Fedoseev, G. A. and V. N. Gol'tsev. 1969. Age-sex structure and reproductive capacity of the population of the Pacific walrus. Zool. Zhur. 48:407-413. (transl. by F. H. Fay)

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As a result of intensive harvest of the walrus in the 19th century and first half of the 20th century, its numbers everywhere were greatly reduced. At present, judging from the literature (Fay, 1957; Scheffer, 1958; Mansfield, 1959; Fedoseev, 1962 etc.), the number of walruses throughout the Arctic does not exceed 100 thousand. walruses in the Despite the fact that the commercial cropping of USSR is now on the verge of prohibition, the problem of protecting and restoring . these animals remains extremely essential. The fact of the matter is that the harvest of walruses is done by the native population, and discontinuance of it is not possible, because the meat of the walrus is an essential food product for the Eskimos and coastal Chukchi in a number of localities. Further utilization of walruses must be carried out with calculation of the biologically sound, rate of harvest. And this in turn requires detailed study of a series of problems concerning the dynamics of the species.

In this report an attempt is made to characterize the age-sex structure, reproductive capacity and segregation of the Pacific walrus (Odobaenus rosmarus divergens Illiger, 1815) population.

On the basis of work under our supervision conducted on ice and coastal haulouts of walruses in the Bering and Chukchi seas, materials on the age composition of the harvest were gathered in the autumn of 1964 (teeth from 541 animals), as well as some data from the literature.

Many investigators (Arsen'ev, 1927; Belopolskii, 1939; Freiman, 1940; Nikulin, 1940; Yablokov and Bel'kovich, 1962; Krylov, 1965; Collins, 1940; Fay, 1957; etc.) noticed that the herds of walruses on the ice and on coastal hauling grounds in the summer-autumn period were not of uniform composition. They observed two basic types of congregations: "mixed", composed of females with young and immature animals of both sexes, and "all male", in which were found only adult males. They determined also that, in summer, the Anadyr Gulf (Rudder and Meechken hauling grounds) and the northeastern coast of the

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Chukchi Peninsula are inhabited principally by males. It is recorded that only males lay on the Rudder hauling ground (Arsen'ev, 1927; Ni kulin, 1940; Yablokov and Bel'kovich, 1962, etc.). V. I. Krylov (1966) determined that the males with lumpy skin ("shishkari") are adults, and that on Rudder hauling ground, up to 8 - 10% of the animals were young up to 3 years old. Part of the males disperse into the northwestern Chukchi sea (near arangell Island), where females and immature animals of both sexes also reside.

Thanks to the development of a method for determination of age of walruses by the number of cementum layers in the teeth (Chapskii, 1941; Mansfield, 1959; Krylov, 1965; etc.), it has become possible to discriminate in greater detail the composition of the walrus population on the basis of analysis of the harvest. Our data on the age composition of harvested males (Fig. 1) demonstrate that, on the Rudder hauling ground in August-September, the

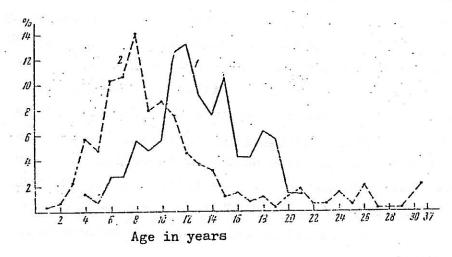


Fig. 1 Age composition of harvested walruses (males) on Blossom (1) and Rudder (2) coastal hauling grounds.

animals are predominantly 6 to 11 years old (about 60%), while at the same on Wrangell Island (Blossom hauling ground), up to 73% of the animals are 11 to 19 years old. It is interesting that, on the Rudder hauling ground, up to 10% are composed of old males of ages 21 to 37 years old, which were nearly absent on the wrangell hauling ground.

The data of V. I. Krylov (1965) on the age composition of walruses on the ice in 1960 to 1962 (Fig. 2) attest to the fact that, p. 409 in the western part of the Chukchi Sea, males 11 to 20 years old prevailed.

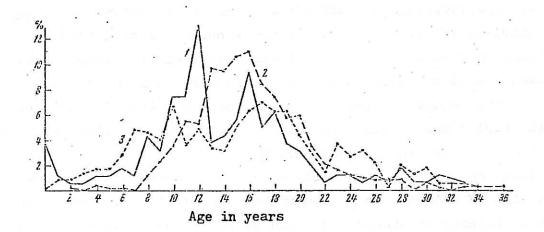


Fig. 2 Age composition of males in harvests from the ice haulouts in the Chu kchi sea (data from V. I. Krylov, 1965). 1-1960, 2-1961, 3-1962.

Inasmuch as the data on age composition of male walruses were obtained from analysis of the harvests, naturally the question arises: Are the indicated differences the result of selection in the harvest, or do the walruses in the different regions differ in age composition? V.I. Krylov (1965) writes that, in the Chukchi Sea, the hunters endeavor to take the largest animals. As a result of that, immature animals are less well represented than the mature animals in the kill. Moreover, V.I. Krylov noted that old ones of both sexes occurred singly in the kill in the northwestern Chukchi Sea.

Certainly, selection has a place in the harvest of walruses, but this hardly can be a major cause of so clear a difference in age composition of those taken from the Rudder hauling ground, on the one hand, and from the Blossom hauling ground and ice haulouts of the western part of the Chukchi Sea, on the other. It seems to us that, under the circumstances of the harvest, when walruses lie very close together without any segregation by age, the hunters would have difficulty shooting animals of a specific age (for example, only 6 to 10 years or 11 to 13 years), for the difference in size of these animals is not great

(10 to 30 cm). Whereas walruses 6 to 10 years of age are taken in large numbers in the vicinity of Rudder Spit, those

shot in the Chukchi Sea are predominantly 11 to 15 years of age. This difference in composition is shown in Fig. 1. Evidently, selection took place only in that the hunters in the western part of the Chukchi Sea, as well as in the Rudder area harvested almost no immature animals 1 to 5 or 6 years of age.

It is appropriate to recall the remark of I. Veniaminov (<u>fide</u> P.G. Nikulin, 1940), who, in characterizing the distribution of walruses in Alaska in summer, noted that it was "extremely remarkable that the walruses coming to Alaska are essentially all males, both young and very old, and that females never have been seen among them." Further, P. G. Nikulin (1940) was inclined to think that this congregation was made up of animals not participating in mating.

Thus, one probably can speak of definite segregation of the Pacific population of walruses in the summer-autumn period. In Anadyr Gulf (in the vicinity of Rudder and Meechken spits) and, evidently, in Alaska in summer remain principally maturing males or young adults that have not yet reached physical maturity (6 to 11 yrs), as well as very old males 20 years old and older. In small quantities with them remain immature animals 3 to 5 years old. To the western part of the Chukchi Sea (vicinity of Wrangell Island) go the females, physically mature males, and immature animals of both sexes. In addition, adult males on the ice haulouts not infrequently form separate groups.

Data on the representation of age classes in different populations are scarce. K.K. Chapskii (1936) attempted to determine the magnitude of the annual increment in the Atlantic population. He thought that the adults comprised 50% of the total population and that only half of the adult females gave birth annually (according to K.K. Chapskii, females mature at 4 to 6 years of age, males a year later). From such original data, K.K. Chapskii determined that the annual production of offspring did not exceed 12.5%, and with allowance for sterility and natural mortality, not more than 10%.

S. Yu. Freiman (1940), on the basis of examination of a large group of Pacific walruses, concluded that ratio of age groups was: adults 59%, immatures 24%, young 17%. Sexual maturity in the females, according to S. Yu. Freiman, sets in in the third year of age; males mature at 5 to 6 years.

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V. I. Krylov (1965) determined that the annual increment of the Pacific walrus population comprises not more than 6.3%. The proportions of age-sex groups in mixed herds (according to V. I. Krylov) is: adults 71.1%, of which 36% are females and 35.1% are males; immatures of both sexes amount to 28.9%. In his ultimate work, V.I. Krylov (1967) brought forth new data on the annual increment of the walrus population as 11.2%. In addition, he assumed that the adult part of the stock comprised 70% and that the proportion of males to females was 1:1.

Sexual maturity of walruses, according to the data of V. I. Krylov (1967), sets in in males at the age of 7 to 9 years (in the majority at 8 yrs.); in females at the age of 6 to 8 years (but the greatest part of them matures at 7 yrs. of age). Only 35% of the mature females give birth each year.

According to the data of foreign investigators, the crude birth rate of the Pacific walus is 11% (Scott et al., 1959) to 14% (Burns, 1965); in the Atlantic walrus it is 8% (Mansfield, 1959). It should be noted that, according to Burns' data, about 47% of the adult females give birth each year, i.e. 12% more than indicated by V. I. Krylov's data.

We attempted to define the rates of birth and of recruitment to the adult population of Pacific walruses on the basis of the shape. of the curve of age structure of the population, which in turn was calculated from the age composition of the harvest. The proportion of males and females in the populations, as already noted above, comprises 1:1. Therefore the composition of the population is the same if we construct the curve on the basis of the data of age composition of either the males or the females, separately or together. Our collections of aged material were of males, and on that basis, we determined the structure of the population. First, we combined the data of age composition of the Anadyr sample with that from the western Chukchi Sea. By combination of these materials, we determined the proportion of age groups, representative of the adult part of the stock, that is the mature animals. Further, utilizing the data of Burns (1965) and V. I, Krylov (1967) on the annual amount of fertile females, we determined the birth rate (15 to 17% of the entire population). However, the highest mortality apparently occurs in the first year of life of walruses, as in other pinnipeds. For example, the natural mortality in the first

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year of life of hooded seals is more than 50% (Rassmusen, 1961); in the fur seal it is 40% (Severtsov, 1941); and in the ringed seal the average is 35% (Fedoseev, 1966).

The age of sexual maturity in the walrus, if we accept as the mean value, that calculated on the basis of the data of V. I, Krylov and Burns, is 5 to 8 years in females (the majority at 6 to 7 years), and is 6 to 9 years in males, i.e. nearly the same as in the ringed seal (EcLaren, 1958; Fedoseev, 1964; Nazarenko, 1965). The maximal longevity of walruses is 37 to 38 years; in ringed seals of the Okhotsk sea it is 32 years, and in the Canadian sector of the Arctic, 41 years (McLaren, 1958). Apparently, the magnitude of natural mortality in walruses also does not differ greatly from that of the ringed seal. Therefore, we assume that the mortality in the first year of life of walruses is the same as in the ringed seal ie35%. Possibly, this quantity is somewhat high for walruses.

Knowing the quantity of offspring and the natural mortality in the first year of life, we determined the relative number of yearlings in the population. Further, we estimated the relative quantity of animals 2 to 7 years of age, allowing that the population curve of walruses in the immature part of the population represents an exponential curve, as in other long-lived species of mammals (Severtsov, 1941). The curve of the adult part of the population was constructed from the mean of the data on age composition of the harvest sample. As a whole, the overall population curve of the Pacific walrus is of the exponential type (Fig. 3(1)).

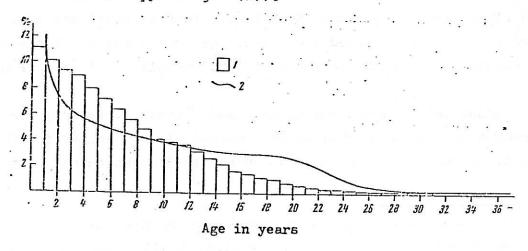


Fig. 3. Age structure of the Pacific walrus population.

1 - composition of the overall population;

2 - probable structure in the absence of harvests.

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For a long time, the effect of intensive harvests on the age structure of the walrus population has been juvenization, because those cropped were principally adults.

For this reason, the age structure of the population has been considerably modified. In the absence of harvests or with non-selective harvests, the population age curve of walruses apparently would have a curve of the intermediate type \frac{1}{(\text{Fig. 3(2)})}. The difference between the exponential curve and the curve of intermediate type is that the natural mortality of adults in the curve of the latter type is considerably lower than in the immature animals. The intermediate type, the relative number of adults in the stock is larger. However, with the exponential curves, comparatively more immature animals would be present.

It cannot be assumed that the proportions of the age classes in the stock always are accurate representations of the typical curve of composition, for the magnitude of each age class, although relatively stable over a long period, is not the same from year to year. In this connection, the curves (of age structure), which we have shown in Fig. 3 characterize the average age composition of the population over a specific period, but not in one given year.

In the modern population of the walrus, the magnitude of the estimated annual increment of newborn young, according to our calculations, amounts to 15 to 17%, and for animals one year old, the mean 11% of the population. Recruitment to the adult part of the population does not exceed 9.0%, i.e. the productive females are replenished by approximately 4.5% of the overall population each year.

Taking into account the natural and harvest mortality, the actual increment to the stock will be considerably less than our indicated amount. According to the data of Burns (1965), the annual mortality

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^{1/} In designation of curves of components of the population, we utilize the terminology of S. A. Severtsov (1941), who for mammals and a series ofother animals described three basic types of curves; exponential (curve of exponential function), logistic or s-shaped, and intermediate, occupying a middle position between the two preceding types of curves.

of the walrus averages 12 to 13%, on which basis, the increment to the population would comprise not more than 3%. With addition of the overall harvest losses, the mortality evidently exceeds the increment.

In the period from 1957 to 1960, the number of the Pacific walruses was estimated at 50 thousand head (Fedoseev, 1962; Fay, 1957). According to Brooks (1963) and Burns (1965), the number amounted to 70 to 90 thousand. If we take the average number of animals to 70,000, then the increment of the stock with calculation of natural mortality stands at 2.1 to 2.8 thousand head.

The mean annual catch amounts to 2.6 thousand head (in the territorial waters of the USSR it is about 1.1 thousand; in coastal Alaska, about 1.5 thousand). Moreover, at the time of harvest, up to 30% of the animals sink. Therefore, the overall harvest removal from the stock amounts to not less than 3 thousand head.

Thus, the number of animals in the Pacific walrus population apparently continues to be slowly reduced.

Certainly we cannot pretend that our computations are precise, but they, nevertheless, attest to the tense state of the walrus stocks. On the whole, there is a need for more precise enumeration of the animals in coming years, monitoring repeatedly by the method of aerial photographic census. $\frac{2}{}$ Also required are more precise data on the magnitude of natural mortality. The coefficients of natural mortality obtained by American investigators apparently are too high, for they were calculated on basis of aged material from a population strongly affected by harvests. If the coefficient of natural mortality is calculated from the maximal age in the sample (method of F. I. Baranov, modified by P. V. Tiurin, 1963), then it does not exceed 8 to 10 per cent (maximal age 40 years), on the average. However, this estimate of natural mortality cannot be unconditionally accepted, since the maximal age under the influence of the harvest also is lowered. In addition to calculation of population size, studies of the age structure of the population should be continued, for this offers the best basis for calculation of the magnitude of the increment and of diminution of the stock.

^{2 /} the first calculation of walruses by the method of aerial photographic census was conducted in 1960 (Fedoseev, 1962).

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AGE-SEXUAL STRUCTURE AND ABILITY OF REPRODUCTION IN THE PACIFIC WALRUS POPULATION

G. A. FEDOSEEV and V. N. GOLTZEV

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Summary

In the modern walrus population the increment amounts to 15—17% of the whole population numbers, as calculated by new born walruses, and to 11%, as calculated by yearlings. The increment of the sexually mature specimens amounts to 9%. While taking into account the natural mortality the increment in the walrus population does not exceed 3%. In territorial waters of the USA and of the USSR 2.5—3 thousands of walruses are caught per year what exceeds slightly the increment.

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G. A. Fedoseyev, and V. N. Goltsev

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возрастно-половая структура И ВОСПРОИЗВОДИТЕЛЬНАЯ СПОСОБНОСТЬ ПОПУЛЯЦИИ ТИХООКЕАНСКОГО МОРЖА

Г. А. ФЕДОСЕЕВ и В. Н. ГОЛЬЦЕВ

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В современной популяции моржа величина пополнения, исчисляемая по новорожденным, составляет 15—17%, а по зверям годовалого возра--11% от численности всей популяцин. Пополнение половозрелой части популяции составляет 9%. С учетом естественной смертности прирост в популяции моржа не превышает 3%. В территориальных водах СССР и США добывается 2,5—3 тыс. голов моржа в год, что незначительно превышает прирост.

В результате интенсивного промысла моржа в XIX и первой половине XX вв. его численность повсеместно сильно сократилась. В настоящее время, судя по литературным данным (Fay, 1957; Scheffer, 1958; Mansfield, 1959; Федосеев, 1962 и др.), численность моржей во всей Арктике не превышает 100 тыс. голов. Несмотря на то, что промышленная добыча моржей как в СССР, так и за рубежом запрещена, вопрос об охране и восстановлении численности этих животных остается весьма актуальным. Дело в том, что промысел моржей производится местным населением, и прекращение этого промысла невозможно, так как мясо моржа для эскимосов и береговых чукчей в ряде мест является одним из основных продуктов питания. Дальнейшее использование моржей должно производиться с учетом биологически обоснованных норм добычи. А это, в свою очередь, требует детального изучения ряда вопросов динамики численности вида.

В настоящем сообщении делается попытка характеристики возрастно-половой структуры, воспроизводительной способности и дифференциации популяции тихоокеанского моржа (Odobaenus rosmarus diver-

gens Illiger, 1815).

В основу работы положены наши наблюдения, проведенные на ледовых залежках и береговых лежбищах моржа в Беринговом, Чукотском морях, материалы по возрастному составу побоек, собранные осенью 1964 г. (зубы от 541 животного), а также некоторые литературные данные.

Многие исследователи (Арсеньев, 1927; Белопольский, 1939; Фрейман, 1940; Никулин, 1940; Яблоков, Белькович, 1962; Крылов, 1965; Collins, 1940; Fay, 1957 и др.) обратили внимание, что образуемые моржами ледовые залежки и береговые лежбища в летне-осенний период не одинаковы по составу животных. Наблюдаются два основных типа скоплений: смешанные, состоящие из самок с детенышами и неполовозрелых особей обоего пола; самцовые, в которых встречаются только взрослые самцы. Установлено также, что в летнее время в Анадырском заливе (Руддерское, Меечкенское лежбище) и у северо-вос-

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Age-sex structure and reproductive capacity of the Pacific walrus population

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In the present walrus population, the recruitment based on the number of newborn amounts to 15—17%, and the recruitment based on the number of one-year-olds amounts to 11% of the total numbers of the population. The recruitment of the sexually mature part of the population is 9%. With the natural mortality taken into account, the increment in the walrus population does not exceed 3%. In the territorial waters of the USSR and USA, 2500—3000 walruses are killed annually; this number is slightly higher than the increment.

As a result of intensive exploitation of the walrus in the 19th and the first half of the 20th centuries, its numbers have greatly diminished everywhere. Judging from the literature (Fay, 1957; Scheffer, 1958; Mansfield, 1959; Fedoseyev, 1962, etc.), the numbers of the walrus throughout the Arctic today do not exceed 100,000 head. Despite the fact that commercial utilization of the walrus has been banned both in the USSR and abroad, the question of protecting and restoring the numbers of these animals is still a rather pressing one. The point is that the walrus is utilized by the local population, and it is impossible to stop this, since walrus meat is one of the staple foods of the Eskimo and coastal Chukchi in some places. Future utilization of the walrus should be carried out only on

the basis of biologically substantiated rates of harvesting. This calls for a detailed study of the population dynamics of this species.

This paper is an attempt to characterize the age—sex structure, reproductive capacity and differentiation of the Pacific walrus population (Odobaenus rosmarus divergens Illiger, 1815).

The paper is based on our own observations carried out at the ice rookeries and coastal hauling-out grounds of the walrus in the Bering and Chukchi seas, material on the age composition of walrus takes (teeth from 541 animals, collected in the autumn of 1964), as well as data from the literature.

Numerous researchers (Arsenyev, 1927; Belopolsky, 1939; Freiman, 1940; Nikulin, 1940; Yablokov, Belkovich, 1962; Krylov, 1965; Collins, 1940; Fay, 1957, etc.) have noted that the ice rookeries and coastal hauling-out grounds formed by the walruses during the summer-autumn differ in the composition of the animals. Two main types of groups are noted, namely mixed groups consisting of females with their pups and sexually immature individuals of both sexes, as well as male groups consisting exclusively of adult males. It has also been established that mainly male walruses are found in the Anadyr Gulf (Rudder, Meyechken hauling-out grounds) and on the northeastern shores of the Chukchi Peninsula during the summer. It has been noted that only adult males haul out at the Rudder grounds (Arsenyev, 1927; Nikulin, 1940; Yablokov, Belkovich, 1962, etc.). V.I. Krylov (1966) has established that along with the adult males, up to 8-10% of the herd at the Rudder grounds consists of juveniles up to 3 years of age. Some of the males migrate to the northwestern part of the Chukchi Sea (near Wrangel Is.), which is also inhabited by females with their pups and sexually immature individuals of both sexes.

Thanks to the method of age determination by tooth cement layers (Chapsky, 1941; Mansfield, 1959; Krylov, 1965, etc.), a more detailed differentiation of the walrus population based on analysis of walrus takes has become possible. Our data on the age composition of the harvested male walruses (see ,Fig. 1) show that 6—11-year-old animals predominate (approximately 60%) at the Rudder grounds in August—September, whereas 11—19-year-olds comprise up to 73% of the animals on Wrangel

Is. (Blossom hauling-out grounds) during the same period. An interesting fact is that old males 21—37 years of age, which are hardly ever encountered on Wrangel Is., constitute up to 10% of the walruses at the Rudder grounds.

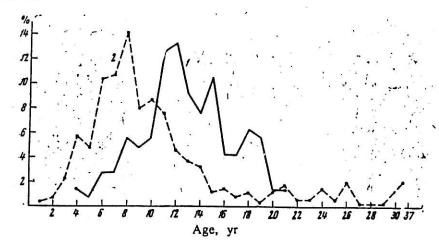


Fig. 1. Age composition of the takes of male walruses at the Blossom (1) and Rudder (2) hauling-out grounds

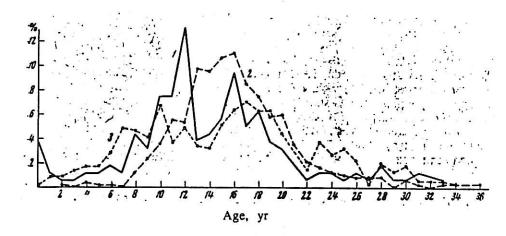


Fig. 2. Age composition of the takes of male walruses at ice rookeries in the Chukchi Sea (based on the data of V.I. Krylov, 1965): 1 - 1960, 2 - 1961, 3 - 1962

V.I. Krylov's data (1965) on the age composition of the walruses at the ice rookeries during 1960—1962 (Fig. 2) indicate that 11—20-year-old animals also predominate among the male walruses in the western part of the Chukchi Sea.

Since the data on the age differentation of male walruses are based on the analysis of walrus takes, one naturally wonders whether these differences in the age composition of walruses from one area to the next are the result of the selectiveness of hunting. V.I. Krylov (1965) believes that the hunters of the Chukchi area strive to get the largest animals. As a result of this, fewer young animals and more adults are killed. Krylov also notes that old male and female walruses are only occasionally encountered among the animals killed in the northwestern parts of the Chukchi Sea.

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There is no doubt that selectivity plays a certain role in the walrus hunt, but it is not likely to be the main cause of such a sharp difference in the age composition of the walrus takes from the Rudder grounds on the one hand, and those from the Blossom grounds and ice rookeries of the western part of the Chukchi Sea on the other. In our opinion, when the walruses are crowded together without any age differentiation, it is difficult for the hunter to shoot off animals of a specific age (e.g. only 6-10-year-olds or 11-13-year-olds), since the difference in their size is insignificant (10-30 cm). Meanwhile, 6-10-year-old walruses were harvested in larger numbers near the Rudder grounds, while 11-15-yearolds predominated in the takes from the Chukchi Sea. It is the animals of these age groups that account for the differences in the composition of the takes graphed in Fig. 1. The selectiveness of the hunt apparently consisted only in the fact that hardly any sexually immature animals (i.e. from 1 to 5-6 years of age) were killed by the hunters either in the western part of the Chukchi Sea or in the Rudder area.

It is appropriate to mention the comments of I. Veniaminov (after P.G. Nikulin, 1940) who, characterizing the summer distribution of walruses in Alaska, notes that the walruses landing in Alaska are essentially all males, juveniles and aged animals, never females. Furthermore, P.G. Nikulin (1940) is inclined to believe that these groups are formed by bachelor walruses which do not participate in mating.

Consequently, there probably is some differentiation of the Pacific walrus population during the summer—autumn period. Predominantly maturing males or young sexually mature walruses that are not quite physically mature (6—11 years old), as well as aged males 20 years of age and older, remain in the Anadyr Gulf (Rudder area and the Meyechken spit) and apparently along the Alaskan coast for the summer. A few sexually immature walruses (3—5 years old) remain with them. The

females, physically mature males and sexually immature male and female walruses migrate to the western part of the Chukchi Sea (around Wrangel Is.). At the same time, adult males often form separate groups at the ice rookeries.

Data on the ratio of different age groups in various populations are scarce. K.K. Chapsky (1936) attempted to determine the annual increment in the Atlantic walrus population. He assumed that the sexually mature animals made up 50% of the total population, and that only one-half of the females bore pups annually (according to Chapsky, female walruses mature in the fourth—sixth year of life, and male walruses mature a year later). With these initial data, Chapsky determined that the annual number of offspring does not exceed 12.5%, and with non-breeders and natural mortality taken into account, not more than 10%.

S.Yu. Freiman (1940), on the basis of a study of a large group of Pacifical walruses, quotes the ratio of age groups as 59% adults, 24% sexually immature individuals, and 17% juveniles. According to S.Yu. Freiman, sexual maturity sets in at the age of 3 year in female walruses, and 5—6 years in male walruses.

V.I. Krylov (1965) determined that the increment of the Pacific walrus stock amounted to not more than 6.3% of the total herd. The age—sex ratio in the mixed walrus rookeries (according to V.I. Krylov) was 71.1% sexually mature animals (36% females and 35.1% males) and 28.9% sexually immature walruses of both sexes. In his most recent paper (1967), V.I. Krylov presented new data on the increment of the walrus population, which was 11.2% of the total herd. At the same time, he indicated that the sexually mature part of the herd made up 70% of the animals with a 1:1 ratio of males and females.

According to V.I. Krylov (1967), sexual maturity in walruses sets in at the age of 7—9 years (mostly 8 years) in male walruses, and at the age of 6—8 years in female walruses (but the greater part of the females begins to breed at the age of 7). Only 35% of the sexually mature females bear pups annually.

According to the data of foreign authors, the number of offspring amounts to 11% (Scott et al., 1959) and 14% (Burns, 1965) in the Pacific walrus, and to 8% of the whole population in the Atlantic walrus

(Mansfield, 1959). According to Burns, about 47% of the sexually mature females breed annually (12% more than indicated by V.I. Krylov).

We have attempted to determine the number of offspring and recruitment of the sexually mature part of the Pacific walrus stock by plotting a population curve which, in turn, was based on the age composition of the walrus takes. As we have already noted, the male/female ratio in the walrus population is 1:1. Therefore, the type of the walrus population curve will not change if we plot a curve on the basis of the age composition of the males and females separately or together. In our samples, the age material pertained mostly to the males, and the structure of the population was plotted on the basis of this material. At first, we combined the data on the age composition of the walrus takes from the Anadyr Gulf and from the western part of the Chukchi Sea. Combined, this material allows us to establish the age-group ratio characteristic of the sexually mature part of the herd, or, in other words, the population curve for the sexually mature animals. Later, having used Burns' (1965) and Krylov's data (1967) on the annual number of pupbearing females, we determined the number of offspring (15-17% of the total population). However, in walruses, as in other pinnipeds, the highest mortality is observed during the first year of life. For example, the natural mortality in the first year is over 50% in the hooded seal (Rassmusen, 1961), 40% in the fur seal (Severtsov, 1941), and an average 35% in the ringed seal (Fedoseyev, 1966).

The age of onset of sexual maturity in walruses, if we go by the averages based on Krylov and Burns' data, will be 5—8 years (mostly 6—7 years) for the female walruses, and 6—9 years for the males, i.e. almost the same as in the ringed seal (McLaren, 1958; Fedoseyev, 1964; Nazarenko, 1965). The maximum known age is 37—38 years for the walrus, 32 years for the ringed seal of the Sea of Okhotsk, and 41 years for the seal of the Canadian sector of the Arctic (McLaren, 1958). Apparently, the natural mortality of the walrus does not differ much from that of the ringed seal. Therefore, we have accepted the mortality of the walrus during its first year of life as equal to that of the ringed seal, i.e. 35%. This figure may be slightly overestimated for the walrus.

Knowing the number of offspring and the natural mortality in the first years of life, we determined the relative abundance of yearlings in the population. We later calculated the relative number of 2—7-year-olds, assuming that the population curve in the sexaully immature part of the walrus population is an exponential curve as in other long-lived species of mammals (Severtsov, 1941). The population curve of the sexually mature part of the walrus population was plotted on the basis of the average data on the age composition of the walrus takes. On the whole, the population curve for the present Pacific walrus population proved to be an exponential curve (Fig. 3, 1).

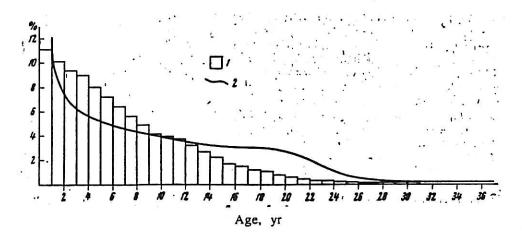


Fig. 3. Age structure of the Pacific walrus population

1 - present population, 2 - conjectural structure with no hunting

Under the effect of prolonged intensive exploitation of the walrus, the age structure of the walrus population has undergone significant rejuvenation, since predominantly adult animals were killed off. Because of this, the type of the population curve has changed considerably. In the absence of hunting, or with nonselective hunting of the walrus, the population curve for the walrus is apparently of the intermediate type! (Fig. 3, 2). The difference between the exponential curve and the intermediate curve lies in the fact that the natural decrease in the sexually

¹We haved used S.A. Severtsov's terminology (1941) for the walrus population curves. He described three main types of curves for mammals and a number of other animals: the exponential curve (curve of the exponential function), the logistic or S-shaped curve, and the intermediate curve which lies between the two previous types.

mature part of the herd by the intermediate type of curve progresses much more slowly than in the sexually immature part of the population. Because of this, the relative abundance of sexually mature animals in the herd is greater. With the exponential curve, there is a certain relative increase in the number of sexually immature animals, which alters the ratio.

One should not assume that the ratio of individual generations in the herd will always give the correct population curve of this or that type, since the size of individual generations, though relatively stable over a long period, cannot be absolutely invariable. Therefore, the types of population curves (age structure) presented in Fig. 3 characterize the mean age composition of the population for a given period, not for any year as a whole.

In the present walrus population, the recruitment, which is calculated by the number of newborn, amounts to 15—17% by our estimates, while the recruitment based on the number of yearlings averages 11% of the total population. The recruitment of the sexually mature part of the population does not exceed 9.0%, i.e. the relative recruitment of breeding females is approximately 4.5% of the total numbers of the population.

If we take the natural mortality and the number of animals killed by hunters into account, the actual increment of the herd will be substantially smaller than indicated by our recruitment figures. According to Burns (1965), the annual mortality of the walrus averages 12—13%. With this taken into account, the increment of the walrus population will not exceed 3%; if we take into account the number of animals killed by hunters, the total losses will apparently exceed the increment.

During 1957—1960, the Pacific walrus population was estimated at 50,000 head (Fedoseyev, 1962; Fay, 1957). According to Brooks and Burns (J.W. Brooks, 1963; J.J. Burns, 1965), the Pacific walrus population numbered 70,000—90,000 head. If we take 70,000 as the average number of walruses, the increment of the herd with natural mortality taken into account will be 2100—2800 head.

The average annual take by hunters is 2600 head (about 1100 in the territorial waters of the USSR, about 1500 off the coast of Alaska). In addition, up to 30% of the animals drown during the hunting season.

Therefore, the total removal from the herd during the hunting season amounts to at least 3000 head.

We can therefore say that the numbers of the Pacific walrus population are obviously continuing to decrease slightly.

Of course, we do not claim that our estimates are highly accurate, but nevertheless, they do indicate that the walrus stocks are dwindling. To get a more accurate estimate of their numbers, the walrus count should be repeated by aerial photographic survey within the next few years2. The data on natural mortality also require verification. The coefficients of natural mortality derived by American researchers are apparently overestimated, since they were calculated on the basis of the age data for a population highly rejuvenated by hunters. If we were to calculate the coefficient of natural mortality by the maximum age in the samples (F.I. Baranov's method modified by P.V. Tyurin, 1963), its value would probably not exceed 8-10% on the average (maximum age 40 years) for the walrus population. However, even this value of natural mortality cannot be accepted unconditionally, since the maximum age has also decreased under the influence of hunters. In addition to population surveys, we should continue to study the age structure of the walrus population; this would make it possible to obtain a well-founded calculation of the increment and losses in the herd.

²The first aerial photographic survey of walruses was carried out in 1960 (Fedoseyev, 1962)

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З ООЛОГИЧЕСКИЙ ЖУРНАЛ

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ВОЗРАСТНО-ПОЛОВАЯ СТРУКТУРА И ВОСПРОИЗВОДИТЕЛЬНАЯ СПОСОБНОСТЬ ПОПУЛЯЦИИ ТИХООКЕАНСКОГО МОРЖА

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В современной популяции моржа величина пополнения, исчисляемая по новорожденным, составляет 15—17%, а по зверям годовалого возраста—11% от численности всей популяции. Пополнение половозрелой части популяции составляет 9%. С учетом естественной смертности прирост в популяции моржа не превышает 3%. В территориальных водах СССР и США добывается 2,5—3 тыс. голов моржа в год, что незначительно превышает прирост.

В результате интенсивного промысла моржа в XIX и первой половине XX вв. его численность повсеместно сильно сократилась. В настоящее время, судя по литературным данным (Fay, 1957; Scheffer, 1958; Mansfield, 1959; Федосеев, 1962 и др.), численность моржей во всей Арктике не превышает 100 тыс. голов. Несмотря на то, что промышленная добыча моржей как в СССР, так и за рубежом запрещена, вопрос об охране и восстановлении численности этих животных остается весьма актуальным. Дело в том, что промысел моржей производится местным населением, и прекращение этого промысла невозможно, так как мясо моржа для эскимосов и береговых чукчей в ряде мест является одним из основных продуктов питания. Дальнейшее использование моржей должно производиться с учетом биологически обоснованных норм добычи. А это, в свою очередь, требует детального изучения ряда вопросов динамики численности вида.

В настоящем сообщении делается попытка характеристики возрастно-половой структуры, воспроизводительной способности и дифференциации популяции тихоокеанского моржа (Odobaenus rosmarus divergens Illiger, 1815).

В основу работы положены наши наблюдения, проведенные на ледовых залежках и береговых лежбищах моржа в Беринговом, Чукотском морях, материалы по возрастному составу побоек, собранные осенью 1964 г. (зубы от 541 животного), а также некоторые литературные данные.

Многие исследователи (Арсеньев, 1927; Белопольский, 1939; Фрейман, 1940; Никулин, 1940; Яблоков, Белькович, 1962; Крылов, 1965; Collins, 1940; Гау, 1957 и др.) обратили внимание, что образуемые моржами ледовые залежки и береговые лежбища в летне-осенний период не одинаковы по составу животных. Наблюдаются два основных типа скоплений: смешанные, состоящие из самок с детенышами и неполовозрелых особей обоего пола; самцовые, в которых встречаются только взрослые самцы. Установлено также, что в летнее время в Анадырском заливе (Руддерское, Меечкенское лежбище) и у северо-вос-

точных берегов Чукотского п-ова обитают в основном самцы. Отмечается, что на Руддерском лежбище залегают только взрослые самцы (Арсеньев, 1927; Никулин, 1940; Яблоков, Белькович, 1962 и др.). В. И. Крылов (1966) установил, что, наряду со взрослыми моржами— «шишкарями», на Руддерском лежбище до 8—10% поголовья составляют молодые до 3 лет. Часть самцов уходит в северо-западный район

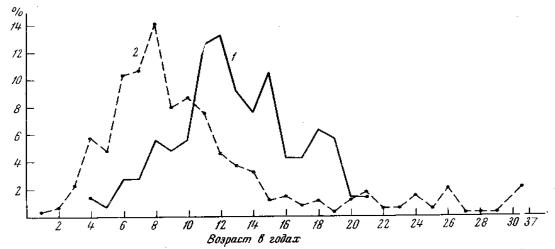


Рис. 1. Возрастной состав побоек моржей (самцы) на Блоссомском (1) и Руддерском (2) береговых лежбищах

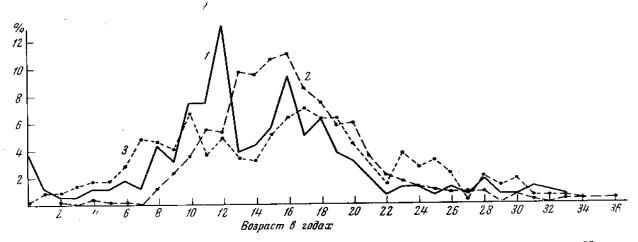


Рис. 2. Возрастной состав самцов в побойках моржа на ледовых залежках в Чукотском море (по данным В. И. Крылова, 1965) I=1960 г., 2=1961 г., 3=1962 г.

Чукотского моря (вблизи о-ва Врангеля), где обитают также самки с детенышами и неполовозрелые животные обоего пола.

Благодаря разработке методики определения возраста моржа по наслоению цемента зубов (Чапский, 1941; Mansfield, 1959; Крылов, 1965 и др.) стало возможным более детально разобраться в дифференциации популяции моржа на основе анализа побоек. Наши данные по возрастному составу побоек самцов (рис. 1) показывают, что на Руддерском лежбище в августе-сентябре преобладают звери 6—11 лет (около 60%), в то время как на о-ве Врангеля (Блоссомское лежбище) до 73% составляют животные 11—19 лет. Интересно, что на Руддерском лежбище до 10% составляют старые самцы в возрасте 21—37 лет, которых почти не было на о-ве Врангеля.

Данные В. И. Крылова (1965) по возрастному составу моржей на ледовых залежках в 1960—1962 гг. (рис. 2) свидетельствуют о том, что

в западной части Чукотского моря среди самцов также преобладают животные \pm возрасте 11-20 лет.

Поскольку данные о возрастной дифференциации самцов моржей получены на основе анализа побоек, естественно, возникает вопрос: не являются ли указанные выше различия в возрастном составе моржей по отдельным районам следствием селективности промысла? В. И. Крылов (1965) считает, что в Чукотском море зверобои стараются бить наиболее крупных зверей. В результате этого неполовозрелых зверей в побойках меньше, чем взрослых. Кроме того, В. И. Крылов отмечает, что старые особи обоего пола в северо-западной части Чукотского моря в побойках единичны.

Безусловно, селективность имеет место при добыче моржей, но вряд ли это может быть главной причиной столь четкого различия в возрастном составе побоек моржей с Руддерского лежбища, с одной стороны, и с Блоссомского лежбища и ледовых залежек западной части Чукотского моря, — с другой. Нам представляется, что в условиях промысла, когда моржи залегают очень плотно, без какой-либо дифференциации по возрасту, зееробою трудно отстрелять животных определенного возраста (например, только 6-10 лет или 11-13 лет), так как разница в размерах этих животных невелика (10—30 см). Между тем, моржи в возрасте 6-10 лет в большем количестве добывались в районе Руддерского лежбища, в то время как в Чукотском море в побойках преобладали звери 11-15 лет. Именно за счет животных этих возрастов наблюдается различие в составе побоек, представленных на рис. 1. Очевидно, селективность промысла проявлялась лишь в том, что зверобои как в западной части Чукотского моря, так и в районе Руддера почти не добывали неполовозрелых особей, т. е. животных в возрасте от 1 года до 5-6 лет.

Уместно напомнить замечания И. Вениаминова (по П. Г. Никулину, 1940), который, характеризуя распределение моржей у Аляски в летнее время, отмечает: «весьма замечательно, что моржи, приходящие на Аляску, суть все самцы, молодые и престарелые, и никогда не видели между ними самок». Более того, П. Г. Никулин (1940) склонен полагать, что эти скопления образуются холостяками, не участвующими в спаривании.

Таким образом, вероятно, можно говорить об определенной дифференциации тихоокеанской популяции моржа в летне-осенний период. В Анадырском заливе (район Руддера и косы Меечкен) и, очевидно, у Аляскинского побережья на лето остаются преимущественно созревающие самцы или молодые половозрелые, не достигшие достаточной физической зрелости звери (6—11 лет), а также престарелые самцы 20-летнего возраста и старше. В небольшом количестве с ними остаются неполовозрелые — 3—5 лет. В западную часть Чукотского моря (район о-ва Врангеля) уходят самки, физически зрелые самцы и неполовозрелые ссоби обоего пола. При этом взрослые самцы на ледовых залежках нередко образуют обособленные группы.

Данные о соотношении возрастных групп в различных популяциях скудны. К. К. Чапский (1936) сделал попытку определить величину ежегодного прироста в атлантической популяции моржа. Он полагал, что половозрелые составляют 50% от всей численности популяции и только половина езрослых самок щенится ежегодно (по К. К. Чапскому, самки созревают на 4—6-м году жизни, самцы — на год позже). При таких исходных данных К. К. Чапский определил, что величина ежегодного приплода не превышает 12,5%, а с учетом яловости и естественной смертности — не более 10%.

С. Ю. Фрейман (1940) на основании обследования большой группы тихоокеанских моржей приводит следующее соотношение возрастных групп: взрослые — 59%, неполовозрелые — 24%, молодняк — 17%. По-

ловая зрелость у самок моржа, по данным С. Ю. Фреймана, наступает

в 3-летнем возрасте, самцы созревают в 5—6 лет.

В. И. Крылов (1965) определил, что прирост стада тихоокеанского моржа составляет не более 6,3% от общего поголовья. Соотношение возрастно-половых групп в смешанных залежках моржей (по В. И. Крылову) следующее: половозрелые — 71,1%, из них самок — 36%, самцов — 35,1%, неполовозрелые обоего пола — 28,9%. В последней работе (1967) В. И. Крылов привел новые данные по приросту популяции моржа — 11,2% от общей численности поголовья. При этом принималось, что половозрелая часть стада составляет 70% при соотношении самцов и самок 1:1.

Половая зрелость у моржей, по данным В. И. Крылова (1967), наступает: у самцов в возрасте 7—9 лет (в массе в 8 лет); у самок — в возрасте 6—8 лет (но большая часть из них начинает размножаться в 7-летнем возрасте). Ежегодно щенится только 35% половозрелых самок.

По данным зарубежных исследователей, величина приплода у тихоокеанского моржа — 11% (Scott et al., 1959) и 14% (Burns, 1965), а у атлантического моржа — 8% (Mansfield, 1959) от численности всей популяции. Отметим, что, по данным Бёнса, в размножении ежегодно участвует около 47% половозрелых самок моржа, т. е. на 12% больше, чем

по данным В. И. Крылова.

Нами предпринята попытка определения величины приплода и пополнения половозрелой части стада тихоокеанского моржа на основе построения кривой населения, которая, в свою очередь, была построена по возрастному составу побоек. Соотношение самцов и самок в популяции моржа, как уже отмечалось выше, составляет 1:1. Поэтому тип кривой населения популяции моржа не изменится, если мы будем строить кривую на основе данных возрастного состава самцов и самок порознь или вместе. В наших сборах возрастной материал был в основном по самцам, на его основе и была построена структура популяции. Вначале мы объединили данные возрастного состава побоек из Анадырского залива и из западной части Чукотского моря. Эти материалы в совокупности позволяют установить соотношение возрастных групп, характерное для половозрелой части стада, или, иными словами, кривую населения половозрелых животных. Далее, использовав данные Бенса (1965) и В. И. Крылова (1967) о количестве ежегодно плодоносящих самок, определили величину приплода (15—17% от общей численности популяции). Однако на 1-м году жизни у моржей, по-видимому, как и у других ластоногих, наблюдается наиболее высокая смертность по сравнению с последующими годами. Например, естественная смертность на 1-м году жизни у хохлача более 50% (Рассмусен, 1961), у котиков — 40% (Северцов, 1941) и у кольчатой нерпы в среднем — 35% (Федосеев, 1966).

Возраст наступления половой зрелости у моржей, если принять его по средним значениям, вычисленным на основе данных В. И. Крылова и Бёнса, для самок будет 5—8 лет (в массе созревают в 6—7 лет), для самцов — 6—9 лет, т. е. почти такой же, как и у кольчатой нерпы (МсLaren, 1958; Федосеев, 1964; Назаренко, 1965). Предельный известный возраст у моржа 37—38 лет, у кольчатой нерпы Охотского моря — 32 года, а у нерпы канадского сектора Арктики — 41 год (МсLaren, 1958). По-видимому, и величина естественной смертности у моржей резко не отличается от таковой у кольчатой нерпы. Поэтому смертность на 1-м году жизни у моржей мы приняли такой же, как и у кольчатой нерпы, — 35%. Возможно, эта цифра для моржей несколько завышена.

Зная величину приплода и естественной смертности на 1-м году жизни, мы определили относительную численность годовиков в популяции. В дальнейшем вычислили относительную величину животных 2—7-летнего возраста, допустив, что кривая населения у моржей в неполовозре-

дой части популяции представляет экспоненциальную кривую, как и у других долгоживущих видов млекопитающих (Северцов, 1941). Кривая населения половозрелой части популяции была построена по средним данным возрастного состава побоек. В целом кривая населения для современной популяции тихоокеанского моржа получилась экспоненциального типа (рис. 3, 1).

Под длительным воздействием интенсивного промысла возрастная структура популяции моржа в значительной степени омоложена, так как добывались преимущественно взрослые животные. В связи с этим тип кривой населения в значительной мере видоизменен. При отсутствии промысла или его неселективном воздействии кривая населения в попу-

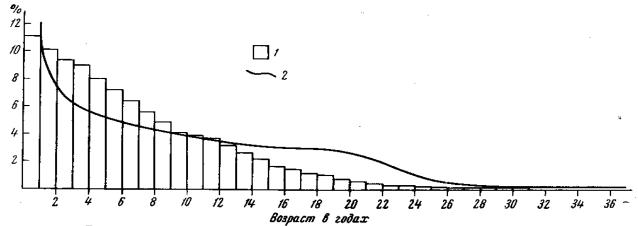


Рис. 3. Возрастная структура популяции тихоокеанского моржа I — население в современной популяции, 2 — предполагаемая структура при отсутствии промысла

ляции моржа, по-видимому, имеет вид кривой промежуточного типа 1 (рис. 3, 2). Различие между экспоненциальной кривой и кривой промежуточного типа состоит в том, что естественная убыль в половозрелой части стада по кривой последнего типа идет значительно медленнее, чем в неполовозрелой части. В связи с этим относительная численность половозрелых животных в стаде больше. При экспоненциальной кривой соотношение меняется в сторону некоторого относительного увеличения количества неполовозрелых животных.

Не следует полагать, что соотношение отдельных генераций в стаде всегда может давать правильную кривую населения того или иного типа, так как величина отдельных генераций, хотя и имеет относительную стабильность в течение длительного периода, все же не может быть абсолютно одинаковой. В связи с этим типы кривых населения (возрастная структура), которые мы приводим на рис. 3, характеризуют осредненный возрастной состав популяции на определенный период, а не на какой-либо отдельный год.

В современной популяции моржа величина пополнения, исчисляемая по новорожденным, по нашим расчетам, составляет 15—17%, а исчисляемая по зверям годовалого возраста—в среднем 11% от численности всей популяции. Пополнение половозрелой части популяции не превышает 9,0%, т. е. относительная величина размножающихся самок пополняется примерно на 4,5% от общей численности популяции.

¹ В названии кривых населения популяции мы пользуемся терминологией С. А. Северцова (1941), который для млекопитающих и ряда других животных описал три основных типа кривых: экспоненциальная (кривая показательной функции), логистическая, или S-образная, и промежуточная, занимающая среднее положение между двумя предыдущими типами кривых.

Если учесть естественную и промысловую смертность, то фактический прирост стада будет значительно меньше приведенных нами показателей пополнения. По данным Бёнса (1965), ежегодная смертность у моржа в среднем 12—13%. С учетом этих данных, прирост в популяции моржа составит не более 3%, а с учетом промысла общая убыль, очевидно, превысит прирост.

На период 1957-1960 гг. численность поголовья в тихоокеанской популяции моржа оценивалась в 50 тыс. голов (Федосеев, 1962; Fay, 1957). По данным Брукса и Бенса (J. W. Brooks, 1963; J. J. Burns, 1965), численность тихоокеанских моржей составляет 70-90 тыс. голов. Если принять среднюю численность поголовья за 70 тыс. голов, то прирост стада с учетом естественной смертности составит 2,1—2,8 тыс. голов.

Промысловая добыча в среднем ежегодно составляет 2,6 тыс. голов (в территориальных водах СССР добывается около 1,1 тыс. голов, у берегов Аляски — около 1,5 тыс. голов). Кроме того, во время промысла до $30\,\%$ животных тонет. Поэтому общее промысловое изъятие из стада составляет не менее 3 тыс. голов.

Таким образом, численность поголовья в тихоокеанской популяции

моржа, по-видимому, продолжает незначительно сокращаться.

Безусловно, наши расчеты не претендуют на большую точность, но тем не менее, они свидетельствуют о напряженном положении запасов моржа. В целях уточнения численности поголовья в ближайшие годы следует повторить учет моржей методом аэрофотосъемки 2. Нуждаются в уточнении и данные о величине естественной смертности. Коэффициенты естественной смертности, полученные американскими исследователями, по-видимому, завышены, так как расчет проводился на основе возрастного материала сильно омоложенной промыслом популяции. Если вычислить коэффициент естественной смертности по предельному возрасту в пробах (метод Ф. И. Баранова, модифицированный П. В. Тюриным, 1963), то в среднем для популяции моржа ее величина, по-видимому, не превысит 8—10% (предельный возраст 40 лет). Однако и эта величина естественной смертности не может быть безоговорочно принята, так как предельный возраст под влиянием промысла также уменьшился. Кроме работ по учету численности, следует продолжить изучение возрастной структуры популяции, на основе которой представилось бы возможным более обоснованное расчисление величин прироста и убыли в стаде.

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AGE-SEXUAL STRUCTURE AND ABILITY OF REPRODUCTION IN THE PACIFIC WALRUS POPULATION

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Summary

In the modern walrus population the increment amounts to 15-17% of the whole population numbers, as calculated by new born walruses, and to 11%, as calculated by yearlings. The increment of the sexually mature specimens amounts to 9%. While taking into account the natural mortality the increment in the walrus population does not exceed 3%. In territorial waters of the USA and of the USSR 2.5-3 thousands of walruses are caught per year what exceeds slightly the increment.