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Feeding of Bearded Seals in the Bering and Chukchi Seas and Trophic Interaction with Pacific Walruses

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ABSTRACT. Current and historical information about food habits of bearded seals, *Erignathus barbatus*, are presented. Shrimps, crabs, and clams are overall the most important prey. Proportions of different prey in the diet vary with age of seals, location, and time of year. Foods of male and female seals are similar. Young seals eat proportionally more shrimps than do older animals. Recently, clams were important in the diet only in Norton Sond and near Wainwright, and only during late spring and summer. Greatest quantities of food were found in stomachs of seals which had eaten mostly clams. In Bering Strait, seals taken in spring 1958 and 1967 had consumed large quantities of clams, but this item was only a minor fraction of foods in 1975-79. Walruses, *Odobenus rosmarus*, have increased steadily in numbers since 1960. Whereas Bering Strait was mainly a route through which walruses migrated in spring and autumn, this region is now an area in which large numbers (up to 80,000) spend portions of the summer and autumn. The walruses feed mainly on clams. Increased foraging activity of walruses may have reduced availability of this food item for bearded seals. The walrus population currently appears to be exhibiting indications of stress. These indications may be a reflection of walrus numbers at or in excess of the ability of the clam resource to withstand current predation by walruses. Indices of population condition in bearded seals have remained stable, perhaps due to their more euryphagous habits.

RÉSUMÉ. Les auteurs présentent la documentation actuelle et historique au sujet des habitudes alimentaires des phoque barbus. Leurs plus importantes proies sont, par dessus tout, les crevettes, les crabes et les parlourdes.

Les proportions entre ces différentes proies dans leur régime varient avec l'âge, la région et l'époque de l'année. Males et Femelles ont des habitude alimentaires semblables. Les jeune phoques mengent proportionellement plus de crevettes que les animaux plus âgés le font. Récémment la palourdes étaient un élément important dans leur régime, seulement dans le "Norton Sound" et près de Wainwright et cela seulement à la fin du printemps et en été. Les quantités les plus grandes de nourriture se trouvaient dans les estomacs de phoques qui avaient surtout mangés des paloudes. Dans le détroit de Bering, les phoques pris aux printemps 1958 et 1967 avaient consommé de grandes quantités de parlourdes mais ce n'était qu'une fraction mineure de leur nourriture pendant les années 1975 à 1979. La population des morses a augmenté constamment depuis 1960. Alors que le détroit de Bering était la route principale de migration pour les morses au printemps et à l'automne, cette région est maintenant un lieu de séjour pendant une partie de l'été et de l'automne, pour un grand nombre d'entre eux (jusqu'a à 80,000 individus). Les morses se nourrisent surtout de paloudes. Ceci peut avoir reduit la quantité de cette nourriture, disponible pour les phoques barbus. À l'heure actuelle le point critique apparaît avec cette population du morses. Ceci yeut dire que les morses peuvent être trop nombreux pour permettre un bonne sauvegarde de la nourriture fournie par les palourdes. La population des morses barbus parait être restée stable, peut être à caise de leurs habitudes "euryphages."
Traduit par Alain de Vendegies, Aquitaine Co. Canada Ltd.

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INTRODUCTION

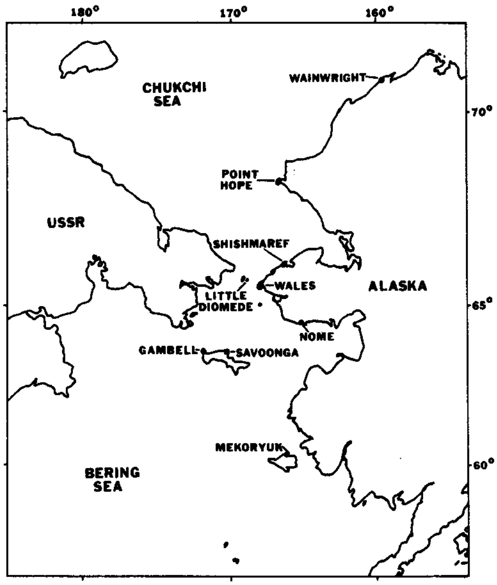
In the northern hemisphere, the Bering Sea supports by far the greatest abundance and variety of pinnipeds. Combined estimates of populations of all species of pinnipeds in the Bering Sea indicate in excess of two million individuals. The majority of species feed on fishes, cephalopods, and shrimps (Scheffer, 1950; Fiscus and Baines, 1966; Lowry and Frost, in press). Only two species, the bearded seal (*Erignathus barbatus*) and the Pacific walrus (*Odobenus rosmarus divergens*) feed primarily on benthic invertebrates (Kosygin, 1977; Fay *et al.*, in press). Both of these species are abundant and large. The mean weight of bearded seals in the Bering and Chukchi Seas is 209 kg for all age classes older than pups, while individuals 6 years old and older average 242 kg (Burns and Frost, 1979). Fay *et al.* (1977) indicated that an "average" Pacific walrus weights about 900 kg. Recent population estimates for the two species in the Bering and Chukchi Seas are 300 000 (Burns, in press) and 209 000 (Krogman *et al.*, 1979), respectively. Both species are considered ice associated and generally follow the seasonal advance and retreat of sea ice (Burns, 1970; Fay, 1974). Bearded seals and walruses are generally most abundant in the northern Chukchi Sea in summer and in the southern Chukchi and northern Bering Seas in winter. Much of the population of both species migrates through Bering Strait twice each year.

Approximately half of the Bering Sea and all of the Chukchi Sea are underlain by the Bering-Chukchi platform. This continental shelf area is one of the largest in the world with an area of about 1.5 million square kilometers. An estimated 250 000 metric tons of bearded seals and walruses derive their annual nutrition from the benthic communities of this area.

Depending on the degree of dietary overlap exhibited by bearded seals and walruses, population size changes in one might be expected to affect the other. The Pacific walrus population has undergone a recent dramatic expansion (Krogman *et al.*, 1979). In this paper we present recent data on foods of bearded seals in the Bering and Chukchi Seas and evaluate, to the extent presently possible, the trophic interaction between bearded seals and walruses.

METHODS AND MATERIALS

Our data on foods of bearded seals are based on direct examination of stomach contents collected primarily between 1975 and 1979. The majority of the stomachs examined were purchased from Eskimo hunters at the villages shown in Figure 1. In addition, the stomach contents of some bearded seals collected for scientific purposes were examined. Stomachs were removed from the animals and tied at the cardiac and esophogeal sphincters. They were then either injected with 10% formalin or frozen and shipped to the laboratory. The collection date, location, and sex were recorded for each animal, and a claw from the frontflipper and an upper canine tooth were collected when possible. Ages of specimens were determined by claw rings and cementum annuli (Burns and Frost, 1979).



In the laboratory, stomachs were slit open and the contents gently washed onto a 1.00-mm sieve. Non-food items (parasites, clotted blood, etc.) were sorted from the food. The remaining items were sorted to the lowest possible taxonomic level and identified using published keys and reference specimens. The volume of each invertebrate taxon and of fish material was determined by water displacement in graduated cylinders. The number of fishes of each taxon was determined from counts of characteristic hard parts such as preopercular bones and otoliths. Data were entered on computer forms and keypunched.

Computer programs were developed to allow sorting of data by collection date, sex, age, and geographical location. Within a specified date/ sex/ location category the data for all seals collected were combined as a single sample. For invertebrate taxa and total fish material the percentage of the total stomach contents which was comprised by each individual taxon was calculated. For individual taxa of fishes the percent of the total number of fishes consumed which was made up by that taxon was calculated. The mean volume of stomach contents in each sample was also calculated. Only stomachs containing food were included in mean volume calculations.

RESULTS

A total of 397 bearded seal stomachs containing food were examined in this study. Of the total, 121 were from four villages and shipboard collections in the Bering Sea, 42 were from two villages in Bering Strait, and 234 were from two villages in the Chukchi Sea. The largest collection (181) was made at the village of Shishmaref. Collections at most other locations were much smaller.

TABLE 1. Scientific and common names of major prey species of bearded seals in the Bering and Chukchi Seas.

General Taxon	Scientific Name	Common Name
Clams	*Clinocardium ciliatum*	cockle
	Serripes groenlandicus	Greenland cockle
	Spisula polynyma	surf clam
Crabs	*Chionocetes opilio*	tanner crab
	Hyas coarctatus	spider crab
	Telmessus chieragonus	hairy crab
Echiuroid worms	*Echiurus echiurus*	
Fishes	*Ammodytes hexapterus*	sand lance
	Boreogadus saida	arctic cod
	Eleginus gracilis	saffron cod
	Family Cottidae	sculpins
	Family Pleuronectidae	flatfishes
	Lycodes sp.	eelpout
Isopods	*Saduria entomon*	
Polychaete worms	*Eunoe* sp.	polynoid worm
	Nephtys sp.	nephthyd worm
	Nereis sp.	nereid worm
Shrimps	*Argis* spp.	crangonid shrimp
	Crangon spp.	crangonid shrimp
	Eualus spp.	hippolytid shrimp
	Pandalus spp.	pandalid shrimp
	Sclerocrangon boreas	crangonid shrimp
Snails	*Buccinum* sp.	whelk
	Natica sp.	moon snail
	Neptunea sp.	whelk
	Polinices sp.	moon snail

Most specimens were collected during the spring-summer period during which active subsistence seal hunting by local residents occurs.

In the presentation and discussion of results we will deal primarily with major taxa of prey. A listing of these taxa and the scientific and common names of the species most frequently eaten by bearded seals is shown in Table 1.

Two sets of samples were used to examine age-related differences in the bearded seal diet. The first included all specimens collected at Shishmaref. The second included all specimens collected in the Bering Sea. Included in the second data set were specimens from Wales and Diomede, both located in the Bering Strait. For each set of data, results were tabularized for each age class from pups to 4-year-olds for all age classes greater than 4 years. Foods

TABLE 2. Major foods of bearded seals by age class. Values represent percent of total stomach contents volume for invertebrate taxa and total fish material and percent of the total number of fishes eaten for individual fish taxa.

	Shishmaref			Bering Sea		
	Pups N = 38	1 and 2 Years Old N = 21	≥3 Years Old N = 91	Pups N = 52	1 and 2 Years Old N = 31	≥3 Years Old N = 50
Clam	4	11	19	2	3	25
Snail			1			2
Shrimp	59	47	30	45	26	27
Brachyuran crab	6	20	24	28	38	27
Isopod	18	9	8	1	*	*
TOTAL FISH	7	11	6	13	26	10
Saffron Cod	51	18	30	41	5	4
Arctic cod	*	*	1	5	2	6
Sculpins	28	55	25	47	89	77
Flatfish	20	25	37	*	1	1
MEAN VOL (ml)	325	462	492	213	578	670

* Indicates values less than 1%.

of 1- and 2-year-old seals were similar as were foods of all age classes 3 or more years old. Results are therefore presented for three age groups: pups, 1- and 2-year-olds, and seals 3 or more years old (Table 2). In both samples the volumetric importance of clams in the diet increased with age. The frequency of occurrence of the primary species of clam eaten, *Serripes groenlandicus,* showed a corresponding increase in older seals. At Shishmaref, *Serripes* occurred in 1 of 38 pups (2.6%), 4 of 21 1- and 2-year-olds (19.0%), and 20 of 91 older seals (22.0%). In samples from the Bering Sea, *Serripes* occurred in 1 of 52 pups(1.9%), 3 of 31 1- and 2-year-olds (9.7%), and 19 of 50 older seals (38.0%). The relative volumetric importance of shrimps in the diet decreased with age. However, the frequency with which shrimps were eaten did not change and ranged from 92 to 100% in all subsamples. The shrimps eaten by bearded seals belong to three families. At Shishmaref, over 98% of the identified shrimps eaten by all age classes belonged to the family Crangonidae. This family of shrimps comprised 42-65% of the identified shrimps eaten by the three age classes of seals taken in the Bering Sea. In this area the volumetric importance of shrimps of the family Hippolytidae decreased from 41% of identified shrimps in pups to 7% in seals 3 or more years old. Correspondingly, the importance of shrimps of the family Pandalidae increased from 10% in pups to 51% in seals 3 or more years old. Generally, the importance of isopods and saffron cod decreased with age, while brachyuran crabs, sculpins and flatfish were of greater importance in the diet of older seals.

TABLE 3. Major foods of bearded seals collected in the Bering Sea sorted by time period. Results are presented as in Table 1. Percent frequency of occurrence (no. stomachs containing item/total no. stomachs in sample x 100) is also given. Only specimens from seals 3 or more years old are included.

	1 May - 30 September N = 46		1 October - 30 April N = 11	
	Percent Volume/No.	Percent Frequency of Occurrence	Percent Volume/No.	Percent Frequency of Occurrence
Clam	28	63	*	9
Snail	2	48	1	27
Shrimp	20	94	53	73
Brachyuran crab	23	80	37	91
TOTAL FISH	16	78	5	82
Saffron cod	3	4	4	36
Arctic cod	9	17	5	27
Sculpins	82	46	76	54
Flatfish	—	—	3	46
MEAN VOL (ml)	662	—	743	—

*Indicates values less than 1%.

TABLE 4. Major foods of bearded seals sorted by sex. Results are presented as in Table 1. Only specimens collected between 1 May and 30 September from seals 3 or more years old are included.

	Bering Sea		Shishmaref	
	Males N = 25	Females N = 17	Males N = 27	Females N = 64
Clam	36	18	20	18
Snail	*	6	*	1
Shrimp	20	20	26	32
Brachyuran crab	23	22	23	25
Echiuroid worm	*	*	19	4
Isopod	—	—	2	22
TOTAL FISH	14	19	6	5
Saffron cod	—	4	28	31
Arctic cod	7	13	—	2
Sculpins	82	80	24	25
Flatfish	—	—	46	38
Eelpout	—	2	*	—
MEAN VOL (ml)	668	712	539	472

*Indicates values less than 1%.

TABLE 5. Major foods of bearded seals at seven locations in the Bering and Chukchi Seas in the spring-summer period. Results are presented as in Table 1. With the exception of Point Hope, only specimens 3 or more years old are included.

	Gambell N = 10	Savoonga N = 7	Nome N = 7	Diomede N = 18	Shishmaref N = 91	Pt. Hope[1] N = 87	Wainwright N = 26
Clam	42	12	69	4	19	38	55
Snail	2	2	*	2	1	2	1
Shrimp	23	33	20	16	30	13	26
Brachyuran crab	17	40	3	34	24	24	5
TOTAL FISH	10	5	2	32	6	2	*
Saffron cod	—	—	24	—	30	—	1
Arctic Cod	1	—	—	10	1	—	11
Sculpins	98	95	76	88	25	—	87
Flatfish	—	—	—	—	37	—	—
MEAN VOL (ml)	654	469	753	646	492	—	715

[1]Data from Johnson *et al.* (1966) for June. Fishes were mostly sculpins with trace amounts of flatfish.

*Indicates values less than 1%.

Due to the limited number of specimens available from other than the spring-summer period, seasonal aspects of feeding could not be examined in detail. Results from samples collected in the Bering Sea from seals 3 or more years old were tabularized for two time periods, 1 May-30 September and 1 October-30 April (Table 3). Major differences occur in the proportions of the various prey items in the diet during the two time periods. The importance of clams and fishes was much less in the autumn-winter than in the spring-summer period. The proportion of the food comprised of shrimps and brachyuran crabs was greater in the autumn-winter period. *Serripes* occured in 20 of 46 (44%) stomachs from seals collected in the spring-summer period but in none of the 11 stomachs from seals collected in the autumn-winter period.

Sex-related dietary differences were examined using the same data sets used for examining age-related feeding patterns. Only seals 3 or more years old collected between 1 May and 30 September were included in the analysis (Table 4). Foods of males and females were generally similar in both areas. Based on volumetric data, clams were of slightly greater importance in the diet of males than of females. However, the frequency of occurrence of *Serripes* was similar for both sexes at Shishmaref (22%), while in the Bering Sea *Serripes* occurred in 36% of male seals and 53% of female seals examined.

Geographical variations in the foods of bearded seals collected at seven villages along the Bering and Chukchi Sea coasts are shown in Table 5. With the exception of Point Hope, only seals 3 or more years old collected between

1 May and 30 September were included in the analysis. Clams, shrimps, and brachyuran crabs combined accounted for more than 70% of the stomach contents volume at all locations except Diomede where fishes were an important food. The proportion of clams in the diet was highly variable, ranging from a high of 69% at Nome to a low of 4% at Diomede. Brachyuran crabs were least important in the diet at Nome and Wainwright, where clams were the main prey.

At three localities, data are available on the foods of bearded seals collected over a period of several years which allow a preliminary assessment of year-to-year fluctuations and changes in prey utilization. Unfortunately, ages are not available for many specimens and sample sizes are small, so that it was not possible to exclude young seals from the analysis. All specimens were collected during the months of May to August. Results are presented as the percent of the total volume and frequency of occurrence of clams in the stomachs examined from each year (Table 6). The results suggest a decline in importance of clams (primarily *Serripes groenlandicus* at Nome and Diomede, and *Spisula polynyma* at Wainwright) in the diet in recent years. The trend is particularly evident at Diomede where clams were a major food item in seals examined in 1958 and 1967 but were a minor food item in seals collected from 1975 to 1979. Ages are available for most of the seals collected since 1975 at Diomede. If only seals 3 or more years old collected at Diomede from 1975 to 1979 are considered, clams still comprised only 4% of the volume of food and *Serripes* occurred in only six of 18 seals examined. At all three localities the relative importance of shrimps in the diet increased when the amount of clams consumed decreased.

TABLE 6. Percent of total stomach contents volume which consisted of clams in bearded seals collected at Nome, Diomede, and Wainwright between 1958 and 1979. Frequency of occurrence (no.of stomachs containing clams/total no. of stomachs in sample) is given in parentheses. Only stomachs from seals collected between May and August are included.

Year	Nome	Diomede	Wainwright
1958	—	One of two primary foods[1] (9/17)	—
1964-1965	—	—	49% (5/7)
1967	—	59% (5/6)	—
1970	40% (1/2)	—	—
1975	48% (1/1)	9% (5/6)	55% (16/22)
1976	87% (4/5)	2% (2/4)	66% (6/7)
1977	44% (5/8)	0% (0/4)	75% (3/3)
1978	—	0% (0/2)	4% (2/4)
1979	* (1/6)	2% (3/8)	32% (12/16)

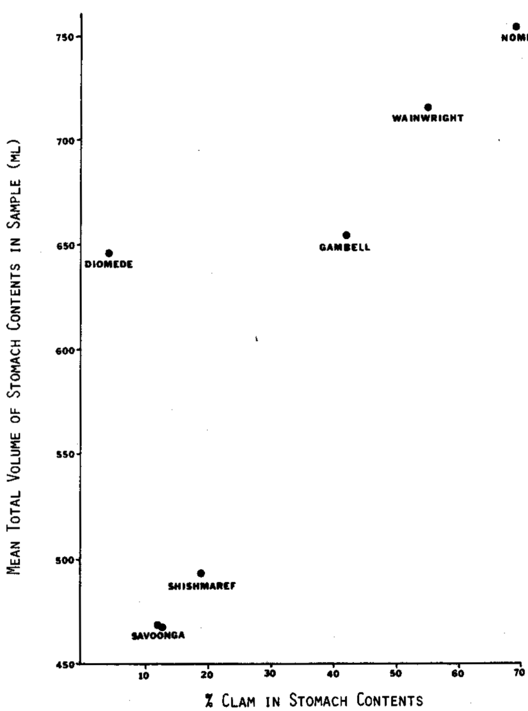
[1]Kenyon, 1962.

*Indicates values less than 1%.

In order to assess the importance of clams to bearded seal feeding, we sorted our data into two subsets: seals whose stomachs contained 50% or more clams, and seals whose stomachs contained less than 50% clams. Seals 3 or more years old collected from 1975 to 1979 at all localities in the Bering and Chukchi Seas were included in the analysis. The mean total volume of stomach contents which consisted of clams was calculated for each subset. The mean volume of contents in seals which had eaten mostly clams was 1047 ml, while the volume of contents in seals which had less than 50% clams in their stomachs when collected averaged 514 ml. This difference was highly significant ($t=5.67$, 175 degrees of freedom, $p<0.01$). The relationship between the proportion of clams in the diet and the mean total volume of stomach contents at six locations is shown in Figure 2. With the exception of Diomede where sculpins are preyed on heavily, the relationship is quite direct: the greater the proportion of clams in the diet, the greater the average quantities of food found in the stomachs.

DISCUSSION

Bearded seals in the norther Bering Sea and Chukchi Sea feed on a wide variety of benthic organisms. However, we found that the bulk of their food is comprised of clams, crabs, and shrimps. Fishes are generally of minor



volumetric improtance in the diet. Those fishes eaten are primarily sculpins, cods, and flatfishes. Other items of minor importance include snails, isopods, echiuroid worms, polychaetes, sponges, eelpout, and sand lance. The results are similar to those reported by Kenyon (1962), Johnson *et al.* (1966), and Burns (1967) for the same general area. Kosygin (1971) reported the stomach contents of 152 bearded seals collected in the Bering Sea during spring 1963-65. His results were similar to ours and others with the exception that he did not report clams as a food item.

Previous investigators have not examined age- and sex-related dietary differences. We found substantial differences in foods of young of the year, 1- and 2-year-old, and older seals. Although clams, crabs, and shrimps are the major foods of all age classes, clams are of greatest importance to older seals. Such differences must be considered when evaluating observed feeding patterns. For example, if Kosygin (1971) examined mostly young seals then the lack of clams in his specimens would be explained. Differences in foods of male and female bearded seals appear to be slight, if any. However, it would be of interest to investigate this question in more detail with large collections of adult seals made at a single location and time period.

Our results indicate marked seasonal changes in the quantities of clams consumed. We found *Serripes* only in seals collected between 1 May and 30 September. Burns (1967) found clams to be important foods of bearded seals collected in July and August but not those collected in May. Johnson *et al.* (1966) working at Point Hope found only trace amounts of clams in stomachs of 26 bearded seals collected between November and May. In June they found that clams comprised of 37.7% of the food volume in 87 stomachs containing food.

Of all major food items consumed by bearded seals, clams appear to be the most variable. The volumetric proportion of clams in the diet varies from 2 to 25% depending on age class, from less than 1 to 28% depending on time of year, and from 4 to 69% depending on location. In addition, the importance of clams in the bearded seal diet seems to have decreased in recent years, particularly in Bering Strait. The principal species eaten in the Bering Sea is *Serripes groenlandicus*. When examining partially digested material, some *Clinocardium ciliatum* may be included with *Serripes*, but from examination of fresh material we are confident that over 90% of the cockles eaten are *Serripes*. Little is known of the biology of this species. It occurrs in the North Atlantic as well as the Bering and Chukchi Seas on generally soft bottoms. Presumably *Serripes* lives on or near the sediment surface since life individuals are not uncommonly caught in otter trawls. It is a slow-growing species requiring 10-17 years to reach a shell length of 7 cm in West Greenland (Petersen, 1978). When consuming *Serripes*, bearded seals usually eat only the foot portion. Apparently this part is exposed and the bearded seals grasp the foot in their mouths and tear it from the shell and viscera. This may involve some learned behavior which could explain the differences in *Serripes* consumption among age classes. Perhaps during autumn and winter *Serripes* burrow more deeply in the sediment or do not expose their feet, therefore making themselves unavailable to bearded seals. Other possible factors such as seasonal changes in palatability and age-related partitioning of feeding areas cannot be ruled out. Geographical variations in consumption of *Serripes* probably relate to the distribution and abundance of the clams. Petersen (1978) reported *Serripes* biomasses ranging from 0 to 250 g /m^2 at several localities in Disko Bugt, West Greenland.

In the Bering Sea, *Serripes* also comprises a large portion of the diet of walruses during the spring-summer period. Fay *et al.* (in press) report the following values for percent (by weight) of *Serripes* in the walrus diet: Gambell 3.9%, Savoonga 33.9%, Nome 97.7%, and Diomede 3.3%. The dietary overlap between bearded seals and walrus is therefore considerable, particularly in Norton Sound near Nome. Unfortunately, no data are available on foods of alruses near Wainwright. Vibe (1950) found little dietary overlap between bearded seals and walruses near Thule, Greenland since he found no large clams in bearded seal stomachs. However, he examined only four bearded seal stomachs from the spring-summer period and these may have been from young animals.

The Pacific walrus population has undergone a recent dramatic expansion. the population in 1975 was estimated at over 200 000 animals (Krogman *et al.*, 1979), more than four times as large as the estimated population in 1940 (Fay, 1957). If the rate of increase has not declined, by 1980 the population may number over 260 000 animals. Fay *et al.* (1977) estimated that a population of 200 000 walruses would crop the estimated standing stock of clams in the Bering or Chukchi Seas at a rate of 20% per year. This is at or above the normal rate of production for the species being consumed (Petersen, 1978). The species of clams consumed live 20 years or more. It seems possible that the increase in the walrus population has been fostered and supported by large standing stocks of old clams accumulated during years of light predation when the walrus population was much smaller. It appears that these stocks may now be epleted in much of what has been considered the normal walrus range.

Major changes in the summer-autumn distribution pattern of the walrus population have become evident in recent years. The region between Bering Strait and Saint Lawrence Island is of particular interest. Walruses are largely excluded from this area in winter due to topographical features and northerly winds which cause convergence of heavy ice in the area (Shapiro and Burns, 1975). During the 1960's walruses migrated through this area on their way to and from summering grounds in the Chukchi Sea but did not remain in the area in significant numbers (Fedoseev, 1962). However, in recent years as many as 80 000 walruses have summered in this area (Gol'tsev, 1972; Alaska Department of Fish and Game, unpublished data), presumably since food was more abundant there than elsewhere. We think that the recent increase in predation by walruses has reduced stocks of *Serripes* in the area, thereby causing the decline in the amount of *Serripes* found in bearded seals taken at Diomede. Apparently, stocks of *Serripes* near Nome and Wainwright have been less severely depleted. However, we expect that, as depletion of food resources causes further distributional shifts in the walrus population, these stocks will be overgrazed as well.

The reduction in availability of *Serripes* has apparently had little effect on the bearded seal population. Estimates of abundance of bearded seals are not sufficiently accurate to detect small changes in numbers. However, good data are available on pregnancy rates and these show a constant rate of about 83% from 1962 through 1978 (Burns and Frost, 1977). This is not surprising since bearded seals forage to a large extent on crabs, shrimps, and sculpins, all of which are abundant and widely distributed in the Bering and Chukchi Seas. In the case of walrus, fairly reliable population estimates show a rapid rate of population increase at least through 1975. However, there are numerous indications that the health and productivity of the population may be declining. In 1965, eight of 160 sexually mature walruses examined were barren. In 1975 this figure has increased to 21 in a sample of 161 (Burns, unpublished data). These differences are statistically significant at the 95% probability (Chi square = 5.279). In addition, many animals are reported to be leaner than in previous years and features of natural mortality and population age distribution may be changing (Fay *et al.*, in press.). Such responses do not seem unlikely since walruses depend so heavily on long-lived slow-growing clams.

Mutual use of clams for food by both walruses and bearded seals has important implications for the former. Bearded seals are euryphagous benthos feeders which consume but depend only moderately upon clams. Walruses, however, are stenophagous and depend on clams for 80% or more of their food. Thus, a reduction of clam resources available to both would probably result only in a change of diet of the bearded seals. For the walruses, such a reduction in primary prey would mean a reduction in carrying capacity of the habitat with a concomitant redistribution (currently occurring) and eventual reduction in the size of the walrus population.

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