Changes in sea urchins and kelp following a reduction in sea otter density as a result of the *Exxon Valdez* oil spill

Thomas A. Dean[1,*], James L. Bodkin[2], Stephen C. Jewett[3], Daniel H. Monson[2], Dennis Jung[1]

[1]Coastal Resources Associates, Inc., 1185 Park Center Dr., Ste. A, Vista, California 92083, USA

[2]Biological Resources Division, U.S. Geological Survey, Alaska Science Center, 1011 E. Tudor Rd., Anchorage, Alaska 99503, USA

[3]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 200 O'Neill Building, Fairbanks, Alaska 99775, USA

ABSTRACT: Interactions between sea otters *Enhydra lutris*, sea urchins *Strongylocentrotus droebachiensis*, and kelp were investigated following the reduction in sea otter density in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill in 1989. At northern Knight Island, a heavily oiled portion of the sound, sea otter abundance was reduced by a minimum of 50% by the oil spill, and from 1995 through 1998 remained at an estimated 66% lower than in 1973. Where sea otter densities were reduced, there were proportionally more large sea urchins. However, except in some widely scattered aggregations, both density and biomass of sea urchins were similar in an area of reduced sea otter density compared with an area where sea otters remained about 10 times more abundant. Furthermore, there was no change in kelp abundance in the area of reduced sea otter density. This is in contrast to greatly increased biomass of sea urchins and greatly reduced kelp density observed following an approximate 90% decline in sea otter abundance in the western Aleutian Islands. The variation in community response to a reduction in sea otters may be related to the magnitude of the reduction and the non-linear response by sea urchins to changes in predator abundance. The number of surviving sea otters may have been high enough to suppress sea urchin populations in Prince William Sound, but not in the Aleutians. Alternatively, differences in response may have been due to differences in the frequency or magnitude of sea urchin recruitment. Densities of small sea urchins were much higher in the Aleutian system even prior to the reduction in sea otters, suggesting a higher rate of recruitment.

KEY WORDS: *Enhydra lutris* · *Strongylocentrotus droebachiensis* · Prince William Sound · Alaska · Keystone species · Top-down control

INTRODUCTION

One of the most well-known paradigms in ecology is that involving interactions between sea otters *Enhydra lutris*, sea urchins *Strongylocentrotus* spp., and kelp (reviewed in Estes & Duggins 1995). Sea otters are considered keystone predators within coastal marine systems of the North Pacific that exert strong top-down control on the structure of the nearshore community (Power et al. 1996). Throughout their range, sea otters reduce densities of large sea urchins, which are a preferred prey. In rocky habitats, this leads to higher densities of kelp, which are less grazed by sea urchins. Thus, the paradigm holds that there are 2 states within the system: one with sea otters, few large sea urchins, and dense kelp; and the other without sea otters, an abundance of large sea urchins, and less dense kelp.

The evidence for the paradigm is mostly of 2 sorts: observations of sea urchins and kelp in (1) nearby areas with and without sea otters (Estes & Palmisano 1974, Estes et al. 1978, Duggins 1980, Breen et al. 1982, Estes

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*E-mail: coastal_resources@compuserve.com

& Duggins 1995), and (2) in a given area before and after recolonization by sea otters after decades of absence (Lowry & Pearse 1973, Laur et al. 1988, Watson 1993, Estes & Duggins 1995, Kvitek et al. 1998). Both types of evidence have led to similar conclusions regarding the generalized effect of the sea otter foraging on kelp forest community structure. Fewer studies have examined the transitions during recolonization by sea otters (Laur et al. 1988, Watson 1993, Estes & Duggins 1995, Konar 2000, in this issue), and only 2 recent studies (Estes et al. 1998, Konar 2000) have examined community response to a reduction in the abundance of sea otters. Yet it is these sorts of observations of dynamic systems that may provide greater understanding of the role of sea otters, and keystone predators in general, in determining community structure.

Here, we describe changes in populations of sea otters, sea urchins *Strongylocentrotus droebachiensis*, and kelp in Prince William Sound, Alaska, following the *Exxon Valdez* oil spill. We present evidence that sea otter densities in heavily oiled parts of the sound remained reduced for at least 9 yr following the spill. We compare sea urchin populations in these areas to those in an unoiled part of the sound, where sea otter densities were about 6 to 15 times higher after the spill, and examine possible cascading effects on benthic algae. We specifically ask (1) Was the observed reduction in sea otter density, maintained over a period of 9 yr, sufficient to result in changes to sea urchins or kelp? and (2) What do observed changes, or lack thereof, suggest regarding the generality of the sea otter-sea urchin-kelp paradigm and the role of keystone predators?

THE SYSTEM

Intense hunting pressure caused sea otters to become nearly extinct during the late 19th century (Riedman & Estes 1988). However, a small remnant population persisted in Prince William Sound (Lensink 1962) and this population expanded during the 1960s and early 1970s. By the late 1980s, sea otters had occupied western Prince William Sound, the area most affected by the oil spill, for at least 2 decades and populations appeared relatively stable (Bodkin et al. 2000). Sea otters in the sound feed mostly on clams, crabs and mussels (Calkins 1978, Garshelis et al. 1986, Doroff & Bodkin 1994), but occasionally prey on sea urchins (Doroff & Bodkin 1994). There are few data on sea urchin densities prior to the expansion of sea otter populations. Intertidal surveys conducted following the 1964 earthquake found sea urchins were 'regular but uncommon' (Haven 1971). However, a survey conducted in 1984 in a portion of the sound not yet oc-

cupied by sea otters found high density patches of large sea urchins in the shallow subtidal (D. B. Irons, J.L.B. and G. R. VanBlaricom unpubl. data). Other diver surveys in shallow water (<30 m) conducted in 1975-76 and 1979, in parts of the sound occupied by sea otters, found few sea urchins (Rosenthal et al. 1977, 1982). Much of the nearshore zone is densely vegetated by kelps *Agarum clathratum*, *Laminaria saccharina*, *Laminaria bongardiana*, and *Nereocystis luetkeana* (Rosenthal et al. 1977, Dean et al. 1996b).

In 1989, the *Exxon Valdez* oil spill killed an estimated 1000 to 2800 sea otters (Garrott et al. 1993). Most of the deaths occurred within Prince William Sound (Garshelis 1997) and mortality was particularly high around northern Knight Island, where an estimated 90% of the sea otters were oiled (Bodkin & Weltz 1990, Bodkin & Udevitz 1994). There was no apparent effect of oil on sea otters within the largely unoiled eastern sound and Montague Island areas.

There was no detectable reduction in sea urchin density as a direct result of the oil spill, and impacts on subtidal kelp were minimal. In surveys conducted a year after the spill, sea urchins were rare at both oiled and unoiled sites, and there was no difference in density between sites (Dean et al. 1996a). Surveys conducted in 1990, 1.5 yr after the spill, indicated that there were proportionally more small plants of some kelp species and higher densities of *Laminaria saccharina* at oiled than at unoiled sites (Dean et al. 1996b). However, there were no differences in either percent cover or biomass for all kelp species combined.

METHODS

Estimates of sea otter abundance. Sea otter densities were compared between a heavily oiled 168 km^2 area around northern Knight Island and an unoiled 90 km^2 area near Montague Island (Fig. 1). Extensive mark-recapture efforts indicated that there was no movement of sea otters between these areas (J.L.B. unpubl. data). The pre-spill estimate of sea otter abundance is based on data from a sound-wide aerial census conducted in June 1973 (Pitcher 1975). We estimated abundance within our study areas by taking subsets of the census data corresponding to these areas. Post-spill estimates are from aerial surveys conducted in July or August in each year from 1993 to 1998 using methods described in Bodkin & Udevitz (1999). A single survey was conducted in 1993 and 1994. Thereafter, 4 to 6 replicate surveys were conducted each year.

There are no reliable estimates of sea otter abundance in our study areas just prior to or just following the spill. Surveys of sea otter abundance along the
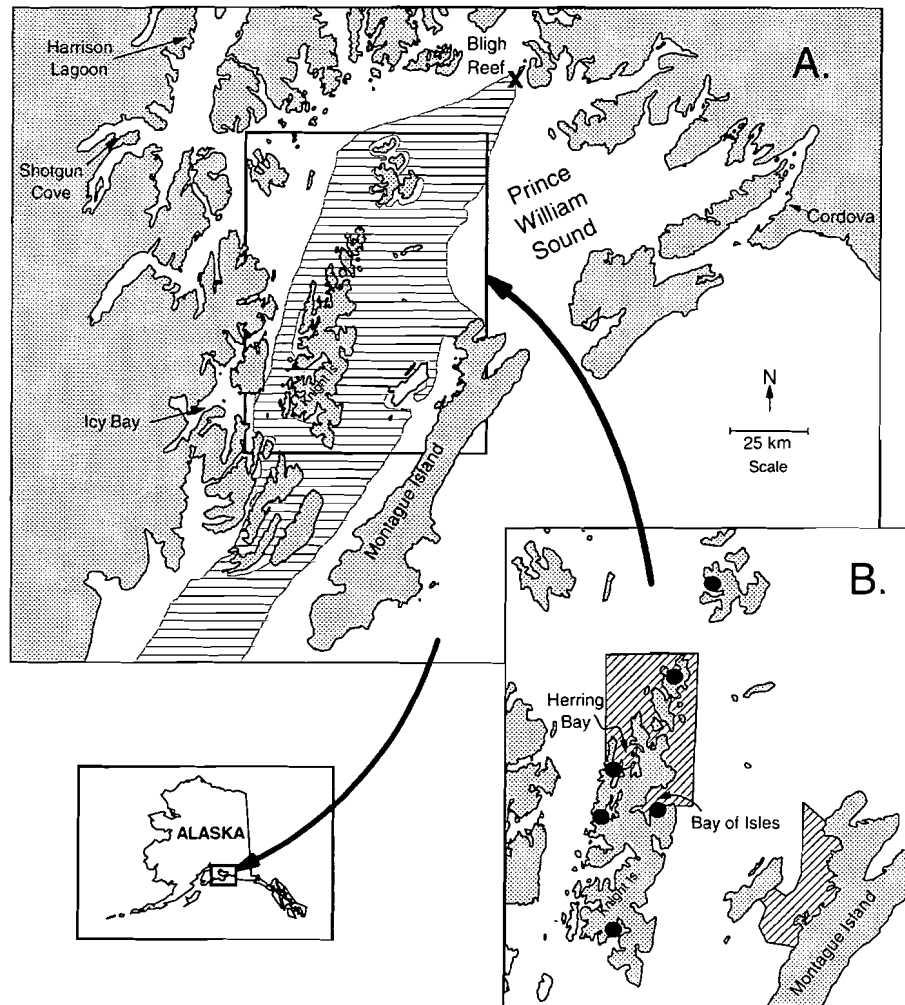
Fig. 1. Location of sampling sites for sea otters, sea urchins, and kelp in western Prince William Sound. The trajectory of oil from the *Exxon Valdez* oil spill is given by the hatched area in (A). This is based on a hind-cast model (Galt et al. 1991) and shoreline oiling surveys (ADEC 1989, ADNR 1991). Survey areas for sea otters are indicated by hatching in (B). Sea urchins were sampled at systematically placed sites along the shorelines in Herring Bay, Bay of Isles, and the hatched area of Montague Island in 1996 and 1997. (●) Sites where kelp and sea urchin density were sampled in 1990, 1993, and 1998

shoreline, conducted from a small boat as an adjunct to sea bird surveys (Burn 1994, unpubl., Johnson & Garshelis 1995), were previously used to estimate the decline in sea otters that resulted from the spill (Garrott et al. 1993, DeGange et al. 1995, Johnson & Garshelis 1995). However, during times when concurrent estimates for the same areas were available for both methods (July 1993, 1996, and 1998), means from aerial surveys differed from boat survey estimates by a factor of 0.3 to 3.6. Boat survey estimates were higher than the aerial survey means in 3 instances and lower in another 3 instances. We chose not to rely on boat survey data because (1) there are known biases in the boat survey methods (Udevitz et al. 1995), (2) boat surveys sampled a smaller proportion of sea otter habitat (generally on the order of 6% vs about 20% for aerial surveys) and inaccuracies were likely to result from small-scale shifts in the distribution of otters, and (3) boat survey estimates did not agree closely with estimates from aerial surveys, which are considered to be more accurate. As a result, we cannot be certain of the relative decline in sea otter density caused by the oil spill. However, the number of sea otters removed from northern Knight Island in 1989 can be estimated, and based on this, we estimate the minimum population density prior to the spill. The number of sea otters removed is probably a close approximation of the pre-spill density given that mortality of sea otters in this region was high (Bodkin & Udevitz 1994) and that considerable effort was made to remove any surviving otters from here because they were either oiled or at risk of being oiled (Bodkin & Weltz 1990).

The number of sea otters removed as a result of the spill is based on the number of carcasses recovered, an estimate of the number of carcasses that were not recovered, and the number of sea otters removed for rehabilitation. We assumed that the number of carcasses drifting out of the study area equaled the number drifting in, and we excluded fetuses and sea otters judged to have died prior to the spill. A number of recovered carcasses and live sea otters removed for rehabilitation, all of which were taken from the sound, did not have specific collection sites identified. We assumed that the proportion of these that was from our study area was equal to the proportion of sea otters with known collection sites that came from our study area. We estimate that 59% of the dead sea otters were recovered. This was based on the model of Garshelis (1997), which estimated carcass recovery rate based on the proportion of beaches that were searched, and the likelihood of finding a beached carcass on searched beaches. DeGange et al. (1994) gave a lower estimate (20%), but this was for the entire spill area, including locations outside of the sound, where search efforts and hence carcass recovery rates were lower. The number of otters removed, compared to the number of otters observed at northern Knight Island in 1993 through 1998, gave a minimum relative reduction in otter abundance that occurred following the spill and was sustained for years afterwards.

Sea urchins in areas of high and low sea otter density, 1996 and 1997. Sea urchin density and size distributions were compared between a heavily oiled area with reduced sea otter densities and an unoiled area where sea otter densities were unaffected by the spill and remained high. Densities and size distributions were estimated from approximately 68 km of shoreline in Bay of Isles and Herring Bay, on northern Knight Island, and along approximately 51 km of shoreline on Montague Island (Fig. 1). These were subsets of the areas in which aerial sea otter surveys were conducted. Twenty-nine to 30 different, systematically selected shoreline segments, each 200 m long, were sampled in each year. On each selected segment, we sampled on randomly placed transects placed within each of 3 depth strata: deep subtidal (−5 to −10 m), shallow subtidal (−0.5 to −5 m), and intertidal (+0.5 to −0.5 m). All depths are relative to mean lower-low water. Subtidal transects were sampled by divers. Sea urchins from within a 50 m long by 0.5 m wide transect, placed parallel to shore, were counted and measured. All movable rocks were turned to search for sea urchins. We could confidently find sea urchins approximately 5 mm or greater, but smaller individuals were difficult to see and were not sampled. Biomass of sea urchins was estimated based on a regression of dry mass versus test diameter from a subsample of 62 sea

urchins ranging in size from 5.0 to 46.8 mm. The resulting function was: dry mass (g) = 0.00065(test diameter $[mm])^{2.52}$, $r^2 = 0.96$.

We also measured sea urchin density in the lower intertidal zone along gently sloping cobble beaches, where we observed widely scattered aggregations of sea urchins that were unlikely to be adequately characterized by our systematic sampling. Based on a visual shoreline census made from a boat, and on aerial photographs, we identified 3100 m and 2200 m of shoreline fitting this description within the Knight and Montague Island study areas, respectively. These shorelines were divided into 100 m segments, and 4 segments from each study area thought to be the most promising sea urchin habitats were sampled along with 8 (at Knight Island) and 9 (at Montague Island) additional randomly selected segments. Six of the 12 segments at Knight Island and 3 of the 13 segments at Montague Island had aggregations of sea urchins. We marked the boundaries and estimated the areal extent of each aggregation, and based on the size and relative density of sea urchins observed, either censused the entire aggregation or sampled within randomly placed quadrats or transects to estimate sea urchin density.

Sea urchins and kelp in an area of reduced sea otter abundance, 1990 to 1998. The density of sea urchins and the percent cover and biomass (blotted wet weight) of kelp were measured at sites in 6 bays within the general region of Knight Island (Fig. 1). The extent of shoreline oiling at these sites varied, but all were within the oil spill's trajectory where the density of sea otters was reduced following the spill. These sites were used to estimate oil spill impacts on kelp and invertebrates in 1990 (Dean et al. 1996a,b) and re-sampled in the summers of 1993 and 1998. There is no comparable time series for sea urchin density from Montague Island, and no kelp density data from Montague Island. Sea urchins were counted within a 2 m swath along each of three 30 m long transects at each site. Visual estimates of percent cover of kelp were made in 4 randomly placed 0.25 m² quadrats on each transect and the kelp within each quadrat were counted by species and harvested for determination of biomass (blotted wet mass). Transects were placed at random positions along the shore and at a random depth between 2 and 11 m. Different randomly selected transect locations were sampled in each year.

Statistical analyses. We tested the null hypothesis of no difference in sea otter density between areas, among years, and their interaction with a 2-way, fixed-effect ANOVA. Only data from 1995 through 1998, in which replicate surveys were conducted, were used in the analysis. Estimates of density from each replicate survey were square-root arcsine transformed to equalize variances. Assumptions of normality and homo-

geneity of variance were met once data were transformed. Bonferroni's multiple comparisons (Milliken & Johnson 1984) were used to contrast years within each study area.

Sea urchins were patchily distributed, and were found at only a small proportion of systematically selected shoreline segments that were sampled. As a result, we were unable to statistically test hypotheses of differences in mean density. Instead, we tested the hypothesis of no differences in the frequency of occurrence of sea urchins between depth strata, sampling areas, years, and their interaction with a 3-way log-linear model (Grizzle et al. 1969) using the SAS®, catmod procedure (SAS 1988). We also tested the hypotheses that, at intertidal sampling sites where sea urchins were present, there was no difference in mean density between areas and years, and no interaction between area and year. Densities were log-transformed in order to equalize variances.

The hypothesis of no difference in the proportion of large sea urchins (>20 mm test diameter) between areas and years was tested using a log-linear analysis as described above. A 20 mm size category was selected because sea otters are size-selective predators, and when larger sea urchins are available, they generally prey on individuals larger than 20 mm (Estes & Duggins 1995). All sea urchins collected from each area were pooled to obtain a reasonable sample size.

Temporal trends in the density, percent cover, and biomass of kelp within the Knight Island area were examined using a 1-way ANOVA. Sites were treated as experimental units and site means were used as replicates. All data met assumptions of normality and homogeneity of variance, and no transformation of the data was required.

RESULTS

Sea otter abundance

The average density of sea otters at northern Knight Island between 1993 and 1998 was 0.46 ind. km^{-2} (77 ind. in a 168 km^2 area), roughly one-third of the 1973 pre-spill estimate of 1.41 ind. km^{-2} (Fig. 2). In contrast, pre- and post-spill population estimates from Montague Island were similar, averaging 5.37 ind. km^{-2} in 1973, compared to 5.21 ind. km^{-2} between 1993 and 1998. From 1995 through 1998, the average density of sea otters at northern Knight Island was the same as in 1993 (0.46 ind. km^{-2}) and there was no significant change in density with time. On the other hand, sea otter densities at Montague Island increased significantly between 1996 and 1997. Even prior to the oil spill, sea otter densities were higher at Montague,
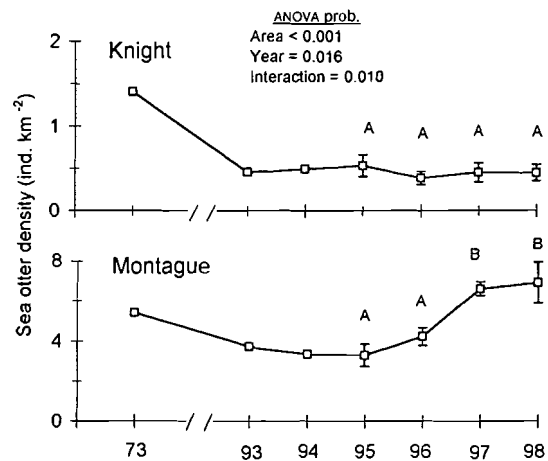

Fig. 2. Population estimates for sea otters in the northern Knight and Montague Island study areas between 1973 and 1998. Replicate surveys were conducted in each year between 1995 and 1998, and error bars are given representing ±1 standard error. The number of surveys conducted varied from 5 (in 1995 through 1997) to 6 (in 1998) at Montague Island, and from 4 (in 1995, 1997, and 1998) to 5 (in 1996) at Knight Island. Results of a 2-way ANOVA conducted to test for differences between areas (Montague and Knight Islands), years (1995 to 1998), and their interaction are given. Like letters indicate yearly means within each area that did not differ significantly based on Bonferroni contrasts of years within areas. Note the difference in scales for Montague and Knight Islands

probably because shorelines are less steeply sloped there and there is proportionally more shallow water where sea otters prefer to feed. After the oil spill, the magnitude of the difference between islands was greater, averaging about a full order of magnitude.

An estimated 165 sea otters were removed from the northern Knight Island area subsequent to the oil spill in 1989 (Fig. 3). Sixty-one oiled sea otter carcasses were recovered from northern Knight Island. We estimate that an additional 24 of the carcasses with unspecified Prince William Sound collection sites came from this area. An estimated 60 sea otter carcasses were not recovered. In addition, 17 sea otters were removed from this study area for rehabilitation. Finally, we estimated that 3 sea otters in rehabilitation with unidentified collection sites came from the study area. This totals 165 sea otters (0.98 ind. km^{-2}) that were removed from the northern Knight Island area. We use this estimate as the minimum pre-spill sea otter density within this area. Based on this minimum, and on the number of sea otters present in 1993 (77), we estimate that there was a relative reduction in sea otter density of at least 53% as a result of the spill. There was a 68% decline in sea otter abundance between 1973 and 1993, but some of this may have occurred prior to the spill in 1989. Alternatively, the numbers of

Table 1. Percentage of sites with sea urchins *Strongylocentrotus droebachiensis* present and geometric mean densities (back-transformed means of log[ind. m^{-2} + 0.1]) of sea urchins within northern Knight and Montague Islands, 1996 and 1997. MLLW: mean lower-low water

Depth stratum	Area	Year	n	% with sea urchins	Geometric mean density (ind. m^{-2})
Intertidal	Knight	1996	30	53.3	0.039
(+0.5 to −0.5 m, MLLW)		1997	30	26.6	0.014
	Montague	1996	30	20.0	0.007
		1997	29	48.3	0.055
Shallow subtidal	Knight	1996	30	10.0	0.003
(−0.5 to −5.0 m, MLLW)		1997	30	10.0	0.003
	Montague	1996	30	3.3	0.001
		1997	28	14.3	0.004
Deep subtidal	Knight	1996	30	10.0	0.002
(−5.0 to −10.0 m, MLLW)		1997	29	3.4	0.001
	Montague	1996	24	0.0	0.000
		1997	22	4.5	0.002

sea otters could have been higher at northern Knight Island before the spill in 1989 than in 1973.

Sea urchin density, size distribution, and biomass

In 1996 and 1997, sea urchins were relatively rare at both the northern Knight Island and Montague study areas. On systematically selected transects, the geometric mean density within every depth stratum, area, and year was less than 0.06 ind. m^{-2} (Table 1). In almost all cases, sea urchins were found under cobble or boulders, and were not visible unless rocks were overturned. There was a significant interaction in the frequency of occurrence of sea urchins between areas

and years (Table 2). Sea urchins were found at significantly more sites at northern Knight Island than at Montague Island in 1996, but the frequency of occurrence did not differ between areas in 1997 (Tables 1 & 2). Overall effects of area (over both years) and year (over both areas) were not significant. The frequency of occurrence of sea urchins was higher in the intertidal zone than in the subtidal (both shallow and deep strata) at both northern Knight and Montague Islands. At intertidal sites with sea urchins present, densities were significantly higher in 1997 than in 1996, but there were no differences in density between northern
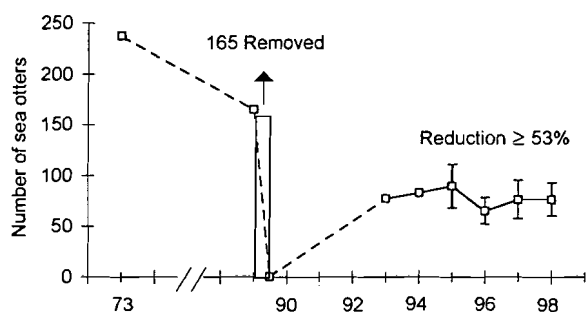

Fig. 3. Numbers of sea otters at northern Knight Island, Prince William Sound, between 1973 and 1998. The 1973 value is from an aerial census. Estimates from 1993 to 1998 are from aerial surveys. Replicate surveys (n = 4 in 1995, 1997, and 1998; n = 5 in 1996) were conducted after 1994 and means ± 1 standard error are given for these. The 1989 data are minimum values based on the estimated number of sea otters removed from the area as a result of the *Exxon Valdez* oil spill. The dashed line indicates uncertainty in trends that result from having only estimated minimums in 1989

Table 2. Results of log-linear categorical analysis of the frequency of occurrence of sea urchins *Strongylocentrotus droebachiensis* within different depth strata (intertidal, shallow subtidal, deep subtidal), areas (Knight and Montague Islands), and years (1996 and 1997)

Source	df	Chi-square	p
Intercept	1	2069.30	<0.001
Depth stratum	2	46.47	<0.001
Area	1	1.05	0.305
Year	1	0.23	0.629
Depth stratum × Area	2	0.29	0.867
Depth stratum × Year	2	0.86	0.649
Area × Year	1	12.20	<0.001
Depth stratum × Area × Year	2	5.69	0.058
Contrasts between depth strata			
Intertidal vs shallow	1	29.51	<0.001
Intertidal vs deep	1	46.24	<0.001
Shallow vs deep	1	1.91	0.167
Contrasts of areas within years			
Knight vs Montague (1996)	1	9.82	0.002
Knight vs Montague (1997)	1	2.74	0.090

Knight and Montague Islands (Fig. 4). Geometric means were less than 0.5 ind. m⁻² in both areas.

Higher densities of sea urchins were found within widely spaced aggregations, especially on Knight Island. Searches of gently sloping intertidal cobble beaches in 1996 revealed 6 such aggregations at Knight Island and 3 at Montague Island. The geometric mean density within these aggregations was 12.11 ind. m⁻² at Knight Island and 0.42 ind. m⁻² at Montague Island and differed significantly between areas (Student's $t = 5.88$, $p < 0.01$). The average areal extent of aggregations was about 2.5 times higher at Knight Island (mean = 253 m² at Knight Island and 104 m² at Montague Island) but did not differ significantly between areas (Student's $t = 1.92$, $p = 0.096$).

Fig. 5. Size-frequency distribution of sea urchins *Strongylocentrotus droebachiensis* at northern Knight and Montague Islands in 1996 and 1997

Few large sea urchins were found at either northern Knight or Montague Islands (Fig. 5). The largest sea urchin had a test diameter of 53 mm. Only 4.9% at Knight Island and 2.9% from Montague Island were greater than 40 mm (based on averaged percentages from 1996 and 1997). The majority of the sea urchins from Montague Island were 15 mm or less, and the majority from Knight Island were 25 mm or less. Size-frequency distributions differed between areas, and the proportion of sea urchins that were larger than 20 mm was higher at Knight Island than at Montague Island (Fig. 4). Also, there were significantly higher frequencies of large sea urchins in 1996 than in 1997 (Fig. 4).

The biomass of sea urchins was low at both northern Knight and Montague Islands, averaging less than 0.06 g dry mass m⁻² at both areas in 1996 and 1997 (Fig. 4). We were unable to test for statistical differences in biomass between areas and years because there were no urchins found at a large number of sites. However, the range in yearly mean biomass overlapped between areas and mean biomass was higher at Knight in 1996 and higher at Montague in 1997 (Fig. 4).
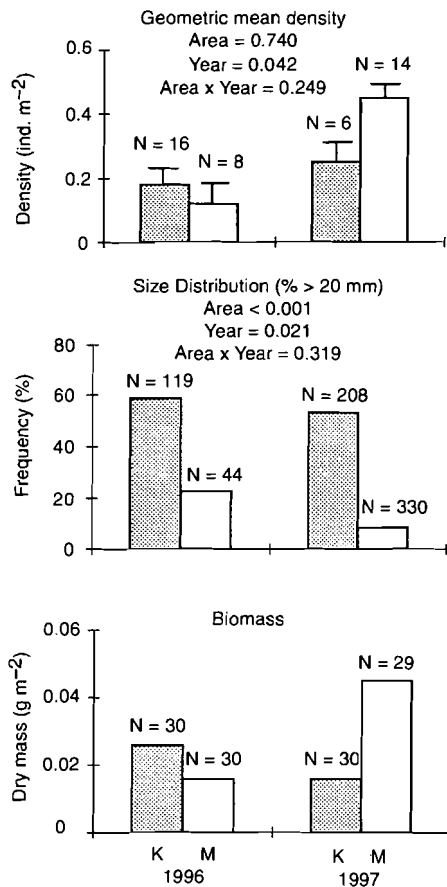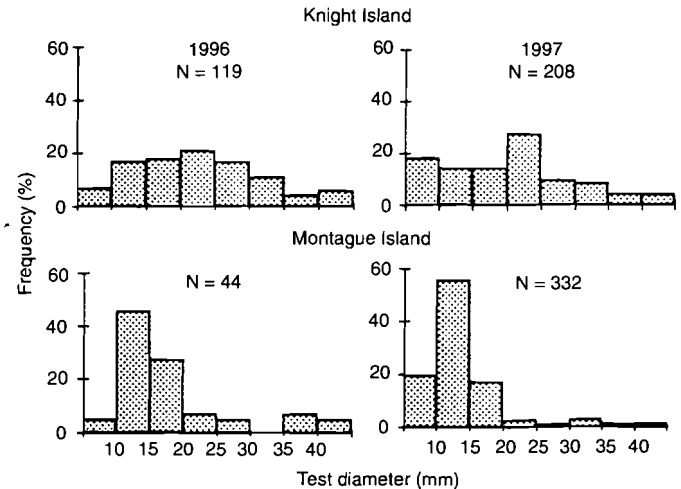

Fig. 4. Density, size distribution, and the mean biomass of sea urchins *Strongylocentrotus droebachiensis* at northern Knight (K) and Montague (M) Islands in 1996 and 1997. Density values are geometric means (plus 1 standard error) for those intertidal sites where sea urchins were present. Size distributions are expressed as the percentage of sea urchins with test diameters greater than 20 mm. Results of a 2-way ANOVA (for density) or a 2-way log-linear analysis (for size distribution) are given

Temporal trends in sea urchins and kelp in an area of reduced sea otter density

Within the area where sea otter densities were reduced, densities of sea urchins remained low and kelp densities remained high in 1990, 1993, and 1998. Geometric mean densities of sea urchins in subtidal surveys conducted at 6 sites within the Knight Island

Table 3. Geometric mean density of sea urchins *Strongylocentrotus droebachiensis* at 6 subtidal sites within the Knight Island. Also given are mean biomass, percent cover, and density of kelp greater than 10 cm in height at these sites in 1990, 1993, and 1998. Standard errors are given in parentheses. Also given are probabilities of no difference in means between years based on 1-way ANOVAs. No test was performed for sea urchin data because of the large number of sites without sea urchins. All sites had reduced densities of sea otters

Year	Sea urchin geometric mean density (ind. m^{-2})	Kelp biomass (g wet mass m^{-2})	Kelp cover (%)	Kelp density (ind. m^{-2})
1990	0.007	1449 (222)	62.9 (3.06)	8.28 (0.85)
1993	0.015	1222 (313)	66.4 (8.02)	12.67 (4.49)
1998	0.002	908 (229)	53.3 (6.13)	10.89 (2.39)
p	No test	0.290	0.272	0.499

area from 1990 through 1998 ranged from 0.002 to 0.015 ind. m^{-2} (Table 3), and were similar to densities observed in subtidal strata at northern Knight Island and Montague Island in 1996 and 1997 (0.004 ind. m^{-2}). The density, percent cover, and biomass of kelp at these sites did not differ significantly among years (Table 3). Algal cover ranged from 53 to 66%. Almost all hard substrata had kelp, and bare areas were largely restricted to sand patches interspersed among cobbles and boulders or nearly vertical rock walls. These surveys were conducted over a limited area, but the lack of sea urchins and relatively high density of kelp within the area of reduced sea otter density were widely observed in non-quantitative surveys conducted over much larger areas. From 1989 through 1998, we made over 1000 dives within the study area, and made qualitative observations over an estimated 40 000 to 50 000 m^2. During these qualitative surveys, only 2 subtidal aggregations of sea urchins were observed and only 1 had an associated barren area with little or no kelp. Both aggregations of sea urchins disappeared after 3 yr as extensive searches of these areas revealed no remaining sea urchins.

DISCUSSION

A keystone species is one that has a large effect on community structure that is disproportionate to its abundance (Power et al. 1996). Many, but not all, are predators that influence structure by consuming prey. The response of a community to a keystone predator depends in part on the abundance of the predator, which at times may be regulated by factors other than prey abundance (e.g. Fagan & Hurd 1994, Estes et al. 1998). Most studies have evaluated the importance of predators on community structure by comparing extremes (with or without the predator). Studies evaluating the effects of intermediate predator densities are

rarer, but suggest that prey often respond in a non-linear manner to changes in predator abundance (Hurd & Eisenberg 1984, Andrew & Underwood 1993, Fagan & Hurd 1994). Even in cases where keystone predators are completely removed from a system, community responses may vary with location or time (reviewed in Power et al. 1996). Understanding the range in variation in response and the causes for this is important for understanding functional relationships between predator and prey and, in particular, in predicting how systems may respond to perturbations of predators.

In rocky subtidal systems of the North Pacific, it has been widely demonstrated that where sea otters are abundant large sea urchins are rare and kelp is abundant. The alternative state is represented by no sea otters, higher densities of large sea urchins, and less abundant kelp (Lowry & Pearse 1973, Estes & Palmisano 1974, Estes et al. 1978, 1998, Duggins 1980, Breen et al. 1982, Laur et al. 1988, Watson 1993, Estes & Duggins 1995, Kvitek et al. 1998). The response of communities during transitions in sea otter abundance (from either low to high or vice versa) is less predictable. In some cases, sea urchin densities have dramatically declined and kelp abundance has increased within a few months of sea otter reoccupation (Laur et al. 1988, Watson 1993). However, little response was observed in the 10 yr following reoccupation by sea otters in the Semichi Islands, Alaska (Konar 2000). An approximate 90% reduction in sea otters in the western Aleutian Islands was followed by a 9-fold increase in sea urchin *Strongylocentrotus polyacanthus* biomass and a nearly 90% reduction in kelp (Estes et al. 1998). In contrast, in both the Knight Island area of Prince William Sound (our study) and the Semichi Islands (Konar 2000), a reduction in sea otter abundance on the order of 50% resulted in no apparent effect on sea urchin biomass, and little or no change in kelp abundance.

Differences in community response to changes in predator abundance may relate in part to the magnitude of the change and the non-linear nature of the response by prey. Both the relative and absolute reductions in sea otter population density observed by Estes et al. (1998) in the western Aleutian Islands were apparently larger than those we observed in Prince William Sound. While reductions in sea otter abundance in heavily oiled parts of Prince William Sound may have approached or exceeded 90% immediately following the oil spill in 1989, we estimate that the population density was about one-third of the pre-spill

(1973) density in 1993 to 1998. The number of remaining sea otters may have been high enough to inhibit sea urchin population growth in our study areas, but not in the western Aleutian Island sites. Even though sea urchin densities within our study areas were low, sea otters continued to prey on sea urchins. In a collection of 102 sea otter scats from western Prince William Sound in winter 1998, 29% had sea urchin remains (J.L.B. unpubl. data). The continuing effect of sea otter predation in our study area was reflected in the size distributions of sea urchins. While there were proportionally more large urchins where sea otter densities were reduced on northern Knight Island, there were very few large sea urchins in either of our study areas.

Differences in community response to changes in sea otter abundance may also result from what has been termed context dependence (Power et al. 1996). The role of a keystone predator can vary with location or time (reviewed in Power et al. 1996), and may depend on the relative frequency or magnitude of recruitment of prey (Menge et al. 1994, Robles 1997). The difference in response to a reduction in sea otters in Prince William Sound versus the western Aleutian Island sites examined by Estes et al. (1998) may have been related to the much higher density of small sea urchins in the Aleutians that was maintained even in the presence of sea otters. Prior to the reduction in sea otters in the western Aleutians, sea urchin densities were upwards of 100 ind. m^{-2}, even where sea otters were abundant for decades (Estes & Duggins 1995). In contrast, densities in Prince William Sound averaged less than 0.06 ind. m^{-2}, and even in denser inter-tidal aggregations on Knight Island, averaged only 12 ind. m^{-2}.

The relatively low density of small sea urchins observed in Prince William Sound is similar to that observed by Estes & Duggins (1995) in Southeast Alaska. At locations near Sitka where there were few sea otters, Estes & Duggins found high densities of large sea urchins, with relatively few smaller individuals. At nearby sites that sea otters had recently colonized, almost all of the sea urchins were eaten and very few individuals remained. They attributed the relative lack of small sea urchins at Southeast Alaska sites compared to the Aleutians to a relative lack of sea urchin recruitment. We have not measured recruitment in Prince William Sound, but it is likely that the relatively low density of small sea urchins, and the lack of response to reductions in sea otters, may be related to relatively low frequency of widespread sea urchin recruitment.

While we suspect that Prince William Sound may support lower rates of sea urchin recruitment than the western Aleutians, there is ample evidence to suggest that sea urchin abundance in Prince William Sound would be higher in the total absence of sea otters. A survey conducted in northern Prince William Sound in 1984 found extremely high densities of relatively large sea urchins in Shotgun Cove, an area not yet reoccupied by sea otters (D. M. Irons, J.L.B. and G. R. VanBlaricom unpubl. data). Densities of sea urchins exceeded 1000 m^{-2} in some areas, 7.8% were over 40 mm test diameter, and the maximum size was 57 mm. In contrast, in nearby Harrison Lagoon, which was recently recolonized by sea otters, sea urchin densities were high (maximum of 296 m^{-2}) but all were small (mean test diameter <15 mm and maximum test diameter = 29 mm). Second, we observed 2 large aggregations of sea urchins during the course of our studies: 1 in Bay of Isles and 1 in the mouth of Icy Bay. In 1995, preliminary observations suggested that maximum densities in these aggregations were in the range of 20 to 50 m^{-2}. Mean test diameters were about 25 mm, near the minimum size usually consumed by sea otters (Estes & Duggins 1995). Each aggregation covered an area of 100 m^2 or more. In spite of obtaining accurate positions for these aggregations, we were unable to relocate any sea urchins at these sites when we returned to do more quantitative surveys in subsequent years. Finally, in 1998, over 700 small (mean test diameter <20 mm) sea urchins were found in several trawl samples from depths of about 30 m at Montague Island (D.H.M. & A. Fukuyama unpubl. data). The area sampled and the efficiency of the trawl could not be accurately determined, making it impossible to accurately estimate sea urchin density. However, it is likely that the density of sea urchins was over 1 m^{-2}, and probably much higher. These observations suggest that Prince William Sound is capable of supporting locally dense patches of sea urchins, and in the absence of sea otters, sea urchins within these patches can grow to 40 mm or more.

Predation on sea urchins by sea stars and birds may also have contributed to the apparent lack of response by sea urchins to reductions in sea otters. Sunflower sea stars *Pycnopodia helianthoides* and glaucous-winged gulls *Larus glaucescens* are known predators of sea urchins (Duggins 1980, Irons et al. 1986) and both are abundant in Prince William Sound (Wiens 1995, Dean et al. 1996a). *P. helianthoides* densities averaged more than 0.1 m^{-2} in rocky subtidal habitats, and were greater than 1 m^{-2} at some sites (Dean et al. 1996a). In the intertidal zone, densities of adult *P. helianthoides* averaged 0.16 m^{-2} at Knight Island and were significantly higher than the 0.03 m^{-2} at our Montague Island sites (p < 0.01, *t*-test, T.A.D. & S.C.J. unpubl. data). Sea urchins are rarely found in the stomachs of *P. helianthoides* collected from Prince William Sound (Gage 1998, S.C.J. unpubl. data), but we cannot rule out that sea star or bird predation helped to limit sea urchin populations.

We also cannot dismiss the possibility that the lack of a stronger response by sea urchins in Prince William Sound was related, in part, to impacts associated with the oil spill. While Dean et al. (1996a) found no evidence of an impact of oil on sea urchin populations, very few sea urchins were found at either oiled or unoiled sites, and the power to detect differences was low. For several more abundant intertidal and subtidal invertebrates, for which differences were more easily detected, higher densities were observed in unoiled versus heavily oiled areas (Dean et al. 1996a, Highsmith et al. 1996, Jewett et al. 1999).

While we observed no substantial increase in sea urchin biomass or decrease in kelp biomass in the 9 yr following the reduction in sea otters in 1989, future changes are possible. The number of sea otters at northern Knight Island has remained low, and a strong recruitment year for sea urchins could result in an increase in sea urchin biomass. Thus, we may have observed a long lag in response to a reduction in predators, rather than a lack of response. Such lags are expected in cases where recruitment of prey is episodic.

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