Final Report to Eskimo Walrus Commission

REPRODUCTIVE SUCCESS AND FEEDING HABITS OF WALRUSES TAKEN IN THE 1982 SPRING HARVEST, WITH COMPARISONS FROM PREVIOUS YEARS

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ABSTRACT

Reproductive tracts from 248 females, and stomach contents from 76 males and females taken in the 1982 spring harvest at Alaskan Eskimo communities were analyzed and the results compared with those from previous years. The findings in the reproductive tracts indicated that the percentage of the harvest made up by females giving birth was much higher in 1982 than in 1980, but that the rate of success of the animals in carrying their fetuses to full-term still was low, mainly due to abortions and premature births. The percentage of females in new pregnancy also continued to be low. The stomach contents were similar to those in 1980, supporting the notion that the walruses are continuing to take somewhat less of the clams and more of the other types of invertebrates and fishes than they were in earlier years. The unit weights of prey continued to be about the same as in 1980 but lower than those in 1975. Males and females were taking virtually the same kinds and sizes of prey, whereas their diets apparently were quite different as recently as 1975. As a whole, these findings, combined with data from other sources, suggest that the productivity of the Pacific walrus has declined significantly in recent years, probably due to a high proportion of old, less productive females in the population and, perhaps, a depleted food supply. We conclude that the observed changes are characteristic of a population that is no longer growing but has reached or is tending to reach a stationary state.

INTRODUCTION

The Pacific walrus, *Odobenus rosmarus divergens* Illiger, inhabits the ice-covered Bering and Chukchi Seas, between western Alaska and eastern Siberia, where it has been harvested in small numbers by coastal natives for several thousand years. The dependence of those people on the walrus as a subsistence resource remains strong today. For that reason the governments of the United States and the Soviet Union protect and manage the walrus population primarily for native use.

Management of the Pacific walrus requires that both the U.S.A. and the U.S.S.R. maintain continuous surveillance of the size of the walrus population and its biological characteristics, including the number and sex/age composition of the annual harvests. For history has shown that this resource is highly susceptible to depletion by over-harvesting (Fay, 1957; Kleinenberg, 1957), and that it has been recovering in recent years from such depletion (Krylov, 1968; Fay, 1982).

One aspect of management surveillance is the collection of biological samples from the harvested animals. Those samples are used to assess the current reproductive status and performance of the females, as well as the age composition, physical condition, and feeding habits of the animals in the catch. Such samples were collected and analyzed for about 20 years (1959-79) by the State of Alaska's Department of Fish and Game, to provide scientific guidance for regulation of harvests and restoration of the walrus population to its optimal sustainable level. Similar sampling was conducted by the U.S. Fish and Wildlife Service (FWS) in the spring of 1980 and by the Eskimo Walrus Commission (EWC) in cooperation with the FWS in 1982.

The following is a report on some of the biological samples obtained during the 1982 spring harvests at Little Diomede, Wales, King Island, Nome, Gambell, Savoonga, and Mekoryuk (Fig. 1). Included are the results from analyses of stomach contents and reproductive organs, with a discussion of the significance of those results by comparisons with the data from samples obtained in previous years.

METHODS

The samples were collected, labelled, and preserved by the EWC and FWS field personnel in April-June 1982 and were made available to us within about one month after collection. Our analyses were begun immediately upon the arrival of the samples in Fairbanks and were completed within about two months.

Reproductive Tracts

The reproductive tracts from females had been preserved in 10% formalin; each tract had been labelled with accession number and date. Most of the uteri had been excised just anterior to the cervix, leaving the uterine horns joined at the cervical end and the ovaries still attached to the tubal end. In many instances, the supporting ligaments had been trimmed away to reduce the weight and volume for shipping. Tracts from most of the females which had recently given birth had been further reduced in size by removal of all or part of the enlarged parturient horn.

In our laboratory, we soaked each of the tracts in fresh water for a few hours before processing, to remove some of the formalin and to soften the tissues for easier handling. Insofar as possible, each horn and ovary

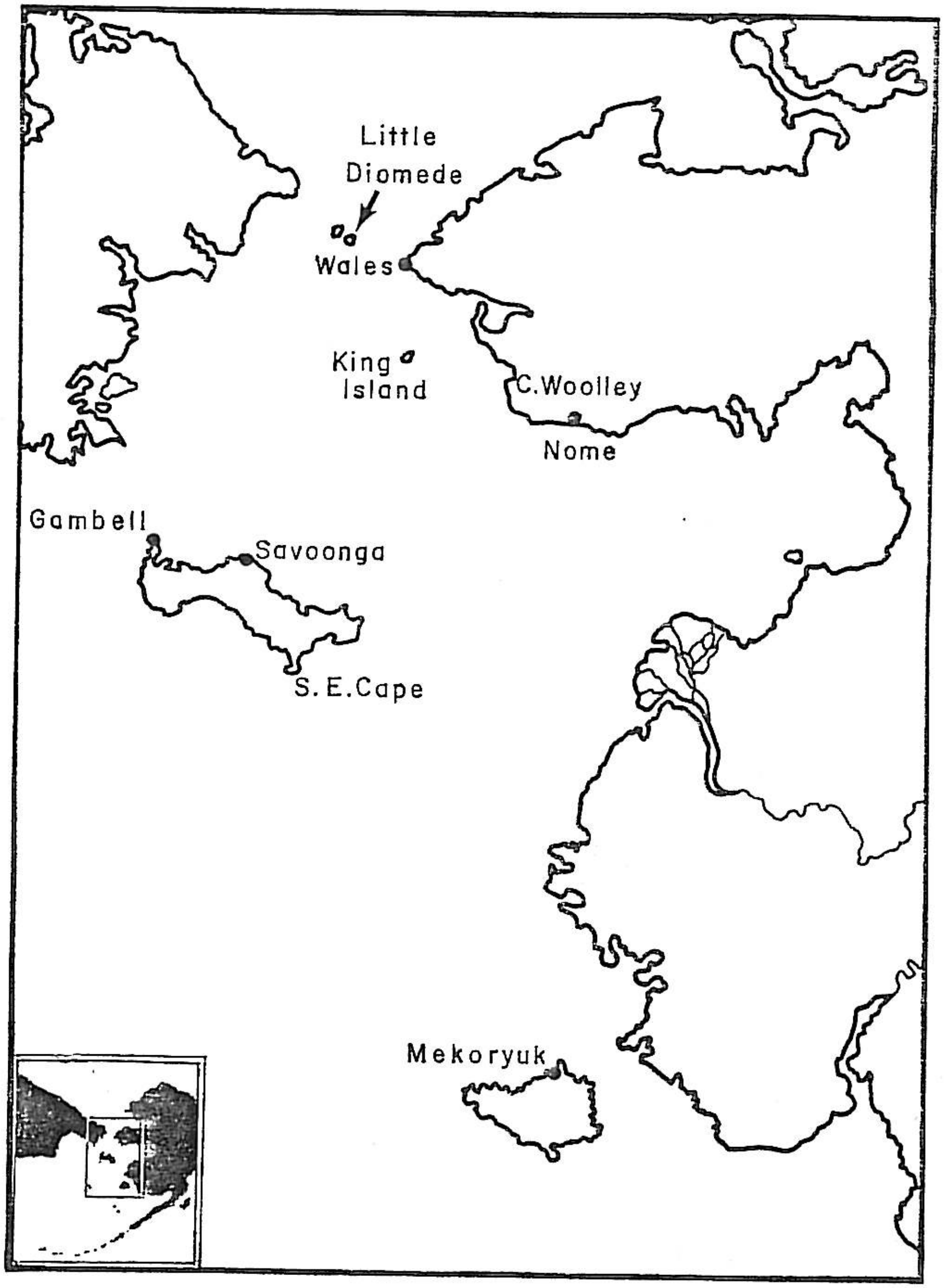

Fig. 1. Locations from which biological samples were obtained during the 1982 spring harvest of walruses by Alaskan natives. The area encompassed by the map is shown at lower left (insert).

per pair was identified as "right" and "left", or if this was not feasible, as "A" and "B". The principal reason for this was to maintain the correct relationship between the ovarian and uterine features on each side of the uterus, for these are of importance for interpreting the individual animal's reproductive history. The length and diameter of each uterine horn were then recorded. Length was measured along the anterior curvature, from the middle of the bifurcation to the tubal end; diameter was measured about midway of the length. The purpose of those measurements was to obtain an estimate of the date when birth or abortion had taken place, based on the rate of reduction in size of the uterus following parturition (Fig. 2).

The uterine horns were then separated by cutting through their junction, and the right (or "A") ovary was removed, trimmed of surrounding tissues, and examined superficially for ovulation scars. The ovary then was sectioned longitudinally in 2-mm-thick slices with a sharp knife; each cut was to the depth of the suspending ligament, leaving the slices interconnected by the ligament. The internal features of the ovary were then examined visually, by leafing through the slices successively, from one side of the ovary to the other. In this process, the kinds and dimensions of the vesicular follicles, corpora lutea, and corpora albicantia were assessed and recorded. The uterine horn then was sectioned longitudinally and inspected for placental scars, endometrial condition, lumenal contents, and embryos. These processes then were repeated with the left (or "B") ovary and horn, following which the ovaries and samples of the placental scars were labelled and stored in 5% formalin for future reference.

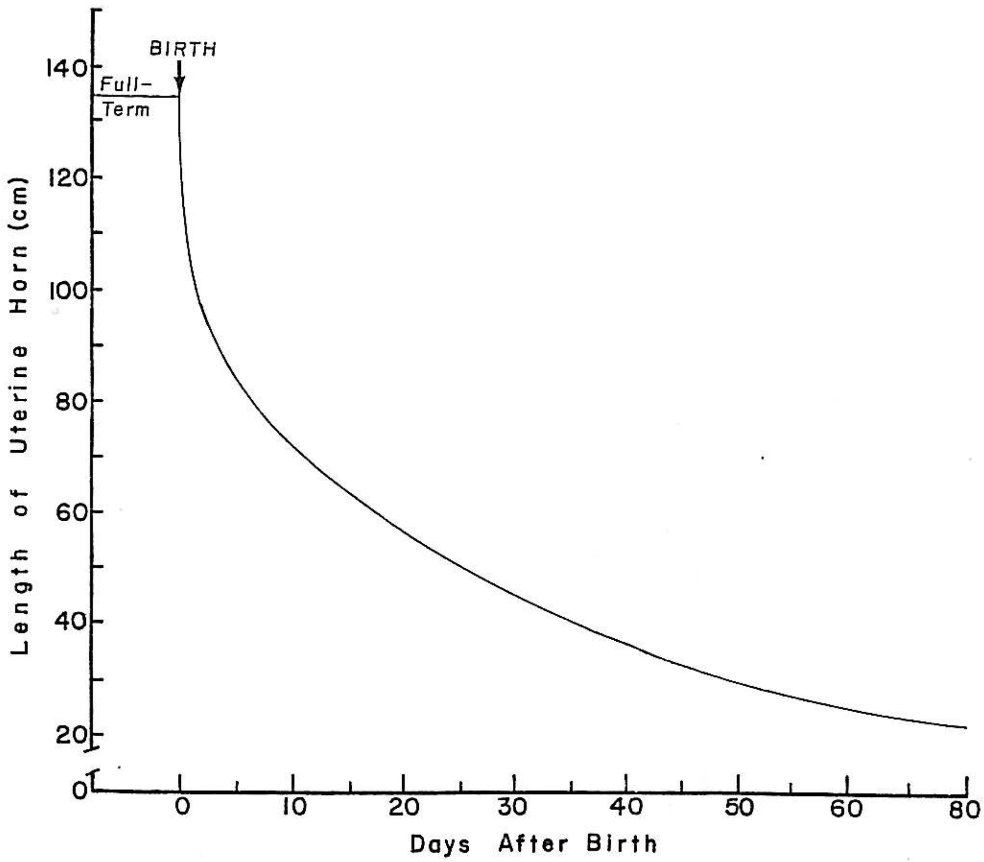

Fig. 2. Involution of the parturient horn of the uterus of the Pacific walrus, following birth. Curve is estimated mean length along the anterior curvature, based on known lengths at full-term and at completion of involutional contraction, with extrapolation of intermediate lengths from proportional values reported by Gier and Marion (1967).

Specific Features

The features in the ovaries and uteri provide a long-term, semi-permanent record of reproductive performance. Both caution and experience are required for their interpretation. Our identifications of those features were based on the following criteria (from Harrison and Weir, 1977; Fay, 1982; Fay and Stoker, 1982):

Ripening follicles.- In nearly all ovaries of adult and subadult walruses, some vesicular follicles can be seen in the cortical layer. These follicles vary considerably in size, in relation to the reproductive status of the animal. "Healthy", ripening follicles have the appearance of more or less spherical cysts, filled with a slightly opaque liquor which, with formalin fixation, has a soft, gelatinous texture. In anestrous animals, these usually are up to 5 mm in diameter; in estrous animals, one or more of the follicles enlarges further to as much as 25 to 30 mm. In the present study, for an index of reproductive condition, we routinely measured only the largest follicle in each ovary.

Degenerate follicles.- These are similar to the foregoing, except that the follicular liquor is very milky, often with a yellowish to pinkish coloration. With formalin fixation, the liquor becomes rather firm and "cheesy". Degenerate follicles often are very large (15 to 20 mm) and occur most frequently in post-estrous animals.

Corpus luteum of new pregnancy.- These were identified by their nearly spherical shape, large size (17 to 38 mm in diameter), softness (i.e., lack of fibrous tissue), usually irregular perimeter, bright yellowish color (sometimes with a pinkish center), and fresh ovulation scar in the adjacent tunic of the ovary, through which the ovum had been released. Pregnancy was confirmed in a few cases by the presence of a newly implanted embryo in the adjacent horn of the uterus. In most cases, however, we were unable to confirm that the animal was pregnant, because the unimplanted blastocyst was too small to be seen with the naked eye. Implantation generally takes place in June, about one month later than the time when most of these specimens were taken.

Accessory corpus luteum.- The accessory corpora were identical in color and texture to the corpus luteum of pregnancy, with which they occurred in the same or opposite ovary. However, they usually were much smaller (3 to 17 mm) and lacked the ovulation scar (i.e., the ovum had not been released).

Corpus atreticum.- Like the foregoing, these were mostly small (1-16 mm) and each lacked an ovulation scar. They differed in that, where they occurred with a corpus luteum of new preganncy, their development was not in concert with the latter. That is, they showed signs of incomplete development or degenerative retrogression, usually with extensive invasion by reddish-brown thecal tissue and some tough, fibrous scar tissue.

Corpus luteum of false pregnancy.- When first formed, these are identical to and indistinguishable from a corpus luteum of new pregnancy, including the presence of an ovulation scar. Hence, they are difficult to identify in cases where pregnancy can not be confirmed by the presence of an implanted embryo. Our basis for identification of a corpus luteum of false pregnancy was its being degeneratively out of phase with the corpora lutea of new pregnancy. That is, even though an ovum had been released and a corpus luteum had formed, that corpus already was showing retrogressive changes, like those in the corpora atretica, presumably because the ovum had not been fertilized or the blastocyst had died or been expelled.

Corpus luteum of term pregnancy.- The corpus luteum at term usually was very large (15-43 mm), very firm (from fibrous invasion), and subspherical, with a smooth, regular border. Generally, one-third to one-half of the corpus was whitish fibrous tissue, often arranged in a stellate pattern, and the remaining patches of lutein cells tended to be more orange than yellowish. The adjacent uterine horn was very large and thick-walled; the opposite horn was much smaller, its endometrium was intensely vesiculate, and its lumen usually contained a large amount of mucous, sometimes mixed with blood.

Corpus luteum/albicans, postpartum.- Following the birth of the calf (or abortion of the fetus), the corpus luteum gradually shrinks to about half of its former size, its lutein cells are depleted, and it becomes a mass of whitish scar tissue — the corpus albicans. This process requires about 3 to 6 months. Early in that period, some thecal invasion also takes place, imparting a somewhat brownish color to the waning patches of lutein cells. The uterus, at the same time shrinks to its former size (which takes about 2 months), and the placental lesion gradually heals.

The presence of a corpus albicans in the ovaries is not reliable evidence that a pregnancy has been completed, however, for any of the five types of corpora described in the foregoing can become a corpus albicans. The corpora albicantia vary greatly in size and appearance, probably because of their different origins. They also vary greatly in duration, some apparently disappearing within 2 to 4 years, whereas others may persist for 15 to 20 years. We presume that the larger, more persistent ones are those derived from corpora lutea of pregnancy, for this often is borne out by their correlation with placental scars for at least the first few years. We counted all corpora albicantia, but we did not accept any as firm evidence of previous pregnancy without the corroborating evidence from a placental scar in the adjacent uterine horn.

Placental scars.- The broad, zonal placenta of the walrus encircles the fetus *in utero* and is intimately attached to the uterine wall. At birth, it tears free from the uterus, leaving behind a raw, bloody lesion in the endometrium and an associated hematic contusion in the underlying tissues. The lesion evidently heals within a month, becoming a "placental scar", dark reddish-brown in color from the residue of hemoglobin and its derivitives in the tissues. Gradually, over a period of 4 to 5 years, the pigments are removed or fade, and the scar becomes successively paler, then disappears.

In the formalin-preserved uteri from the 1982 spring sample, the placental scars were separable into at least six distinct types, on the basis of their size and coloration and the condition of the uterine horn:

1. "Scar" broad (3 to 15 cm wide), rough, dark brown and bloody, found in animals at full term pregnancy or having recently (within 30 days) given birth. Both uterine horns were greatly enlarged, and the endometrium of the non-pregnant horn, in particular, was extremely vesiculate. In the ovary adjacent to the largest horn (with the scar) was a corpus luteum of term pregnancy.

2. Scar smooth to slightly rough, dark brown to reddish-brown, 1.5 to 4.5 cm wide (N = 19, mean ± SE = 2.62 ± 0.14 cm). The uterine horn with the scar ranged from normal non-pregnant size up to 7 cm in diameter. Usually both horns contained some free blood and/or mucous in the lumen, and the endometrium of both was moderately to highly vesiculate. In the ovary adjacent to the horn with the scar was a corpus with structure and appearance intermediate between the corpus luteum of term pregnancy and the corpus albicans. From the size of the horn with the scar and the retrogressive state of the corpus luteum-albicans, these were judged to have aborted or given birth 40 to more than 60 days before the date of collection, well before the normal mid-April to mid-June calving season.

3. Scar orange-brown, smooth to slightly rough, 1.3 to 3.3 cm wide (N = 31, mean ± SE = 2.38 ± 0.10 cm); uterine horn of normal progestational size with no free blood or vesiculation of the endometrium. In the adjacent ovary were one or more corpora albicantia, usually one of which was considerably larger and more rounded than the others, presumably having developed most recently from retrogression of the corpus luteum of term pregnancy associated with the scar. These scars were judged to be about 1 year old (i.e., from term pregnancy in 1981).

4. Scar bright to dull orange, smooth, 1.0 to 4.0 cm wide (N = 56, mean ± SE = 2.31 ± 0.08 cm); uterine horns of progestational size, with no free blood or vesiculation. In the adjacent ovary were one or more corpora albicantia, usually one of which was slightly larger than the others, more dense, and more rounded to oval. These scars were judged to be 2 years old (term pregnancy in 1980).

5. Scar pale orange, smooth, 1.2 to 3.0 cm wide (N = 28, mean ± SE = 1.86 ± 0.09 cm); uterine horns of progestational size, with no free blood or vesiculation. In the adjacent ovary were one or more corpora albicantia, sometimes one of which was slightly larger than the others, more dense, and more regular in outline. These scars were believed to be 3 years old (term pregnancy in 1979).

6. Scars usually very faint, with patchy coloration of endometrium but often with a distinct pale orange band in the muscular layer beneath it, 0.5 to 2.3 cm wide (N = 26, mean ± SE = 1.46 ± 0.09 cm). One or more irregularly shaped corpora albicantia were in the adjacent ovary, sometimes one of which was slightly larger and more dense than the others. These scars were believed to be 4 years old (term pregnancy in 1978).

Numerous other uteri contained no evident placental scars or pigment in the uterine wall, though most had a number of corpora albicantia in their ovaries. These animals were judged not to have been pregnant for more than 4 years.

Stomach Contents

Each sample of stomach contents from one walrus was in a separate, nylon, paint-strainer bag, labelled with accession number, date, and (in most cases) the sex of the animal. Most of these were 5-pound subsamples which had been taken from the cardiac end of the stomach (whereas in 1980, each had been an aliquot from the mixed total contents). This method of collection from the cardiac end was employed, because the materials in that end of the stomach are least affected by digestion.

Each sample was analyzed in the same manner and with the same equipment used by Fay *et al.* (1977) and Fay and Stoker (1982) in their analyses of samples from the 1975 and 1980 spring walrus harvests in the same region. First, each sample was placed in a bucket of fresh water to dilute the formalin and separate the pieces, most of which had congealed together into a more or less solid mass. After decanting some of the liquid, the larger solid parts were removed by hand and sorted into taxonomic groups. The remaining particulate material was then decanted from the sediments (sand and gravel) and poured through a 2-mm-mesh sieve. The materials caught in the sieve also were then sorted into taxonomic groups, insofar as possible.

Then, the number of individual prey represented in each taxonomic group was counted, and after the excess water had been drained and blotted from it, each group was weighed to the nearest gram. Each taxon was identified to the lowest possible nomenclatural level (usually to genus), based on comparison with reference specimens in the University of Alaska's marine collections. Since walruses usually do not ingest whole gastropods and bivalve mollusks, our identifications of those mollusks were based mainly on the soft parts (feet and siphons) or, in the case of the gastropods, on the attached operculum.

For each sample, we recorded the accession number, date, sex, and the name, number of individuals, and total weight for each taxon of prey. Also recorded were the weights of molluscan shell fragments, bottom sediments, and unidentifiable organic digesta.

RESULTS

Reproductive Tracts

Of 249 specimens provided (Appendix I), 198 consisted of all or most of the uterine horns with attached ovaries, 9 consisted of only one uterine horn and/or ovary, 38 were ovaries alone, 3 were uteri without ovaries, and 1 was a piece of meat and fat with no reproductive organs at all. Most of these had been well labelled and well preserved, and 243 of them were sufficiently complete for diagnosis of the current reproductive status of the animals from which they were taken.

Three of the 243 diagnostic specimens were sexually immature animals (NW-15P, DW-213, WL-A). The remaining 240 were 100 from Little Diomede, 9 from Wales, 18 from Nome/King Island, 87 from Gambell, 24 from Savoonga, and 2 from Mekoryuk. All of these were sexually mature "adults", as indicated by the fact that each had at least one corpus luteum or corpus albicans in its ovaries. The following analysis is based on the findings in those adults.

Current Reproductive Status

Of the 240 adult females, 160 (67%) had become pregnant in 1981, and 138 (86%) of those were in full-term pregnancy or had given birth within a few days or weeks of the time when they were killed (Table 1). That is, they had completed or nearly completed a full term of pregnancy and had given birth (or were about to give birth) within the normal mid-April to mid-June calving period. Those conditions were evident from the fact that, in each case, both uterine horns were greatly enlarged and thickened, and

Table 1. Summary of reproductive status of female walruses obtained in each locality during the 1982 spring harvest.

Locality	Total no.	Term or recent birth[1]	Abortion or early birth[2]	New pregnancy[3]	Barren[4]	Immature	Incomplete[5]
Nome/King I.	23	3	1	11	3	1	4
Gambell	88	64	6	9	8	0	1
Savoonga	24	9	5	8	2	0	0
Diomede	101	57	9	26	8	1	0
Wales	10	3	1	4	1	1	0
Mekoryuk	2	2	0	0	0	0	0
Totals	248	138	22	58	22	3	5

[1]In full-term pregnancy or having given birth within the normal mid-April to mid-May calving period.

[2]Fetus aborted in winter or calf born permaturely, before the normal calving period.

[3]Normal, new pregnancy from the 1982 breeding season, not including new pregnancies in animals that aborted early in gestation.

[4]Mature animals, neither in term nor new pregnancy, and not including those which aborted.

[5]Lacking in diagnostic materials sufficient for determination of current reproductive status.

the ovary that was attached to the largest horn contained a retrogressive corpus luteum, typical of those in females at term pregnancy or recent parturition.

Of these term to postpartum females, 126 (91%) were accompanied by newborn calves; nine apparently had lost their calves, and three were still pregnant with a full-term fetus.

The other 22 animals (14% of the 1981 pregnancies) either had given birth to their calves unusually early in 1982, or they had aborted their fetuses at some time during the winter, well before the gestation was completed. This was indicated in each case by (a) the presence of a recent (brown or reddish-brown) placental scar in the uterus, (b) contraction of the uterine horn with the placental scar to or nearly to its normal non-pregnant size, and (c) our finding that the associated corpus luteum-albicans was more fibrous and consolidated than those of animals known to have given birth within the normal mid-April to mid-June calving period.

The contracted uterus in 13 of those specimens indicated that they had aborted very early, possibly in January, February, or early March. None of those 13 was accompanied by a calf, hence we assume that their aborted fetuses had not survived. Nine of these females were in estrus again, and two that apparently had aborted very early in the winter were pregnant again at the time when they were killed. Each of the latter two, taken in early June, had a large, new corpus luteum of pregnancy in one ovary, and a small embryo already implanted in the adjacent uterine horn.

In the last nine animals that had conceived in 1981, the size of the uterus suggested that they had given birth or aborted the fetus in late March or early April. Only four of those animals were accompanied by calves; the calves of the other five apparently had not survived or had been separated from the mother.

In addition to the two new pregnancies among the aborting animals, 58 others (24% of the total adults) also were newly pregnant. Each of these had a large (17-38 mm in diameter), new corpus luteum in the ovaries, and three had one or more accessory corpora, as well. The uteri of 37 of these animals, taken between 5 May and 14 June, did not contain any embryos large enough to be seen with the unaided eye, but we assume that a microscopic blastocyst was present in each. However, 19 others taken between 21 May and 9 June, did contain small embryos, most of which were in an early stage of implantation (Table 2). The status of two specimens could not be determined, because the uterine horns had been removed.

At least 5 of these 58 newly pregnant females were accompanied by newborn calves, obviously not their own but apparently taken in fosterage. At least 44 others were not with calves; the status of the other 9 was not recorded.

Lastly, 22 animals (9% of the total adults) were classified as "barren", because they had not become pregnant within the past year, nor had they given birth or aborted more recently than one year earlier. Nine of these appeared to be in estrus, for their ovaries contained ripening follicles 7 to 15 mm in diameter. The ovaries of two of those and three others contained several atretic follicles; two more had corpora of false pregnancy, and eight showed no signs of recent reproductive activity, although they had several corpora albicantia from ovulations in previous years.

Six of these 22 barren females were reported to have been accompanied by newborn calves, which they may have taken in fosterage. Twelve had no calves with them, and the status of the other four was not recorded.

Table 2. Frequency of occurrence of free and implanted embryos in relation to date of collection of walruses, during the 1982 spring harvest.

Condition of embryo	May				June	
	5-10	13-19	21-25	27-30	2-7	8-14
Free	3	4	8	11	4	7
Implanted	0	0	2	4	1	14
Total	3	4	10	15	5	21

Current Fertility

Approximately 93 of the animals in this sample were potentially capable of being bred in the 1982 breeding season. Included were the 22 classified as "barren", 58 identified only as "new pregnancies", and the 13 that aborted early in the winter. Of those, 60 (64%) appeared to have been bred successfully, 2 (2%) experienced false pregnancy, 16 (17%) were still in estrus, and 15 (16%) were reproductively inactive at the time when they were killed.

Of 63 ovulations which had taken place in the 1982 breeding season, 60 (95%) probably were fertilized successfully, judging from the presence in each case of a well developed, functional corpus luteum of new pregnancy in the ovaries. The other 3 (5%) were not successfully fertilized, as indicated in two cases by the presence of a corpus of false pregnancy and, in the third, by an accessory corpus from which the ovum had been released. Because about two-thirds of the cases of probable success had not yet reached conception (= implantation, in which some further failures could be expected), the actual rate of success in new pregnancy could have been slightly lower than 95%, had these animals survived. The rate also would have been lowered, had any of those in estrus shed their ova, for the probability of fertilization during the spring and summer is extremely low, because of the scarcity of fertile males at that time.

Recent Fecundity

The recent reproductive history of individual walruses has been interpreted previously by two methods: (1) counts of corpora albicantia in the ovaries (Chapskii, 1936; Burns, 1965; Gol'tsev, 1975), and

(2) assessment of placental scars in the uterus (Fay, 1982). Because the corpora albicantia may persist in the ovaries for the lifetime of some animals, one is tempted to count them in each individual and interpret this as the full record of the number of pregnancies that the individual has completed. Unfortunately, as Burns (1965), Krylov (1966), and Fay (1982) have observed, such counts tend to overestimate fecundity (birth rate), because the corpora albicantia can be formed not only from corpora lutea of pregnancy but from accessory, atretic, and false pregnancy corpora, as well. For example, in this 1982 sample, several young females that had one or two large corpora albicantia in their ovaries obviously had not given birth to any calves, for their uteri were sinuous and of very small diameter (1.5 cm), typical of sexually immature individuals, and there were no placental scars in their uterine horns. Previous experience has shown that, following at least one pregnancy, the uterine horns of young females do not contract to their former, immature condition but become stouter (2-3 cm in diameter) and are smoothly arched, rather than sinuous.

Placental scars are more dependable as indicators of past pregnancies than the corpora albicantia, because each scar is firm evidence that a placenta was attached to the uterine wall for all or most of a gestation. Their main disadvantage is that they apparently do not persist longer than about 4 years; hence, they are indicative of only that much of the past reproductive performance. Furthermore, in the enlarged parturient horn of females that have recently given birth, the placental scars from previous pregnancies are obscured by congestion and discoloration of the uterine wall. For that reason, the record of previous pregnancies in the postpartum females tends to be incompletely detectable by visual means and to underestimate past reproductive performance.

The most complete, reliable record of past reproductive performance from placental scars is found in the uteri of barren, newly pregnant, and abortive animals, for all of the scars from the past four years are clearly visible. Judging from the placement of those scars and of the newly implanted embryos, successive placentations in the same horn may be adjacent to but not overlapping one another. That is, there is a tendency for new implants to be situated near but not overlying any earlier placentations. Hence, the number of detectable scars in these animals appears not to be affected by newer ones overlying any of the old (contrary to our earlier prediction: Fay and Stoker, 1982). In this 1982 sample, the number of scars evidently was equal to the actual number of near- to full-term pregnancies that each animal had experienced in the previous 4 years. Because those animals were not taken selectively by the hunters (except for tusk size), they probably tended to approximate a random historical sample, representative of the population at large (Fay, 1982).

There were 99 such specimens in this 1982 spring sample. Of those, 51 had only one placental scar, 24 had two scars, 4 had three scars, and 20 had none. Nineteen of these scars were from pregnancies that had ended in the current year (i.e., from early births and abortions), 20 had ended in 1981, 39 in 1980, 12 in 1979, and 19 in 1978. The average percentage of these females that had completed or nearly completed a pregnancy per year, from 1978 to 1981 was about 31% (Table 3). This was not the rate of live births, however, for it included fetuses that were born dead, as well as abortions and premature births, which have been very common in recent years.

Table 3. Percentages of near-to full-term pregnancies per year, for the past five years, indicated by placental scars in the uteri of walruses taken in the 1982 spring harvest.

Sample	Year pregnancy completed				Total
	1978	1979	1980	1981	
Sample size	59	68	76	83	286
No. of pregnancies	19	12	39	20	90
Percentage	32.2	17.6	51.3	24.1	31.5

Information gained from this and a previous study (Fay and Stoker, 1982) has indicated that the percentage of gestations ending in failure due to abortion and premature birth amounted to at least 27% in 1980 and 11% in 1982. In addition, Fay (1982) estimated earlier that about 2% of the full-term fetuses are born dead. With that kind of mortality, the live birth rate during 1978 to 1981 could have been as low as 23 to 25%, rather than 31%. That it actually was very low is indicated further by the fact that, of the 111 pregnancies recorded, at least 25 (22%) had ended in failure. Of those, 15 were animals that had aborted early in 1982 and were not accompanied by calves (i.e., their abortuses apparently had died). The failure of the other 10 was implicite in the fact that each of the animals had been pregnant in two successive years. Walruses can breed in successive years only when the first fetus is aborted early enough in gestation (e.g., December-January) for the female to ovulate again in February or March of that winter. In such cases, the probability of survival of the aborted fetus appears to be extremely low.

Other Comparisons with Previous Years

The spring harvests have been monitored most effectively for the longest period at Gambell and Little Diomede, beginning in 1952 in both localities and continuing to the present. The walrus hunters at Gambell apparently have always been highly selective in their harvests of female walruses, preferentially taking those with newborn calves whenever possible (Fay, 1958). They do this traditionally because the flesh of the calves is cherished as dried meat for human consumption during the summer, and the skins are required for making rawhide lines for their harpoons and lashings for their walrus hide boats. For that reason, the annual catch of adult females near Gambell has tended to be made up predominantly of postpartum animals, accompanied by newborn calves. At Little Diomede, however, the hunters apparently do not usually select primarily for females with calves (Kenyon, 1958), for their traditions differ from those of the St. Lawrence Islanders. Nevertheless, about half of their annual catch of adult females also has tended to be of full-term and newly postpartum animals, possibly because those are better represented in the herds available at the time of the hunt.

From the 1950's to late 1960's, the proportion of full-term and postpartum females in the catches at both Gambell and Diomede appeared to be comparatively stable, tending to cluster around means of about 83% at Gambell and 47% at Diomede (Fig. 3). More recently, however, the proportions taken at both localities have been highly erratic and apparently have varied about substantially lower means (e.g., 42% and 37%, respectively, from 1979 to 1982). Remarks from the hunters about a scarcity of calves as early as 1977 (J. J. Burns, unpublished notes) suggest that this change was underway by that time, and that it was not due to any difference in hunter-selection but to a general decrease in the availability of postpartum animals. Such a decrease in availability could have been caused by (1) a general decline in the productivity of the population, (2) inacessibility of the animals because of weather or ice conditions unfavorable to the hunters, or (3) a change in the migration routes used by the term and postpartum females. To the best of our knowledge, neither (2) nor (3) were viable options in this case; neither the weather, the ice, nor the migration routes appeared to be remarkably different than they had been in

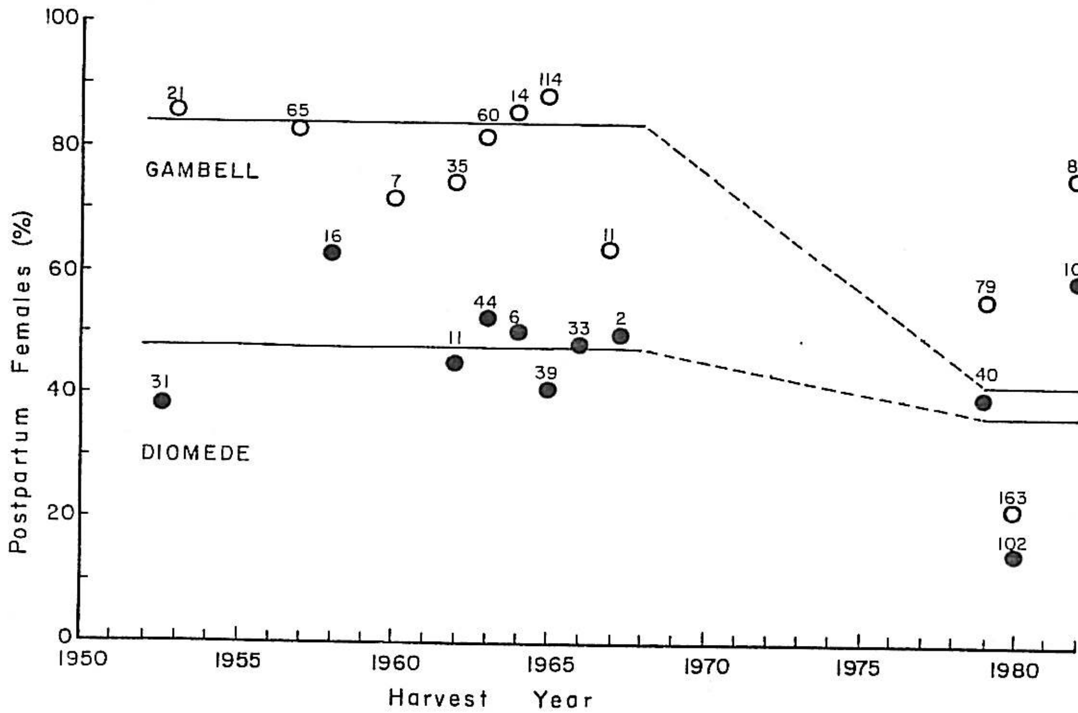

Fig. 3. Proportions of full-term and postpartum individuals (combined) in the catches of adult female walruses at Gambell (o) and Little Diomede (•), spring 1952-68 and 1979-82. The number of specimens in each sample is indicated above each symbol. Solid lines are the means for those time periods in each locality; dashed lines suggest the trends that occurred in the intermediate period, 1969-78. (From J. J. Burns and F. H. Fay, unpublished data)

the 25 years prior to 1977. Option (1), however, is supported both by our findings and by those of the Alaska Department of Fish and Game, as regards comparative reproductive success from the 1950's to early 80's (Burns, 1965 and unpublished data; Fay, 1982; Fay and Stoker, 1982 and this report). Those findings are as follows:

Pregnancy rate.- Because the duration of pregnancy in walruses is about 16 months, the individual female does not normally breed each year but tends to breed in alternate years (biennially) or less often (Brooks, 1954; Mansfield, 1958). For that reason, nearly half of a *random, representative* sample of the adult females taken in any spring will tend to be made up of newly pregnant individuals (i.e., bred in the current year), a slightly smaller proportion will be of individuals at full-term or postpartum (i.e., bred in the previous year), and a much smaller proportion will be of reproductively inactive (barren) animals. The percentage of newly pregnant animals in such a sample can be taken as an estimate of the "pregnancy rate" for the entire adult female segment of the population; that is, as an estimate of the percentage of females that became pregnant that year.

Unfortunately, such "random, representative" samples are very difficult to obtain (Fay, 1982), but an index of the pregnancy rate can be derived from the harvest samples. Because of hunter-selection, the harvests tend to contain an over-representation of postpartum females and an under-representation of newly pregnant and barren animals, as noted earlier. If we exclude the postpartum animals, however, the remainder of each harvest sample should tend to approach a random sample of the ratio between newly pregnant and barren animals, for there is no chance for selective taking of either of those classes. There will be some bias toward older animals, because of selection for large tusks, but that should be similar in all of the samples.

In harvest samples of non-postpartum animals, the average proportion of new pregnancies during the 1950's and early 60's was about 72% per year (Fig. 4). By the late 1970's and early 80's, however, that proportion had declined to about 60% per year. This is a highly significant difference ($X^2 = 6.69$, $p < .01$), which indicates that a definite change took place, either in the pregnancy rate of the overall population, or in the average age of the females in the harvest (or both). We believe that the age composition of the samples did change during that period, and that the change was a reflection of conditions in the population as a whole, for the following reasons:

1. The percentage of newly pregnant females in each age class varies greatly, being highest in the 7- to 10-year olds and successively lower in the older animals (Table 4). That is, the older the female, the less likely she is to be pregnant — a fact that every seasoned walrus hunter is well aware of. Therefore, if the recent harvest samples were made up predominantly of older animals than those taken in the 1950's and 60's, one would expect the percentage of new pregnancies to be lower in the recent than in the earlier samples. The hypothesis, then, is that the age composition of the samples did change.

2. In the reproductive organs examined by us and by the Alaska Department of Fish and Game, over the years, the number of corpora lutea and albicantia in the ovaries of each specimen was recorded. Because most of the corpora albicantia in the ovaries persist for many years, their number in each

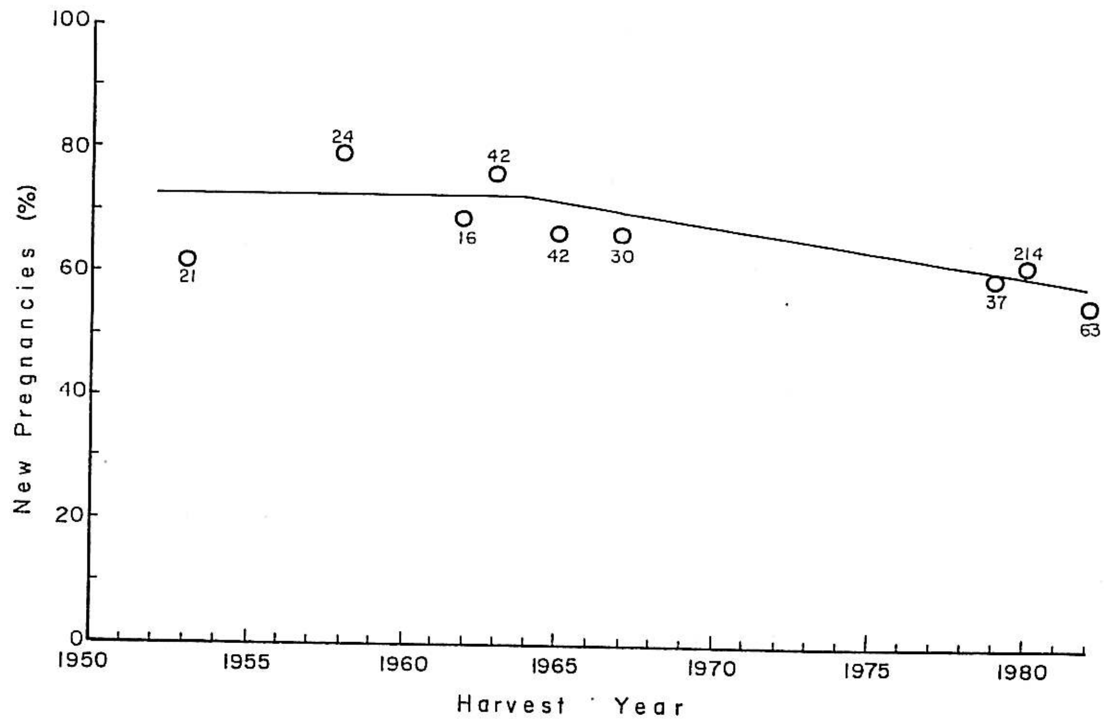

Fig. 4. Proportions of new pregnancies among the non-postpartum females in the catches of walruses at Alaskan native villages, 1952-68 and 1979-82. The number of specimens in each sample is indicated above the symbols. Curve is suggested trend. (From J. J. Burns and F. H. Fay, unpublished data)

Table 4. Estimated average proportions of walruses in each age class from 4 to 20 years achieving estrus, conception, and birth.

Age (yrs)	Ovulating[1] (%)	Conceiving[2] (%)	Bearing[3] (%)
4	10.7	4.7	2.4
5	41.2	26.0	15.9
6	54.6	41.5	29.9
7	65.1	55.3	44.2
8	61.0	54.9	47.8
9	59.3	55.7	50.7
10	55.2	53.0	49.8
11	52.0	49.9	47.4
12	49.0	46.1	42.9
13	47.0	43.2	38.4
14	45.0	40.0	33.6
15	43.0	37.0	29.6
16	41.0	34.0	25.8
17	39.0	31.6	23.1
18	38.0	29.6	20.7
19	37.0	27.8	18.6
20	35.0	25.2	16.4

[1]Percentage of females ovulating that developed a corpus lutem (from Fay, 1982, table 34).

[2]Percentage of females achieving implantation of an embryo in the uterus, based on graphic interpolation of average values from rates of conception success (from Fay, 1982, table 35).

[3]Percentage of females that successfully completed a full term of pregnancy and gave birth to a live calf, based on graphic interpolation of average values from observed rates of success in gestation (from Fay, 1982, table 35).

animal tends to increase in cumulative fashion, as the animal grows older (Burns, 1965; Krylov, 1966). Given that the relationship between age and number of corpora is known (Fay, 1982: Fig. 125), then we can compare samples among years to test the hypothesis that the age composition of the samples changed. The results of that test, taking the samples from Diomede and Gambell, indicate that, whereas the modal number of corpora per individual was about 2 (probable age = 8 to 10 years) in the 1950's and early 60's, it had risen to about 5 (probable age = 14 to 18 years) by the early 1980's in both localities (Fig. 5). The respective average numbers were about 3.4 (age 9-10 yrs) and 5.6 (age 17-20), and that difference appears to be significant.

Thus, a shift in age composition of the catch to older animals in recent years is clearly indicated, and the fact that it took place in the same way both at Gambell and at Diomede, in spite of different selective practices, suggests that it has been a population-wide phenomenon.

Reproductive success.- The comparative success of female walruses in achieving fertilization of the ovum, implantation of the blastocyst, and gestation of the fetus to normal birth also appears to vary considerably with age (Fay, 1982). Because we have not yet determined the ages of the individuals in the recent samples, we have not been able to compare this among the samples, age-class-by-age-class, but we did derive some overall estimates (Table 5). These suggest that the percentage of ovulations that resulted in formation of a corpus luteum has not changed significantly in recent years, but the percentage of gestations resulting in normal births has decreased significantly. That decrease apparently has been the result primarily of an order of magnitude increase in abortion and premature

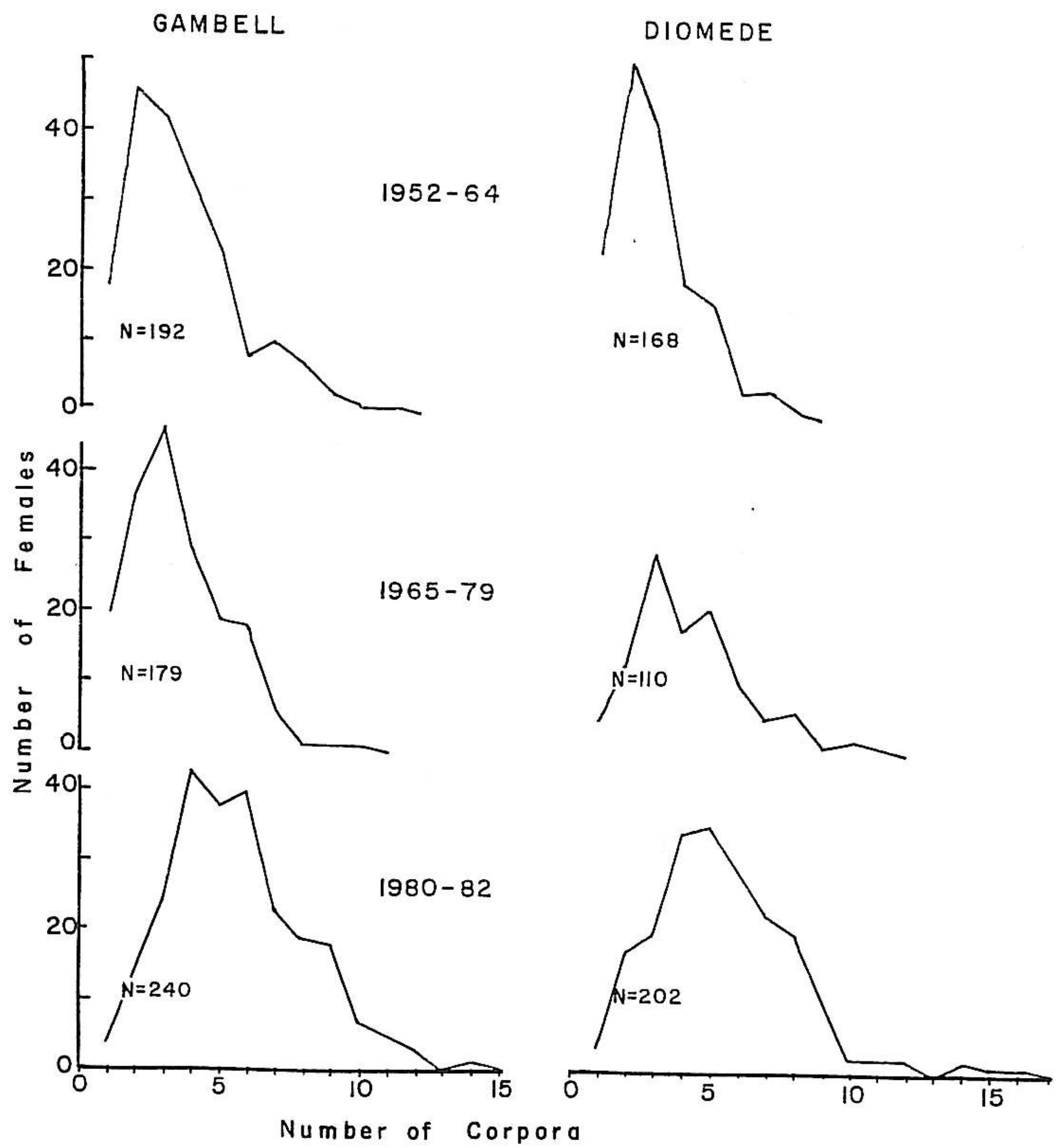

Fig. 5. Comparative frequency of occurrence of numbers of corpora (lutea and albicantia, combined) in the ovaries of adult females from the spring harvests at Gambell and Little Diomede, 1952-82. Sample sizes (N) are shown for each curve. (From J. J. Burns and F. H. Fay, unpublished data)

Table 5. Observed average rates of success in pregnancy of walruses taken during the native harvests from 1952 to 1982.

Stage of pregnancy	Harvest years A 1952-1968	B 1975-1979	C 1980-1982	Probability of difference (A:C)	
Fertilization:					
No. of ovulations	312	99	216		
% successful[1]	84.3	89.9	89.4	χ^2=2.77	p<.10
Gestations:					
No. implanted	203	80	230		
% carried to birth[2]	98.5	90.0	83.5	χ^2=28.47	p< .025

[1] Ovulations resulting in formation of a corpus luteum of pregnancy.

[2] Pregnancies resulting in birth during the normal calving season or prematurely if the calf apparently survived.

births, from about 1.5% to 16.5% of the fetuses per year. A change of that magnitude might have been caused by an increase in the age composition of the catch, if that increase were as great as suggested in the foregoing analysis. The older females appear to have much lower success in carrying a fetus to full-term than do those in the 9- to 12-year-old range (Table 4).

Live births.- From 1952 to 1966, Burns and Fay (unpublished data) personally observed that all but 10 (6%) of 156 term and postpartum females taken at Gambell and Little Diomede during the spring hunts were accompanied by living calves or contained a living fetus. In the spring hunts of 1980 and 82, all but 12 (7%) of 169 such females taken principally at Gambell and Diomede had calves or fetuses. Since these proportions are not significantly different, we conclude that the rate of late fetal mortality and/or loss of calves soon after birth, in the normal mid-April to mid-June calving period, has remained stable for the past 30 years.

Overview.- The reproductive data from the spring harvest samples, obtained principally at Gambell and Little Diomede over the past 30 years, may be summarized as follows:

The estrous females achieved pregnancy with about the same level of success throughout that period, but the proportion of females breeding each year declined significantly toward the end of the period. The percentage of those pregnancies that were successfully completed also decreased sharply, mainly due to a large increase in abortions and premature births. Of the pregnancies that were successfully carried to completion, the proportion resulting in stillbirths and death or loss of newborn calves during the period of birth did not change.

That these conditions were reflective of the population as a whole and not simply artifacts of hunter-selection in the harvests is indicated by the fact that the samples from both Gambell and Diomede showed similar changes, though the selective processes differ in those two localities. The implications of the findings are that the walrus population now contains a much larger proportion of old adults than it did 20 or 30 years earlier, and that its productivity has declined, principally as a consequence of that condition. We suspect that other factors may have played a part in that decline, as discussed later in this report.

Regional Comparison

The walrus population in winter tends to be divided into two major segments, one of which resides in the northcentral Bering Sea, generally to the west and southwest of St. Lawrence Island (Fig. 6), and the other in the southeastern Bering Sea, in the vicinity of Bristol and Kuskokwim Bays (Fay, 1982). At the time of the spring walrus hunt, the animals from these two segments are in migration northward to summer feeding grounds in the Chukchi Sea. Those from the northcentral area become available to the hunters at Gambell, usually from late April to late May, as the animals move up through Anadyr Strait (between St. Lawrence Island and the Chukchi Peninsula). The same animals become available to the hunters at Little Diomede, generally from mid-May to early June, as they pass through western and central Bering Strait.

The southeastern wintering segment is hunted in the vicinity of Nunivak Island in April to early May and by the hunters of Savoonga, Nome, and King Island, generally from mid-May to mid-June, as they pass through

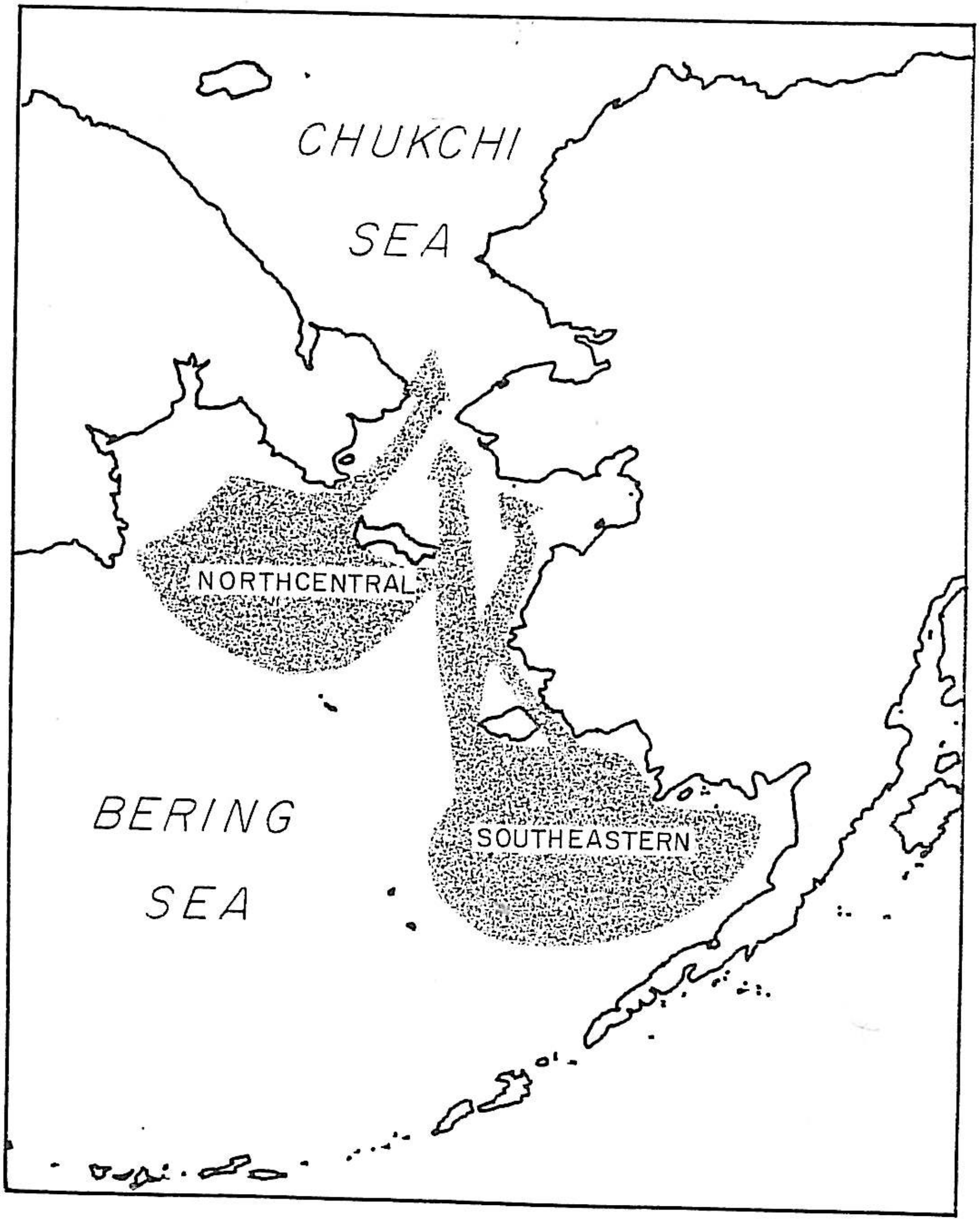

Fig. 6. Suggested spring migration routes of walruses from the two principal wintering areas in the Bering Sea. (Based on Fay, 1982:figs. 5-9)

the northeastern Bering Sea, including outer Norton Sound. They become available to the hunters at Wales and Little Diomede in late May to mid-June, when they pass through eastern Bering Strait. Thus, taking into account the timing of the catch and the location in which it was taken, one can divide the harvest sample approximately into two parts, each of which was drawn from one of the main wintering segments of the population. Since the mating season of these animals is in winter, when the two segments appear to be geographically isolated from each other, Fay (1982) has suggested that they may be reproductively discrete subpopulations which should be considered separately in any management scheme. Whether this idea is valid or not, they certainly occupy different habitats and are likely to be influenced by different ice and feeding conditions, which could affect their survival and productivity differently.

Based on these considerations, we divided the 1982 harvest samples into two parts, the first (northcentral segment) from the catch at Gambell and at Little Diomede up to 5 June, and the second (southeastern segment) from Mekoryuk, Savoonga, Nome-King Island, Wales, and Diomede after 5 June. The results (Table 6) indicate, first, that a significantly greater proportion of the catch from the northcentral than from the southeastern segment was made up of cows that had recently given birth or were still in term pregnancy ($X^2 = 23.76$, $p < .01$). This is to be expected, because of the selection practiced by the Gambell hunters for cows with newborn calves. Probably that same selection was responsible for the significantly higher proportion of those cows that were accompanied by calves ($X^2 = 5.44$ $p < .05$), and for the tendency for a lower proportion of pregnancies begun in 1981 which ended in abortion or premature birth ($X^2 = 3.51$, $p < .10$). The

Table 6. Comparative reproductive parameters of females drawn from the two principal wintering segments of the Pacific walrus population during the 1982 spring harvest.

Wintering segment and sample size (N)	Term and postpartum Total	Term and postpartum With calves	Aborted or permature births	New pregnancies	Barren
Northcentral[1] (N=142)	100	97	11	21	10
Southeastern[2] (N=98)	38	32	11	37	12

[1] From the harvest at Gambell and from Diomede up to 5 June.

[2] From harvests at Mekoryuk, Savoonga, Nome-King Island, Wales, and from Diomede after 5 June.

proportion of "potentially pregnant" females that had been fertilized successfully did not differ significantly between samples. Hence, we conclude that the productivity of both segments probably was about equal.

Stomach Contents

Of the 79 stomach content samples received, 27 were from Little Diomede, 3 from Wales, 2 from King Island, 2 from Cape Woolley, 2 from Nome, 33 from Gambell, 4 from Savoonga, 1 from Southeast Cape (St. Lawrence I.), and 5 were from Mekoryuk (Appendix II). One of those from Nome (N-1) and two from Gambell (G-163, G-233) consisted only of congealed blood and/or stones, hence they were discarded without further analysis. The remaining 76 samples comprised about 120.1 kg, of which 109.7 kg were organic matter and 10.4 kg were inorganic sediments (sand and gravel). Since most of the samples were 2 to 3 liter aliquots drawn from much larger volumes, these weights are not representative of the total weight of materials in the 76 stomachs, though they are representative of the proportions of prey. Some 16,750 individual prey were identified in the samples, and these represented at least 45 genera of benthic organisms from 12 phyla (Table 7). The diversity of prey from each locality was proportional to the number of samples, as might be expected. The greatest diversity (32 genera) was at Gambell, from which the most samples (31) were obtained; the lowest diversity (4 genera) was at Cape Woolley, from which only two samples were obtained.

Included in the weight of organic matter were about 4.2 kg of fragmented digesta not identifiable to taxon, and 71 g of molluscan shell fragments, most of which were identifiable to genus. Loose periostracum (4.8 kg) from siphons of *Mya* spp. and *Hiatella* was included in the respective

Table 7. Frequency of occurrence and diversity of prey in the stomach contents of walruses taken in each locality, spring 1982.

Taxon	Diomede (N=27)	Gambell (N=31)	S.E. Cape (N=1)	Savoonga (N=4)	Cape Woolley (N=2)	King Island (N=2)	Nome (N=1)	Wales (N=3)	Mekoryuk (N=5)
Coelenterata									
Anthozoa	3	2	0	0	0	0	0	0	2
Scyphozoa	4	0	0	0	0	0	0	0	0
Annelida									
Nephthys	7	8	0	2	0	1	1	0	2
Arenicola	0	4	0	2	0	0	0	0	2
Phyllodoce	0	0	0	0	0	0	0	0	0
Lumbrinereis	0	2	0	0	0	0	0	0	1
Brada	0	1	0	0	0	0	0	0	0
unidentified	1	2	0	0	0	0	0	0	1
Sipunculida									
Golfingia	10	3	0	1	0	0	0	0	0
Echiurida									
Echiurus	5	6	1	3	2	0	0	0	1
Priapulida									
Priapulus	11	8	1	3	0	1	1	1	1
Nemertinea									
unidentified	0	1	0	1	0	0	0	0	0
Mollusca									
Neptunea	8	13	0	3	0	0	0	0	0
Buccinum	4	11	0	2	0	0	0	0	0
Natica	11	10	1	2	0	2	0	0	0
Polinices	14	16	1	3	0	1	0	0	0
Turitella	0	0	0	0	0	0	0	0	3
Margarites	0	1	0	0	0	0	0	0	1
Serripes	14	27	1	3	0	1	1	0	0
Mya	27	27	1	2	2	2	1	0	1
Spisula	0	11	1	0	0	0	1	3	3
Tellina/Macoma	6	11	1	2	0	1	0	0	1
Hiatella	13	0	0	0	1	1	1	1	2
Yoldia	0	2	0	2	0	1	0	0	0
Siliqua	0	0	0	0	0	0	1	0	0
Nucula	0	0	0	1	0	0	0	0	2
Octopus	4	2	0	0	0	0	0	0	0

Table 7. Continued

Taxon	Diomede (N=27)	Gambell (N=31)	S.E. Cape (N=1)	Savoonga (N=4)	Cape Wooley (N=2)	King Island (N=2)	Nome (N=1)	Wales (N=3)	Mekoryuk (N=5)
Crustacea									
Anonyx	0	2	0	0	0	0	0	0	0
Byblis	1	1	0	0	0	0	0	0	0
Ampelisca	0	1	0	0	0	0	0	0	0
Argis	2	6	1	1	0	0	0	0	2
Pagurus	3	5	0	2	0	0	0	0	0
Hyas	1	5	1	1	0	1	0	0	0
Echinodermata									
Cucumaria	16	5	1	0	1	1	1	3	3
Urochordata									
Pelonaia	0	1	0	0	0	0	0	0	0
Brachiopoda									
unidentified	0	0	0	0	0	0	0	0	1
Vertebrata									
Ammodytes	0	9	0	1	0	0	0	0	0

total weights for each of those genera. Not included in either the total numbers or weights were 297 gastropod operculae and 15 octopus beaks, weighing about 50 g. These were recorded only as "trace" occurrences, inasmuch as such indigestible hard parts apparently are retained in the stomach for some time after the fleshy parts have been digested.

Regional Comparison

About two-thirds or more of the identified prey in nearly all of the areas were bivalve mollusks (Table 8). Of those, clams of the genus *Mya* predominated in most of the samples. As a whole, the samples from the Bering Strait region had a high proportion of holothurians (sea cucumbers); the samples from Cape Wooley and eastern St. Lawrence Island also contained a large proportion of echiurid worms. At Mekoryuk, the principal non-molluscan prey were anemones. Fishes occurred in significant amounts only in the samples from Gambell, but were present in trace amounts at Savoonga, as well.

Comparison With Results From Previous Years

The contents of the 1982 samples did not differ markedly from those obtained in the same localities in 1975 and 1980 (Table 9). In each year, bivalve mollusks made up the largest proportion by far of the ingesta, with most of the other invertebrate taxa poorly represented. This year, one class (Scyphozoa) of coelenterates was represented for the first time. These organisms (jellyfish) were present in small but significant amounts (532 g) in four of the samples from Little Diomede. At St. Lawrence Island, fishes (*Ammodytes*) were found more frequently and in larger amounts than they were

Table 8. Regional comparison of principal stomach contents from walruses taken in the 1982 harvest.

Locality	No. of stomachs	Total weight (kg)	Percentage by weight of identified prey		
			All mollusks	Principal bivalves	Principal non-molluscan
Diomede	27	6.8	85	*Mya*-67, *Serripes*-15	Holothureans-12
Wales	3	2.4	94	*Mya*-94	Holothurean-6
King Island	2	2.8	92	*Mya*-72, *Serripes*-8	Holothureans-8
Cape Woolley	2	2.8	7	*Mya*-7	Holothureans-58 *Echiurus*-34
Nome	1	2.0	94	*Mya*-78, *Macoma*-15	Holothureans-5
Gambell	31	43.4	92	*Mya*-61, *Serripes*-21, *Spisula*-5	Fishes-4
Savoonga	4	4.6	69	*Mya*-35, *Serripes*-28	*Echiurus*-27
S.E. Cape	1	0.9	93	*Mya*-22, *Spisula*-66	*Echiurus*-3 Holothureans-2
Mekoryuk	5	14.3	70	*Mya*-24, *Tellina*-39	Anemones-28

Table 9. Comparative percentages by weight of prey in stomach contents of walruses taken in spring harvests at three localities in 1975, 1980, and 1982.

Location	Diomede			Savoonga			Gambell		
Year	1975	1980	1982	1975	1980	1982	1975	1980	1982
Sample size	71	15	27	14	25	4	13	47	31
Scyphozoa	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0
Anthozoa	0.0	0.1	0.2	0.0	0.5	0.0	0.0	0.3	0.2
Polychaeta	0.6	1.7	0.4	0.1	0.5	2.8	1.0	1.6	1.6
Sipunculida	0.6	3.3	0.4	0.1	0.6	0.5	0.3	tr	tr
Echiurida	tr	0.3	0.1	0.2	0.2	24.5	tr	5.4	0.2
Priapulida	0.2	0.8	0.5	0.4	2.2	0.5	0.8	0.8	0.3
Gastropoda	1.1	2.8	1.1	0.3	2.7	2.2	1.1	3.7	2.6
Bivalvia	84.0	85.8	77.3	80.6	79.9	61.7	65.2	61.7	75.5
Cephalopoda	tr	0.2	0.1	0.0	0.0	0.0	tr	tr	tr
Crustacea	tr	0.1	0.2	0.3	0.6	tr	3.3	5.2	0.3
Holothuroidea	0.4	0.6	11.2	0.7	0.7	0.0	2.7	0.8	0.8
Urochordata	0.0	tr	0.0	0.0	0.0	0.0	0.0	0.1	tr
Fishes	0.0	0.0	0.0	0.0	tr	tr	0.0	0.2	3.4
Mammals	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sediments	2.0	3.5	4.7	0.7	10.4	3.5	2.0	16.3	11.6

in 1980, when they were detected for the first time in the stomach contents. About 1,475 g of these fishes were recovered from nine of the 31 samples (29%) from the Gambell area, and trace amounts were found also in one of the four samples from Savoonga. The increasing importance of fishes in the diet in recent years has been indicated by a rising percentage of walruses infected by anasakid nematodes ("codworms") in the stomach. The proportion of animals found infected in this year's samples was about the same as in 1980-81 (Table 10), and the difference between those and the findings in 1964-75 was very highly significant ($X^2 = 11.42$, $p < .001$).

The tendency toward increased use of invertebrates other than bivalves, which was suggested by the comparison of the 1975 and 1980 data (Fay and Stoker, 1982) was evident again in this year's samples (Table 11). The percentage by weight of non-bivalve prey apparently increased from a low of 4 to 5% in 1975 to at least 10 to 20% by 1982, in both male and female walruses. This year, further increase took place mainly in the use of jellyfish, sea cucumbers, and fishes. Along with that shift to alternate, non-bivalve prey, there has been a trend of reduction in use of the smaller bivalves, particularly by females. From the 1950's at least until 1975, the females appeared to be taking the smaller forms, such as *Hiatella*, *Astarte*, *Yoldia*, and the tellinids, to a much greater extent than were the males (Brooks, 1954; Fay *et al.*, 1977). Apparently, that tendency no longer holds, for our findings in both the 1980 and 1982 samples showed no significant difference between males and females; both appeared to be feeding primarily on the larger forms, such as *Mya* and *Serripes*.

The recent tendency toward more similar choice of prey by males and females has been suggested also by comparisons of the average unit weights

Table 10. Comparative frequency of occurrence and numbers of anasakid nematodes ("cod worms") parasitizing the stomach of walruses taken in the Bering Sea over the past two decades.[1]

Year	No. of walruses	Anasakid nematodes: Frequency (%)	Number per walrus: Range	Number per walrus: Mean	Source
1964-66	95	1.0	5	—	Yurakhno and Treschev, 1972
1975	107	6.5	1-20	6.0	L.M. Shults, unpublished data
1980-81	114	14.0	1-61	14.3	F.H. Fay and S.W. Stoker, unpublished data
1982	76	14.5	1-37	15.8	This study

[1]Since these parasites are acquired by pinnipeds through ingestion of fishes, their comparative frequency of occurrence and relative abundance are indicative of degree of piscivory.

Table 11. Comparative percentage composition by weight of stomach contents from male and female walruses taken in the Bering Strait region in spring 1975, 1980, and 1982.

Prey	From males			From females		
	1975	1980	1982	1975	1980	1982
Anemones	0.0	0.2	0.2	0.0	0.4	0.2
Jellyfish	0.0	0.0	1.0	0.0	0.0	0.1
Worms[1]	1.4	4.3	2.0	2.4	15.8	4.9
Snails/whelks	1.1	1.4	2.1	2.0	3.4	1.9
Clams (total)	96.2	91.5	90.3	95.0	76.4	79.0
Large[2]	91.2	86.9	88.9	39.5	74.0	77.2
Small[3]	5.0	3.6	1.4	55.5	2.4	1.8
Shrimps/crabs	0.5	2.5	0.2	tr	3.3	0.3
Sea cucumbers	0.7	0.9	1.4	0.5	0.6	13.6
Tunicates	tr	tr	tr	0.0	0.1	0.0
Fishes	0.0	0.1	2.9	0.0	0.0	tr

[1]Polychaetes, sipunculids, echiurids, and priapulids.

[2]*Serripes*, *Clinocardium*, *Mya*, and *Spisula*.

[3]*Hiatella*, *Astarte*, *Macoma*, *Tellina*, *Yoldia*, *Nucula*, *Thyasira*, and *Liocyma*.

of those prey in the stomach contents (Table 12). At least since 1980, the males apparently have been taking somewhat smaller prey than before, and the females, larger prey, bringing the males and the females into direct competition with each other.

DISCUSSION

The Pacific walrus population was greatly depleted by over-hunting on two occasions in the past, first by the Yankee whalers between 1849 and 1914, when about 140,000 animals were harvested in addition to those taken by natives of western Alaska and eastern Siberia (Bockstoce and Botkin, 1982). The second depletion was by the Soviet sealing fleet between 1931 and 1960, when the commercial catch again was about 140,000 animals, in addition to those taken by natives (Krylov, 1968). In the interval between those two events, the walrus population probably recovered to some degree, perhaps nearly to its pre-exploited level (Fay, 1982). That recovery was not well documented, but the trend since the 1950's has been recorded or at least inferred by information from several sources.

The results of repeated censuses of the population since the 1950's have suggested that it at least doubled in size, possibly from a low of less than 100,000 to a high of more than 200,000 by 1980 (Fay, 1957; Kenyon, 1960, 1972; Fedoseev, 1962; Krylov, 1968; Gol'tsev, 1972; Estes and Gol'tsev, in press; Johnson and Burns, in prep.). A substantial increase was indicated during that time also by the population's gradual reoccupation of most of its former range in both Soviet and American waters (Gol'tsev, 1968, 1976; Fay, 1982; J. J. Burns, unpublished data). To date, practically all former hauling grounds that were used by the

Table 12. Comparative unit weights (g/individual) of prey in the stomach contents of male and female walruses taken in the Bering Strait region in spring 1975, 1980, and 1982.

Prey Type	From males						From females					
	1975		1980		1982		1975		1980		1982	
	No.	Unit wt.	No.	Unit wt.	No.	Unit wt.	No.	Unit wt.	No.	Unit wt.	No.	Unit wt.
Polychaetes	302	12.8	220	2.4	189	3.6	104	5.6	568	1.8	57	5.9
Sipunculids	941	3.3	170	2.4	17	4.0	135	3.0	200	4.0	42	3.5
Echiurids	67	6.6	286	4.8	18	5.6	13	7.8	811	3.3	278	4.2
Priapulids	196	8.1	140	7.9	22	7.9	42	11.2	63	6.6	21	9.5
Gastropods	1,717	3.8	375	3.1	338	3.1	618	2.1	370	2.9	277	2.6
Bivalves												
Cardiids[1]	3,961	21.8	935	18.4	844	14.9	675	6.2	304	18.8	762	5.4
Myacids[2]	20,182	22.8	7,349	6.7	2,911	11.3	1,193	17.9	1,444	9.9	1,514	16.8
Hiatella	22,586	1.4	4,467	0.5	965	0.3	26,377	1.3	0	—	1,194	0.4
Tellinids	136	2.5	1,389	0.3	1,332	0.3	1,230	1.1	963	0.5	439	0.4
Other small clams	188	0.5	44	0.7	1	1.0	735	0.3	1,219	0.2	72	0.9
Shrimps	71	3.0	426	4.0	17	1.9	4	0.5	345	2.7	17	3.8
Crabs	363	7.5	163	1.8	19	2.5	9	4.0	46	2.7	20	2.4
Holothureans	221	21.0	53	13.4	49	14.7	19	18.2	18	9.6	346	15.0
Overall	50,931	11.8	16,017	4.8	7,395	6.9	31,155	2.1	7,413	4.2	5,066	7.6

[1]Excluding samples from Nome, where cardiids appear to be uniformly of much smaller size than elsewhere and were sampled only from males in 1975 and on from females in 1980 and 1982.

[2]Includes *Mya truncata*, *M. arenaria*, and other large *Mya*-like clams as yet unidentified.

population in historic times have been reoccupied, with the exception of the Pribilof Islands.

Signs of the population's approach to an upper limit were recognized as early as 1975, when the overall pregnancy rate among females taken in the spring harvest was about 31%, suggesting that a substantial decline in productivity already was underway (J. J. Burns, unpublished data). By 1977, the native walrus hunters at St. Lawrence Island were commenting on the leanness of the animals, and they reported that the calves were scarce among the herds seen that spring. In 1978, they and the hunters at Diomede remarked on the finding of unusual food items in the stomach contents and, especially, on a considerable increase in frequency of occurrence of seal remains. In the autumn of 1978, a dramatic rise in natural mortality and fetal abortion in the St. Lawrence Island area was reported and subsequently documented by Fay and Kelly (1980), who also presented evidence in support of the alleged decrease in fatness. This was followed by our finding of further suggestions of change in feeding habits in the 1980 harvest samples and recognition of an exceptionally high percentage of abortions and premature births (Fay and Stoker, 1982). Further documentation of leanness was obtained in that year by Smith (1980) at Little Diomede Island and in the following winter by Fay and co-workers (Fay, 1981a) in the southeastern Bering Sea. In July of 1981, extremely low numbers of each of the juvenile cohorts were documented among the herds summering in the Chukchi Sea (Fay, 1981b), and those findings were confirmed by further compositional counts in September of that year (A. A. Hoover, unpublished data) and again in July and August of 1982 (Fay and Kelly, 1982). The compositional counts indicated further that the poorest production of young had taken place in 1980, and that the 1982 cohort of calves was greater than any others for at least the past 7 years, though still well below the level predicted from the productivity in the 1950's and 60's.

Taken as a whole, the results of those studies, together with the hunters' observations, suggest to us that the Pacific walrus population, which had been recovering in the 1950's, 60's, and early 70's from a depelted state, (1) may have reached its zenith in the late 1970's, (2) probably declined significantly after that, as a consequence of depressed productivity, increased natural mortality, and continuing harvests, and that (3) it is currently trending toward its equilibrium level, in balance with the carrying capacity of its environment. We contend that the data obtained from analysis of the reproductive organs and stomach contents collected during the 1982 spring harvest support that point of view.

Reproductive Analysis

The reproductive efficiency of the female walrus depends not only on the frequency and proper timing of estrus but also on her ability to achieve fertilization of the shed ovum, implantation of the blastocyst, gestation of the fetus to full-term, and birth and nurture of the calf. Success in achieving each of those steps varies considerably with age, being very low in adolescence, highest when physical maturity is attained (at 10 or 11 years), and decreasing again in old age (Fay, 1982). Other factors, such as nutritional deficiency, endocrine imbalance, anatomical defects, trauma, and infectious diseases may play a part in causing reproductive failures at each step along the way (Hafez, 1967).

In this 1982 sample of reproductive organs, we found evidence of a significant reduction in reproductive efficiency, well below that of the population in the 1950's and 60's reported by Burns (1965), Krylov (1966), and Fay (1982). In many respects, it was comparable to that seen in 1979 and 1980 by Fay and Stoker (1982) and Burns (unpublished data). We suspect that most of the resultant decrease in productivity was a function of the age of the animals. The productivity of individual walruses certainly declines in old age, and a shift in age composition of the harvest samples, from primarily young, highly productive adults to older, less productive animals, would tend to lower the overall pregnancy rate of the samples. Our comparative counts of numbers of corpora in the ovaries from harvest samples collected over the past 30 years (Fig. 5) indicate that such a shift in age composition has taken place gradually. A tendency for shift to older animals is indicated also by the known age compositions of walruses of both sexes, taken in the spring harvests at Gambell and Diomede between 1952 and 1968 (F. H. Fay and J. J. Burns, unpublished data). We predict that it will be even more evident, when those data are compared with the age compositions of harvests from the 1970's and early 80's, as those become available.

The observed increase in percentage of abortions and premature births in this and the previous two samples (1979, 1980) may be attributable to the change in age composition, but its magnitude appears to have been much greater than would be predicted from the changes inferred above. Such an age-related change would be likely only if the catch were made up either of very young or very old adults, which may not be applicable in this case. Hence, we suspect that other regulating factors have been involved, and that the most probable of those are nutritional deficiency and/or disease.

That the animals taken in the early 1980's were only about half as fat as those taken much earlier has been documented (though not yet formally reported) with data collected in several samples (Smith, 1980; Fay, 1981a and unpublished). What this means in terms of changing nutrient intakes from past to present is not yet clear, but it is clear that the change was large. Whether it was large enough to cause spontaneous abortion also is not clear, for the evidence is not sufficient from walruses to implicate nutritional deficiency as a proximate cause of abortion. Abortion can be caused in other mammals by poor physical condition and/or nutritional stress of the female, as has been demonstrated experimentally (e.g., see reviews by McDonald, 1961; Belling, 1963; Hafez, 1967). The possibility of its having had a similar effect on the walruses should not be overlooked. Malnutrition also can exert an immunosuppressing influence, in effect opening the door to certain infectious diseases. A newly discovered viral agent in this walrus population bears close resemblance to some others that have been linked with spontaneous abortion in domestic animals and free-living pinnipeds (Smith *et al.*, in press). Conceivably, that agent, in combination with nutrient stress, has played a part in this event.

Analysis of Stomach Contents

The stomach contents of the animals taken in the 1982 spring harvest were more similar to those obtained in 1980 than in 1975, which were the only other large, quantitative samples available for comparison. In all of those samples, the walrus' primary reliance on bivalve mollusks (Chapskii, 1936; Nikulin, 1941; Vibe, 1950) was confirmed again and again. The proportional use of other, alternate prey continued to be high in 1982, as it was in 1980. Coelenterates, which had not been recorded at all in the diet of these animals prior to 1980 (Fay and Stoker, 1982), again made up a significant proportion of the food in the stomachs. Among those were a larger number of scyphozoans (jellyfish), which are bulky but extremely poor in nutrients. Sand lance fishes, which also were recorded for the first time in 1980, occurred more frequently and in larger amounts in this year's samples than before.

In general, the unit weights of the organisms found in the stomachs this year were about the same as in 1980 and considerably smaller than in 1975. Although many of the benthic organisms in this year's samples were large, old adults, the proportion of smaller, younger prey was very high, bringing the unit average down, well below that of the 1975 samples in most cases. This suggests that the supply of the larger, older invertebrates has decreased in the Bering Strait region in recent years. That the total biomass of the benthic fauna in this region has decreased significantly since the early 1970's has been suggested also by comparative sampling of that fauna (H. M. Feder and S. W. Stoker, unpublished data).

We interpret the high proportion of benthic sediments in this year's and the 1980 stomach content samples as another indication of a depleted food supply. That is, we believe that the amount of sediment ingested with each meal tends to be proportional to the amount of effort expended by the walrus in obtaining its food. This is an untested hypothesis, based only on the logic that, with a decrease in the size of the prey, the walrus will need to take more individuals to make up the volume required for sustenance; since the sediments are ingested incidentally during the process of capturing the prey, the amount ingested probably is proportional to the number of prey taken.

We also interpret the convergent predation by males and females on the same kinds and size classes of bivalves in recent years as further indication of a reduced food supply for walruses in this region. Our logic in that interpretation is as follows:

Walruses feed primarily on bivalve mollusks. If the bivalve populations in the Bering Strait region had not changed or had increased in abundance, the walruses would not have changed their feeding habits. A change in feeding habits would have taken place, only if there had been a decrease in the supply of bivalves. With a decrease, the males which formerly were taking primarily the large, mature individuals of the larger growth forms (e.g., *Mya* and *Serripes*), would be obliged to take more of the smaller, younger individuals of those genera to make up the volume required for sustenance. The females, which formerly fed mainly on the largest individuals of the smaller growth forms (e.g., *Hiatella* and *Astarte*), would be obliged to take more individuals of the larger growth forms to make up their required volume. Such change in the females would have been necessary, because predation on the younger, smaller individuals of the small growth forms would have been energetically inefficient; that is, the energy expended in obtaining them would have exceeded the energy gained from eating them. Given all of those conditions, we believe that the size of the prey taken by both sexes would tend to approach unity, as the prey populations continued to decrease in abundance.

Implicite in this logic is our suspicion that, not only has there been a decline in the supply of bivalves in this region, but that it has been caused by the walruses, themselves. We believe that the walruses could be responsible for this change, because their use of this region has increased greatly in the past 30 years. Whereas in the 1950's and early 60's, they simply passed through the Bering Strait region on migration, large numbers of them have been residing there throughout the summer and autumn, since the late 1960's (J. J. Burns, V. N. Gol'tsev, and A. A. Kibal'chich, unpublished data). For example, more than 67,000 individuals were recorded on the Arakamchechen, Nunyangan, Naukan, and Big Diomede hauling grounds on 21 September 1975 (Gol'tsev, 1976). The impact of such numbers on the benthic fauna of this region, even for just a few weeks, would have been enormous.

Adequacy of the Harvest Samples

Whether the harvest samples are reflective of the population as a whole is open to question. Certainly, for reproductive information they are biased in some respects by the hunter's selection for females with calves at Gambell and for animals with the larger tusks in all localities. For that reason, they obviously are not random, representative samples of the population at large, but they should tend to reflect any major changes that take place in either productivity or age composition of the whole population. Since tusk size tends to increase with age, selection for that character by the hunters would have biased all of the samples equally toward the older age classes, if the population were not increasing in size. If the population were growing, the bias would have been increasing annually, for there would have been more animals available, hence greater opportunity for exercising the selection. If the population had reached an upper, stationary level or even declined because of reduced recruitment, it would have contained a higher *proportion* of old animals, hence provided even greater opportunity for the hunters to exercise that selection. One characteristic of a stationary or declining mammalian population is a high proportion of old individuals (Dublin and Lotka, 1936).

The selection at Gambell for females with calves should result always in their taking a preponderance of the most productive age classes (8-11 yrs) if the population were stationary (i.e., not growing), hence to bias the harvest samples equally in all years. In an actively growing population, that bias would be enhanced. Since the composition of a growing population tends to be heavily weighted on the younger age classes, and the age at first pregnancy is low, each harvest sample would be composed mainly of the younger adults. Upon approaching or reaching its upper limit, however, the population would be expected to decline in productivity through the combined effects of (1) a rising proportion of older, less productive animals, (2) increasing age at first pregnancy, and (3) decreasing reproductive efficiency due to a variety of density-dependent extrinsic factors, such as poor nutrition, trauma, and disease. Under the latter circumstances, the hunter's selection for females with calves would continue to exert a biasing effect on the composition of the harvest, but the selection both for large tusks and for cows with calves would tend to increase the proportion of older animals in each successive sample.

Thus, despite the distorting influence of hunter-selection, the composition of periodic samples of reproductive organs from the harvests should reflect even gradual changes in structure, productivity, and status of the population, given a baseline of data from previous years for comparison. The precision of those reflections as indicators of the direction of change obviously will vary with the size of the samples. Their accuracy, as representations of actual population parameters, will vary somewhat with other conditions. Ice, weather, and sea state limit the hunters' ability to conduct their annual harvests, and those conditions probably also influence the migration rates and routes taken by the walruses, thereby affecting the availability of the animals to the hunters. Occasionally, those conditions lead to very small harvests in one or more localities, in which case there may be little or no opportunity for the hunters to take the animals selectively. Then, the harvest will approach a random sample of those available.

As an index of changes in feeding habits, the harvest samples to date have been minimally acceptable. Their main deficiency has been the small sample size per locality. In some instances, the variance in composition of the stomach contents among individuals from the same locality has been very large, clearly demonstrating that small samples (i.e., from small numbers of individuals) are not reliable indicators of the feeding habits in that locality. Ideally, samples from at least 50 males and 50 females in each locality should be analyzed. Because the largest samples in the past have been from Gambell and Diomede, future samples for monitoring this aspect of the population's activities probably should be obtained only from those areas.

Another weakness of the stomach content samples is the wide variation in quality of the collected materials. Digestion of food in the stomach of walruses evidently takes place very rapidly, and it can continue long after the animal is killed. Collections of food from the cardiac end of the stomach tend to be the least affected by digestion, hence the most useful for comparative purposes. This was the method used in 1982; the samples taken in 1980 were aliquots of the mixed stomach contents, hence they tended to be more affected by digestion, as were the 1975 samples, which were of the entire stomach contents.

The difference between years in the methods used to collect the samples raises questions about the validity of comparing them directly, without weighting the results in some way. Digestion does tend to remove the smaller organisms first, because of their large surface/volume ratio (Fay and Lowry, 1981), and does tend to depress unit weight of the larger organisms. It probably also leads to a greater ratio of sediments/organics, because the ingested gravel apparently tends to remain in the stomach long after the organic matter has been digested. On the basis of those observations, we would have expected the 1975 and 1980 results to have been the most similar, because they were about equally affected by digestion. Yet, they were the most different in composition. Conversely, because of the better quality of the 1982 samples, we expected them to differ the most from the other two. That they differed the least in composition from the 1980 samples gives some confidence that the changes observed between 1975 and 1980 were real, and that, even with samples of different quality, major changes in feeding habits can be detected if the samples are large enough.

Overview

Given that the comparison among years of information from the harvest samples can be interpreted in terms of parameters of the walrus population as a whole, we conclude from the foregoing analyses that the population has taken a turn in recent years, away from its former growth mode, toward a stationary condition. We believe that the turn came about as a consequence of two factors — lowered productivity and nutritional stress, which may have been interactive. Much of the decline in productivity appears to have been a natural result of an increasing proportion of old adults, which simply are less productive than the younger animals. Conceivably, part of it may have been caused by the poor physical condition of many of the animals, perhaps synergistically coupled with disease.

A population-wide decrease in productivity certainly would have exerted some influence on the reproductive composition of the harvests in all localities, comparable to the average changes seen at Gambell and Diomede. But we think this would not explain the wide oscillations in composition that apparently took place in those two areas in recent years. The extremely low proportions of postpartum females taken in 1977 (according to hunter reports) and in 1980, compared with the moderate to high proportions in 1979 and 1982, suggest to us that the proximate cause of the oscillations may have been synchronous breeding. That is, we suspect that a large proportion of the adult females was induced to breed in one year, followed by a small proportion in the succeeding year, and so forth, rather than the previous balance of about equal numbers of breeders each year. Presumably, synchronization of breeding could come about by chance alone, but it would be more likely to occur if some additional factor such as disease or environmental stress were involved. That is, we suspect that an unusual set of conditions affected reproductive success of either the estrous or the pregnant females in one winter, tending to bring most of the females into breeding synchrony in the following year. Synchronization of breeding could result in pulses of high production of calves at 2- to 3-year intervals, with low production in the intermediate years, at least for a time until a new balance is achieved.

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LITERATURE CITED

Belling, T. H. 1963. Reproduction efficiency in the hereford cow. *J. Am. Vet. Med. Assoc.* 142:494-501.

Bockstoce, J. R. and D. B. Botkin. 1982. The harvest of Pacific walruses by the pelagic whaling industry, 1848-1914. *Arctic and Alpine Research* (in press).

Brooks, J. W. 1954. A contribution to the life history and ecology of the Pacific walrus. Special Rep. 1, Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks. 103 pp.

Burns, J. J. 1965. The walrus in Alaska, its ecology and management. Alaska Department of Fish and Game, Juneau. 48 pp.

Chapskii, K. K. 1936. The walrus of the Kara Sea. *Trudy Vsesoiuz. Arkt. Inst.* 67:1-124.

Dublin, L. I., and A. J. Lotka. 1936. *Length of Life. A Study of the Life Table.* Ronald Press, New York, NY.

Estes, J. A. and V. N. Gol'tsev. (in press). Abundance and distribution of the Pacific walrus (*Odobenus rosmarus divergens*): results of the first Soviet-American joint aerial survey, autumn 1975. *In* F. H. Fay and G. A. Fedoseev (eds.), *Soviet-American Cooperative Studies on Marine Mammals, Vol. 1, Pinnipeds.* NMFS Circular.

Fay, F. H. 1957. History and present status of the Pacific walrus population. *Trans. N. Am. Wildl. Conf.* 22:431-443.

Fay, F. H. 1958. Pacific walrus investigations on St. Lawrence Island, Alaska. Processed rept., Alaska Cooperative Wildlife Research Unit, University of Alaska, Fairbanks. 54 pp.

Fay, F. H. 1981a. Modern populations, migration, demography, trophics, and historical status of the Pacific walrus. Annual rept. R.U. #611. NOAA Outer Continental Shelf Environmental Assessment Program, Boulder, CO. 38 pp.

Fay, F. H. 1981b. Distribution, age/sex composition, and associated behaviors of Pacific walruses in the eastern Chukchi Sea, 14-29 July 1981. Institute of Marine Science, University of Alaska, Fairbanks. 14 pp.

Fay, F. H. 1982. *Ecology and biology of the Pacific walrus, Odobenus rosmarus divergens Illiger.* N. Am. Fauna No. 74. U.S. Fish and Wildlife Service, Washington. 279 pp.

Fay, F. H., H. M. Feder, and S. W. Stoker. 1977. An estimation of the impact of the Pacific walrus population on its food resources in the Bering Sea. PB 273-505. National Technical Information Service, Springfield, VA. 38 pp.

Fay, F. H. and B. P. Kelly. 1980. Mass natural mortality of walruses (*Odobenus rosmarus*) at St. Lawrence Island, Bering Sea, autumn 1978. *Arctic* 33:226-245.

Fay, F. H. and L. F. Lowry. 1981. Seasonal use and feeding habits of walruses in the proposed Bristol Bay clam fishery area. Final Rept., Contract 80-3, North Pacific Fisheries Management Council, Anchorage, AK. 61 pp.

Fay, F. H., and S. W. Stoker. 1982. Analysis of reproductive organs and stomach contents from walruses taken in the Alaskan native harvest, spring 1980. Final Report, Contract 14-16-0007-81-5216. U.S. Fish and Wildlife Service, Anchorage, AK. 86 pp.

Fedoseev, G. A. 1962. On the status of the stocks and the distribution of the Pacific walrus. *Zool. Zhur.* 41:1083-1089.

Gier, H. T., and G. B. Marion. 1967. Uterus of the cow after parturition: involutional changes. *Am. J. Vet. Res.* 29:83-96.

Gol'tsev, V. N. 1968. Dynamics of coastal walrus herds in connection with the distribution and numbers of walruses. *In* V. A. Arsen'ev and K. I. Panin (eds.), *Pinnipeds of the Northern Part of the Pacific Ocean,* pp. 205-215. Food Industry, Moscow.

Gol'tsev, V. N. 1972. Distribution and assessment of numbers of the Pacific walrus, autumn 1970. *In* Tezisy Dokl. 5th Vsesoiuz, Sovesch. Morsk. Mlekopit., 1:25-28 (Abstract). Akad. Nauk SSSR, Makhachkala.

Gol'tsev, V. N. 1975. Reproduction of the Pacific walrus. *In* Tezisy Dokl. Vsesoiuz. Sovesch. Biol. Resur. Dal. Vost. Mor., pp. 113-115 (Abstract). TINRO, Vladivostok.

Gol'tsev, V. N. 1976. Aerial surveys of the Pacific walrus in the Soviet sector during autumn 1975. Unpublished report. TINRO, Magadan. 22 pp.

Hafez, E. S. E. 1967. Reproductive failure in domestic mammals. *In* K. Benirschke (ed.), *Comparative Aspects of Reproductive Failure,* pp. 42-95. Springer-Verlag, New York.

Harrison, R. J. and B. J. Weir. 1977. Structure of the mammalian ovary. *In* Lord Zuckerman and B. J. Weir (eds.), *The Ovary,* vol. 1, 2nd ed., pp. 113-217. Academic Press, New York.

Kenyon, K. W. 1958. Walrus and other marine mammal studies at Little Diomede Island, Alaska, 11 May to 14 June 1958. Unpublished report. U.S. Bureau of Sport Fisheries and Wildlife, Seattle. 112 pp.

Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. U.S. Bureau of Sport Fisheries and Wildlife, Seattle. 39 pp.

Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6-16 April 1972. U.S. Bureau of Sport Fisheries and Wildlife, Seattle. 79 pp.

Kleinenberg, S. E. 1957. On preserving the walrus. *Priroda* 1957(7):101-103.

Krylov, V. I. 1966. The sexual maturation of Pacific walrus females. *Zool. Zhur.* 45:919-927.

Krylov, V. I. 1968. Present condition of the Pacific walrus stocks and prospects of their rational exploitation. *In* V. A. Arsen'ev and K. I. Panin (eds.), *Pinnipeds of the Northern Part of the Pacific Ocean,* pp. 189-204. Food Industry, Moscow.

McDonald, I. W. 1961. Physiological limitations on reproduction in the sheep. *Austral. Vet. J.* 37:99-104.

Mansfield, A. W. 1958. The biology of the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus) in the eastern Canadian Arctic. Manuscr. Rept. Ser. (Biol.) 653. Fisheries Research Board of Canada, Montreal. 146 pp.

Nikulin, P. G. 1941. The Chukchi walrus. *Izv. TINRO* 20:21-59.

Smith, A. W., D. G. Ritter, G. C. Ray, D. E. Skilling, and D. Wartzok. (in press). New calicivirus isolates from walrus (*Odobenus rosmarus*). *J. Wild. Dis.* 19.

Smith, T. E. 1980. Walrus study project 1980 field collection report Diomede, Alaska. U.S. Fish and Wildlife Service, Anchorage, AK. 15 pp.

Vibe, C. 1950. The marine mammals and the marine fauna in the Thule District (Northwest Greenland) with observations on ice conditions in 1939-41. *Medd. om Grønl.* 150(6):1-115.

Yurakhno, M. V. and V. V. Treschev. 1972. An investigation of the helminth fauna of the Pacific walrus. *In* Tezisy Dokl. 5th Vsesoiuz. Sovesch. Morsk. Mlekopit. 2:280-283. Akad. Nauk SSSR, Makhachkala.

APPENDIX I

LIST OF REPRODUCTIVE TRACTS FROM FEMALE WALRUSES TAKEN IN THE SPRING 1982 HARVESTS.

The principal findings in the ovaries and uteri of each of the reproductive tracts obtained during the 1982 spring harvest are listed. Corpora lutea in the ovaries were classified as: N = Corpus luteum of new pregnancy; F = Corpus luteum of false pregnancy; T = Corpus luteum of term pregnancy; C = Corpus atreticum; A = Accessory corpus luteum; and X = Corpus luteum/albicans from abortion or premature birth of the fetus. Absence of these is indicated by a dash in the "corpus luteum type" column.

The number of corpora albicantia is the total for both ovaries. Where indicated as number "+", only one ovary was available, hence the total probably was greater than the number found in the one ovary.

For placental scars less than 1 year old, the age estimate was based in part on the dimensions of the involuting uterine horn. Where the age of the scar is indicated as unknown ("unk"), the uterine horn was not available for diagnosis. For animals in term pregnancy or recently postpartum, the scar is indicated as "New", whether or not the uterine horn was available for inspection. In many young adults, including several of those with one or more corpora albicantia in their ovaries, the uterine horns were comparable with those of the immature animals in being very slender (1.5 cm) with no traces of placental scars. Hence, they were judged not to have been pregnant previously; this is indicated by a dash in the "Age latest placental scar" column. Older animals with no evident scars but with much stouter (2.5-3 cm) uterine horns and numerous corpora albicantia were judged to have been pregnant ">4" years earlier.

The diameter of the largest healthy follicle (i.e., not including degenerate follicles) is the largest for the pair of ovaries. Where the follicle was irregular or oval in outline, the size given is the best estimate of the diameter of it as a sphere.

Information on presence ("Yes") or absence ("No") of the calf with the female was extracted from the data sheets provided by K. Lourie. This information apparently was based on reports from the walrus hunters. Where no information was given or there was uncertainty as to which of several females was accompanied by the calf, this is indicated as "unk".

Non-pregnant animals having one or more healthy follicles 7 or 8 mm in diameter or larger were regarded as being "Estrous". This is tantamount to being "Barren", since the probability of fertilization of an ovum in May or later appears to be near zero. A few of the animals at "Term" or "Postpartum" also had such large follicles, for there is a postpartum estrus, ordinarily not resulting in pregnancy. Animals were regarded as being in "New pregnancy" if they had an ostensibly normally developed corpus luteum with ovulation scar in one ovary; many of those also had an implanted embryo in the uterus. Some that had no implanted embryo may have been "False pregnancy", since several of those also had large, ripening follicles indicative of continuing estrus. Animals were considered to have "Aborted" where the condition of their uterine horns and corpus luteum/albicans was indicative of birth of the fetus in March or earlier; "Premature" births had taken place in early April.

Specimens from Nome-King Island-Cape Woolley
23 May to 8 June 1982

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
NW-1	5/23	N,A	4	>4	13	No	New pregnancy
NW-9	5/30	T	3	New	3	Yes	Postpartum
NW-11	5/29	unk	4+	1	2	No	One ovary missing
NW-14P	5/30	N	5	1	8	Yes	New pregnancy
NW-15P	5/30	—	0	—	3	No	Immature
NW-12	6/07	unk	unk	2	unk	unk	Ovaries missing
NW-13	6/07	unk	unk	—	unk	unk	Ovaries missing
NW-14	6/07	—	3	2	9	unk	Estrous
NW-15	6/07	N	7	2	5	unk	New pregnancy
NW-20	6/08	X,N	1	>0.2	4	No	Aborted; New pregnancy
CN-1	5/30	N	4	1	3	No	New pregnancy
CN-2	5/30	unk	1+	1	unk	No	One ovary missing
FD-2	5/30	T	0	New	5	No	Postpartum
KI-2	5/25	N	5	unk	3	No	New pregnancy
KI-3	5/25	N	0	unk	7	No	New pregnancy
KI-4	5/25	—	6	unk	12	No	Estrous
CW-1	6/08	N	6	>4	2	No	New pregnancy
CW-2	6/08	N	5	4	4	No	New pregnancy
CW-3	6/08	N	4	2	3	unk	New pregnancy
CW-4	6/08	C	0	—	4	unk	Barren
CW-5	6/08	N	9	>4	2	unk	New pregnancy
CW-JT	6/08	N	2	2	3	unk	New pregnancy
CW-JT	6/08	T	6	New	<1	unk	Postpartum

Specimens from Gambell area
5 May to 5 June 1982

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
GW-14	5/05	T	4	New	3	Yes	Postpartum
GW-15	5/05	T	4	New	3	Yes	Postpartum
GW-16	5/05	T	3	New	4	Yes	Postpartum
GW-17	5/05	X	4	>0.2	2	No	Aborted
GW-18	5/05	X	4	>0.2	7	No	Aborted; Estrous
GW-19	5/05	T	1	3	3	Yes	Postpartum
GW-20	5/05	N	7	2	3	No	New pregnancy
GW-21	5/05	T	5	New	1	Yes	Postpartum
GW-30	5/05	T	5	New	3	Yes	Postpartum
GW-31	5/05	T	8	New	3	Yes	Postpartum
GW-38	5/07	T	3	New	4	Yes	Postpartum
GW-40	5/07	T	2	New	2	Yes	Postpartum
GW-41	5/07	T	0	New	2	Yes	Postpartum
GW-43	5/07	T	3	New	5	Yes	Postpartum
GW-46	5/09	T	2	New	4	Yes	Postpartum
GW-47	5/09	T	4	New	3	Yes	Postpartum
GW-50	5/10	T	4	New	7	No	Postpartum
GW-51	5/10	T	4	New	3	Yes	Postpartum
GW-53	5/10	T	5	New	4	Yes	Postpartum
GW-54	5/10	T	3	New	4	Yes	Postpartum
GW-56	5/10	N	8	2	2	No	New pregnancy
GW-57	5/10	T	6	New	4	Yes	Postpartum
GW-58	5/10	N	9	1	<1	Yes	New Pregnancy
GW-62	5/10	Meat, fat and vascular tissues only					
GW-63	5/10	—	4	3	<1	Yes	Barren
GW-64	5/10	T	3	New	3	Yes	Postpartum
GW-65	5/10	T	1	New	4	Yes	Postpartum
GW-66	5/13	T	2	New	3	Yes	Postpartum
GW-68	5/13	T	5	New	2	Yes	Postpartum
GW-71	5/13	N	6	2	2	Yes	New pregnancy
GW-72	5/13	F	6	1	1	Yes	Barren; False pregnancy
GW-73	5/13	N	10	2	5	Yes	New pregnancy

Specimens from Gambell area
5 May to 5 June 1982
(continued)

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
GW-74	5/13	T	1+	New	unk	Yes	Postpartum
GW-76	5/13	T	2+	New	unk	Yes	Postpartum
GW-77	5/13	T	3	New	3	Yes	Postpartum
GW-78	5/13	T	3	New	3	Yes	Postpartum
GW-79	5/13	T	1	New	6	Yes	Postpartum
GW-80	5/13	T	8	New	3	Yes	Postpartum
GW-81	5/13	T	2	New	3	Yes	Postpartum
GW-82	5/13	T	4	New	3	Yes	Postpartum
GW-84	5/13	T	4	New	4	No	Postpartum
GW-85	5/13	F,A,A	9	4	4	Yes	Barren; False pregnancy
GW-86	5/13	X	3	>0.1	3	Yes	Premature
GW-87	5/13	T	1+	New	unk	Yes	Postpartum
GW-89	5/13	T	5	New	2	Yes	Postpartum
GW-90	5/13	T	3+	New	unk	No	Postpartum
GW-91	5/13	T	3	New	4	Yes	Postpartum
GW-92	5/13	—	1	unk	2	Yes	Barren
GW-93	5/13	T	4	New	2	Yes	Postpartum
GW-94	5/13	T	3	New	3	Yes	Postpartum
GW-95	5/13	T	2	New	3	Yes	Postpartum
GW-96	5/13	T	4	New	4	Yes	Postpartum
GW-102	5/14	N	7	1	4	Yes	New pregnancy
GW-103	5/14	T	7	New	2	Yes	Postpartum
GW-104	5/14	T	4	New	4	Yes	Postpartum
GW-105	5/14	T	4+	New	unk	Yes	Postpartum
GW-106	5/14	T	5	New	3	Yes	Postpartum
GW-107	5/14	T	4	New	5	Yes	Postpartum
GW-108	5/14	T	3	New	3	Yes	Postpartum
GW-109	5/14	T	6	New	4	Yes	Postpartum
GW-111	5/14	T	6	New	3	Yes	Postpartum
GW-112	5/14	T	2	New	2	Yes	Postpartum
GW-113	5/14	—	6	1	7	Yes	Estrous

Specimens from Gambell area
5 May to 5 June 1982
(continued)

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
GW-141	5/21	N	5	4	4	No	New pregnancy
GW-142	5/21	X	5	>0.2	1	No	Aborted
GW-143	5/21	T	8	New	5	Yes	Postpartum
GW-144	5/21	T	3	New	2	Yes	Postpartum
GW-145	5/21	T	1	New	3	Yes	Postpartum
GW-146	5/21	unk	1+	unk	unk	Yes	One ovary only
GW-147	5/21	T	4	New	3	Yes	Postpartum
GW-149	5/22	—	4	unk	10	Yes	Estrous
GW-150	5/22	T	5	New	6	Yes	Postpartum
GW-151	5/22	T	5	New	4	Yes	Postpartum
GW-152	5/22	T	4	New	4	Yes	Postpartum
GW-153	5/22	T	unk	New	unk	Yes	Postpartum
GW-157	5/23	T	5	New	3	Yes	Postpartum
GW-158	5/23	T,A	7	New	1	Yes	Postpartum
GW-159	5/23	T	3	New	3	Yes	Postpartum
GW-161	5/24	X	5	>0.2	5	No	Aborted
GW-164	5/22	T	3	New	3	Yes	Postpartum
GW-165	5/23	X	5	>0.2	8	No	Aborted; Estrous
GW-166	5/23	C,C,C,C	8	4	9	No	Estrous
GW-167	5/23	N	4	3	6	No	New pregnancy
GW-168	5/23	T,A	2	New	4	Yes	Postpartum
GW-169	5/23	T	5	New	4	Yes	Postpartum
GW-171	5/25	T	4	New	5	Yes	Postpartum
GW-174	5/25	N	5	1	8	No	New pregnancy
GW-176	5/25	T	6	New	5	Yes	Postpartum
GW-237	6/05	—	2	3	6	No	Barren

Specimens from Savoonga area
27 May to 17 June 1982

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
SV-1	5/27	T	4	New	3	Yes	Postpartum
SV-2	5/27	X	7	>0.2	6	No	Aborted
SV-9	5/27	T	2	New	3	Yes	Postpartum
SV-13	5/27	T	4	New	3	No	Postpartum
SV-14	5/27	T	2	New	1	Yes	Postpartum
SV-20	5/27	N	8	2	3	No	New pregnancy
SV-21	5/27	N	6	2	5	No	New pregnancy
SV-22	5/27	T	3	New	3	No	Postpartum
SV-23	5/27	T	4	New	5	Yes	Postpartum
SV-24	5/27	N	5	2	11	No	New pregnancy
SV-25	5/27	N	10	>4	7	No	New pregnancy
SV-29	5/27	T	6	New	1	Yes	Postpartum
SV-33	5/27	X,N	2	>0.2	1	No	Aborted; New pregnancy
SV-34	5/27	N	6	>4	3	No	New pregnancy
SV-35	5/27	—	2	1	15	No	Estrous
SV-37	5/27	T	1+	New	unk	No	Postpartum
SV-42	5/27	T	2+	New	unk	No	Postpartum
SV-43	5/27	X	4	>0.2	7	No	Aborted; Estrous
SV-50	5/30	N	6	1	5	No	New pregnancy
SV-51	5/30	N	6	>4	9	No	New pregnancy
SV-52	5/30	X	1	>0.2	9	No	Aborted; Estrous
SV-53	5/30	N	3	>4	3	No	New pregnancy
SV-101	6/17	X	8	>0.2	2	No	Aborted

Specimens from Little Diomede area
19 May to 13 June 1982

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
DW-1	5/19	N	5	4	4	No	New pregnancy
DW-2	5/22	T	3	New	<1	Yes	Postpartum
DW-3	5/23	T	4	New	3	Yes	Postpartum
DW-4	5/23	T	2	New	3	Yes	Postpartum
DW-11	5/23	N	8	>4	5	No	New pregnancy
DW-12	5/23	N	7	2	8	No	New pregnancy
DW-13	5/23	T	3	New	3	Yes	Postpartum
DW-14	5/23	T	2	New	5	Yes	Postpartum
DW-15	5/23	T	5	New	2	Yes	Postpartum
DW-18	5/23	T	6	New	5	Yes	Postpartum
DW-19	5/23	T	4	New	3	Yes	Postpartum
DW-22	5/24	T	5	New	4	Yes	Postpartum
DW-23	5/24	T	5	New	4	Yes	Postpartum
DW-24	5/24	T	4	New	5	Yes	Postpartum
DW-25	5/24	T	1	New	2	Yes	Postpartum
DW-27	5/24	N,A,A,A	5	2	<1	Yes	New pregnancy
DW-28	5/25	T	5	New	6	Yes	Postpartum
DW-30	5/25	T	3	New	1	Yes	Postpartum
DW-31	5/25	N	8	3	3	No	New pregnancy
DW-32	5/25	N	2	—	3	No	New pregnancy
DW-33	5/27	T	2	New	3	Yes	Postpartum
DW-34	5/27	X	7	>0.2	1	No	Aborted
DW-35	5/27	N	2	—	2	No	New pregnancy
DW-36	5/27	T	3	New	5	Yes	Postpartum
DW-37	5/27	N	1	—	3	No	New pregnancy
DW-38	5/27	X	5	>0.2	9	No	Aborted; Estrous
DW-39	5/27	X	2	>0.2	7	Yes	Aborted; Estrous
DW-40	5/27	N	1	—	4	No	New pregnancy
DW-43	5/27	T	5	New	3	Yes	Postpartum
DW-44	5/27	T	5	New	3	Yes	Postpartum
DW-45	5/27	X	3	>0.1	10	Yes	Premature; Estrous
DW-46	5/27	—	6	2	5	No	Barren

Specimens from Little Diomede area
19 May to 13 June 1982
(continued)

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
DW-47	5/27	T	1	New	5	Yes	Postpartum
DW-49	5/27	T	2	New	3	Yes	Postpartum
DW-50	5/27	N	1	2	5	No	New pregnancy
DW-51	5/27	T	8	New	<1	Yes	Full-term
DW-52	5/27	—	5	1	5	No	Barren
DW-53	5/27	X	7	>0.2	10	No	Aborted; Estrous
DW-54	5/27	T	6	New	1	Yes	Postpartum
DW-56	5/27	T	3	New	2	Yes	Postpartum
DW-57	5/27	T	5	New	5	Yes	Postpartum
DW-58	5/27	T	3	New	5	Yes	Postpartum
DW-59	5/27	T	3	New	4	Yes	Postpartum
DW-60	5/27	T	3	New	4	Yes	Postpartum
DW-61	5/27	T	6	New	6	Yes	Postpartum
DW-62	5/27	T	3	New	3	Yes	Postpartum
DW-63	5/27	T	1	New	4	Yes	Postpartum
DW-64	5/27	T	4	New	3	Yes	Postpartum
DW-77	6/02	N	9	3	4	No	New pregnancy
DW-94	6/04	T	4	New	4	Yes	Postpartum
DW-101	6/05	T	3	New	7	Yes	Postpartum
DW-102	6/05	T	4	New	3	Yes	Postpartum
DW-103	6/05	N	5	2	5	No	New pregnancy
DW-104	6/05	T	5	New	3	Yes	Postpartum
DW-105	6/05	T	6	New	5	Yes	Postpartum
DW-107	6/07	T	4	New	5	Yes	Postpartum
DW-108	6/07	C,C,C	6	>4	9	No	Estrous
DW-110	6/07	T	4	New	9	Yes	Postpartum
DW-120	6/07	T	3	New	7	Yes	Postpartum
DW-121	6/07	T	3	New	3	Yes	Postpartum
DW-122	6/07	T	3	New	5	Yes	Postpartum
DW-123	6/07	T	5	New	6	Yes	Postpartum

Specimens from Little Diomede area
19 May to 13 June 1982
(continued)

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
DW-124	6/07	—	14	>4	5	No	Barren
DW-125	6/07	X	7	>0.2	7	No	Aborted; Estrous
DW-126	6/07	N	1	—	4	No	New pregnancy
DW-127	6/07	N	7	2	5	No	New pregnancy
DW-184	6/09	T,A	5	New	7	Yes	Postpartum
DW-185	6/08	N,A,A,A,A	10	4	3	No	New pregnancy
DW-186	6/08	—	5	1	3	No	Barren
DW-187	6/08	T	2	New	4	Yes	Postpartum
DW-188	6/08	N	3	2	7	No	New pregnancy
DW-189	6/08	X	7	>0.2	12	No	Aborted; Estrous
DW-191	6/08	T	6	New	3	Yes	Postpartum
DW-192	6/08	T	3	New	4	Yes	Postpartum
DW-193	6/08	T	0	New	7	Yes	Postpartum
DW-194	6/08	T	3	New	4	Yes	Postpartum
DW-195	6/08	N	3	3	<1	No	New pregnancy
DW-196	6/08	—	5	1	2	No	Barren
DW-200	6/08	X	3	>0.2	2	No	Aborted
DW-201	6/08	N	4	2	2	No	New pregnancy
DW-202	6/08	C,C,C,C	7	>4	2	No	Barren
DW-203	6/08	T	6	New	7	Yes	Postpartum
DW-204	6/08	N	4	4	2	No	New pregnancy
DW-207	6/08	T	7	New	3	Yes	Postpartum
DW-208	6/08	X	3	>0.2	10	No	Aborted; Estrous
DW-209	6/08	T	3	New	2	Yes	Postpartum
DW-210	6/08	N	1	—	5	No	New pregnancy
DW-211	6/08	N	5	1	5	No	New pregnancy
DW-212	6/08	N	1	—	10	No	New pregnancy
DW-213	6/08	—	0	—	4	No	Immature
DW-214	6/08	—	3	2	8	No	Estrous
DW-215	6/08	N	6	2	5	No	New pregnancy

Specimens from Little Diomede area
19 May to 13 June 1982
(continued)

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
DW-221	6/08	N	4	3	7	No	New pregnancy
DW-222	6/08	N	4	1	3	No	New pregnancy
DW-223	6/08	T	3	New	3	Yes	Postpartum
DW-224	6/08	T	4	New	5	Yes	Postpartum
DW-225	6/08	T	5	New	3	Yes	Postpartum
DW-226	6/08	T	4	New	5	Yes	Postpartum
DW-227	6/08	T	5	New	3	Yes	Postpartum
DW-228	6/09	T	3	New	4	Yes	Postpartum
DW-229	6/09	N	4	2	4	No	New pregnancy

Specimens from Wales area
23 May to 14 June 1982

Field no.	Date	Corpus luteum type	No. of corpora albicantia	Age latest placental scar (yrs)	Diameter largest follicle (mm)	With calf	Status
WL-A	5/23-26	—	0	—	3	unk	Immature
WL-B	5/23-26	N	5	2	3	unk	New pregnancy
WL-C	5/23-26	T	3	New	3	unk	Postpartum
WL-1	6/14	T	6	New	7	unk	Postpartum
WL-2	6/14	X	3	>0.2	8	Yes	Premature; Estrous
WL-4	6/14	N	4	2	7	unk	New pregnancy
WL-5	6/14	N	2	1	2	unk	New pregnancy
WL-X	6/14	N	8	3	5	unk	New pregnancy
WL-Y	6/14	C,C,C,C	7	>4	1	unk	Barren
WL-Z	6/14	T	8	New	3	unk	Postpartum

Specimens from Mekoryuk area
29 April 1982

MK-4	4/29	T	3+	New	unk	unk	Postpartum
MK-5	4/29	T	1	New	3	Yes	Full-term

Location unknown, possibly S.E. Cape

SEC-10?	unk	—	10	>4	9	unk	Estrous

APPENDIX II

LIST OF KINDS, NUMBERS, AND WEIGHTS OF FOOD ITEMS IN STOMACH CONTENTS OF WALRUSES FROM THE SPRING 1982 HARVEST.

The following is a list of numbers and weights of prey found in samples from each of the 76 walruses whose stomach contents were adequate for analysis. The number of individual prey ("No.") is the maximum identifiable with certainty. All weights ("Wt.") are in grams. Insofar as possible, each type of prey was identified to genus; otherwise, identification to higher taxonomic rank was possible. Where only the indigestible hard parts of an organism were present, presumably left from an earlier meal, these were indicated only as trace occurrence ("tr"). Most of these were operculae from gastropods (snails). In many instances there were several gastropod feet which lacked the diagnostic operculum, hence were not certainly identifiable to genus. These are indicated as "Gastropoda unidentified". The last category "Sediments" includes only the inorganic materials (sand and gravel).

Results from analysis of stomach contents of walruses from the Little Diomede area, 24 May to 13 June 1982

Field no.	DW-22		DW-93		DW-94		DW-108		DW-109		DW-155		DW-156	
Sex	♀		♀		♀		♀		♀		♂		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Scyphozoan	—	22	—	—	—	—	—	—	—	—	—	—	—	—
Nephthys	—	—	—	—	—	—	—	—	—	—	—	—	2	2
Polychaete unid.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Golfingia	—	—	—	—	—	—	1	1	—	—	—	—	3	7
Echiurus	—	—	—	—	—	—	1	1	—	—	—	—	2	17
Priapulus	—	—	—	—	—	—	1	19	5	30	1	12	—	—
Neptunea	8	42	—	—	4	44	—	—	—	—	—	—	—	—
Buccinum	tr	tr	—	—	2	5	—	—	—	—	—	—	—	—
Natica	—	—	—	—	8	7	1	1	1	1	—	—	1	1
Polinices	tr	tr	—	—	10	7	—	—	—	—	—	—	3	1
Gastropod unid.	14	28	—	—	57	68	1	2	—	—	—	—	4	3
Serripes	23	242	24	464	95	843	2	12	—	—	—	—	—	—
Mya	1	10	27	593	32	45	50	801	42	809	113	2,010	67	2,291
Tellinidae	—	—	8	8	—	—	—	—	—	—	—	—	—	—
Hiatella	—	—	—	—	60	10	1,103	401	2	1	—	—	10	3
Bivalve unid.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	2	4	—	—	1	18
Byblis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pagurus	—	—	—	—	—	—	—	—	—	—	—	—	1	6
Hyas	—	—	—	—	—	—	—	—	8	30	—	—	—	—
Cucumaria	4	75	6	85	3	34	15	113	5	42	—	—	—	—
Meat fragments	—	74	—	40	—	120	—	2	—	38	—	12	—	19
Shell fragments	—	6	—	—	—	1	—	4	—	2	—	—	—	—
Sediments	—	50	—	206	—	265	—	80	—	427	—	5	—	30
Totals	50	549	65	1,396	271	1,449	1,175	1,437	65	1,384	114	2,039	94	2,398

Results from analysis of stomach contents of walruses from the Little Diomede area,
24 May to 13 June 1982
(continued)

Field no.	DW-157		DW-158		DW-159		DW-160		DW-161		DW-162		DW-163	
Sex	♀		♀		♀		♀		♀		♀		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	6	10	—	—	—	—	4	68	—	—	—	—	—	—
Scyphozoan	—	—	—	—	—	—	—	—	—	—	—	—	1	6
Nephthys	6	24	—	—	—	—	1	3	—	—	—	—	15	163
Polychaete unid.	—	—	—	—	—	—	—	—	—	—	—	—	4	9
Golfingia	6	28	4	6	—	—	7	25	—	—	—	—	—	—
Echiurus	2	13	—	—	—	—	1	8	—	—	—	—	2	20
Priapulus	1	12	3	22	—	—	—	—	1	48	—	—	1	24
Neptunea	—	—	—	—	1	4	1	1	—	—	tr	tr	—	—
Buccinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natica	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polinices	1	1	—	—	—	—	1	1	1	1	2	1	—	—
Gastropod unid.	3	7	2	2	7	17	6	14	—	—	4	5	—	—
Serripes	4	17	—	—	—	—	—	—	—	—	—	—	5	16
Mya	28	997	62	1,455	59	1,246	48	1,288	99	2,045	57	1,344	33	1,305
Tellinidae	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hiatella	—	—	1	1	—	—	—	—	—	—	—	—	—	—
Bivalve unid.	—	—	—	—	—	—	—	—	—	—	—	—	8	32
Octopus	—	—	—	—	—	—	—	—	—	—	1	3	1	27
Byblis	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Argis	—	—	1	9	—	—	—	—	—	—	—	—	—	—
Pagurus	—	—	—	—	2	6	—	—	—	—	—	—	—	—
Hyas	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cucumaria	55	877	29	418	26	310	43	683	24	305	24	337	32	625
Meat fragments	—	22	—	30	—	103	—	49	—	31	—	20	—	90
Shell fragments	—	—	—	3	—	—	—	—	—	—	—	2	—	—
Sediments	—	50	—	132	—	117	—	27	—	50	—	58	—	20
Totals	112	2,058	102	2,078	95	1,803	113	2,168	125	2,480	88	1,770	102	2,337

Results from analysis of stomach contents of walruses from the Little Diomede area, 24 May to 13 June 1982 (continued)

Field no.	DW-184		DW-190		DW-200		DW-206		DW-216		DW-228		DW-230	
Sex	♀		♂		♀		♂		♂		♀		♂	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	—	—	—	—	—	—	1	18
Scyphozoan	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nephthys	—	—	—	—	5	8	—	—	—	—	—	—	—	—
Polychaete unid.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Golfingia	2	10	—	—	16	50	—	—	—	—	—	—	3	9
Echiurus	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Priapulus	—	—	—	—	—	—	—	—	1	4	1	18	—	—
Neptunea	—	—	—	—	—	—	—	—	—	—	—	—	3	15
Buccinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natica	—	—	1	1	—	—	tr	tr	—	—	1	1	—	—
Polinices	—	—	—	—	—	—	tr	tr	—	—	1	1	—	—
Gastropod unid.	1	1	—	—	3	8	—	—	—	—	3	2	3	22
Serripes	—	—	—	—	5	17	—	—	—	—	—	—	8	145
Mya	73	2,060	55	1,741	30	394	32	791	47	952	71	1,662	53	1,750
Tellinidae	1	3	—	—	—	—	—	—	—	—	—	—	—	—
Hiatella	—	—	—	—	—	—	—	—	—	—	18	7	43	10
Bivalve unid.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Byblis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argis	—	—	—	—	—	—	—	—	—	—	2	15	—	—
Pagurus	—	—	—	—	—	—	—	—	—	—	—	—	2	8
Hyas	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cucumaria	11	230	—	—	53	804	—	—	4	60	—	—	18	240
Meat fragments	—	20	—	83	—	42	—	13	—	47	—	132	—	32
Shell fragments	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Sediments	—	10	—	11	—	156	—	83	—	80	—	17	—	6
Totals	88	2,335	56	1,836	112	1,479	32	887	52	1,143	97	1,855	134	2,255

Results from analysis of stomach contents of walruses from the Little Diomede area, 24 May to 13 June 1982 (continued)

Field no.	DW-231		DW-232		DW-233		DW-234		DW-235		DW-236	
Sex	♂		♂		♂		♂		♂		♂	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	—	—	—	—	—	—
Scyphozoan	—	—	—	—	—	—	1	4	—	—	—	500
Nephthys	—	—	2	2	—	—	—	—	—	—	1	1
Polychaete unid.	—	—	—	—	—	—	—	—	—	—	—	—
Golfingia	—	—	9	45	1	3	—	—	—	—	—	—
Echiurus	—	—	—	—	—	—	—	—	—	—	—	—
Priapulus	—	—	1	20	1	21	—	—	—	—	—	—
Neptunea	—	—	1	6	—	—	4	11	—	—	—	—
Buccinum	—	—	—	—	—	—	tr	tr	tr	tr	—	—
Natica	1	2	—	—	5	8	3	6	1	1	—	—
Polinices	6	5	1	3	5	5	9	10	5	3	—	—
Gastropod unid.	30	42	3	7	2	2	23	46	15	21	9	18
Serripes	33	845	32	912	87	698	45	815	46	893	21	515
Mya	19	791	13	408	9	259	19	800	14	850	4	253
Tellinidae	2	3	6	17	1	1	1	1	—	—	—	—
Hiatella	5	2	8	2	586	230	140	27	53	13	125	41
Bivalve unid.	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	—	—	—	—
Byblis	—	—	—	—	—	—	—	—	—	—	—	—
Argis	—	—	—	—	—	—	—	—	—	—	—	—
Pagurus	—	—	—	—	—	—	—	—	—	—	—	—
Hyas	—	—	—	—	—	—	—	—	—	—	—	—
Cucumaria	—	—	—	—	—	—	—	—	—	—	—	—
Meat fragments	—	27	—	42	—	20	—	47	—	30	—	22
Shell fragments	—	—	—	—	—	3	—	—	—	—	—	—
Sediments	—	12	—	8	—	290	—	13	—	5	—	8
Totals	96	1,729	76	1,472	697	1,540	245	1,780	134	1,816	160	1,358

Results from analysis of stomach contents of walruses from the Wales area, 14 June 1982.

Field no.	WL-1		WL-3		WL-4	
Sex	♀		♀		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.
Priapulus	1	2	—	—	—	—
Mya	240	1,545	20	320	20	365
Tellinidae	8	10	—	—	—	—
Cucumaria	1	2	2	10	9	132
Sediments	—	12	—	12	—	25
Totals	250	1,571	22	342	29	522

Results from analysis of stomach contents of walruses from the King Island area, 25 May 1982

Field no.	KI-1		KI-4	
Sex	♂		♀	
Taxon	No.	Wt.	No.	Wt.
Nephthys	—	—	2	2
Priapulus	1	3	—	—
Natica	tr	tr	tr	tr
Polinices	—	—	5	4
Serripes	—	—	570	1,296
Mya	110	885	19	207
Tellinidae	—	—	3	5
Hiatella	5	4	—	—
Yoldia	—	—	8	2
Hyas	1	1	—	—
Cucumaria	20	205	—	—
Meat fragments	—	75	—	—
Sediments	—	70	—	—
Totals	137	1,243	607	1,516

Results from analysis of stomach contents of walruses from the Cape Woolley area, 8 June 1982.

Field no.	CW-1		CW-5	
Sex	♀		♀	
Taxon	No.	Wt.	No.	Wt.
Echiurus	15	60	25	260
Mya	13	65	1	2
Tellinidae	1	1	—	—
Cucumaria	31	545	—	—
Meat fragments	—	50	—	—
Sediments	—	970	—	900
Totals	60	1,691	26	1,162

Results from analysis of stomach contents of a walrus from the Nome area, 30 May 1982.

Field no.	NW-15	
Sex	♀	
Taxon	No.	Wt.
Nephthys	5	5
Priapulus	4	10
Serripes	6	10
Mya	229	1,590
Tellinidae	112	310
Yoldia	78	24
Cucumaria	27	100
Totals	461	2,049

Results from analysis of stomach contents of walruses from the Gambell area, 25 April to 25 May 1982.

Field no.	GW-1		GW-2		GW-11		GW-12		GW-13		GW-36		GW-37	
Sex	♂		♂		♂		♂		♂		♂		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nephthys	—	—	—	—	—	—	2	5	—	—	—	—	—	—
Arenicola	—	—	—	—	—	—	1	3	—	—	—	—	—	—
Lumbrinereis	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Brada	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polychaete unid.	—	—	—	—	—	—	27	24	—	—	—	—	—	—
Golfingia	—	—	—	—	2	3	—	—	—	—	—	—	—	—
Echiurus	—	—	—	—	—	—	—	—	—	—	1	5	—	—
Priapulus	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Neptunea	tr	tr	—	—	—	—	—	—	—	—	—	—	1	2
Buccinum	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Natica	—	—	—	—	—	—	27	40	2	2	—	—	—	—
Polinices	1	2	—	—	—	—	2	2	—	—	—	—	6	9
Margarites	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gastropod unid.	1	1	—	—	1	4	—	—	—	—	—	—	—	—
Serripes	12	63	—	—	1	6	8	95	—	—	9	316	1	8
Mya	61	783	143	1,899	120	1,295	3	31	91	849	59	1,216	127	847
Spisula	—	—	—	—	—	—	19	470	1	32	3	26	—	—
Tellinidae	—	—	—	—	1	1	5	2	1,264	344	—	—	—	—
Yoldia	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Anonyx	—	—	—	—	—	—	—	—	—	—	—	—	1	1
Byblis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ampelisca	—	—	—	—	—	—	—	—	—	—	—	—	2	1
Argis	6	19	—	—	—	—	1	5	—	—	—	—	14	40
Pagurus	—	—	—	—	—	—	—	—	—	—	—	—	7	4
Hyas	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cucumaria	1	2	—	—	—	—	—	—	—	—	—	—	—	—
Pelonaia	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ammodytes	—	—	—	—	56	373	370	670	—	—	4	10	—	—
Meat fragments	—	70	—	—	—	107	—	40	—	36	—	16	—	90
Shell fragments	—	4	—	13	—	11	—	—	—	—	—	2	—	—
Sediments	—	76	—	22	—	45	—	tr	—	55	—	9	—	8
Totals	82	1,020	143	1,934	181	1,845	466	1,388	1,358	1,318	76	1,600	159	1,010

Results from analysis of stomach contents of walruses from the Gambell area, 25 April to 25 May 1982. (Continued)

Field no.	GW-48		GW-49		GW-67		GW-69		GW-70		GW-75		GW-86	
Sex	♂		♂		♂		♂		♂		♂		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	14	73	—	—	—	—	—	—
Nephthys	—	—	—	—	1	4	—	—	2	30	2	9	—	—
Arenicola	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lumbrinereis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Brada	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Polychaete unid.	—	—	—	—	—	—	—	—	1	3	—	—	—	—
Golfingia	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Echiurus	—	—	—	—	—	—	8	42	—	—	1	6	—	—
Priapulus	—	—	—	—	—	—	—	—	—	—	3	25	—	—
Neptunea	—	—	—	—	21	190	3	47	—	—	—	—	tr	tr
Buccinum	—	—	—	—	1	3	1	3	—	—	—	—	tr	tr
Natica	—	—	—	—	1	1	—	—	—	—	—	—	—	—
Polinices	4	6	1	7	—	—	—	—	—	—	—	—	tr	tr
Margarites	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gastropod unid.	—	—	—	—	4	17	1	3	6	87	5	10	65	280
Serripes	—	—	—	—	21	352	43	497	3	108	67	907	7	50
Mya	256	1,183	245	1,660	61	910	70	895	61	1,512	17	142	25	60
Spisula	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tellinidae	36	4	10	3	—	—	—	—	—	—	—	—	100	25
Yoldia	—	—	—	—	—	—	—	—	—	—	—	—	8	2
Octopus	—	—	—	—	1	10	—	—	—	—	—	—	—	—
Anonyx	—	—	—	—	—	—	1	1	—	—	—	—	—	—
Byblis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ampelisca	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argis	—	—	—	—	—	—	3	6	—	—	—	—	—	—
Pagurus	—	—	—	—	3	6	—	—	—	—	—	—	—	—
Hyas	—	—	—	—	1	13	2	4	—	—	—	—	—	—
Cucumaria	—	—	—	—	—	—	—	—	2	80	—	—	—	—
Pelonaia	—	—	4	10	—	—	—	—	—	—	—	—	—	—
Ammodytes	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Meat fragments	—	20	—	—	—	62	—	37	—	28	—	76	—	108
Shell fragments	—	2	—	—	—	—	—	—	—	—	—	—	—	—
Sediments	—	10	—	5	—	5	—	44	—	25	—	70	—	—
Totals	296	1,225	260	1,685	115	1,573	146	1,652	75	1,873	95	1,245	205	525

Results from analysis of stomach contents of walruses from the Gambell area, 25 April to 25 May 1982. (Continued)

Field no.	GW-88		GW-97		GW-98		GW-99		GW-101		GW-110		GW-147	
Sex	♂		♂		♂		♂		♂		♂		♀	
Taxon	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.	No.	Wt.
Anemone	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Nephthys	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Arenicola	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lumbrinereis	—	—	—	—	—	—	—	—	—	—	1	2	—	—
Brada	—	—	—	—	—	—	—	—	4	1	—	—	—	—
Polychaete unid.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Golfingia	1	6	—	—	—	—	—	—	—	—	—	—	—	—
Echiurus	—	—	—	—	2	15	—	—	—	—	1	1	—	—
Priapulus	—	—	2	12	2	11	1	3	—	—	—	—	—	—
Neptunea	4	16	—	—	1	6	tr	tr	1	1	—	—	tr	tr
Buccinum	tr	tr	—	—	—	—	—	—	tr	tr	3	5	tr	tr
Natica	—	—	—	—	—	—	—	—	tr	tr	3	4	tr	tr
Polinices	—	—	1	3	—	—	1	1	4	5	4	6	tr	tr
Margarites	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gastropod unid.	6	45	—	—	—	—	4	5	1	2	4	9	7	14
Serripes	23	433	12	172	17	145	45	446	4	75	25	573	2	10
Mya	96	1,421	190	1,705	139	1,067	60	619	5	57	4	92	142	1,078
Spisula	—	—	—	—	—	—	—	—	30	159	8	170	—	—
Tellinidae	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Yoldia	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Octopus	—	—	—	—	—	—	tr	tr	—	—	—	—	—	—
Anonyx	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Byblis	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ampelisca	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Argis	—	—	—	—	—	—	—	—	5	2	—	—	—	—
Pagurus	—	—	—	—	—	—	—	—	tr	tr	—	—	—	—
Hyas	—	—	—	—	—	—	2	5	5	2	—	—	—	—
Cucumaria	—	—	1	48	3	85	—	—	—	—	—	—	—	—
Pelonaia	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ammodytes	—	—	—	—	—	—	—	—	3	1	108	110	—	—
Meat fragments	—	28	—	26	—	60	—	125	—	54	—	25	—	—
Shell fragments	—	2	—	—	—	—	—	2	—	—	—	—	—	—
Sediments	—	—	—	5	—	25	—	64	—	1,380	—	26	—	—
Totals	130	1,951	206	1,971	164	1,414	113	1,270	62	1,739	163	1,025	151	1,102