

Sea otters versus sea stars as major clam predators: evidence from foraging pits and shell litter

Sarah B. Traiger^{1,*}, Brenda Konar¹, Angela Doroff², Lauren McCaslin²

¹University of Alaska Fairbanks, Fairbanks, AK 99775, USA

²Kachemak Bay National Estuarine Research Reserve, Alaska Center for Conservation Science, University of Alaska, Homer, AK 99603, USA

ABSTRACT: Sea otters *Enhydra lutris* and sea stars both excavate clams and leave behind foraging pits. If the source of pits can be determined with confidence, they may provide information about benthic foragers without direct foraging observations. Our objectives were to determine (1) if pits can be attributed to either predator (sea otters or sea stars) using pit dimensions; (2) how pit shape changes over time; and (3) whether shell litter can be used to distinguish the relative clam predation by sea otters and sea stars. Naturally occurring pits were tagged and measured at 4 subtidal and 2 intertidal sites in Kachemak Bay, Alaska, USA, every 2 wk from May to August 2014. To determine how pit dimensions change over time, experimental sea otter and sea star pits matching published descriptions were dug at each site and measured after 2 wk. Additionally, we collected and analyzed shell litter at each site to determine the source of their mortality. Cluster analysis on pit dimensions showed that none of the measured parameters could identify pit source for the 109 pits measured. Consistent with this finding, the experimental pit types were indistinguishable after 2 wk. In contrast, shell litter proved useful in quantifying predator-specific predation. Consumption of clams by sea otters and sea stars was equal at all but one site. Only 2.4 % of overall clam predation was attributed to other predators besides sea otters or sea stars. The significant sea star predation should be taken into account when making policy decisions concerning shellfish harvests and sea otter population management.

KEY WORDS: *Enhydra lutris* · *Pycnopodia helianthoides* · Clams · Foraging pits

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INTRODUCTION

Sea otters *Enhydra lutris* and sea stars both excavate clams in the low intertidal and shallow subtidal zones (Smith 1961, Calkins 1978, Kvitek et al. 1992), which can impact clam fisheries and soft and mixed substrate habitat dynamics (Kvitek et al. 1992, Ross et al. 2002). In habitats with unconsolidated benthic substrate in Alaska, USA, clams comprise 71 to 100 % of sea otter diet (Calkins 1978, Kvitek et al. 1992, Doroff & DeGange 1994, Wolt et al. 2012) and are also important prey for several northeast Pacific coast sea stars including sun stars *Pycnopodia helianthoides*, North Pacific sea stars *Asterias amurensis*, rain-

bow stars *Orthasterias koehleri*, and short-spined stars *Pisaster brevispinus* (Mauzey et al. 1968, Sloan & Robinson 1983). Where sea otters or sea stars have high predation rates on clams, clam harvest limits may need to be adjusted to maintain healthy clam populations. To better examine the ecological role of sea otters versus sea stars in soft-sediment habitats and to incorporate this predation into ecosystem-based management of clam fisheries, it is important to have accurate methods to determine foraging rates on clams.

Healthy and recovering sea otter populations have often been associated with reductions in the abundance and size of their prey, including clams (Hines &

Loughlin 1980, Kvitek et al. 1992, Doroff & DeGange 1994). However, clam populations have also been able to persist and sustain otter populations for many years despite otter-associated mortality. In Prince William Sound, Alaska, sea otters reduced crab populations quickly after recolonizing but continue to be sustained at an equilibrium density in the region where clam populations exist (Garshelis et al. 1986). Sea otters have been perceived as a threat to commercial and recreational clam fisheries. In California, USA, the recolonization of sea otters prevented the opening of a recreational clam fishery (Wendell et al. 1983). In the Czech Republic, fishers' attitudes toward the recovering Eurasian otters *Lutra lutra* were negative, although damage to fish stocks by the otters was not as severe as perceived (Vaclavikova et al. 2011). Understanding and accounting for primary sources of mortality in native bivalve populations will help resource management agencies inform human harvest levels in coastal Alaska.

Sea stars are diverse and abundant in the intertidal and subtidal in the North Pacific and in Kachemak Bay, Alaska (Chenelot et al. 2007, Iken et al. 2010) and, like sea otters, may be major clam predators. *P. helianthoides* are generalist predators, and burrowing clams are a large component of their diet in soft-substrate habitats (Shivji et al. 1983), contributing up to 72% of their diet in the subtidal zone (Mauzey et al. 1968). *P. brevispinus*, *Evasterias troschelii*, and *O. koehleri* feed on clams in Washington, USA (Mauzey et al. 1968, Smith 1961), and these species also occur in Alaska (Chenelot et al. 2007). *A. amurensis* dig shallow pits for clams and have reduced commercial clam stocks in Tasmania, Australia, where they are invasive (Ross et al. 2002). As one of the most common and active sea stars in Alaska, *P. helianthoides* is the most likely sea star to prey on clams at levels comparable to those of sea otters. Foraging by sea otters can facilitate *P. helianthoides* predation on clams by allowing easier access to remaining small clams excavated and not consumed by the sea otters (Kvitek et al. 1992). However, in habitats with high population densities of both sea stars and sea otters, predation pressure on all clam size-classes may be elevated. Further information on prey competition or facilitation between sea otters and sea stars such as *P. helianthoides* is needed to assess their respective impacts on clam resources.

Foraging pits can provide information about clam consumption by benthic foragers without direct foraging observations. For example, the presence and density of foraging pits has been used to determine sea otter foraging rates and locations (Kvitek et al. 1992) and to assess their potential exposure to lingering oil in oil spill-impacted areas (Boehm et al. 2007, Bodkin et al. 2012). Substrate disturbance through pit digging has ecological consequences across a range of terrestrial and marine habitats (woodlands: Eldridge & Mensinga 2007; ponds: Adamek & Marsalek 2013; marine soft-sediments: Oliver & Slattery 1985). However, determining the source of foraging pits based on measured dimensions may be difficult. There is a high degree of overlap and a wide range of values in described characteristics of sea otter and sea star pits in the literature (Table 1). Sea otter pits have been described as oblong with excavated sediment piled on one end of the pit (Kvitek et al. 1992); however, their dimensions have not been consistently reported among studies. Similar to sea otters, *P. helianthoides* also excavate pits while foraging for clams (Mauzey et al. 1968, Sloan & Robinson 1983). *P. helianthoides* push sediment aside with their arms and extend half of their arms into the pit (Sloan & Robinson 1983). Their pits have been described as being rounder and shallower than otter pits, with sediment piled in a ring around the pit (Kvitek et al. 1992). This description has been used by others to distinguish between otter pits and *P. helianthoides* pits (Boehm et al. 2007). In British Columbia, Canada, *P. helianthoides* were observed digging pits 6 to 14 cm deep (Sloan & Robinson 1983). Variation in observed pit dimensions among studies could be due to differences in sea otter foraging behavior, depth of the prey being targeted, or other factors affecting pit persistence such as the physical processes of wave action, currents, and sedimentation.

Table 1. Literature descriptions of sea otter and sea star foraging pits by pit dimension along the Pacific coast and in Alaska, USA

Sediment distribution	Area/size	Pit depth (cm)	Shape
Sea otter pits			
Sediment piled on one side of pit rim ^a	1300–2000 cm ^{2a} 15 to 45 cm across ^b 14 000 cm ² on average ^c	Up to 50 ^b 10–15 ^d	Elongate ^a
Sea star pits			
Sediment evenly around perimeter ^a	Smaller than otter pits ^a	6–14 ^e 5–23 ^f	Circular ^a
Literature basis: ^a Kvitek et al. (1992), ^b Calkins (1978), ^c Kvitek et al. (1988), ^d Boehm et al. (2007), ^e Sloan & Robinson (1983), ^f Mauzey et al. (1968)			

A major challenge in using foraging pits as a metric of foraging activity is that pit persistence is uncertain. Experimental pits dug around Kodiak Island, Alaska, were present after 6 mo but were gone after 12 mo (Kvitek et al. 1992). However, no detailed measurements or analyses were done on these pits since pit persistence was not the focus of that study. Foraging pits in the northern Knight Islands, Prince William Sound, Alaska, may persist for 1 yr based on photographs taken 1 yr apart (Boehm et al. 2007), while experimental pits at mean lower low water (MLLW) in western Prince William Sound persisted for approximately 4 to 6 mo (Bodkin et al. 2011). In Elkhorn Slough, California, recently made otter pits had claw marks on the inner walls, which wore away over time (Kvitek et al. 1988), but this characteristic of foraging pits has not been reported elsewhere. If foraging pits actually fill in and are replaced by new pits by the time researchers return to a site, foraging activity could be underestimated. Foraging pit persistence may vary with environmental factors such as water motion or sediment grain size. In mixed grain size gravel beds, smaller particles are sorted through the interstitial spaces between larger particles (Buscombe & Masselink 2006). Foraging pits may fill in more quickly in areas with high amounts of interstitial space in the sediment. High water motion would also likely facilitate sediment movement. In addition, pits may change shape due to *P. helianthoides* foraging activity, as there is clear evidence that *P. helianthoides* are attracted to otter pits (Kvitek et al. 1992). They are chemoreceptive (Brewer & Konar 2005), quickly aggregate at experimentally dug pits, and prey on the smaller clams that sea otters leave behind (Kvitek et al. 1992). While foraging for remaining smaller clams within a sea otter pit, *P. helianthoides* could change the shape of the pit, or how the sediment mounds around the pit. This will make distinguishing between sea otter and *P. helianthoides* pits difficult and may lead to inaccurate designation of predators. Without a better understanding of pit persistence and changes in pit dimensions over time, studies using pit dimensions as a metric of foraging intensity on clams are not able to draw accurate conclusions about their predators. The use of foraging pits for determining otter predation on clams needs to be validated by comparing estimates with other methods, as was done for time–depth recorder data (Tinker et al. 2007).

Shell litter has also been used to determine the source of foraging pits (Kvitek et al. 1992, Boehm et al. 2007). Sea otters break clam shell valves or the hinge when feeding (Calkins 1978), while a labora-

tory study showed that *P. helianthoides* always leave the shell intact (Kvitek et al. 1992). Previous studies have used the presence of otter-cracked shells next to a pit as an identifying characteristic of otter pits (Kvitek et al. 1992, Boehm et al. 2007). However, sea otters eat their prey on the surface, and in areas with large tidal currents the shell litter may not fall directly next to the foraging pit from which they obtained their prey. For this reason, the use of shell litter for determining individual pit source may be inappropriate; however, these materials may be used for predation source at the site level.

Gaps in our knowledge about the origin and persistence of foraging pits currently limits our ability to quantify the relative contribution of sea otters, sea stars, and other consumers to local clam predation. While previous studies have attempted to draw conclusions on clam predation events based on pit dimensions, questions regarding clam predation still remain: (1) Can sea otter and sea star foraging pits be distinguished using quantitative dimensions? (2) How long do characteristics distinguishing sea otter and sea star foraging pits persist? and (3) Can shell litter be used to determine the relative importance of sea otters and sea stars as clam predators? Here, we hypothesize that recent (2 wk old or less) foraging pits can be distinguished based on measurable characteristics (major axis, minor axis, pit depth, and how sediment is piled) and that after 2 wk sea otter and sea star pits can still be distinguished. Lastly, we hypothesize that shell litter can be used to assign relative clam predation by sea otters and sea stars.

MATERIALS AND METHODS

Study area

This study was conducted in Kachemak Bay, a large estuary in southcentral Alaska with a tidal range of approximately 9 m. Sea otters were extirpated from this area by 1792 (Lensink 1962), and after the close of the commercial fur trades for sea otter pelts, the region recovered through natural recolonization processes during the late 1960s and 70s (Schneider 1976, Gill et al. 2009). Between 2002 and 2008, the population increased by 26% yr⁻¹, reaching 3.9 otters km⁻² (Newsome et al. 2015). Based on this last estimate, the Kachemak Bay population is below its carrying capacity based on estimated available food sources (Gill et al. 2009, Newsome et al. 2015). Since then, the sea otter population has continued to grow in this region at approximately

13% yr⁻¹ (USFWS and USGS unpubl. data). *Saxidomus gigantea* and *Leukoma staminea* are the most popular clams for recreational fishing in Kachemak Bay (ADFG 2009). Surveys of clam populations in Kachemak Bay in 2007 and 2008 found that *S. gigantea* was abundant (up to 58 m⁻²) and *Macoma balthica*, *Mya truncata*, and *L. staminea* were also observed (Stewart et al. 2014). *Pycnopodia helianthoides* are common in Kachemak Bay and can reach densities of 0.1 to 0.28 m⁻² (Brewer & Konar 2005, S. B. Traiger & B. Konar unpubl.).

Sampling sites in this study were located at 10 m depth (referenced to MLLW) at 4 sites (Port Graham, PG; Peterson Bay, PB; McDonald Spit, MS; and Kasitsna Bay, KB) and at 2 intertidal sites (0 m depth at MLLW) (MS and KB; Fig. 1). These water depths were chosen because sea otters and sea stars often forage there (Mauzey et al. 1968, Calkins 1978, Sloan & Robinson 1983, Kvitek et al. 1992) and clams are common (Stewart et al. 2014). Sites were chosen to standardize substrate as much as possible.

Distinguishing unknown pit sources using quantitative dimensions

Foraging pits that were recently made (within the last 2 wk) were tagged, counted and measured along three 10 × 2 m permanent transects every 2 wk from May to August 2014 at all 6 sites. The center of each pit was marked with a landscaping flag so that it could be revisited and so that new pits could be distinguished from those previously sampled. For each

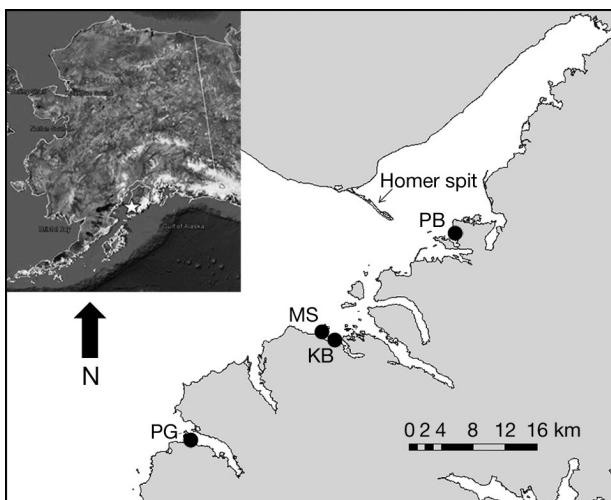


Fig. 1. Locations of the 4 study sites within Kachemak Bay. White star on the inset map shows the location of Kachemak Bay within Alaska, USA. PG: Port Graham; PB: Peterson Bay; MS: McDonald Spit; KB: Kasitsna Bay

pit, the lengths of the major axis, minor axis and depth in the middle of the pit were recorded. Surface area was calculated using the equation for area of an ellipse. As an indicator of pit shape, we calculated the percent difference between the major axis and the minor axis as [(major–minor)/major] × 100. The size of the sediment pile on the edge of each pit was quantitatively binned by the proportion of the pit edge encircled by sediment mound (0, 1–25, 26–50, 51–75, 76–100%). Approximately every 2 wk, new pits were measured and marked as previously described. Thus, the maximum age of pits surveyed after the initial sampling was known, except for those identified the first time the survey was conducted. Only pits of known maximum age were used in our analysis. If a previously marked pit was totally filled in with sediment and no longer recognizable as a foraging pit, it was recorded as ‘filled in’ and the marker was removed.

To determine whether the natural pits fell into distinct groups representing sea otter and sea star pits, the multivariate data cloud of pit dimensions was analyzed in Primer (PRIMER v. 6; Clarke & Gorley 2006). Major axis and minor axis were strongly correlated with surface area ($r = 0.95$ for both) and were excluded from analysis. Variables were normalized before analysis. We used CLUSTER analysis with group averages on Euclidean distance similarity matrix and SIMPROF test to determine whether there were significant subgroups within the data cloud (Clarke et al. 2014). A principal coordinate analysis (PCO) plot was used to visualize the data. A 1-way analysis of similarity (ANOSIM) test was used to detect differences in pit dimensions among sites (random, 5 levels: MS 0 m, KB 10 m, MS 10 m, PB, and PG).

Persistence of characteristics distinguishing experimental sea otter and sea star foraging pits

To test the persistence of pits in Kachemak Bay, experimental pits were constructed on May 28, 30, 31, and June 1, 2014. A total of 6 replicate sea otter and sea star pits were dug at all 6 sites. The dimensions selected for the experimental pits were based on descriptions of naturally occurring sea otter and *P. helianthoides* pits (Kvitek et al. 1992, Boehm et al. 2007). Specifically ‘sea otter’ pits were constructed to be 20 cm deep, with major and minor axes of 26 and 23 cm, respectively. For these pits, sediment was piled on one end of the oval pit, and all clams larger than 20 mm were removed from the excavated sediment to model the removal of clams by otters (Kvitek

et al. 1992). Target dimensions for the experimental sea star pits were 10 cm deep and had a 20 cm diameter. For these, sediment was piled evenly around the edge of the round pit and all clams were removed from the excavated sediment to model the clams that would be removed by sea stars (Kvitek et al. 1992). Pairs of experimentally dug sea otter and sea star pits were placed side by side every 2 m along the depth contour. The side of the transect on which a pit was placed was determined randomly. Pits were numbered and marked with flagging tape on stakes in the sediment.

Experimental pit dimensions were measured immediately after digging the pits. Partly because of infill while digging and larger rocks in the substrate, actual dimensions varied from the target dimensions. Actual dimensions were typically within 10 cm of the target but ranged from 12 cm below and 35 cm above the target dimension. Even with the infill, average starting dimensions for the 2 experimental pit types were significantly different (permutational multivariate ANOVA, PERMANOVA, $p = 0.0007$; Table 2).

To monitor short-term changes in experimental pit dimensions, pits were measured approximately 2 wk after set-up as previously described for naturally occurring pits. If an experimental pit was totally filled in with sediment and the sediment pile was gone, it was recorded as 'filled in'. Presence and activity of sea stars in all experimentally dug pits were noted and classified as described previously. Differences between experimental sea otter and sea star pits at

the initial set up and after 2 wk were tested using the PERMANOVA procedure based on a Euclidean distance matrix in Primer. Variables were normalized before analysis. Variables were checked for correlation using Draftsman plots and Spearman correlations and subsequently removed from the analysis if correlations ≥ 0.9 occurred. Differences between experimental sea otter and sea star pits (Type) were tested at set-up and after 2 wk and among sites in a 3 factor design. The factors were Type (fixed, 2 levels: Otter, Star), Sampling event (random, 2 levels: Set-up, After 2 wk), and Site (random, 6 levels: KB 0 m, KB 10 m, MS 0 m, MS 10 m, PB, and PG). To further compare the degree of change among sites, percent change was calculated for each dimension of each pit by dividing the 'After 2 wk' measurement by the 'Set-up' measurement and multiplying by 100. Differences in percent change among sites were tested with a PERMANOVA on a Euclidean distance matrix with Site as a random factor.

The rates at which experimental pits fill in or change dimensions may be influenced by water motion. To assess relative water motion at each site where experimental pits were dug, 3 replicate clod cards were deployed at each site and at each depth contour (Denny 1985). Clod card cubes were made of Plaster of Paris using ice cube trays (plaster to water ratio of 1:1 based on manufactures instructions), glued to plastic sheets, and attached to bricks. After the cards were assembled, they were cured in seawater for 2 d, then dried for 1 wk and weighed twice to ensure they were fully dried before they were deployed in the field for approximately 2 wk. Handling controls were taken to the sites (either intertidal or subtidal) and then returned to the lab and placed in still sea water for 2 wk. Average weight loss of controls for each site was subtracted from the weight loss of the field-deployed clod cards. Weight loss of clod cards was compared among sites using ANOVA with Tukey's pairwise comparisons to assess relative water motion (Thompson & Glenn 1994) using the R program (R Development Core Team 2008).

The rates at which experimental pits fill in may also be influenced by substrate composition. To assess percent cover of substrate grain size at each site, sediment grain size (sand [< 2 mm], gravel [2–6 mm], cobble [6–100 mm], boulder [10 cm–1 m], or bedrock [> 1 m]) was determined at 5 to 10 random points in 5 replicate haphazardly placed 625 cm² gridded quadrats. To calculate percent cover of each grain size for each replicate quadrat, the number of points for each grain size was divided by the total number of points and multiplied by 100. Grain size bins were

Table 2. (A) Comparison of pit dimensions between experimental sea otter and sea star pits (Type) across and within sampling events (Set-up, After 2 wk) and sites using a 3-way PERMANOVA (**bold** values are significant assuming $\alpha = 0.05$). (B) Pairwise comparison of the interaction between experimental pit type and sampling event using PERMANOVA (**bold** values are significant assuming $\alpha = 0.05$)

(A) Source	df	SS	Pseudo-F	p
Type	1	48.57	1.68	0.216
Sampling event	1	88.96	3.31	0.073
Site	5	54.17	0.40	0.930
Type \times Sampling event	1	22.74	4.84	0.022
Type \times Site	5	45.39	1.92	0.134
Sampling event \times Site	5	136.95	8.23	<0.001
Type \times Sampling event \times Site	5	23.64	1.42	0.141
Residual	112	372.55		
Total	135			
 (B) Type \times Sampling event				
		<i>t</i>		<i>p</i>
Otter, Star at Set-up		4.09		<0.001
Otter, Star after 2 wk		0.77		0.532

based off the Wentworth scale (Wentworth 1922). Differences in grain size distribution among sites were tested using a 1-way PERMANOVA based on a Euclidean distance matrix with site as a random factor.

Predator importance based on shell litter

To assess if shell litter can be used to determine the relative importance of sea otters and sea stars as clam predators, shells were collected along the permanent transects in mid-June, and at the end of July and August. Only recently deposited shells (no fouling on the shell) were collected, as these would have the greatest chance of being related to recent foraging activity in the same area. Shells were collected in plastic bags and brought back to the lab where they were recorded as 'otter-cracked' if at least 1 valve or the hinge was broken or cracked (Kvitek et al. 1992) and as 'star-preyed' if both halves of the shell were intact, open and not drilled. Drilled shells have boreholes that are indicative of predation by moon snails or octopus (Ambrose et al. 1988). To provide further insight into the species and sizes of clams preyed on by sea otters and sea stars, shells were identified to the lowest taxonomic level possible and shell width was measured. The size frequency distributions of otter-cracked and star-preyed shell widths were compared using a 2-sided Kolmogorov-Smirnov (KS) test. Densities of shells (shells per 10 m²) were calculated by dividing the number of shells collected along a transect by the transect area (20 m²) then multiplying by 10. To determine which predator is responsible for the most clam predation, we compared densities of shell litter by type (otter-cracked, star-preyed, or bore-holed) using 1-way ANOVAs in R (R Development Core Team 2008) for all sites combined and within each site.

To determine whether sea star density is an indication of sea star predation, all sea stars were counted and identified along the transects at the same time that shell litter was collected. Only *P. helianthoides* were used in our analysis because the other 2 stars that were found, *Evasterias troschelii* and *Orthasterias koehleri*, occurred at very low densities. We tested for Spearman correlations between shell litter (total shell litter and star-preyed shells) and *P. helianthoides* abundance. We also compared density of *P. helianthoides* across sites using ANOVA in R (R Development Core Team 2008). Since surveys of shell litter and *P. helianthoides* abundance at the 0 m sites were performed during low tide, these sites were excluded from the correlation analysis. *P. heli-*

anthoides can move into the intertidal zone during high tide to feed but typically retreat to the subtidal zone as the tide drops (S. B. Traiger, B. Konar, A. Doroff pers. obs.); hence, surveys of their abundance at low tide probably do not reflect their true use of the habitat.

RESULTS

Distinguishing unknown pit sources using quantitative dimensions

Foraging pits (n = 109) were measured across all four 10 m sites and one of the 0 m sites from May to August 2014. Although sea otters were seen in the area, no pits were observed at the KB 0 m site during the study. There were no significant clusters within the data set of measured pits based on the CLUSTER analysis and SIMPROF test (p = 0.174), and no clusters were apparent from the PCO plot either (Fig. 2A) so pit source could not be determined. Most pits were elongate with the major axis on average 18 ± 13% (SD) longer than the minor axis. Major axes ranged from 0 to 56% longer than minor axes. Fourteen percent of pits were perfectly round. Although most pits surveyed (53%) had no sediment pile, 26% had up to 25% of the pit edge with piled sediment, which is indicative of sea otters. This contrasts with only 2% of pits having sediment piled on 76–100% of the pit edge, which is indicative of sea stars. Pit depths averaged 11.8 ± 4.7 cm (SD) and ranged from 3 to 27 cm. Surface area averaged 958 ± 674 cm² (SD) and ranged from 71 to 3533 cm².

There were some differences in pit dimensions among sites (ANOSIM, R = 0.095, p = 0.006), so separate CLUSTER analyses and SIMPROF tests were run for each site (excluding MS 0 m due to low sample size). There were no significant clusters within KB 10 m, MS 10 m, or PG (SIMPROF, p = 0.727, 0.710, and 0.430, respectively). There were 3 significant clusters within the pits measured at PB (Fig. 2B). There was a wide range of values for each dimension in Cluster a, so we were unable to determine the source of pits in this cluster (Fig. 2C). The pits in Cluster b were deep compared to pits in Cluster a (13.5 ± 2.1 cm [SD] vs. 7.9 ± 3.0 cm [SD]), both pits had 26–50% of the rim covered in sediment mound, surface area was large relative to Cluster a (834 ± 180 cm² [SD] vs. 468 ± 369 cm² [SD]) and both pits were perfectly round (%major axis > minor axis = 0) while pits in Cluster a had major axes 11% longer than minor axes on average (7% SD; Fig. 2C). Due to

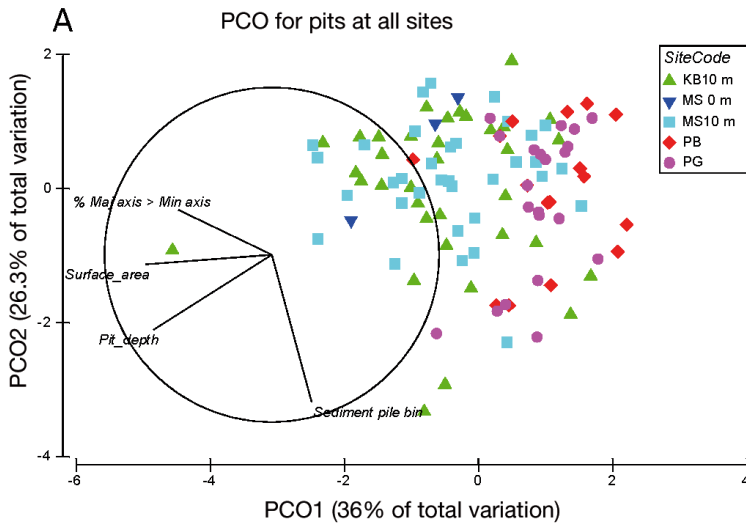
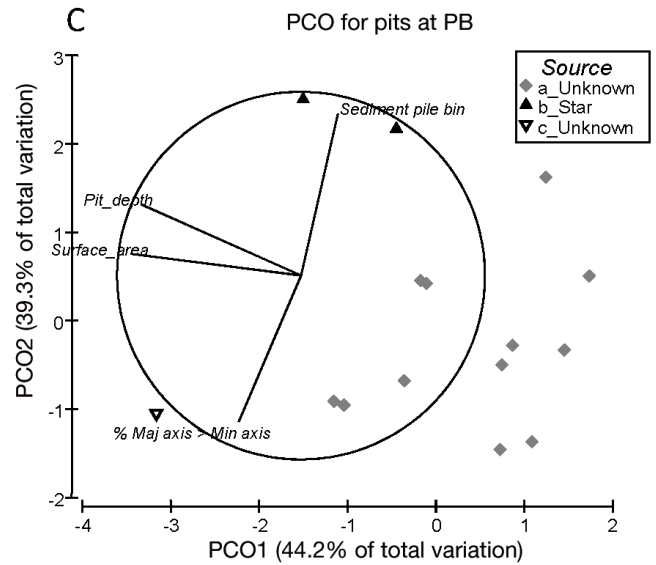
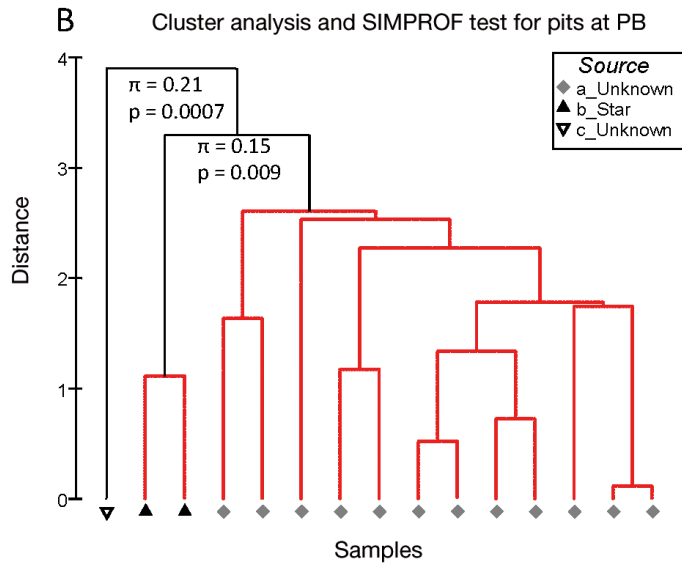


Fig. 2. (A) Principal coordinate analysis (PCO) plot based on Euclidian distance of dimensions of surveyed foraging pits color coded by site. Each point represents one pit. Solid lines represent vectors of pit dimension variables. (B) Dendrogram of foraging pits at Site PB. Black nodes represent divisions of statistically significant subdivisions determined by SIMPROF tests, resulting in 3 clusters (a_Unknown, b_Star, and c_Unknown). Sample symbol corresponds to the cluster in which it was placed by the CLUSTER analysis. Test statistic (π) and p values are listed below statistically significant nodes. (C) PCO plot of foraging pits at Site PB, with symbols corresponding to clusters generated by CLUSTER analysis. See Fig. 1 for full site names



the round shape of the pits and the presence of sediment on more than 1/4 of the pit perimeter, we assigned this cluster as sea star source. Cluster c had one pit, which was large (surface area 1236 cm²), had a major axis 22% larger than the minor axis, was 10 cm deep, and had sediment mounded on 50–75% of the pit perimeter, which was more than any other pit at PB. We were unable to assign a source to this pit because the characteristics of sediment mound and pit shape give conflicting indications of pit source based on literature descriptions of pits (Table 1). The sediment mound value indicates a sea star source; however, the pit shape indicates sea otter source, and size of the pit is very close to the lower limit of pit size observed by Kvitek et al. (1992).

Pit flag loss rate occurred and varied across sites. Flag loss was highest at the MS 0 m site, where 6 of the 7 flags deployed were lost in mid-July. Flag loss

also occurred at PG from June to July when 4 of the 7 flags deployed at the time were lost. Flag loss was lower at PB (3 out of 20) and MS 10 m (8 out of 56). There was no flag loss at KB 10 m.

Persistence of characteristics distinguishing sea otter and sea star foraging pits

After 2 wk, the 2 experimental pit types (otter vs. sea star) did not have significantly different dimensions from each other (Table 2, Fig. 3). There were significant differences in the degree of change in pit dimensions among sites (Table 3) with most of these differences being between intertidal and subtidal sites. At 0 m, all of the experimental pits at KB were filled in after 2 wk. At MS 0 m, 67% of experimental sea star pits were filled in, while all 6 of the experi-

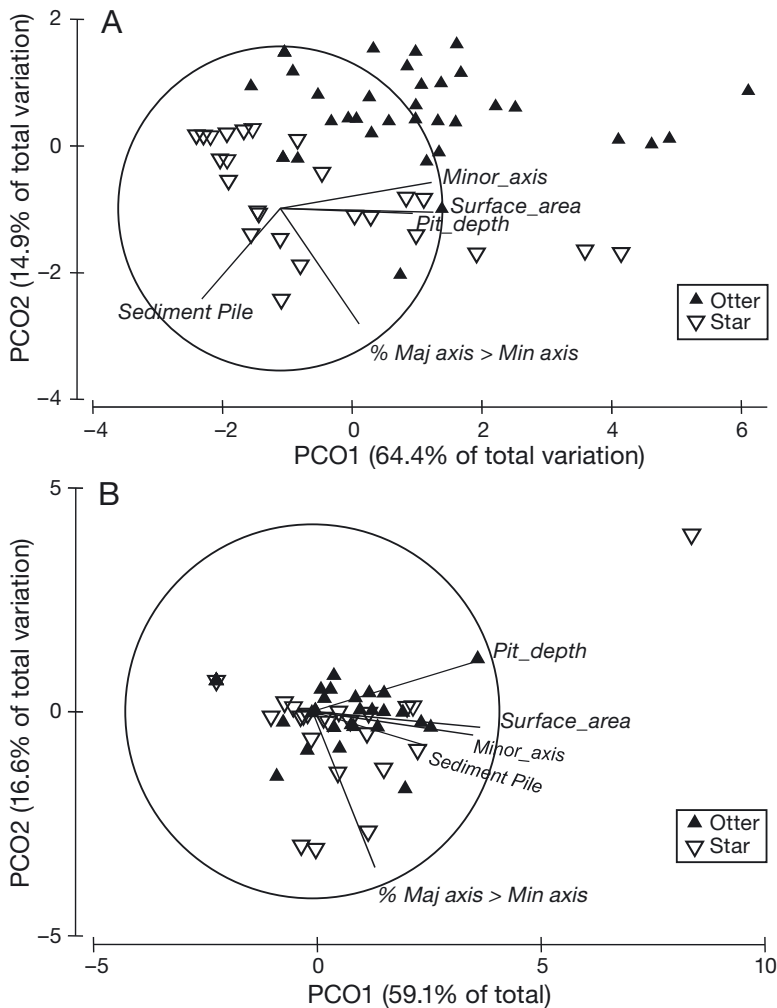


Fig. 3. (A) PCO plot showing clear separation in starting dimensions between experimental otter and sea star pits just after they were dug (Initial Set-up). (B) PCO plot showing that after 2 wk, the experimental otter and sea star pits are indistinguishable. In both plots, each point represents 1 pit

mental sea otter pits were still present. Across all sites, 90% of the experimental pits dug at 10 m were still visible after 2 wk. The pit characteristics that changed the most were pit depth (average -44% change) and sediment pile. After 2 wk, no sediment

Table 3. Comparison of percent change in dimensions of experimental pits among 2 intertidal and 4 shallow subtidal sites in Kachemak Bay, Alaska, USA. The analysis was a 1-way PERMANOVA with a random factor (Site), performed with 9999 permutations (**bold** values are significant assuming $\alpha = 0.05$)

Source	df	SS	MS	Pseudo-F	p
Site	5	3.87×10^5	77 492	5.97	<0.001
Residual	59	7.66×10^5	12 979		
Total	64	1.15×10^6			

pile remained at 72% of sea otter pits and 62% of sea star pits.

There were no significant differences in clod card weight loss among sites, indicating there may be no differences in relative water motion (ANOVA, $p = 0.199$, $F = 1.699$), although our sample size was low. Sediment grain size composition was significantly different among sites (Table 4). Mean percent cover of sand, cobble, and boulders ranged from 4–92, 4–52, and 0–4%, respectively. Bedrock was not observed at any site. The KB 0 m site had the lowest percentages of sand and gravel (4% for both) and the highest cover of cobble at 52%. The MS 0 m site and PG had the next highest covers of cobble at 32 and 27%, respectively.

Predator importance based on shell litter

A total of 125 shells were collected over the study period. Fifty-six percent of the shells were otter-cracked, 42% were star-preyed, and 2% contained bore-holes. Across all sites, there was a significantly lower density of bore-holed shells than otter-cracked or star-preyed shells (ANOVA, $p < 0.001$ and $p = 0.011$, respectively) (Fig. 4). Density of otter-cracked and star-preyed shells was only different at PG (ANOVA, $p = 0.002$) (Fig. 4), with 70% of the shells

being otter-cracked at this site. This indicates that sea otters and sea stars are of equal importance as predators of clams at most of our sites, while at PG, sea otters are more important. Clam species preyed on by both sea stars and sea otters included *Clinocar-*

Table 4. Comparison of sediment grain size composition among 2 intertidal and 4 shallow subtidal sites in Kachemak Bay, Alaska, USA. The analysis was a 1-way PERMANOVA with a random factor (Site) performed with 9999 permutations (**bold** values are significant assuming $\alpha = 0.05$)

Source	df	SS	MS	Pseudo-F	p
Site	5	46 740	9347.9	9.96	<0.001
Residual	24	22 522	938.42		
Total	29	69 262			

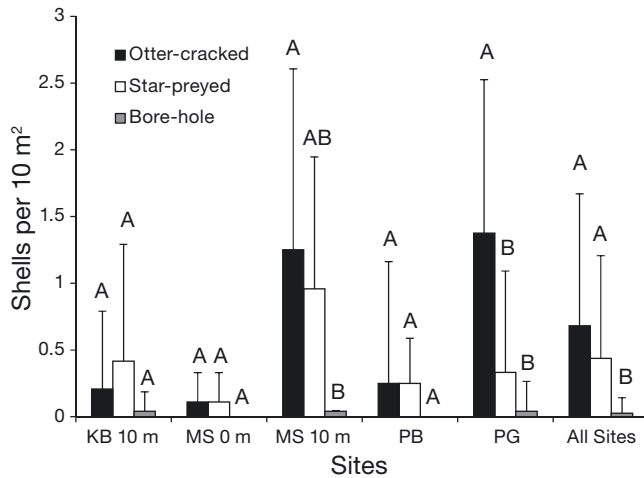


Fig. 4. Densities of star-preyed and otter-cracked shells collected along same 2×10 m transects where foraging pits were surveyed. Separate ANOVAs were performed to compare density of otter-cracked, star-preyed, and bore-holed shells across all sites, and within each site. Letters above bars indicate significant differences for each separate test. See Fig. 1 for full site names

dium sp., *Humilaria kennerleyi*, *Mya truncata*, *Saxidomus gigantea*, and *Serripes groenlandicus*. Sea stars included a wider range of clams in their diet and additionally preyed on *Diplodonta* sp., *Hiatella arctica*, *Leukoma staminea*, *Lyonsia* sp., *Macoma* sp., and *Mactromeris polynyma*. *S. gigantea* was the most common species in both otter-cracked and star-preyed shell litter (Table 5). The shell width of otter-cracked shells ranged from 27.07 to 94.72 mm with a mean of 57.26 ± 13.63 mm (SD), while star-preyed shells ranged from 11.45 to 102.00 mm with a mean

Table 5. Proportions of clam species preyed on by sea otters, sea stars, and moon snails or octopus as shown by shell litter. n: number of shells. For star-preyed shells, 'other' includes *Hiatella arctica*, *Leukoma staminea*, *Lyonsia* sp., *Mactromeris polynyma*, and *Serripes groenlandicus*, which each made up 1.9% of star-preyed shell litter. Blank cells: 0

Species	Otter-cracked (n = 70)	Star-preyed (n = 52)	Bore-holed (n = 3)
<i>Clinocardium</i> sp.	2.9	17.3	
<i>Diplodonta</i> sp.		3.8	
<i>Humilaria kennerleyi</i>	4.3	3.8	
<i>Macoma</i> sp.		7.7	33.3
<i>Mya truncata</i>	2.9	5.8	
<i>Saxidomus gigantea</i>	88.6	48.1	33.3
<i>Serripes groenlandicus</i>	1.4	1.9	
Unknown		3.8	33.3
Other		5.8	

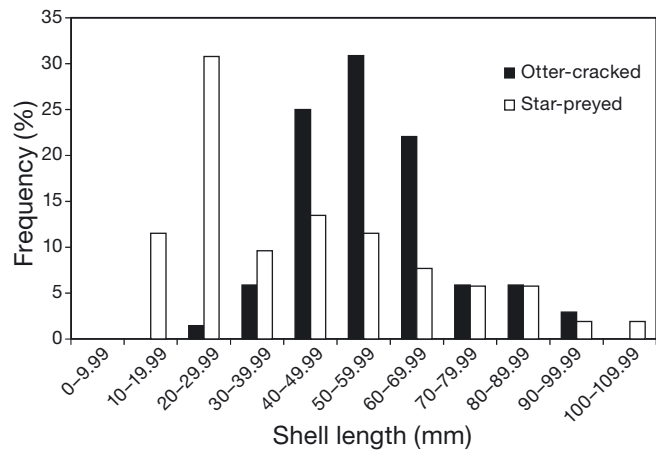


Fig. 5. Range of sizes of clams preyed on by sea otters and sea stars as shown by shell litter. All shells collected with bore-holes ($n = 3$) were in the 20–20.99 mm size category (data not shown)

of 42.47 ± 22.75 mm (SD) (Fig. 5). There was a significant difference in the frequency distribution of shell widths of otter-cracked and star-preyed shells (KS test, $D = 0.5237$, $p < 0.001$).

There was no correlation between star-preyed shells and density of *P. helianthoides* (Spearman, $p = 0.686$). *P. helianthoides* density was higher at MS 10 m than PG (ANOVA, $p = 0.003$), but star-preyed shells were not more abundant than otter-cracked shells at MS 10 m. Density of *P. helianthoides* does not appear to be an indicator of the magnitude of sea star clam predation.

DISCUSSION

The results of this study showed conclusively that shell litter, but not pit dimensions, could be used to estimate clam predation by sea otters and sea stars in Kachemak Bay, Alaska. Distinguishing characteristics between experimental sea otter and sea star pits disappeared and many pits filled in within 2 wk. We conclude that shell litter is a more useful and less ambiguous method for determining sea otter and sea star clam predation in the intertidal and subtidal without direct observation. Our study indicates that sea stars contribute to clam mortality as much as sea otters; however, further research is needed to examine possible biases due to difference in shell litter deposition. This finding contrasts to the common perception that sea otters are the only significant clam predators in Alaska.

Our hypothesis that recent (2 wk old or less) foraging pits can be distinguished based on measurable

characteristics was not supported. We did not observe any patterns in the multivariate data cloud of pit dimensions that indicated that different types of predators were making them. We also found that the multivariate data did not align with any of the existing literature descriptions (Table 1). For example, the amount of piled sediment increased toward the lower right end of the PCO plot, which could indicate that pits in this portion of the graph are sea star pits (Kvitek et al. 1992); however, pit shape (% major axis > minor axis) and surface area do not show clear decreasing values in that direction (compare vector directions on Fig. 2). As such, we do not recommend using foraging pits to determine levels of clam predation by sea otters and sea stars separately. There is not enough quantitative information in the literature to clearly distinguish the types of pits made by each predator, and the lack of clustering in the pit dimensions indicates that either both predators make pits of very similar size and shape, or that one predator is responsible for all the pits observed. Foraging pits are more useful for determining the role of individual predators in study systems where only one pit digging predator occurs (Hines et al. 1997, Eldridge & Mensinga 2007, Dor et al. 2014), or there are large differences in the sizes of pits produced by different predators (Nelson et al. 1994).

Our hypothesis that after 2 wk, sea otter and sea star pits can still be distinguished was not supported. After 2 wk, experimental sea otter and sea star pits were no longer significantly different from each other, largely because the differences in roundness and amount of piled sediment that distinguished pits at the beginning of the experiment were not present after 2 wk. These results suggest that the metrics typically found in the literature to differentiate foraging pits are likely not accurate for pits older than 2 wk. Since sediment piles are quickly eroded, previous studies using sediment piles to distinguish pits may be underestimating the contribution of sea stars to foraging pits. As a result, the role of sea stars in shaping soft-sediment communities could be underappreciated in areas with sea otters. More than half of the recent shells that were collected were a result of sea star predation, indicating that they are currently important predators of clams at these sites in Kachemak Bay. The high degree of change in pits we observed over 2 wk is likely an important reason why we could not distinguish foraging pits. Very frequent resurveys would be necessary to accurately distinguish the source of foraging pits and to accurately quantify foraging pit dimensions, regardless of their source. In other study systems, surveys of foraging

pits have involved frequent resampling (4 d, Hines et al. 1997; 24 h, O'Shea et al. 2012). In contrast, surveys of foraging pits attributed to sea otters have been repeated every 2 wk (Kvitek et al. 1988) or have not been repeated, using a snapshot approach (Kvitek et al. 1992, Boehm et al. 2007, Bodkin et al. 2012). A snapshot approach, combined with an inaccurate estimate of pit persistence, could result in underestimation of foraging. Appropriate sampling frequency will depend on infill rates, which may be influenced by sediment grain size, water motion, and potential for continued use of the pit.

The changes we observed in pit dimensions over-time may have been influenced by a lack of sea star activity in the pits (given that sea star activity can prevent infill), water motion, and sediment grain size. Sea stars were never observed using pits that had been previously marked with a landscaping flag or in our experimental pits, which were marked slightly differently, with a nail with flagging at the edge of the pit. While it is possible that the landscaping flag placed at the center of the pits deterred further use of the pits by sea stars or sea otters, we believe that the rate of pit reuse is low in our system, due to the lack of activity in our experimental pits. We also do not believe that *Pycnopodia helianthoides* would be deterred by landscaping flags because we have observed them overturning bricks and large rocks in order to dig for clams underneath. We do not know of any evidence of sea otters reusing pits. The high rate of pit in-fill in this study differs from previous studies that found sea otter foraging pits persisting for 4 mo to 1 yr (Kvitek et al. 1992, Boehm et al. 2007, Bodkin et al. 2011). Pit persistence has also been studied in Australia, where most stingray foraging pits filled in within 7 d, but some pits became larger from continued use by the stingrays (O'Shea et al. 2012). Although *P. helianthoides* have been shown to be attracted to foraging pits (Kvitek et al. 1992), it seems that they were not attracted to our experimental pits since most experimental pits became smaller or filled in over time.

Wave exposure was relatively similar among our sites in Kachemak Bay, but this may explain the longer pit persistence in Kodiak Island and Prince William Sound, where tidal driven currents are weaker due to smaller tidal ranges. Stingray pits in Australia also filled in more quickly at exposed than at protected sites (O'Shea et al. 2012). We also observed differences in experimental pit persistence between the intertidal and subtidal sites with a higher rate of experimental pit disappearance at 0 m depth than at 10 m, but there was no difference in

relative water motion. However, there were differences in sediment grain size with a higher proportion of cobble at KB 0 m. The larger sized rocks in the intertidal may cause pits to fill in more quickly than subtidal pits at the same site, which had a higher proportion of sand and gravel. Sediment transport is affected in part by sediment grain size (Larson & Kraus 1995). Larger sediment grains enable more water percolation than saturated small grain size sediment, leading to greater transport rates of sediment (Larson & Kraus 1995).

The difference in pit persistence across depth contours has important implications for interpreting foraging pit data. It should not be assumed that foraging pits are indicators of foraging over the same time span at intertidal and subtidal sites because of these differences in their persistence. In contrast to western Prince William Sound, where intertidal foraging pits persisted several months (Bodkin et al. 2011), foraging pits at our intertidal sites may only represent foraging activities within the last 2 wk or less. Similarly, foraging pits and furrows formed by walrus in Bristol Bay are not observed in areas with dynamic sediment movement, even though walrus are known to forage in those areas (Bornhold et al. 2005). While we observed fewer pits at our intertidal sites (zero at KB and 3 at MS), we may be missing some foraging activity due to high infill rates. KB has a 9 m tidal range, so at high tide, the intertidal is very accessible to sea otters. Indeed we expected to see higher numbers of foraging pits in the intertidal since other studies using foraging pits and radio tags recorded frequent foraging in the intertidal (Bodkin et al. 2007, Gilkinson et al. 2011). The number of foraging pits may also have been low at our intertidal sites if clam abundance was low due to previous sea otter or sea star predation, recreational clam fishing, or other factors. We also found low numbers of shells at our intertidal sites (zero at KB and 4 at MS), which may also be indicative of low prey abundance.

Our hypothesis that shell litter can be used to assign relative clam predation by sea otters and sea stars was supported. We observed very few shells with indications of other predators and were able to classify predation source for all shells collected. We did not observe any shells with contradicting predation signs (i.e. a shell with both bore-holes and otter-cracks). Like any method of determining predation rates, using shell litter has potential biases. Sea otters eat clams on the surface, so otter-preyed shells may be distributed farther from their origin than star-preyed shells, resulting in underestimation of sea otter predation. In California, sea otters were ob-

served to move away from shore to eat on the surface after collecting clams in shallower water (Kvitek et al. 1988). Small clam prey of sea otters may also be underestimated because sea otters have been observed to consume whole clams 3 to 5 cm long (Calkins 1978). However, these potential biases are outweighed by the higher confidence in identifying the source of clam mortality and benefits of additional information gained compared to using foraging pits. Surveys of shell litter provide the added benefit of being able to identify small individuals, which can be difficult in observational studies (Dean et al. 2002, Wolt et al. 2012). Unlike counts of foraging pits, shell litter can also be directly linked to the number of predated clams. Shell litter can be used to determine recent foraging activity of sea otters on clams, as in this study, as well as historical predation of clams at a site (Kvitek et al. 1992, Stewart et al. 2014). While shell litter is useful for distinguishing between sea otter and sea star clam predation, it does not account for all predation on clams. Clams are important diet items for wintering sea ducks, which consume small clams (≤ 4 cm) whole, so their fecal pellets need to be sampled to assess their predation on clams (Lewis et al. 2007). Crabs prey on clams by chipping away the edge of the clam valves (Boulding 1984, R. G. Kvitek pers. comm.); however, at the sites we sampled, only 1 *Saxidomus gigantea* was found chipped in this way. Larger crab species, such as Tanner crab *Chionoecetes bairdi* generally would be found in deeper water than our sampling sites.

Multiple methods of determining sea otter foraging should be used to account for method biases. For example, Elliott Smith et al. (2015) found that estimates of diet specialization differed between stable isotope and observation methods, with stable isotopes providing less biased estimates of specialization. Shell litter, when combined with other methods, could help provide a more complete view of sea otter foraging on clams. In contrast to shell litter, direct foraging observations are time consuming, and clam species may be impossible to identify from great distances, although statistical methods can be used to account for these biases (Tinker et al. 2012). Observations also allow for a more complete prey dataset, which include soft-bodied organisms (Dean et al. 2002). Scat collections are often done to determine sea otter prey, but these data are limited to sea otter haul out sites, and only prey with hard parts are observed (Faurot et al. 1986, Green & Brueggeman 1991, Doroff et al. 2012). Pairing shell litter with direct observations and scat collections will ensure that

soft-bodied and small size class organisms are incorporated (Green & Brueggeman 1991).

To better predict changes in clam populations, we need to understand the relative contributions of sea otters and sea stars to their mortality. In KB, according to the shell litter, sea stars are as important as sea otters for clam predation, and as such, clam mortality due to sea stars should be considered in clam management strategies. In addition to preying on equal number of clams, sea stars also prey on a wider range of species and sizes of clams, including *Diplodonta* sp., *Hiatella arctica*, *L. staminea*, and *Mactromeris polynyma*. Size-specific predation pressure evident from the shell litter could be built into population models for clams. While the KB sea otter population has been rising since recolonization (Gill et al. 2009), its impact on clam populations is unknown. As the sea otter population recovers in KB, public perception is mixed, and there is concern that the population recovery is a threat to local clam fisheries. Sea otters also prey on Tanner crabs *C. bairdi*, fat innkeepers *Urechis unicinctus*, sea stars such as mottled stars *Evasterias troschelii*, green urchins *Strongylocentrotus droebachiensis*, octopus (*Octopus* sp.), mussels (*Mytilus* spp.), and fish (Calkins 1978, Garshelis et al. 1986, Green & Brueggeman 1991, Dean et al. 2002, Gill et al. 2009, Doroff et al. 2012), which are also present in KB. Although clams are a high-energy food source (Oftedal et al. 2007), sea otters may target prey-types that do not require excavation while they are still abundant.

Ecosystem-based management approaches require an understanding of natural sources of mortality for clams and reasonably accurate estimates of mortality from different predators. For example, in the North Sea, lesser sandeels are preyed on by predatory fish, sea birds, seals, and are fished by humans (Furness 2002). Predatory fish consume more sandeels than sea birds, seals, and the fishery, so management decisions made for predatory fish could have more effect on sandeel stocks than changing fishing practices on sandeels themselves (Furness 2002). Clams and shellfish in general have been a major component of the subsistence, recreational and commercial fisheries (valued at approximately \$4 billion USD) across Alaska (Salomon et al. 2007, Donkersloot 2012), and these fisheries are managed by Alaska Department of Fish and Game. Shell litter data could be used to determine predation rates by both sea otters and sea stars, and this information could then be factored into clam harvest limits. All field methods for studying sea otter foraging, including direct observation and scat samples, are time consuming and carry biases. If sea

stars are not accounted for, the use of foraging pits to assess sea otter foraging in soft bottom habitats will probably result in overestimates of sea otter foraging that may be detrimental to local management efforts. If the goal is to determine clam mortality in the intertidal and shallow subtidal due to non-human predation, we recommend conducting surveys of shell litter in conjunction with scat and direct observations. Using shell litter surveys, we have shown that sea stars are equally important predators as sea otters in KB and should be included in clam management strategies; however, further research is needed to investigate potential biases in shell litter due to difference in shell deposition.

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