

**Testing a charismatic paradigm:  
Consequences of a growing sea otter population for nearshore benthic communities  
along the south shore of the Strait of Juan de Fuca.**

**Final Project Report  
Marine Ecosystem Health Program**

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**Abstract**

Sea otters are known to have ecologically and economically significant effects on coastal ecosystems of the North Pacific Rim as a result of their foraging activities and preferences. The sea otter population off Washington State was hunted to extinction early in the twentieth century, but was restored by translocation from Alaska in 1969 and 1970. The population now numbers about 550 animals and ranges from Cape Flattery to Kalaloch on the outer coast of Washington. During winter months between 1995 and 2000, a large group of subadult male sea otters occupied nearshore habitat on the western portion of the south shore of the Strait of Juan de Fuca (SJDF). The group of otters returned to outer coast habitats each spring during the period. In each successive year during the period, the area of occupancy by the sea otters was farther to the east. By winter of 2000 sea otters were seen as far east as Pillar Point. Since 2001, winter occupation of western SJDF by sea otters has not occurred. The purpose of this project was to resample abundances and size distributions of benthic invertebrates and algae at nineteen sites on the south shore of the central SJDF between Kydaka Point and Port Angeles. The sites were first established and surveyed in summer 1997, before any sea otters had been observed within the range of the sites. By the time of our resurvey, done in summer 2001, the westernmost eleven of the nineteen sites were within the range occupied by sea otters during winter months between the surveys. The 2001 resurvey data were compared with survey data gathered in 1997 to test hypotheses regarding direct effects of sea otters on prey populations and shellfish fisheries, and indirect effects of sea otter foraging on kelp forest communities in the region. We found that patterns of change in preferred sea otter prey populations in the eleven westernmost sites between 1997 and 2001 differed from patterns in the easternmost eight sites, and were generally consistent with known effects of sea otter predation based on studies in other locations. In the case of sea urchins, effects of harvest by the urchin fishery complicate our ability to definitively attribute observed changes to sea otter foraging. Changes in kelp forest communities between 1997 and 2001 were generally not consistent with predictions of models linking sea otter foraging with increased abundance, diversity, and productivity in kelp forest ecosystems. We conclude that continued use of SJDF habitats will cause reduction in preferred prey populations and reduced yields in fisheries for crabs, clams, and possibly sea urchins. We conclude that factors regulating kelp forest community structure in SJDF relate primarily to storm disturbance and substratum instability, and not to effects of sea otter predation on dominant grazers. The enigmatic pattern of use of SJDF habitat by sea otters since 2001 adds uncertainty to long-term predictions for interactions of sea otters and coastal ecosystems in SJDF. Long-term predictions are also complicated by the potential for eventual merging of the Washington sea otter population with the growing sea otter population on the outer coast of Vancouver Island, British Columbia, Canada.

## Introduction

The sea otter population off the Washington coast once ranged from the Columbia River to Discovery Bay and the San Juan Islands, but was hunted to extinction between 1741 and 1911 during a poorly regulated multinational fur trade. The 1911 Treaty for the Preservation and Protection of Fur Seals (37 Stat. 1542) included an Article protecting sea otters from further harvesting. The treaty effectively ended the harvest of sea otters and allowed remnant populations to begin recovery. At a workshop in 1997, total sea otter numbers were estimated to be 126,000 worldwide, (Gorbics et al. 2000), with much of the original North American range still uninhabited. As a consequence of recent downward trends in Alaskan populations, total sea otter numbers are now thought to be in rapid decline.

In the summers of 1969 and 1970, fifty-nine sea otters (forty-one females, eighteen males) were reintroduced to Washington from Alaska (Bowlby et al., 1988). The first group was released in the open ocean near Point Grenville where fourteen of the otters died a few days after release as the result of fur soiling and stress of travel, and two died from gunshot wounds (Kenyon 1969). The second group was released in more favorable sea otter habitat within the coastal portion of Olympic National Park at La Push. No immediate fatalities were documented following the release at La Push (Jameson, 1998b). However, no more than ten otters were counted in Washington waters through 1976 (Jameson et al. 1982, Bowlby et al. 1988) when the first pups were discovered. From the first systematic survey in 1977 through the 1980s, the Washington population of sea otters increased steadily with a maximum annual growth rate of 20% per yr (Jameson et al. 1986, Jameson 1998a).

The Washington population of sea otters now numbers about 550 animals and, until 2001, was growing at an estimated annual rate of 8.8%/yr (Biological Resources Division, US Geological Survey [BRD/USGS], unpublished data). The 2002 survey indicated a reduction of population growth rate, with little change in numbers between 2001 and 2002. The recent surveys have found sea otters ranging from Destruction Island northward to Tatoosh Island and Cape Flattery (BRD/USGS, unpublished data). During winter seasons from 1995 to 2000, a large group of male otters was observed in the western Strait of Juan De Fuca (SJDF). In each successive year after 1995, the winter group of sea otters was found farther to the east in SJDF. By winter 2000, sea otters were found as far east as Pillar Point (BRD/USGS, unpublished data; Washington Department of Fish and Wildlife, unpublished data). In each subsequent spring season, the male group returned to outer coast habitats south of Cape Flattery. Since winter 2000, very few sea otters have been found within SJDF, and the pattern of winter use of western SJDF apparently has ended, at least temporarily.

Sea otter predation may alter nearshore communities both directly and indirectly. The direct effects include significant reductions in prey density, shifts in size frequency distribution toward smaller individuals, and increased prey populations in cryptic habitats such as cracks and crevices where prey items are protected from sea otters (Ebert, 1968; Lowry and Pearse 1973; Estes and Palmisano 1974; Estes and Duggins 1995; Kvittek et

al. 1989, Kvitek et al. 1998, Fanshawe et al. 2003). Benthic surveys along the Washington coast have indicated that typical prey species for sea otters are significantly more abundant to the north and east of the sea otter's current range than within that range or to the south (Kvitek et al. 1989, Kvitek et al. 1998.).

Extensive work has been done to assess the link between direct ecological effects of sea otter foraging with indirect effects resulting from removal of prey by sea otters. Indirect sea otter effects have been examined in several types of natural communities in California, British Columbia, Alaska, and Russia as well as along the Washington coast. In some kelp forest communities, foraging sea otters limit the number, size, and microhabitat distribution of sea urchin populations, thereby controlling grazing and facilitating the proliferation of diversity and biomass in algal species (e.g. McLean 1962, Estes and Palmisano 1974, Estes et al. 1978, Breen et al. 1982, VanBlaricom and Estes 1988, Watson 1993, Estes and Duggins 1995, Kvitek et al. 1998). Kelp forests enhanced by the reduction of grazing support higher secondary productivity, promoting increased growth rates of suspension feeders (Duggins et al, 1989), increased biomass and diversity of fishes, habitat for reef fishes and nursery grounds for young *Sebastes* spp. (Bodkin 1988, Ebeling and Laur 1988). In soft bottom communities (e.g. Wade 1975, Estes et al. 1981, VanBlaricom 1987, 1988, Kvitek and Oliver 1988, 1992, Kvitek et al. 1988, Jameson 1995), sea otters excavate large volumes of sediment while foraging, creating pits in which scavengers aggregate and feed. Additionally, shells discarded while feeding create an increase in hard substratum for recruitment of laminarian kelps and sessile invertebrates such as anemones. In the rocky intertidal community VanBlaricom (1988) discovered that sea otters create gaps in mussel beds while foraging, freeing space for competitively inferior species, and thereby fostering increased local species diversity.

Sea otters often prefer to forage on benthic invertebrate species that are also taken in fisheries. The result is a number of circumstances in which conflicts exist between shellfish fishery interests and sea otter populations (e.g., Estes and VanBlaricom 1985). Dungeness crabs, geoducks and other clam species, sea cucumbers and sea urchins are the most important invertebrate fisheries in SJDF. The fisheries include tribal subsistence and commercial harvests, as well as non-tribal commercial and recreational harvests (Clallam County Marine Resources Committee, 2001). A review by Gerber and VanBlaricom (1999) indicated a strong and economically significant potential for future conflicts between a growing sea otter population and the Dungeness crab and sea urchin fisheries in SJDF. Effects of sea otters on clam and cucumber fisheries were described as more difficult to predict, but were also expected to be significant.

In 1997, nineteen sites in SJDF were surveyed as the first step in assessing the potential for sea otters to influence prey populations and benthic communities (Figure 1). At that time, none of the sites had been occupied for any significant time period by sea otters. Results of the 1997 surveys were described by Carter and VanBlaricom (1998), a copy of which is appended to this Final Report. Between 1997 and 2001, sea otters were observed to range across eleven of these study sites during the winter months. We completed a resurvey of the nineteen sites in summer 2001, with funding from the Marine Ecosystem Health Program and the Washington Cooperative Fish and Wildlife Research

Unit. Here we report observed changes in invertebrate and algal populations between 1997 and 2001. We discuss observed changes between surveys in the context of recent patterns of habitat use in SJDF by sea otters, with consideration of other environmental factors that may account for changes in our study sites. Our principal goals are to test the hypotheses that the presence of sea otters in SJDF has: 1) altered abundances and size distributions of preferred prey populations in the manner seen in other locations at other times as indicated above; 2) enhanced local biodiversity through various indirect effects associated with foraging as described above; and 3) influenced prey populations in a manner that will cause conflict with tribal, commercial, and recreational fisheries.

## **Methods**

### *General approach*

Our general approach is to compare patterns of change in surveyed benthic populations between 1997 and 2001. We focus on examination of differences in community dynamics between sites in two categories: 1) those that lacked sea otters prior to 1997, but were occupied by sea otters at some time between 1997 and 2001. Sites 1 through 11 (counting from west to east in Figure 1) are in this category; and 2) those that have not been occupied by sea otters at any time in recent history, to our knowledge. Sites 12 through 19 are in this category.

Carter and VanBlaricom (1998) described results of the 1997 surveys, reporting that plant communities at the study sites in the Strait were dominated by ephemeral species, or by juveniles of perennial species. They also reported a prevalence of physically unstable substrata (sand, gravel, and cobble) over solid rocky substrata. In comparable studies in the Strait, Shaffer (1999) reported very high densities of perennial species and a high variance of plant density over time in permanent study sites. Collectively, these results suggest important roles for substratum instability and frequent physical disturbance during winter in structuring kelp-dominated benthic communities within our study areas. In soft substrata, Carter and VanBlaricom reported variable but often high densities of large infaunal clams, especially gapers, roughneck piddocks, and geoducks.

Based on the 1997 data, we established an analytical framework intended to distinguish between two principal hypotheses for relationships of sea otters and benthic communities in our study areas:

1. Disturbance hypothesis: In the disturbance hypothesis, reoccupation of sites by sea otters should have little effect on major features of community structure. Whereas substratum type and other unknown factors may be strongly associated with patterns in benthic communities as seen in 2001, the presence or absence of sea otters in study sites between 1997 and 2001 will not associate strongly with patterns of change in the benthic data.
2. Paradigm hypothesis: In the paradigm hypothesis, changes in densities and sizes of sea otter prey (especially sea urchins, crabs, and clams) should be strongly

associated with pattern of presence of sea otters in the study sites between 1997 and 2001. Such patterns should prevail regardless of substratum type. In the case of rocky substrata, major increases in the densities of adult perennial kelps and associated invertebrates should be associated with sites occupied by sea otters during the period between surveys.

### *Site location and schedule*

During the summer and early autumn of 2001 we conducted benthic surveys along the south coast of SJDF with the purpose of repeating the 1997 surveys. The 1997 sites were located between Kydaka Point and Port Angeles (Figure 1). In 2001, surveys required fifty-two person-dives and a total of thirty-five diver-hours. Work was done primarily from a 5.2 m open skiff. Sites surveyed in 1997 (Carter & VanBlaricom, 1998) were relocated using Global Positioning System (GPS) coordinates that were recorded during the 1997 surveys. The 1997 location data were generated using two different types of GPS unit. Location data for sites 1 through 10 (Kydaka Point eastward to Twin Rivers) were recorded using a Magellan 5000 GPS unit. The Magellan unit was not equipped with differential location capability, and provided data with a minimum error of  $\pm 30$  m. Location data for sites 11 through 20 (Twin Rivers eastward to Port Angeles) were obtained with a Rockwell Precision Lightweight Global Receiver (PLGR). The PLGR was among the earliest GPS units made available to researchers with differential location capability, guaranteeing positional accuracy with a minimum error of  $\pm 3$  m. At that time, differential GPS technology was classified, and our use of the differential PLGR required explicit permission from the U.S. Department of Defense, through a cooperative arrangement with the U.S. Geological Survey.

Since 1997, differential GPS capability has been declassified by the U.S. government, and is now available without restriction. During our 2001 surveys, we used a Garmin GPSMAP 76 differential GPS unit to relocate the sites first surveyed in 1997. The Garmin unit generates location data with precision similar to the PLGR used in 1997. A directional indicator within the GPS unit allowed us to approach the position of each study site. When the GPS unit indicated that we were positioned within 3 meters of the site, the skiff anchor was deployed. The anchor then served as the starting point for the survey at that site. During the 1997 surveys the mean depth at study sites was 9.1 m (30 ft). When approaching sites in 2001, we sometimes found that the location of indicated site coordinates was at water depths other than 9.1 m as indicated by the skiff fathometer. In such cases, we motored perpendicular to the shoreline until we came to a depth of 9.1 m. In these cases new site coordinates were recorded from the GPS unit (see Table 1).

In the selection of the original study sites in 1997, the south coastline of SJDF between Kydaka Point and Port Angeles was partitioned into five intervals of equal length using Washington Coastal Kelp Resource Maps W-7 – W-13 (Ecoscan Resource Data, PO Box 1046, Freedom, CA 95019 USA). Maps are based on infrared aerial photographs of kelp canopies taken in October 1989. The five linear strata were then subdivided into 0.25 km intervals. In each stratum, four study site intervals and several alternate intervals were chosen at random. Stratified random site selection was used in order to minimize

clumping of sites and maximize the sampling coverage throughout the study area. During the 1997 survey, one primary site was not sampled and a second was replaced with an alternate site, in both cases because of hazardous tidal currents at the primary sites during sampling visits. The result was a survey of nineteen sites in the study area. We utilized the same nineteen sites during the 2001 surveys (Table 1).

### *Sampling methods*

In the interest of maintaining consistency among different projects with similar goals, we modeled our benthic survey protocols after protocols developed jointly by the University of California, Santa Cruz (UCSC), and the Biological Resources Division of the US Geological Survey (USGS). The UCSC/USGS criteria were, however, developed for application specifically to benthic habitats with rocky substrata. Because we anticipated encountering gravel, sand, or mud habitat prior to the 1997 surveys, and because sea otters are known to forage in benthic habitats with soft substrata as well as rocky, the UCSC/USGS protocols were modified so that samples on soft substrata could be accommodated. The modified protocols, described here, were used both in 1997 and 2001.

At all sites, transect lines were extended from the skiff anchor along the bottom at a depth of 9.1 m below mean lower low water. Lines generally were oriented parallel to shoreline. At each site, a sample consisted of surveys of twenty quadrats randomly spaced along the 50 meter transect tape running east or west (parallel to shoreline, direction chosen at random for each site) from the anchor. Quadrats were 0.25 m<sup>2</sup> in area. Spacing of the quadrats was based on a pre-determined random number of fin-kicks by survey divers between successive quadrats. During the 1997 field work, we were forced to terminate sampling work at one site before surveys of all twenty quadrats were completed. We terminated work prematurely at three sites in 2001. In all cases, abrupt increases in local tidal currents made continued survey work physically impossible.

Within quadrats, macroalgae and large invertebrates were sampled (Table 2). Visible macroalgae were sorted into size classes of small (<0.1m maximum length), medium (0.1-1m) and large (>1m). Clams were sampled by counting visible siphons. Red algae and encrusting invertebrates are often colonial, with a clear definition of individuals not apparent. In such cases we estimated percentage bottom cover in the quadrat, rather than counting individuals. Percent cover of fleshy red algae, coralline red algae, and encrusting invertebrates were recorded using a scale of 0-6 (0=0%, 1=1-5%, 2=5-25%, 3=25-50%, 4=50-75%, 5=75-95%, 6=95-100%). Percent cover of three different substratum types (sand, mixed [particles ranging from fine gravel to cobble <12in diameter], and bedrock) were recorded using the same scale. The cover units are displayed as modal values in all tables and figures provided in this report.

In addition to the quadrat based sampling, three species of urchins (*Strongylocentrotus franciscanus*, *S. purpuratus*, and *S. droebachiensis*) were counted and measured along a single 50 meter transect. The transect line extended from the anchor in the opposite direction from the quadrat survey transect line. We counted all urchins encountered

within 1 m of the line on either side. Thus, urchin transects at each site covered a total area of 100 m<sup>2</sup>. All enumerated urchins were also measured individually during dive surveys (maximum test diameter in mm as determined with Vernier calipers), and were immediately replaced on the substratum following measurement.

### *Analyses*

We calculated means and variances by data category (species or taxon) for quadrat data gathered at each study site. Multivariate analyses of variance were used to evaluate differences by site between data sets collected in 1997 and 2001. Main factors in the analysis were substratum type, and presence of sea otters between the surveys of 1997 and 2001 as reported by the sea otter research project of the Biological Resources Division, U.S. Geological Survey. Cover variables were not included in analyses because coverage was measured by index values rather than actual measurements. Within substratum type, if sites with sea otter presence during winter months were significantly different from those not utilized by sea otters, data were interpreted as consistent with the paradigm hypothesis. If differences among sites did not match with sea otter distribution during winter, data were interpreted as consistent with the disturbance hypothesis.

## **Results**

### *Substratum characteristics*

In both 1997 and 2001 the predominant substratum type was sand or mixed in the seven most westerly sites (From Pillar Point to the west), and predominantly mixed substrata in the remaining twelve sites (Table 3). There was a trend toward higher cover by sand across all stations between 1997 to 2001. The most dramatic changes in substrate type were at sites 1, 3, 4, 5, 6, and 97-A. In all cases except site 4, the observed change was an increase in sand cover. At site 4, substratum cover shifted from primarily sand to primarily mixed.

### *Patterns of abundance and individual size*

Considered across all sites without regard to substratum type or degree of prior occupation by sea otters, the most abundant benthic plants enumerated were kelps and the brown alga *Desmarestia ligulata* (Table 4). The most abundant large invertebrates were bivalves and stars (Table 4). Urchins were found at only three sites and were relatively uncommon (Tables 4 and 5). The distributions of test diameters for urchins (Table 5) were typical for the each species in the region, and generally similar to data collected on test diameters in 1997.

Within substratum type patterns generally were similar to the overall pattern, with variation among substratum types along expected lines (Table 4). Bivalves were most abundant in sand and mixed substrata, and less common on rocky substrata. The predominant perennial understory kelp, *Pterygophora californica*, and the surface canopy kelps *Nereocystis luetkeana* and *Macrocystis integrifolia* were more abundant on rocky

substrata than other substratum types. However, kelps and other algae were present on all substratum types.

### *Patterns of change*

Multivariate analyses of variance indicated significant effects of substratum type, sea otter presence, and the substratum – sea otter interaction (Table 6). Effects of the substratum factor were expected, and were generally consistent with known habitat preferences of surveyed species. The analytical result is consistent with a strong effect by sea otters on benthic organisms, with the strength of the effect varying among the three categories of benthic substratum.

Possible effects of sea otters can be considered for two categories of species, those known to be sea otter prey, and those not consumed by sea otters. Of the latter, a response to sea otter presence was expected for species of algae known to be grazed by sea urchins, which are, in turn, a known preferred prey of sea otters. Thus, we separately consider results for species known or suspected to be directly affected by sea otters (prey species), and for species known to be indirectly affected by sea otters (species consumed by sea otter prey species).

In the case of direct effects, we found that changes in species abundance were consistent with the paradigm hypothesis in most, but not all, cases (Tables 7 & 8, Figures 2, 3, & 4). Sea otters are known to prey intensively on sea urchins, bivalves, and crabs. Results for direct effects are summarized by these three major prey categories as follows:

*Urchins*: Sea urchin densities declined in mean abundance between 1997 and 2001 on all types of substratum. Distribution of urchins also declined between the two surveys. Urchins were present in twelve of nineteen sites (63%) in 1997, but only three of nineteen sites (16%) in 2001. Of the sites with urchins present in 1997 that lacked urchins in 2001 (n=9), six were in areas occupied by sea otters during the interval between surveys, with the remaining three in locations not known to be affected by sea otter foraging in recent history. Distributions of urchin test diameter did not differ substantially between surveys for any of the three species observed in quadrats or transects (Table 5).

*Bivalves*: In the case of bivalves in sandy substrata, densities in sites 1 through 11 (utilized by sea otters between surveys) declined substantially between surveys, while densities in sites 12 through 19 increased substantially between surveys. In mixed substrata, bivalve densities declined in all sites between surveys. In rocky substrata, bivalves (mainly rock scallops) declined in sites 1 through 11 and were unchanged in sites 12 through 19 between surveys.

*Crabs*: In areas occupied by sea otters between surveys, crab densities declined on all three substratum types. In areas not used by sea otters between surveys, crabs were unchanged on rocky substrata, declined on mixed substrata, and increased slightly on sandy substrata.

The primary indirect effect of interest is the potential increase in algal abundance resulting from reduction in sea urchin density by sea otters. The paradigm hypothesis predicts substantial increases in kelps as a result of reduction in sea urchin abundance by sea otters. Of the eight categories of large algae surveyed and analyzed in our study (Tables 7 & 8), none provided data fully consistent with the hypothesis. A result consistent with the hypothesis would include two components: 1) a substantial *absolute* increase over time in kelp densities in areas used by sea otters between surveys; and 2) a substantial *relative* increase in kelp densities in sites used by sea otters between surveys as compared to sites not used by sea otters between surveys. In the case of rocky and mixed substrata, where the paradigm hypothesis should most clearly explain variation in the data between surveys, the data were consistent with the hypothesis in only four of sixteen possible taxon/substratum combinations (Tables 7 & 8). In the case of sandy substrata, where linkages of direct and indirect effects of sea otters are expected to be less clear, data were consistent with the paradigm hypothesis for only two of eight taxonomic categories evaluated.

## **Discussion**

Our data are consistent with significant direct effects of predation by sea otters on large benthic invertebrates in the western SJDF. Species such as clams, crabs, and urchins are known sea otter prey, and are known to indicate strong demographic responses to effects of sea otter predation in other locations. For two reasons, we urge restraint in attributing observed changes solely or primarily to effects of sea otter predation. First, we do not have direct observations of sea otter foraging activities during winter months between 1997 and 2001 in SJDF. Thus, we cannot describe either the diet of sea otters or the precise locations of foraging activities in SJDF during the interval between benthic surveys. Second, there are patterns in our data that suggest important effects of other ecological factors on benthic populations in SJDF between surveys. For example, sea urchin size distributions were similar among the three sites in which urchins were found in 2001. Two of these sites were among the eleven subject to potential sea otter effects between surveys, while the third apparently has not been influenced by foraging sea otters in recent decades. Modified size distributions in urchin populations are known to be one of the most consistent and predictable effects of sea otter predation. Although urchin populations disappeared from six sites apparently utilized by sea otters for foraging between 1997 and 2001, they also disappeared from three sites not foraged by sea otters. Survey data for clams and crabs generally were more consistent with significant direct effects by sea otters as compared to data for urchins.

Patterns in data for sea otter prey species lead us to conclude that sea otter predation likely contributed to reductions in density of prey between surveys in sites one through eleven. The effect seems most clear for clams and crabs. In the case of urchins, sea otter predation may have been only one of several possible factors influencing patterns of change observed between surveys. The ongoing harvest of urchins in SJDF can be an important source of mortality, from which recovery of urchin populations can be quite slow (Carter and VanBlaricom 2002). Thus, harvest of urchins may complicate efforts to

understand effects of sea otter predation on urchin populations in SJDF. For all taxa surveyed, we must acknowledge the probable important role of other key demographic factors, such as recruitment variation and effects of other natural predators, in variations observed between surveys.

Our data from SJDF provide no meaningful support for the widely celebrated paradigm that sea otters enhance kelp forest productivity, diversity, and habitat by controlling sea urchin populations. We suggest that the most likely explanation for our observations is the unstable nature of the predominant substratum in most of our surveyed areas. Kelps may settle and thrive on small pieces of solid substratum, such as cobble or shell fragments, during summer months when water movements are relatively benign. However, winter storm activity can move such substratum categories easily, causing abrasion and probable death of most attached kelps. Our data for kelp populations in SJDF are clearly more consistent with our disturbance hypothesis than with our paradigm hypothesis.

Following is a summary of our results in the context of various hypotheses posed herein:

*General Hypothesis 1:* Sea otter predation is the principal explanation for observed changes between surveys in abundances and size distributions of preferred prey populations in the manner seen in other locations at other times as indicated above.

*Result:* Qualified support for the hypothesis, with the caveat that other factors, possibly including urchin harvest, clearly are influencing demographic patterns in some prey categories over time.

*General Hypothesis 2:* Foraging by sea otters results in enhanced local biodiversity in SJDF nearshore communities through various indirect effects associated with foraging as described above.

*Result:* No meaningful support for the hypothesis.

*General Hypothesis 3:* Sea otter foraging is influencing prey populations in SJDF in a manner that will cause conflict with tribal, commercial, and recreational fisheries.

*Result:* Qualified support for the hypothesis, with the caveat that other factors, possibly including urchin harvest, clearly are influencing demographic patterns in some prey categories over time.

*Alternative hypotheses: “Paradigm” vs. “Disturbance”:*

*Result:* Data for kelp communities in SJDF are clearly more consistent with the disturbance hypothesis than the paradigm hypothesis.

Our project results may be of value to managers charged with decisions regarding long-term conservation options for sea otters, nearshore benthic communities, and shellfish

fisheries in SJDF. As anticipated, we find that future expansion of sea otter populations into SJDF will likely cause reduction in benthic invertebrate species sought by commercial harvesters. In this context, our data are most convincing for clam and crab populations, but less so for urchin populations. Continuing harvest of urchins at intensive levels complicates possible conclusions regarding long-term effects of sea otters on the urchin fishery.

One of the most frequent arguments in favor of expanded sea otter populations is the documented augmentation of kelp forest diversity, productivity, and habitat observed in many locations following recovery of sea otter populations. Our data indicate that managers and conservation interests should not anticipate this effect in SJDF. Because of substratum instability and effects of winter storm activity, the structure of kelp forests in SJDF is much more likely to be affected by patterns in the physical environment than by the effects of foraging by sea otters.

The enigmatic recent behavior of the Washington sea otter population has led to differing estimates of carrying capacity for the population (Laidre et al. 2002, Gerber et al. in press), and to uncertainty about the ultimate significance of SJDF as sea otter habitat. Over the long term, sea otters may eventually move into SJDF once more and establish permanent occupancy. If this occurs, our conclusions and predictions outlined above will become directly relevant to considerations for ecosystem management. However, SJDF may be used on sporadically by sea otters, to the extent that food resources occasionally become sufficient to support groups of sea otters for relatively brief periods. This latter case is perhaps the better characterization of the importance of SJDF to Washington's sea otters over the past decade. In this case it may be reasonable to attach less significance to sea otter predation over the long term, in comparison to other factors important to ecosystem structure, such as storm disturbance, harvest intensity, and human population growth. Finally, we take note of the continued growth of the sea otter population in British Columbia (BC), Canada. The BC population's southern limit is now the Barkley Sound region, and there is evidence that the population continues to grow steadily. A merging of the Washington and BC populations is a realistic possibility over the long term. Such a merger likely will alter habitat use and growth patterns of the combined population and reopen the question of long-term use of habitats in SJDF.

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Table 1. GPS coordinates recorded at study sites in 1997 and 2001. 1997 data are from Carter and VanBlaricom (1998). In all cases, relocation of study sites was based initially on coordinates recorded in 1997. In those cases where the 1997 coordinates resulted in inappropriate positioning (i.e., incorrect water depth), the skiff was moved perpendicularly to shoreline until to correct depth was obtained, and a new set of coordinates was recorded. The 1997 coordinates were retained for all other sites.

Site	1997		2001	
	North	West	North	West
1	48° 16.61'	124° 20.24'	48° 16.61'	124° 20.24'
2	48° 16.43'	124° 19.24'	48° 16.43'	124° 19.24'
3	48° 15.48'	124° 16.69'	48° 15.48'	124° 16.69'
4	48° 14.95'	124° 11.92'	48° 14.95'	124° 11.92'
5	48° 14.66'	124° 11.06'	48° 14.63'	124° 11.12'
6	48° 14.02'	124° 09.41'	48° 14.00'	124° 09.43'
7	48° 12.62'	124° 05.75'	48° 12.62'	124° 05.75'
8	48° 10.94'	124° 01.73'	48° 10.94'	124° 01.73'
9	48° 10.37'	123° 55.91'	48° 10.37'	123° 55.91'
10	48° 10.20'	123° 55.31'	48° 10.20'	123° 55.31'
11	48° 09'52.43"	123° 50'48.63"	48° 09.01'	123° 55.81'
97-A	48° 09'46.88"	123° 43'28.68"	48° 09.78'	123° 43.47'
13	48° 10'07.07"	123° 42'33.96"	48° 10.11'	123° 42.51'
14	48° 09'57.87"	123° 41'45.54"	48° 09.96'	123° 41.76'
15	48° 09'44.13"	123° 40'14.76"	48° 09.73'	123° 40.24'
16	48° 09'40.38"	123° 39'53.38"	48° 09.67'	123° 39.88'
17	48° 08'29.23"	123° 30'54.83"	48° 08.50'	123° 30.15'
18	48° 08'04.27"	123° 30'09.14"	48° 08.07'	123° 30.15'
19	48° 08'05.01"	123° 29'55.83"	48° 08.08'	123° 29.93'

Table 2. List of taxa recorded during the 2001 surveys in the Strait of Juan de Fuca.

**Plants**

Kelps

Surface canopy species:	Nereocystis luetkeana Macrocystis integrifolia
Understory species:	Pterygophora californica Alaria marginata Laminara spp. Costaria costata Pleurophycus gardneri Agarum clathratum
Other algae or algal categories:	Desmerestia ligulata Encrusting red algae (coralline and noncoralline) Foliose red algae Articulated coralline red algae
Other plants:	Zostera marina

**Invertebrates**

Large solitary invertebrates:

Echinoderms:

Urchins:	Strongylocentrotus droebachiensis (green urchin) S. franciscanus (red) S. purpuratus (purple)
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Stars:

	Henricia leviuscula Mediaster aequilis Orthasterias kohleri Pycnopodia helianthoides Solaster sp.
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Cucumbers:

	Cucumaria miniata Parastichopus californicus
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Crabs:

	Scyra acutifrons Pugettia gracilis Oregonia gracilis Cancer spp. Other unidentified species
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Chitons:

	Cryptochiton stelleri
--	-----------------------

Gastropods:

	Haliotis kamtschatkana
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Bivalves:

	Chlamys sp. Panopea abrupta Tresus nuttallii Zirphaea pilsbryi Other unidentified species
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Encrusting invertebrates (recorded as a single category. Includes unidentified sponges, tunicates, bryozoans, hydroids, and other colonial encrusting organisms).

Table 3. Summary of substratum type by study site for 1997 and 2001 surveys. For each site/survey combination, data represent tallies of the predominant substratum type in each quadrat sampled. Totals are less than 20 quadrats in cases where abrupt increases in tidal current strength made completion of the sample physically impossible.

<b>Site</b>	<b>2001</b>			<b>1997</b>				
	<b>Sand</b>	<b>Mixed</b>	<b>Bedrock</b>	<b>Total</b>	<b>Sand</b>	<b>Mixed</b>	<b>Bedrock</b>	<b>Total</b>
<b>Site 1</b>	4	12	0	16	12	6	2	20
<b>Site 2</b>	15	1	1	17	9	4	7	20
<b>Site 3</b>	19	0	1	20	5	15	0	20
<b>Site 4</b>	4	12	4	20	15	5	0	20
<b>Site 5</b>	20	0	0	20	11	5	4	20
<b>Site 6</b>	12	8	0	20	20	0	0	20
<b>Site 7</b>	20	0	0	20	20	0	0	20
<b>Site 8</b>	0	15	5	20	1	16	3	20
<b>Site 9</b>	0	20	0	20	0	20	0	20
<b>Site 10</b>	0	16	4	20	0	20	0	20
<b>Site 11</b>	0	20	0	20	0	19	1	20
<b>Site 97-A</b>	0	20	0	20	18	2	0	20
<b>Site 13</b>	0	11	9	20	0	8	9	17
<b>Site 14</b>	0	7	13	20	0	16	4	20
<b>Site 15</b>	0	20	0	20	0	19	1	20
<b>Site 16</b>	0	10	8	18	0	11	9	20
<b>Site 17</b>	0	20	0	20	0	20	0	20
<b>Site 18</b>	4	16	0	20	0	20	0	20
<b>Site 19</b>	1	19	0	20	1	19	0	20

Table 4. Mean densities (#/0.25m<sup>2</sup> or modal substratum cover code as defined in text) with standard deviations, by substratum type, for the most abundant taxa surveyed in 2001 quadrat counts along with data for the three urchin species. See Table 2 for a complete listing of taxonomic categories surveyed. Overstory kelps include *Nereocystis* and *Macrocystis*. The Laminariales group includes *Laminaria spp*, *Costaria*, *Agarum*, *Alaria*, and *Pleurophycus*.

Group	Bottom Type					
	Sand		Mixed		Bedrock	
	avg.	std. dev.	avg.	Std. dev.	avg.	std. dev.
Sm Overstory kelps	0.05	0.17	0.19	0.47	0.30	0.39
Lg Overstory kelps	0.02	0.06	0.05	0.11	2.17	5.24
Sm <i>Pterygophora</i>	0.76	0.91	2.61	3.05	4.15	5.46
Lg <i>Pterygophora</i>	0.79	2.29	0.65	1.05	0.28	0.38
Sm Laminariales grp.	3.39	5.78	3.45	2.54	3.18	4.50
Lg Laminariales group	0.98	2.25	0.68	0.95	0.54	0.57
sm <i>Desmarestia</i>	1.22	2.44	1.82	2.35	0.72	1.80
lg. <i>Desmarestia</i>	0.00	0.00	0.41	1.47	0.45	1.21
% Fleshy Reds	0.00	0.94	0.00	0.76	0.00	1.49
% Art. Coralline Algae	0.00	1.02	0.00	1.87	0.00	2.05
% Encrusting Inverts	0.00	0.00	0.00	0.27	0.00	1.77
Clams	0.58	1.47	0.14	0.33	0.00	0.00
Crabs	0.12	0.30	0.06	0.21	0.14	0.38
Cucumbers	0.00	0.00	0.09	0.24	0.00	0.00
Stars	0.10	0.29	0.10	0.21	0.38	0.73
<i>S. franciscanus</i>	0.00	0.00	0.00	0.00	0.00	0.00
<i>S. droebachiensis</i>	0.00	0.00	0.00	0.00	0.11	0.30
<i>S. purpuratus</i>	0.00	0.00	0.13	0.29	0.29	0.60

Table 5. Summary of urchin transect survey data. Abundance data are counts for the total area surveyed per site (50\*2 m<sup>2</sup>). Test diameters are in mm. Transect counts for urchins were zero for all species at all sites not indicated.

		Mean test diameter	#/100 m <sup>2</sup>
<b>Otter sites</b>			
Site 8	red	125	15
	purple	65	7
	green	0	0
<b>Non otter sites</b>			
Site 13	red	93	20
	purple	79	24
	green	71	9
Site 16	red	167	3
	purple	55	3
	green	0	0

Table 6: Results of MANOVA statistical test of sea otter presence and substrate type on invertebrate and algal abundance between studies completed in 1997 and 2001.

<b>Effect</b>	<b>Method</b>	<b>F ratio</b>	<b>P-value</b>
Substratum	Pillai's Trace	2.71	<0.001
	Wilk's Lambda	5.96	<0.001
	Hotelling's Trace	11.09	<0.001
	Roy's Largest Root	24.9	<0.001
Sea otters	Pillai's Trace	10.51	<0.001
	Wilk's Lambda	10.51	<0.001
	Hotelling's Trace	10.51	<0.001
	Roy's Largest Root	10.51	<0.001
Interaction	Pillai's Trace	4.79	<0.001
	Wilk's Lambda	6.23	<0.001
	Hotelling's Trace	7.85	<0.001
	Roy's Largest Root	15.82	<0.001

Table 7: Results of *post hoc* analyses of variance for source of significance between survey data from 1997 and 2001.

<b>Parameter</b>	<i>Otters</i>			<i>Substrate</i>			<i>Otters * Substrate</i>		
	<b>DF</b>	<b>F</b>	<b>Sig.</b>	<b>DF</b>	<b>F</b>	<b>Sig.</b>	<b>DF</b>	<b>F</b>	<b>Sig.</b>
Urchins	1, 21	.636	.434	2, 21	1.639	.218	1, 25, 26	.042	.839
Clams	1, 21	1.256	.273	2, 21	3.385	.053	1, 25, 26	.332	.570
Crabs	1, 21	1.120	.302	2, 21	4.520	.023 <sup>2</sup>	1, 25, 26	.553	.464
Cucs	1, 21	11.591	.003 <sup>1</sup>	2, 21	11.890	.000 <sup>3</sup>	1, 25, 26	1.662	.209
Stars	1, 21	1.192	.287	2, 21	.759	.481	1, 25, 26	2.214	.149
Overstory kelps	1, 21	3.807	.065	2, 21	5.695	.011 <sup>4</sup>	1, 25, 26	1.450	.240
Understory kelps	1, 21	.717	.407	2, 21	1.291	.296	1, 25, 26	.040	.844

<sup>1</sup> Pairwise comparisons yielded the same P-value (.003) for otter and non-otter sites

<sup>2</sup> Pairwise comparisons yielded significance between bedrock and mixed substrate (P = .021)

<sup>3</sup> Pairwise comparisons yielded significance when comparing bedrock to either mixed (P = .000) or sand (P = .007)

<sup>4</sup> Pairwise comparisons yielded significance when comparing bedrock to mixed (P = .009)

Table 8. Summary of changes ( $\#/0.25\text{m}^2$ ) between the 1997 and 2001 surveys sorted by substratum type and use of sites by sea otters between surveys. “Present” indicates site was used by sea otters between surveys. “Absent” indicates site was not used by sea otters between surveys.

Parameter	<i>bedrock</i>		<i>mixed</i>		<i>sand</i>	
	present	absent	present	absent	present	absent
Small Overstory	-0.86	14.33	-0.22	-0.33	-0.08	0.00
Large Overstory	7.00	0.55	0.04	-0.59	0.03	0.00
Small <i>Pterygophora</i>	1.03	-0.08	1.06	1.72	0.30	2.13
Large <i>Pterygophora</i>	-1.43	5.28	-0.73	-0.10	1.31	0.00
Small Laminariales	-3.89	-1.95	-4.72	-10.10	-3.53	-9.89
Large Laminariales	-2.29	-11.23	0.59	-1.53	1.21	-3.89
Small <i>Desmarestia</i>	-2.00	-1.17	-0.48	-0.36	-16.92	-0.89
Large <i>Desmarestia</i>	0.00	-2.76	0.00	0.59	0.00	0.00
Clams	-4.86	0.00	-2.27	-0.18	-2.29	2.79
Crabs	-0.95	0.00	-1.14	-1.39	-0.14	0.06
Cucumbers	-0.86	-0.44	-0.15	-0.67	-0.05	0.00
Stars	0.00	-4.33	-0.41	-0.39	0.10	0.05

FIGURES



Figure 1. Locations of study sites (shaded red circles). Major landmarks are noted with orange squares.

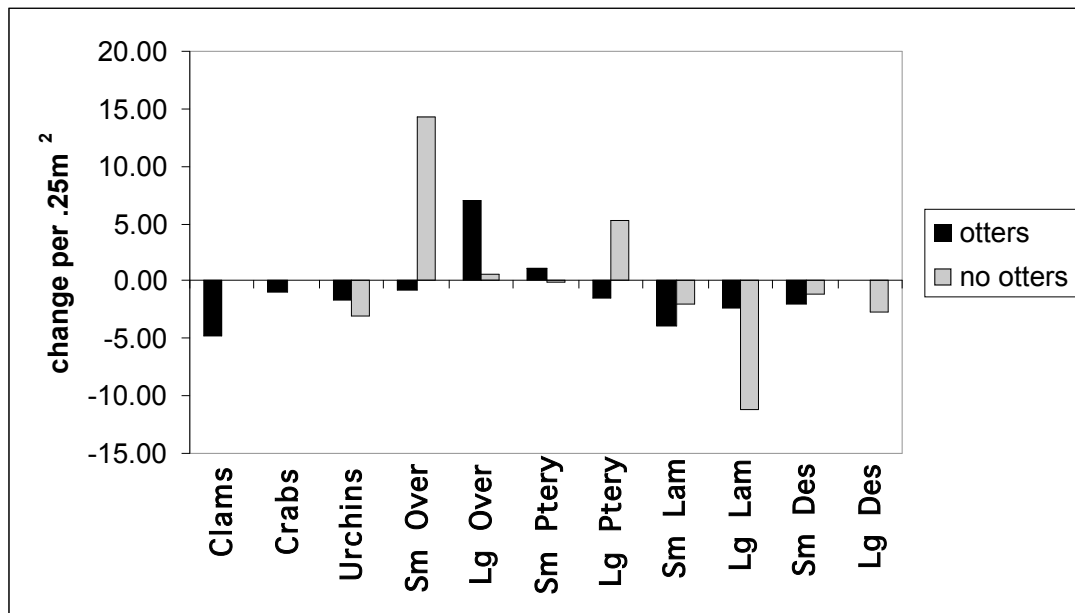


Figure 2. Changes in invertebrate and algal densities, per quadrat, on bedrock substrata between the surveys of 1997 and 2001. Data designated “otters” were collected at sites utilized by sea otters between 1997 and 2001. Data designated “no otters” were collected at sites not used by sea otters in recent decades.

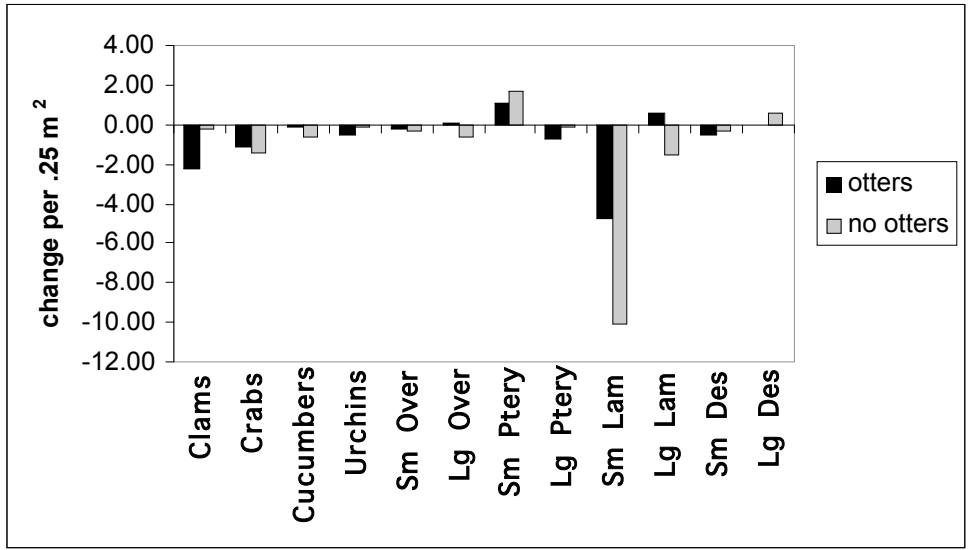


Figure 3. Changes in invertebrate and algal densities, per quadrat, on mixed substrata between the surveys of 1997 and 2001. Data designated “otters” were collected at sites utilized by sea otters between 1997 and 2001. Data designated “no otters” were collected at sites not used by sea otters in recent decades.

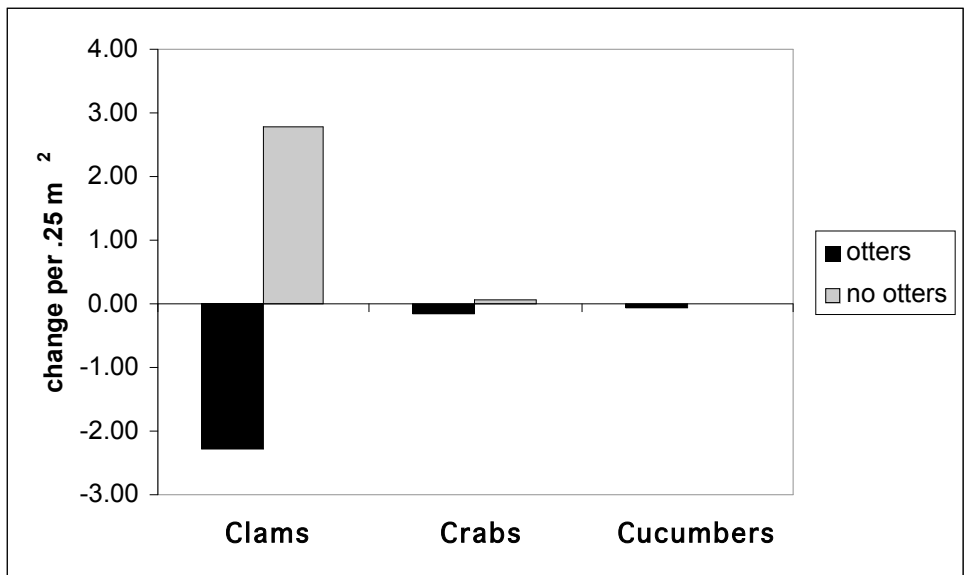


Figure 4. Changes in invertebrate densities, per quadrat, on sandy substrata between the surveys of 1997 and 2001. Data designated “otters” were collected at sites utilized by sea otters between 1997 and 2001. Data designated “no otters” were collected at sites not used by sea otters in recent decades.

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