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Final Report

CHANGES IN SOFT-BOTTOM PREY COMMUNITIES ALONG A GRADIENT IN SEA OTTER PREDATION AROUND KODIAK ISLAND, ALASKA.

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1986 Cooperative Agreement (No. 14-16-0009-86-948)

Between

U. S. Fish & Wildlife Service, Department of the Interior

And

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ABSTRACT .

Sea otters, *Enhydra lutris*, have a dramatic impact on bivalve prey populations and non-prey infaunal communities around Kodiak Island. The major prey species was the clam, *Saxidomus giganteus*, which had the highest biomass of all prey in the study area. Otters preferred the largest individuals of this species. Feeding grounds with the longest history of sea otter foraging had the lowest biomass and generally smaller size of *S. giganteus*. Recently invaded feeding grounds had intermediate biomass of clam prey. Relatively unexploited feeding grounds had the highest prey biomass and largest individual size. Otters first exploited *S. giganteus* in shallow-water feeding grounds, and later switched to *Macoma* spp. in deeper water. Sea otters rarely consumed the deepest burrowing clam, *Tresus capax*, which apparently had a depth refuge from otter predation. *Mya truncata* was the preferred prey at only one site, where their siphons were highly conspicuous and burrow depths were restricted to < 20 cm. The reduction in total prey biomass from the heavily exploited to the unexploited feeding grounds was highly significant.

Excavation of clam prey disturbed as much as 12% of the sea floor at recently invaded feeding grounds. Several unexploited feeding grounds were covered with dense tube mats of sabellid polychaetes, which also harbored many clam prey. These mats will probably be destroyed by future feeding activities of otters. When otters disturbed the dense tube mat, the sea star, *Pycnopodia helianthoides*, fed on infaunal animals where the tube mat was exposed in the feeding pit. Otters also discarded clam shells on the sediment surface and exposed old, buried shells during excavation. Surface shells provided attachment sites for large anemones and kelp.

INTRODUCTION

The community effects of sea otters, *Enhydra lutris*, including their interactions with prey populations are known primarily from rocky shores (VanBlaricom and Estes in press). Sea otters also forage extensively in soft-sediment environments (Kenyon 1969, Calkins 1978, Wild and Ames 1974, Miller et al. 1975, Stephenson 1977, Hines and Loughlin 1980, Estes et al. 1981, Garshelis 1983, Estes and VanBlaricom 1985, VanBlaricom in press, Kvitek et al. in press, Kvitek and Oliver in press), where there is little known about their effects on prey populations and community structure (Kvitek and Oliver in press). Sea otter populations made dramatic recoveries during the last 75 years after intensive commercial exploitation (Kenyon 1969). Otters are still recolonizing historical feeding grounds throughout their range. The recolonization of historical feeding grounds provides unique opportunities to explore the effects of otters on prey populations, communities and habitats. Unfortunately, this process has not been well documented in rocky or soft-sediment environments. There is, however, excellent information on differences in prey populations and communities in rocky habitats with and without sea otters (Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978, Simenstad et al. 1978), but there are no comparable observations from soft-sediment environments.

Thousands of sea otters forage around the Kodiak Archipelago and are recolonizing historical feeding grounds. Although otters have not spread around the entirety of Kodiak Island, they have already exploited hundreds of square kilometers of benthic feeding grounds (Schneider 1976). Large fronts of

foraging otters have spread southward from Shuyak Island and are invading relatively unexploited feeding grounds in southern Afodnak Island and north and northwestern Kodiak Island (Schneider 1976). We use this gradient of sea otter foraging to describe the changes in soft-sediment prey communities from heavily exploited old feeding grounds, to recently exploited new sites, to relatively unexploited feeding grounds. By substituting space for time in this natural experiment, we document shifts in bivalve prey species, sizes and abundances that were probably caused by otter predation. In addition, we consider the community effects and extent of sea otter foraging disturbance, including disruption of the primary substrate through prey excavation and the addition of hard substrate to soft sediment habitats via discarded shells.

METHODS

Study Sites and Sea Otter Patterns

The study region was around Raspberry Island in the Kodiak archipelago, where there was an influx of sea otters during recent years resulting in two major types of feeding grounds: old and frontal areas (Figure 1). Otters fed extensively for several years in the old feeding grounds, which included sites now abandoned by otters and sites still occupied by otters. Frontal areas were only recently invaded by sea otters and contained heavily exploited and relatively unexploited patches of prey. Specific study sites were selected based on past and present otter movements and densities, and on scuba surveys (Figure 1). Observations on the movements and numbers of sea otters in the study area where made by local residents and by the U.S. Fish and Wildlife Service.

Shell Record

Bivalve shells were collected to determine the prey species and sizes eaten by otters. Divers swam haphazardly over study sites and picked up all shells from the sediment surface. Shell were sorted to species and relative age categories. Fresh shells had remnants of soft tissue attached, usually a small part of the mantle or adductor muscles. Recent shells were those with no remnant tissues and with little or no signs of shell breakdown or fouling by invertebrates or algae. The old category included shells with clear signs of shell breakdown and/or fouling with attached animals and plants. Shell collections were further divided into broken and whole shells. All shells were measured to the nearest mm.

Live Prey

Prey densities, sizes and biomass were measured at six sites (Selief Bay, Bukti Pt., Rolling Pt., Shoal Pt., Back Bay 5m and 10m). All sites were sampled between 28 June and 6 July, 1986. Haphazardly placed circular 0.25 m^2 quadrats (an open-ended 55 gal oil drum cut in half) where excavated to a depth of 50 cm by divers. A fire hose was used to liquify the sediment within the barrels and dislodge clams which then came to the sediment surface where they were collected. Water was pumped through a 35m x 2.5" hose by a 8 hp Briggs and Stratton powered irrigation pump. Ten replicates were taken at all sites except Rolling Point (N = 8). Bivalves were sorted to species and shell length measured to the nearest mm. Wet meat weight was recorded to the nearest gram. *Tresus capax* siphon counts/m^2 were also made by divers at the mouth of Selief Bay.

Observations of feeding otters were made from land with either a 40x or 80x spotting scope at five sites. Otters consume their prey at the surface, making it relatively easey to document prey type (Calkins, 1978).

Community Disturbance

Foraging sea otters disturb the bottom by creating pits and discarding shells on the sediment surface. Divers counted and measured otter feeding excavations along 10m x 2m transects at Selief Bay, Bukti Pt., Rolling Pt., Shoal Pt. and the Back Bay sites. Dense tube mats of infaunal invertebrates were sampled with diver-held cores (0.0075 m^2) to a depth of 15 cm at the unexploited sites in Back Bay (5m and 10m). Samples were screened through 0.5 mm mesh and fixed in 10% formalin in the field. Later they were switched to 95% ethanol, sorted to species, counted and wet weight recorded.

Sea otters also exposed old, buried shells during excavation. These shells were counted in 15, one meter square quadrat pairs at Bukti Point: one quadrat was placed over a single pit and the other placed 2 m from the same pit. Divers also categorized the attachment substrate (cracked shell, unbroken shell, or rock) of all kelps encountered on one dive, and counted the number of kelp plants in 13 one meter square quadrats at Bukti Point. The attachment substratum (shell or rock) and the density of the anemone *Metridium senile* was sampled along 6 transects (10x2m) at Laida Rocks.

RESULTS

Sea Otter Movements

Sea otters were observed in small numbers in Raspberry Strait and Kupreanof Strait in the mid 1970's (Schneider, 1978). The number of animals remained high in numbers in both areas through the 1970's and 1980's. Many animals were present in Kupreanof Strait during our visit. Only about 50 individuals were observed during our visit (Table 1). Hundreds of individuals were observed feeding and rafting in Selief Bay as late as 1984, but have not been observed by local residents since then. Coincident with the decline in Raspberry Strait, the numbers of feeding and rafting animals increased markedly in Afognak Strait in 1985 and 1986 (Simon-Jackson et al., 1986, USFWS unpubl.), where they rapidly depleted beds of intertidal clams used by local residents. The general pattern of sea otter movement through the study area is shown by the large arrows in Figure 1 (also see Table 1).

The movements and feeding activities of otters indicate several types of feeding grounds in the study area. Selief Bay was heavily used by otters in the past, but is not used today. Bukti Point, Laida Rocks, Naugolka Point, and Rolling Point were heavily used by otters in the past and many otters still forage there today. Rolling Point was probably the most recently exploited of the old feeding grounds (Table 1). All the above sites are called old feeding grounds because they were heavily exploited by otters in past years. In contrast, Shoal Point was used heavily by otters only in the last 1-2 years. The Back Bay sites were relatively unexploited by sea otters, but are within the Afognak Strait foraging front where there were several hundred otters, primarily males, foraging on benthic prey (Tables 1 and 2).

Live Prey

Saxidomus giganteus accounted for 81% of the clam biomass throughout the study area (Table 3). Its biomass and average size was greatest in the relatively unexploited feeding grounds in the Back Bay area (Tables 3

and 4) (Kruskal-Wallis, p < .0001; SNK, p < .05). The biomass of clams was lowest at the four heavily exploited sites if the deep-burrowing *Tresus capax*, which was rarely consumed by otters (see Live vs Dead Record), was excluded from the data (Table 3)(Kruskal-Wallis, p < .0001; SNK p < .05). The number of clams was lowest at the oldest feeding grounds, Selief Bay, and highest in the unexploited Back Bay 10m feeding grounds (ANOVA, p < .0001; SNK, p < .05). Although living bivalve populations were not sampled at Laida Rocks and Naugolka Point, two old feeding grounds, qualitative observations of scuba divers revealed these sites to be similar to Bukti Point and Selief Bay, with relatively few siphons of large clams.

Qualitative observations by scuba divers indicated a positive relationship between the number of large clams and the quantitative biomass and size size values obtained via excavation (Tables 3 and 4). The siphons and siphon burrows of large *Saxidomus giganteus, Mya truncata* and *Tresus capax* were easily identified by divers.The siphons of *S. giganteus* were most conspicuous to divers in the Back Bay areas. Large *M. truncata* were most conspicuous at Back Bay 10m. The siphons of *T. capax* were most conspicuous at Rolling Point. We also found a dense bed of *T. capax* in Raspberry Strait just outside Selief Bay in 20 m of water (18.3 ± 3.94 SD siphons/ m^2; N=19).

Surface observations showed clams were the most frequent prey taken by sea otters at five sites, comprising 75% - 100% of the identified prey items observed.

Shell Record

Shells were collected from the sea floor to determine the species and sizes of prey eaten by otters. However, for the shell record to be used as a reliable indicator of the sea otter diet, otter predated shells must be distinguished from those of other mortality sources. Although many whole shells were clearly discarded by feeding otters (Table 5), some of these shells could be produced by other potential sources of prey mortality. Therefore, we present only the broken record as a conservative estimate of the foraging activities of sea otters (see Shell Record in the Discussion).

A significantly higher proportion of both the fresh and recent shells were broken by sea otters versus unbroken at all sites (Tables 5 and 6)(G = 52.236, DF = 1, p << .001). While this pattern varied between sites (G heterogeneity = 50.144, DF = 7, p << .001) at no location did whole shells out number otter broken shells (Tables 5 and 6). For this reason, none of our major findings are changed by including or excluding the whole shell record. Although the mean shell lengths of the recent unbroken record were generally smaller than those of the recent broken record (Table 6, ANOVA, p ≤ .001), this size difference disappears when only the fresh record is considered (Table 5, ANOVA, p = .747). The fresh record most accurately represents the sizes of shells broken and left whole by otters, because only otters discard shells with attached flesh.

There were two distinct patterns in the proportions of recent and old shells in the study area. First, there were no recent shells in Selief Bay, only old shells (Table 7). Hundreds of sea otters were observed in the bay as late as 1984 by local residents, and no large groups have been there since 1984 (Table 1). In contrast, there were no old shells at the deeper Back Bay site, only recent shells (Table 7). The proportion of recent and old shells were relatively similar at most of the other feeding ground, except the shallow Back Bay site,

which had a large proportion of old shells (Table 7). These shells may be quite old and periodically covered and uncovered by the gravel deposit there. This site appeared to have a highly mobile sediment.

The proportion of recent versus old shells and the species composition of clam prey was correlated with water depth at two sites (Table 8). Apparently, *Saxidomus giganteus* was first consumed in shallow water, where there was a high proportion of older shells (Chi^2 = 10.1, DF = 1, p < .01), and *Macoma secta* was later consumed in deeper water, where there was a high proportion of recent shells (Chi^2 = 54.02, DF = 1, p < .001). The depth pattern occurred at both Laida Rocks and Naugolka Point (Table 8).

Live vs Dead Record

A comparison of the size of live and fresh shells of *Saxidomus giganteus* indicates that sea otters select larger individuals (multi-way ANOVA, p < .0001) (Figure 2). We only located large numbers of fresh shells at two study sites. Fresh shells give the best benthic record of sea otter diet. No other local ecological process produces shells with remnants of fresh soft tissue attached to clam shells (see Discussion). In addition to the fresh shells, recent and old otter broken shells of *S. giganteus* are also larger than the shells of live clams (ANOVA, p < .0001)(Table 7).

Saxidomus giganteus was the most abundant large clam (Tables 3 and 4) and the most abundant sea otter prey in the study area (Figures 3 and 4, and see Table 2 for the bivalve fraction of the sea otter diet). This species accounted for 68 % of all the broken shells we collected (N=1032). This percentage was at times lower than the percentage of *S. giganteus* among the live clams (Table 7, Figures 3 and 4), because the live clams included many small individuals that were probably not common sea otter prey (Figure 2).

Comparison of live and dead records show *S. giganteus* was consumed by otters in proportion to the abundance of individuals of edible size (≥ 40 mm) at the three sites most recently occupied by otters; Rolling Pt., Shoal Pt. and the 5m Back Bay site (Chi^2 = .021, DF = 2, p > .95) (Figures 3 and 4). (Minimum edible size, >40mm, is the mean of the smallest *S. giganteus* found in the dead record at each site). However, this minimum size does not apply to all situations as we found scat samples with shell fragments of very small *Saxidomus* and *Macoma* spp. at Rolling Point, an old feeding grounds at which the average size of *Saxidomus* clams was smallest (Table 4).

Nevertheless, sea otters apparently reduced the numbers of *S. giganteus* at the older heavily exploited sites, such as Bukti Pt. and especially Selief Bay (Figure 3) where the proportions of live *Saxidomus* (≥ 40 mm) were less than those in the dead record (Chi^2 = 45.67, DF = 1, p ≤ .001). Although *Humilaria kennedeyi* of edible size was common at Bukti Point (Tables 3 and 4), it was rarely consumed by sea otters (Figure 3). At the deeper Back Bay area *S. giganteus* was supplanted by *Mya truncata* as the most numerous shell on the sea floor (Figure 4). This was the least exploited feeding ground, and the only one where *S. giganteus* was not the most abundant shell in the dead record.

Community Disturbance

Sea otters disturbed bottom communities by excavating clam prey and by discarding clam shells on the sediment surface. Discarded and exposed shells were colonized by a number of sessile organisms. Shells were the most common substrate for the large sea anemone, *Metridium senile*, and brown

algae, Laminariales, at two study sites (Table 9). *M. senile* was the dominant macrofauna at Laida Rocks, but without those individuals attached to shells (78%) it would be out numbered by the sea pen, *Ptilosarcus gurneyi*, which do not require hard substrata for anchorage.

Shells broken by otters accounted for over 30% of the algal colonized shells at Bukti Point, where 96% of the kelp was attached to shells (Table 9). Again, many of the unbroken shells probably were discarded by feeding otters (e.g., Table 5). Furthermore, because sea otters expose shells buried in the sediment while excavating infaunal prey, most of the shells were likely the direct or indirect result of sea otter foraging. At Bukti Pt. more shells (8.3 shells/m^2) were found associated with recent feeding pits than away from pits (0.9 shells/m^2) (paired t-test, N = 15, p < .0001).

This same pattern of algal enhancement by shell litter was qualitatively observed in even shallower water in the Shoal Pt. feeding grounds. However, unlike at Bukti Pt., green and brown algae attached to shells formed mats up to one meter thick on the sea floor. Fronds were so densely packed that circulation within the mat was sufficiently retarded to make the underlying water anoxic, indicated by a scum of bacterial ooze frequently found in the lower portions of the matted algae. This condition appeared to cause large *Saxidomus giganteus* found in the underlying sediments, to come to the surface, where they were observed gaping and dying on the sea floor, further increasing shell litter.

Sea otters made many pits as they excavated clam prey (Table 10). The density of pits was greatest at Shoal Point (ANOVA, p < .0001; SNK, p < .05), where we also observed the most recent pits and a group of about 400 rafting and feeding otters. Plumes of suspended sediment and turbid water occurred above and within these new pits. These recently made pits covered over 12% of the sea floor. The largest number of fresh shells was also collected at Shoal Point (Table 5 and Figure 2). Otter pit sizes were comparable at all sites (Table 10)(ANOVA, p = .12), and could easily be distinguished from *Pycnopodia* pits. The latter were also numerous but generally smaller and more circular with the excavated sediment evenly distributed in a ridge around the perimeter. Otter pits, however, were more elongate with the displaced sediment piled at one end of the long axis. The density of feeding pits indicated the feeding grounds with high levels of recent feeding activity (Figure 5).

Non-bivalve infaunal densities and biomass were also very high at sites relatively undisturbed by otter foraging. Both Back Bay areas were dominated by dense assemblages of polychaete worms, and overwhelmingly by tubiculous species, especially sabellids (Table 11). *Myxicola infundibulum* formed a nearly continuous cover at much of the 5m site, as did *Schizobranchia insignis* and *Potamilla occelata* at 10m. The tubes of the latter two species formed a thick (15-20 cm), spongy mat in which all the large bivalves were embedded. No large clams were found below the depth of the mat. Comparable densities of these same sabellid species were only observed at one other site, Shoal Pt., also within the recently exploited frontal area. However, due to the extensive substrate disturbance by otters (Table 10), rather than being a near continuous sheet of suspension feeders, the area was a mosaic of tube mat punctuated with nearly defaunated sea otter feeding pits. Divers saw no worm tubes or

feeding tentacles within these pits. Unfortunately, core samples from these pits were lost during shipping.

DISCUSSION

A Natural Experiment

There is a gradient in the movements and feeding activities of sea otters in soft sediment feeding grounds that corresponds with a gradient in the biomass of clam prey and the disturbance of bottom communities (Figure 5). The movements of otters through the study area around Kodiak Island were not quantified, but were observed by a number of local residents (Figure 1 and Table 1). There are no quantitative information on the structure of prey communities before sea otters moved into the study area. Therefore, the effects of otters on prey communities are inferred from the changes in prey communities along this known gradient of sea otter colonization and feeding.

The inference of temporal patterns from spatial gradients is confounded by site variations and unknown initial conditions. Nevertheless, this approach has provided an excellent impression of the community role of sea otters along rocky shores (Estes and Palmisano 1974, Dayton 1975, Estes et al. 1978, Simenstad et al. 1978). These general results were later verified in manipulative field experiments (Duggins 1980). Although there were know doubt some community differences in the pre-otter conditions of our study sites we believe the demonstrable similarities warrant the comparison. All sites were near-shore, soft sediment habitats where otters were observed to feed almost exclusively on large clams. In addition, the species assemblages of both the live bivalve communities and the otter predated shell records were similar and dominated by Saxidomus giganteus. The only exception to this species pattern were found at the ends of the gradient and can be explained by otter predation.

Our observations conform to the generalized view of sea otter expansion and prey exploitation. As an otter population increases, groups of male (fronts) establish themselves in prey rich regions at the population periphery (Wild and Ames 1974, Miller 1980, Garshelis et al. 1984, Jameson in review). Here they forage on the largest size classes of preferred prey (Hines and Pearse 1982). When these are depleted, progressively less desirable prey types are utilized (Ebert 1968, Vandevere 1969, Ostfeld 1982, Wild and Ames 1974, Estes et al. 1981), until the majority of the otter group moves on (Garshelis et al. 1984).

The structure of prey communities and the benthic feeding record in soft-sediment habitats show distinct differences between old feeding grounds, recently invaded feeding grounds and relatively unexploited sites. These differences are clearly related to the activities of sea otters, which provide the best explanation for the observed patterns. The lowest biomass of live clams, the oldest shell record, the largest difference between the size of live and discarded shells, and the fewest recent feeding pits were found in the old feeding ground at Selief Bay, where otters foraged heavily until 1984 but not since then. The highest biomass of live prey, a sparse shell record, the smallest difference between the size of live and discarded shells, and few feeding pits were found at the least exploited feeding grounds in the Back Bay area. Intermediate biomass, a well developed shell record with many recent shells, and many fresh feeding pits were found at sites where sea otters forage heavily today (Bukti, Rolling, and Shoal Points). Shoal Point was the most recently invaded of the heavily utilized feeding grounds. It had the largest number of

fresh shells and feeding pits. Our qualitative observations from other sites (e.g., Laida Rocks and Naugolka Point) conform to the same general patterns that were quantified at the main study sites.

Shell Record

The bivalve shell record discarded by otters gives an excellent impression of the foraging activities of sea otters in soft-sediment feeding grounds, but must be interpreted cautiously. To represent the prey species and sizes exploited by otters, several potentially confounding factors must be considered: 1) other significant otter prey species that do not leave durable records (e.g. fish), 2) additional sources of bivalve mortality (e.g. sea star predation), and 3) mechanisms by which older buried shells of unknown mortality are brought to the sediment surface (exposed while otters excavate infaunal prey). The first problem is unimportant; bivalves were the most important prey at our study sites around Kodiak Island. Divers found no other abundant prey species at any of the sites. Because otters are known to consume their prey at the sea surface, direct observations of feeding otters in the study area also confirmed that bivalves comprised 75% or more of the prey items consumed by otters (Table 2). In terms of biomass consumed by otters, the results would probably be even more dramatic as most non-bivalve food items were very small.

Sea star predation and exposure of old shells killed *in situ* can also be eliminated as confounding factors by presenting only the broken record as a conservative estimate of sea otter predation. Sea otters open large bivalve prey by either cracking the shell or prying the valves apart with their paws and teeth (Kvitek et al. in press), and as a result, produce both a broken and unbroken shell record. However, whereas otter predation is the only likely explanation for the broken shells, both exposure of buried shells and sea star predation contribute to the unbroken shell assemblage. We show that significant numbers of buried shells are unearthed by foraging otters. Many of these shells were whole and probably died *in situ* from unknown causes. *Pycnopodia helianthoides* also contribute shells of all sizes and species to the unbroken record. These predatory stars, the only other major consumers of bivalves at the study sites, were frequently observed eating clams of all available size classes and discarding clean (no remnant tissue), unbroken shells. Although many whole shells were clearly discarded by feeding otters (Table 5), by using only the broken shell record as an estimate of sea otter foraging activities, our results do not contain other sources of prey mortality.

None of our major findings are changed by including or excluding the whole shell record. This is because a significantly higher proportion of the shells were clearly broken by sea otters when recent and fresh collections at all sites are compared, and at no location did whole shells out number otter broken shells. Although the mean shell lengths of the recent unbroken record are generally smaller than those of the recent broken record, this is likely due to the inclusion of shells discarded by *Pycnopodia*. Divers often observed these stars eating several very small clams (< 40 mm) at once. Furthermore, this size discrepancy is not found in the fresh record, the most accurate reflection of the sizes of shells broken and left whole by otters. For the above reasons, we believe the broken shell record is the best indicator of spatial changes in sea otter foraging patterns at the study sites. The problems with sampling and

interpreting the benthic feeding record have been previously discussed for walruses (Oliver et al. 1983) and sea otters (Kvitek et al. in press).

Prey Preferences and Predation Effects

Based on the shell record, large individuals of *Saxidomus giganteus* are the preferred clam prey. This was the major prey species at all the heavily utilized feeding grounds and was generally consumed in proportion to its abundance (Figures 3 and 4) and biomass (Table 3). The fresh shells at both Rolling and Shoal Points were significantly larger than the live shells (Figure 2), indicating otters were selecting larger individuals ($\geq$ 40 cm). In addition, the size of discarded shells was significantly larger than the live *S. giganteus* at all the heavily exploited feeding grounds (Table 7).

Heavy sea otter feeding appeared to have a dramatic impact on prey populations. The biomass of prey was lowest where the feeding activities of otters was known to be highest (old feeding grounds and Shoal Point), and was highest at the least exploited feeding grounds in the Back Bay area (Table 3, Figure 6). These unexploited sites also had the smallest difference between the size of live and discarded shells, suggesting that relatively sparse feeding had not caused a change in the size of prey which had apparently occurred at the heavily utilized feeding grounds (Table 7).

Comparison of the live and dead records also shows that not all prey were selected in proportion to there density or biomass. This was true of *Humilaria kennerleyi* at Bukti Pt. and *Tresus capax* at Rolling Pt., suggesting a component of prey preference in addition to size and abundance. It is not clear why otters should avoid *H. kennerleyi* other than it is found in the presence of a larger and more abundant prey, *Saxidomus*. In Elkhorn Slough of central California, the burrowing piddock, *Zirphaea pilsbury*, is found in a large (0.1 km2) dense (>50/.25m^2) unexploited patch bounded on either side by less dense populations of *Saxidomus nuttalli* (2-5/.25m^2) preyed on by sea otters (Kvitek and Anderson, unpublished data)Within this patch, *Z. pilsbury*, although smaller than *S. nuttalli*, is vastly more abundant, represents much higher biomass and is far more easily excavated (the sediment is fine, unconsolidated silt versus the hard, shell, gravel and clay matrix the *Saxidomus* are embedded in). Yet there is no evidence the otters ever feed on *Zirphaea*. It may be an unpleasant taste, or the presence of a larger more widely distributed prey that protects some bivalves from otters. Or perhaps in the case of *Zirphaea*, the otter's unwillingness to dig in a messy and smelly sediment that may foul and degrade the thermal protection of its coat. This latter consideration is not relevant to *Humilaria* since at Bukti Pt. it co-occurs with *S. giganteus*.

Tresus capax, however, which accounted for as much biomass as *Saxidomus* at Rolling Pt., apparently has a depth refuge from sea otter predation around Kodiak Island. *Tresus* was the deepest burrowing bivalve prey in the study area and therefore the most difficult to excavate. It was the only large, deep burrowing clam occurring in relatively high numbers in the heavily utilized feeding grounds. The densest patch was found outside Selief Bay in Raspberry Strait, where large numbers of otters fed for over 10 years. Discarded shells of *T. capax* were also rare, indicating little otter predation on this species. In contrast, we located no dense patches of live *Saxidomus giganteus* and many discarded shells of this major prey throughout Raspberry Strait and in Selief Bay (e.g. Table 7). Kvitek et al. (in press) documented a similar refuge

from otter predation for deep-burrowing bivalves in California. There the refuge was mediated by an otter foraging strategy which maximized the biomass obtained per volume of sediment excavated. Otters preferred a patch of smaller individuals restricted to a relatively shallow burrow, over an adjacent patch of the same but more abundant species, which contained larger but more deeply buried individuals. Similarly, it may not be efficient for otters to excavate the deepest bivalves around Kodiak Is. as long as there are other suitable prey.

This depth refuge may be particularly important for the *Tresus capax* in our study site. Its protruding and hard tipped siphon make it much more conspicuous than the flush siphon of *Saxidomus giganteus* , and otters foraging either visually or by touch should find *Tresus* easily.

Comparison of the live and dead *Mya* spp. shell record at the Back Bay 10m site suggests that a more conspicuous siphon can place an otherwise rare but large and accessible species at risk. At this site, all bivalves were found within the 20cm thick sabellid worm tube mat and therefore all equally accessible. However, although large, live Mya were very rare in this essentially unexploited area (Tables 3 and 4), they made up the majority of the dead record which was composed of only recent shells (mean size = 70 ± 7 mm) (Figure 4). Furthermore, this was the only site where the proportion of *Saxidomus* in the shell record was significantly less than in the live record (Figure 4), suggesting an early preference for a rare but large, conspicuous and accessible prey. Hines and Loughlin (1980) proposed a similar pattern of predation in Monterey Harbor, California where, after ten years of otter occupancy, the once high *Tresus nuttallii* densities had been reduced to only 5% of the *Saxidomus nuttalli* numbers despite the two species being found at deep but similar sediment depths (to 50cm). Six years later, Kvitek and Oliver (in press) resurveyed the area and found both species to be rare.

Foraging Site Preferences

Our quantitative and qualitative observations suggest that otters prefer to forage in shallow water and move into deeper waters when shallow-water prey are heavily exploited. This pattern was quantified at Laida Rocks and Naugolka Point where *Saxidomus giganteus* was consumed first in shallow water (20m), and *Macoma secta* was later consumed in deeper (30m) water (Table 9). Our qualitative observations in Afognak Strait indicate that otters primarily exploited the intertidal and very shallow (several meters) subtidal feeding grounds and had not feed heavily in the slightly deeper and offshore sites, such as the 10m Bay Bay area. Here the major prey was *S. giganteus* at all depths.

Current speed may be a more important factor than water depth in determining foraging site selection within the frontal area. Although differences in water depth between these sites are slight, current speeds vary greatly. The 10m Back Bay site, which was surveyed extensively by towed divers, was dominated by a bivalve rich, polychaete tube mat extending down the long axis of the main channel for many hundreds of meters. This central channel was characterized by extremely strong tidal currents (5-8 kts, Walt Cunningham, pers. com.) which may effectively discourage otter foraging, and explain why this was the richest but least exploited study site.

Community Disturbance

Sea otter foraging disturbance affects the ecology of soft-sediment feeding grounds via the addition of hard substrata and excavation of the

sedimentary habitat. While foraging on bivalve prey, otters expose high numbers of shells buried in the sediment and also discard the shells of their prey. This process creates hard substrate on an otherwise soft bottom, and increases the abundance of otherwise rare species that attach to shells. At water depths below the photic zone at Laida Rocks, the shell substrate enabled the anemone *Metridium senile* to become the dominant macrofauna, outnumbering the sea pen, *Ptilosarcus gurneyi*, which do not require hard substrata for anchorage. In shallower water at Butki Pt., 98% of kelps were also found attached to shells.

We observed the potential destruction of clam beds by the development of a dense algal canopy at Shoal Pt. Algae attached to shells and formed such dense mats on the sea floor that circulation was reduced and anoxic conditions developed. As a result,*Saxidomus giganteus* were found dead or nearly dead at the sediment surface, further increasing shell litter. If this interpretation is correct, the foraging activities of sea otters may produce the dynamic mosaic of clam beds and algal patches encountered throughout the study area.

Sea otters must displace large numbers of other infaunal species while excavating bivalve prey. Over 12% of the sea floor was disturbed by otter foraging at Shoal Pt., the site exposed to the greatest feeding intensity during our study. This level of disturbance is of comparable intensity to that caused by two other benthic feeding marine mammals also know to greatly influence their prey communities, gray whales (Johnson and Nelson, 1984; Oliver and Kvitek, 1984; Oliver and Slattery 1985; Kvitek and Oliver 1986) and walrus (Oliver et al. 1985; Kvitek et al. in prep).

Because otters must excavate sediment to the depth of their prey, the dense, infaunal communities in the frontal area (Table 11) may not persist under heavy sea otter predation. Much of the Back Bay sites were carpeted with dense sabellid worm mats, which otters, like divers, would have to rip up to obtain the embedded clams. Woodin (1978) found other polychaete assemblages to be highly susceptible to substrate disturbance as a result of crab foraging (*Limulus* and *Callinectes*). If otters begin feeding at the Back Bay sites, they will displace the non-bivalve species which represent as much biomass as the embedded bivalve prey (Tables 3 and 11). Although no pits were available to sample in the Back Bay 10m area, qualitative observations of the five pits found at the 5m site indicated complete removal of the tube mat within otter excavations. No tube mates of any kind were observed at the older heavily exploited sites. It seems unlikely that infaunal communities found in the frontal areas, characterized by high densities of relatively long-lived, sessile polychaetes, will persist in the presence of heavy otter excavation.

Sea otters may facilitate the death of many other infauna by increasing the foraging efficiency of the sea star, *Pycnopodia helianthoides*. These "formidable engines of destruction" (Ricketts et al. 1986) were frequently observed excavating prey within previously dug otter pits. *Pycnopodia* excavate infaunal prey by sweeping away sediment with their arms and tube feet (personal observation). This predation is impeded by the presence of dense polychaete worm tubes (e.g., Woodin 1978, personal observations). Although *Pycnopodia* roamed over the tube mats at all three frontal sites, their feeding was confined almost exclusively to the edges of the mat or to the exposed edges of otter pits. At one pit edge, we found a *Pycnopodia* with 12

clams on its tube feet. *Pycnopodia* also responded quickly to diver-made excavations, approaching and feeding on the exposed tube mat. VanBlaricom (1982) documented a similar commensal behavior between foraging rays and surf perch. The digging activities of rays made burrowing amphipods available to perch, which rarely consumed these prey in the absence of rays.

In summary, sea otters appear to have a dramatic impact on the biomass and size patterns of their major bivalve prey. They may also destroy dense communities of tube-building infauna during the excavation of prey, help to develop algal reefs that may clog clam beds, and allow sea stars to prey on many animals that are usually unavailable to them.

ACKNOWLEDGEMENTS

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Table 1. Sea otter invasion chronology and present population status for the Kodiak Archipelago study areas.

Location	year Invaded	maximum number observed since invasion		Information source	1986 maximum Ind	present population status 1986
		ind	yr			
Old Feeding Grounds						
Raspberry Strait (heavy feeding)	mid 1970's	350	1980	Schauf pers. comm., Schneider 1976	~50	females, pups, reproductive males
Selief Bay (heavy feeding)	mid 1970's	low hundreds	1983	Grucheu, pers. comm.	0	
Bukti Point (heavy feeding)	mid 1970's	?	?	Schneider, 1976; Cunningham pers. comm. Stanford pers. comm.	95	females, pups, reproductive males
Rolling Point (heavy feeding)	mid-late 1970's	?	?	U.S. Fish & Wildlife Service, unpublished	~25	males
Naugolka Point	mid-late 1970's	?	?	U.S. Fish & Wildlife Service, unpublished	~75	males
Laida Rocks	mid 1970's	?	?	U.S. Fish & Wildlife Service, unpublished	~50	females, pups, reproductive males
Frontal Area						
Shoal Point (heavy feeding)	1983-84[1]	400	1986	Shepard pers. comm. U.S. Fish & Wildlife Service, unpublished	400	males
Back Bay 5m (intermittent feeding)	1983-84			Shepard pers. comm.	few[2]	
Back Bay 10m (rare feeding)	1983-84			Shepard pers. comm.	few	

[1] occasionally present in small numbers at least since mid 1970's

[2] presence in Back Bay sometimes related to strong easterly winds

Table 2. Sea otter diet at Kodiak Archipelago study sites based on direct observations of feeding otters.

Location	clam	limpet or chiton	crab	mussel	urchin	fish	other	N
Prey Observed Eaten By Sea Otters percent of identified items								
Old Feeding Grounds								
Buktl Point (heavy feeding)	74.3%	6.6%	2.0%		6.1%		11.0%[1]	393
Rolling Point (heavey feeding)	100.0%							89
Naugolka Point	77.6%	19.0%					3.4%	58
Bare Island	95.8%		2.1%		1.1%	1.1%		95
Frontal Area								
Shoal Point (heavey feeding)	92.1%	1.2%	1.2%	5.5%				254

[1] mostly small gastropd snails

Table 3. Biomass and number of individuals of the common bivalve prey found at six sites around the Kodiak Archipelago. Old feeding grounds were heavily exploited by otters in the past, and Selief Bay no longer had otters present in 1986. The frontal areas were recently exploited by otters either heavily, intermittently or rarely. Mean grams or individuals per .25 m^2 (standard deviation). N = 10 replicate samples per site, except Rolling Pt. (N = 8).

			Major Bivalve Prey Species											
			Saxidomus giganteus		Macoma spp.[1]		Mya spp.[2]		Humilaria kennerleyi		Protothaca staminea		Tresus capax	
Location	Total Bivalves													
	gms	Ind	gms	Ind	gms	Ind	gms	Ind	gms	Ind	gms	Ind	gms	Ind
Old Feeding Grounds														
Selief Bay (heavy feeding)	86 (93)	5 (4.9)	14 (35)	1 (1.9)	35 (50)	2 (3.3)	33 (41.7)	2 (2.1)	0 (0)	0 (0)	0 (0)	0 (0)	2 (7)	<1 (<1)
Bukti Point (heavy feeding)	110 (56)	7 (3.3)	85 (69)	4 (2.0)	0 (0)	0 (0)	5 (14.5)	0.2 (.4)	17 (16.0)	3 (2.5)	0 (0)	0 (0)	0 (0)	0 (0)
Rolling Point (heavy feeding)	277 (93)	18 (15)	127 (81)	14 (12)	0 (0)	0 (0)	2 (4)	1 (2)	0 (0)	0 (0)	3 (3)	2 (4)	146 (136)	1 (1)
Frontal Area														
Shoal Point (heavy feeding)	137 (89)	8 (2.7)	123 (88)	5 (2.3)	0 (0)	0 (0)	4 (4.5)	1 (1.1)	0 (0)	0 (0)	3 (5.9)	0.6 (1)	7 (22)	<1 (<1)
Back Bay 5m (intermittent feeding)	562 (235)	11 (4)	558 (232)	10 (3.6)	0 (0)	0 (0)	3 (7.9)	0.1 (.3)	0 (0)	0 (0)	2 (3.9)	0.2 (.4)	0 (0)	0 (0)
Back Bay 10m (rare feeding)	632 (146)	46 (22)	562 (156)	19 (6.8)	13 (22.3)	23 (17.5)	14 (10.5)	1 (.7)	9 (16.2)	0.3 (.5)	23 (20.0)	3 (3.1)	0 (0)	0 (0)

[1] *Macoma nasuta, Macoma secta, Macoma balthica*

[2] *Mya truncata, Mya arenaria*

Table 4. Shell lengths of the live, common bivalve prey found at the six study sites listed in Table 2. Mean shell lengths given in mm (standard deviation).

Location	Mean Shell Lengths of Live Bivalve Prey Species					
	Saxidomus giganteus mm	Macoma spp.[1] mm	Mya spp.[2] mm	Humilaria kennerleyi mm	Protothaca staminea mm	Tresus capax mm
Old Feeding Grounds						
Selief Bay	49	59	66	0	0	58
(heavy feeding)	(12.6)	(12.0)	(12.3)	(0)	(0)	
N	8	22	17	0	0	1
Bukti Point	54	0	55	43	30	0
(heavy feeding)	(18.0)	(0)	(43.1)	(8.4)		
N	39	0	2	27	1	0
Rolling Point	36	20	27	0	20	116
(heavy feeding)	(17.2)	(4.7)	(9.9)	(0)	(12.8)	(12.5)
N	110	6	7	0	16	6
Frontal Area						
Shoal Point	59	22	33	0	35	93
(heavy feeding)	(15.8)	(4.4)	(13.0)		(10.9)	
N	54	6	10	0	6	1
Back Bay 5m	80	0	86	0	41	19
(intermittent feeding)	(15.5)				(10.6)	
N	104	0	1	0	2	1
Back Bay 10m	66	27	56	76	37	0
(rare feeding)	(14.2)	(5.7)	(10.6)	(10.0)	(8.9)	(0)
N	186	228	9	3	28	0

[1] Macoma nasuta, Macoma secta, Macoma balthica

[2] Mya truncata, Mya arenaria

Table 5. The shell record composition of freshly eaten *Saxidomus giganteus* from two sites around Kodiak Island where sea otters were feeding and discarding shells. Proportions and mean sizes (standard deviations) are given for broken and unbroken shells with remnant tissues attached.

| | Fresh *Saxidomus giganteus* Shell Record | | | | |
| | Broken Shells | | Whole Shells | | |
Location	percent of shell record	shell length mm	percent of shell record	shell length mm	N
Rolling Pt.	52%	61	48%	63	50
(SD)		(13.7)		(11.7)	
Shoal Pt.	91%	75	9%	75	90
(SD)		(13.2)		(12.5)	

Table 6. The shell record composition of recently eaten *Saxidomus giganteus* from six sea otter feeding grounds around Kodiak Island. Proportions and mean shell lengths (standard deviations) are given for broken and unbroken shells in good condition with no fouling organisms attached.

	Recent *Saxidomus giganteus* Shell Record				
	Broken Shells		Whole Shells		
Location	percent of shell record	shell length mm	percent of shell record	shell length mm	N
Old Feeding Grounds					
Bukti Pt.	63%	72	37%	59	120
(heavy feeding)		(12.3)		(11.8)	
Rolling Pt.	70%	68	30%	60	86
(heavy feeding)		(10.1)		(14.0)	
[1]Naugolka Pt.	51%	73	49%	67	92
		(11.5)		(12.6)	
Frontal Area					
Shoal Pt.	79%	72	21%	56	24
(heavy feeding)		(13.9)		(12.1)	
Back Bay 5m	57%	75	43%	32	14
(intermittent feeding)		(24.1)		(7.2)	
Back Bay 10m	52%	77	48%	84	29
(rare feeding)		(12.7)		(9.2)	

[1] There was no recent shell record at Selief Bay and no live clams were sampled at Naugolka Pt., only shell record.

Table 7. The live shells and otter broken record of recent and old *Saxidomus giganteus* shells from six sea otter feeding grounds around Kodiak Island. Proportions and mean shell lengths (standard deviations) are given for recent (those in good condition with no fouling organisms attached) and old (worn and fouled) shells.

	Live and Otter Broken *Saxidomus giganteus* Shell Record							
	Live Record			**Recent Shells**		**Old Shells**		
Location	percent of live record	shell length mm	N	percent of *S. giganteus* shell record	shell length mm	percent of *S. giganteus* shell record	shell length mm	N
Old Feeding Grounds								
Sellef	16%	49	50	0%	0	100%	81	108
(heavy feeding)		(13)			(0)		(18.4)	
Bukti Pt.	53%	54	74	42%	72	58%	73	180
(heavy feeding)		(18)			(12.3)		(11.1)	
Rolling Pt.	75%	36	146	31%	68	69%	71	195
(heavy feeding)		(17)			(10.1)		(8.6)	
Frontal Area								
Shoal Pt.	70%	59	75	56%	72	44%	75	34
(heavy feeding)		(16)			(13.9)		(14.9)	
Back Bay 5m	95%	80	110	5%	75	95%	86	171
(intermittent feeding)		(16)			(24.1)		(8.1)	
Back Bay 10m	40%	66	462	100%	77	0%	0	15
(rare feeding)		(14)			(12.7)		(0)	

Table 8. Composition by age and major prey species of the otter predated shell record found in shallow (20m) and deep (30m) water at two feeding sites on Kodiak Island.

Location	Otter Cracked Shell record				
	Shell Record Age		Major Prey Species		
	Recent percent of shell record	Old percent of shell record	*Saxidomus giganteus* percent of shell record	*Macoma secta* percent of shell record	N
Laida Rks					
shallow	29%	71%	81%	0%	27
deep	76%	24%	3%	94%	63
Naugolka					
shallow	58%	42%	90%	3%	69
deep	95%	5%	11%	82%	168

Table 9. Percentages of laminarian kelps and *Metridium senile* anemones found on shells and rocks at two soft sediment foraging sites. The density per square meter of shells with algae and sea anemones is also shown as mean and (standard deviation).

| Species Location | Attachment Substrates | | | | | Abundance | |
| | Shells | | | Rocks | N | | |
	otter cracked	unbroken	total shells			no./m^2	N
Laminariales Bukti Point	32%	64%	(96%)	4%	174	3.6(2.43)	13
Metridium senile Laida Rocks			78%	22%	37	0.3(0.11)	6

Table 10 Sea otter feeding excavation at six sites around Kodiak Island. Means and (standard deviations) based on sample sizes of N. No evidence of recent otter foraging was found at either Selief or the 10m Back Bay site.

	Sea Otter Feeding Excavations		
Location	Pit Density pits/20m²	Pit Size m²	Percent Area Disturbed
Old Feeding Grounds			
Selief (heavy feeding)	0	0	0
Bukti Pt. (heavy feeding) N	1.6 (1.92) 8	0.16 (0.078) 13	1.3% (1.75) 8
Rolling Pt. (heavy feeding) N	6.5 (1.0) 4	0.20 (0.120) 26	2.2% (0.83) 4
Frontal Area			
Shoal Pt. (heavy feeding) N	14.2 (4.34) 10	0.18 (0.103) 142	12.5% (4.79) 10
Back Bay (5m) (interminttent feeding) N	0.5 (0.53) 10	0.13 (0.0) 5	0.3% (0.33) 10
Back Bay (10m) (rare feeding)	0	0	0

Table 11. Biomass and number of individuals of the non-bivalve infauna found at two sites within the frontal feeding area at Kodiak Island. Mean grams and individuals per .25 m^2 (standard deviation). N = 6 replicate samples per site.

					Non-Bivalve Infauna							
			Sabellid		other tubiculous		errant				other	
Location	**Total Infauna**		polychaetes		polychaetes[1]		polychaetes[2]		Crustaceans		groups[3]	
	gms	Ind	gms	Ind	gms	Ind	gms	Ind	gms	Ind	gms	Ind
Back Bay 5m[4]	82.2	9388	52.7	5658	16.7	1917	9.9	562	1.4	1097	1.6	188
	(34.2)	(3771)	(32.0)	(3347)	(14.0)	(1175)	(6.8)	(163)	(0.9)	(496)	(2.1)	(148)
Back Bay 10m[5]	655	23992	532.5	13223	72.5	5248	32.6	2505	9.8	1663	8.0	698
	(67.6)	(3940)	(113.9)	(2570)	(40.0)	(2058)	(9.2)	(623)	(5.6)	(416)	(7.2)	(612)

[1] ampharetids, owenids, cirratulids, maldanids
[2] philadocids, sylids, mephtids, glycerids, ophelids
[3] sipunculid worms, nemertean worms, echiuroid worms
[4] dominant sabellid species: *Myxicola infundibulum*
[5] dominant sabellid species: *Schixobranchia insignis* and *Potamilla occelata*

Figure 1. Map of the Kodiak Island study area showing the old, recent and unexploited feeding grounds and the general location of the active foraging front around Afognak Strait. The arrows indicate the general movement of the sea otter population into this part of Kodiak Island.
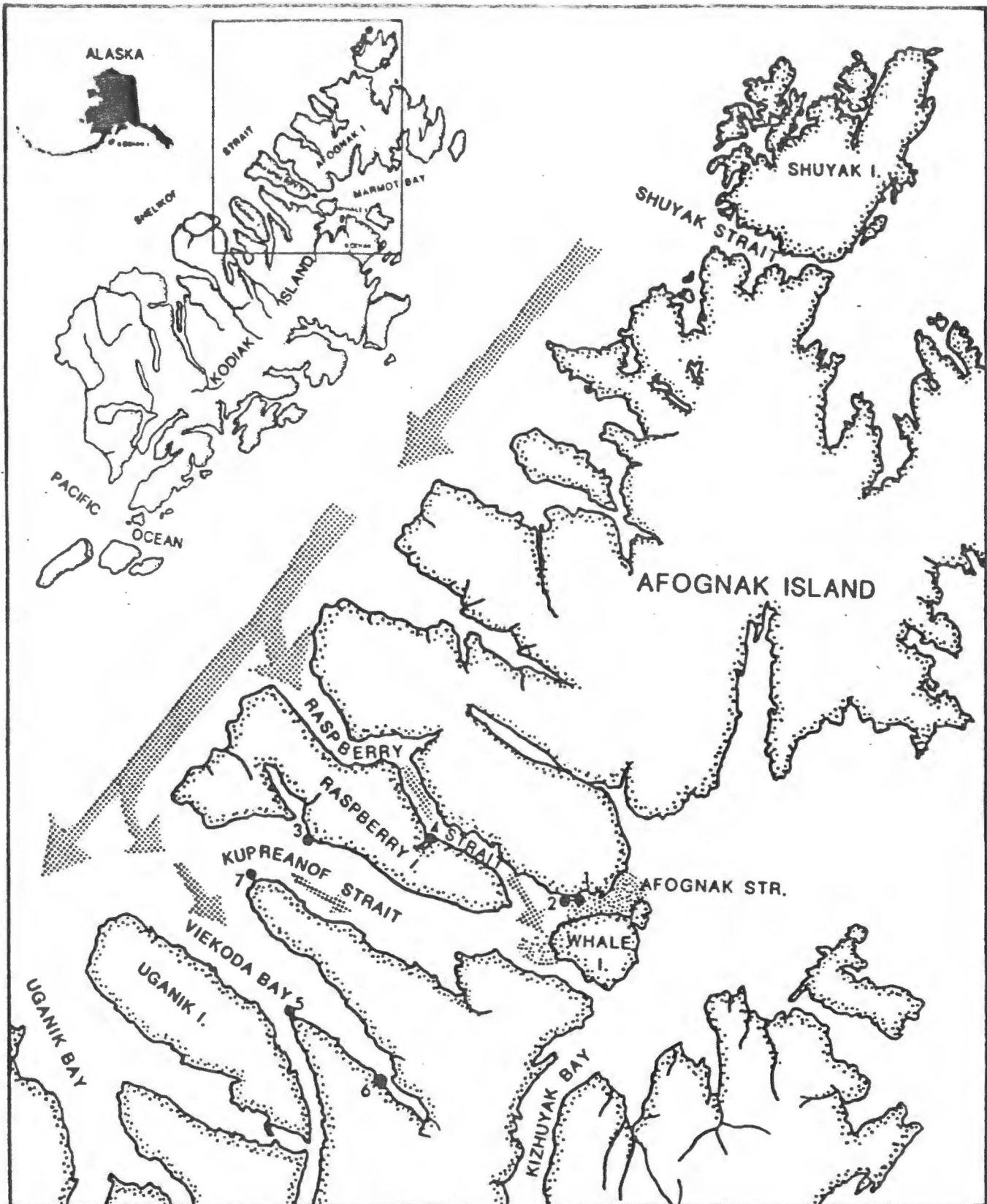
1. BACK BAY 2. SHOAL PT. 3. BUKTI PT. 4. SELIEF BAY 5. NAUGOLKA 6. ROLLING PT.
7. LAIDA RKS

▨ SEA OTTER EXPANSION ▨ OTTER FRONT
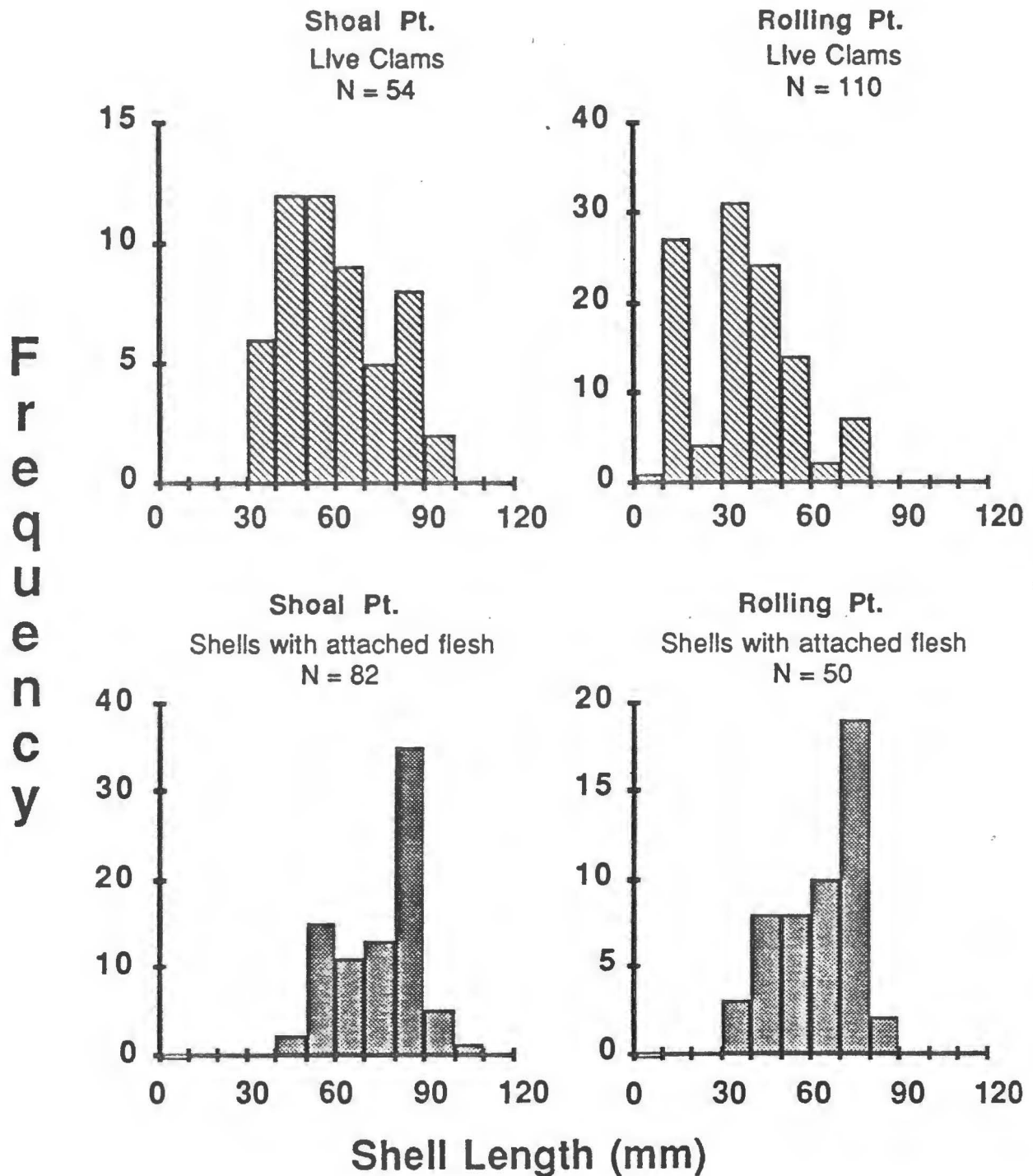
Saxidomus giganteus Shell Records

Figure 2. Size distribution of live and freshly otter predated <u>Saxidomus giganteus</u> clams at two sites where sea otters were observed eating bivalves and discarding shells. Clams freshly killed by sea otters still had attached adductor muscle tissure.

Old Feeding Grounds

Available Prey and Otter Broken Shell Record
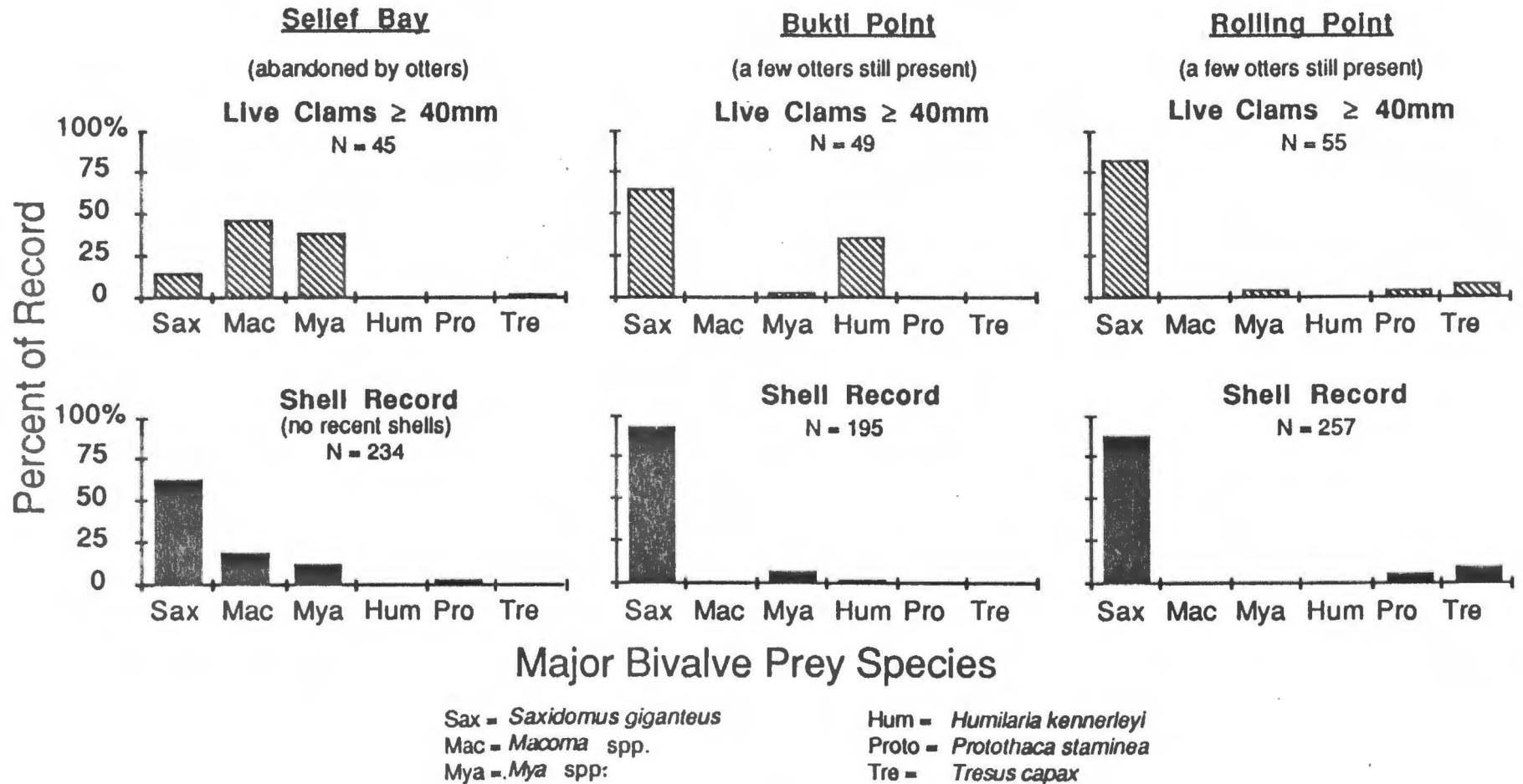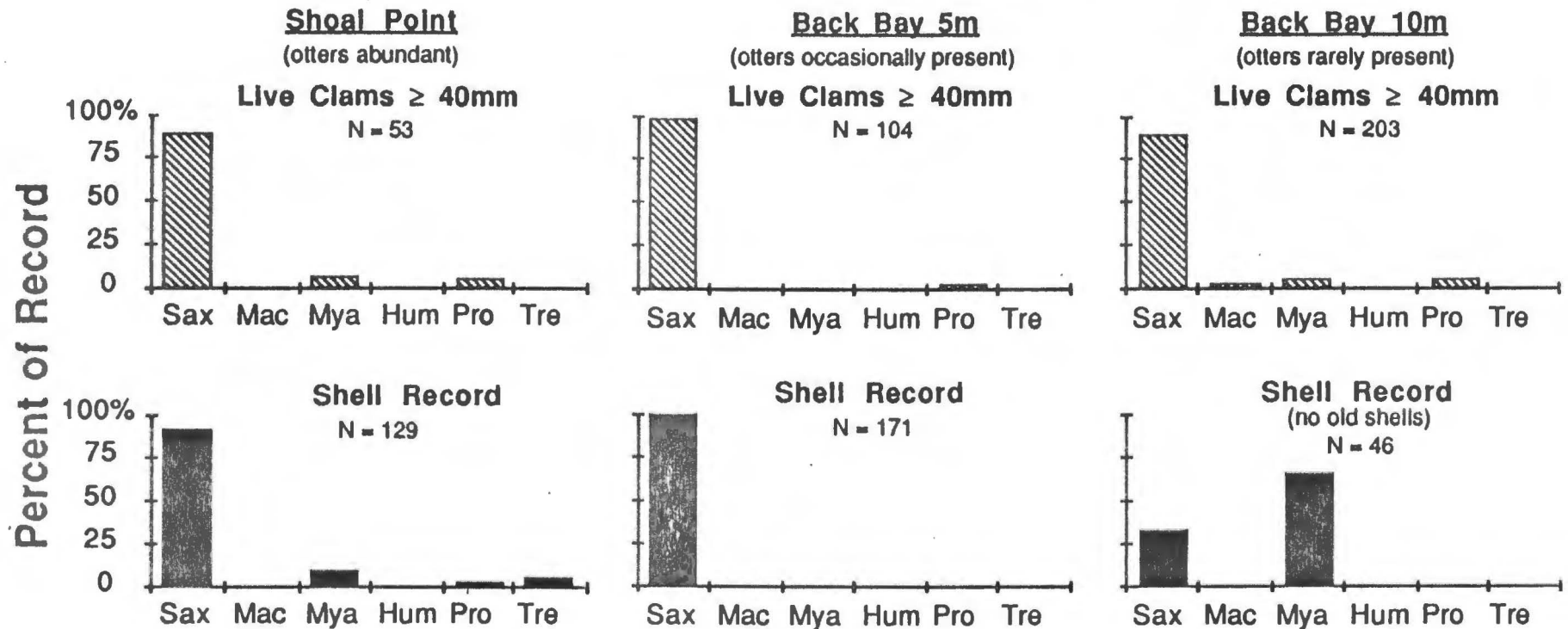
Species composition by percent

Figure 3. Species composition by percent of the available live bivalve prey and otter borken shell records found at three old feeding grounds that had been heavily exploited by otters in the past. Sea otters were still present at Bukti and Rolling Point, but had not used Selief Bay for several years.

Frontal Area

Available Prey and Otter Broken Shell Record

Species composition by percent

Shoal Point
(otters abundant)

Back Bay 5m
(otters occasionally present)

Back Bay 10m
(otters rarely present)

Live Clams ≥ 40mm   N = 53

Live Clams ≥ 40mm   N = 104

Live Clams ≥ 40mm   N = 203

Shell Record   N = 129

Shell Record   N = 171

Shell Record
(no old shells)   N = 46

Sax Mac Mya Hum Pro Tre

Major Bivalve Prey Species

Sax = *Saxidomus giganteus*
Mac = *Macoma* spp.
Mya = *Mya* spp.

Hum = *Humilaria kennerleyi*
Proto = *Protothaca staminea*
Tre = *Tresus capax*

Figure 4. Species composition by percent of the available live bivalve prey and otter borken shell records found at three sites in the Afognak Strait frontal area. Otters were abundant at Shoal Point but only occasionally and rarely at the Back Bay 5m and 10m sites respectively.
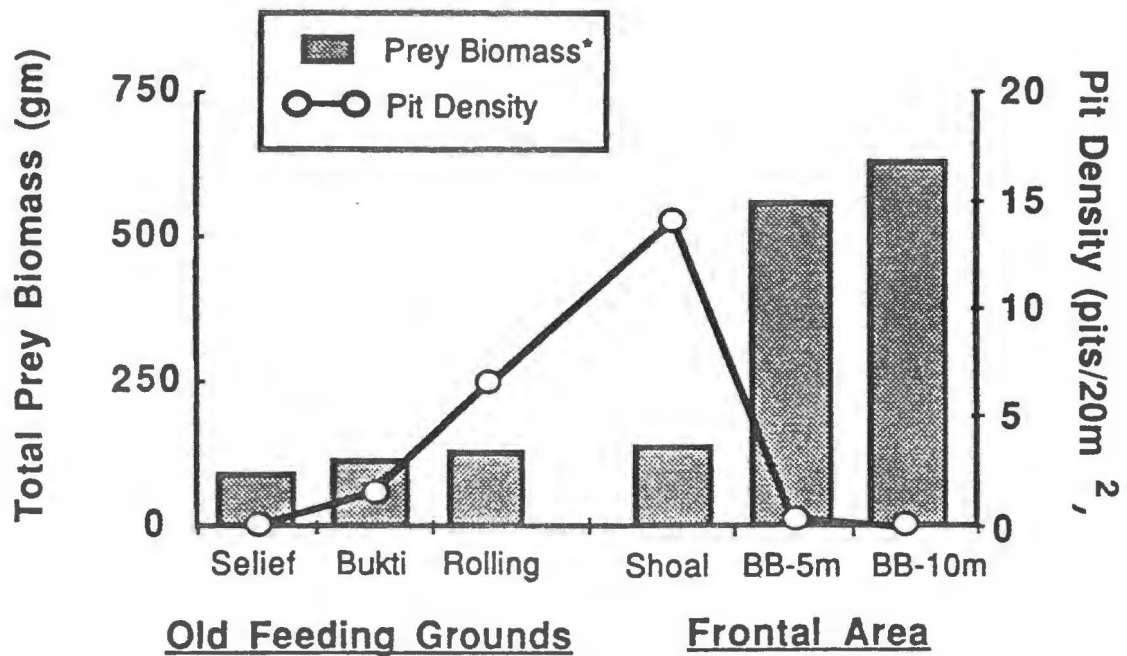
Figure 5. Comparison of available bivalve prey biomass and sea otter feeding intensity (number of foraging pits per 20 square meters) along a gradient of otter occupancy. Biomass is highest at least exploited sites.