## INTERTM REPORT

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ANALYSIS OF WALRUS REPRODUCTIVE ORGANS AND STOMACHS
FROM THE 1980 SPRING HARVEST IN THE BERING STRAIT REGION

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

Management of the Pacific walrus requires that both nations maintain continuous surveillance of the numerical status and biological characteristics of the walrus population, including the quantity and quality of the harvests by man. For history has shown that this resource is highly susceptible to depletion by over-harvesting (Fay, 1957), and that it has been recovering in recent years from such depletion (Krylov, 1968; Fay and Kelly, 1980). One aspect of management surveillance is the collection of biological samples from harvested animals, with which to assess their current reproductive status and performance, as well as their age composition, physical condition, and feeding habits. Collections of that type were made by Fish and Wildife Service personnel in 1980, during the spring walrus harvests at native vilLages in the St. Lawrence Island to Bering Strait region. This was done with the assistance and cooperation of the Eskimo Walrus Commission.

The following is a report on analyses of some of the materials collected from the walruses taken during the 1980 spring harvest. Those materials included 104 samples of stomach contents from animals taken at Little Diomede, Wales, Nome, Savoonga, and Gambell, and reproductive organs from 173 females taken at Gambell. Analyses of an additional 110 sets of reproductive organs
from females taken at Diomede and Nome will be included in the final report.

The materials were preserved and labelled in the field by the FWS personnel and were stored for about one year, before being made available to us in June 1981. After their arrival in Fairbanks, they were stored for about 2 months in $10 \%$ formalin in a refrigerated space, before being analyzed.

METHODS

## Reproductive Tracts

The reproductive tracts from Gambell were received as preserved (in $10 \%$ formalin), labelled (with accession number and date), pairs of ovaries with all or part of the adjacent uterine horns still attached. Before processing, these were soaked in fresh water for a few hours to remove some of the formalin and to soften the tissues for easier handing. After soaking, each pair was separated, and the individual horns were identified as "right" and "left". The ovary was removed from the right horn, sectioned serially in 1- to 2-mm-thick longitudinal slices with a sharp knife, and inspected visually, before the adjacent uterine horn was hemisected longitudinally. Then the same process was repeated with the left ovary and horn. The reasons for this sequence were: (1) if an ovary was found to contain a new corpus luteum of pregnancy, the adjacent horn could be opened very carefully, so that it could be searched for the associated embryo without damaging it, and (2) for the sake of maintaining the correct relationship between structures in each ovary and its adjacent uterine horn, the right and left organs
were handled separately. The latter is important for interpreting the individual animal's reproductive history.

Each sectioned ovary and uterine horn were inspected visually, and all features relevant for interpretation of reproductive history and status were recorded. For the ovaries, these records included the kinds and dimensions of the vesicular follicles, corpora lutea, and corpora albicantia; for the uteri, they included the width and color of any placental scars, presence of embryos, blood, or mucous in the lumen, condition of the endometrium, and when appropriate, the outside diameter of the horns.

In nearly all ovaries of juvenile subadult and adult walruses, some vesicular follicles can be seen without magnification in the creamy-brown cortical layer. These follicles vary considerably in size and condition, and this variability is related to the reproductive status of the animal (Fay, in press). "Healthy" or ripening follicles tend to contain a slightly opaque, gelatinous liquor, whereas the liquor in degenerate follicles is very milky and firm when fixed in $10 \%$ formalin. Degenerate follicles with firm, milky liquor (sometimes with a pinkish-yellowish tinge) often are very large and are found most often in postestrus individuals. Apparently, these are follicles which ripened nearly to maximal size but degenerated spontaneously or after release and fertilization of an ovum from another follicle in the same or opposite ovary.

The quality of healthy, vesicular follicles in the ovaries appears to have no relationship to the individual's reproductive capability, for the ovaries of immature females 2 to 3 years old usually contain as many or more than those of the adults (Fay, in press). The size of the largest healthy follicles, however, is a strong indicator of the individual's being in or
out of estrus. Hence, we routinely recorded the size of the largest healthy follicle in each ovary in the present series.

A corpus luteum can be formed from (a) an unruptured follicle, (b) a ruptured follicle the ovun of which was not fertilized, or (c) a ruptured follicle the ovum from which was fertilized. That is, the development of a corpus luteum is not necessarily indicative that the female will give birth to a calf. For various reason, the ovum may not be fertilized, the blastocyst may not implant, or the conceptus may be aborted, resorbed, or born dead (Hafez, 1967). Hence, we identified each type of corpus luteum for the purpose of gathering comparative information on reproductive performance, in this case, the percentage of ovulations resulting in pregnancy. In the ovaries, a corpus luteum of new pregnancy (i.e., from the 1980 mating season) was recognized by its large size ( $18-34$ mm in diameter), irregular perimeter, bright yellowish color (sometimes with pinkish center), and fresh ovulation scar in the adjacent tunic. Accessory corpora lutea, in the same ovary with the corpus luteum of pregnancy (or occasionally in the opposite ovary), were identical in structure with the primary corpus but were less than half as large and had no ovulation scar. Corpora atretica resembled the accessory corpora in size and lack of an ovulation scar, but when present with a corpus luteum of pregnancy, they were not in the same stage of development; in most instances, they were alone in the ovary and most were in a retrogressive state. Corpora lutea of false pregnancy also were small and retrogressive but did have an associated ovulation scar, indicating that an ovum had been shed but not fertilized. Finally, corpora lutea of term pregnancy, in animals that were still carrying a full-term fetus or had recently given birth, were large ( $21-43 \mathrm{~mm}$ ), with a regular
border, and generally contained $50 \%$ or more fibrous tissue, usually arranged in a stellate pattern. In these, the patches of remaining lutein cells tended to appear more orange than yellowish.

In each instance where a corpus luteum is formed, whether or not correlated with a pregnancy, it eventually becomes a corpus albicans - a mass of whitish, fibrous tissue (Harrison and Weir, 1977). Following normal pregnancy in the walrus, retrogression of the corpus luteum to a corpus albicans takes place over a period of more than 2 but less than 7 months after the birth of the calf (Fay, in press). Presumably, the other types of corpora lutea also require several months to make this change. For several years thereafter, the corpus albicans continues to shrink in size and, eventually, disappears. Since the corpora albicantia derived from retrogression of corpora atretica, corpora accessoria, and corpora of false pregnancy cannot be distinguished reliably from those derived from corpora lutea of pregnancy, and because each type eventually disappears, the number of corpora albicantia in the ovaries of a walrus is not a reliable index of that animal's productivity. Although the number of corpora may tend to approximate the number of ovulations, it is not dependable as an indicator of the number of pregnancies completed. For these reasons, although we recorded each corpus albicans, we did not attempt to interpret the meaning of their numbers. Only those still in a stage of development from a retrogressing corpus luteum (i.e., still containing some lutein cells and/or thecal elements) lent themselves to interpretation.

More useful for interpretation of reproductive history are the placental scars, since these are reliable indicators of past pregnancy. Their appearance in fresh specimens was described earlier by Fay (in press), who
observed that they change in color and tend to diminish in size with increasing age. Their coloration is due to deposits of hemosiderin in the contused endometrium and uterine wall, at the site of detachment of the zonal placenta. The change in color is due to gradual removal of the hemosiderin, over a period of 3 to 4 years in the endometrium and about one year longer in the deeper muscular layers.

In the preserved uteri from the 1980 Gambell sample, the scars were separable into seven distinct types:

1. Broad (about 5 to $>20 \mathrm{~cm}$ wide), rough, dark brown and bloody, found in animals at full term pregnancy or having recently (in spring 1980) given birth. In these cases ( $\mathrm{N}=36$ ), both 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. Smooth to slightly rough, dark brown to reddish-brown, 1.5 to 4 cm wide ( $\mathrm{N}=13$, mean $\pm \mathrm{SE}=24.3 \pm 2.4 \mathrm{~mm}$ ), in uterine horns ranging from normal progestational (non-pregnant) size up to 7 cm in diameter. Usually both horns contained some free blood 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 diameter 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 earlier, well before the normal mid-April to mid-June calving season.
3. Orange-brown, smooth to slightly rough, 1.5 to 3.5 cm wide $(\mathrm{N}=28$, mean $\pm \mathrm{SE}=26.0 \pm 0.85 \mathrm{~mm}$ ), in a 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 1979).
4. Bright to dull orange, smooth, 1.8 to 3.3 cm wide $(\mathrm{N}=28$, mean $\pm \mathrm{SE}=$ $23.1 \pm 0.63 \mathrm{~mm}$ ), in uterine horns of progestational size, with no free blood or vesiculation. In the adjacent ovary were one or more corpora albacantia, 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 1978).
5. Pale orange, smooth, 1.3 to 3.5 cm wide $(\mathrm{N}=22$, mean $\pm \mathrm{SE}=20.7 \pm$ 1.07 mm ), in 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 1977).
6. Usually very faint, patchy coloration of endometrium, but with a distinct pale orange band in the circular muscular layer beneath it, 1.2 to 3.3 cm wide $(\mathrm{N}=17$, mean $\pm \mathrm{SE}=16.8 \pm 1.18 \mathrm{~mm}$ ). 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 1976).
7. No distinct coloration of the endometrium, but very pale yellowish to orange band or blotches in the circular muscle beneath it. Where measurable, these ranged in width from 0.9 to $2.3 \mathrm{~cm}(\mathrm{~N}=15$, mean $\pm$ S.E $=14.5 \pm 1.10 \mathrm{~mm}$ ). The adjacent ovary contained one or more irregular shaped corpora albicantia, sometimes one of which was slightly larger or more dense than the others. These scars were believed to be about 5 years old (term pregnancy in 1975).

Numerous other uteri contained no evident placental scars or hemosiderin 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 at least 6 years.

## Stomach Contents

The samples of stomach contents apparently also had been preserved in $10 \%$ formalin, although the fixation of some was extremely poor, as if they had not been immersed long enough or in a strong enough solution. Each sample was in a separate, nylon "paint strainer" bag, labelled with accession number, date, and (in most cases) the sex of the animal. Apparently, all of these were subsamples (aliquots) from larger volumes, but in only a few instances was this stated on the label.

Of the 104 stomach content samples, 15 were from Little Diomede, 11 from Wales, 3 from Nome, 25 from Savoonga, and 50 were from Gambell. Nine of the 11 samples from Wales were improperly preserved (or not preserved at a11) and had to be discarded. Three of the 50 from Gambell consisted only of congealed blood and gravel and one contained only gravel; these also were discarded. The remainder were analyzed in the following manner:

First, each sample was dumped from its container into a bucket of fresh water to dilute the formalin and separate the pieces, most of which had congealed together into a 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 $2-m m-m e s h$ 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.

For each sample, we recorded the accession number, date, sex (when given), 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 particulate material.

## RESULTS

## Reproductive Tracts

Of the 173 specimens provided from Gambell, 163 consisted of all or part of both uterine horns with attached ovaries, 7 consisted of only one uterine horn and ovary, and 3 were simply pieces of meat, fat, and vascular tissue having no relationship to the reproductive organs (Appendix I). These had been well labelled and well preserved, and 167 of them were
sufficiently complete for diagnosis of current reproductive status of the animals from which they were taken. Four of those (Nos. 36, 117, 132, and 321) were from infertile, nulliparous, immature individuals, as indicated by (a) their slender ( $1-1.5 \mathrm{~cm}$ ) uterine horns lacking any trace of placental scars, (b) the absence of any corpora lutea or albicantia, and (c) the presence only of small (up to $3-5 \mathrm{~mm}$ ) follicles in their ovaries. The remaining 163 tracts were from fertile animals of breeding age, which had ovulated at least once. Of those, one (No. 12) had ovulated for the first time in 1979; one other (No. 76) had ovulated for the first time in 1980. All others had ovulated two or more times, and most had been pregnant more than once before (multiparous).

## Current Reproductive Status

Of the 163 tracts of adults that were complete enough for diagnosis of reproductive status, 36 (22\%) were either in full-term pregnancy or had recently given birth to a calf in 1980. This was evident from the fact that both uterine horns were greatly enlarged and thickened, and that one of the attached ovaries contained a corpus luteum of the type typical of term pregnancy and parturition. Because only a small part of the parturient horn was provided; however, we were unable to identify in most instances whether the fetus was still in utero or had recently been born. Only where the parturient horn obviously was reduced in size from term pregnancy dimensions were we able to confirm that birth had taken place sometime before the animal was killed.

Another 13 animals (8\%) which had conceived in 1979 apparently had either given birth to their calves unusually early in 1980 or had aborted
the fetus during the winter, before the gestation was completed. This was indicated in each case by the fact that (a) a recent (brown or reddish brown) placental scar was present in the uterus, (b) the uterine horn with the placental scar had contracted to or nearly to its normal non-pregnant size, and (c) 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. Two of these animals had ovulated again in the current (1980) breeding season, which suggests that they had aborted very early in the winter; one other was about to ovulate (ripening follicles to 9 mm in diameter). Of the two which already had ovulated, one apparently had not been fertilized, as indicated by its shrunken, retrogressive corpus atreticum and a large (11 mm) degenerate follicle; the other had been fertilized and contained a large, normally functional corpus luteum of new pregnancy. The remaining 10 abortive animals were not in estrus and had not ovulated in the current year.

In addition to the one animal which had aborted early in pregnancy and had become pregnant again in the current year, 68 others ( $42 \%$ ) also were newly pregnant. Of those, 60 had ovulated only once in the current year and become fertilized successfully, as indicated by the presence of a single, large corpus luteum of new pregnancy. Five others had ovulated twice and had been fertilized successfully at the second ovulation, as indicated by the presence of a small, retrogressive corpus atreticum and a large, normally developed, new corpus luteum of pregnancy. Three others had one or more small, accessory corpora lutea, in addition to the large primary one. The uteri of most of these newly pregnant animals were not enlarged and did not contain any macroscopically visible embryos, although we assume that a microscopic blastocyst was present in each. Only three, taken on 27-28 May,
contained visible embryos in an early stage of nidation (implantation).
In those, the uterus was slightly swollen at the implantation site. Their embryos were elliptical blastocysts, about $6-7 \mathrm{~mm}$ long and $4-5 \mathrm{~mm}$ in diameter, which apparently had not yet reached the "primitive streak" stage of organization.

The remaining 46 animals (28\%) were classified as "barren", inasmuch as they had not been pregnant within the past year and were not likely to become pregnant in the current year. Although six of them appeared to be in estrus (with ripening follicles 8 to 14 mm in diameter), these probably would not have been fertilized successfully, since rutting males are scarce after April (Fay, in press). Eight of these barren females apparently had ovulated earlier, during the normal, mid-winter mating season but had not been fertilized successfully, as indicated by the presence of a corpus atreticum in their ovaries.

The findings in this sample are markedly different from those in spring harvest samples from Gambell in previous years (Table l). Because of a strong tendency for selective harvest of cows with newborn calves, the Gambell hunters in the past always took a high proportion (80-90\%) of females that were in term pregnancy or had recently given birth (Fay, 1958; Burns, 1965). In the 1980 sample, however, presumably taken with the same selective effort, the proportion of adults with newborn calves or in full-term pregnancy was only about one-fourth that of the earlier years. This suggests that either the desired parturient cows with calves were unavailable for some reason, or that the method of selection has changed. To the best of our knowledge, the latter is not the case, hence we assume that parturient females were less available in 1980 than during the $1950^{\prime} \mathrm{s}$ and $1960^{\prime} \mathrm{s}$.

Table 1. Comparative proportions of births, new pregnancies, and unproductive animals in spring harvest samples of adult female walruses from Gambell, 1952-1980.

| Harvest <br> years | Sample <br> size | \% Bearing <br> new calf | \% Newly <br> pregnant | early birth, <br> or barren | Source |
| :--- | :---: | :---: | :---: | :---: | :---: |
| $1952-61$ | 93 | 83 | 11 | 6 | F. H. Fay, unpubl. data |
| $1962-64$ | 109 | 80 | 15 | 5 | J. J. Burns, unpubl. data |
| 1965 | 114 | 89 | 7 | 4 | J. J. Burns, unpubl. data |
| 1980 | 163 | 22 | 42 | 36 | This study |

Of the 127 females that were not in term pregnancy and had not recently given birth, 69 (54\%) were newly pregnant, and 58 (46\%) were barren, had aborted, or had given birth unusually early. The respective proportions of these classes in previous years, based on a comparable sample of 206 specimens reported by Fay (in press), were $68 \%$ and $32 \%$. The difference between these samples is significant ( $\mathrm{X}^{2}=6.25, \mathrm{p}<0.025$ ). It suggests that the pregnancy rate in this segment of the population has declined in recent years, and that the proportion of unproductive animals has increased, as was implied also by the foregoing.

## Current Reproductive Performance

The reproductive efficiency of the female 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. The rate of success in achieving each of these steps varies considerably with the age of the mother, being highest in walruses at 8 to 15 years of age and lowest in the youngest and oldest breeders (Fay, in press). Probably, the reproductive efficiency of all age classes is depressed by stresses, such as disease and nutritional deficiencies, which could be prevalent at high population densities and absent or minimal at low densities.

In this series of sexually active females from the 1980 spring harvest at Gambell, at least 49 had conceived in 1979, and of those, 36 (73\%) apparently had successfully completed the full pregnancy and given birth to a calf in the normal spring season. Most of those calves probably were born alive, though judging from past performance, a few (1 or $2 \%$ ) could have been born dead (Fay, in press). The remaining 13 animals (27\%) that
conceived in 1979 evidently had either given birth unusually early or had aborted the fetus prematurely. In 10 of those specimens, the uterus already had contracted to the normal progestational (non-pregnant) size, indicating that birth or abortion had taken place during the winter, not later than mid-March. In 3, the uterine size suggested birth or abortion in late March to the first days of April. Although some prematurely born calves apparently can survive (Burns, 1965; Fay, in press), most of them probably expire. Abortuses that were sighted in late February and early March 1981, during the Zvyagino cruise, were dead or dying, and no living calves were sighted.

The proportion of early births or abortions suggested by this sample is significant greater than was indicated by comparable samples obtained in the 1950's and 1960's. In those earlier samples, the proportion of conceptions ending in gestational failure due to abortion, premature birth, and fetal death was only about $5 \%$ (Fay, in press), in contrast to the $27 \%$ for abortion and premature births alone in this 1980 sample.

This sample also suggests a much higher percentage of reproductive failures taking place between ovulation and conception (implantation) than was seen in the earlier samples. Of 84 ovulations recorded in this 1980 series, only 69 ( $82 \%$ ) appeared to have been fertilized successfully; 15 (18\%) were unsuccessfully, as indicated by the presence of a corpus atreticum. Because most of the cases of successful fertilization had not yet reached the stage of conception (implantation), in which some further failures could be expected, the actual rate of reproductive failure between ovulation and conception probably was somewhat higher, perhaps about $20 \%$. In comparable samples taken in the 1950 's and $1960^{\prime}$ s, the percentage of preconception failures was a little over $10 \%$ (Fay in press).

Because the placental scars persist in the uterus for several years and change in color in a consistent manner, the past reproductive performance of each individual can be determined in part from the presence and character of those scars. Confidence in interpretation of them, however, diminishes with the age of the scars, for the presence of old scars may be masked by newer ones in the same location. This interpretive problem can be circumvented by including in the sample only those animals in which there is no possibility of such masking. For example, to estimate from the present (1980) series the proportion of animals which conceived in 1978 and carried a fetus to or nearly to term in 1979 the sample would include only those animals having placental scars that were 1 year old or older; for estimation of the proportion conceived in 1977 and carrying to term in 1978 , the sample would include only those with scars 2 years old and older, etc. Because there is no possibility of the Gambell hunters' selection having any biasing effect on this historical record (Fay, in press), each such sample can be regarded as random and representative of the population at large.

The results of this analysis (Table 2) suggest that the pregnancy rate (percentage per year of animals carrying a fetus to or nearly to term) since 1976 has been between about 23 to $29 \%$, though it may have been as high as $37 \%$ in 1975. Only the latter proportion is comparable to the rate derived by Fay (in press) from samples taken in the $1950^{\prime} \mathrm{s}$ and $1960^{\prime} \mathrm{s}$, when the mean pregnancy rate was about $38 \%$ per year. This contrast suggests that the pregnancy rate in the segment of the population harvested by the Gambell hunters declined markedly after 1975 and has not yet returned to its former magnitude.

Table 2. Pregnancy rates indicated for the past five years by placental scars in the uteri of females walruses taken in the 1980 spring harvest at Gambell.

|  | Year of Birth |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Specimens | 1975 | 1976 | 1977 | 1978 | 1979 |
| Sample size | 17 | 37 | 56 | 77 | 109 |
| No. pregnant | 10 | 9 | 13 | 22 | 30 |
| $\%$ pregnant | 37.0 | 24.3 | 23.2 | 28.6 | 27.5 |

## Stomach Contents

## Regionat differences

The 15 samples from Little Diomede contained about 29 kg of prey remains and 1 kg of bottom sediments (sand and gravel). At least 3,722 individual prey, representing at least 33 taxa, were identified (Table 3). By far, the largest proportion of these were mollusks, which made up about $86 \%$ of the number and $89 \%$ of the weight of the contents. Nearly 3,000 of the identifiable prey were clams and cockles, principally of the genera Mya, Serripes, Macoma, Tellina, and Hiatella. In terms of weight, Mya and Sempipes predominated, making up more than 16 and 6 kg , respectively, or about $80 \%$ of the identifiable animal remains. of the non-molluscan prey, polychaete and sipunculid worms were most abundant and made up about $5 \%$ by weight of the total contents.

The two stomachs from Wales that were adequately preserved for analysis contained a total of 860 g of ingesta. Bivalves made up a large part of this, accounting for about $47 \%$ of the number and $30 \%$ of the weight of the prey (Table 3). These bivalves were tellinid clams of the genera Macoma and Tellina, together with Mya spp. In greater abundance; however, were worms of the genus Echitoms, which made up more than $50 \%$ of the number and $36 \%$ of the weight of prey in the stomachs.

The dominant prey in the stomach content samples from the Nome area were bivalve mollusks, principally cockles of the genus Serripes, of which more than 1,000 were identified. These made up nearly $85 \%$ of the 1,252 prey and $67 \%$ of the total of 4.7 kg of food in the stomachs. Second in abundance were clams of the genus Mya, followed by crangonid shrimps and gastropods.

Table 3. Quantitative analysis of the stomach contents of 91 walruses taken in native harvests in the Bering Strait region, spring 1980.

| Loca-/No. of tion/stomachs Total no./wt. (g) of prey | $\frac{15 / \mathrm{Di}}{}$ | $\xrightarrow{\text { omede }}$ | 2/W | Nales | 1,252/4 | Home | 25/Savoonga | $\frac{\text { voonga }}{\text { /33,916 }}$ | $\frac{46 / \mathrm{Ga}}{8.731}$ | mbell |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Proportional composition per taxon | \% no. | \% wt | \% no. | \% wt | \% no. | \% wt | \% no | \% wt | \% no. | \% wt |
| Anthozoa | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.5 | 0.3 | 0.3 |
| Polychaeta | 3.1 | 1.7 | 1.4 | 0.8 | 0.0 | 0.0 | 0.2 | 0.5 | 7.2 | 0.6 |
| Sipunculida | 8.2 | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.6 | 0.6 | 0.1 | 0.1 |
| Echiurida | 0.3 | 0.3 | 50.6 | 36.0 | 0.0 | 0.0 | 0.2 | 0.2 | 9.1 | 5.2 |
| Friapulida | 0.4 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.9 | 2.2 | 1.0 | 0.9 |
| Mollusca Gastropoda | 6.7 | 2.1 | 0.8 | 0.4 | 1.6 | 1.0 | 2.5 | 2.6 | 11.5 | 4.0 |
| Bivalvia Serripes | 9.6 | 20.4 | 0.0 | 0.0 | 84.6 | 67.4 | 5.6 | 30.2 | 3.2 | 8.4 |
| Tya | 28.7 | 60.5 | 10.7 | 26.6 | 11.4 | 11.9 | 45.4 | 38.5 | 30.4 | 44.9 |
| Spisula | 0.3 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.0 | 2.2 |
| Hiatella | 4.8 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 41.2 | 5.2 | 0.0 | 0.0 |
| Tellinidae ${ }^{\text {l }}$ | 34.1 | 1.6 | 36.5 | 3.3 | 0.0 | 0.0 | 2.0 | 0.3 | 6.1 | 0.3 |
| Yoldia | 2.3 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.5 | 0.1 |
| Astarte | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 13.2 | 0.5 |
| Liocyma | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.1 | 0.1 |
| Thyasira | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 |
| Bivalve <br> fragments | - | 3.3 | - | 0.0 | - | 4.5 | - | 6.0 | - | 2.7 |
| Ceminalopoda | 0.2 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 |
| Crustacea Amhinoda | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 |
| Cranconids | 0.0 | 0.0 | 0.0 | 0.0 | 1.3 | 1.2 | 0.4 | 0.4 | 8.0 | 4.9 |
| Crabs | 0.1 | 0.1 | 0.0 | 0.0 | 0.1 | 0.1 | 0.4 | 0.2 | 2.9 | 0.7 |
| Holothurcidea | 0.4 | 0.6 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.6 | 0.3 | 0.8 |
| Urochordata | 0.1 | 0.1 | 0.0 | 0.0 | 0.6 | 0.2 | 0.0 | 0.0 | 0.2 | 0.1 |
| Fishes | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 1.8 | 0.2 |
| Aninal matter unidentified | 1.7 | 0.8 | - | 2.8 | - | 13.7 | 0.1 | 1.7 | 0.8 | 5.6 |
| Sottom sediments | - | 3.5 | - | 30.0 | - | 0.0 | - | 10.2 | - | 17.5 |

1 Includes both Yacoma spp. and Tellina sp., the soft parts of which are not readily separable in all cases.

The 25 samples from Savoonga had a total weight of 33.9 kg , of which about $10 \%$ was sand and gravel and the rest was animal matter (Table 3). Mollusks were by far the most abundant prey, making up about $97 \%$ of the number and $83 \%$ of the weight. Dominant among these in terms of numbers were the clam genera Hiatella and Mya, which were represented by about 4,300 and 4,700 individuals, respectively, out of a total of about 10,400 prey. By weight, however, Mya and Serripes dominated, amounting to 38 and $30 \%$, respectively, of the total.

Finally, the 46 analyzable samples from Gambell made up nearly 49 kg , of which 50 kg ( $82.5 \%$ ) was animal matter. Again, the most abundant prey were mollusks, but in this area they made up only about $69 \%$ of the number and $63 \%$ of the total weight. Of these, bivalves of the genera Mya and Astarte were most numerous, comprising 2,658 and 1,157 individuals, but Mya, Serpipes and Spisula predominated by weight, making up about 45, 8, and $2 \%$; respectively, of the total. Also present in significant quantities were echiurid worms and crustaceans, each of which made up 5 to $6 \%$ of the weight.

Comparison with 1975 results
Area by area and as a whole, these findings are not markedly different from those in a comparable series of samples obtained in most of the same localities in the spring of 1975 (Fay et al., 1977). The proportions of the ingesta made up by bivalve mollusks in the Diomede and Nome areas appear to have been about the same or slightly greater in 1980 , whereas they were about the same or slightly lower in the Savoonga and Gambell areas (Table 4). Some tendency toward increased utilization of other taxa is suggested,

Table 4. Comparative proportions (by weight) of prey taxa in stomach contents of walruses taken in spring harvests at four localities in 1975 and 1980.

| $\frac{\text { Location }}{\text { Year }}$ | Diomede |  | Nome |  | Savoonga |  | Gambell |  | Trend |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | 1975 | 1980 | 1975 | 1980 | 1975 | 1980 | 1975 | 1980 |  |
| Sample Size | 71 | 15 | 7 | 3 | 14 | 25 | 13 | 46 |  |
| Anthozoa | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 0.3 | + |
| Polychaeta | 0.6 | 1.7 | tr | 0.0 | 0.1 | 0.5 | 1.0 | 0.6 | no change |
| Sipunculida | 0.6 | 3.3 | 0.0 | 0.0 | 0.1 | 0.6 | 0.3 | 0.1 | + |
| Echiurida | tr | 0.3 | 0.0 | 0.0 | 0.2 | 0.2 | tr | 5.2 | $+$ |
| Priapulida | 0.2 | 0.8 | 0.4 | 0.0 | 0.4 | 2.2 | 0.8 | 0.9 | $+$ |
| Gastropoda | 1.1 | 2.1 | 0.7 | 1.0 | 0.3 | 2.6 | 1.1 | 4.0 | + + |
| Bivalvia | 84.0 | 86.4 | 73.5 | 83.8 | 80.6 | 80.3 | 65.2 | 59.0 | no change |
| Cephalopoda | tr | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | tr | tr | $+$ |
| Crustacea | tr | 0.1 | tr | 1.3 | 0.3 | 0.6 | 3.3 | 5.7 | +H+ |
| Holothuroidea | 0.4 | 0.6 | 0.0 | 0.0 | 0.7 | 0.6 | 2.7 | 0.8 | - |
| Urochordata | 0.0 | 0.1 | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.1 | H+ |
| Fishes | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | tr | 0.0 | 0.2 | + |
| Mammals | 1.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | - |
| Sediments | 2.0 | 3.5 | 0.2 | 0.0 | 0.7 | 10.2 | 2.0 | 17.5 | $+$ |

and, in some cases the prey found in the 1980 samples had not been recorded earlier. For example, anthozoan coelenterates (sea anemones), urochordates (tunicates), and fishes (sand lance) are three groups of prey which were not present at all in the 1975 samples but appeared in small but significant amounts in the 1980 series. In all areas, the quantities of gastropods (snails) and crustaceans (especially crangonid shrimps) were markedly greater in 1980 than in 1975 , and moderate to large increases were shown also in the use of echiurid and priapulid worms. These differences suggest that the diets of the animals in these four areas have shifted slightly toward the use of "alternate" prey, though they still are relying primarily on the bivalves. Conceivably, the much higher proportions of benthic sediments in most of the 1980 samples also were related to this use of alternate prey.

Some differences were apparent between years also in the average unit weights of the principal molluscan prey. Those in the 1980 samples tended to be markedly lighter (smaller, younger) than those in the 1975 samples (Table 5). Whereas such difference could occur between small samples, as a consequence of the stomach contents being in different stages of digestion, that source of error should be evenly distributed in samples of large size such as these. These differences suggest that the walruses in 1980 were preying on clams and cockles that were substantially younger than those in 1975.

## DISCUSSION

Since the late $1950^{\prime}$ s, the Pacific walrus population appears to have been recovering from a greatly depleted state. That depletion was brought

Table 5. Comparative unit weights of primary prey taxa in stomach contents of walruses taken in the Bering Strait region in spring 1975 and 1980.


[^0]about by the Soviet Union's overharvests during the $1930^{\prime} \mathrm{s}$ to $1950^{\prime} \mathrm{s}$, the magnitude of which was comparable to that taken by the Yankee whalers in the late 19th century (Krylov, 1968; Bockstoce and Botkin, in press). By the $1950^{\prime} s$, the population probably was at its lowest numerical level in history (Fay, in press), and it is from that low point that it has been recovering in recent years.

Results of repeated aerial censuses of the population since 1958 have indicated rapid increase in numbers, possibly from a low of less than 100,000 to more than 200,000 animals by 1980 (Kenyon, 1960,$1972 ;$ Fedoseev, 1962; Krylov, 1968; Estes and Gol'tsev, in press; A. W. Johnson, pers. comm.). This trend of increase has been indicated also by the population's gradual reoccupation of most of its former range in both Soviet and American waters (Gol'tsev, 1968; Estes and Gol'sev, in press; Fay, in press; J. J. Burns, pers. comm.). To date, practically all former hauling grounds that were used by the population in historic times have been reoccupied, with the exception of the Pribilof Islands.

Beginning about 1978, the native walrus hunters of western Alaska (particularly at Gambell) complained about the scarcity of newborn calves and the leanness of the adults, and they reported that the animal's feeding habitats also had changed in some degree. Those observations, coupled with a mass mortality of walruses at St. Lawrence and the Punuk Islands in the autumn of 1978, led the hunters to suspect that the population had overshot the carrying capacity of its environment and was likely to decline again, this time from natural causes (Fay and Kelly, 1980). Although a major decline seemed unlikely in such a long-lived, apparently $X$-selected species as this, there was no known precedent on which to base more than a theoretical
judgement (e.g., see Estes, 1979). The walrus is, afterall, different from the other pinnipeds, in that it is a "grazer" dependent on a sedentary, slowly growing food base (bivalve mollusks), rather on a highly mobile, productive, and rapidly growing base, such as fishes or krill. Because of this difference, a rapidly expanding walrus population may be capable of depleting its resources by overgrazing, to the extend that several years may be required for the depleted mollusk populations to recover (Fay et aZ., 1977). In that event, the walrus population itself might decline for some years, before reaching a new balance with its food supply.

Our findings in the present study, compared with those from the $1950^{\prime}$ s to mid-70's, indicate further that some major changes have taken place in the productivity of the population and suggest that the quality and quantity of its food may have changed, as well. Rates of reproductive failure appear to have increased significantly, having approximately doubled between ovulation and conception and risen to at least five times the former level during gestation. The concommittent pregnancy rate appears to have declined by at least $30 \%$, and the scarcity of parturient females in the highly selective (for females with new calves) harvest at Gambell suggests that the live birth rate or survival of new calves may have fallen even lower than that.

The stomach contents of the animals taken in the 1980 spring harvest were not markedly different from those obtained in 1975 , but they did show a tendency toward the animals' utilization of both smaller clams and a wider variety of other, non-molluscan prey in all areas. Such changes could be interpreted in several ways. Although they might have no relationship to
the population status of the walruses, they are nevertheless the kinds of changes one might expect to take place if the walrus population were exerting pressure on its food base. As the larger clams are removed, the walruses would be obliged to take ever smaller ones and, presumably, to seek out larger, alternate prey, some of which had been utilized in small amounts before, whereas others had not been utilized at all by walruses.

The changes in feeding habits suggested by these findings do not appear to be great enough to have any significant impact on the health of the walruses, yet an average decrease in fatness of about $50 \%$ has become clearly apparent in recent years. Whereas the thickness of the sternal blubber in animals taken in 1958-73 ranged from about 3 to 10 cm (Fay and Kelly, 1980), the same measurement on animals taken during 1980 and 1981 ranged from about 0.5 to 7.5 cm (Smith, 1980; Fay, 1981). This is a large and highly significant difference, which indicates clearly that the walruses today are either obtaining much less food or are working much harder to get it, or both. In numerous instances in the 1980 samples, we found that the animals had eaten hundreds of tiny clam meats weighing no more than 0.1 to 0.2 g . These were much smaller than any we had encountered in the 1975 samples, and we questioned the efficiency of a $1,000 \mathrm{~kg}$ walrus, seeking and consuming such tiny prey, one by one:

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Gw-187". P12 —. 12,10,8,8,7. $11,10,4$. 15 R.Br None. 21 60-189 "923-12,11 . 11,8,8,7 (cuthothat) Nows 32 ©0-1945/2180-P42in. 8 (cuttratit) (costashet) 21 $6 \omega-1975 \% \% 80$ Pa9 - $9 \cdot 19$ (cutshort) (athori) $<1<1$ 601-198 " - P27. 21 None (cut shat) (cidey) Br fily 52

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Appendix I continued
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 $610-3435 \% / 27 \% 0-N 26 \cdot 17,10,10$. Nons 28 Orft Nozie 11 mutypiseus;


Analysis of stomach contents from walruses taken in the spring 1980 harvest

## Little Diomede 11 may- 11 June 1980



Anemone titi. Neither
Lembrintreis - - - - - - - - - - - - - - - - - Plyflodoce


Totals $\quad 154.1,723 \quad 2783,4835 \quad 631,672 \quad 182 \quad 3,495 \quad 272.3,042 \quad 274 \quad 2,504-51 \quad 882$


Wales 29 may - 3 Jurc 1930



Totals 1,061 $\quad 3,190 \quad 128 \quad 1,116 \quad 63 \quad 418$

## Appendix II continued

Sevocugh 15 may - 3 Juns 1980



|  |  | $\begin{aligned} & S t w \cdot 192 \\ & \mathrm{No}_{0}^{\mathrm{cr}} \mathrm{ly} \end{aligned}$ | $\begin{aligned} & 9 w_{i}-195 \\ & \text { No. } \mathrm{of} \end{aligned}$ | $\begin{aligned} & \text { Sin- } 196 \\ & \text { No, at. } \end{aligned}$ | $\begin{array}{ll} 6 & \text { swo-197 } \\ \text { it. } & \text { N4. } \end{array}$ | $\begin{aligned} & s v \omega=200 \\ & H_{0}{ }^{\circ} \text { unt } \end{aligned}$ |  |
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| Anenone mid. | - - |  |  |  |  | - - | - - |
| Nepltys | - - |  |  |  |  |  | 5 |
| Lanbminereis | - - |  | - |  |  | - | - - |
| Pectinaria - | - - | - - | - - |  |  |  | - - |
| Polychate unid. | - - | - $=$ | - - | - | - - | - |  |
| Golfingia | - - | - - | - - |  | 1 | - - | $\therefore$ - |
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| Primpulas | 5 | - | 4. 30 | $36 \quad 33$ | $336-5 \quad 42$ | 3-28 | 2. 14 |
| Neptunca | 7. 4 | - - | $t r l_{\text {r }} t_{r}$ | 3 | 13. it tr | -12. 104 | 6.15 |
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| Cinhidiopsis |  |  |  |  |  | - | - |
| Margarites |  |  |  |  |  |  |  |
| Gastropedurid. Sterripes | $\begin{aligned} & 5 \\ & 42 \end{aligned}$ | $\begin{array}{r} 2 \\ -99 \end{array}$ | $25$ | $4$ | $\begin{array}{cc} 4 & 1 \\ 166 & 12 \end{array}$ | 55 | $\begin{aligned} & 18 \quad 45 \\ & 60 \quad 839 \end{aligned}$ |
| Clincterdiuse |  |  | - |  |  |  |  |
| mysa | 32.45 | 34 57 | 12._131 | -70.30 | $302 \times 328-565$ | -44 198 | 50-341 |
| mucesestilline | - . | $13 \quad 10$ | - - | - - | - - - | - - | - - |
| Hiatella | - |  | - | -- - | 89 | - - | - |
| Yoldia | --. |  | - | - | - - - | - - |  |
| Leorgma |  |  |  | 1 | 1- $=$ | $=$ | - |
| Binaluetrasind. | 30 | 130 | - 162 | 22 | 226 | 343 | 155 |
| Crangonids | 8.2 | 3.7 | - - - | 2. | 2 |  | - - |
| Hyas |  |  | 1.0 .5 |  | - - - | - - | - - |
| Pajurus |  |  |  |  |  |  | - - |
| Cucumaria |  | - - |  | - - | - - |  | - - |
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| Alimual friosuasts. | - | - - | 79 | - 5 | 5 - | 1 |  |
| Sodiments | - . 40 | - ... 50 | - 0 | - | - $\quad 585$ | - | - 17 |
| Fotals | 108. 186 | $103 \quad 1,706$ | $42 \quad 1086.5$ | 127 1,05 | $1755^{2}$-442. 1,390 | 1251,5 | $144 \quad 1,134$ |


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| :---: | :---: |
| Anenone mid. - - - | $\ddot{\sim}$ |
| Mepattrys .-. | 3 |
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| Pectiraria - - - | 1 |
| Pelyshacte urid. | 2 |
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| Mrewetelina - - - - |  |
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| Liocyma - - - | 1 |
| Bintlettulicd. - 114 - 123 |  |
| Crangonids -.6.6. | 11 |
| Hyas ..... 181 - | 5 |
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| Avimens unid. | - |  |  |  |  |  |  |  |  |
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| Bricurice | 1 | tr. $t_{r}$ | 3.6 | - | 116.74 | 69826 | 104412 |  |  |
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| Astaste | - - - |  |  |  |  |  |  |  |  |
| Yeletsias |  |  |  |  |  | 21 |  |  |  |
| Thyasciar |  |  |  |  |  |  |  |  |  |
| Licequia |  |  | 6.9 |  |  |  | - . |  |  |
| Biablut frags. | - - | - | 31 | 20 | - | - - | - - |  |  |
| Cotetus | - - | - | - - | - - | - |  | - - |  |  |
| Anmicx | - - | - | - - |  |  |  | - - |  |  |
| Hippoineters | - |  | - - | - - |  |  | - - |  |  |
| Belcusidia |  | - | - - | - - | - |  | - - |  |  |
| Gigis |  | - - | - | - - |  |  |  |  |  |
| Crazgmid uid. | $172 \quad 387$ | $20-27$ | - | 31.93 | - | $9-10$ | - - |  |  |
| Hyas | 1.-2 | - - - | - - | 1 | 2 | - - |  |  |  |
| Roguces |  |  | - - | - - |  | - | - - |  | 1 |
| Cruftarcan fuess |  |  |  | - |  |  | $1 \quad 0.5$ |  |  |
| Helthurcan wnid. | - | - - | - | - - | - |  |  |  |  |
| Plonaia |  |  | - | - - |  |  |  |  |  |
| Urechond ate mid. | 2 . 7 |  | - - | - - |  |  |  |  |  |
| Aurectates | - - | - | - - |  | - - |  |  |  |  |
| Animal matter | - - | 280 | - - | - - | - 35 | 67 | 9102 |  |  |
| wood fraqs |  |  | - - | - - | - - | - - | - - |  |  |
| Setiments | - 0 | - 0 | -. 130 | - .-. 0 | 246 | - $\quad 100$ | $=140$ |  | - 2 |
| Totals | $\pi 6.516$ | 82 | ma | , 6 | 132 | - | $0 \times 1$ |  | 4 |








[^0]:    ${ }^{1}$ Includes Serripes spp. and Clinocardium spp.
    ${ }^{2}$ Includes Tellina lutea and Macoma spp.

