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SEA OTTERS AND BENTHIC PREY COMMUNITIES IN WASHINGTON STATE

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ABSTRACT

An August 1987 benthic survey of otter-free and otter-occupied areas along the outer coast of Washington State's Olympic Peninsula confirms that this area has been as profoundly influenced by sea otters as other rocky, nearshore communities studied in California, Canada, and Alaska. Prey density, size, and biomass were found to be negatively correlated with sea otter abundance, suggesting that the re-introduction of sea otters to this area in 1969–1970 has profoundly affected invertebrate prey abundance and distribution, particularly that of the red sea urchin, *Strongylocentrotus franciscanus*. Red urchin distribution appears to influence algal groups differently and in a manner consistent with current otter/urchin/kelp theory. Foliose red algal abundance was negatively related to urchin numbers and coralline crusts were positively correlated. Aerial photographs of *Macrocystis integrifolia* cover at Cape Alava suggest an increase since the introduction of sea otters. Given the present distribution of prey along the Olympic Peninsula coast, we conclude that as the sea otter population continues to grow, range expansion is more likely to occur to the north, which may also lead to possible conflicts with an increasing sea urchin fishery and Native American set net activity.

Key words: sea otter, *Enhydra lutris*, Washington State, community structure, invertebrate prey, benthic, rocky habitats, predation.

The successful re-introduction of sea otters to the Washington coast has provided an excellent opportunity to increase our understanding of sea otter community ecology. The distribution of otters along the coast is well documented (Bowlby *et al.* 1988), making it possible to identify and exploit a gradient of sea otter predation as a natural experiment. In 1969–1970, 59 sea otters were translocated from Alaska to the outer coast of the Olympic Peninsula, Washington State (Jameson *et al.* 1982). Current estimates place the population at approximately 100 individuals (Bowlby *et al.* 1988) with a 16.5% annual rate of increase (Jameson *et al.* 1986). Prior to this study, no quantitative benthic survey had been conducted along the Olympic coast to assess sea otter prey availability, or the impact of otters on their communities. Such a study was warranted for a variety of reasons. Sea otters have been characterized as a keystone species (*sensu* Paine 1969) in rocky, kelp communities where their importance is disproportionately large with respect to their numbers (Estes and Palmisano 1974, Estes *et al.* 1978, Duggins 1980, Estes and Harrold 1988). Although widely accepted as a paradigm (but see Foster and Schiel 1988), the scenario of increasing kelp cover with the reduction of herbivorous invertebrates by sea otter predation is based primarily on comparisons of Alaskan and Canadian areas with and without sea otters (Estes *et al.* 1978, Duggins 1980, Breen *et al.* 1982), small-scale experimental manipulations of sea urchins or kelp (*e.g.*, Dayton 1975, Duggins 1980), and reconstruction of changes following natural sea otter range expansions from historical records (VanBlaricom 1984). Laur *et al.* (1988) represents the only published quantitative comparison of prey and algal differences in rocky communities before and after sea otter occupation.

Expanding sea otter populations are known to compete with man for economically important invertebrate prey (see Estes and VanBlaricom 1985 for review) often resulting in heated and costly conflicts between conservationists and fisheries. Such a potential exists along the Olympic coast due to the recent development and growth of the sea urchin fishery in the Strait of Juan de Fuca (Fig. 1). Finally, sea otters are viewed as a “threatened” species by many conservationists as a result of their extirpation during the fur trade and susceptibility to human induced mortality (*e.g.*, oil spills and gill nets) (U.S. Fish and Wildlife Service 1987).

Given the paucity of critical tests, the need to test the paradigm in other geographic areas, the potential for fisheries conflicts, and the reduced numbers of this species, there is a need for more information regarding the impact of sea otters on their prey communities and the factors important to the re-establishment of this species (Levin 1988).

Our research had three primary objectives: (1) the assessment of prey resources within the sea otters range; (2) the comparison of prey abundance and community structure among areas of high, low and no otter numbers as a correlative test of the otter/grazer/kelp paradigm; (3) the compilation of subtidal community baseline data and the establishment of permanent, long-term monitoring stations within and outside the present sea otter range.

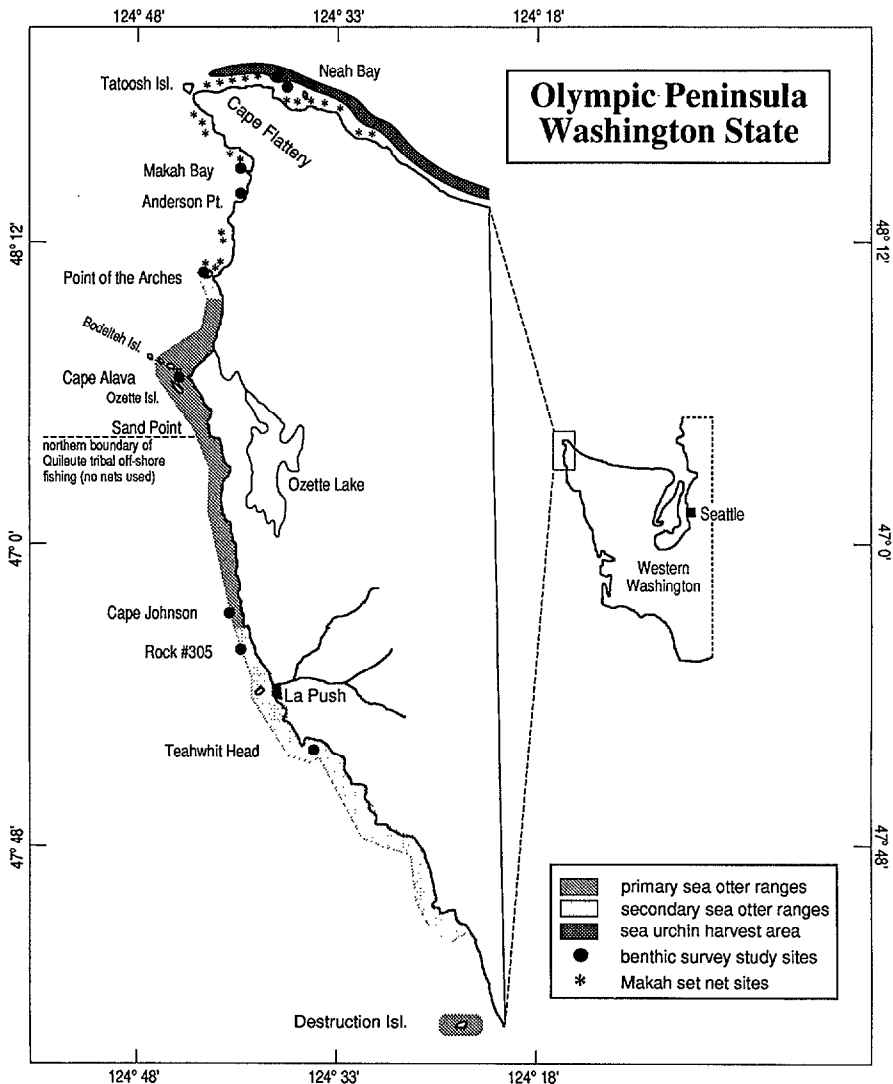


Figure 1. Map of the Olympic Peninsula outer coast, Washington State, showing primary and secondary sea otter ranges, benthic survey study sites, commercial sea urchin fishing grounds, and Native American fishery areas. These are no coastal gill net sites south of Point of the Arches.

METHODS

STUDY SITE SELECTION

Three types of study areas were selected with respect to the current range of the Washington State sea otter population (Fig. 1). To characterize benthic communities within areas of high, low and no otter occurrence, sites were selected along a gradient of otter occupancy (Fig. 2). Area designations (defined in Bowlby *et al.* 1988) are primary range (mean otters sighted/region/aerial survey

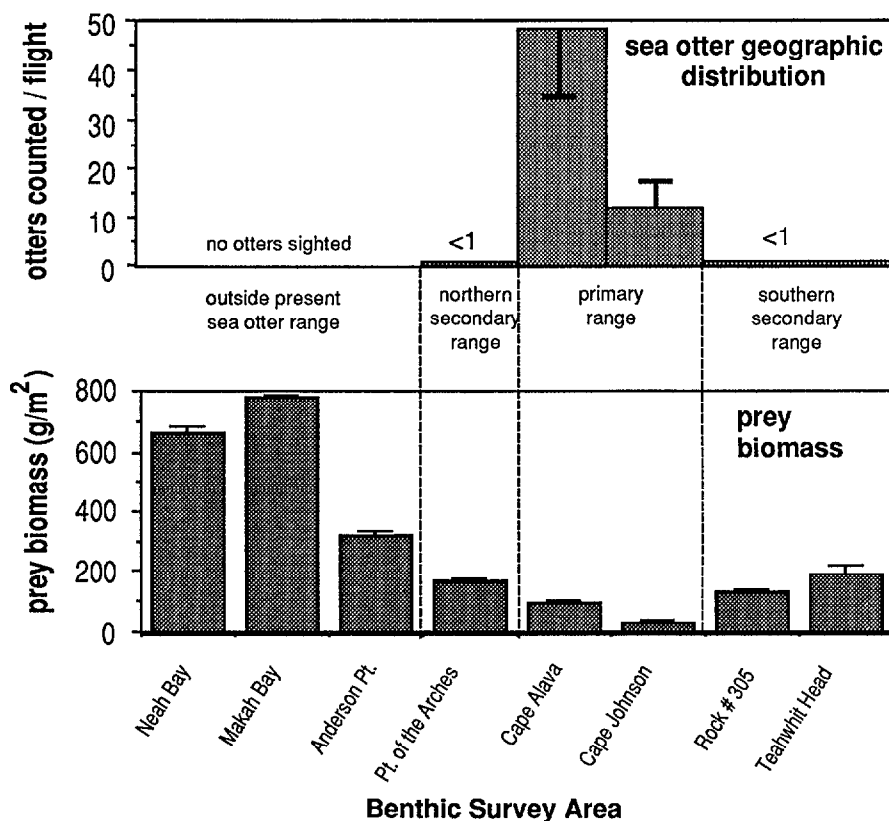


Figure 2. Prey biomass was lowest at sites within the sea otter primary range (>3 otter sightings/aerial survey on 7 flights between March and October 1987, Bowlby *et al.* 1988). Prey biomass was intermediate at sites within the secondary range (actual otter sightings <1 /flight, Bowlby, personal communication) and was highest outside the sea otter range (no sightings). Mean otter counts (error bars = SE) are for geographic ranges (Fig. 1) which include the corresponding benthic survey areas.

>3), secondary range (mean otters sighted/region/aerial survey <3) and outside the range (no otter sightings). (Although Bowlby *et al.* define secondary range as <3 otters sighted/flight, actual sightings were <1 /flight in the regions identified as secondary range.) Within the otters' primary range, sites at Cape Johnson and Cape Alava were chosen which had been identified as principal feeding areas (Bowlby *et al.* 1988) (Fig. 1). Scuba was then used to survey the area and specific sampling sites were located in the region of highest prey concentrations.

Sites outside the primary range of otters were selected based on the following criteria: protection from swell via headlands or offshore islands, water depth and substrata similar to within range sites, and the highest concentrations of prey given the first two constraints. Areas of high prey abundance were chosen because these would be the most likely to be exploited and thereby influenced by otters. The southern secondary range sites (Fig. 1) were placed at Teahwhit Head and

Rock #305 (U.S. Fish and Wildlife Service 1970). The northern secondary range site was located at Point of the Arches. Outside the otter range and to the north, sampling was done at Anderson Point, Makah Bay and Neah Bay (Fig. 1). At Neah Bay two sites were used, one inside an area in which commercial urchin fishing is prohibited by the Makah tribe, and one outside. A large area at each site was extensively surveyed qualitatively using scuba to insure the specific study location (transect site) was representative of the general area. Although a small resident otter population (< 10) is known to occupy Destruction Island (Fig. 1) (Bowlby *et al.* 1988), this area was not included in the quantitative survey due to its peripheral status and remote location.

Three sites, one in each type of study area were selected as principal study sites, and were more thoroughly sampled than the other locations. These included Anderson Pt. which was outside the present otter range and to the north, and the two permanent monitoring sites, Cape Alava within the primary range, and Teahwhit Head in the southern secondary range.

TRANSECT LAYOUT AND INSTALLATION

To facilitate the comparison of our results with those of researchers in other geographic areas and thus enhance the ability to generalize about the impact of sea otters on their prey communities, transect layout and data collection procedures followed the protocol used by U.S. Fish and Wildlife Service in their monitoring of sea otter habitats (U.S. Fish and Wildlife Service 1987) whenever possible.

All field work was done during the last two weeks of August 1987 with the exception of Neah Bay which was sampled November 4, 1987.

Two types of transect layouts were used, permanent and temporary. Permanent transect markers were installed at Cape Alava and Teahwhit Head. These consisted of a 50-m baseline with five 14-m transect lines projecting from alternating sides every 10 m. The end of each line was marked with a stainless steel 0.25" \times 4" eye-bolt and numbered stainless steel tag. At all other sites, temporary transects (25 or 50 m) were deployed and their positions well noted with surface line-ups such that they could be relocated within at least 50 m.

DATA COLLECTION

Quadrat counts—At the permanent transect sites, ten 1-m² quadrats were placed end to end on both sides of each transect line providing 20 quadrats per line and 100 per site. A two-meter-long section at each end of the 14-m transect lines was excluded to account for any disturbance that may have resulted from the bolt installation process. At the temporary sites, quadrats were placed end to end in a single row. Invertebrates identified as likely sea otter prey were counted by species within each quadrat.

Point contact—A point contact method was used to quantify biotic cover, water depth and substratum type at the two permanent monitoring stations (Cape Alava and Teahwhit Head) and at Anderson Pt. At these sites, a meter

tape was stretched out along each transect line and the type of cover found directly under the tape was recorded at points every 20 cm along the entire length of the line. Cover was noted as foliose red algae, crustose coralline algae, brown algae, sessile invertebrate, or bare rock. If more than one type of cover was found under a single contact point, each was recorded. Percent cover of each type was calculated for each of the principal study sites. Percentages were arcsine transformed and between site comparisons made via ANOVA and Fisher PLSD multiple range tests. Cover at Neah Bay was qualitatively noted.

Water depth was measured at one meter intervals along each transect line and then corrected to mean low water. Substratum type was also noted every meter and classified as either sand, gravel, cobble (5–10 cm), small rocks (10–50 cm), large rocks (50–150 cm), boulders (>150 cm), or bed rock. Mean percent cover of each type was then computed for each site. Substratum relief was characterized by a rugosity index. This was the ratio of the bottom contour distance between the end points of each transect line and the straight line distance (14 m) between the points. The contour distance was determined by attaching a meter tape to one end of the transect line and then following the bottom topography with the tape until reaching the other end of the transect.

Prey size distributions and biomass—Size distributions of the major benthic invertebrates were compiled at each site. Individuals were either measured *in situ* or collected and measured on shore. In addition to sizes, total weights and wet mean weights were obtained for likely sea otter prey species. These measurements were then used to calculate size/weight regressions and combined with density data to compute sea otter prey biomass concentrations at each site.

Aerial kelp canopy survey—A comparison of pre- and post-sea otter introduction cover of *Macrocystis integrifolia* was made based on an aerial photograph taken of the Cape Alava study site on 13 July 1959 from 500 ft (V. Scheffer, in National Marine Mammal Laboratory archives, Seattle, Washington) and an 11 June 1986 aerial photograph of the same area taken from the same altitude. Percent cover of *M. integrifolia* was computed by projecting the photographs onto a pattern of random dots divided into quadrats (4 and 3 respectively) and counting the proportion of dots contacting kelp canopy.

RESULTS

INVERTEBRATE PREY

Abundance—At sites north of the sea otter range, overall invertebrate prey abundance patterns were dominated by the red sea urchin, *Strongylocentrotus franciscanus* (Table 1). Numbers of urchins increased significantly along a south to north gradient from Cape Alava (ANOVA and Fisher PLSD multiple range test, $P < 0.05$). At Cape Alava and to the south, urchin densities were very low (0.02–0.22/m²) and although more were found in the southern secondary range than in the primary otter range, this difference was not significant at the $P = 0.05$ level (Table 1). Within the primary and southern secondary range, prey items were generally small species. Gastropods, limpets, small chitons and

Table 1. Sea otter invertebrate prey abundances [individuals/m²], means and (SD), at sites within and outside of the primary sea otter range along the outer coast of Washington State. Commercial harvesting of sea urchins is not permitted inside of the Makah reserve.

| Site | <i>Strongylo-</i> <i>centrotus</i> <i>franciscanus</i> | Sea cucumbers | <i>Crypto-</i> <i>chiton</i> <i>stellerii</i> | <i>Hinnities</i> <i>giganteus</i> | Gastro- pods | Limpets | Small chitons | Crabs | Total prey | <i>n</i> |
|------------------------------------|--|--------------------|---|--------------------------------------|-----------------|---------|------------------|--------|---------------|----------|
| North of sea otter range | | | | | | | | | | |
| Neah Bay inside | 21.1A ^a | 0.24C ^b | 0.04B | 0.0B | 0.70C | 0.0.24B | ns | 0.0B | 22.4A | 50 |
| Makah reserve | (9.36) | (0.59) | (0.20) | (0.0) | (2.17) | (0.59) | | (0.0) | (10.16) | |
| Neah Bay outside | 12.3B | 0.36C ^b | 0.04B | 0.0B | 0.56C | 0.40B | ns | 0.0B | 13.5B | 50 |
| Makah reserve | (9.66) | (0.66) | (0.20) | (0.0) | (1.07) | (0.86) | | (0.0) | (9.91) | |
| Makah Bay | 6.69C | 0.10C ^c | 0.06B | 0.02B | 0.59C | 0.67A | 0.33B | 0.0B | 8.5C | 49 |
| | (3.63) | (0.31) | (0.24) | (0.14) | (1.72) | (1.01) | (0.46) | (0.0) | (4.45) | |
| Anderson Pt. | 3.33D | 0.27C ^c | 0.02B | 0.0B | 0.29C | 0.06C | 0.04C | 0.0B | 4.0E | 99 |
| | (2.61) | (0.59) | (0.14) | (0.0) | (0.70) | (0.31) | (0.20) | (0.0) | (2.99) | |
| Northern secondary sea otter range | | | | | | | | | | |
| Pt. of Arches | 4.42D | 0C ^c | 0.11B | 0.0B | ns | 0.0C | 0.0C | 0.0B | 4.5E | 35 |
| | (5.02) | (0.0) | (0.32) | (0.0) | | (0.0) | (0.0) | (0.0) | (5.07) | |
| Primary sea otter range | | | | | | | | | | |
| Cape Alava | 0.02E | 0.93B ^c | 0.0B | 0.03B | 3.95A | 0.65A | 0.59A | 0.18A | 6.4A | 100 |
| | (0.14) | (1.65) | (0.0) | (0.22) | (4.79) | (1.18) | (0.85) | (0.50) | (5.81) | |
| Cape Johnson | 0.0E | 0.22C ^c | 0.02B | 0.14A | 0.32C | 0.16B | 0.20B | 0.0B | 1.1F | 50 |
| | (0.0) | (0.82) | (0.14) | (0.76) | (0.55) | (0.47) | (0.25) | (0.0) | (1.54) | |
| Southern secondary sea otter range | | | | | | | | | | |
| Rock #305 | 0.10E | 1.06B ^c | 0.1B | 0.1A | 1.18B | 0.96A | 0.30B | 0.02B | 3.8E | 50 |
| | (0.30) | (1.82) | (0.3) | (0.36) | (1.79) | (1.84) | (0.43) | (0.14) | (3.18) | |
| Teahwhit Hd. | 0.22E | 1.31A ^c | 0.26A | 0.19A | 2.01B | 0.06C | 0.10B | 0.15A | 4.3E | 100 |
| | (0.61) | (2.21) | (0.5) | (0.46) | (3.77) | (0.28) | (0.27) | (0.5) | (4.67) | |

^a Means within a column with the same letters are not different ($P > 0.05$, ANOVA and Fisher PLSD multiple range test).

^b *Stichopus californicus*.

^c *Cucumaria miniata*.

ns = not sampled.

sea cucumbers (the only large prey) were the most abundant species found (Table 1). Bowlby *et al.* (1988) noted sea cucumbers in the diets of sea otters at both Cape Alava and Cape Johnson. Cape Alava had the highest overall prey densities of the sites within the otter range, but gastropods accounted for >60% of the prey individuals sampled (Table 1).

Prey biomass and size distributions—The highest concentrations of large prey items and total prey biomass were found outside the primary range, especially to the north (Table 2 and Fig. 2). North of Cape Alava total prey biomass was much higher, and prey individuals > 5 cm in size generally represented >80% of the prey sampled. The lower percentage of large prey items at the Neah Bay site outside the Makah reserve probably was due to the removal of urchins in the 8–13 cm size classes as a result of the commercial urchin harvest going on at the time of our sampling. South of Cape Johnson, in the southern secondary range, biomass increased by approximately a factor of two, but prey size remained small, with half or more of the prey being <5 cm. The smallest overall prey size (Cape Alava, 77% of the items <5 cm) and the lowest biomass (Cape Johnson, 31 g/m²) were found in the primary range.

BIOTIC COVER

Foliose red algal cover was negatively correlated with the presence of sea urchins whereas coralline algal crust and bare rock cover was positively correlated with urchin abundance (Table 3). No pattern was found in the distribution of brown algal or sessile invertebrate substratum cover between sites.

KELP CANOPY COVER

Macrocystis integrifolia cover was significantly less (*t*-test, $P = 0.014$) at Cape Alava in July 1959 ($31.5\% \pm 8.8$) ten years before the re-introduction of sea otters, than in June 1986, 16 yr following the translocation ($58.7\% \pm 3.2$).

PHYSICAL CHARACTERISTICS

The three principal study sites (those sampled most intensively) were similar in water depths (4.0–4.8 m MLW) (Table 4) and all other study sites were within this depth range. Rugosity was somewhat higher at Cape Alava and Teahwhit Head than Anderson Pt. which had a higher percentage of small rocks and gravel (Table 4). Large rocks, boulders and sculptured bed rock varyingly contributed to the high bottom relief found at Teahwhit Hd., Rock #305, Cape Johnson, Cape Alava, Point of the Arches, Makah Bay and the Neah Bay outside site. Neah Bay (inside) had a hardpan and bed rock bottom with numerous low ridges and occasional boulders.

DISCUSSION

PREY ABUNDANCE

This study extends the geographic range of nearshore benthic habitats significantly influenced by sea otters to Washington State's outer coast, and estab-

Table 2. Percentages of prey items > 5 cm observed consumed by feeding sea otters (Bowlby *et al.* 1988) reflect the reduced prey sizes found at sites within the primary range and the otters' preference for larger prey items.

| Site | Prey size | |
|------------------------------------|--|--|
| | Benthic survey percent of prey individuals > 5 cm | Feeding otters percent of prey individuals > 5 cm |
| North of sea otter range | | |
| Neah Bay (inside reserve) | 83% | |
| Neah Bay (outside reserve) | 66% | |
| Makah Bay | 87% | |
| Anderson Pt. | 89% | |
| Northern secondary sea otter range | | |
| Pt. of the Arches | 92% | |
| Primary sea otter range | | |
| Cape Alava | 23% | 45% <i>n</i> = 139 |
| Cape Johnson | 44% | 73% <i>n</i> = 135 |
| Southern secondary sea otter range | | |
| Rock #305 | 43% | |
| Teahwhit Head | 51% | |

lishes a baseline for future testing of the sea otters' role in structuring these communities. As in other studies comparing areas with and without sea otters (Estes *et al.* 1978, Duggins 1980, Breen *et al.* 1982), results of this survey suggest that sea otters have greatly reduced prey abundance within their present range (Fig. 2). The general pattern that emerges is one of very low prey numbers and small prey sizes within the primary range versus dramatically higher prey numbers, sizes and biomass outside the range to the north and moderately larger prey sizes and higher biomass within the secondary range (Table 2). Jameson *et al.*'s (1986) survey of the Washington otter population and qualitative habitat description in 1985 described the Cape Alava area as the primary range of the population with characteristically low prey densities. A site 2 km south of Cape Johnson, however, was described as a secondary site typical of one recently occupied by otters due to the observed abundance of large and accessible prey, especially red sea urchins. A more recent survey of sea otter distribution along the coast has classified Cape Johnson as primary otter range and areas south of Cape Johnson as secondary range (Bowlby *et al.* 1988). The majority of the otter population now moves seasonally between Cape Johnson in the summer and Cape Alava during the winter (Bowlby *et al.* 1988).

Our benthic prey survey results at Cape Johnson and Rock #305 are consistent with this observed pattern of usage. We found Cape Johnson to have the lowest

Table 3. Algal and invertebrate cover as determined by point contacts ($n = 250$ per station) at the three principal study sites (Anderson Pt., Cape Alava and Teahwhit Head). Neah Bay values are based on qualitative observations made while sampling benthic prey. Percent cover sums may exceed 100% due to layering.

| Site | Biotic cover at the principal study sites | | | | |
|--|---|--------------------|----------------|--------------------|--------------------|
| | Folios red algae | Coralline crust | Brown algae | Inverte- brates | Bare rock |
| High urchin density (21 individuals/m ²) | | | | | |
| Neah Bay (inside Makah reserve and north of otter range) | 0% | 100% | nr | nr | nr |
| Moderate urchin density (3 individuals/m ²) | | | | | |
| Anderson Pt. (north of otter range) | 27%B ^{a**} | 18%A ^{**} | 25%A | 11%A | 24%A ^{**} |
| Low urchin densities (<0.2 individuals/m ²) | | | | | |
| Cape Alava (primary ot- ter range) | 73%A | 5%B | 14%B | 8%A | 10%B |
| Teahwhit Hd. (southern secondary otter range) | 66%A | 9%B | 34%A | 4%B | 13%B |

nr = not recorded.

^a Means within a column with the same letters are not different ($P > 0.05$, ANOVA and Fisher PLSD multiple range test).

^{**} $P \leq 0.01$.

prey numbers and biomass of any site surveyed. No red urchins were seen anywhere in the area. The Rock #305 site, in the same vicinity as Jameson's dive site, 2 km south of Cape Johnson (Jameson *et al.* 1986), showed increased biomass but small prey, supporting Jameson's conclusions. The few urchins (*Strongylocentrotus droebachiensis*, *S. franciscanus*, *S. pupuratus*) that were found at otter occupied sites were always in crevices or within rock burrows and thus inaccessible to sea otters. This is in dramatic contrast to areas outside the otters' range where urchins of all species were exposed and accessible to otters. Unlike the study of Hines and Pearse (1982), spatial refugia for larger prey species are rare along the outer coast of Washington, which may account for the virtual absence of red urchins and other large prey within otter occupied areas.

The relatively greater abundance of small sized prey at primary range sites was reflected in the sizes of observed diet items of the feeding otters (Table 2). At Cape Alava where only 23% of the prey sampled was >5 cm in length, 55% of prey items observed being consumed by otters were <5 cm (Bowlby *et al.* 1988). At Cape Johnson where the proportion of prey >5 cm was 62% higher than at Cape Alava, the proportion of prey >5 cm consumed by otters was also higher (91%) than at Cape Alava. The fact that at both otter sites the proportion of consumed items >5 cm was higher than the proportion of this size range found in the available prey indicates that the otters were selecting larger prey. Otters were rarely observed eating very large prey (large crab and octopi) at Cape Alava or Cape Johnson (<4% and <3% of the observed diet

Table 4. Depths (means and SD, $n = 50$ point contacts per site) and substratum distributions ($n = 250$ point contacts per site) are given for transects at the three principal study sites. The rugosity index, a measure of substratum relief, is the ratio of the contour distance between two points on the sea floor *vs.* the straight line distance between the points.

| Site | Depth (m) | Rugosity index | Physical characteristics of the principal study sites | | | | | Bed rock |
|------------------------------------|------------|----------------|---|------------------|------------------------|-------------------------|---------------------|----------|
| | | | Substrate (% cover) | | | | | |
| | | | Sand and gravel | Cobble (5–10 cm) | Small rocks (10–50 cm) | Large rocks (50–150 cm) | Boulders (> 150 cm) | |
| North of sea otter range | | | | | | | | |
| Anderson Pt. | 4.0 (0.43) | 1.2 (0.08) | 6% | 18% | 22% | 16% | 6% | 28% |
| Primary sea otter range | | | | | | | | |
| Cape Alava | 4.8 (0.52) | 1.4 (0.14) | 0% | 14% | 10% | 28% | 44% | 4% |
| Southern secondary sea otter range | | | | | | | | |
| Teahwhit Hd. | 4.4 (0.44) | 1.4 (0.09) | 0% | 4% | 4% | 8% | 38% | 42% |

respectively, Bowlby *et al.* 1988), although such rare occurrences may account for a significant portion of the caloric intake of otters in areas of reduced prey abundance (Garshelis *et al.* 1986).

COMMUNITY STRUCTURE

The sea otter's ability to greatly reduce densities of herbivorous invertebrates, especially sea urchins, has long been implicated as an important factor in determining the structure of nearshore algal communities (see VanBlaricom and Estes 1988). Areas with otters are generally portrayed as having low numbers of invertebrate grazers and abundant algal cover, whereas in areas without otters, grazing pressure has been shown to greatly limit algal biomass, especially kelps (Duggins 1980, Dayton 1975). Our results support this generalized view. In this study as in others, sea urchin densities varied inversely with otter presence. Consistent with other investigations of the otter/urchin/algal paradigm (*e.g.*, Laur *et al.* 1988) we found a negative relationship between urchin densities and foliose red algal cover and a positive one between urchins and coralline crust cover (Table 3). There was also consistent agreement with respect to *Macrocystis integrifolia* cover. Although *Macrocystis* canopy cover is known to vary between years, comparison of *M. integrifolia* canopy cover at Cape Alava from aerial photographs taken 10 yr before and 16 yr after the re-introduction of sea otters to the coast suggests a significant increase in percent cover as predicted by theory (VanBlaricom 1984).

Sea otters as rocky substratum disturbers—Qualitative observations at Cape Alava suggest that sea otters were turning over rocks in order to obtain prey and thereby influencing the structure of their prey communities. Considerable numbers of the large rocks (50–100 cm) in the area had sessile invertebrates, normally found on the undersides, on the tops and foliose red algal species were on the undersides. Due to the scarcity of large exposed prey at this site, it is not unreasonable that otters were turning over rocks to obtain hidden food items (*e.g.*, crabs, octopus, *Cucumaria miniata*). Wave disturbance of rocky benthic communities in both the intertidal (Sousa 1979) and subtidal (Kennelly 1987a, 1987b) has been shown to influence patterns of species richness and abundance. Otter disturbance of this sort may produce considerably different patterns than wave disturbance because the two events are mostly likely to occur at different times of the year, *i.e.*, otters of the Washington coast shift their range seasonally to avoid exposure to the prevailing swell (Bowlby *et al.* 1988).

THE SEA OTTERS' FUTURE ON THE WASHINGTON COAST

Although the Washington State sea otter population is likely just above the brink of extinction ($\cong 100$ individuals, Bowlby *et al.* 1988), continued growth at the present estimate of 16.5%/year (Jameson *et al.* 1986) will ultimately result in range expansion due to social interactions or prey reduction. A comparison of the otter's present distribution versus that of their prey (Fig. 2)

suggests that expansion to the north would provide the greatest increase in prey biomass over what appears to be a depleted resource within their current range.

If the otters extend their range to the north, they will not be passive participants in the communities they invade, and it is therefore worth considering the consequences. The northern limit of the present sea otter range is already at the southern boundary of the Makah set net fisheries operating out of Neah Bay (Dave Sones, Makah Tribal Council Fisheries, Neah Bay, personal communication) (Fig. 1). Although there have been no reports of sea otter deaths as a result of these nets, entanglement in commercial gill nets has been identified as a source of sea otter mortality in California and implicated as a factor restricting the growth of the southern sea otter population (Wendell *et al.* 1985). Furthermore, the new and growing sea urchin fishery developing in the Strait of Juan de Fuca may also be impacted by northern expansion of otters (Fig. 1). The sea urchin catch in the Neah Bay area has increased from 20,000 pounds landed in the 1982–1983 season to 1.6 million pounds landed during the first three months of the 1987–1988 season (A. Bradbury, Washington Department of Fisheries, personal communication).

Given these factors; an expanding otter population, diminished prey within the otters' present range, a gradient of both prey abundance and human fishing activity increasing to the north, and the tendency for otters and humans to compete for shellfish resources; the outer coast of Washington State's Olympic Peninsula will be an area of human/otter interactions. Agencies responsible for balancing the competing values held by conservationists concerned with the sea otter's recovery and protection, and shellfishermen who view the otter as a formidable competitor, face a difficult task (Levin 1988). Because these interactions have developed into conflicts in other regions (see Estes and VanBlaricom 1985 for review), planning for the management of these potential problems should begin before they arise.

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LITERATURE CITED

- BOWLBY, C. E., B. L. TROUTMAN AND S. J. JEFFRIES. 1988. Sea otters in Washington: distribution, abundance, and activity patterns. Washington State Department of Wildlife, Olympia, WA. Final Report to National Coastal Resources Research and Development Institute, Newport, Oregon.
- BREEN, P. A., T. A. CARSON, J. B. FOSTER AND E. A. STEWART. 1982. Changes in

- subtidal community structure associated with British Columbia sea otter transplants. *Marine Ecology Progress Series* 7:13–20.
- DAYTON, P. K. 1975. Experimental studies of algal canopy interactions in a sea otter-dominated kelp community at Amchitka Island, Alaska. *Fisheries Bulletin* 73:230–237.
- DUGGINS, D. O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61:447–453.
- ESTES, J. A., AND J. F. PALMISANO. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–1060.
- ESTES, J. A., AND C. HARROLD. 1988. Sea otters, sea urchins, and kelp beds: some questions of scale. Pages 116–150 in J. A. Estes and G. A. VanBlaricom, eds. *The community ecology of sea otters*. Springer-Verlag, Berlin.
- ESTES, J. A., AND G. A. VANBLARICOM. 1985. Sea otters and shellfisheries. Pages 187–235 in J. Beddington, R. A. Beverton and D. Lavigne, eds. *Conflicts between marine mammals and fisheries*. Allen and Unwin, London.
- ESTES, J. A., N. S. SMITH AND J. F. PALMISANO. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822–833.
- FOSTER, M. S., AND D. R. SCHIEL. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall. Pages 92–115 in J. A. Estes and G. A. VanBlaricom, eds. *The community ecology of sea otters*. Springer-Verlag, Berlin.
- GARSHELIS, D. L., J. A. GARSHELIS AND A. T. KIMKER. 1986. Sea otter time budgets and prey relationships in Alaska. *Journal of Wildlife Management* 50:637–647.
- HINES, A. H., AND J. S. PEARSE. 1982. Abalones, shells, and sea otters: dynamics of prey populations in central California. *Ecology* 63:1547–1560.
- JAMESON, R. J., K. W. KENYON, A. M. JOHNSON AND H. M. WIGHT. 1982. History and status of translocated sea otter populations in North America. *Wildlife Society Bulletin* 10:100–107.
- JAMESON, R. J., K. W. KENYON, S. JEFFERIES AND G. A. VANBLARICOM. 1986. Status of a translocated sea otter population and its habitat in Washington. *Murrelet* 67: 84–87.
- KENNELLY, S. J. 1987a. Physical disturbances in an Australian kelp community. I. Temporal effects. *Marine Ecology Progress Series* 40:145–153.
- KENNELLY, S. J. 1987b. Physical disturbances in an Australian kelp community. II. Effects on understory species due to differences in kelp cover. *Marine Ecology Progress Series* 40:155–165.
- LAUR, D. R., A. W. EBLING AND D. A. COON. 1988. Effects of sea otter foraging on subtidal reef communities off central California. Pages 150–168 in J. A. Estes and G. A. VanBlaricom, eds. *The community ecology of sea otters*. Springer-Verlag, Berlin.
- LEVIN, S. A. 1988. Sea otters and nearshore benthic communities: a theoretical perspective. Pages 202–209 in J. A. Estes and G. A. VanBlaricom, eds. *The community ecology of sea otters*. Springer-Verlag, Berlin.
- PAINE, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103:91–93.
- SOUSA, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239.
- U.S. FISH AND WILDLIFE SERVICE. 1970. Washington Island Wilderness. Maps and boundary description. Nisqually National Wildlife Refuge Complex. Olympia, Washington.
- U.S. FISH AND WILDLIFE SERVICE. 1987. Final environmental impact statement: proposed translocation of southern sea otters. U.S. Fish and Wildlife Service Sacramento, CA.
- VANBLARICOM, G. A. 1984. Relationships of sea otters to living marine resources in California: a new perspective. In V. Lyle, ed. *Collection of papers presented at the Ocean Studies Symposium, November 7–11 1982, Asilomar, California, California*.

Coastal Commission and California Department of Fish & Game, Sacramento.
361 pp.

VANBLARICOM, G. A., AND J. A. ESTES. 1988. The community ecology of sea otters.
Springer-Verlag, Berlin.

WENDELL, F. E., J. A. AMES AND R. A. HARDY. 1985. Assessment of the accidental
take of sea otters, *Enhydra lutris*, in gill and trammel nets. Unpublished report.
Maine Resources Branch, California Department of Fish and Game.

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