Fedoseev, G. A. 1982. Dynamics of range and ecological segregation of the population of Pacific walruses. Ekologiya 1982(1):45-51. (Transl. by F.H. Fay)

ABSTRACT

In the end of winter and early spring, walruses inhabit offshore polynyas, where the ice is thin and open. Their range in different years varies with the ice conditions. In the course of the annual cycle of life, walruses form associations (elementary groups, herds, coastal haulouts, and large discrete concentrations, confined to highly productive regions of the sea). Also recorded are segregations of animals by sex, age, and ecological zones.

Investigations of distribution of the Pacific walrus in the spring, summer, and autumn have been dealt with in many studies (Elliott, 1875; Allen, 1880; Clark, 1884; Suvorov, 1914; Belopol'skii, 1939; Collins, 1940, Nikulin, 1940; Fay, 1957; Yablokov and Bel'kovich, 1962; Fedoseev, 1962, 1966; Krylov, 1968; Gol'tsev, 1968; Burns, 1970). The winter habitat of walruses has not been well studied. Nevertheless, L. O. Belopol'skii (1939) suggested that walruses in winter concentrate in the vicinity of St. Lawrence Island. This was confirmed by aerovisual observations in later years, and in time, other areas of winter and early spring habitation were discovered in Bristol and Kuskokwim Bays, about Nunivak Island, along the southern coast of the Chukchi Peninsula, and on the Koryak Coast (Kenyon 1972; Braham et al., 1978; Fedoseev, 1979). As a whole, the works cited above give a full presentation of the limits of range of the walrus. Nevertheless, until now the annual variation in range has not been considered, apart from the synoptic account on this question presented by Fedoseev (1978). In that communication, based on many years of data (since 1960), as well as on literature review, an attempt was made to portray and explain the seasonal and annual dynamics of distribution of the Pacific walrus, together with estimation of the spatial arrangement of the animals and their segregation by age and sex.

DYNAMICS OF RANGE

The Pacific walrus lives for the greater part of the year on the shelf of the Bering Sea. In the summer-autumn period (June to October), its range expands to include the Chukchi Sea and, in some years, the eastern part of the East Siberian Sea and part of the western Beaufort Sea. The principal concentrations of walruses are confined to specific zones (Fig. 1).

In the end of winter and first half of spring, when the Bering Sea is maximally covered by ice, walruses tend to be centered in the southeastern part (Bristol and Kuskokwim Bays and Nunivak Island) and in the vicinity of the southern coast of the Chukchi Peninsula and St. Lawrence Island. In recent years, there have been small concentrations of walruses (up to 10-15 thousand head) on the ice from Cape Navarin to Khatyrka and farther south in Olyutorksii and Karaginskii Gulfs. Solitary walruses and groups (up to 7 to 15 animals) are sparsely distributed over all of the Bering Sea shelf, along the meandering leads that, like rivers, stretch in different directions over the whole mass of ice in the Bering Sea.

The recorded features of the distribution in the period of maximal ice cover indicate that walruses are not capable of living in vast fields of thick ice. For emersion onto the surface of the ice or for respiration between dives to the bottom for food (walruses feed on benthic animals), they can penetrate only gray (thickness 10-15 cm) and, in rare cases, gray-white (thickness 15-30 cm) ice. The most favorable conditions for them in winter and early spring are found (1) in offshore polynas, (2) amidst gray ice with an admixture of gray-white and white ice, and (3) in massifs containing large amounts of finely broken white ice. Naturally, in addition to this, an important role is played also by the presence of food.

In the Bering sea, offshore (coastal) polynyas as a rule are formed in the cold part of the year off the southern coasts of the Asiatic and American mainlands and islands, specifically in response to the predominantly northern and northwestern winds on Chukotka and northern or northeastern winds in Alaska. Under the influence of those winds, the newly formed ice is constantly carried away. In the southeastern part of the Bering Sea, thinning of the ice and formation of polynyas are aided also by the existing system of currents.

It can be assumed that good conditions for habitation by walruses in these regions are determined not only by ice conditions. Areas with persistent polynyas apparently have the best productivity as well. For this hypothesis there is a sound basis. As a result of the active atmospheric circulation, the waters in the polynyas are cooled, probably resulting in vertical circulation of the water mass, with the more dense, cooler waters saturated with oxygen sinking to the bottom. Under the influence of this process, the near-benthic layer is enriched with oxygen,

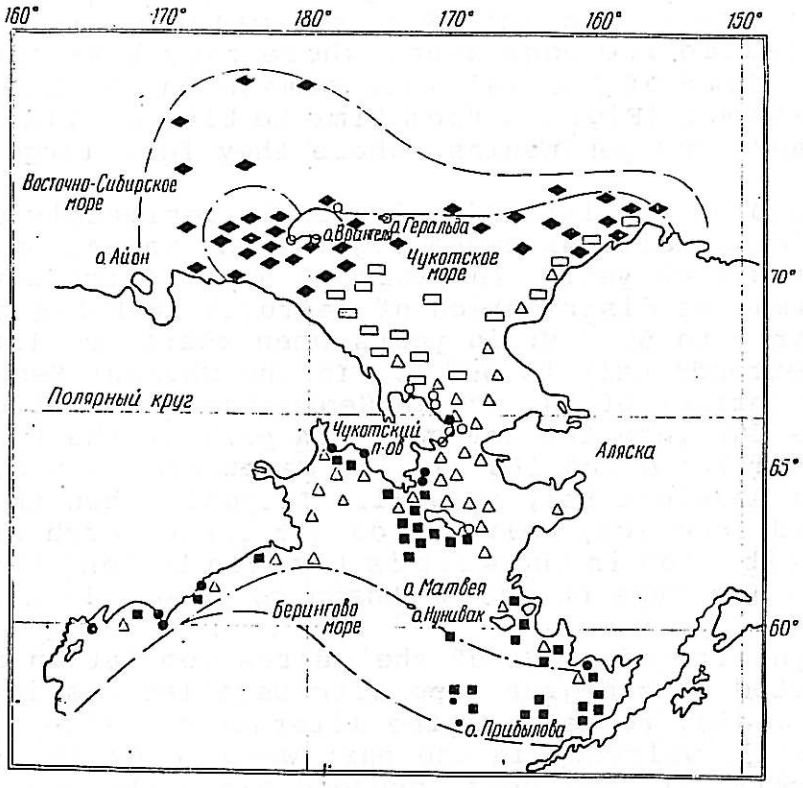

Fig 1. Dynamics of range of the Pacific walrus.

— — — limit of maximal dispersion; —.—.— limit of minimal dispersion; ● coastal haulouts filled in summer and autumn; ○ coastal haulouts formed in autumn. Areas of high concentrations of walruses: ■ in March-April; △ in May-June; ▭ in July; ◆ in August-September.

which is very significant for the bethic fauna (the basic food of walruses), ordinarily deficient in oxygen during the winter.

Thus, the presence of favorable ice and favorable feeding conditions lead to concentrations of walruses in specific areas in the end of winter and in early spring.

In the last ten days of April and in May, when the thermal and dynamic processes begin to destroy the ice, walruses make their way to Bering Strait and then into the Chukchi Sea, where they migrate in two directions: (1) along the coast of Alaska to the vicinity of Point Barrow, and (2) into the western part of the sea to Wrangel Island (Belopol'skii, 1939; Nikulin, 1940; and others). In the Chukchi Sea, the walruses as a rule reside in the so-called ice edge zone, where they have open, massive ice floes. Some of the walruses remain in the Bering Sea for the whole summer (Fig. 1), from time to time hauling out to rest on the islands and peninsulas, where they form large herds.

Inasmuch as the life of walruses is intimately connected with ice, ice conditions cause significant variation in the range of the walrus each year. In years of maximal ice coverage, the southern limit of distribution of walruses in February-March extends nearly to 55 ^{o} N; in years when there is little ice, the limit extends only to 60^{o} N. In the Chukchi Sea, at the time of maximal retreat of the ice in September, the walruses in some years range far into the northeastern part of the East Siberian Sea, reaching 74^{o} N and 166^{o} E, and penetrate into the western part of the Beaufort Sea, as well. In years when the Chukchi Sea is not freed from ice, walruses do not range north of 71^{o} N; and their distribution in the west is limited to Long Strait and in the east to Ice Cape on the northern coast of Alaska.

The dynamics of range of the walrus population are interconnected to a degree also with oscillations in size of the stock. According to data in the literature (Elliott, 1875; Suvorov, 1914), walruses in the past were found in large numbers in Karaginskii Gulf and were recorded along the eastern shore of Kamchatka, south to 52^{o} N. From those areas, they penetrated into the Okhotsk Sea, where their presence in the past is a recorded fact (Arsen'ev, 1976). Up to the period of mass destruction of walruses, which took place in 1870-1880, they penetrated into the coastal waters of northern Alaska and Canada, as far as the Mackenzie River; in the south, they appeared in large numbers at the Pribilof Islands and ranged into the Gulf of Alaska (Fay, 1957).

In years of depressed numbers, such as were recorded in the end of the 40's and beginning of the 50's of our present century, walruses very rarely were observed south of Cape Navarin. In the 1970's, with increase in numbers, however, they have occurred persistently on the coast of eastern Kamchatka (Pinigin and Pryanishnikov, 1975).

ASSOCIATION AND SEGREGATION OF WALRUSES

Walruses are gregarious animals. Their high sociality is a function of (1) the duration of their training as young (after 1 to 1.5 years of being raised on milk, the young walruses still remain a long time with their mother),(2) their collective protection from predators (polar bears and killer whales), (3) their joint involvement in obtaining food, and (4) their mutual thermoregulation (walruses warm each other during lengthy rests on ice in cold weather.)

The size of groups of walruses can vary from a few animals to thousands, depending on the time in their reproductive cycle and the season of the year. The basic group is 3 to 5 animals; in the majority of cases, these are females with their young of different ages. Analogous groups are formed, not on a sexual basis but by individuals' ties with each other. The number of animals in such groups can be somewhat more (from 7 to 10), and they can be not only of mixed sexes but of males alone.

The functional role of the primary group of walruses is in mutual harvesting of food. Such a system of feeding is connected with the fact that young walruses are not capable of harvesting food independently, because their tusks are not long enough. The practice of mutual harvesting of food apparently is instinctively fixed and conserved in mature animals; this does not, however, exclude the option of solitary feeding, as well.

The scanty makeup of the primary groups is a function of the process of mutual feeding; larger groups would inhibit rapid satisfaction. The least expense of time in feeding, followed by a long rest, are extremely important for walruses; without them they could not accumulate the thick, insulative layer of fat necessary for existence in the cold climate of the Arctic. The primary groups are most often found swimming in the feeding areas. On the ice they are rare, because walruses associate in larger companies (herds) when they rest. The functions of the herd are defense against predators and energetic economy in maintenance of constant body temperature (walruses resting on the ice lie very close together, and by that means they warm one another especially in cold weather).

The herds are formed from different numbers of elementary groups, and they can be made up of males alone or of mixed sexes. The number of animals per herd ranges from less than 50 to more than 500. The quantity of animals in a herd depends in many instances on the size of the ice floe and, possibly, on the presence of predators and how often they disturb the walruses. In the mating season the composition of the herds is influenced substantially by the polygamy of walruses (Freiman, 1940; Nikulin, 1940; Burns 1965; Fay et al., 1978). The ratio of adult males to females in the areas where mating takes place amounts to 1:10. At the same time, in peripheral areas inhabited by subadult males, the ratio of males to females was 27:1 (Fay et al., 1978). Undoubtedly, the polygamy of walruses influences the

formation of herds, not only in the season of reproduction but in other periods of the annual cycle, as well.

The haulouts of walruses on shore represent a different association than the "herd", although they are similar in a functional sense. In either case, the animals congregate to rest and their defense from predators (polar bears) depends on that association. Nevertheless, the haulouts on shore include much larger numbers of animals than those on ice, and they are formed in areas where there is no ice. On the basis of the frequency of their use, the haulouts on shore are divisible into continuous and intermittent (Nikulin, 1940; Gol'tsev, 1968). Continuous haulouts differ from intermittent, in that they (1) are occupied earlier, (2) are situated close to rich feeding areas, and (3) function for a prolonged time. Intermittent haulouts are occupied usually during the fall migration, function for a short time, and occasionally are numerous in unexpected places. For example, in the autumn of 1964 on the coast and islands of Chukotka, walruses hauled out in 30 places. With growth of the stock in recent years, the number of walruses on the haulouts has increased considerably. For example, in some instances the numbers reached 35 to 40 thousand head on Arakamchechen Island and on Cape Blossom (Wrangel Island). Furthermore, they have reestablished continuous haulouts in some locations that had not been used for many years, especially in southern areas.

For a long time, the walruses that lay on haulouts on the Bering Sea coasts of Chukotka and Alaska in summer were known to be males (Elliott, 1875; Nikulin, 1940; Fay, 1957; Yablokov and Bel'kovich, 1962). Conversely, those using haulouts on ice in the Chukchi Sea always have been predominantly females with young, with only a few males (Fedoseev, 1962; Krylov, 1968; Fedoseev and Gol'tsev, 1969).

Analysis of the age composition of animals harvested or found dead on the haulouts has shown the following: in the Chukchi Sea in summer, physically mature males (12 to 20 years of age) are found in mixed herds on ice with females and young, as well as in purely masculine groups. On Rudder and Meechkin haulouts, juvenile and subadult males (4 to 12 years of age) predominate; very old animals (over 20 years of age) also are present. Conversely, on haulouts in Bering Strait (Arakamchechen Island), physically mature males, (12 to 20 years of age), predominate.

In addition to the seasonal segregation of walruses by sex and age, there is a more complex segregation of the population into spatially separated reproductive zones, each of which has a specific set of conditions. One of these zones is located in the southeastern part of the Bering Sea (Bristol and Kuskokwim Bays and west of there); the second extends from St. Lawrence Island to the southern coast of the Chukchi Peninsula, as far as Kresta Bay. In the end of the 19th century, a concentration of walruses existed also on the Koryak Coast (Elliott, 1875; Suvorov, 1914), but whether it contained any breeding females is unknown. At

present, that concentration of walruses is regenerating, and individual females with calves have been encountered there in April (Fedoseev, 1979). The overwhelming majority of animals residing there, however, are males, which haulout on shore.

One can assume that the separate concentrations of walruses in the breeding season provide the ecological basis for some degree of genetic differentiation within the Pacific population. This hypothesis is based on the fact that the conditions for reproduction in each area are distinctive. We shall not consider all of those features here but simply note that the southeastern part of the Bering Sea is strongly influenced by the warm California current, whereas southern Chukotka and St. Lawrence Island are affected by a severe climate.

Thus, the materials presented above allow us to conclude that the dynamics of range of the walruses depend on the ice regime in the area normally occupied, and on the size of the population. The gregarious way of life, which is linked with polygamy, the collective systems for defense against enemies and for harvest of food, as well as the pecularities of thermoregulation, all contributed to association of walruses in diverse, temporary groups, the behavioral and ecological aspects of which account for the sex- and age-related morphological features of the animals.

The life of walruses is closley linked with the ice. Nevertheless, the males depend on it to a lesser degree than do the females, which have a long-term involvement in rearing the young. Therefore in the Bering and the southern part of the Chukchi Sea in summer, when there is no ice, only males are present. Because of the strength of their polygamy, those males are segregated into companies of physically mature animals, on the one hand, and of juvenile, subadult and old-aged, on the other.

The females and sexually immature animals of both sexes, together with some of the physically mature males, leave the Bering Sea in spring as the ice melts, and go to more northern areas for the summer, reaching the eastern part of the East Siberian Sea and the western part of the Beaufort Sea. In the end of October and November, those walruses migrate back to the Bering Sea, where they concentrate during the breeding season in three areas.

The marked organization and sexual segregation of the herds are tangible grounds for selective hunting of walruses, which can play a significant role in regulation of their numbers and rational utilization of their stocks.

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