

WALRUS, *ODOBENUS ROSMARUS*, FEEDING IN THE BERING SEA: A BENTHIC PERSPECTIVE

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ABSTRACT

Walrus, *Odobenus rosmarus*, feed primarily on benthic bivalves and create a distinct record of their feeding activities on the sea floor. The record consists of furrows, pits, and discarded bivalve shells which were observed and sampled with scuba. Documentation of this benthic feeding record suggested that walrus commonly search for visually conspicuous prey by sight; that, in addition to "rooting" with the snout and vibrissae, walrus excavate bivalve prey by hydraulic jetting; that tusks are not used to excavate prey; and that all prey are excavated before consumption, which generally occurs close to the site of excavation. The mechanism of consumption appears to involve suction from between the shells. Continuous pit-furrow systems indicate the number of prey consumed in single dives, and suggest that a walrus can locate, excavate, and consume more than six clams per minute. The abundance of small infauna that are not walrus prey (e.g., polychaete worms, small bivalves, and crustaceans) was lower inside all excavations, indicating that the structure of bottom communities is highly modified by the extraction of a few large prey.

Marine mammals are observed primarily at the sea surface. Yet many important activities, especially feeding, occur underwater beyond the view of surface observers. While informative glimpses of feeding activities are sometimes obtained at the water surface (e.g., Watkins and Schevill 1976, 1979; Würsig and Würsig 1980), and the types of foods consumed are indicated by contents of gastrointestinal tracts (e.g., Lowry et al. 1980; Lowry and Frost 1981), knowledge of foraging behavior and the community role of marine mammals is generally poor. Electronic tags, depth recorders, and other instrumentation are improving this limited view (e.g., Watkins et al. 1981; Kooyman 1981). However, the greatest opportunities for studying the feeding ecology of marine mammals may involve species that prey on benthic organisms.

Bottom-feeding marine mammals often feed in shallow water, where general feeding grounds usually are known and local feeding areas can be relocated. Because benthic habitats and bottom prey are relatively immobile, prey communities can be sampled with considerable accuracy and precision, and can be experimentally manipulated as well. Largely for these reasons, we understand more about the community role of the sea otter, *Enhydra lutris*, a bottom feeder, than any other marine mammal (Estes and Palmisano 1974; Dayton 1975; Estes et al. 1978, 1982; Simenstad et al. 1978; Duggins 1980). In contrast to

the very few species of bottom feeders, most marine mammals feed on mobile prey in the water column where foraging activities are difficult to observe, and no record is made. Nektonic prey are extremely difficult to sample quantitatively. Even if a feeding event were observed, the dynamic nature of prey patches and the pelagic habitat preclude direct measurement of the effect of mammal predation on prey communities.

Some bottom-feeding marine mammals leave a record of their feeding activities in soft-sediment environments. The record primarily consists of pits and furrows made in the sea floor. For example, the gray whale, *Eschrichtius robustus*, produces large, bowl-shaped pits while feeding on benthic infauna, especially amphipod crustaceans (Oliver et al. 1983). Gray whales capture and consume invertebrate prey by suction, but also kill, injure, and displace nonprey, modify local habitats, and attract scavenging animals to these excavated bottoms. Walrus; bearded seals, *Erignathus barbatus*; sea otters; dugongs, *Dugong dugon*; and manatees, *Trichechus* spp., also feed in soft-sediment habitats, but only the walrus and gray whale depend primarily on infaunal prey (Anonymous 1978).

Walrus are a common and conspicuous element of the marine mammal fauna inhabiting arctic and subarctic waters of the Northern Hemisphere. They are particularly abundant in the Bering and Chukchi Seas, where they forage among the bivalve communities found on the broad Beringian platform. The contents of numerous gastrointestinal tracts indicate

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that bivalve mollusks are the primary prey (Fay 1982). However, because gastrointestinal samples are extremely difficult to relate to a particular feeding habitat and walrus feeding has not been observed in the field, present knowledge of foraging behavior largely depends on morphological arguments and observations of captive animals (Fay 1982). We cannot evaluate walrus disturbance of bottom communities from gastrointestinal samples. The diet and feeding method of walrus provide an opportunity to explore their feeding ecology by examining records of foraging activity on the sea bottom.

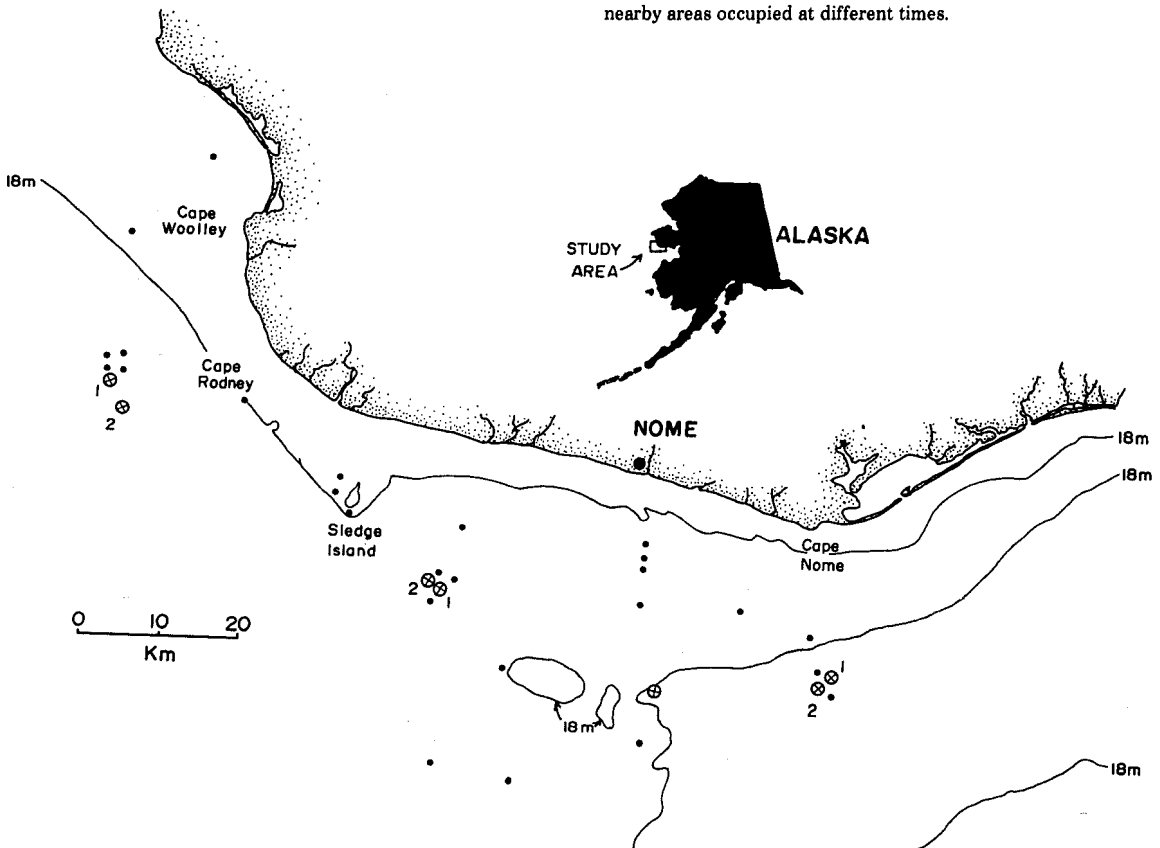
There are three principal objectives of this paper: 1) To describe the benthic feeding record of the walrus; 2) to demonstrate that the record provides important insights into patterns of searching, capturing, and consuming prey; and 3) to suggest the roles walrus play in structuring soft-bottom communities.

STUDY AREA

All of our observations and sampling were done near Nome, Alaska, in the northern Bering Sea (Fig.

1). The bottom is gently sloping, with extensive flat regions of fine and muddy sand (Sharma 1974). Bottom waters are cold (1° - 8° C), and temperatures fluctuate seasonally (Muench et al. 1981). Water clarity is poor, usually allowing 0.5 to 1.5 m of visibility, but is occasionally 2 to 8 m. Sea ice forms during the fall and persists until late spring or early summer. Fast ice is relatively persistent nearshore, but offshore ice patterns are highly variable, particularly the occurrence and movement of the pack ice (McNutt 1981; Stringer 1981; Ray and Dupré 1981). No ice gouging of bottom sediments or gas cratering occurs in the study area (Larsen et al. 1979). Walrus are strongly associated with sea ice, where they haul out to care for young and to rest, often between foraging activities (Fay 1982). Large numbers of walrus pass through the study area, particularly during the spring northward migration (May-June). Small numbers may be present there during other months as well (Fay 1982; pers. obs.). Bearded seals are also abun-

FIGURE 1.—The major diving stations (large open circles with X in center) and other sites (small closed circles) surveyed by divers in May-June 1981 near Nome, Alaska. Numbered stations refer to nearby areas occupied at different times.



dant in the area during the spring (Lowry et al. 1980), but gray whales are seen infrequently (pers. obs.). The biomass of benthic animals is dominated by bivalve molluscs and echinoderms with large numbers of a few sedentary polychaete worms (Stoker 1978). The number and biomass of crustaceans are much lower in the study area compared with the central and western parts of the northern Bering Sea (Stoker 1978).

Field work was done from 22 May to 7 June 1981. Remnants of shore-fast ice moved away from Nome several days before our arrival. Well-developed pack-ice and large groups of walrus were observed in the general study area during the preceding month. These animals probably fed in the region for at least a month before our arrival. Therefore, the benthic feeding record was likely to be quite recent. No walrus were seen in the study area after the sea ice moved offshore around 15 May 1981.

METHODS

Thirty-three dives were made south and west of Nome (Fig. 1). At each site, divers using scuba thoroughly searched the bottom for traces of walrus feeding activity. The benthic feeding record was quantified at only several sites where feeding traces were found. Here, discarded bivalve shells were collected, and the distance to the nearest pits and furrows was recorded. Pit and furrow dimensions were measured, as well as the number of pits in a patch, and the area of bottom containing each distinct patch of pits. A patch of pits was considered distinct when no additional pits were found within 5 m of the group. Water clarity of <1 m limited the patch size observations in all areas except Cape Nome. Shell lengths and breaking strengths (using a hinged plate that was calibrated to pounds of pressure) were measured at the laboratory.

Small benthic infauna that are not walrus prey were sampled directly in feeding excavations, and in adjacent undisturbed bottoms with hand-held corers

(area = 0.0075 m²; depth = 12-15 cm). Samples were washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Animals were identified to the lowest possible taxon and counted. Although juvenile bivalves and small species were adequately sampled by the corers, larger individuals were not, particularly the major walrus prey, *Macoma* spp., *Mya truncata*, and *Serripes groenlandicus*. However, the siphons and siphon burrows of the deep-burrowing clam, *M. truncata*, were counted in 1 m² areas to estimate the abundance of these large individuals. Sediment consolidation was measured with a simple penetrometer, which was a weighted rod (0.5 kg) dropped through a cylinder resting on the bottom. Penetration was estimated as distance of rod penetration into the surface sediments (e.g., Ronan 1975).

RESULTS

Benthic Feeding Record

We observed two basic types of excavations, furrows and pits. In both cases, shells of the excavated clams were discarded close to excavations. Therefore, different pits and furrows were easily linked to the species of excavated bivalve prey. There were three principal bivalve prey, *Mya truncata*, *Serripes groenlandicus*, and *Macoma* spp. (mostly *M. calcareo*). These groups are recognized as major prey by Vibe (1950) and Fay (1982). Feeding records generally contained one or two types of excavations: Furrows, *Mya* pits, or a mixture of *Mya* and *Serripes* pits. The relative abundance of discarded shells corresponded to the primary type of excavation in each area. For example, 92 to 100% of the shells were *Mya truncata* at stations that primarily had *Mya* pits; 76 to 83% of the shells were *Macoma* spp. at stations that primarily had *Macoma* furrows; and *Mya truncata* and *S. groenlandicus* shells were both abundant at stations that had mixed pits (Table 1). Bivalve prey thus were identified by discarded shells and by ex-

TABLE 1.—Excavation type and percentages of discarded shells from the three major prey found at the main feeding sites near Nome, Alaska. Percentages are based on the number of reconstructed whole clams.

Location	Depth (m)	Primary ¹ excavation type	Percent of discarded shells			No. of bivalves
			<i>Mya truncata</i>	<i>Serripes groenlandicus</i>	<i>Macoma</i> spp. ²	
Cape Rodney-1	24	<i>Mya</i> pit	100	0	0	17
Cape Rodney-2	24	furrow	18	6	76	17
Sledge Island	24	furrow	10	10	83	41
Nome	24	mixed pit	41	54	5	35
Cape Nome-1	17	<i>Mya</i> pit	92	4	4	28
Cape Nome-2	17	mixed pit	21	79	0	164

¹Areas contained either mostly *Mya* pits, mixed pits of *Mya* and *Serripes*, or mostly furrows with *Macoma*.

²Primarily *Macoma calcareo*.

cavation morphology. Each excavation was linked to a particular species of clam, and a larger region (dive station) was characterized both by the primary type of excavation and by the most abundant shells. Because each of two divers traveled at least 50 m and often over 100 m per dive, the primary type of excavation was easily assessed, albeit qualitatively, despite the poor water clarity. Benthic feeding records were located on 18 of 33 dive sites, but were only well quantified at 6 of the 18 sites (Table 1).

Furrows

The most extensive and distinct furrows were found near Sledge Island (Table 1). Water clarity in this area was relatively poor (about 1 m), but was adequate to see furrow widths and to trace lengths. By swimming rapidly over a long distance (>50 m), we estimated qualitatively that at least 40% of the bottom was furrowed at one Sledge Island dive site. Furrows generally formed a complex maze of excavations, but discarded shells always were abundant (as many as 5-10/10 m²) within and along the furrow edges and were rare (<1/10 m²) on undisturbed bottoms between furrows. The average furrow width was 45 cm and depth was 17 cm (Table 2). *Macoma* spp. were primarily excavated from furrowed bottoms (Table 1).

TABLE 2.—Morphological differences between the three major types of excavations of the walrus. Means and 95% confidence limits (sample size).

	Diameter or width (cm)	Depth (cm)
<i>Mya truncata</i> pit	30±1 (30)	32±3 (10)
<i>Serripes groenlandicus</i> pit	14±2 (9)	11±3 (14)
<i>Macoma</i> spp. furrow	45±3 (7)	17±2 (7)

Pits

Three distinct types of pits were made in excavating *Mya truncata*, *Macoma* spp., and *Serripes groenlandicus*. The pits differed in diameter or depth (Fig. 2, Table 2), reflecting a species position in the sediment.

Mya pits had a deep central shaft (Fig. 2). Divers readily identified these pits by thrusting a fist into a shaft. *Mya truncata* has a long, tough siphon and lives deep in the sediment (about 30 cm). Eighty-nine percent ($n = 190$) of the *Mya* pits contained only a *Mya* shell within 1 m of the pit.

Macoma pits were similar in diameter to *Mya* pits,

but lacked the central shaft. They were relatively rare, as furrows were the primary excavations associated with *Macoma* shells (Table 1). *Macoma* spp. generally lives <20 cm into the sediment, and has a shorter siphon than *Mya truncata*.

The largest *Serripes* pits were much smaller than the *Mya* and *Macoma* pits (Fig. 2). Small *Serripes* pits were impossible to distinguish from sea star pits and surface irregularities. Some large *Serripes*-type pits may be made by larger sea stars (*Lethasterias* and *Asterias*). This bivalve has a short siphon, is a shallow burrower, and commonly occurs at the sediment surface. *Serripes* shells were conspicuous on the sediment surface. Therefore, although either the shells or pits of *Mya truncata* and *Macoma* spp. could be counted to estimate prey consumption, only the shells provided an adequate estimate of the number of *S. groenlandicus* eaten by walrus.

Pit-Furrows

Pit-furrow systems consisted of a series of pits connected by a shallow, continuous, and distinct furrow (Fig. 3). These systems were less common than the isolated pits or deeper furrows, and were found only at Cape Nome. Species excavated in the pit-furrow systems were primarily *Mya truncata* and *S. groenlandicus*.

Shells

The shells of primarily three groups of bivalves, *Mya truncata*, *Serripes groenlandicus*, and *Macoma* spp., were observed on the sea floor (Fig. 4). *Macoma* and *Serripes* shells were commonly attached at the umbus. About 6 to 8% of the shells from these groups were broken, while 78% of the *Mya* shells were broken (Table 3). Greater breakage of *Mya* shells appeared to be related to shell hardness (Table 3), and not necessarily to a different feeding method. The outer lining of the siphon (the periostracum) was attached to 83% of the *Mya* shells ($n = 65$), and the distal end of the siphon commonly was intact.

TABLE 3.—Percentage of broken shells found in major prey species (based on number of reconstructed whole shells), and an index of shell hardness.

	No. of bivalves	Percent broken	Shell hardness ¹
<i>Mya truncata</i>	96	78	4.9±1.7
<i>Macoma</i> spp.	32	6	7.2±2.3
<i>Serripes groenlandicus</i>	154	8	7.2±1.2

¹ Pounds of pressure required to break a single valve. Means and 95% confidence limits in 10 trials.

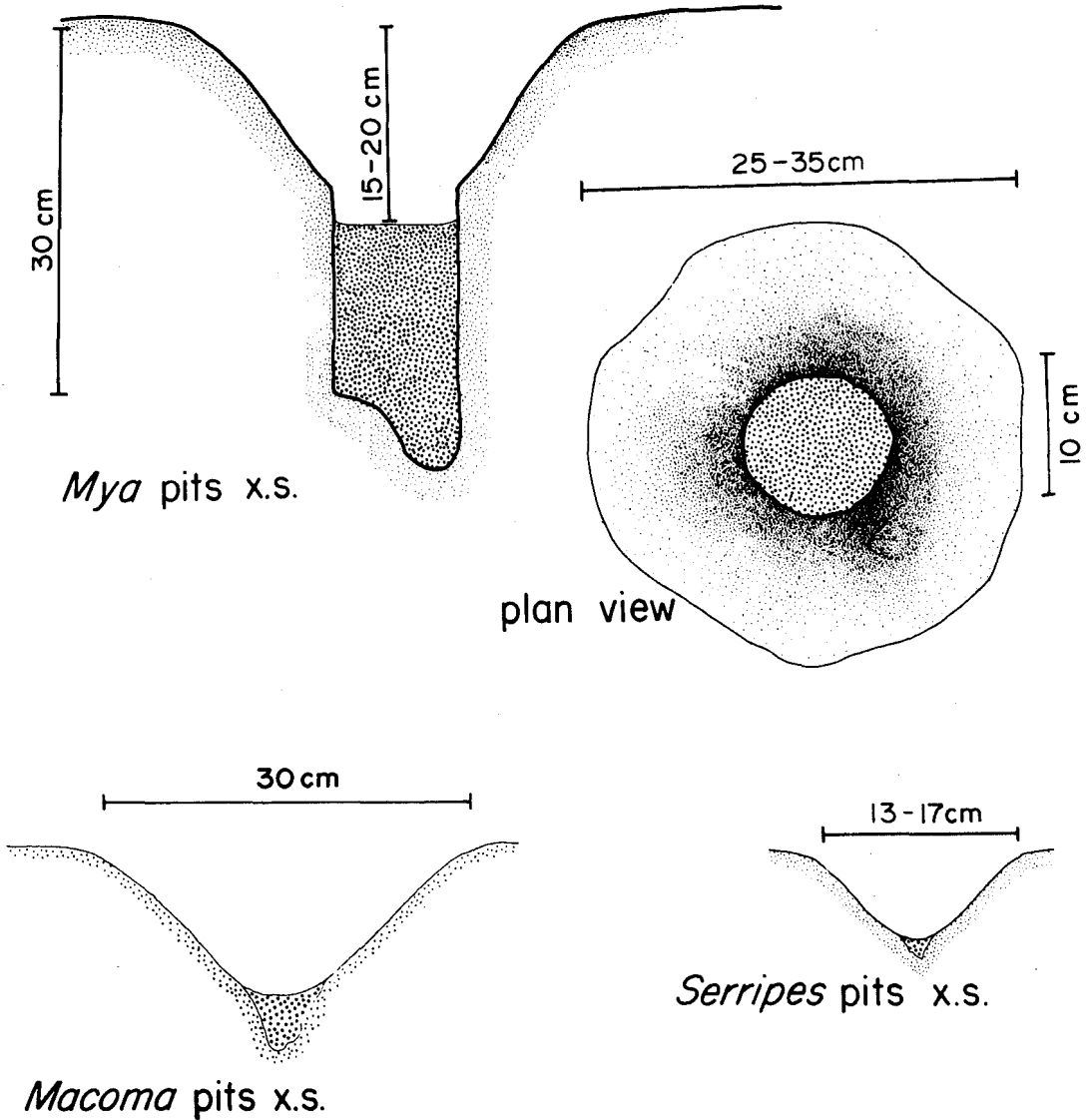


FIGURE 2.—Illustrations of the large *Mya truncata* and *Macoma* spp. pits, and the smaller pits created by excavating *Serripes groenlandicus*.

Evidence for Single Diving Events

Mya pits generally were found in distinct groups with a distance of at least 5 m between patches of pits. There was no significant difference between the number of pits per patch or the area covered by a group of pits when two similar dive sites were compared from Cape Nome (Table 4). Patches included from 1 to 20 pits, which may represent the activities of a walrus during a single dive.

We found one excellent record of the number of clams taken in a single feeding event in a pit-furrow

TABLE 4.—Number of *Mya* pits found per group and area of the patches in two similar locations near Cape Nome. Means and 95% confidence limits in *N* samples.

	<i>N</i>	Cape Nome-2	<i>N</i>	Cape Nome-1	Prob. ¹
Pits per patch	15	6.1±2.6	12	5.6±3.2	<i>P</i> >0.3
Patch area (m ²)	15	10.6±7.6	12	18.0±9.8	<i>P</i> >0.2

¹Probability of difference in *t*-test.

system located off Cape Nome (Fig. 3). The pits or shells of 19 *M. truncata* and 15 *S. groenlandicus* were located in this continuous pit-furrow. Unfortunately, we could not survey the entire system because of a

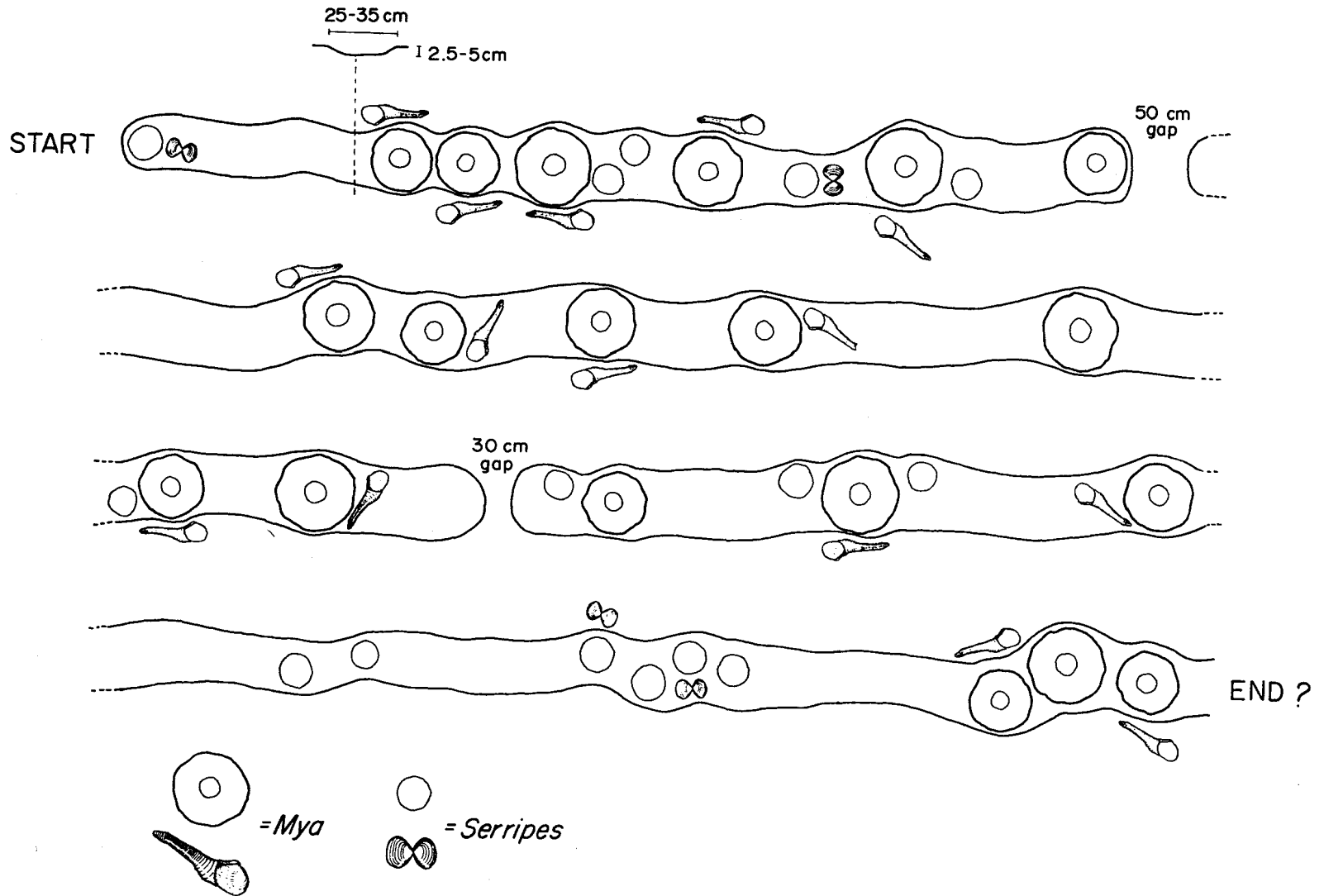


FIGURE 3.—A continuous pit-furrow system made by a feeding walrus showing pits found with and without bivalve shells. Divers did not reach the end of the system.

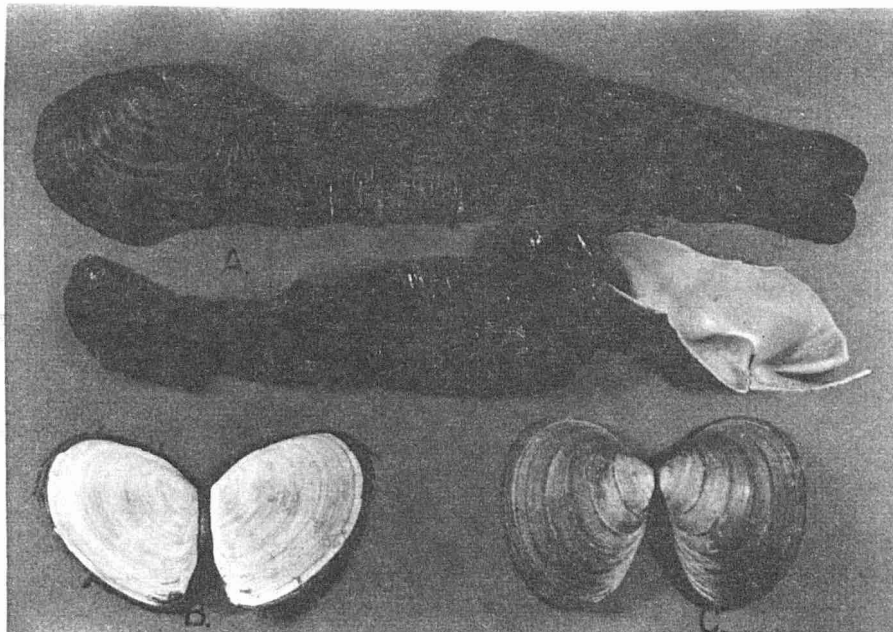


FIGURE 4.—Shells of *Mya truncata* (A), *Macoma calcaria* (B), and *Serripes groenlandicus* (C) discarded by feeding walrus.

low air supply. Nevertheless, this incomplete record is the most accurate estimate of the number of clams it is possible for a walrus to excavate during a single dive.

Effects on Benthic Communities

Walrus undoubtedly have a significant effect on abundance and size distribution of bivalve prey. Because we did not obtain adequate samples of the large individuals in living bivalve populations, we could not compare availability of various sizes of prey with the sizes of prey consumed. Nevertheless, discarded shells indicated that walrus consumed relatively large individuals from the three principal groups of bivalves (Fig. 5).

It is important to determine whether walrus disrupt different nonprey populations while feeding in different local habitats. Core samples were taken to document the species composition and relative abundance of the smaller infauna, which could be displaced, injured, or killed during excavation of the large bivalve prey. These samples indicate that benthic infaunal communities were strikingly different at the major feeding sites near Nome (Table 5). The western areas were near Cape Rodney and were numerically dominated by tube-building polychaete worms, *Myriochele oculata*, and *Polydora flava flava*.

TABLE 5.—Abundant infauna found at the three major feeding sites of walrus. Mean numbers per 0.0075 m² with standard deviations in parentheses. P = polychaete; C = crustacean; O = ophiuroid; T = tunicate; Pr = protozoan.

	Cape Rodney-1 (24 m)	Sledge Island-2 (24 m)	Cape Nome-2 (17 m)
<i>Myriochele oculata</i> (P)	133 (55)	45.7 (10.6)	448 (116)
<i>Polydora</i> cf. <i>flava flava</i> (P)	302 (171)	0	0
<i>Exogone</i> sp. (P)	9.7 (3.5)	0	0
Sabellidae (P)	8.3 (5.1)	0	1.3 (1.0)
<i>Syllis</i> sp. (P)	7.7 (1.8)	0	0
<i>Amphiodia craterodmeta</i> (O)	1.7 (1.2)	205 (48)	5.7 (2.3)
<i>Leucon nasica</i> (C)	0	18.3 (0.4)	0
Oligochaeta	0	14.0 (11.0)	0
<i>Rhizomogula</i> sp. (T)	0	0	201 (71)
<i>Protomedea fasciata</i> (C)	1.7 (1.2)	4.7 (2.7)	51.3 (47.5)
<i>Gromia</i> sp. (Pr)	4.7 (1.8)	0	34.2 (8.7)
Podocopids (C)	3.3 (2.0)	2.0 (1.0)	14.0 (4.2)

We located an excellent record of *Mya* pits and shells there (Table 1), and observed the siphons and siphon-burrows of large, living *M. truncata*. At Sledge

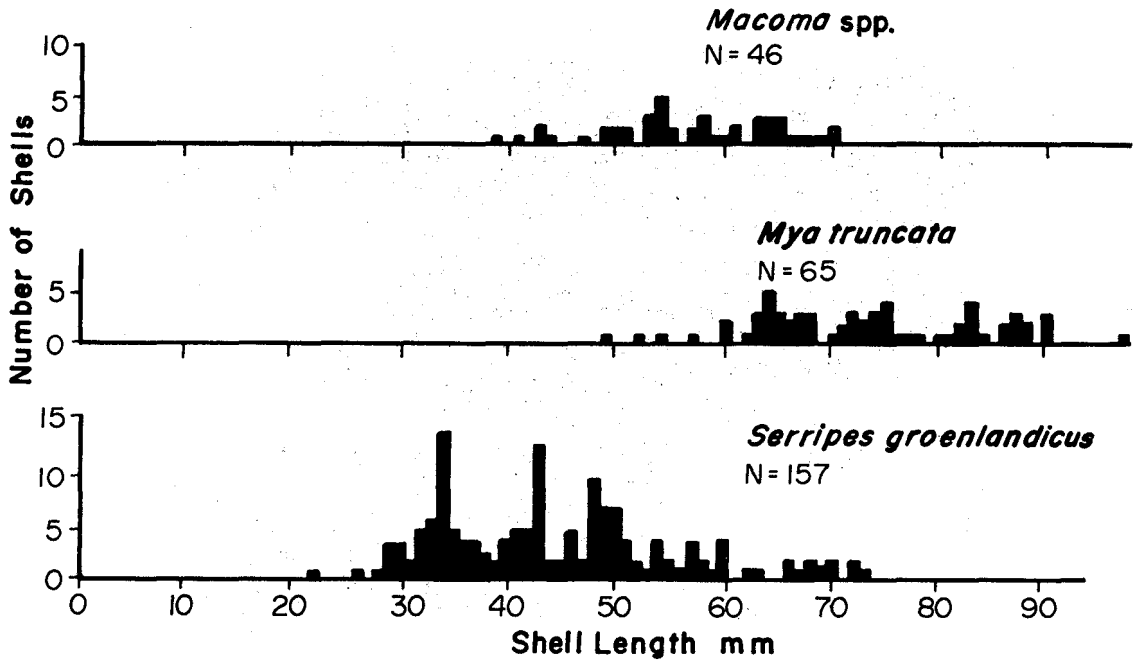


FIGURE 5.—Shell size of three groups of clams consumed around Nome, Alaska. Shells are from the benthic feeding record.

Island, the small ophiuroid, *Amphiodia craterodmeta* (disc diameter = 1.4 cm) was the most abundant species, and there was a record of furrowed sediment and *Macoma* shells (Table 1). Qualitative observations indicated few large, living bivalves, mostly *Macoma* spp. and fewer *Mya truncata*. Instead of a visually conspicuous tube mat of polychaetes, the bottom was covered with a dense carpet of interwoven ophiuroid arms. At Cape Nome, *Myriochele oculata*; the tube-building amphipod crustacean, *Protomedea fasciata*; and the infaunal tunicate, *Rhizomogula* sp., were relatively abundant. *Mya truncata* was the major walrus prey taken at Cape Nome (Table 1) and was the only abundant large bivalve living here ($>5/m^2$). The number of sea stars, primarily *Asterias amurensis*, increased from Cape Rodney to Cape Nome. They were the predominant large epifaunal animals.

The feeding activities of walrus produced similar changes in the structure of these different benthic communities. The feeding excavations we discovered probably were <1 mo old (see section on Study Area), and occurred in highly mixed gravel and sand, in sand, and in sandy mud. Sediments were significantly less consolidated ($t = 10.2, P < 0.0001$) in *Mya* pits (penetration = 11.9 cm; $n = 15$) than in undisturbed sediments (penetration = 4.4 cm; $n = 15$). The biogenic structure of surface sediments in ex-

cavations was poorly developed compared with the adjacent bottom.

Despite differences in the structure of nonprey communities, most infauna were less abundant inside the recent walrus excavations from all feeding sites. With few exceptions, the abundances of major groups (Fig. 6) and numerically dominant species (Fig. 7) were lower inside pits (Cape Rodney, Nome, Cape Nome) and furrows (Sledge Island). One exception was the polychaete worm *Myriochele oculata* at one Sledge Island site (Figs. 6, 7). These individuals were not recently settled, but were large adults in well-developed tubes. Because this species was relatively immobile, tubes probably were concentrated passively in the furrow bottom during walrus feeding. The small (diameter <1 cm) infaunal tunicate *Rhizomogula* sp. was very abundant in the Cape Nome region, and apparently rolled into *Mya* pits during and after excavation. Its abundance was significantly higher ($t = 5.1, P < 0.01$) in the bottoms of pits ($\bar{X} = 576$ per core inside, 251 outside; $n = 6$). One or two larger epifaunal anemones also occurred in many excavations. We observed several of these individuals rolling across the sediment surface in strong currents. Scavenging lysianassid amphipods were abundant in only two cores from recent excavations at Cape Nome (61 and 43/core; $1/133 m^2$). These amphipods were rare in most core samples (<1 /core;

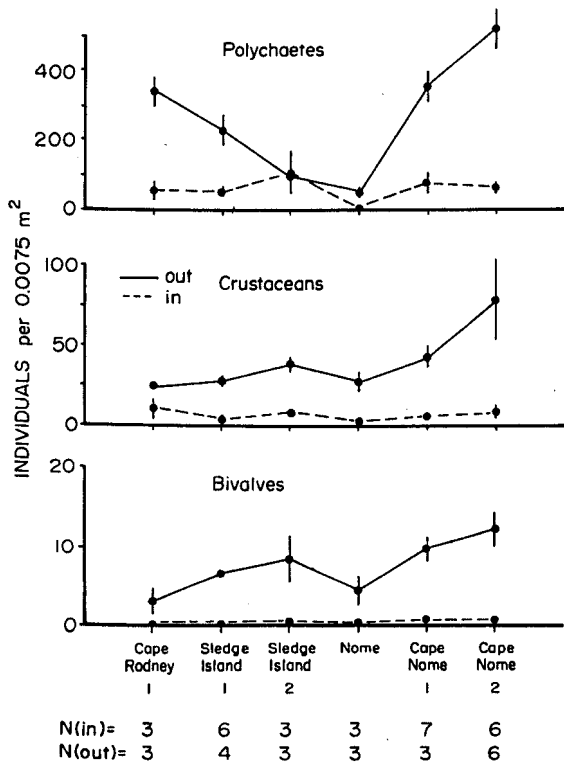


FIGURE 6.—Abundances of major infaunal groups inside and outside the furrows dug for *Macoma* spp. (Sledge Island), and the pits excavated for *Mya truncata* (all other areas). Means and standard errors in N cores.

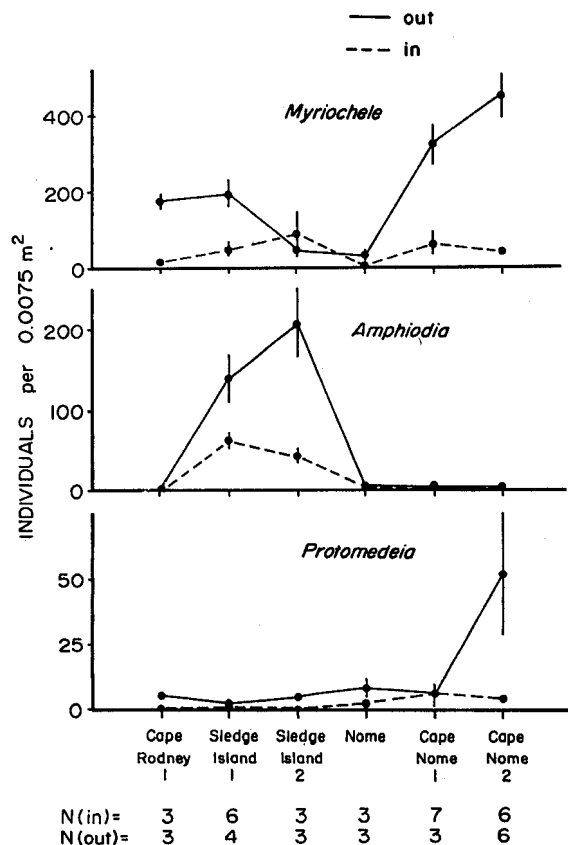


FIGURE 7.—Abundances of three numerically dominant infaunal species inside and outside walrus excavations. The polychaete worm *Myriochele oculata*, the ophiuroid *Amphiodia craterodmeta*, and the crustacean *Protomedeia fasciata*. See Figure 6 legend.

$n = 26$ cores). Lysianassids respond to various disturbances and are voracious scavengers (pers. obs.) that probably were attracted to the tissue on a discarded bivalve shell.

DISCUSSION

Walrus Feeding Behavior

Walrus are highly specialized for feeding on benthic infauna, especially bivalve molluscs (Fay 1982). Of other marine mammals, only the diet of bearded seals overlaps with the bivalve prey of walrus near Nome, but bearded seals have a much broader diet than do walrus (Lowry et al. 1980). Because bearded seals eat certain shallow-burrowing clams (e.g., *Serripes groenlandicus*) and rarely eat deep burrowers (e.g., *Mya truncata*), they cannot account for the diverse feeding records observed near Nome. No other biological or physical process can account for the record of excavations and discarded shells. While some large sea stars can make pits as large as the larger *Serripes* pits,

none of the *Mya* and *Macoma* pits or the furrowed bottoms are produced by sea stars.

The low water clarity in the Bering and Chukchi Seas and the poorly developed eyes of walrus suggest that prey are not located by sight (Fay 1982). However, the benthic feeding records suggest that walrus often search for certain bivalves by sight. The most important evidence was the presence of many distinct, isolated pits with no indication of bottom disturbance between pits. These pits were made in excavating *Mya truncata*, the same species that divers routinely located by sight because of the large, conspicuous siphons. Apparently, walrus used the snout and vibrissae to search for prey without conspicuous siphons or shells (Fay 1982), as extensive furrowing only occurred in excavating *Macoma* spp., clams with small and cryptic siphons. These "rooting" activities clearly disturbed surface sediments and infaunal communities. Even the move-

ments of hermit crabs, gastropods, and sea stars produced distinct traces in surface sediments. Because the bottom was undisturbed around the isolated pits made in extracting the visually conspicuous prey, the snout and vibrissae were probably unimportant in locating these species.

The feeding excavations of walrus clearly indicate that clams are not excavated with the tusks. Fay (1982) gave a convincing argument based on anatomy and tusk abrasion patterns that the tusks are not used to excavate prey. Their main function apparently involves aggressive interactions, especially among the males (Miller 1975). None of the furrows or pits we discovered could be produced by plowing or digging with the tusks. As suggested by Vibe (1950) and Fay (1982), most excavations probably involve "rooting" with the snout and vibrissae. According to Fay³, snout widths of subadult and adult walrus range from 29 to 41 cm for males and 23 to 35 cm for females. These sizes correspond exactly to the diameter of the upper portion of *Mya* pits and the width of furrows if the snout is swung in a narrow arc during excavation (Table 2).

We hypothesize that in addition to "rooting," a pulsing jet of water also was used to excavate prey. The walrus' mouth and tongue are well adapted for sucking and expelling water (Fay 1982) (a well-known fact to visitors who are sprayed regularly at Sea World Park in San Diego). Hydraulic jetting is the only feasible mechanism for producing the deep (30 cm) central shafts of *Mya* pits. These hydraulic pulses also may be used to produce furrows and other pits, probably in conjunction with snout and vibrissae movements. This idea was tested by constructing a suction-jet similar to the clam guns used to extract bait from intertidal mudflats. By manipulating the nozzle diameter and the volume of water exchanged per stroke, divers have produced excavations similar to the pits and furrows made by walrus.⁴ A similar jetting process was observed in bat rays by Gregory et al. (1979), who suggested that it was used to excavate infaunal prey.

All clams were excavated prior to consumption. Shells were found on the surface of the sediment in a nonliving orientation. There was no evidence that biting (Vibe 1950) or suction was used to remove the soft parts of the clam while the shell was held in the sediment. Soft parts were clearly consumed near the sea floor, because discarded shells were closely as-

sociated with pits and furrows. The soft parts of clams probably were sucked from between the two shells (Vibe 1950; Fay 1982).

Perhaps the most exciting potential of the benthic feeding record is to quantify the activities of a single dive. The continuous pit-furrow system we discovered showed the location, excavation, and consumption of 34 clams along >60 m of the bottom. Over half of these clams (19) lived 30 cm deep in the sediment. At this water depth average dive times are about 5 min (Fay 1982), which suggests that one walrus ate more than six clams per minute. Divers can locate a number of long, continuous pit-furrow and furrow systems where the species, size, and number of prey can be measured. These may be the most accurate records of the diving and foraging activities of any marine mammal.

Effects of Bottom Disturbance

Walrus have an obvious impact on their large bivalve prey, but they also displace many of the small and abundant infauna that are not walrus prey. All the furrows and pits we observed were probably <1 or 2 mo, and probably <1 mo old (see section on Study Area). While there were dramatic differences between the structures of nonprey communities at the major feeding sites, the abundances of most small infauna were significantly lower inside all of the recent excavations (Figs. 6,7). The few exceptions were either immobile species that were passively concentrated in the excavations (e.g., *Myriochele oculata* and *Rhizomogula* sp.), or more motile species that may be attracted to the excavations or to scavenging events inside excavations (e.g., lysianassid amphipods). Walrus disturbance clearly produces new habitats, opens considerable space, and modifies resources that influence subsequent patterns of colonization. The tissue that remains attached to discarded shells may be an important source of food for several benthic scavengers, including asteroids, ophiuroids, and crustaceans.

Interactions Among Marine Mammals

Walrus may interact trophically with a number of other bottom-feeding marine mammals (Lowry et al. 1980; Lowry and Frost 1981). Gray whales and bearded seals share the walrus' feeding grounds in the Bering and Chukchi Seas, while the sea otter and walrus overlap in the southeastern Bering Sea. Because these other large predators produce a benthic feeding record that is distinct from the walrus, potential interactions can be examined by comparing

³F. H. Fay, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. May 1982.

⁴Oliver, J. S., and E. F. O'Connor. Hydraulic excavation of bivalve prey by walrus. Unpubl. manuscr. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

benthic feeding records in areas where the species do and do not overlap.

Walrus and sea otters may compete for food in the southeastern Bering Sea, where sea otters forage extensively in soft-sediment habitats. In contrast to the situation in rocky shores (e.g., Estes et al. 1982), the feeding ecology of sea otters in soft sediments is poorly understood. Along the California coast, sea otters feed on several species of bivalves, including Pismo clams, *Tivela stultorum*; Washington clams, *Saxidomus nuttallii*; and gaper clams, *Tresus nuttallii* (Stephenson 1977; Hines and Loughlin 1980), on tellinid clams *Tellina* sp. in Prince William Sound (G. A. VanBlaricom⁵), and on razor, *Siliqua alta*, and surf, *Spisula polynma*, clams along the Alaska Peninsula (pers. obs.). They excavate pits with the forelimbs and commonly produce sediment piles next to the excavation. Unlike the sea otter, walrus pits do not have piles of extracted sediment. Because otters break shells to extract soft parts, the discarded shells of walrus and sea otters are easily separated as well. Walrus feed along the northeastern portion of the Alaska Peninsula,⁶ while sea otters occur more to the southwest. However, their ranges do overlap in the central area. Therefore, feeding records can be quantified in areas of overlap and non-overlap for both species.

Walrus and bearded seals may compete for bivalves in the northern Bering and Chukchi Seas (Lowry et al. 1980). Although we have not observed the benthic feeding record of bearded seals, we predict that it is distinct from the walrus record, and thus amenable to the same sampling scheme outlined for the sea otter-walrus feeding grounds in the southern Bering Sea.

Gray whales do not consume large bivalves, but they may have a negative effect on the walrus food resource by reducing the recruitment or survival of walrus prey. One possible hypothesis is that gray whale feeding kills clams by direct burial, or by clogging feeding structures. We predict that this hypothesis is incorrect. A more likely hypothesis is that gray whale disturbance has a positive influence on several species of amphipod crustaceans, and that these crustaceans decrease the recruitment of young bivalves by predation, trampling, or some less direct interference. This idea can be tested by excluding whales from a bottom area with a large (perhaps 20 × 20 m) canopy made of net on a pipe frame. Walrus

feeding probably has little or no effect on gray whales.

This discussion speculates broadly about the usefulness of the benthic feeding record. But much of the speculation can be formulated into hypotheses that are subject to critical tests. Comparable ideas about most other marine mammals, especially the non-bottom-feeding species, are extremely difficult to test, either by manipulative experiments or by sampling natural contrasts. For this reason, the benthic feeding record will undoubtedly make important contributions to our understanding of foraging behavior, community roles, and interactions among marine mammals.

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