1980 and downward in 1982.

The proportion of pregnancies that resulted in successful births decreased significantly in the interval between 1952-68 and 1980-82 (200/203:192/230; $X^2=28.47$, $p<0.001$). Most of that decrease apparently was the result of an order of magnitude increase in abortions and premature births, which rose from about 1.5% of the fetuses per year in the 1950's and 60's to about 16.5% in 1980 and 1982 (Fay and Stoker, 1982a,b).

As a whole, each of the data sets indicates a trend of decrease in productivity in recent years and increased irregularity, with intermittent years of very high and very low production. The overall trend of decrease in productivity, if gradual could have been entirely a function of age composition of the samples. As shown earlier, the older females reproduce less often and are less successful than the younger ones in carrying out a full pregnancy (Fay, 1982). The increased irregularity in the productivity of the samples, however, does not appear to be attributable to increased age; it seems to be due to synchronization of breeding, with a high proportion of females in estrus one year, a low proportion in the next, etc. We suggest that the synchrony may have been brought about by a very high rate of reproductive **failures** in one year, resulting in a very high proportion of the females coming into estrus the following year.

Recruitment.--Walrus reproduce very slowly, relative to other **pinnipeds**, and for that reason they are presumed to have very high survivorship and recruitment rates (Mansfield, 1958). Those rates are impossible to estimate from catch samples, because of the biases of selective hunting, but as **Chapskii** (1936) recognized they can be estimated from visual sampling of the sex/age composition of the population at large. Because the harvesting of walrus usually is not aimed at the cohorts of immature animals from 1 to about 5 years old, that part of the population is practically unaffected by man and is influenced only by natural mortality. The relative abundance of those young cohorts in the population, therefore, should be indicative of their natural survival rate and should reflect also the general magnitude of recruitment to breeding age, at least for the females, most of which mature at 6 to 7 years of age.

Using visual methods, we conducted compositional surveys of summering walrus in the **Chukchi** Sea, during five research cruises there. We also obtained a compositional sample by observation of the autumnal migrants on the **Punuk** Islands. In each of those samples, the young animals were classified visually as 0-, 1-, 2-, 3-, and 4 to **5-year-olds**, without regard for sex. Females 6 years old and older were regarded as adults. The data gathered during shipboard surveys were of groups on the ice, and in each case we included only the counts from groups that were completely classified. The importance of including only the completely classified groups to

avoid sampling bias is discussed elsewhere in this report. With incomplete classification, there is a tendency for bias in favor of overrepresenting the younger age classes. The only non-shipboard sample, which was from the **Punuk** Islands, was made up of ten different **subsamples** of animals on the periphery of very large herds that were lying on shore. Because those were not complete classifications of whole herds, and because there is a tendency for immature animals to be most numerous on the edges of the herd and for females with calves to be most numerous there, as well (**Popov**, 1960; **Miller**, 1975; **Miller and Boness**, 1983), the Punuk sample probably was biased toward higher than random proportions of females with young.

Before conducting the first survey in 1981, we assumed that we would find at least 25% of the females with calves of the year, at least 20% with **1-year-olds**. That assumption was based on the knowledge that the pregnancy rate was at least 35% per year during the late 1970's and at least 30% per year early in the 1980's (**Fay and Stoker**, 1982a,b), and that the **survivorship** of the first and second year young had been estimated to be at least 80% (**Chapskii**, 1936). Thus, our findings in the first survey (July 1981) of only 5 to 6% of the females with calves of the year and only about 3% with **1-year-olds** were completely unexpected (Table 10). Because they differed significantly from the expected findings, we sampled at every subsequent opportunity, to obtain further data and seek clarification of the situation. All of the results from the additional surveys were very similar to those from the first survey; even our most optimistically biased sample from the **Punuk** Islands suggested that, in recent years, either the prenatal mortality has been higher than **Fay and Stoker's** (1982a,b) data indicated, or the early postnatal survival of calves has been extremely low (or both).

The relative size of the successive cohorts in a given year and of the same cohorts in successive years indicates that the birth and/or survival rates of the calves had been declining at least since 1976, had reached their nadir in 1980, and have been rising slowly ever since then. The cohort with the poorest representation (1980) was produced in the same year in which the catch samples indicated the lowest birth rate on record.

Change in Diet---Large samples of stomach contents were obtained from walrus taken in the vicinity of **Gambell**, **Savoonga**, and **Little Diomed** in 1975, 1979, 1980, and 1982. Each year in each locality, 60 to 90% by weight of the food items in the stomachs were bivalve mollusks; the rest were mainly **polychaetes**, **sipunculids**, **echiurids**, gastropod, crustaceans, and **holothureans** (**Fay et al.**, 1977; **Lowry and Frost**, 1981; **Lowry et al.**, 1982; **Fay and Stoker**, 1982a,b).

In general, the relative amounts of bivalves in the stomachs tended to decrease and the amounts of non-bivalves tended to increase in each successive sample. Fishes were found in the stomach contents for the first

Table 10. Relative abundance of the younger cohorts of walruses in visually classified samples from the Bering and **Chukchi** seas, 1981-83.

Date and location	No. of adult females	Number of young per cohort (and expressed as % of adult females)							
		1976	1977	1978	1979	1980	1981	1982	1983
July 1981, E. Chukchi	1208	167 --(13.8)--		77 (6.4)	56 (4.6)	39 (3.2)	66 (5.5)		
Sept 1981, E. Chukchi	278	22 --(7.9)--		14 (5.0)	6 (2.2)	4 (1.4)	8 (2.9)		
Nov 1981, Punuk Is.	374	69 -(18.4)--		44 (11.8)	36 (9.6)	16 (4.3)	53 (14.2)		
July 1982, E&W Chukchi	456				15 -(;?6)--	8 (3.3)	32 (7.0)	108 (23.7)	-
Aug 1982, E&W Chukchi	881		52 -(5.9)--		31 (3.5)	14 (1.6)	63 (7.2)	94 (10.7)	-
Aug 1983, W. Chukchi	326			27 --(8.3)--		9 (2.8)	8 (2.4)	24 (7.4)	36 (11.0)

time in 1980, but only in trace amounts. By 1982, however, they were present in significant amounts (3.4% by weight) at **Gambell**, where they were present in 9 of 31 stomachs. Further evidence of their growing importance in the diet was shown also by the rising frequency of infection of the walruses by anasakid nematodes (Table 11), parasites that reside in the walrus' stomach and can be acquired only by eating fishes, the intermediate hosts. In addition to the fishes, such apparently unusual prey as **anthozoans** were present frequently and in large amounts in the 1980 and 1982 samples, whereas they had been found only once before. Also, jellyfish (**Scyphozoa**) appeared for the first time and in large amounts in the 1982 sample. At the same time, **holothureans** occurred more often and in larger quantities by weight than before.

Table 11. Comparative frequency of occurrence and numbers of **anasakid** nematodes parasitizing the stomach of Pacific walruses in spring harvest samples, 1964-1982.

Anasakids in stomach					
Year	No. of walruses	Frequency (%)	Number <u>per</u> walrus Range	Mean	Source
1964-66	95	1.0	5		Yurakhno and Treschev (1972)
1975	107	6.5	1-20	6.0	L. M. Shults , (unpublished data)
1980-81	114	14.0	1-61	14.3	Fay & Stoker, (1982b)
1982	76	14.5	1-37	15.8	Fay & Stoker, (1982b)

From 1975 to 1982, an apparent trend of decreasing average size of all types of prey in the stomachs also was reported by (Fay and Stoker **(1982b)**). Concurrently, the diets of males and females appeared to be convergent on the same types and sizes of prey, whereas they evidently had been quite divergent earlier (Fay et al., **1977**). A peculiar increase in the frequency of occurrence of seal-eating walruses also took place in the late 1970's and early 80's (Lowry and Fay, 1984), but we are not yet sure how much of that can be attributed to use of "alternate'" prey. That is, **much** of it might have been due to unusual environmental conditions that brought the walruses and seals together.

The full significance of the findings concerning feeding habits, as regards their relationship to population status, will not be known until the data have been **re-analyzed** in more appropriate ways. That task is underway (J. L. Sease, in prep.). In the meantime, we suggest only that they do indicate change, and that the change may have been associated with the rapid growth of the walrus population and its increased pressure on existing food supplies, as suggested also by Lowry et al. (1980).

Blubber Thickness.--The blubber or hypodermic of the skin of **pinnipeds** serves the combined functions of (1) storage depot for fats, (2) thermal insulating layer, and (3) smoothing of body contours for hydrodynamic efficiency. In the adult males, the fat tends to be thickest in the beginning of the breeding season. At that time, it may also serve a social function, since dominance is partly a correlate of body size (Miller, 1975). For the breeding bulls, **it** also serves as a nutrient supply while they fast during the rut. In addition, it may be **useful** to them as padding, dampening and distributing some of the shock of tusk strikes by their opponents. In females, the blubber tends to be thickest at the time of parturition, when its main function presumably is as a nutritive reserve for both mother and calf in the first weeks of lactation.

As in other wild mammals, the amount of fat on the body is an indicator of the general health of the individual and of the quality and quantity of the food supply. For that reason, we and others have routinely measured blubber thickness **mid-ventrally** over the sternum on many of the specimens that we have examined. We compared those measurements from walruses taken during the 1950's to early 1970's with those from animals taken more recently. The results (Table 12), when tested by a **Kruskal-Wallis** non-

Table 12. Comparative sternal blubber thickness of Pacific walruses, 1958-1983.

		1958-72 (Jan-Sept)	1980 (May-Jun) ¹	1981 (Feb-Mar)	1983 (Jul-Aug)
MALES	N	8	22	85	56
	Range	25-76	4-60	15-54	10-37
	Mean	49.6	27.4	32.6	24.4
	S.D.	14.08	11.73	7.70	5.76
FEMALES	N	18	122	87	321
	Range	30-102	12-75	24-68	13-59
	Mean	57.3	38.9	39.6	29.5
	S.D.	21.61	10.81	8.98	7.83

¹ Unpublished U. S. Fish and Wildlife Service data by T. E. Smith.

parametric ANOVA, indicated that the animals taken in recent years have been significantly ($P < 0.02$) leaner than those taken earlier. Although some of the difference among samples can be attributed to seasonal change (Fay, 1982), even the recent winter specimens (which should have been the **fat-test**) were much leaner than the earlier ones. The implication is that the walruses are not as well fed as they were before, possibly because food is scarcer, lower in nutrients, or requires more effort to obtain. We interpret the greater leanness as a correlate of increase in size of the population.

Distribution and Composition

Monthly Distribution

The following is a **resumé** of distributional information obtained by us in this and related projects and of some contributed by other observers. This information is new since Fay's (1982) compilation, which included all of the data available to him up to 1979. We use that compilation as a background for our description here, because it was done on a monthly basis. Consideration of the distribution per month is most useful for identification of major concentrations and migration routes.

January.--The details of distribution of the Pacific walrus population in this month still are unknown. The few sightings reported up to 1979 were mainly from interviews with Eskimos at **Diomedé**, St. Lawrence, and **Nunivak** islands. The lack of data elsewhere is mainly due to lack of effort (Fig. 15, JAN). Most of the reports near the islands were of **subadult** and adult male walruses. The location of the females and young is not known for this month. Because the height of the mating season appears to be in January and February (Fay, 1982; Fay *et al.*, 1984), we assume that the distribution in this month is similar to that in the following one.

The only new information that we have for this month is from an aerial survey of the Bristol Bay area, which was done for a complementary project (Fay and Lowry, 1981). The northern half of the Bay was ice-covered at the time, and the only walruses sighted in the entire area were three on the ice, just east of **Hagemeister** Island. Their sex and relative age were not determined.

February.--A substantially greater amount of data was available up to 1979 for the month of February, most of it from **Kenyon's (1960a)** first aerial survey and from three icebreaker cruises on which walrus sightings had been recorded (F. H. Fay, B. P. **Kelly**, R. A. Ryder, **unpubl.**). Each of those data sets suggested a regularity to the pattern of distribution, in which the animals were clumped in two areas: (1) from the St. Lawrence **polynya** southward and (2) in the area south of Nunivak Island and **Kuskokwim**

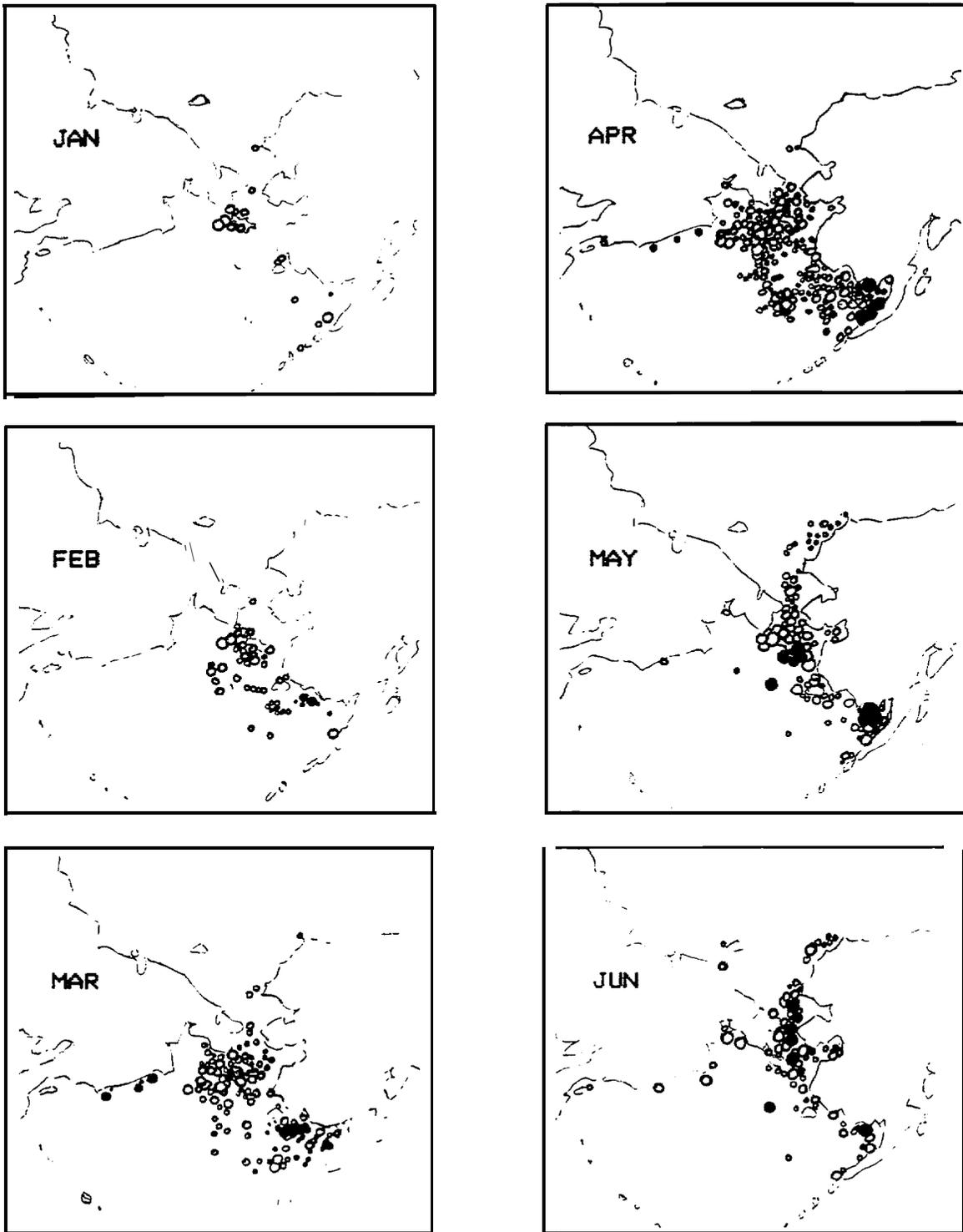


Figure 15. Distribution of the Pacific walrus population, January to June. Open circles are from Fay (1982); black dots are new data from various sources. Size of symbols is proportional to number of animals sighted.

Bay (Fig. 15, **FEB**). A clear preponderance of adult females and young had been seen in the first area; the animals in the second area at **first** were assumed to have been males from the Bristol Bay summering herds. Through aerial photography in 1972, however, they were found to include females and young, as well (**Fay, 1982**).

Fay and Lowry's (1981) aerial survey of Bristol Bay in this month again showed only one small group on the ice in the northwestern part of the Bay. A few days later in that same year, however, we found (via the ZRS **ZVYAGINO**) a clump of some thousands farther to the northwest, just off the Kuskokwim estuary. These were mostly herds of females and young, accompanied by a few adult males, and the sex ratio of adults was like that in the St. Lawrence wintering area (i.e., about 1 male/10 females). These were breeding herds; many of the males were engaged in courtship displays in the water, alongside the herds of females.

March.--The distribution was better known up to 1979 for the month of March than for the previous month. It appeared to be essentially the same or very similar to that in February, with the principal clumps of walruses in the St. Lawrence Island and Nunivak-Kuskokwim-Bristol Bay regions (Fig. 15, **MAR**). Our observations during an icebreaker survey of the St. Lawrence area in 1972 had confirmed that the animals there were mostly females and young, with a number of males still conducting courtship displays (**Fay et al., 1984**). In some years, the beginning of northward movement was evident **from** the increase in number of animals north of St. Lawrence Island, usually by the end of the month (**Fay, 1982**).

On the Soviet side, **Kibal'chich** (1981) and co-workers found numerous small groups (mostly 5 to 15) of males in the ice along the Koryak coast from just south of Cape **Navarin** to the vicinity of **Natalia** Bay. Fay and Lowry (1981) also found about 700 males in Bristol Bay in this month, which was a large increase over the number present in January and February. At the same time, however, some breeding herds still were in place, south of **Kuskokwim** Bay, and many males still were displaying there. Nearer the southern edge of the pack ice were small groups of **subadult** males.

April.--The documentation of distribution up to 1979 was better in this month than in the previous three combined (Fig. 15, **APR**), principally due to **Kenyon's** aerial surveys. Again, it indicated essentially the same two clusters, one to the south of St. Lawrence Island and the other in Bristol and Kuskokwim Bays, but the clusters appeared to be spreading and linking together, **to** a greater extent than before.

The northward migration clearly is underway by the middle of this month in all years. It is most evident in the north, for the animals wintering near St. Lawrence Island begin to move by the thousands through Anadyr Strait, between **Gambell** and Cape Chaplin. The herds of females and

young from the Bristol-Kuskokwim wintering area also begin to move northward in the first half of this month, some passing through **Etolin** Strait and others around the western end of **Nunivak** Island.

Our additions to the distributional data in this month were only in Bristol Bay, where two aerial and one shipboard surveys in 1980-81 showed the numbers of males to be greater than in the previous month. A total of about 15,000 animals were congregated at Round Island, on Cape **Seniavin**, and in the nearshore waters along the northern coast of the Alaska Peninsula (**Fay** and Lowry, 1981). We presume that those males had moved there from the breeding aggregations south of **Kuskokwim** Bay.

May.--The distribution in the eastern Bering and eastern **Chukchi** seas was well documented in this month by **Fay's** (1982) compilation, but there was little information from Soviet waters. That continues to be the status, today. The apparent concentration of animals along the Alaskan coast (Fig. 15, MAY) probably does not fully portray the location of the whole population, for some must also be in the Anadyr area at that time; others are said to penetrate into the western **Chukchi** Sea as far as Cape **Serdtshe-Kamen** (**Krylov et al.**, 1964). Most of the animals passing through Bering Strait in this month are females and young from the St. Lawrence wintering area. Those from the Bristol-Kuskokwim wintering area are still moving up the eastern side of the Bering Sea, into the vicinity of eastern St. Lawrence Island and Norton Sound. Any of the males that have migrated north with either group seem to move only as far as Anadyr Gulf and the **Chirikof** Basin, where they congregate on the remaining ice, long after the females and young have passed by.

Fay and Lowry's (1981) aerial surveys of Bristol Bay in this month, in both 1980 and 1981, confirmed again the presence only of the summering cluster of adult and subadult males. The numbers appeared to be approximately the same as in April. To the west, another, smaller summering group of males has recently **re-occupied** the St. Matthew - **Hall** Island area (**D. Irons**, pers. **comm.**), apparently for the first time in more than 30 years.

June.--Practically all of the females and young and a few of the subadult and adult males have passed through Bering Strait by the end of this month. Those remaining behind in the Bering Sea are mainly adult males, who summer principally in Anadyr Gulf, Bristol Bay, western **Chirikof** Basin, and Bering Strait. Again, the concentration of sightings on the Alaskan side (Fig. 15, JUN) is due principally to shortage of data from Soviet waters. According to **Krylov et al.** (1964), about 8,000 males begin to use the Rudder Spit hauling ground in Anadyr Gulf by the end of this month, and many of the migrants into the **Chukchi** Sea have moved as far as Long Strait by this time.

In an aerial survey of Bristol Bay, Fay and Lowry (1981) found the males still abundant and clustered mainly in the northern part of the Bay, near the Walrus Islands. To the west, D. Irons (pers. **comm.**) observed about 400 males in the St. Matthew-Hall Island area, and we saw a few more in the vicinity of the Penuk Islands, just east of St. Lawrence Island.

July-September--- Both Soviet and American data have indicated that practically all of the females and young are in the Chukchi Sea by July, and that they remain there at least through September (Fig. 16, JUL, AUG, SEP). They appear to congregate there in two large areas, (1) from about 170°W to the vicinity of Point Barrow and (2) along the northern coast of **Chukotka** to Long Strait and **Wrangell** Island. Many of those along northern **Chukotka**, at least as far as **Inchoun** and **Kolyuchin** Bay, are males; farther to the west and north in the pack ice they are mostly females and young. The animals remaining in the Bering Sea at that time are virtually all males (Brooks, 1954; Fedoseev, 1962; Burns, 1965; Gol'tsev, 1968).

The results from aerial surveys in Bristol Bay in 1980 indicated that the number of males there still was about 15,000 during these three months (Fay and Lowry, 1981). At least 400 males also have been present on St. Matthew and Hall islands (D. Irons, R. D. Jones, pers. **comm.**), and we saw a few near the **Penuk** Islands, as well. At Arakamchechen and **Nunyangang** islands, off the Soviet coast, at least 4,000 males and four adult females were present in 1983 (Fay et al., 1983).

October.--Southward migration of the animals usually begins in this month (**Krylov et al.**, 1964). The data available up to 1979 suggested that practically all of the animals that had summered in the eastern and western **Chukchi** Sea converged on the northern coast of **Chukotka** before moving southeastward toward Bering Strait (Fig. 16, OCT). That same pattern is inferred also by newer data from the Soviet side (**Fedoseev**, 1981).

Fay and Lowry's (1981) aerial survey for this month in Bristol Bay indicated a substantial decline in number of animals (males) there. Concurrently, the number at the Penuk Islands grew to nearly 1,000 (Fig. 17).

November.--The data on walrus distribution for November still are sparse (Fig. 16, NOV). Up to 1979, nearly all of the information for that month had been obtained by interview with Alaskan Eskimos, for there had been none from either aerial or shipboard surveys and none from the Soviet side. We have added to this the observations from an aerial survey of Bristol Bay (Fay and Lowry, 1981), and from our monitoring of the autumnal migration at the **Penuk** Islands. A high proportion of the 10,000 or more animals arriving on the Penuk haulout were adult females, which presumably swam there via Bering Strait from their summering areas in the **Chukchi** Sea. We know, however, that some of the adult males that arrived there had migrated northward, rather than southward, for at least three of them had

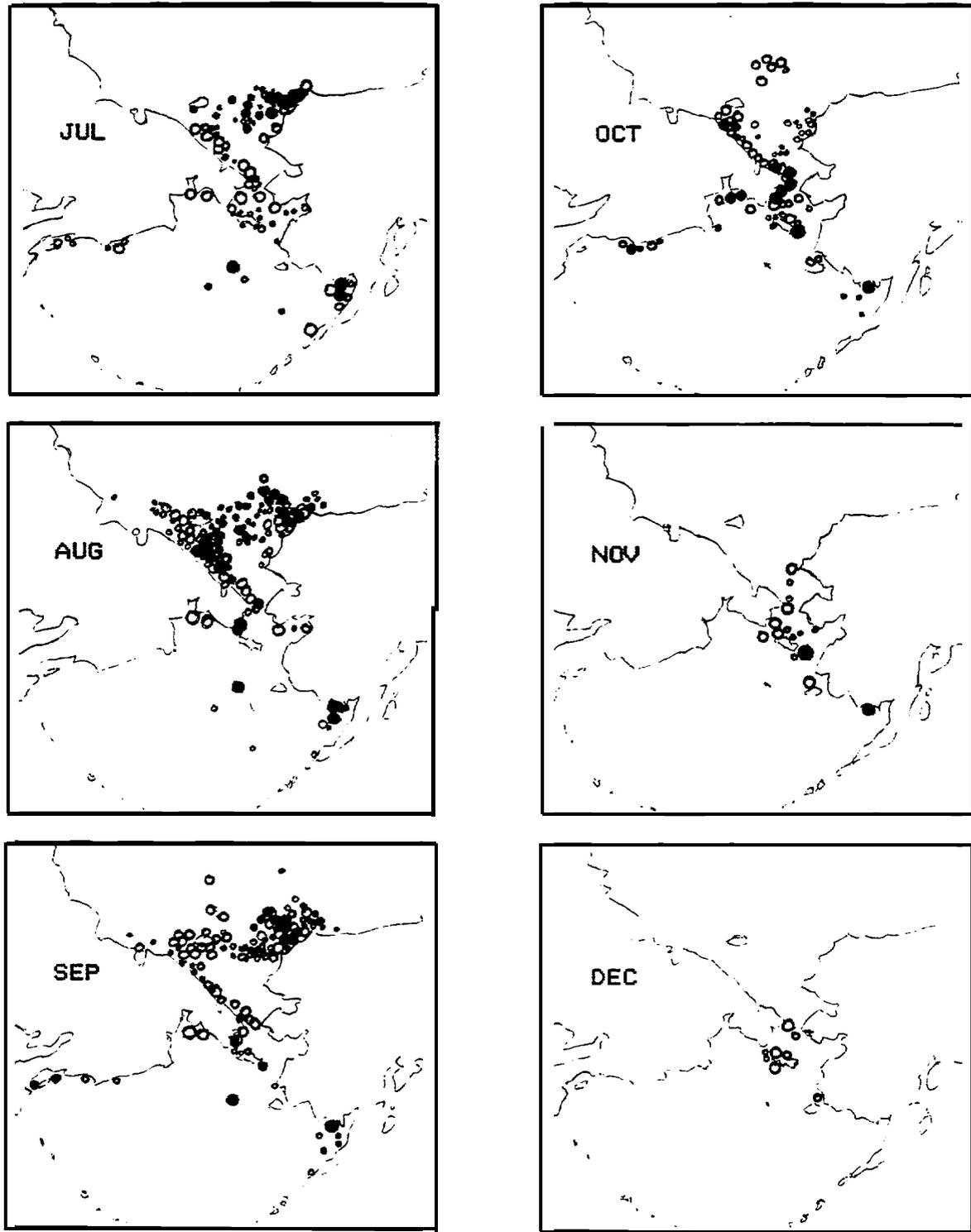


Figure 16. Distribution of the Pacific walrus population, July to December. Open circles are from Fay (1982); black dots are new data from various sources. Size of symbols is proportional to number of animals sighted.

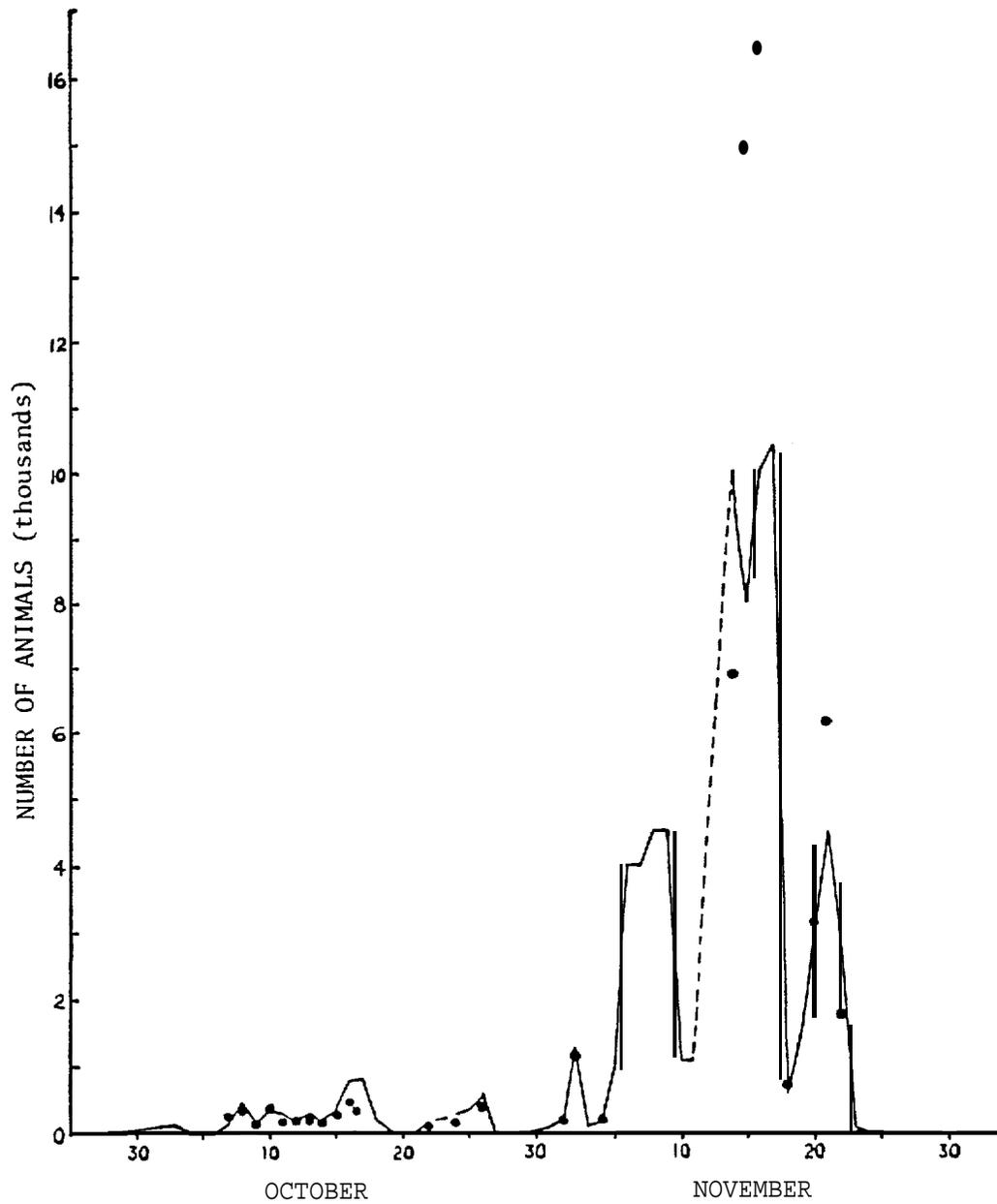


Figure 17. Numbers of walrus on the **Punuk haulout** each day, 28 September to 30 November 1981. Line connects numbers actually counted or extrapolated from sample counts. Dots are estimates based on area occupied, assuming 2 m² per walrus.

been radio-tagged at Round Island, Bristol Bay, a few months earlier (J. Taggart and C. Zabel, pers. **commun.**). The last of the animals left the **Punuk** Islands on November 23rd, and the haulout there became ice-bound the following day.

December. --The distribution in December is practically unknown (Fig. 16, **DEC**), and we were not able to contribute anything positive to improve on that situation.

Time of Mating

The time of mating of walruses is in mid-winter, rather than in the spring. This was discovered about 30 years ago, partly as a result of **Fay's** (1955) observation that the testes of the mature males were already showing seasonal retrogression by May, and of Mansfield's (1958) finding that some adult males were becoming fertile as early as November. By tracing the histological stages in the annual **spermiogenetic** cycle of the males from November to August, Fay (1982) observed that the adults reached their peak of fertility about the end of December, apparently were in rut during January and February, and generally were showing signs of retrogression as early as March. The adolescent males, conversely, appeared to reach their peak of testicular development about two months later than the adults. Thus, assuming that the breeding season must coincide with the rut, Fay concluded that the females probably were in estrus in January-February, rather than in May and June as presumed by most previous investigators.

The data from females were fewer and less complete, but they were supportive of the schedule implied by the males. The ovaries of some of the potentially estrous females (i.e., the adults that were not already pregnant with an advanced fetus) that were obtained by Fay (1982) in November, December, and the first days of January contained some slightly enlarged vesicular follicles, which were suggestive of the beginning of **estrus**, but none was clearly near ovulation. One of two potentially **estrous** females taken by E. **Muktoyuk** (Alaska Department of Fish and Game) in mid-February, however, already had ovulated approximately 2 weeks earlier; the other apparently was barren. Three more taken in late March and early April by Fay (1982) and co-workers had fully formed new corpora lutes of pregnancy from ovulations that had taken place at least one month earlier. That is, these few specimens indicated that ovulation was taking place mainly in late January to early February.

Although a few females taken in April, May, and June had some very large vesicular follicles, suggestive of estrus, they were a distinct minority. Practically all of the potentially estrous females taken at that time already had very large, fully developed corpora lutes of pregnancy,

and in some cases their embryos already were beginning to implant. None showed any evidence of having ovulated any later than early March. The results from the females, therefore, also indicated that the breeding season of the Pacific walrus began in January and ended not later than early March. Even though a few females had come into **estrus** after that time, apparently none of them had been bred (Fay, 1982).

The concept of a breeding season in winter was novel and contradicted all previous reports, notably by Allen (1880), **Belopol'skii** (1939), Collins (1940), **Nikulin** (1941), **Freiman** (1941), Brooks (1954), **Tikhomirov** (1964a), **Krylov et al.** (1964), **Krylov** (1969), and Fedoseev (1976). Soviet biologists were skeptical of the new findings as late as 1976, and they remained skeptical, even after **Gol'tsev** (1978) reported that the series of specimens taken on the first Soviet-American walrus research cruise in March-April 1976 confirmed the existence of an earlier (than March-April) mating season.

For various reasons, mainly logistic, the investigation of the breeding season of the Pacific walrus still is incomplete, but the weight of confirming evidence is now much heavier and more widely accepted. The Soviet biologists finally confirmed to their own satisfaction that walruses breed in winter, not spring, and that they are polygynous, not monogamous. That took place during another Soviet-American cruise, in late **February-early March** 1981. Nearly all of the potentially estrous females that were taken (between 25 February and 10 March) had well-developed corpora lutes, and the advanced development of those corpora indicated that ovulation had taken place at least 2 weeks to a month earlier. A few other females still had large vesicular follicles in their ovaries, indicating that they were still in **estrus**; a few more were reproductively inactive (barren). During that same cruise, additional confirming evidence was obtained also from the males. Nearly all of the adolescent and adult males taken had spermatozoa in their epididymides, but the sperms in many of the older adults were non-motile, indicating that they were no longer fertile. High motility of the sperms in the younger males, however, showed that they still were in an active state of rut, again confirming that the adolescent males come into rut later than the adults.

Location of the Breeding Areas

We suspect that the males, most of whom summer in the Bering Sea, meet up with the females, all of whom summer in the **Chukchi** Sea, in October-November. That meeting seems to take place primarily in the Bering Strait region, from St. Lawrence, Pujuk, and Arakamchechen islands to the East Cape and **Inchoun** hauling grounds. Apparently, it takes place as a result of the males' coming northward from their summering areas and the females coming southward from theirs. The northward movement of males on the

Soviet side was reported earlier by Soviet biologists, who observed major shifts of male herds in late summer and autumn between the Rudder, **Arakamchechen**, and **Inchoun** areas (Nikulin, 1947; Krylov et al., 1964; Gol'tsev, 1968). On the Alaskan side, it was detected for the first time during this study, when males radio-tagged in Bristol Bay in summer were sighted at the **Punuk** hauling ground in November. About that same time, a large proportion of the Bristol Bay males apparently left that area, and they did not return until March and April (Fay and Lowry, 1981; **Fay**, 1982).

Their further progress into the wintering areas and in establishing organized breeding groups is unknown, but we presume that the animals are influenced greatly in both of those events by the development of the seasonal pack ice. Depending on the timing and extent of ice formation, the entire population may be in the Bering Sea and distributed in their wintering areas as early as the end of November, in some years; **in** other years, they may not settle into the wintering/breeding pattern until January. To describe that pattern precisely, **however, is** not possible at present. Without fuller information on the means and extremes of distribution of the animals during November, December, and January, we can only guess at their location in a very general way.

As noted above, practically all of the mating that results in pregnancy seems to take place during January and February and may extend into the first days of March. We know the general distribution in March with some precision and know that it can be related to ice conditions in a predictable way (Burns et al., 1980; Fay, 1982). Hence, we assume that the **north-south** extent of the distribution will tend to increase from January to March, because of the gradual increase in extent of the pack ice. Because the variation among years in extent of ice is even greater than that among months in this period (Brewer et al., 1977; Burns et al., 1980, 1981), the estimation of location of the mating herds is more appropriately linked with extent of the ice than with time.

Our best estimates of the location of the breeding herds under minimal, mean, and maximal extents of winter ice (Fig. 18) are based on distribution in relation to ice conditions, as reported by Wartzok and Ray (1980) and **Braham et al.** (1984), as observed and photographically documented during **Kenyon's** (1960a, 1972) aerial surveys, and as observed by us and by J. J. Burns, G. C. Ray, R. A. Ryder, and S. W. Stoker (**pers. comm.**) during seven different cruises via American icebreakers and Soviet sealers in the winter ice of the Bering Sea.

The estimate of breeding areas during the minimal extent of winter ice has nonempirical basis, for there have been no surveys of breeding herds under that condition. We have guessed at the location, based on our belief that the animals choose areas that are well within the pack, on the leeward side of ice-forming zones. There, divergence of the ice continually per-

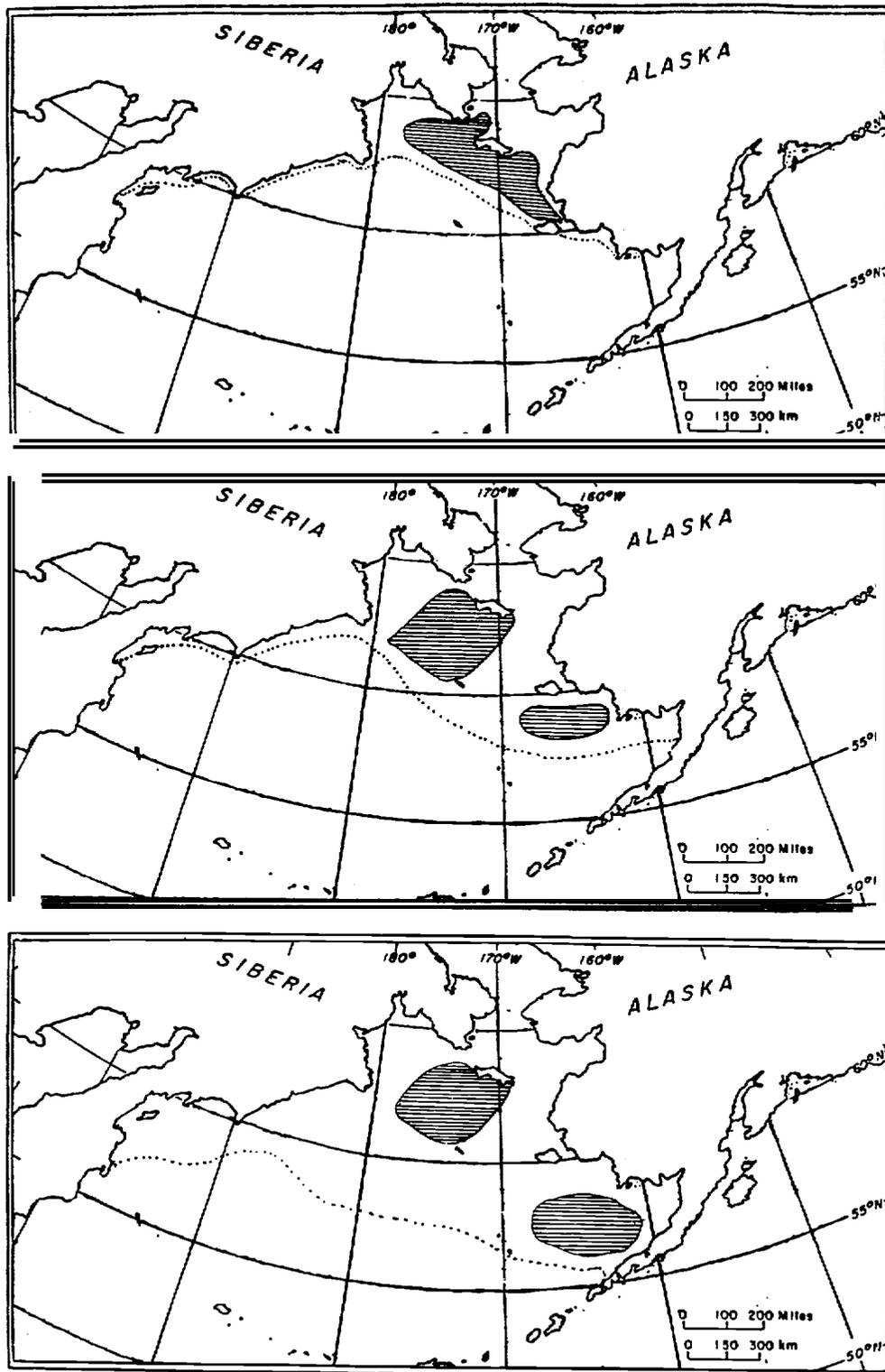


Figure 18. Estimated location of mating herds (cross-hatched), January-March, during minimal (top), median (center), and maximal extent of the pack ice. Dotted line is approximate location of ice edge.

mits leads and **polynyas** to form, and the floes are thick enough to be supportive and dry. Presence of food in some abundance may be another factor in selection of an area, but we feel that it is secondary to choice of the ice habitat.

Apparently, all of the adult females and most of the adult males are concentrated in those mating areas, during at least January to early March. There, the females and young tend to stay together in groups of about 10 to 50 individuals, and each of those groups is attended by one or more large, mature males. When the herd hauls out onto the ice to rest, the bulls station themselves in the water alongside the floe. There they perform their courtship displays (Fay et al., 1984). Each display lasts 2 to 3 min, and consists of an underwater, acoustical **portion, in which a series** of pulses ("clicks" or "knocks") and bell-like sounds are made (Ray and Watkins 1975), followed by a surface portion, in which the bull raises his head above the water and emits one or more single pulses, then a short, harsh whistle, before diving again. Each such male displays continuously, for as long as the females remain at rest. Presumably, the displays serve as advertisement to the females of the males's sexual readiness and as a warning to other males in the vicinity to stay away. We saw females leave the herd and join a displaying male in the water. After some preliminary play (nuzzling, mounting), they dove beneath the surface, where copulation probably took place (Fay et al., 1984).

When more than one bull was displaying before a herd of females, each bull maintained a distance of about 7 to 10 m from the other(s) and each performed his displays in a fixed location. Invasion of one male's display site by another male resulted in agonistic interaction, with each male visually threatening the other by posturing, showing its tusks. That was followed by violent *fighting* and, finally, **withdrawal of the "loser"**. We frequently saw bulls with bleeding wounds, which suggested that the fights between bulls often result in physical injury to one or both of the combatants (Fay et al., 1984).

The observed ratios of adult males to potentially available mates in the breeding areas, from late February to early April, have ranged from about **1 male:5** females to **1:15** (average, about **1:10**). Adolescent males were absent within the mating areas but were abundant outside the mating areas. Juvenile males up to 6 or 7 years old were numerous within the herds of females and young, but they were too immature to function as breeders or to interact with the adult **males**.

The adult males evidently begin to leave the breeding areas in March, for they start to **re-appear** then in large numbers in Bristol Bay (Fay and Lowry, 1981). By late April, practically **all** of the males that summer in Bristol Bay have returned there, presumably from the Bristol-Kuskokwim wintering/breeding area. The females, by that time, have begun their

northward migration, and apparently many of the adolescent males, which by then are in rut, migrate with them.

Time and Place of Birth

For a long time, the birth of walrus has been known in a general way to take place in spring, principally in May, but that knowledge was based more on inference than on observation (**Chapskii**, 1936; **Nikulin**, 1941; **Mansfield**, 1958; **Burns**, 1965; **Krylov**, 1969). Drawing on all available data, **Fay** (1982) estimated that nearly all births take place between mid-April and mid-June, with a probable peak just before the middle of May. At that time, females of the Pacific walrus population are in migration from the Bering to the **Chukchi** Sea.

Most of the recorded instances of births and of newborn (<12 hr old) calves in the **Bering-Chukchi** region have been from the vicinity of St. Lawrence Island, probably because of more concentrated effort there. A much broader survey of possible calving areas is needed for further documentation of both the time and the place of birth. Our best estimate of the place of birth (Fig. 19), is based on the knowledge of distribution in that period. Because of varying ice conditions, the actual area occupied in any given year will be less extensive but will be within the area shown.

Within that area, the parturient females are not stationary but are in motion, slowly migrating from south to north. Their progress is made principally by swimming, and they haul out frequently on ice floes to rest. Apparently, birth of the young usually takes place on the ice, not in the water (**Fay**, 1982). Often, the females giving birth to calves haul out individually, in isolation from all other walrus. Others may give birth within herds. Apparently, within a day or two after the birth, the mother and calf generally join up with large "nursery herds" of other females and newborn young (**Burns**, 1965, 1970).

For the first few days or weeks after parturition, the female tends the calf very closely, defending it vigorously, carrying it on her back or under her arm in the water, pushing it into the water ahead of her when danger threatens, and calling it back or following when it strays. The new calf probably is tended by its mother most closely in the first few days or weeks after birth. By mid-summer, the calf seems to assume the primary responsibility for maintaining the maternal bond, by following its mother closely and calling loudly to her when unable to follow (**Gehrich**, 1984).

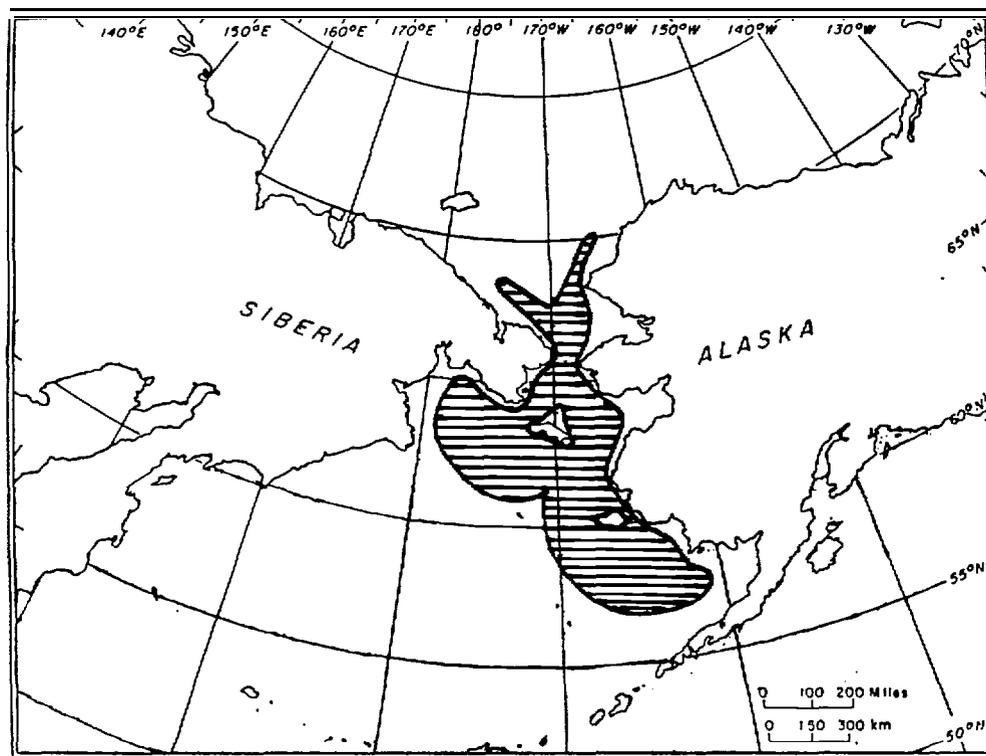


Figure 19. Estimated maximal extent of calving areas (cross-hatched) of the Pacific walrus population in mid-April to mid-June.

Sex/Age Composition

Most of our efforts in this part of the study were directed at gaining understanding of the sex/age composition of walrus summering in the eastern **Chukchi** Sea. There, they congregate in the transportation corridor used by vessels traveling to and from the Canadian and American Beaufort Sea oil fields. There, also, they may eventually be affected by oil exploration and development activities in the Barrow Arch lease area.

Earlier, both Collins (1940) and Brooks (1954) had indicated that most of the walrus taken by Eskimos in the vicinity of Barrow in July and August were adult males, though females and young were said to linger to the south, near Point Franklin. Farther south near Wainwright, Burns (1965 and unpublished) found females and young abundant in July, and G. C. Ray (**pers. comm.**) found them common also in the ice northwest of there in July. The implication of those reports was that sexual segregation prevailed, with the males clumped near Barrow and the females farther south and west, but this needed clarification. From the herds of females and young, we hoped also to obtain information on survivorship of the young cohorts and of the recruitment to the breeding population, as explained earlier in this report.

During our first compositional survey, via the CGC POLAR STAR on 16 to 28 July 1981, we began by searching the pack ice from Barrow to **169°W**, using both the ship and its helicopters to probe into the ice up to 75 km north of its edge. We found a few walrus deep within the pack, but most of the animals were less than 20 km from the southern edge (Fig. 20). Sexual segregation within that area was apparent (Table 13). Males occurred more often than expected in the groups nearest Barrow (east of **159°W**) and very significantly less often than expected in the farthest west sector (west of **163°W**) ($\chi^2=22.629$, 2 d. f., $P < 0.001$). Throughout the whole area, nearly all of the groups that we met were made up only of adult females and their dependent young.

During that survey, we sighted a total of 516 groups of walrus, containing more than 5,000 animals. The majority of animals sighted in the water were in groups of only one or two individuals, whereas most of those on the ice were in larger groups (Table 14). We were able to classify to sex and age 2,179 of the animals in 324 groups. These included 216 groups from which every member was classified (i.e., "complete groups") and 108 for which only partial classification was possible ("**incomplete** groups").

We had greater success in classifying groups that were on the ice than in classifying those in the water. Our level of success in completely classifying groups on the **ice** was inversely related to group size; for in-water groups, the success was disproportionately high for group size 2,

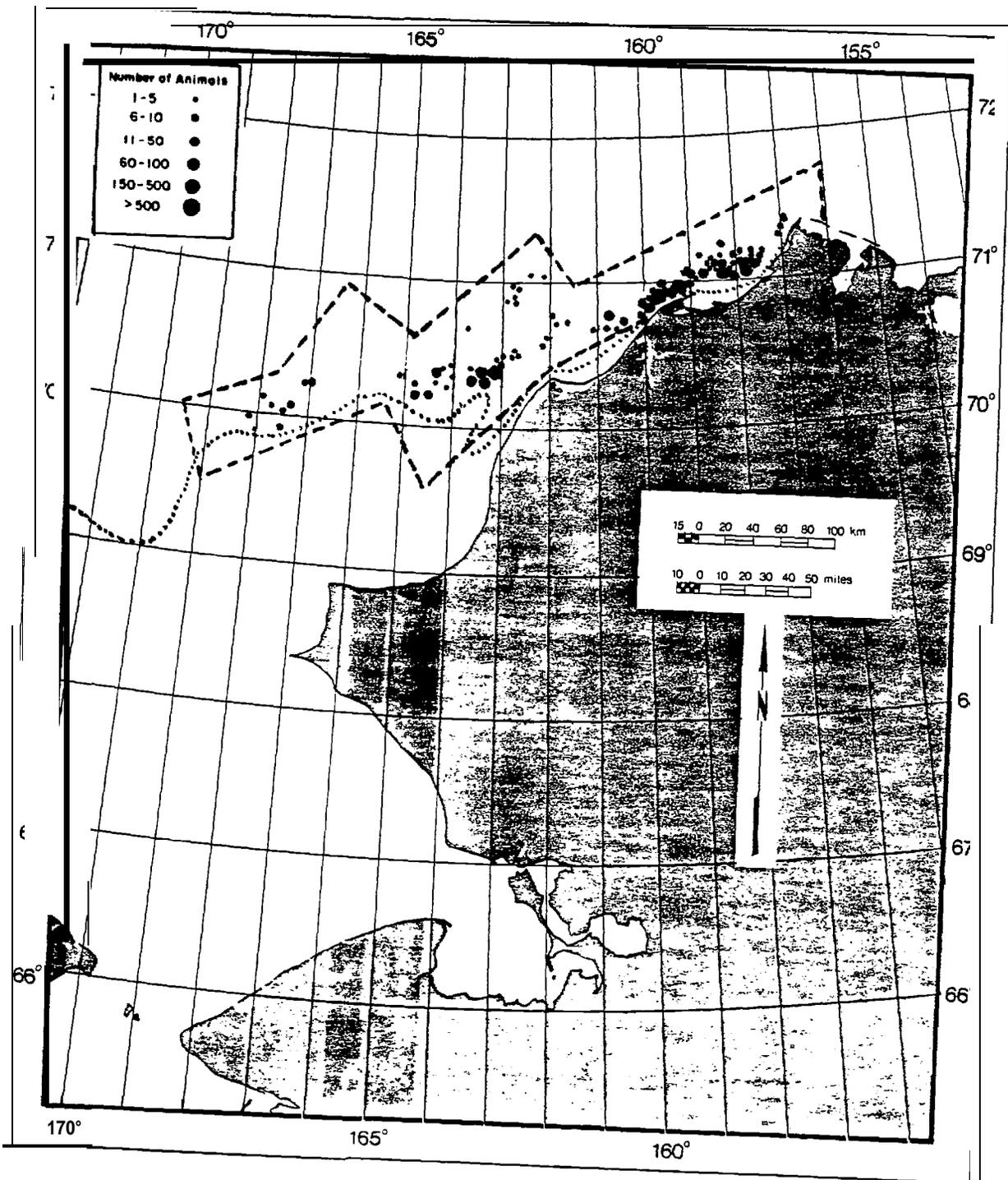


Figure 20. Chart of northeastern Chukchi Sea, showing location of walrus herds, 16-28 July 1981. Dashed line is the boundary of the surveyed area. Dotted line indicates the position of the ice edge.

Table 13. Comparative composition of walrus groups in five sectors of the pack ice of eastern **Chukchi** Sea in late July 1981.¹

Longitude	Total no. of animals	Percentage per sex/age class			
		Females & young		Subadult & adult males	
		No.	%	No.	%
156-159°W	1235	1136	91.98	99	8.02
159-161°W	177	162	91.53	15	8.47
163-166°W	313	311	99.36	2	0.64

¹Limited to completely classified groups on ice. Sample sizes were too small in sectors 161-163°W (n=2) and 166-169°W (n=3) to be tested by the **chi-square** method, since expected values for males were <1.

Table 14. Percentage frequency of occurrence of group sizes of walruses on ice versus in the water, eastern **Chukchi** Sea, 16-28 July 1981.

Location of group	No. of groups	Group size (no. animals/group)							
		1	2	3-4	5-9	10-20	21-50	51-200	
On ice	285	10.2	14.4	16.5	22.8	17.5	12.3	6.3	
In water	231	25.5	38.5	20.8	10.8	3.0	0.8	0.4	

in which cow-calf pairs (which are the most easily identified) predominated (Fig. 21). Apparently as a result of that bias, the proportion of calves in both the completely and the incompletely classified in-water groups was five times that from the completely classified groups on ice (Table 15). Since we regard the completely classified groups on ice as our most reliable sample, we rejected the in-water sample as entirely biased and unreliable and turned to comparison of the on-ice samples.

Table 15. Percentages of walrus in each **sex/age** class per compositional sample, eastern **Chukchi** Sea, July 1981.

Type of sample	No. of animals	Sex/age class (yrs)						
		Both sexes					Females	Males
		0	1	2	3	4-5	6 and older	6 and older
On-ice:								
Completely classified	1691	3.8	2.3	3.3	4.5	9.8	69.3	6.9
Incompletely classified	348	9.2	4.0	3.2	6.0	11.2	55.2	11.2
In-water:								
Completely classified	104	19.2	5.8	2.9	1.9	10.6	57.7	1.9
Incompletely classified	36	44.4	16.7	2.8	5.7	8.3	22.2	0.0

The composition of the incompletely classified groups on ice was similar to that shown by the completely classified groups, but it indicated a much lower proportion of adult females and higher proportions of males and young animals than did the completely classified sample. This was not due to disparate sample sizes but to the field method. In most instances, we routinely classified the youngest animals first, then the subadult and adult males, and lastly, the adult females. In doing so, we frequently were able to classify all or most of the young and the males but did not have time to confirm that all the rest were adult females, before the group dispersed. For that reason, we rejected the incomplete sample as unreliable and accepted only the completely classified groups on ice as being representative of the population in the area surveyed.

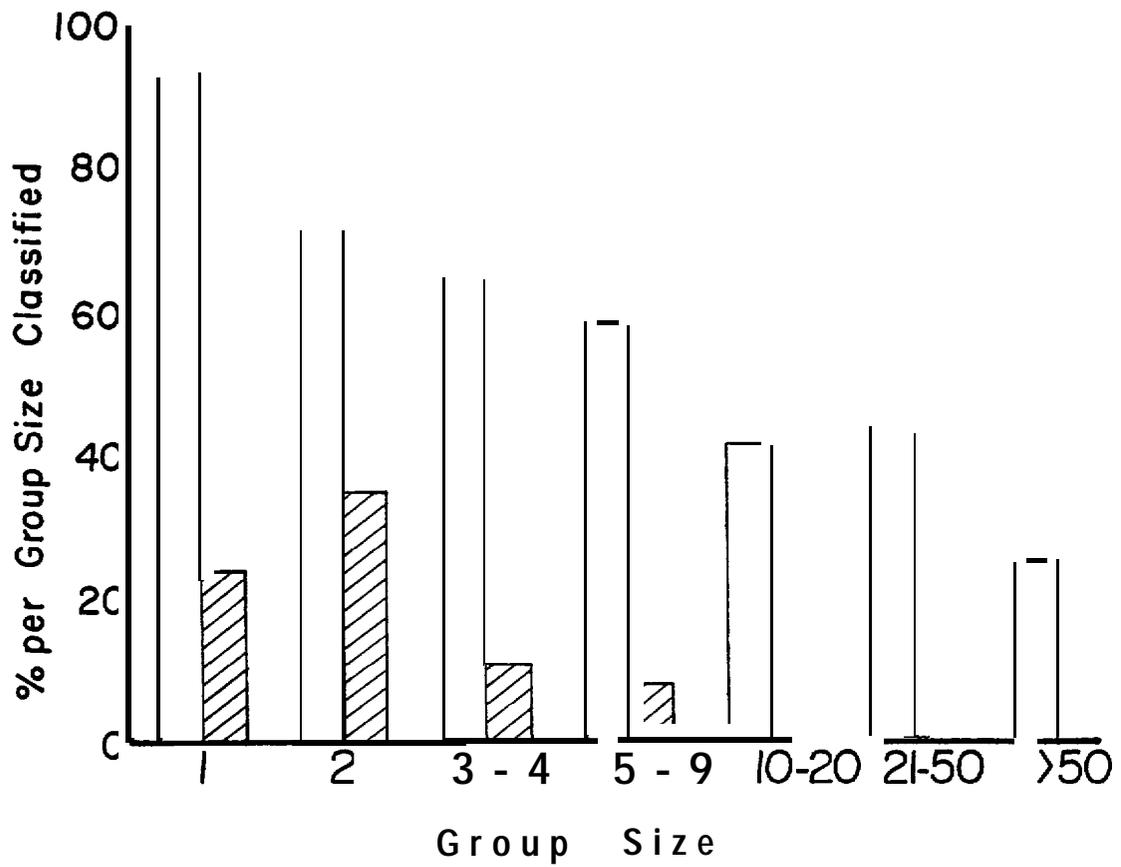


Figure 21. Proportions of animals per group size that were visually classified to **sex/age**. Bars show percentages completely classified: open = groups on ice; **hatched** = groups in water.

The composition of groups on ice that were completely classified tended to vary somewhat with group size (Table 16). Animals in the three youngest age classes did not occur singly, but they were about equally represented in groups of two or more individuals. Independent juveniles 3 to 5 years old tended to be most numerous in groups of 1 to 4 animals, usually not including any older or younger individuals. Subadult and adult males were found mainly in the smallest (1-2) and largest (>50) groups; adult females were most numerous in groups of 10 or more. Had our sampling of groups of different sizes been very unequal, those variations might have biased the results of our survey, but we think they did not in this case. Hence, our findings suggested that the early postnatal survivorship of the young had fallen to a very low level and that it had been that way for at least 6 years. Only about 5.5% of the adult females were accompanied by calves of the year, instead of the expected 30-35% (Fay, 1982), and the successively older cohorts were even smaller.

Table 16. Percentage representation of sex/age classes of walruses in completely classified groups on ice, in relation to group size, eastern **Chukchi** Sea, 16-28 July 1981.

Group size	No. of animals	Sex/age classes						
		0	1	2	3	4-5	M 6+	F 6+
1	27	0.0	0.0	0.0	7.4	40.7	14.8	37.0
2	58	1.7	5.2	1.7	8.6	19.0	12.6	51.7
3-4	105	3.8	1.0	4.8	11.4	13.3	5.7	60.0
5-9	254	3.1	4.3	5.5	6.3	10.6	9.4	60.6
10-15	149	3.4	2.7	2.7	2.0	11.4	6.7	71.1
16-30	456	3.3	2.0	3.9	4.4	9.2	0.9	76.3
31-50	136	7.4	2.2	2.9	2.9	9.6	3.7	71.3
>50	506	4.4	1.6	1.8	3.0	6.1	11.3	71.9

We considered that those results might have been incorrect, perhaps because our sample was not representative of the whole population. That is, we had no basis for assuming that animals summering in the eastern **Chukchi** Sea were typical of the entire population. The possibility of their being a unique group with lower productivity than the rest of the female population could not be discounted. We clearly needed to survey in other areas to determine whether the low **survivorship** was population-wide or peculiar to just the eastern **Chukchi** group.

We sampled again in the eastern **Chukchi** Sea in September 1981, via the N/S OCEANOGRAPHER, and during the southward migration in November 1981 from our field camp on the **Punuk** Islands. The results were similar to those from the first survey, except that the proportion of cows with calves (14.2%) at Punuk was higher than in either of the **Chukchi** surveys. At the time, we did **not** know whether that was attributable to its being more representative of the population or, perhaps, to its being biased by incomplete classification and other circumstances, such as segregation. The latter seemed especially probable, because the **Punuk** sample was made up of ten incomplete counts of animals in the periphery of large herds, where females with young calves tend to cluster (Popov, 1960; Miller and Boness, 1983).

The opportunity to sample both the eastern and the western **Chukchi** Sea came in the following summer, when we were invited to participate in a joint Soviet-American survey of marine mammals in the entire **Chukchi** ice edge. The vessel, K/S ENTUZIAST, was not an icebreaker but a whale catcher, so it was not able to go far into the ice. Nonetheless, with the winds from the south most of the time, the ice was compacted and the animals were abundant in the edge, where they were easily reached. Not only were we able to cover both the eastern and the western ice, we did so twice, two weeks apart, and each time with a different group of observers. Our results from the western part of the Chukchi Sea were very similar to those from the eastern part (Table 17), indicating that the herds in the eastern **Chukchi** probably are representative of the whole female population, hence that the low survivorship of young probably was a population-wide phenomenon. As in **each of** the previous samples, the 1980 cohort, then 2 years old, was by far the smallest.

Thus, by means of our compositional counts, we confirmed that male walrus are more common near Barrow than farther west, but we clearly identified the walrus inhabiting the Barrow Arch lease area as predominantly adult females and dependent young. Judging from the 1975 and 1980 census results in that area, as described earlier, the eastern Chukchi animals constitute about half of the total female population. We also have documented an extremely low survival rate of calves that has been taking place at least since the early 1970's. That poor survival appears to have

led to very low recruitment into the breeding population, at least since the mid-1970's. That low recruitment probably has contributed to the predominance of elderly animals in the population.

Table 17. Percentage composition of walrus herds in the eastern and western **Chukchi** Sea, July-August 1982.

Area	N	Both sexes (yrs)					Males	Females
		0	1	2	3	4-5	6 and older	6 and older
East of 170°W	1520	11.2	5.3	1.1	2.8	5.0	1.1	73.4
West of 170°W	315	8.5	4.7	1.6	1.3	4.7	9.5	69.1

Feeding Habits

The information available on seasonal and regional feeding habits of Pacific walruses up to 1978 was reviewed by Fay (1982). Most of that information was not very detailed, and nearly all of it was from the Bering Strait region in spring. Some additional spring data from that region were obtained in the meantime by Lowry and Frost (1981) and by Fay and Stoker (1982a,b); some winter and spring data were obtained in the southern Bering Sea by Kibal'chich (1981), by Fay and Lowry (1981), and by us. Lastly, we recently obtained some information on feeding habits in summer in the western and central **Chukchi** Sea (Fig. 22).

Winter, Southeastern Bering Sea

During the cruise of the ZRS **ZVYAGINO** in February-March 1981, we observed more than 5,000 walruses in the pack ice south of Nunivak Island and **Kuskokwim** Bay. Most of those were females and young, which seemed to be rather synchronous in their feeding, though they did not follow a circadian schedule. A tabulation of our sightings each day indicated that nearly all of the animals tended to be in the water feeding for 24 to 36 hours, then to spend 36 to 48 hours at rest on the ice (Table 18). The feeding forays usually took place about the time of passage of a storm front through the area; the periods of rest were mainly in the periods of fair weather between storms.

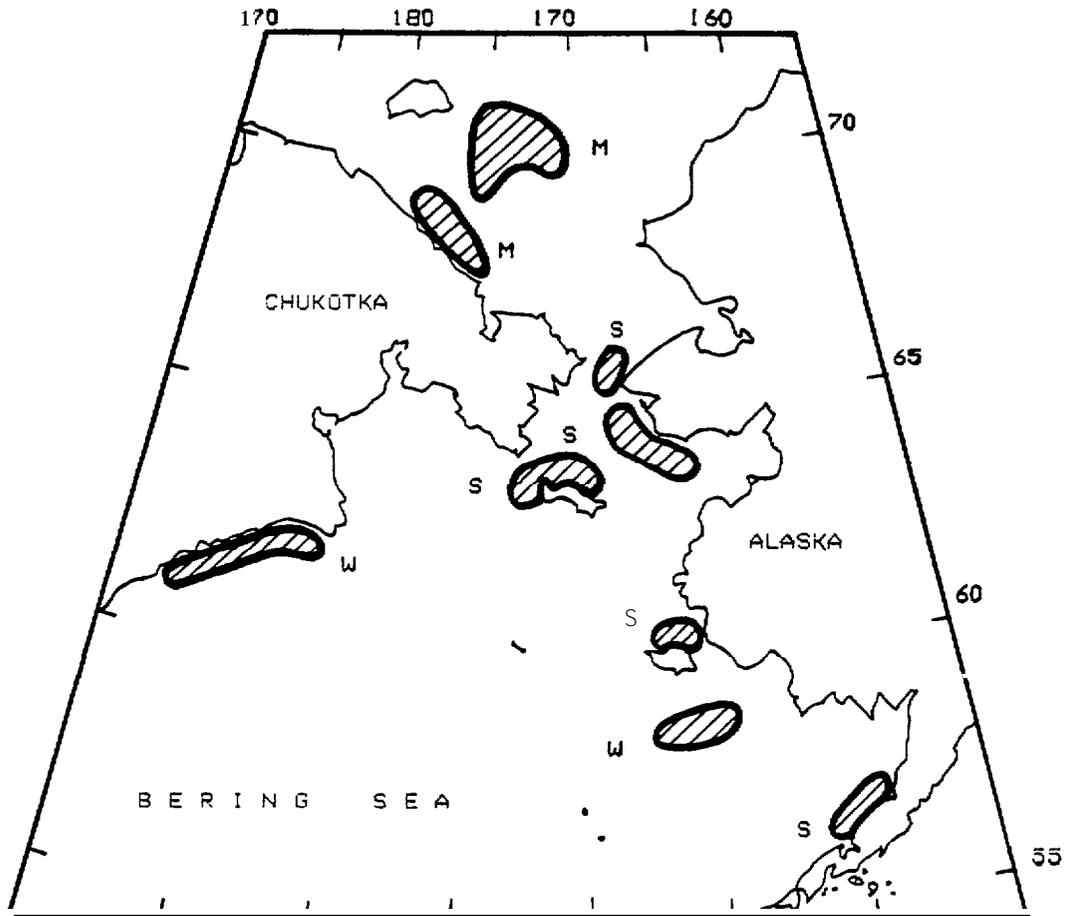


Figure 22. Locations from which walrus stomach contents were obtained by this and complementary projects: in winter (w), spring (S), and summer (M).

Table 18. Daily compilation of sightings of walrus within 1 km of the ship's track, in relation to activity. Animals on the ice were most sleeping; those **in** the water were mostly feeding. ZRS ZVYAGINO, southeastern Bering Sea, winter 1981.

Date	Walrus sighted		
	N	% on ice	% in water
25 February	272	98.5	1.5
26 February	169	83.4	16.6
27 February	599	2.0	98.0
28 February	15	100.0	0.0
1 March	129	94.6	5.4
2 March	369	98.6	1.4
3 March	400	25.5	74.5
4 March	139	76.3	23.7
6 March	63	52.4	47.6
7 March	13	53.8	46.2
8 March	231	100.0	0.0
9 March	44	93.2	6*8
10 March	155	36.1	63.9
11 March	63	95.2	4.8
12 March	36	19.4	80.6
13 March	484	51.4	48.6
14 March	2,144	98.4	1.6
15 March	94	73.4	26.6
Totals	5,419	73.7	26.3

From 180 specimens taken during that cruise, about 120 km offshore in waters 25 to 45 m deep (Fig. 22), we obtained 15 samples of stomach contents. All previous winter and spring samples in southeastern Bering Sea had been obtained much farther south, in deeper water (Tikhomirov, 1964b; Fay, 1982). About 95% by weight of the foods in the 15 stomachs consisted of four kinds of bivalve mollusks: the Alaska tellin (Tellina lutea), surf clam (Spisula polynyma), Greenland cockle (Serripes groenlandicus), and razor clam (Siliqua alta). The tellins predominated by far, in both numbers and weight (Table 19). Of lesser importance by weight but frequent in occurrence were echiurids (Echiurus echiurus), polychaetes (mainly Nephtys

Table 19. Contents of the stomachs of 15 walrus taken in outer Kuskokwim Bay, during February-March 1981.

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Anemones	1	4	13
Polychaetes	9	150	254
Echiurids	11	114	813
Snails	12	53	87
Tellins	15	4,839	20,184
Surf clams	15	283	5,352
Cockles	12	162	2,221
Razor clams	13	229	985
<u>Astarte borealis</u>	2	3	<1
Crustaceans	9	30	52
Meat fragments	15		3,182
Shell fragments	15		59
Inorganic sediments	15		1,200
Totals		5,867	34,402

spp.), whelks (Neptunea spp., Buccinum spp.), and moon snails (Natica spp., Polinices spp.). The stomachs of two 9-month-old calves contained only milk.

Three of the 15 animals with food in **the** stomach were males; the rest were females. The males that contained food ranged in age from 1 to 16 years, and they made up 13.3% of the 24 animals in that age range; none of the 66 older males contained any food. Conversely, the 12 females that had food in the stomach were randomly distributed throughout the age range of the whole sample (**N=90**), of which-they made up 12.5%. The implication of those findings is that the young males feed about as much as the females during the breeding season, but the adult males eat very infrequently or not at all. That implication was supported further by the shrunken condition of the digestive tracts of the adult males. The tracts in the largest males were smaller than those in the adult females and in any but the youngest (1 to 3 yrs old) of the immature animals. Those shrunken organs indicated that the adult males had been fasting for a long time, which was indicated also by their leanness. The blubber on the adult males was significantly thinner than on the adult females, even excluding those with a near-term fetus, which are fattest (Table 20).

Table 20. Comparative thickness of sternal blubber in adult male and adult female walruses taken in southeastern Bering Sea, February-March 1981.

Sex	N	Blubber thickness (mm)		
		Range	Mean	S.D.
Males	65	15-54	32.5	8.25
Females¹	27	31-54	41.0	6.70

¹ Excluding the pregnant females with a nearly full-term fetus.

Many of the snails and bivalves in the stomachs were complete enough to indicate that the walruses had eaten all of the fleshy parts, not just the feet or siphons as Vibe (1950), Brooks (1954), Fay (1955), and Mansfield (1958) had supposed earlier. That is, they had eaten everything but the shells. Shells were absent, except for a few chips from the edges of

the valves. Those chips made up only 0.2% of the weight of the ingesta, whereas the entire shells of the bivalves would have made up 50 to 75% of the total weight, had they been eaten. That scarcity of shells was not due to digestion, for the chips were in virtually undigested condition. Indeed, the shells are more resistant to digestion than are the meats. Frequently, we have found that the shells even of very tiny mollusks pass through the digestive tract with little change, whereas the meats of even the largest ones are fully digested.

Winter, Southwestern Bering Sea

Stomach contents from an unknown number of walruses were collected during the cruise of the ZRS **ZAGORSKII** in the pack ice of the **Koryak-Kamchatka** region in March-April 1980. Those animals were all males, the majority of them **subadults**. Their principal foods were Greenland cockles, soft-shelled clams (*Mya spp.*), and possibly razor clams (**Kibal'chich**, 1981). Although some small clams, such as *Hiatella arctica* and *Macoma* spp. have been reported as abundant in that area, they were not found in any of the stomachs.

Spring, Eastern Bering Sea

Bristol Bay.--During our aerial surveys of Bristol Bay in April 1980 and 81, as **well as** on the cruise of the R/V RESOLUTION there in April 1981, we observed several thousand males in the water, and most of them appeared to be feeding. Nearly all were adults in small groups of 1 to 7 individuals (mean, 3). We obtained stomach contents from four of those males, (Table 21).

Table 21. Contents of the stomachs of four male walruses taken in Bristol Bay, April 1981 (after Fay and Lowry, 1981).

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gin)
Anemones	1	16	1,806
Polychaetes	3	5	4
Echiurids	1	1	6
Snails	3	55	146

Table 21. Continued

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Tellins	3	2,209	2,921
Surf clams	4	1,013	12,635
Cockles	2	6	54
Razor clams	1	20	219
<u>Mya truncata</u>	2	15	368
Crustaceans	2	6	75
Holothureans	1	3	81
Meat fragments	4		2,177
Shell fragments	4		42
Inorganic sediments	4		593
Totals		<u>3,349</u>	<u>23,401</u>

The foods in their stomachs were very similar to those in the winter sample from Kuskokwim Bay, except that the proportions differed. Here, surf clams predominated by weight, and **tellins** and hydrozoans made up most of the rest of the identifiable prey. Because these walruses had been feeding when they were taken, part of their stomach contents was not yet affected by digestion. Again the fleshy parts of the bivalves were found to be nearly complete, but the shells were absent. That is, the walruses had eaten practically all of the meats -- not just the feet and siphons, but the mantles, gills, viscera, and even the adductor muscles. Only the shells were missing, and their absence clearly was not due to digestion.

Nonetheless, digestion apparently had altered the condition of some of the foods, for the larger meaty parts were more numerous in each stomach than were the smaller ones from the same clams. Noting that, Fay and Lowry (1981) **re-examined** the Kuskokwim Bay sample and observed that the smaller **tellins** were best represented in the freshest samples, and the larger surf clams predominated in the more digested samples, indicating that digestion had affected the composition of the stomach contents.

Nunivak Island.—Stomach contents from five male walruses taken in the vicinity of **Mekoryuk** and **Etolin** Strait contained mainly **tellins, soft-shelled clams**, and some large anemones, **possibly of the genus Metridium** (Table 22). Next in order of abundance were razor clams. In much smaller

Table 22. Contents of the stomachs of five male walruses taken in the vicinity of Mekoryuk and **Etolin** Strait, **Nunivak** Island in May and June 1982 (after Fay and Stoker, **1982b**).

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Anemones	2	204	3,500
Polychaetes	2	25	31
Echiurids	1	2	25
Priapulids	1	1	2
Brachiopods	1	2	3
Snails	4	24	35
Tellins	2	2,671	4,744
Surf clams	1	3	50
Cockles	1	11	122
Razor clams	2	518	768
Mya spp.	3	176	2,904
Crustaceans	2	12	13
Holothureans	3	8	66
Meat fragments	5		1,187
Inorganic sediments	5		876
Totals		<u>3,657</u>	<u>12,978</u>

quantities were Greenland cockles, surf clams, **holothureans** (Cucumaria spp.), moon snails, **polychaetes** (especially Nephtys spp., Phyllodoce sp.), and **echiurids**.

St. Lawrence Island.—Stomach contents from 108 walruses taken in the vicinity of **Gambell** and **Savoonga** in May and June of 1980 and 1982 suggested again that walruses in the St. Lawrence Island region feed on a very wide variety of prey (Table 23).

Table 23. Contents of stomachs of 108 walruses taken in the vicinity of St. Lawrence Island, April-June 1980 and 1982 (after Fay and Stoker, 1982a,b).

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Anemones	10	68	401
Nemertean	1	1	1
Polychaetes	30	955	1,814
Sipunculids	16	73	257
Echiurids	38	1,209	4,202
Priapulids	59	212	1,419
Snails	98	1,624	4,146
Tellinids	35	2,696	838
Surf clams	14	551	3,496
Cockles	91	1,494	24,602
<u>Mya</u> spp.	96	10,102	63,130
<u>Hiatella</u>	8	4,288	2,356
<u>Yoldia</u>	10	104	48
<u>Nucula</u>	1	1	1

Table 23. Continued

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
<u>Thyasira</u>	1	1	1
<u>Liocyma</u>	3	7	10
octopus	3	3	10
Amphipods	7	14	17
Shrimps	35	785	2,641
Crabs	45	230	703
Holothureans	30	61	992
Tunicates	9	22	43
Fishes	12	811	1,581
Meat fragments	89		8,298
Shell fragments	9		49
Inorganic sediments	79		17,871
Totals		25,312	138,927

In general, 68% by weight of this sample was made up of bivalve mollusks, especially of the genera *Mya* and *Serripes*. Most of the other prey were **polychaetes**, **echiurids**, snails, crustaceans, and fishes (sand lance, *Ammodytes hexapterus*). Inorganic sediments made up nearly 13% of the total weight.

Nome - King Island.--The stomachs of eight specimens taken in 1980 and 1982, from just south of Cape Nome to the vicinity of King Island, contained mainly Greenland cockles and soft-shelled clams (Table 24). **Tellins**, **echiurids**, and **holothureans** ranked next; other kinds of prey were present in trace amounts.

Table 24. Stomach contents of eight walruses taken from the vicinity of Nome to King Island, May 1980 and 82 (after Fay and Stoker, 1982a,b).

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Polychaetes	2	7	7
Echiurids	2	40	320
Priapulids	2	5	13
Snails	4	21	43
Cockles	3	1,635	4,490
Mya	7	515	4,172
Tellinids	3	116	316
<u>Hiatella</u>	1	5	4
<u>Yoldia</u>	2	86	26
Shrimps	2	22	56
Crabs	2	2	6
Holothureans	3	78	850
Tunicates	1	7	12
Meat fragments	2		125
Inorganic sediments	3		1,940
Totals		<u>2,539</u>	<u>12,380</u>

Bering Strait.--The stomach contents of 50 walruses taken in Bering Strait, between Cape Prince of Wales and the Diomed Islands in May-June 1980 and 82, had the greatest variety of prey (Table 25). Again, clams of

the genus Mya predominated by weight, making up 62.5% of the total; second in importance were cockles at 14.4%; third were **holothureans** at 6.5%. Peculiar to this sample were jellyfish (**Scyphozoa**), which were present in considerable quantities in four stomachs.

Table 25. Stomach **contents** of 50 walruses taken in Bering Strait, May-June 1980 and 82 (after Fay and Stoker, **1982a,b**).

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Anemones	6	18	122
Jellyfish	4	102	510
Polychaetes	17	156	755
Sipunculids	17	356	1,172
Echiurids	12	200	1,179
Priapulids	18	34	478
Snails	40	539	1,299
Tellinids	14	1,425	618
Surf clams	1	11	50
Cockles	27	789	12,498
<u>Mya</u> Spp.	49	2,698	54,280
<u>Hiatella</u>	16	2,333	843
<u>Yoldia</u>	2	50	30
<u>Thyasira</u>	1	1	tr
octopus	9	8	101
Amphipods	2	3	4
Shrimps	2	3	24

Table 25. Continued

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Shrimps	2	3	24
Crabs	4	16	64
Holothureans	29	387	5,621
Tunicates	1	1	1
Meat fragments	44		2,628
Shell fragments	8		22
Inorganic sediments	44		4,525
Totals		9,130	86,814

Summer, Chukchi Sea

During the cruise of the ZRS ZYKOV in July-August 1983, we obtained stomach contents from 40 walruses. Half of those walruses were taken in the west-central part of the Chukchi Sea, from just east of Herald Shoal to about 55 km east of Wrangell Island (Fig. 22). The other half were taken along the northern coast of Chukotka, from the vicinity of Vankarem to the eastern part of Long Strait.

The sample from the west-central Chukchi was made up principally of three food types: whole polychaetes (especially malidanids and terebellids), fleshy parts of moon snails (mostly of the genus Polinices), and strips and chunks of flesh from ringed seals (Phoca hispida) (Table 26). Sipunculids, priapulids, crustaceans, tunicates, and fleshy fragments from pennatularian polyps (sea pens), each made up greater proportions of the ingesta than did the bivalves, which were scarce and mostly of very small size. Most of the stomachs contained large amounts of inorganic solids (sediments), but unfortunately we were not able to measure those amounts. The terebellids and pennatularians had not been identified previously as walrus foods.

Table 26. Stomach contents of 20 walruses taken in west-central **Chukchi** Sea, July-August 1983.

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Sea-pens	10	unknown	661
Polychaetes	13	2,191	3,293
Sipunculids	7	135	462
Echiurids	4	4	25
Priapulids	4	25	474
Snails	19	3,246	2,776
Tellinids	1	1	tr
Cockles	9	61	191
<u>Mya</u> Spp .	1	1	17
<u>Astarte borealis</u>	8	105	18
<u>Yoldia</u> sp.	1	9	4
<u>Nucula</u> sp.	3	3	tr
<u>Nuculana</u> sp.	8	39	1
octopus	9	8	172
Amphipods	1	2	1
Shrimps	6	50	83
Crabs	16	243	277
Tunicates	3	112	562

Table 26. continued

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Seal	3	3	2,345
Shell fragments	8		19
Totals		6,238	11,308

The nearshore sample from northern **Chukotka** was made up about equally of **polychaetes**, **priapulids**, snails, bivalves, **tunicates**, and seal flesh (Table 27). As in the more northern sample, the **polychaetes** were mainly **maldanids** and **terebellids**, the snails predominately **Polinices**, and the seals were ringed seals. Crustaceans were abundant but tiny.

Although bivalves and snails were by far the most abundant prey, they were mostly of very small size. The mean weight of the bivalves was less than 0.2 g. Even so, the meats had been neatly separated from the shells, with the exception of some of the smallest clams of the genera **Nucula** and **Nuculana**, which had been swallowed whole.

Table 27. Stomach contents of 20 walruses taken along the northern coast of **Chukotka**, from Vankarem to Long Strait, July-August 1983.

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Polychaetes	14	495	1,334
Sipunculids	3	18	53
Echiurids	11	12	35
Priapulids	14	387	1,247

Table 27. Continued

Kind of prey	Frequency of occurrence	No. of individuals	Weight (gm)
Snails	19	1,674	1,489
Tellinids	16	2,096	386
Cockles	12	249	245
<u>Mya</u> Spp.	6	65	157
<u>Hiatella arctica</u>	2	2	2
<u>Astarte borealis</u>	13	3,335	337
<u>Yoldia</u> sp.	6	379	52
<u>Nucula</u> sp.	2	2	tr
<u>Nuculana</u> sp.	1	1	tr
octopus	1	2	4
Cumaceans	3	51	5
Amphipods	12	86	36
Shrimps	7	31	82
Crabs	9	146	217
Holothureans	1	8	120
Tunicates	12	954	1,057
Seals	2	2	2,344
Meat fragments	7		42
Shell fragments	6		12
Totals		9,997	9,244

The high proportion of seal-eating walruses in these summer samples from the western **Chukchi** Sea is remarkable but perhaps not unusual. The only previous data from that area were collected by **Krylov** (1971) nearly 20 years ago, and in his sample of 35 stomachs, he found 3 that contained seal flesh. Although seal eating is regarded as unusual in the Bering Sea (Lowry and Fay, 1984), it maybe a very common practice in summer in the western **Chukchi** Sea, where the **benthic** prey appear to be mostly very tiny. Seal eating generally has been regarded as a masculine habit in walruses, but only three of our five seal eaters were males; the other two were females. **Chapskii** (1936) also observed that both males and females were feeding on seals in the Kara Sea in summer.

Amount Eaten in Relation to Age, Sex, and Season

The quantity of food consumed by a single walrus per day or for a longer period of time cannot be measured in the natural environment at present. For that reason, we turned to the records of food intake by walruses reared in captivity, for they at least provide a tangible basis for estimating the intake by wild walruses (**Fay**, 1982). Many walruses have been reared successfully in captivity in the present century, some of them to more than 20 years of age. Two pairs at Marineland in California also have reproduced several times, for the first time in history. The daily feeding records for those pairs and their surviving offspring, from 1974 to 1982, were made available to one of us (**PHG**) by the management of that facility.

The kinds and quantities of foods eaten by each of the Marineland walruses was recorded after each feeding bout. The animals were fed varying proportions of whole, oily fishes and shucked (shell-free) clams. Converting those foods into gross caloric content, we estimated that the walruses consumed energy at mean annual rates ranging from about 25,120 **kcal/day** in a 2-year-old female to 70,310 **kcal/day** in an 18-year-old male. The annual mean of daily intakes increased with age at about the same rate in both sexes, up to 7 or 8 years. From that point, their consumption rates diverged, the females' tending to level off, and the males' rising again until about 15-16 years of age, before leveling off (Fig. 23). Females consumed more when pregnant or lactating than when non-pregnant or non-lactating. Even so, they usually ate less than the adult males.

The body weights of walruses reared in captivity do not differ from those of wild walruses (**Fay**, 1982), hence we assumed that the total body weight (**TBW**) of each of the **Marineland** animals was about the same as the mean **TBW** for wild walruses of the same age and sex. On that basis, we estimated their daily intakes of energy per unit of body weight. Those estimates ranged from about 240 to 470 **kcal/kg^{3/4} TBW** per day (Fig. 24).

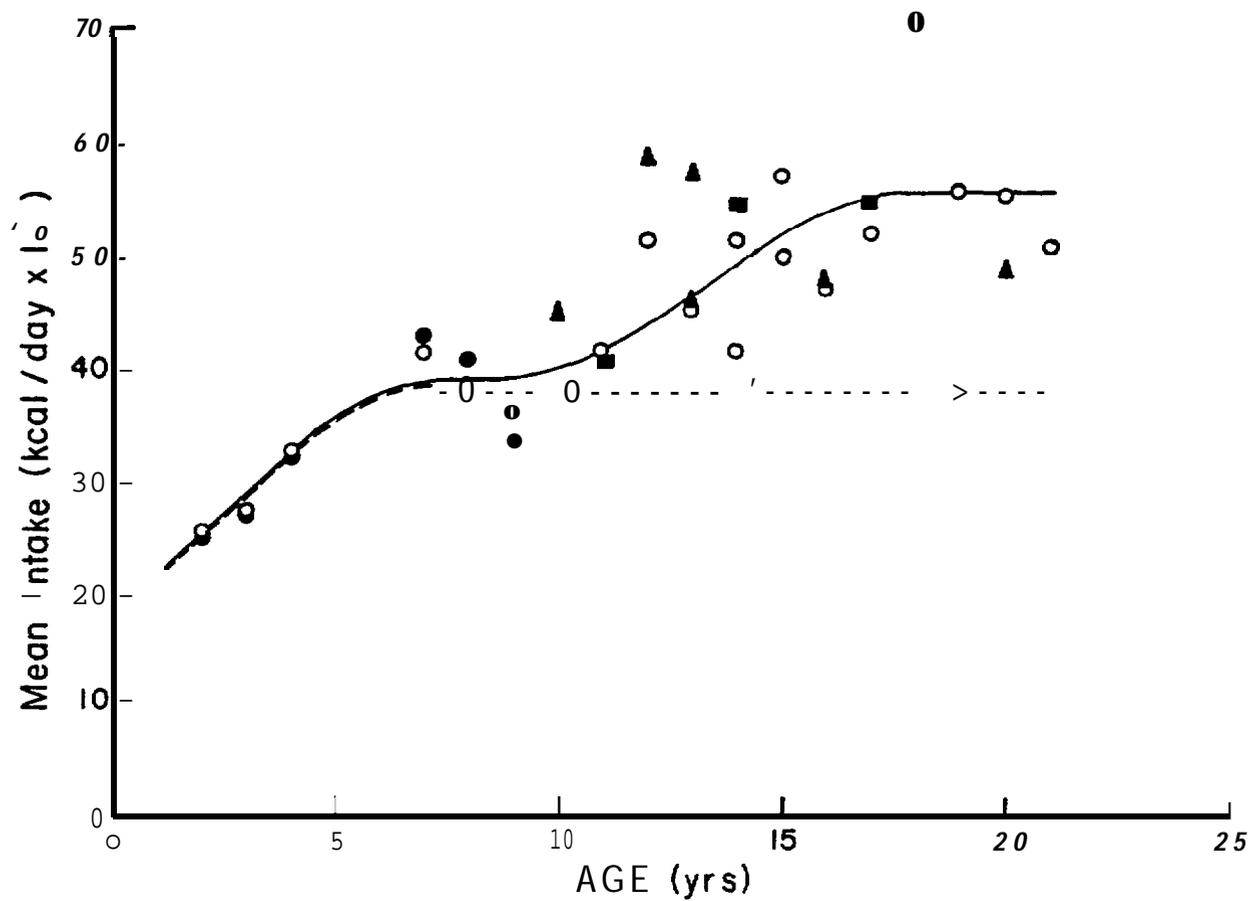


Figure 23. Mean daily energy intake of male (o) and female (● non-pregnant, ▲ pregnant, ● lactating) walrus per calendar year at Marineland, in relation to age (after Gehrich, 1984).

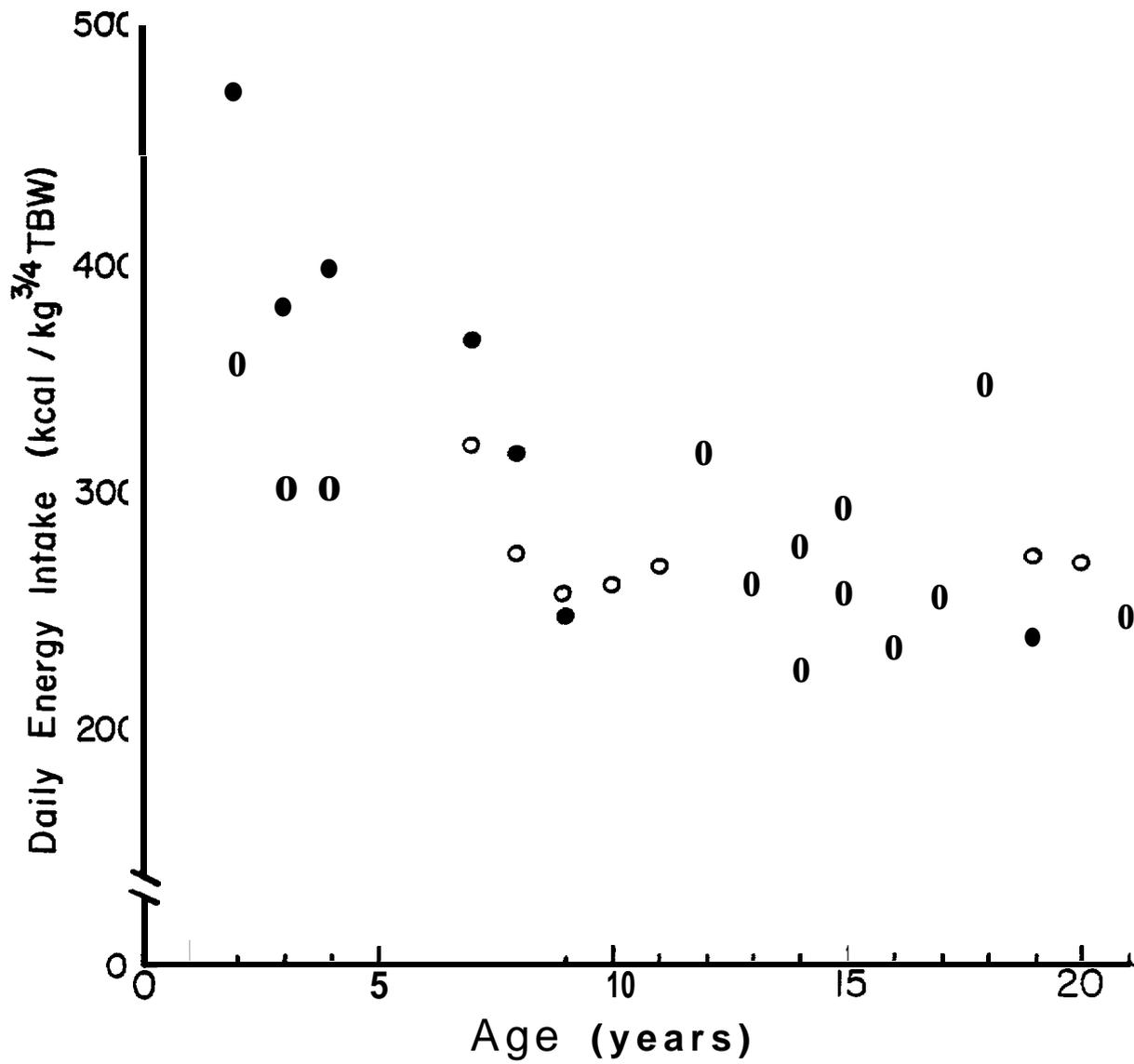


Figure 24. Mean daily gross energy intake per age, in relation to estimated unit body weight, for male (o) and female (.) walrus reared at Marineland (after Gehrich, 1984).

The highest intakes per unit weight were in the youngest, growing individuals; the lowest were in the mature adults.

The young animals' daily intake of energy was comparatively uniform throughout each year, at least up to 4 years of age; it became more variable after that time (Fig. 25). The variation in later years apparently was correlated mainly with reproductive status. For example, the daily energy intake of the adult females usually dropped to zero for several days about the time of **estrus**, then rose again to the previous level. The males also fasted during those days of the females' estrus (**Gehrich**, 1984). Following estrus and mating, the females' consumption of energy increased **steadily** through the spring, summer, and fall, usually reaching its maximum in mid-term gestation (November - December). The mean rate of intake during that mid-term maximum for the two females in five different pregnancies ranged from about 52,500 to 69,300 **kcal/day**. For the next 4 or 5 months, feeding rates decreased again somewhat erratically, then fell to zero for several days about the time of birth. It usually remained very low and very erratic for some days or weeks thereafter. Often there was a brief period of fasting also in August, about the time of the **post-partum** estrus (cf. Fay, 1982). After that, the trend was upward to a new level that persisted with little change through the rest of lactation.

The mean **daily** energy intake during each of those five pregnancies, from the time when the intake began to increase in April or May, until it fell off a year later at calving, ranged from 49,250 to 57,960 **kcal/day** (Table 27). Those intakes amounted to 40 to 50% increases over the means for the same animals when they were non-pregnant and not lactating (**Gehrich**, 1984). The females also consumed about 50% more energy when lactating than they did when not pregnant or lactating. Their intakes during the first year of lactation ranged from about 50,480 to 55,500 **kcal/day**. Immediately after separation from the calf, their intakes fell to the normal non-pregnant, non-lactating level.

The males' energy intakes also became very unstable and variable in adulthood. Both of the males as adults tended to eat very little during a 3- to 5-month period in the winter (Fig. 26). On many days in that period, they ate nothing. That intermittent fasting took place from December or January to April or May, corresponding to the time of rut in the wild males. It took place slightly earlier in the old than in the young male. The younger male was nearly 7 years old when he started this fasting, but it was rather brief and unremarkable until his 10th winter. At that time, he first bred the female successfully.

In both males, the fasting has tended to increase in intensity and duration each year, as they have grown older. Although they have eaten less each year during the breeding season, they have counterbalanced that

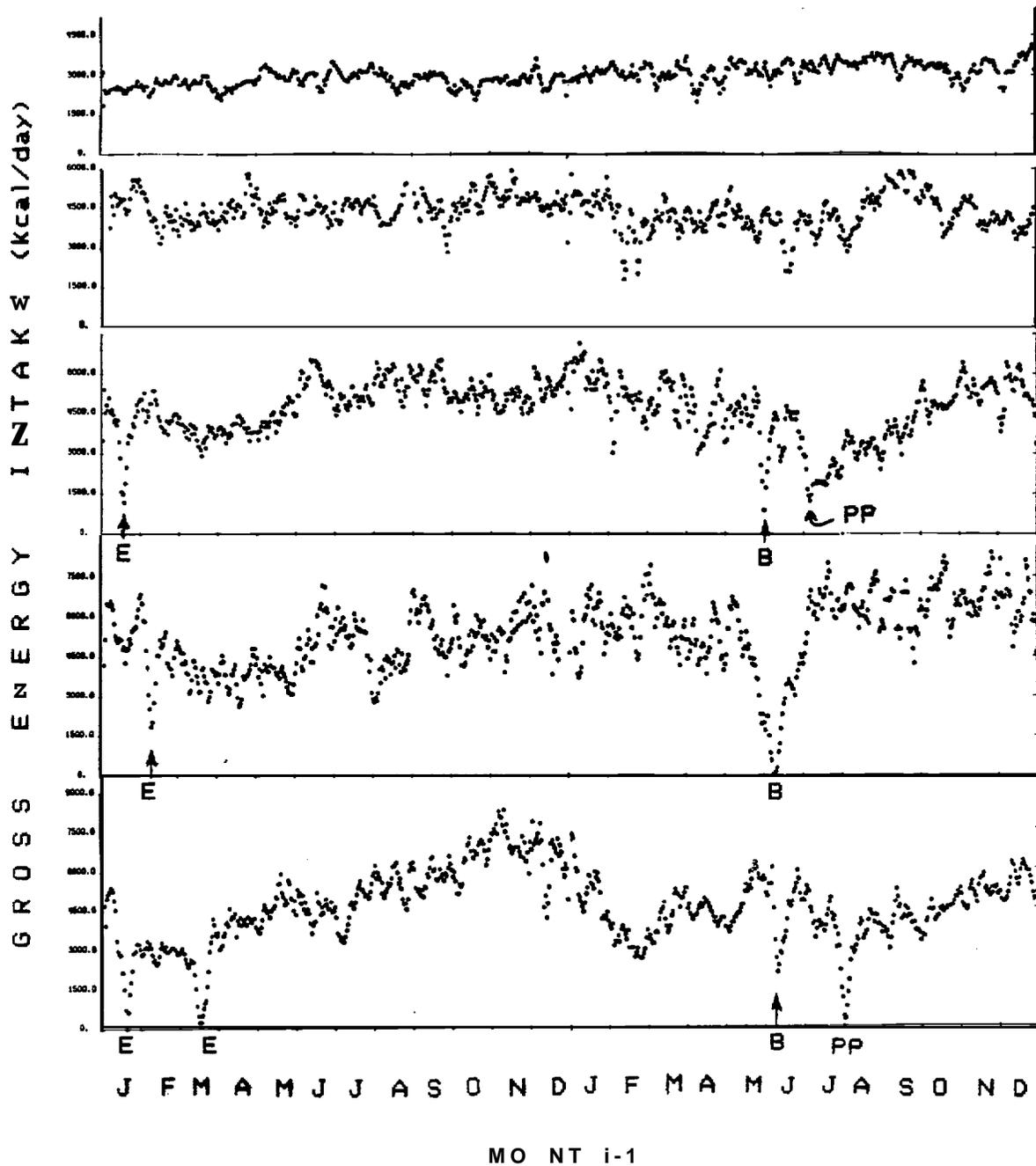


Figure 25. Five day running averages of gross energy intakes for female walrus at Marineland at different ages. Top two in fourth and seventh years; bottom three as adults, during three pregnancies. Deviations linked with estrus at mating (E), birth (B), and postpartum estrus (PP) are indicated.

Table 28. Mean daily energy intakes by pregnant and lactating female walruses at Marineland. Intakes by the same individuals when not pregnant or lactating are shown for comparison.

Age of female (years)	Mean energy intake (kcal/day)		
	Non-pregnant, non-lacteal	Pregnant	Lactating
Female A			
7	43,011		
8	40,995		
9	33,685		
10		50,787	
11			50,477
13		49,250	
Female B			
13		57,963	
14			54,764
16		50,873	
17			55,498
19	36,834		
20		52,385	

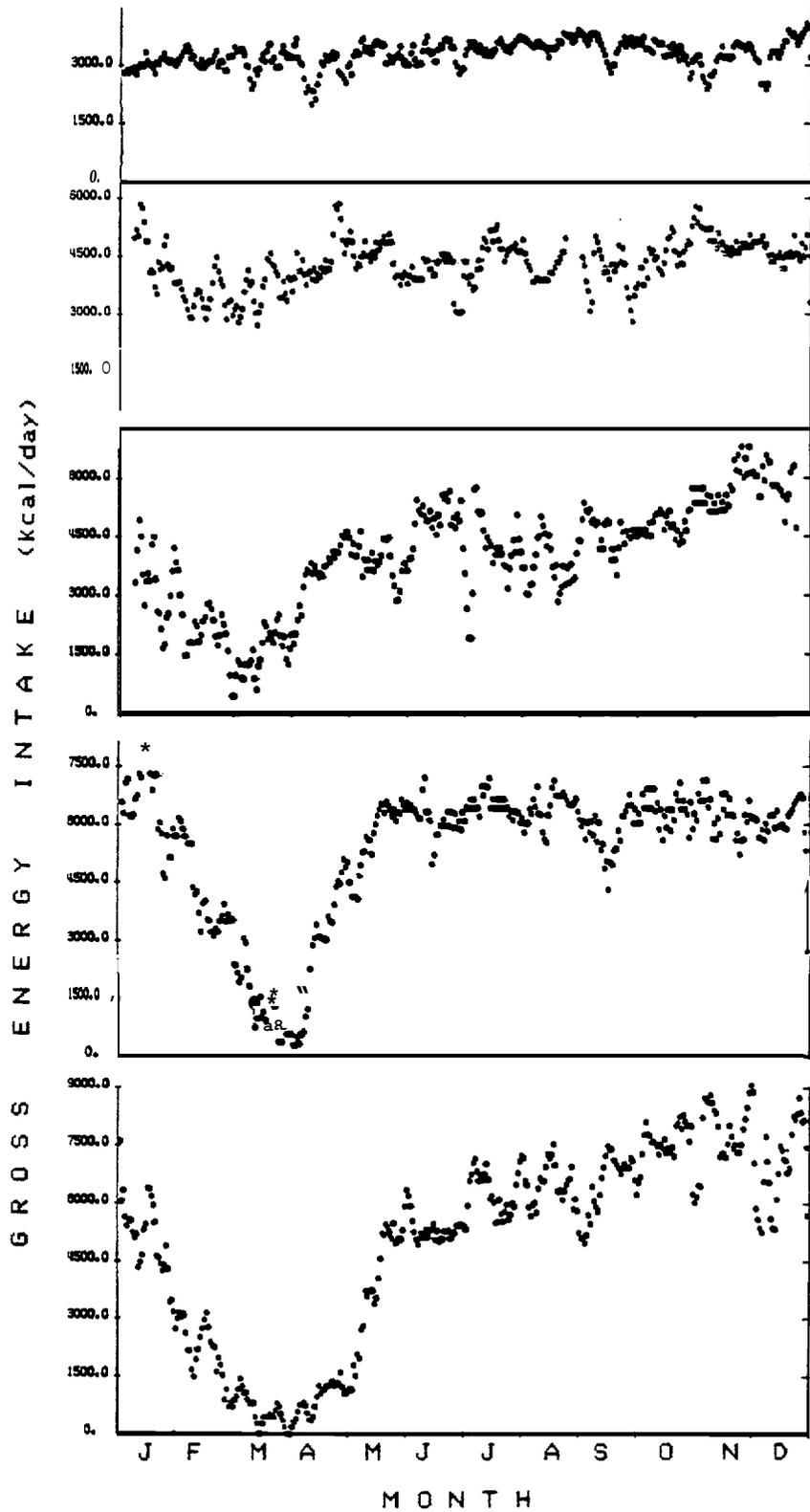


Figure 26. Five day running averages of gross energy intakes for male walruses at Marineland at different ages. Top to bottom: in fourth, seventh, tenth, twelfth, and fifteenth years (Marineland, Los Angeles, unpubl. data).

by steadily increasing their energy intake outside the breeding season (Gehrich, 1984). Like the females, their maximal intake during the year has tended to be in November-December, which corresponds to the time of the autumnal migration of the wild walrus.

Responses to Man-made Disturbance

Man-made disturbances apparently are perceived by walrus principally through the senses of smell, sight, and hearing. That their sense of smell is **keenest** is suggested by their quick response to odors at great distances and in the absence of other stimuli (Loughrey, 1959). Their hearing also is keen. "One needs only to step onto the ice and take several steps, whereupon all of the resting animals are awakened, as if by command" (Bel'kovich and Yablokov, 1961:55). But it is common knowledge that vision is poor and that they do not respond in the same way all of the time.

On ice or on shore, males tend to be less shy than females and individuals less shy than groups. Weather appears to play a part in affecting the response. The animals appear to be more alert in windy or stormy conditions than in fair weather. The length of time that they have been out of the water also seems to play a part; that is, they seem to be more easily frightened when they first haul out than after they have been out for a few hours. In the water, where they usually are awake and alert, they tend to be more trusting, evidently feeling more secure there than on land or ice (Fay and Ray, 1968). Their responses to disturbance when in the water appear to be much more predictable than on ice or land. Visually, they appear to be influenced in their response not only by the distance of the disturbing object from them but by its shape, size, and motion.

Females with calves appear to be the most sensitive to disturbance (Popov, 1960; Salter, 1979; Miller, 1982), and animals lying on shore are more sensitive than those lying on the ice (Loughrey, 1959). Disturbance of animals on ice or on shore usually leads to temporary abandonment of the **haulout**; i.e., the animals withdraw to the comparative safety of the water. Chronic disturbance may lead to permanent abandonment of the **haulout** (True, 1899; Bissett 1968 in Salter, 1978; Gol'tsev, 1968, 1975a). In **Chukotka**, several former **haulouts** are no longer in use, apparently because of persistent disturbance by ships and aircraft. Stampedes from a **haulout** can result in trauma-induced abortions, injuries, and death (Tomilin and Kibal'chich, 1975; Fay and Kelly, 1980).

In this project, we did not experiment with any of those conditions but did make some effort to observe closely and record our observations, in the course of our other work. Our results were as follows:

On Ice, in Winter

During the cruise of the ZRS ZVYAGINO (Feb-Mar 1981), we observed that, when the ship was breaking ice and approaching the walrus upwind, they appeared to awaken when the ship was up **to** 2 km away. Evidently they **were** awakened by the sound alone, since they could not have smelled it upwind and could not have seen it when asleep. **We** also observed that the animals were less easily awakened when the ship was operating in open water than when it was breaking ice. That is, the walrus appeared to be reacting more to the sound of the ice than to the ship's engines. Other **pinnipeds** of the pack **ice** also appear to be alerted more by the sound of breaking ice than by the steady, low frequency sounds of diesel engines.

When first awakened by the approaching ship, the adult males usually just raised their head, looked at the ship briefly, then lay down again until the ship was within about 100 to 300 m. Then, they usually looked again before going into the water, without hesitation. Groups of females and young were more wary, usually watching the ship's approach to about 0.5 to 1 km, whereupon they entered the water and swam away. A similar difference between sexes was evident when the hunters approached the animals on foot over the ice. By approaching upwind and taking cover behind ice ridges, they frequently approached within 2 or 3 m of sleeping males, but they rarely came closer than 20-30 m of females and young.

On **Ice**, in Spring and Summer

From the **CGC** POLAR STAR in the open pack ice south of St. Lawrence Island in May 1980 and in the **Chukchi** Sea in July 1981, we observed that the herds of females and **young** could be approached upwind by the ship in open water at very slow speeds (3-4 kt or less) usually to within about 200 m. When approached faster (6-12 kt), the walrus left the ice at distances of 5-600 m ahead of the ship, indicating that the speed of the disturbing object was a factor in their response. Since we could hear the throb of the ship's engines up to **5**km away, we assumed that the animals could hear it at least as well. Hence, the inescapable conclusion was that the walrus were not frightened as much by the sound of the ship as they were by the nearness (sight) of it (or a combination of those).

On downwind approach in open water, however, the animals left the ice at distances of 1.5 to 2 km, apparently irrespective of the ship's speed (Table 29). Several times, **we** also observed that herds at those distances entered the water and swam away when the exhaust cloud from the **ship's** stack crossed their position. That is, the importance of odor as a stimulus was **confirmed** as foremost. Where odor was the primary factor, the animals fled at distances about ten times those from upwind approaches, where only sight and sound could have played a role.

Table 29. Flight distances (meters) of walrus herds when disturbed by the ship, its helicopters, and two types of small boats, during the cruise of the CGC POLAR STAR in the open ice of the **Chukchi** Sea, **July** 1981.

Vehicle	Direction of approach				Remarks
	N	Upwind	N	Downwind	
Ship	5	100-650	4	1500-2000	Speed <3 kt
Ship	>5	500			Speed >5 kt
Survey boat	4	40-60	1	600	All slow speed
Zodiac	5	10-20	2	200-300	With engine
Zodiac	2	1-3			With paddles
Helicopter	3	400-600	7	1000-1800	Altitude 500 ft

We observed a similar differentiation among their responses to odors, sights, and sounds when we were working among the herds with small boats. With slow, upwind approach, the 30-ft Arctic Survey Boat could go within about 60 m of **the** herds, without causing any apparent disturbance. But with downwind approach, irrespective of speed or sound, the animals took flight at distances of 5-600 m or more. On several occasions, observers in a Zodiac were able to paddle upwind to within 1-3 m of drowsy animals without alerting them; however, with the outboard engine running, 25 m was the minimal distance upwind before the animals were aroused and began to flee. Downwind, even the Zodiac caused some herds to flee at 300 m or more, especially when the boat was moving at moderate to high speeds.

During the cruise of the K/S ENTUZIAST in the **Chukchi** Sea in July-August 1981, the herds again appeared to be aroused and to respond to the approach of the ship at significantly greater distances downwind than upwind (Table 30). The distance at which they responded when the ship approached them across the wind was virtually the same as upwind. That is, where the sense of smell could not possibly have contributed to the animals' assessment of the source of the disturbance, their flight distance tended to be about half to a third as great as it was when odor was a

factor. That difference was not as great as was measured from the POLAR STAR, possibly because the **ENTUZIAST** was a much smaller, **less** smoky ship.

Those findings suggest that the intensity of the animals' response varies with the size of the vessel, as well as its direction and speed, and that the response is least to sight and sound and greatest to the combination of sight, sound, and odor. For audible cues, the quality of the sound seems to be important. Low-frequency, diesel engines appear to cause less disturbance than high-frequency outboard engines. The sound of aircraft engines and the sight of an aircraft moving rapidly overhead appear to be particularly disturbing.

Table 30. Flight distances (meters) of walrus when they were approached upwind, crosswind, and downwind by the K/S **ENTUZIAST** in the ice edge of the **Chukchi** Sea, July-August 1982.

Statistic	Direction of approach		
	Upwind	Crosswind	Downwind
N	39	49	21
Range	15-300	7-400	8-800
Mean	70.8	93.8	206.6
Std. error	12.06	12.21	49.29
95% conf. lim.	46.7-94.9	69.4-118.2	108.0-305.2

On Shore, in Spring, Summer, and Fall

At Cape **Seniavin** in Bristol Bay, we observed a herd of about 1,000 males at rest on the beach at 1000 hours on 8 April 1981. Within 8 hours, that number was reduced to zero by the passage of three fixed-wing aircraft and one **helicopter**, each at "sight-seeing" altitudes of 60 to 80 m. By 0800 hrs on 9 April, about 100 animals were back on the **haulout**, but about half of them left when another fixed-wing craft passed them at less than **100m**. About 100 were present also at 1100 hrs on 10 April, but those were stampeded into the water about an hour later by another passing aircraft. By evening, only 30 animals had returned, and they did not stay long.

On the **Punuk** Islands in October-November 1981, we observed only one man-made disturbance of herds on the beach. That happened on 8 November at 0845 hours, when a twin-engine aircraft made three passes over the walrus at an altitude of about 60 m. At that time, there were about 4,500 animals on the beach. About 1,000 of them raised their head when the aircraft passed, but less than 100 of them went into the water. That same day, two other aircraft passed within hearing range but caused no apparent response among the walrus.

In Water, All Seasons

Walrus in the open water, unlike the animals on the ice, usually showed little concern about an approaching vessel, unless the ship was about to run over them. At that, they simply dove and swam off to the side. Often when a ship was stationary, walrus swam to **within 20 m** of it. Frequently, they dove under it and emerged on the other side, apparently more curious than concerned.

Walrus in ice-covered waters, however, often scrambled rapidly onto the ice, rather than diving under it, when a ship was breaking ice toward them. That kind of response appears to be common among **pinnipeds** inhabiting the pack ice, for we have seen it in meetings not only with walrus but with both ringed and bearded seals, as well. The reason for it is unknown, but we presume that it has survival value in the pack, when the ice is compacting, breaking, and ridging under pressure.

The Consequences of Disturbance

To estimate the consequences of man-made disturbances on walrus is difficult. Certainly they range from very minor to major, depending on the circumstances. The most obvious possibility **of** potentially major importance in our experience was the abandonment of dependent young, which probably starve to death. Of more than 300 groups on the ice that were frightened by the ships and put to flight, only three groups left a calf behind and did not return to retrieve it while we had them in view. Earlier, Fay (1982) had observed during the spring walrus hunt at St. Lawrence Island that six calves were abandoned when some 50 herds of females and young were driven off the ice by hunters. This is a much higher rate of abandonment per group, but it may not have been higher per individual, for the herds tend to be larger in spring than in other seasons.

If the shipping traffic is heavy enough through an area in which walrus herds are concentrated, the number of calves abandoned presumably will be a multiple of the number of ships passing. For example, in the shipping lane from Icy Cape to Barrow, where walrus can be abundant in

July to October (**Fay**, 1982), the effect could be significant. The number of abandoned calves in that area has been unusually high over the past three years, according to reports from the North Slope Borough and U. S. Fish and Wildlife Service. Possibly, this can be attributed to that kind of disturbance, with increased shipping to and from the Beaufort oil fields.

We do not know whether abandonment is likely to take place more often or with greater effect in one season of the year than another. Not enough is known yet about the possibility of seasonal changes in strength of the cow-calf bond. From studies of walruses in **captivity at Marineland** and from our more extensive but less rigorous observations of wild females with calves, we judge that the probability of the mother's abandoning a calf increases with time after birth. That is, the bond appears to be strongest in the beginning, when it is maintained primarily by the mother. With passage of time, the calf apparently assumes increasing responsibility for maintaining **it** by following closely and vocalizing when in need of assistance. Thus, we think that the probability of abandonment is less during the calving period than it is later in the year. This needs to be examined more thoroughly, however.

Another, related consequence of disturbance in the **Chukchi** ice is predation by polar bears (**Ursus maritimus**). We observed one incident of that type, when a calf was captured from a ship-disturbed herd by a bear. The bear apparently had been stalking the walruses and had lain in ambush behind an ice ridge on an adjacent floe. At the instant when the disturbed herd was entering the water, the bear leaped to their floe, took the calf in its mouth, and carried **it** away some distance before killing it with a bite to the head. Whether the bear could have caught the calf without the *'aid*' of the ship, of course, is not known. Apparently, the bears in their own hunting for young walruses routinely rush the herds and stampede them into the water, relying on some calves being left behind (**Nikulin**, 1941; pOpOV, 1958, 1960b). We observed that a calf was the last to enter the water in 6 of 84 herds put off the ice by ships, and we assume that some bears would not fail to make use of that advantage. Some of the bears in the **Chukchi** Sea are notoriously unconcerned by ships and tend to occur in some numbers in the vicinity of the shipping lanes and the walruses on both the Soviet and American sides.

Finally, the question of interference of man-made disturbance with mating activities in the wintering areas remains unanswered. We assume that some inhibition of communication through garbling or "drowning out" of underwater vocalizations could take place, as it does in harp seals (Ronald and Dougan, 1982), if the noise level were high enough. Mansfield (1983) suggests that the noise alone may be sufficient to drive the animals out of areas where oil and **LNG** developmental activities are intense.

DISCUSSION AND CONCLUSIONS

Demographic History

Understanding of the population dynamics of large, wild mammals has advanced greatly in recent years (e.g., see **Fowler** and Smith, 1981), and the walrus can now be placed in that context. Like other **K-selected** species, walruses are long-lived, slow to mature, and have low fecundity, which must be coupled with very high survivorship. The social, reproductive, and demographic similarities of Pacific walruses to African elephants, for example, are striking (Table 31). Although the elephants have a much longer life-span than the walruses and consequently more prolonged development, the similarities between them otherwise are much greater than their thick skin and long tusks. Both require about 15 to 35% of their potential longevity to reach maturity; both have long intervals between single births, becoming longer with age; the calves of both are weaned at 2 or more years, and whereas the young females remain with the adults, the young males leave and form all-male groups about the time of puberty. The basic social groups of both walruses and elephants are matriarchal, consisting mainly of adult females and their young; small groups of males often are **bimodal** in age, with one old male and **the** rest much younger; single females usually are very old, but single males can be of any age; adult survival in elephants is fixed at an extremely high rate, and we surmise that the same is true also in walruses.

Populations of large mammals, when in equilibrium, can weather minor changes in their environment very well, because of their very high adult survival rates (Goodman, 1981). Their late maturity and very low recruitment rates, however, place them at a distinct disadvantage when major environmental changes take place suddenly, for they usually are unable to respond quickly enough to adapt to them. This is because their populations in equilibrium tend to be made up mainly of old animals which reproduce very infrequently. Such a population is very susceptible to over-harvesting, especially of adult females, for it **is** incapable of reproducing rapidly to compensate for the mortality (DeMaster, 1981; Goodman, 1981; Murphy and **Jarrell**, 1983).

We surmise that the primitive, **pre-exploitation** population of Pacific walruses also was in equilibrium with its environment, and that it must have been dominated by elderly, comparatively unproductive animals. We think that it was not greatly affected by the catches of the Russian merchant companies in the 126 years before the sale of Alaska to the United States, for they took only about 45,000 animals, or an average of about 360 animals per year. That could not have had much impact on the size of the primeval population, but at times it might have altered the sex ratio somewhat, because the catches were mainly of adult males. The succeeding

Table 31. Comparative social, reproductive, and demographic characteristics of Pacific walrus and African elephant populations.¹

Character	Elephants	Walruses
1st breed	12-23 yrs	4-11 yrs
Calving interval	3-9 yrs	2-5 yrs
Gestation	22 mos	15 mos
Calves/birth	1	1
Weaning	2 or more yrs	2 or more yrs
Males leave at age	8-10 yrs	5-7 yrs
Basic social group	2-29 ♀♀&yg	2-5 ♀♀&yg
Adult survival	94-96 %	~95 %?
Longevity	60-70 yrs	30-40 yrs

¹From Laws et al. (1975), Laws (1981a), Fay (1982 and **unpubl.** data).

catches by the Yankee whalers, conversely, must have had a catastrophic effect, for they were directed principally at the most sensitive part of the population (the adult females), and they amounted to removal of at least 130,000 in 12 years (average, **11,000/yr**). By the time the whalers stopped their catching, the walrus population apparently had been brought to extreme depletion, for even the strategically situated walrus-hunting Eskimos of the Bering Strait region starved to death in large numbers.

The whalers' reduction of the population also changed its age composition by removing principally the older adults (for their large tusks) and leaving the younger animals. We think that, in doing so, they made it more resilient and more responsive than it was before, for in its reduced state, it was broadly based in the younger, most productive age classes. Hence, it probably was on the increase again by the mid-1880's, when the whalers had all but ceased their catching.

The population was subjected to further pressure, however, about a decade later, when the arctic traders began their work. And they continued their taking, well into the present century, again mainly of the older animals. During their 30+ years of commercial harvesting, the traders certainly depressed the population, but because of its youthfulness and resiliency, they may not have depleted it to as great a degree as the whalers had, for the walrus-hunting natives at the same time were still getting their subsistence harvests, without registering any major complaints of the population's being depleted, at least until the 1920's. The traders, by directing much of their taking at first on the adult males in the southern Bering Sea (whose ivory and hides were most marketable), actually may have contributed to the population's eventual recovery by helping to restore its proper sex ratio. And when they lowered their pressure on the walruses in the early 1920's, the population must have been still broadly based, with a high proportion of young, productive females. We surmise this because it evidently recovered very rapidly and probably was still in a steep climb when the Soviets began their intensive harvesting in 1931.

Although the harvests by the Soviets were nearly **as** large as those by the Yankee whalers', they did not bring the population down **as** rapidly, probably because of **its** youthful resilience. That is, the animals were better able to withstand the excessive catches, because their productivity was very high. Eventually, the population was depleted by those harvests, perhaps to the lowest level in history, but in that depleted state **it** evidently maintained its youthfulness and productivity, for it "exploded" when the Soviets lowered their pressure on it around 1960. That explosion took about 20-25 years, which probably was prolonged somewhat, because the animals still were being cropped at a low rate. The growth of the population during that time was aided in part also by a reversal of the sex ratio of **the** catches. On both sides of the Bering Sea, the **earlier catches** had been mainly of females, but by the early 1960's they were changed by **regulation** in both Alaska and Chukotka to about 75% males (Burns, 1965, 1973; **Krylov**, 1968). We and Lowry et al. (1980) think that the food supply also played a part in helping the rapid response. For a long time, the walrus population had been too small to place much pressure on its food resources and was not using them at all in some areas. That the walruses were much fatter in the 1950's and 60's than they are now speaks of a greater abundance and/or better quality of food in those years.

By the **mid-** to late 1960's, walruses were **re-appearing** in places where they had not been seen for 25 to 40 years. That **re-expansion** into their former range apparently continued well into the late 1970's and early 80's. It may still be underway. At the same time, the results of both the Soviet and American aerial surveys indicated a rapid increase in numbers. The rate of increase appeared to be more rapid than was possible, according to

Kosygin (1975), Estes and Gilbert (1978), and De Master (1984), but we think that the data were not interpreted correctly. Only the Soviet estimates of numbers on their side of the Bering and **Chukchi** seas appear to have been comparable from year to year, and they suggested about a 7% rate of increase in the 1950's and 60's (which is plausible: cf. Mansfield, 1966) and a decelerating rate thereafter. The estimates of the total population, which were generated from the American surveys up to 1972 and from the joint surveys in later years, suggested a much higher rate of increase, but we feel that all or most of that "higher rate" was due to changes in the American census methods, equipment, and analytical procedures.

The expansion of range and Increase in size of the population were accompanied by a gradual shift upward in average age and downward in physical condition, from principally fat, young adults, to lean, old animals. The change in condition apparently was the result of gradually increasing pressure on the food supply; the increase in average age is attributable to declining recruitment. The two causes probably are linked, for reproduction of mammals is influenced by nutrition. Because female walrus become less and less productive as they grow older, this was a self-reinforcing process, resulting in **ever** lower productivity and recruitment. We believe that the population reached its maximal size in the late 1970's, being very large but made up mostly of rather old-aged animals. By 1980, the recruitment was extremely low and fecundity began to vary widely from year to year. We think that for most of the females to have become synchronized into a high production mode in some years and unusually low production in others would have been extremely improbable, unless there had been some extraneous, synchronizing factor. We suggest that the factor was disease and that the newly discovered **calicivirus** of walrus (Smith *et al.*, 1983) was the agent. Neutralizing antibodies to that virus were detected at titres of **1:10** to **1:20** in 3/40 animals (7.5%) sampled in 1976 and at **1:10** to **1:80** in 17/173 (9.8%) in 1981 (*Ibid.*; Smith, Fay, and **Skilling**, unpublished). That increase probably was not significant but illustrates the fact that the virus was widespread in the population. The virus is closely related to the San Miguel sea lion virus (**SMSV**) and vesicular exanthema of swine virus (**VESV**), known or implicated as a cause of abortion and other pathologic conditions. We suppose that it could have lowered reproductive success enough in one year (1980?) to cause synchronous production by a high proportion of females in some subsequent years.

The very low recruitment that we have detected in our compositional surveys also is difficult to rationalize as a function of age alone of the mothers. It appear to have been significantly below the predicted level, at least since the mid-1970's. It seems to be a result of extremely poor survivorship of calves, and about two-thirds of the calf mortality seems to have been taking place in the first 2 months after birth. High infant mortality is not unusual in some other **pinnipeds** in the first few weeks

after birth. Although it seems exceptional for walruses, the comparative basis for that **judgement** was gained during the rapid growth of the population in the 1950's and 60's, and it may have been representative only of that growth phase. That is, high infant mortality may be perfectly normal for a walrus population when it is at or near **K**.

The progress of the population into the future is difficult to predict, without some **modelling**. Since the late 1970's, the walruses have shown distinct signs of decreased fertility, highly variable fecundity, poor recruitment, declining physical condition, change in feeding habits, increase in average age, and increased natural mortality, all of which are characteristic of stabilization or decline (**Eberhardt** and **Siniff**, 1977). We think that the population already reached its peak in the late 1970's, and that it is on the way down again at this time. That its decline already has begun is suggested by the somewhat **larger** cohorts of young since the nadir in 1980, by the Eskimos' reports of increasing fatness, and by an apparently declining annual mortality on the **Punuk** Islands. We think that the population will continue to decline for some years, because the recruitment still is very low, the catches on both sides of the Bering Sea are still going up, and many of the adults are nearing the end of their natural life-span. The fecundity rate probably will continue to decrease for some years yet, for the majority of females are well past their prime and capable only of producing less, not more each year. But calf survival probably will rise markedly and soon result in substantial increases in recruitment. Meanwhile, the population will continue in a downward trend, until the new recruits are abundant enough to produce cohorts sufficiently large to counterbalance **the** high mortality.

Distribution and Movements

In our efforts to fill the gaps in the distributional information for the Pacific walrus population, we accomplished much less than we had hoped for in the autumn-winter period. That gap may remain forever, if a specific effort is not made to fill it.

We were able to confirm that the southeastern wintering-breeding area lies well inside the pack, in the ice-generating zone of that region, and that the sex ratio of adults in the breeding herds there is about 1 **male:10** females, as it is in the north-central (St. Lawrence) breeding area (**Fay et al.**, 1984). We assume that the breeding males in the southeastern **wintering/breeding** area are those that summer in Bristol Bay, for **Fay** and **Lowry** (1981) learned that they leave the Bay in autumn and do not return until after the breeding season has ended. We also learned that some of those males come at least as far north as the **Punuk** Islands in autumn, presumably to meet up with the southbound females, before the beginning of the breeding season. The **Rudder** and **Arakamchechen** males on the Soviet side appar-

ently perform the same kind of reverse migration in autumn (Nikulin, 1947; Krylov et al., 1964; Gol'tsev, 1968), and we presume that they are mainly the breeding males of the north-central (St. Lawrence) wintering/breeding area.

The new distributional information obtained by us and by other OCSEAP and MMS investigators (Leatherwood et al., 1983; Brueggeman et al., 1984; etc) has not contributed further to understanding of the location and extent of calving areas in spring. The population is distributed somewhat differently each year at calving time, depending on ice conditions, and the distributional information currently available is not sufficient to define the full range of that variation. We feel that better definition can only be obtained through a major, dedicated effort.

Recent reports of calving in mid-winter (Lukin, 1978; Brueggeman et al., 1984) are not reliable, since they were based on aerial surveys in which the coincidence of young animals and bloody ice were assumed to have been indicative of recent birth. Young walrus in their first winter (6-10 months old) can easily be misidentified from the air as newborn calves, and bloody ice in the wintering areas is not produced by births but by bulls who have been wounded in battles for courtship sites.

In the **Chukchi** Sea in summer, we confirmed repeatedly that the main concentrations of herds in July and August tend to be near the Alaskan and **Chukotkan** coasts, rather than in the center of the **Chukchi** Sea. We found that nearly all of the animals in both the eastern and the western **Chukchi** pack ice were females with dependent young, but males were common near shore, off Barrow, as reported earlier by Collins (1940) and Brooks (1954), and near the coast of **Chukotka**.

Feeding

The walrus is a **K-selected** predator that feeds primarily on **K-selected** prey (bivalve mollusks), most of which (1) require about as many years as the walrus to reach maturity and (2) live nearly as long as the walrus (Peterson, 1978; Fay and Stoker, 1982b). It is axiomatic that **K-selected** species with **K-selected** prey must inhabit stable environments, and that they are more likely to be upset by major changes in their environment than are the more responsive, opportunistic **r-selected** species with **r-selected** prey even **K-selected** species with **r-selected** prey (Laws, 1981b). Because of the long lag time required by both the walrus and their prey to recover from depletion, any significant change in one will have a great influence on the other. We think that the depletion of the walrus in the 1930's to 1950's allowed their prey populations, especially in the Bering Strait region, to increase greatly and attain a new equilibrium structure, made up mainly of large, old individuals. When the first large samples of

walrus stomach contents were collected for quantitative analysis at St. Lawrence and Little **Diomede** islands in 1975, those animals had been feeding in a region that had been used only during the spring and fall migrations for the previous 30 years. Since then, however, the area has been heavily used throughout the summer, as well, by several thousand males (Lowry et al., 1980). We estimate that those males increased the impact on the **food** supply there by at least 50%, and that, with the growing population of migrants as well, the total impact has more than doubled. The reported changes in feeding habits of the spring migrants from 1975 to 1982 presumably took place as a result of that greatly increased pressure on the abundant but limited supplies (Fay and Stoker, **1982a,b**).

In the western **Chukchi** Sea, however, no evidence of change was detected in a comparison of our recent findings with those of **Krylov** (1971) and **Tomilin** and **Kibal'chich** (1975), from samples collected 10 to 20 years earlier. In each case, the amount of food per stomach was very small and the prey mostly very tiny. Bivalves often were not the predominant prey. The fact that at least half of the females and young summer in the western **Chukchi** suggests that the apparently meager food supply there may not be of critical importance to them in that season. Moderate to low food intakes in summer have been suggested also by our studies of walruses in captivity, but we are not sure how far those findings can be extrapolated to wild walruses. Because wild walruses molt during the summer (Mansfield, 1958; Fay and Ray, 1968; Fay, 1982 and unpublished), however, they may tend to eat less at that time, as other pinnipeds do (**McLaren**, 1958; Mansfield, 1967).

From the records of daily food intake by captive walruses, we now know that they do not feed at a constant rate per unit of body weight at all ages, as claimed by Fedoseev (1976). Like other mammals, they reduce their proportional intake with age. The amounts consumed, relative to **body** weight, are about the same as those reported for domestic animals (**Kleiber**, 1961), being largest during early growth and smallest for maintenance in adults. During pregnancy, the females increased their intake by 40-50% over maintenance, and they also increased about 50%, during lactation. This suggests that the wild walruses, which often are both pregnant and lactating concurrently, may eat nearly twice as much food at that time as their non-pregnant, non-lactating peers (**Gehrich**, 1984).

Response to Disturbance

The walrus' basic response to disturbance amounts to escape, which usually translates into diving into the water from the ice or shore, or if already in the water, diving under the surface and swimming away. This kind of reaction is easily documented and, for that reason, would lend

itself well to experimentation. By opportunistic observation, we obtained enough data of that kind to confirm **Loughrey's** (1959) and **Bel'kovich and Yablokov's** (1961) conclusion that scent is the strongest stimulus resulting in disturbance, with or without acoustical and/or visual cues. We also obtained strong indications that response to visual disturbance depends on the size, speed, and direction of movement of the disturbing object. Sounds also seemed to vary in effect, depending more on quality than quantity.

The long-term consequences of disturbances are much more difficult to document. Soviet reports of permanent abandonment of **haulouts** due to chronic disturbance seem plausible enough, but they have not yet been supported by any data. We think that separation of mother and calf could be a very important result of disturbance by ships and aircraft, but we have no real basis for estimating its total effect. Although our data suggest that for every 100 walrus groups disturbed only about 1 calf will be abandoned, we think the real rate probably is higher, because our data were from herds that withdrew in a comparatively orderly, peaceful manner, rather than being stampeded. The more usual situation is that the ship or aircraft approaches them rapidly and noisily, with the result that the animals stampede into the water. Stampedes can result not only in abandonment but in fatal injury to the young (**Tomiliñ and Kibal'chich**, 1975; Fay and Kelly, 1980).

The ultimate effects of abandonment may be non-lethal and only slightly disruptive, if the separation is only temporary or if the calf is quickly adopted and fostered by another cow. Separation can be lethal (due to starvation) for the calf if it is not adopted or is not fostered by the adoptee. We suspect that most separations lead to death of the calf, but we have no data to support that notion. To determine the outcome of separation usually is not feasible.

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APPENDIX A.

Chi-square contingency table analysis of **parturient**, newly pregnant, and barren female walruses harvested at Little **Diomed** and **Gambell** from 1952 to 1982.

DIOMEDE	Year of catch						
	1952-58	1962-64	1965	1966-68	1979	1980	1982
N	47	61	39	35	40	102	100
Parturient							
Observed	22	31	16	17	16	15	57
Expected	19.33	25.09	16.04	14.40	16.45	41.55	41.14
Chi-sq.	0.368	1.391	0.000	0.471	0.013	16.962	6.119
New.Preg.							
Observed	18	19	16	9	16	63	26
Expected	18.56	24.08	15.40	13.82	15.79	39.88	39.48
Chi-sq.	0.017	1.073	0.024	1.680	0.003	13.411	4.603
Barren							
Observed	7	11	7	9	8	23	17
Expected	9.11	11.83	7.56	6.79	7.75	19.58	19.39
Chi-sq.	0.489	0.058	0.042	0.723	0.008	0.598	0.294
Overall chi-square = 48.343 with 12 d.f. ; P <.001							

GAMBELL	Year of catch							
	1952-61	1962-64	1965	1966-68	1975	1979	1980	1982
N	93	109	114	11	43	29	163	87
Partur.								
Obser.	77	87	101	7	33	16	36	64
Expec.	60.33	70.71	73.95	7.14	27.89	18.81	105.7	56.44
Chi-sq.	4.607	3.754	9.894	0.003	0.935	0.420	45.393	1.014
N. Preg.								
Obser.	10	16	8	3	8	6	68	9
Expec.	18.34	21.50	22.48	2.17	8.48	5.72	32.15	17.16
Chi-sq.	3.794	1.406	9.330	0.318	0.027	0.014	39.983	3.879
Barren								
Obser.	6	6	5	1	2	7	59	14
Expec.	14.33	16.80	17.57	1.70	6.63	4.47	25.12	13.41
Chi-sq.	4.842	6.939	8.989	0.285	3.229	1.434	45.715	0.026
Overall chi-square = 196.831 with 14 d.f. ; P <.001								