

TIME AND LOCATION OF MATING AND ASSOCIATED BEHAVIOR OF  
THE PACIFIC WALRUS, *ODOBENUS ROSMAREUS DIVERGENS* ILLIGER

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and

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## ABSTRACT

Management of the Pacific walrus population by the Soviet Union and the United States has been based up to now on several untenable assumptions concerning the time and place of mating, the social system during the mating season, and the sex and age composition of the population. The condition of reproductive organs of males and females taken throughout the late autumn, winter, and spring indicates that the principal period of mating is January-February, rather than April-June as has been assumed. During **late** winter, virtually all of the adult females and most of the adult males are situated in the north-central and southeastern pack ice of the Bering Sea. The sex ratio of adults in those areas is about 1 male: 10 females. Most of the subadult males are in peripheral and intervening areas. Adult females and young within the two concentration areas in March associate in tightly knit herds, which move about apparently in search of food and in response to movements of the pack ice. One or more adult males associates with each such herd. These bulls engage in ritualized visual and acoustical displays in the water, **especially** when the females are at rest on ice. While displaying, they maintain a distance of about 5 to 10 m from each other; closer intrusion is met by threat, followed by fighting. Individual females enter the water and engage in facial and bodily contact with **the** displaying males, after which, presumably, copulation takes place underwater. The social organization appears **to** be unique among otarioid **pinnipeds**, more closely resembling a **lek than** a "harem" system.

## ВРЕМЯ И МЕСТО СПАРИВАНИЯ И АССОЦИАТИВНОЕ ПОВЕДЕНИЕ ТИХООКЕАНСКОГО МОРЖА

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### /Резюме/

Регулирование популяции тихоокеанского моржа производимое Советским Союзом и США основывалось на некоторых несостоятельных предположениях касающихся времени и места спаривания, поведения и полового состава популяции в этих районах. Сведения полученные во время осмотра половых органов самок и самцов, взятых поздней осенью, зимой и весной, указывают что основной период спаривания протекает в январе-феврале, а не в апреле-июне, как это считалось ранее. Поздней зимой почти все взрослые самки и самцы обитают на северо-центральной и юго-восточном паковом льду Берингова моря. Половая пропорция в этих местах почти 1 самец: 10 самок. Большинство созревающих самцов находится в периферийных районах. Взрослые самки с молодняком собираются в этих районах в марте в плотные стаи и добывая пищу постепенно продвигаются со льдами. Один или несколько взрослых самцов опекают одну из таких групп, издавая при этом ритуальные звуки и взгляды из воды, когда самки отдыхают на льду. В это время самцы сохраняют держатся друг от друга на расстоянии от 5 до 10 м., а при вторжении начинается преследование и драки. Самки по одиночке сходят в воду прикасаются лицом и телом к самцам коопулируют с ними под водой. Более молодые самцы, которые позже приходят в течку, чем взрослые самцы, вероятно оплодотворяют тех самок, которые овулируют после окончания пика спаривания.

## INTRODUCTION

The formulation of a **management** plan for any species requires a thorough knowledge of its natural history, reproductive biology, and population structure. Management of the Pacific walrus by both the United States and the **Soviet** Union has been founded on several basic but inadequately tested assumptions:

(1) *Walruses are polygynous.* Walrus are gregarious and sexually dimorphic, characters typical of polygynous **mammals** (Nutting 1891; **Bertram** 1940; Bartholomew 1970; Trivers 1972; Stirling 1975; Rails 1977). Their closest relatives, the fur seals and sea lions (**Otariidae**) have these characters and are polygynous. However, the otariids congregate on land to mate and bear young, whereas the walrus accomplishes these functions on or near sea ice. The possibility that walruses are monogamous has been proposed by some investigators (e.g. Allen 1880; **Krylov** 1968), apparently on the basis of frequent sightings of small "family groups" during and after the calving period. This proposal has been widely accepted in the Soviet Union but not in the United States. However, the **only** support for either view has been by inference.

(2) *The sex ratio of adults is about 1:1.* Substantial data on the sex ratio of newborn walruses indicate that there are about as many males as females at birth (**Nikulin** 1941; Brooks 1954; Burns 19654). Representative samples of adults have **not** been available, however, since the sexes tend to segregate during most of the year. Because of differential availability and vulnerability of the sexes to hunting, and because of various preferences among hunters, harvest samples tend to be strongly biased and

cannot be assumed to be representative of the population **as** a whole (Burns 1965;<sup>4</sup> Krylov 1965; Gol'tsev 1968). Thus, the sex ratio of the breeding adults is unknown.

(3) *Mating takes place in April to June.* All other pinnipeds, as far as is known, mate within a few days **or** weeks after giving birth. It has been assumed that walruses are not different. Calves are born **mainly** in the month of May (Krylov 1966),<sup>5</sup> and by extrapolation from the size of fetuses obtained in summer and autumn, implantation of the **blastocyst** has been estimated to occur mainly in June (Chapskii 1936; Mansfield 1958). The findings of Brooks (1954), Burns (1965),<sup>4</sup> and Krylov (1969) have confirmed this and have shown that some females have large **Graffian** follicles at that time. Thus, it has been presumed that mating takes place about the same time as birth, that pregnancy lasts about 11 or 12 months, and that, unlike the other pinnipeds, there is no delay in implantation (Harrison 1969).

(4) *There is a "surplus" of males.* Given that the sex ratio at birth is about 1:1, and that there is a high probability of polygyny, there may be a **large** "surplus" of males that **could** be harvested without adversely affecting recruitment of males into the breeding population. This is the basis of management of other polygynous species, especially the northern fur seal, *Callorhinus ursinus* (Roppel and Davey 1965), and it has been at the foundation of management also of the Pacific walrus population in both the United States and the Soviet Union.

The principal weakness in these assumptions lies in their inconsistency with each other and with other relevant findings. For example,

while the sex ratio at birth in most species of mammals is about 1:1, the ratio in the adults usually is unequal (Glucksmann 1974). In marine mammals that are strongly polygynous, adult females greatly outnumber adult males (Carrick et al. 1962; Chapman 1964; Rails et al. 1980). If walruses are monogamous, their adult sex ratio should be near parity; if they are polygynous, then adult females should be considerably more numerous than adult males.

It is now clear that female walruses usually breed at 2- to 3-yr intervals, and that less than half of them bear young in any given year (Freiman 1941; Brooks 1954; Mansfield 1958; Loughrey 1959;<sup>6</sup> Krylov 1962, 1966;<sup>5</sup> Burns 1965)4. This suggests that the period of gestation is longer than one year and points to the possibility of an earlier (than April-June) mating season. The latter was implied also by Mansfield's (1958) finding of fertile adult males in late November and March, and by Fay's (1955) observations that the testes of adult males in April-June were mainly in retrogressive stages.

Because less than half of the females breed in a given year, there could be a large surplus of males, if the adult sex ratio is 1:1. Conversely, if walruses are polygynous, differentially high mortality of males from natural causes is probable (Rails et al. 1980), which could result in a more balanced sex ratio of breeders or in a "surplus" of females. Only 3 to 14% of male elephant seals (*Mirounga angustirostris*) survive to sexual maturity (LeBoeuf 1974); in northern fur seals (*Callorhinus ursinus*), the natural mortality rate of males is more than three times that of females (Chapman 1964; Johnson 1968). The concept of "surplus" deserves careful examination.

In our work, both jointly and separately, over the past several years, we have gathered new data pertaining to the time and place of mating, composition of the breeding adult segment of the population, and social behavior of the mating groups. We present that information here as a contribution to clarification of these matters, which are of vital importance for managing the Pacific walrus population on an international basis.

#### METHODS

We obtained information on the time and place of mating and associated behavior, first, by examination of reproductive organs of walruses taken throughout the winter, spring, and summer; second, by visual and photographic methods during aerial surveys; third, by observation of animals via icebreaking ships; and fourth, by acoustical methods.

Fay obtained testes and epididymides from 111 juvenile, subadult, and adult males at St. Lawrence Island in November to June and at Barrow in July and August, 1952 to 1963. Testes were weighed, and tissue samples were fixed in 10% formalin or AFA, embedded in paraffin, sectioned on a rotary microtome at 7 to 10  $\mu$ , stained with hematoxylin-eosin, and mounted on glass slides. These were examined microscopically to determine seasonal stages of development of the seminiferous epitheliums and the period when spermatozoa were present in the epididymal tubules. Kibal'chich obtained testes from 115 juvenile, subadult, and adult males in southeastern Bering Sea during March-April 1976 via the joint Soviet-American research cruise of the ZRS *Zagorianny*. These were weighed to the nearest gram, and the

presence or absence of spermatozoa was determined microscopically by the impression smear method at the time of collection.

Fay obtained reproductive tracts from 218 adult females taken in the north-central Bering Sea from November to June, 1952 to 1972. The ovaries from these were fixed and stored whole in 10% formalin for one to three months, then sliced into 1- to 2-mm-thick serial sections. They were examined without magnification, to determine the number and size of vesicular follicles and the size and state of development of corpora lutes. Gol'tsev (1978)<sup>7</sup> obtained reproductive tracts from 34 adult females, during the ZRS *Zagoriansy* cruise, and treated them in essentially the same way. In all instances, age of the animals was determined from counts of cementum layers in thin sections of the cheek teeth, as described by Mansfield (1958) and Krylov (1965).

Information on the geographical location of the animals during and just after the mating season was obtained mainly from unpublished aero-visual survey data made available by K. W. Kenyon, G. A. Fedoseev, J. J. Burns, and H. W. Braham. These surveys were made during February to April of 1960 to 1972. Additional aerial survey data were obtained by Ray, during flights over the Bering Sea ice in April 1975 and 1976 via National Aeronautics and Space Administration remote-sensing aircraft. These were supplemented by surface observations via iceworthy ships in March-April 1971 (CGC *Glacier*), February-March 1972 (CGC *Burton Island*), and March-April 1976 (ZRS *Zagoriansy*).

Direct observations of social behavior were made by Fay and Ray during March 1972 and April 1971 via the CGC *Burton Island* and CGC *Glacier*, respectively, in the north-central Bering Sea, and in April to June 1952 to 1966 via small boats in the vicinity of the western end

of St. Lawrence Island. **Kibal'chich** and Fay **observed** social behavior of walruses in the southeastern Bering Sea via the ZRS *Zagorianny* in March-April 1976.

## RESULTS

### Time of Mating

Data from the reproductive organs of males taken in the northern Bering and **Chukchi** seas in November to August 1952 to 1963 (Table 1) indicate that (1) the mature adults, 17 to 37 yrs old, were most often fertile, principally in the period November to February, (2) the younger adults, 12 to 16 yrs old, were fertile less often and over a longer period, and (3) the subadults, 5 to 11 yrs old were least often fertile, and their highest fertility occurred about two months later than for the mature males. The cycle of testis weights suggests a peak in development in December or January for the older males and in February or March for the younger individuals (Figure 1). None of the animals younger than 10 yrs old had spermatozoa in the **epididymides**; spermatozoa were present in a few of the 10 to 13 yr olds from December to May and in most of the fertile mature males from November to May. By analogy with other pinnipeds and with other carnivores in general, in which the principal mating period is just after the peak of the testis cycle of the mature males (cf. **Asdell** 1964; Harrison 1969), these findings suggest that the mating of walruses takes place in mid-winter, rather than in spring.

Data obtained from males collected in southeastern Bering Sea between 20 March and U April, during the Soviet-American cruise of the ZRS

Zagorianny, confirmed this in part (Gel'tsev 1978)<sup>7</sup>. Spermatozoa were most often present in the testes of animals 11 to 19 yrs old (71% fertile), whereas the testes of most of the other mature males, 17 to 32 yrs old, were flaccid and in a retrogressive state. Those of the **subadults**, 8 to 10 yrs old, were **mainly** in the beginning stages of spermatogenesis.

The data from 88 sexually mature females that were not carrying a large fetus and had not given birth recently (*i.e.*, within 2 months) are shown in Table 2. Again, the samples per month are small, but the trends seem clear. Their implication is that (1) ovulation may begin as early as December or take place as late as May in some individuals, as indicated by the presence in the ovaries of vesicular follicles larger than 10 mm in diameter, and (2) that fertilization is essentially completed by March, as indicated by the presence of a new corpus **luteum** of pregnancy. All but two of the corpora lutea of these animals taken in February to June already were fully **luteinized**; one from a specimen taken in early April and one in mid-February were incompletely formed, indicating that fertilization had taken place about 2 weeks earlier.

The remaining 164 females that we examined in November to June were either carrying a large fetus (November-April) or had recently given birth (April-June). Only one of these, taken in June, had a **follicle larger** than 10 mm in its ovaries, and none had any new corpora lutes of pregnancy like those in the foregoing group.

Thus, our data from both the males and the females indicate that the period of mating in the Pacific walrus population is principally in mid-winter, probably beginning no earlier than December and ending no later than March.

## Location of Mating

Five aerial surveys of the Pacific walrus population in its wintering area in the Bering Sea were conducted jointly by the U.S. Fish and Wildlife Service and the Alaska Department of Fish and **Game** between 1960 and 1972 (K. W. Kenyon, Biologist, U.S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Seattle, WA. 98115. **Pers. commun.**, 1960-1972). The principal objective of those surveys was to estimate the number of animals in the population, but they provided, at the same time, an overview of the animals' distribution in the pack ice. The greater part of the population was situated in the north-central Bering Sea, mainly to the south and southwest of St. Lawrence Island; most of the remainder was in the southeast, from the vicinity of Nunivak Island and Kuskokwim Bay to inner Bristol Bay (Figure 2). In the intervening and peripheral areas, the animals occurred in low densities. Subsequent surveys in April 1975 and March-April 1976 by Wartzok and Ray (1980)<sup>8</sup> and by **Braham** et al. (this volume), in general, confirmed those findings. The pattern as shown in Figure 2 is described only in the most general way, since the variations in ice conditions from year to year have a strong influence on it (Burns et al. 1980)<sup>9</sup>.

From interpretation of aerial photographs taken during one of those surveys (1972) and from direct observations from ships, we have repeatedly determined that the two generalized areas of high density contain mostly females and young during March and April, whereas the intervening and peripheral areas contain mostly males (Table 3). The ratios of adult males to adult females in the north-central and southeastern areas of high density were about **1:10** and **1:8**, respectively. In the low density

areas, the ratio of males to females was about **27:1**, and most of those males were subadults.

l'bus, it is apparent that, during late winter to early spring, the Pacific walrus breeding population is essentially split into two groups, one of which is located in the north-central Bering Sea and the other is in the southeastern Bering Sea-Bristol Bay region. Further, there are strong indications that the sex ratio of the adult, breeding population contains many more females than males.

#### Associated Behavior

Most of our data on herd structure and social and acoustical behavior are from the north-central high density area during March 1972 and April 1971. We obtained some additional behavioral information in the western perimeter of the southeastern area in March-April 1976. The following are **resumés**, presented in seasonal chronological order, of 13 instances in which we observed **social** behavior relevant to mating in mixed herds.

4 March 1972, 0700 to 0800 hrs, at **62°53'N, 172°06'W**

We encountered about 330 animals in a large openwater lead. About 295 of these were hauled out and most were sleeping in three groups of 20, 75, and 200 on three large floes in the center of the occupied area (Figure 3a). Evidently, these groups had been **lying** in the same position for several hours, as many of the animals had deposits of frost on their exposed surfaces. About 80% of these animals were **subadult** and adult females; the rest were immature young, **1 to 4** or 5 years old. Another group of about 15 females was in the water and apparently feeding,

0.3 km away in the same lead. We saw no adult bulls within any of the groups of females and young; however, there were 19 bulls in the vicinity, within a 0.5 km radius, and these were distributed as follows: 12 sleeping on the ice in groups of 6, 2, 1, 1, 1, and 1; one sleeping in the water with its pharyngeal pouches inflated; 6 active in the water, alongside the floes on which the central groups of females lay. The group of 6 inactive males was made up of one adult and five subadult animals, two of which had much blood on the body and on the snow around them. The 6 active bulls were spaced 7 to 10 m apart, and in a 35-minute period of observation, we saw them dive and surface again many times in the same place.

6 March 1972, 0900 to 1900 hrs, at 63°04'N, 172°23'W

By helicopter we located several large herds totalling about 1,000 animals, most of which were adult females and young. A few adult bulls were present, some of them bloody about the head and leaving blood on the ice wherever they went. When the ship was moved to this position, we had four herds totalling about 500 animals within a 3 km radius. Nearly all were in the water, alternately diving and surfacing in remarkable synchrony and apparently feeding. Only one animal, an adult bull, was on the ice, sleeping, and he remained there throughout the daylight hours. One group of about 50 animals slept in the water near the ship for more than two hours in the afternoon, before moving on. These were mainly females and young, but with them was one adult bull that was active the whole time, alternately diving and surfacing at 2 to 3 minute intervals, in the midst of and about the periphery of the group.

7 March 1972, 0655 to 1900 hrs, at 63°00'N, 172°04'W

At daybreak, we sighted **steam** rising from three herds about 7 km from the ship and moved to that area for observation. All herds were in the water, evidently feeding, and these appeared to be entirely adult females and their young. Several single bulls were sleeping **on** the ice nearby. Between 0820 and 0920, nine other bulls hauled out nearby, two of **them** with **blood** streaming from superficial wounds. Except for two groups of two each, these were all single males which lay separately, about 50 to 100 m apart. Nearly all of these bulls remained in place throughout the daylight hours, whereas the herds of females were continuously moving. In late afternoon, one group of about 250 females and young hauled out to rest on a large floe about 1.5 km from the ship, in an area where we had seen one or two bulls sleeping previously. This group was still there at nightfall.

8 March 1972, 0700 to 1900 hrs, at 63°00'N, 172°12'W

The ship drifted slowly westward with the ice overnight and, at daybreak, was in the same position relative to the floe on which the herd had hauled out the previous afternoon. The resting herd of females and young was still **in** the same place, but most of the single bulls *that we* had seen the previous day were no longer on the ice. We left the ship on foot and took a position a few meters downwind from the resting herd. We found it to be made up of three partly separated groups of about 50, 150 and 50 adult females and young, each of which had in its midst one adult male (Figure 3b). Those bulls slept soundly during our observations, except for occasional jostling of their closest neighbors for resting

space. That is, we detected **no** activity that was even slightly suggestive of mating behavior, and certainly not indicative of a "beach master" role, as applied to **otariids** or elephant seals. We noted several times an emphatic "knock" sound, like that made by striking knuckles on wood, which seemed to come from the seaward edge of the groups. An occasional, short, loud whistle also came from the same location. We moved to the edge of the floe, a few meters from the perimeter of the largest group, where we observed three adult males in the water alongside the herd. These bulls were diving and surfacing at short intervals (1-3 rein), each in **a** fixed location several meters from each other as in the foregoing observations. The dives, because of their brevity, did not appear to be feeding dives, which in our experience tend to be 5 to **10** min long at such depths (about 55 m). We observed these bulls for over an hour, in which their continuous activity contrasted greatly with that of the inactive males on the ice. The females seemed to pay little heed to the diving **bulls**, except when the latter surfaced with a burst of spray, wetting those nearest the edge of the **floe**. However, this only caused some jostling in the seaward edge of the herd.

By means of hydrophore and amplifier, we detected several underwater **sounds**, presumably made by the diving bulls. These sounds consisted of a series of "knocks" and "**bell-like** sounds" (see **Schevill** et al. 1966), but their significance and that of the other sounds made at the surface was not apparent to us at the time.

9 March 1972, 1600 to **1900** hrs, at **62°44'N, 172°02'W**

We located a group of approximately 95 animals in the water and 20 that were just in the process of hauling out onto the ice. By 1800 hrs,

there were about 70 adult females and immature animals on the ice in three groups of 8, **10**, and about 50; two other groups (15 and 22) of females and young remained in the water, apparently feeding. Eight bulls also were **in** the water, "stationed" about 7 to 10 m apart along the edge of the ice where the females and young lay (Figure 3c). On one occasion, male A surfaced close alongside male B, and the two animals faced each other. They held their tusks horizontally, first obliquely to one another, then **parallel**, then directly (Figure **3e**). Immediately thereafter, male B (who was the larger animal and had the larger tusks) rose chest-high out of the water and rapidly struck A three or four times on the head and neck with powerful downward thrusts **of** his tusks. Both animals dove in unison, with much splashing and churning of the water, then surfaced again, whereupon B rose once more and struck A two or three more times. Swiftly, they both dove again, surfaced briefly in a shower of **spray**, then down again, then up and rolling together violently at the surface, then down again and remained beneath the surface for about two minutes. After this, each surfaced at his own station. Earlier, we had noticed a similar encounter between **males** C and D near C's station, and this also ended with each withdrawing to his usual station. It was not clear from our viewpoint on the ship exactly what these bulls were doing when not engaged in such fights, except that each was remaining in virtually the same place and repeatedly diving and surfacing there, as we had seen in the previous instances.

On one occasion, a subadult or young adult female approached bull A and engaged in some facial contact. She then mounted the male's back in what appeared to be a "copulatory" position, with the male and female roles reversed. The two then dove in unison, arching high out of the water. They

remained underwater for about one **minute**, then surfaced (the **male** first) and engaged in further facial contacts; then the female mounted the male again. They dove in unison once more, rolled together for a **minute** or more at a shallow depth, then surfaced slightly separated. The female swam away and hauled out again with a nearby group. Another female engaged male A in the same kind of activity about 30 minutes later.

Once again, underwater listening revealed "knocks" and the "bell-like" sounds. The ship remained overnight in the same position relative to the herd, drifting slowly southeastward with the ice.

10 March 1972, 0700 to 1430, at 62°36'N, 172°08'W

At daybreak, about half of the herd observed the previous evening was still present. The central group of 10 females and 5 youngsters was still on the ice; about 50 others were **in** the water evidently engaged in feeding. One adult male was in the water near the group of **10** females on the ice (Figure 3d); no other males were in sight. We **left** the ship at 0830 and approached on foot to within 30 m of the animals. We remained there about 5 hours. During that time, the animals did not vary their distribution or their activities notably. The adult females and immature animals in the water were continuously engaged in feeding dives, with 1.5 to 2-minute ventilation rests **at** the surface between dives; we did not determine diving times because individuals were difficult to distinguish from each other. Those on the ice mostly slept the whole time, except for a "**crêche**" of 5 first- and second-year youngsters that were engaged in mutual play. The bull repeatedly dove and surfaced in virtually the same place **along-**side the 10 females for the entire 5 hrs, pausing for 7 to 32 sec at the

surface between dives (Figure 4 upper). His average time spent underwater was 2 min 2 sec; his average time at the surface between dives was 25 sec (Ray and Watkins 1975). As the bull surfaced following each dive, he released a large volume of air just beneath the surface and emerged nearly to shoulder height in a massive eruption of air and water. Raising his tusks nearly to the horizontal he made a "knock" which was audible to us for a distance of at least 200 m. At the time of emitting the "knock", he opened and closed his mouth very swiftly, seemingly making the sound by percussion of the cheek teeth. He inhaled deeply, then lowered his head so that only his crown showed above the surface, and lay floating for a few seconds with one pharyngeal air sac inflated and his back exposed. He then raised his head high enough to exhale and inhale noisily through his mouth, followed by another "knock" as he lowered his head again below the surface. He raised his head thus from one to four times during each surface interval, and on the last of these he "knocked", emitted a short whistle through pursed lips (Figure 5 upper), then immediately dove, arching his back and rear flippers high out of the water (Figure 5 lower).

During each dive, we heard the same stereotyped series of underwater pulses and bell-sounds<sup>10</sup> as we had heard on 8 and 9 March, including a distinctive 7-pulse coda (Ray and Watkins 1975). This whole sequence of sounds (Figure 6) was audible to us in air from our position on the ice and was monitored and recorded by hydrophore, as well. Comparable sequences of underwater pulses and bell-sounds of lesser intensity, apparently made by other bulls some distance away and not within our field of vision, were heard via the hydrophore. At 1400, we intentionally disturbed the animals by exposing ourselves to their view and moving to their windward side,

whereupon all of the females and youngsters departed. **However**, the bull continued his displays at his station for about 10 minutes longer, before departing in the direction of the females. Two other bulls, not seen previously, drew close to **the** area, then headed in the same direction.

17 March 1972, 1000 to 1300 hrs, at 62°47'N, 172°28'W

We encountered a group of 49 animals in an area of heavy, continuous ice with very few holes or leads. On the ice were 45 adult females and young, arranged in three groups of 6, 15, and 24; four adult males were situated as shown in Figure 7a. Bull A was sleeping on **the** ice; bull B was sleeping in the water in a round hole about the same diameter as his body. The other two bulls were displaying in the water, as in the previous incidents. Each had one of his **pharyngeal** pouches inflated while he was at the water's surface. We approached on foot and shot a female from each of the larger groups. This **immediately** frightened away all of the others except the displaying males, who continued their displays for a few minutes before moving in the direction of the departing **females**.

20 March 1976, about 1200 hrs, at 57°15'N, 166°05'W

We observed a group of four adults (2 males, 2 females) which lay in pairs, side by side on the ice, very close together but head-to-tail. A third male which swam **to** and attempted to haul out on the same floe was met with raised tusks but no overt aggression. He hauled out about 2 to 3 m apart from the group, whereupon they all lay down and were quiet.

21 March 1972, 0830 to 1300, at **61°27'N, 174°24'W**

We encountered six herds on the ice and approached them on foot at 0830. There were about 250 animals in **all**, including **mostly** females and young on the ice and more than 10 adult males in the water. We concentrated our attention on two groups of 20 and 30 that were attended by 8 bulls (Figure 7b). The group of 20 on the ice consisted of more than 10 adult and **subadult** females, about 8 juveniles (1 to 6 yrs old), and 2 adult males. Nearly all of these animals had a coating of frost on their exposed body surfaces, indicating that they had been sleeping in the same position for several hours. The males in this group continued to sleep throughout the **4.5-hr** period of **observation**, as did most of the females and young. Only a few of the **subadult** and **immature** females were active, entering and leaving the water several times during the day. In the water near the ice edge was an **adult** bull (A) that was engaged in the same kind of dives and acoustical displays as the bulls observed earlier, though he did not stay as consistently in one place as the others had (Figure 4 lower). The subadult and immature females that entered the water from this group often engaged in nose-to-nose and other facial contacts with this bull and **occasionally** dove with him, but we saw no copulation. A second bull (B), which **at** first stayed some 50 m away, later moved toward A's station. However, he did not come **closer** to A than about 10 m, nor did he engage in the display routine or elicit any evident response from bull A or from the young females. Subsequently, bull B returned to his former place, where he remained at the surface, making "bell" sounds with head submerged for about one hour before moving out of view. At 1200, a third bull (C) appeared about 50 m away from A,

but did not approach any closer. This animal did not engage in the same display sequence as the others, though he did dive occasionally and could have been making underwater sounds.

The **larger** group of about 30 animals also was frost-covered and consisted of adult and **subadult** females and immature animals of both sexes. There were no adult males in this group. However, three very large bulls, spaced about 5 m apart in the water **along** the edge of the floe, were continuously engaged in display routines **all** day; two other, smaller bulls in the water at one end of **the** group, displayed irregularly. The one most distant from the females was least active and, for an hour, simply floated at the surface emitting "bell" sounds, like **bull B**. A few of the youngest **adult** or **subadult** females in the resting group went into **the** water and actively engaged the bulls **in** nose-to-nose and other facial contacts. On several occasions, a female "mounted" a **bull**, and they participated together in considerable surface and sub-surface rolling and splashing. We **felt** that copulation could have been taking **place** during *these* encounters, but we could not identify any copulations with certainty from our position.

21 March 1976, 0800 to **1300** hrs, at **56°45'N, 166°00'W**

We observed a group of 5 **adult** females and *young resting on ice* and a group of 9 bulls and 1 juvenile male also on the ice about 8 m away from the first group (Figure **7c**). One bull was in the water about 0.5 **km** away but apparently was feeding, not displaying, since his dives were **long** (9-10 tin) and he made no surface or underwater sounds. The group of females and young, after about 2 hours of our observation, moved along the

ice and joined the **males**, but other **than** some jostling for **position**, there was no interaction between **the** groups. We heard a few knocks and **an** occasional **bell** sound made by one or more of the bulls on the ice. We heard no underwater sounds by hydrophore.

3 April 1971, 1200 to 1800 hrs, at **61°52'N, 171°45'W**

We encountered a congregation of some 300 animals, nearly **all** of which were asleep on the ice. Approaching on foot, we found them **to** be in several groups, the largest containing about 275 females and young and one centrally located, sleeping bull (Figure 7d). Nearby was a smaller group of about 10 females and 2 adult bulls, **also** sleeping. Farther away were two groups of 7 and 8 pregnant (near-term) females, and scattered in groups **of** 1, 1, 2, and 3 within 1 km of the large central group were 7 adult and **subadult** bulls, also sleeping on the ice. A few animals were in the water near the largest group, and at least one of those was a displaying bull. No other **bulls** were sighted in the water.

5 April 1971, 1700 hrs, at **61°20'N, 173°55'W**

We saw another group of 6 females and young on ice, attended by a large bull who was displaying alongside in the water (Figure 7e).

10 April 1976, 1200 hrs, at **57°30'N, 165°40'W**

We sighted three groups of 6, 8, and 15 females and young on adjacent floes. One bull (**A**) was displaying in the water between the two smaller groups; another bull (**B**) was on the ice about **10** m away (Figure 7f). Bull **B** entered the water and approached **A**, displaying; he was promptly attacked

by A, whereupon he withdrew and hauled out again in the same place.

**Underwater** sounds, evidently from bull A, were like those made by **the** displaying **bulls** observed earlier.

#### DISCUSSION

All previous studies of reproduction in the Pacific **walrus** have been conducted entirely in late spring, summer, and autumn. Those studies have demonstrated **clearly** that implantation of the **blastocyst** takes **place mainly** in June and that the calf is born about 11 months later, usually in May (**Belopol'skii** 1939; **Freiman** 1941; **Nikulin** 1941; Brooks 1954; **Krylov** 19665). However, the **time** and place of mating and the nature of breeding behavior have remained uncertain, for lack of specimens and observations during late autumn, winter, and **early** spring. Our specimens and behavioral observations have now provided enough information to indicate (1) that mating occurs mainly in winter rather than in spring, (2) that the population of females usually is split into two discrete groups (**north-central** and **southeastern**) during that period, and (3) that the social organization and behaviors of adults at that time are distinctively different from those in late spring, summer, and autumn.

Presuming that the mating season was in May and June, **Belopol'skii** (1939), **Freiman** (1941), **Nikulin** (1941), and Brooks (1954) speculated that small, loosely organized "harems" may be formed on the ice. They did not observe any such groups, however, and could only reiterate earlier analogies of sexual dimorphism and gregariousness to support their views of an **otariid-like** system of **polygyny**. Neither have we seen any groups suggestive of an **otariid-like "harem"** structure during observations of hundreds of mixed

herds in the Bering and Chukchi seas in late April to early September. That is, in no case did any bull **appear to** be dominating a group of females or defending a territory; rather, the bulls usually were sleeping or jostling for resting space on the ice, or simply swimming or feeding in the water. **In** that period, the majority of males stay in all-male groups, some of which are very large (hundreds or even thousands). Many of these remain in the Bering Sea throughout the summer, while virtually all of the females and young migrate northward into the **Chukchi** Sea. **We** often have seen and heard **subadult** males in such all-male groups "displaying" to each other, as well as to mature males (cf. Miller 1975, pp. 595-597). In those cases, the young animals' displays were "incomplete" and non-stereotyped; that is, they used only fragments of the full, *stereotyped* array of sounds and actions that characterize the displays of mature bulls in winter.

Conversely, we have **observed** that, in winter, **most** of the mature bulls occur singly and that they tend to follow and closely attend the herds of females. When the females are resting either in the water or on the ice, these bulls engage in ritualized visual and acoustical displays in the water near them. We believe that those displays function both as advertisement of the male's sexual readiness and as reinforcement of a dominance hierarchy among competitive males. Our observations indicate that, when bulls are engaged in this activity, they maintain an individual distance of no less than 5 to 10 m; any closer intrusion is met by threat, followed by fighting. We have never seen aggression of such intensity nor the association of displaying bulls with herds of females in any other season of the year.

For the most part, the **subadult** and juvenile males seem to remain outside the areas where the females and adult males congregate in winter. These younger males associate in small groups (2 to 20), some of which also include one adult male. They tend to become sexually active **later** in the season than do the older males, which would seem to be advantageous as protection from direct competition with their elders. We often have seen subadult males associated with females **later** in the spring and summer, after the adult males are no longer in rut and have formed all-male herds. If these younger bulls play a significant role in reproduction, it may be to fertilize cows that come into estrus after the main mating season.

In March, adult female/male interactions suggestive of **pre-copulatory** play occasionally took place when a female entered the water and swam to a displaying male. These interactions were brief (up to 3 rein), and most of the activity took place underwater. Presumably copulation ordinarily occurs there (Scheffer and Kenyon 1963). About 80% of copulations by walruses in captivity take place in the water (E. D. Asper, Curator of Mammals and Birds, Sea World, Orlando, FL. 32809, pers. **commun.**, August 1974).

Apart from these observations, we feel that the evidence for **polygyny** is compelling on several counts. First, we have observed that females outnumber males by about ten to one in the wintering groups, and that the number of bulls attending a herd of cows seems to vary with its size, suggesting that there is some "optimal" sex ratio. There seemed always to be a few "extra" bulls, however, not far from each herd of females. At times, all of the bulls seemed to be resting on the ice, while the females and young *were* feeding. Because the **older bulls** tend *to come into* rut earliest, we suppose that there is a succession of progressively younger bulls in the mating areas as the seasons advance from winter to spring.

Second, **Ralls** (1977) has pointed out the high predictability in mammals between polygyny and sexual size dimorphism. Adult male Pacific walrus are about 20% longer and 50% heavier than adult females; further, they have larger tusks, much thicker, lumpy skin on the neck and shoulders, and are appreciably paler **in** color than the females (Fay 1982). Body and tusk size of males seem to be the principal determinants of social dominance (Miller 1975). **Immature** males tend to resemble the females in size, coloration, and smooth skin. The degree of **sexual** dimorphism is appreciably less than it is in most other polygynous pinnipeds, which suggests that the walrus's social organization is not as rigid, and that the feedback mechanism favoring dimorphism is not as strong as it is, for example, in the otariids (Bartholomew 1970).

Third, the maturing of the sexes at widely different ages generally is a corollary of **polygyny**, provided that all individuals of the sex which matures early are to breed (Wiley 1978). In all pinnipeds, the females apparently become capable of breeding a year or two earlier than the males (Harrison 1969), but by no means are all of them polygynous. The few that are known to be polygynous show an additional, distinctive feature of development that is a more conclusive corollary: secondary acceleration of growth in the males (Laws 1959). While the males of polygynous species become physiologically capable of breeding not long after the females, they are unable to secure positions in the breeding structure until they have undergone this secondary, post-pubertal growth and have reached a competitively large size, several years later. Male walrus, like the **otariids** and *Mirownga*, also undergo secondary growth, reaching their full adult size about 15 yrs of age, some 5 to 6 years

after they become fertile and 7 to 8 years after the females begin to breed (Fay 1982).

Each of these observations strongly indicates polygynous social **organization**, with inter-male competition for access to **estrous** females, but not necessarily the same kind of organization as that of the other polygynous pinnipeds. It clearly differs from the latter in four major respects: first, there is no discernible **limit** to the amount of breeding space available. The winter pack ice of the Bering Sea approaches a million  $\text{km}^2$  in most years, and at least a third of it is inhabitable by walruses (Burns et al. 1980)? Second, the winter pack ice is continually moving (mainly from north to south), and there is no fixed location within it to which the breeding adults can return each year, other than in very broad, general terms. They do seem to congregate with reasonable regularity within the two large areas shown in Figure 2, but the variations from year to year in extent and quality of the ice preclude site tenacity on a finer scale and, occasionally, preclude even the use of one or both of those areas. Third, the females do not congregate for calving just prior to the mating season. Birth of the calves takes place some months later, during the northward migration. Fourth, males on the ice with the females do not engage the females or other males in any behaviors that seem related to mating or defense of breeding territory. For the most part, they simply sleep, paying no heed to either the females around them or the displaying males in the water. Only the bulls in the water are aggressive toward each other and attentive to the presence and actions of the females.

Thus, **the** circumstances under which walruses **mate** are quite different from those of other polygynous pinnipeds, and this has been the

strongest basis for argument in the past against **polygyny** in walruses. For example, Bartholomew (1970) **dismissed** the possibility of a polygynous system being maintained by a species that copulates in the water, since the greater mobility of pinnipeds there than on land excludes the establishment of stable territories. Stirling (1975) felt that pack ice was unsuitable for organized **polygyny** because of (1) unlimited space for **haulouts** and (2) the instability of the ice itself, which is continually in motion. We suggest that the walrus is an exception. In this case, the "territory" seems to be more a matter of a 3-dimensional "individual space" around the male, in which acoustic displays reinforce the dominance established by body and tusk size and by fighting. The inherent gregariousness of the females, evidently irrespective of any influence by the males, assures unity of the breeding group, even in a habitat that is in motion and constantly changing.

The mating system implied by our observations is somewhat suggestive of a **lek** in that (1) the dominant **males** display before the females in a traditional location (albeit a very large and general one), (2) the sub-dominant males take peripheral positions, outside the "arena", and (3) the female appears to take the active role in consorting with the **male** of her choice within the arena (Wiley, 1978). However, it does not seem to conform to the **lek** criterion of a place where males congregate to attract and court females, who come there just for mating (Wilson 1975). Rather, the females seem to congregate in the two large areas in winter more because of suitable ice conditions than for mating per se, and the males simply go there to engage them. Because the displaying males appear to control access to the females by defending their individual spaces along-side

them, the social arrangement could be construed as a form of "female defense polygyny" in which the gregariousness of the females makes possible the monopolization of each herd by one or a few **males** (Bradbury *In Kolata* 1975; **Emlen** and **Oring** 1977). The fact that **males** continued to display after the females had left suggests that a male's "control" over a given herd is very temporary, perhaps lasting only for the period (24-48 hrs) when the females are resting between feeding bouts.

From what we know of **it** now, the mating system of the walrus seems most similar among pinnipeds **to** that of the northern elephant seal, as described by Le **Boeuf** and Peterson (1969), though it differs in some essential points, presumably because of its occurrence in the moving pack ice, rather than onshore.

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TEXT FOOTNOTES

- 4 Burns, J. J. 1965. The **walrus in** Alaska, its ecology **and** management. 48 p. Alaska Department of Fish and Game, Juneau, AK 99802.
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- 9 Burns, J. J., L. H. Shapiro, and F. H. Fay. 1980. The relationships of marine **mammal** distributions, densities, and activities **to** sea ice conditions. Final report, **R.U. 248/249**, 172 p. Outer Continental Shelf Environmental Assessment Program, **NOAA** Environmental Research Laboratories, Boulder, CO 80302.
- 10 In air, walruses sometimes chatter their teeth, like a rodent. We have observed that "knocks" also can be produced when the jaw is moved rapidly as in percussion of the teeth. Nevertheless, we suspect that the knocking sound is produced by some other means. Fay and **Kibal'chich** watched an adult male "knocking" at close range (3 m) on 21 March 1976 but did not detect any jaw motion; rather, the sounds seemed to come

from deeper in the throat. **Kibal'chich** has **observed** that the bell-sound made by walruses in air occurs at **the** time of inflation of one of the pharyngeal air sacs, but this has not been the case in hundreds of Fay and Ray's observations, in which animals floating at the surface, head down were making the sounds without apparently varying the **volume** of air in their inflated sac(s).

TABLE 1.- Number of **male** walrus examined (n) and percentage in **which** seminiferous tubules contained spermatozoa in hi-monthly samples from the northern Bering and **Chukchi** seas, 1952-63.

Age class (yrs)	November- December		January- February		March- April		May- June		July- August	
	n	%	n	%	n	%	n	%	n	%
5 - 11	14	(14)	3	(67)	5	(40)	9	(44)	3	(0)
12 - 16	18	(72)	3	(67)	4	(50)	14	(50)	5	(0)
17 - 37	6	(100)	3	(100)	8	(25)	10	(10)	6	(0)

TABLE 2.- Results of examination of ovaries from female walruses that were not carrying a large fetus and had not recently given birth (northern Bering Sea 1952-63; southeastern Bering Sea 1976) .

Month	Number examined	Findings in ovaries					
		Follicles < 10 mm diam.		Follicles > 10 mm diam.		New corpus luteum	
		n	%	n	%	n	%
November	1	1	(100)	0	-	0	-
December	13	12	(92)	1	(8)	0	-
January	2	2	(100)	0	-	0	-
February	2	1	(50)	0	-	1	(50)
March	12	3	(25)	0	-	9	(75)
April	15	4	(27)	0	-	11	(73)
May	33	5	(15)	4	(12)	24	(73)
June	10	1	(10)	0	-	9	(90)

TABLE 3.- Composition of visually and photographically surveyed walruses  
in Bering Sea during March-April 1971-76.

Area	Month	No. of animals (both sexes)	Immature (both sexes)	<u>Subadults and adults</u>	
				Males	Females
North-central	Mar ch	907	251	90	566
North-central	early April	332	131 <sup>1</sup>	13	188 <sup>1</sup>
North-central	mid-April	1171	4591	40	672 <sup>1</sup>
East-central	mid-April	255	4	240 <sup>2</sup>	8
East-central	March-April	73	11	54 <sup>2</sup>	8
Southeastern	mid-April	621	237 <sup>1</sup>	38	346 <sup>1</sup>

<sup>1</sup> In original field data, adult females and immature males and females were not recorded separately. Numbers shown here were extrapolated from the totals, based on a sample of 857 animals in which 509 (59.4%) were identified as adult females and 348 (40.6%) as immature animals of both sexes.

<sup>2</sup> More than 75% of these were **subadult** males; at least 90% of all others listed were mature males.

## LIST OF FIGURES

FIGURE 1.-Weight in grams of one testis from each of 109 male walruses taken in the northern Bering and Chukchi seas, in relation date of collection. A-males 14 to 37 yrs old; B-males 5 to 13 yrs old. Each symbol represents one specimen. Curves are visually estimated means.

FIGURE 2.-Chart of the Bering Sea, showing the approximate average pattern of walrus distribution in **mid-** to **late** winter (////) and the two areas in which most of the females and adult males were found in mid-February to mid-April, 1960 to 1972 ( \\\).

FIGURE 3.-Charts of the spatial arrangement of mixed herds of Pacific walruses observed in the north-central Bering Sea in March. The number of adult females and young is shown within each herd. Circles represent bulls that were active in the water (0) and those that were inactive or sleeping (●): a-4 March 1972, b-8 March 1972, c-9 March 1972, d-10 March 1972, e-preliminary (tusk display) interactions of bulls A and B of 9 March. Open **water** and thin ice areas are shaded (see text for further description).

FIGURE 4.-Upper: 10 March 1972, group of 10 females and young resting on ice (center), attended by one displaying bull (arrow) who has just surfaced from a dive. Other females and young engaged in feeding are in the water at left (G. C. Ray photo). Lower: 21 March 1972, bull A (center) in mating display adjacent to group of 20 females and young, in which were two sleeping bulls (F. H. Fay photo).

**FIGURE 5.**-10 March 1972, displaying bull. Upper: making terminal "whistle", just prior to dive. Lower: diving after surface display sequence. Note height to which hind flippers are raised out of the water (G. C. Ray photos).

**FIGURE 6.**-**Diagrammatic** representation of a typical acoustical sequence during one display by an adult male. Insets are actual sonograms of parts of the underwater display (after Ray and Watkins, 1975).

**FIGURE 7.**-Charts of the spatial arrangement of mixed herds of Pacific walrus observed in north-central and southeastern Bering Sea during March and April. Symbols and scale are as in Figure 3: a-17 March 1972, b-21 March 1972, c-21 March 1976, d-3 April 1971, e-5 April 1971, f-10 April 1976 (see text for further description).

