

Final Report

CHANGES ROCKY SUBTIDAL COMMUNITIES ALONG A GRADIENT IN SEA OTTER PREDATION ON THE OLYMPIC PENINSULA COAST OF WASHINGTON STATE

Rikk G. Kvitek¹, David Shull², Don Canestro³, Ed Bowlby⁴ and Barry Troutman⁴

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**Olympic National Park,
Washington State Department of Wildlife
and**

Rikk G. Kvitek¹

Project Officers

Olympic National Park

Bruce Moorhead
Olympic National Park
600 Park Avenue
Port Angeles, WA 98362
(206) 452-4501

Washington Dept. Wildlife

Steve Jeffries
Washington Dept. Wildlife
7801 Phillips Rd.
Tacoma, WA 98498
(206) 964-7278

¹ Zoology Dept., NJ-15, University of Washington, Seattle, WA 98195 (206) 543-1649

² Oceanography Dept., University of Washington, Seattle, WA 98195

³ Biological Sciences, University of California, Santa Barbara, CA

⁴ Washington State Dept. Wildlife, 7801 Phillips Rd., Tacoma, WA, 98498

Abstract

Distribution and abundances of benthic species were sampled within and outside of known sea otter feeding areas along the outer coast of the Olympic Peninsula during the summer and fall of 1987. This survey had four main objectives. 1) To install permanent monitoring stations and collect baseline data on important community members. 2) To determine the distribution and abundance of sea otter prey along the coast. 3) To infer changes in benthic community structure as a result of the introduction of sea otters to Washington in 1969-70. 4) To predict future shifts in the distribution and dynamics of the present otter population based on prey abundance patterns as well as human and environmental factors.

The results of this benthic survey suggests that the introduction of sea otters has profoundly affected the distribution and abundance of their prey along the Olympic Peninsula, particularly with respect to the red sea urchin, *Strongylocentrotus franciscanus*. The lowest benthic prey biomass (98 - 31 g/m²) was found at the sites sampled within the primary range of the sea otters (Cape Alava - Cape Johnson areas) where prey species are scarce (1.1 - 6.4 ind/m²), and small (77 - 56% of the prey < 5 cm). At sites within the secondary sea otter range (areas where otters are only occasionally seen) prey was still scarce (< 4.5 ind/m²), but with moderately higher prey biomass (128-191 g/m²) and prey sizes (43-92 % of the prey ≥ 5 cm). The richest prey communities were found at the four sites to the north of the present sea otter range (Anderson Point to Neah Bay). Prey biomass (318 - 776 g/m²) and density (4 - 22 ind/m²) generally increase along a south-north gradient. Prey individuals were also consistently larger north of Cape Alava (66 - 89% of the prey > 5 cm). North of the otters' range, the red sea urchin accounted for most of the prey individuals and biomass. Within the range, urchins were rare, with sea cucumbers (*Cucumaria miniata*) and small gastropods making up most of the available prey items.

The distribution of red urchins appears to affect algal groups differentially. Comparing sites with and without urchins, the abundance of folios red algae was negatively related to urchin numbers whereas that of coralline crusts was positively correlated. Urchin abundance appeared to have little impact on the annual kelp species *Nereocystis*. No significant difference in the percent cover of this species was found between the site in the center of the otter range with the lowest number of sea urchins (Cape Alava, 32±0.5 % cover) and the site with the highest urchin density (Neah Bay, 34±8.8 % cover). Cover of the perennial species, *Macrocystis*, may have increased at Cape Alava since the introduction of sea otters to the outer coast. Significantly higher *Macrocystis* cover was found in aerial photographs of Cape Alava taken on June 11, 1986 (59% ± 3.2) 16 years after the introduction of otters than those taken of the same site on July 13, 1959 (32% ± 8.8) 10 years before the introduction.

If the sea otters of the Olympic Peninsula have reduced the abundance of their benthic prey base and are now faced with an impoverished resource, as a population they have four non-mutually exclusive alternatives: 1) stay where they are but at a reduced population growth rate or in reduced numbers; 2) stay

where they are and maintain the same or higher rate of increase by switching to an alternate prey resource; 3) move south into an only slightly better prey area or 4) move north into the rich and unexploited feeding grounds around Makah Bay, Cape Flattery and into the Strait of Juan de Fuca. The first option may be exercised by all or just a portion of the total population as has been documented in other areas (i.e. it may become a female area). The second option is also possible given the high numbers of fish found at Cape Alava (4.8 ± 3.2 ind/50 m transect). More fish were observed at this site than any other with the exception of Neah Bay. Moving south would provide little advantage in prey and would expose the otters to greater wave exposure (fewer off-shore island than in their present range) as well as increased human contact (Native American net fisheries and boat traffic around La Push). Finally, to move north would appear to offer the greatest rewards in terms of prey and protection from swell (once north of Portage Head and especially inside the Strait of Juan de Fuca). However, human contact may be an important deterrent; Native American fishing activity increases in this region and the Strait is also the site of an active and increasing sea urchin fishery. We conclude that scarcity of prey in the otters' present range, combined with a south to north gradient of greatly increasing prey and fishing activity sets the stage in Washington for another man/otter conflict.

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1. Introduction

In 1969-70, 59 sea otters were translocated from Alaska to the outer coast of the Olympic Peninsula, Washington State (Jameson et al. 1982). Although, prior to our study, no quantitative benthic survey had been conducted along this coast, either to evaluate sea otter prey availability, the impact the otters have had on their communities, or for any other reason, this information is needed for several reasons. Sea otters have been generally characterized as "keystone" predators in rocky, kelp communities where their importance is disproportionately large with respect to their numbers. Although widely accepted, the paradigm of increasing kelp cover with the reduction of grazing invertebrates by sea otter predation is based on comparisons of Alaskan areas with and without sea otters (Estes and Palmisano 1974, Estes et al. 1978) or human manipulations of sea urchins in the absence of sea otters (Duggins 1980, Dayton 1975); it has never been directly tested. In addition, expanding sea otter populations have a tendency to compete with man for the same resources (see Estes and VanBlaricom 1985 for review) often resulting in heated and costly conflicts between conservationists and fisheries. Finally, California sea otters are listed as an endangered species by the US Fish and Wildlife Service, and hence the efforts at translocation to help bolster their numbers and the intense interest of environmental groups in the otters' well being.

Given the lack of critical tests, the potential for man/otter conflicts, and the demonstrated human concern for this species, there is a need for more information regarding the impact of sea otters on their prey communities and the factors contributing to the re-establishment of this species. The successful re-introduction of sea otters to the Washington coast has provided an excellent opportunity to increase our knowledge in these areas. The distribution of otters along the coast is well known (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data), making it possible to identify and exploit a gradient of sea otter predation as a natural experiment. To this end, our project has 4 primary objectives: 1) the evaluation of prey resources within the sea otters range; 2) the comparison of prey abundance and community structure between areas of high, low and no otter densities 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. This long-term approach will provide a more direct test of the theory by allowing us to track changes in communities as the otter population continues to expand. 4) The final objective is to make predictions about the future distribution and movements of otters along the Washington coast based on factors we identify as most important in determining their present range.

2. Methods

2.1. Study Site Selection

Three broad study regions were selected with respect to the current range of the Washington State sea otter population (Figure 1). To characterize benthic communities within areas of high, low and no otter occurrence, sites were selected along a gradient of otter occupancy identified by Bowlby and Troutman (Washington State Dept. of Wildlife unpublished data) (Figure 2).

Areas are designated as primary range (frequent sighting of numerous otters), secondary range (< 1 sea otter observed per survey flight), and outside the range (no otter sightings). Within the otters' primary range, sites at Cape Johnson and Cape Alava were chosen that had been identified by Bowlby and Troutman (Washington Dept. of Wildlife) as principle feeding areas (Figure 1). Specific sampling sites were then placed in the region of highest prey concentrations within each feeding area.

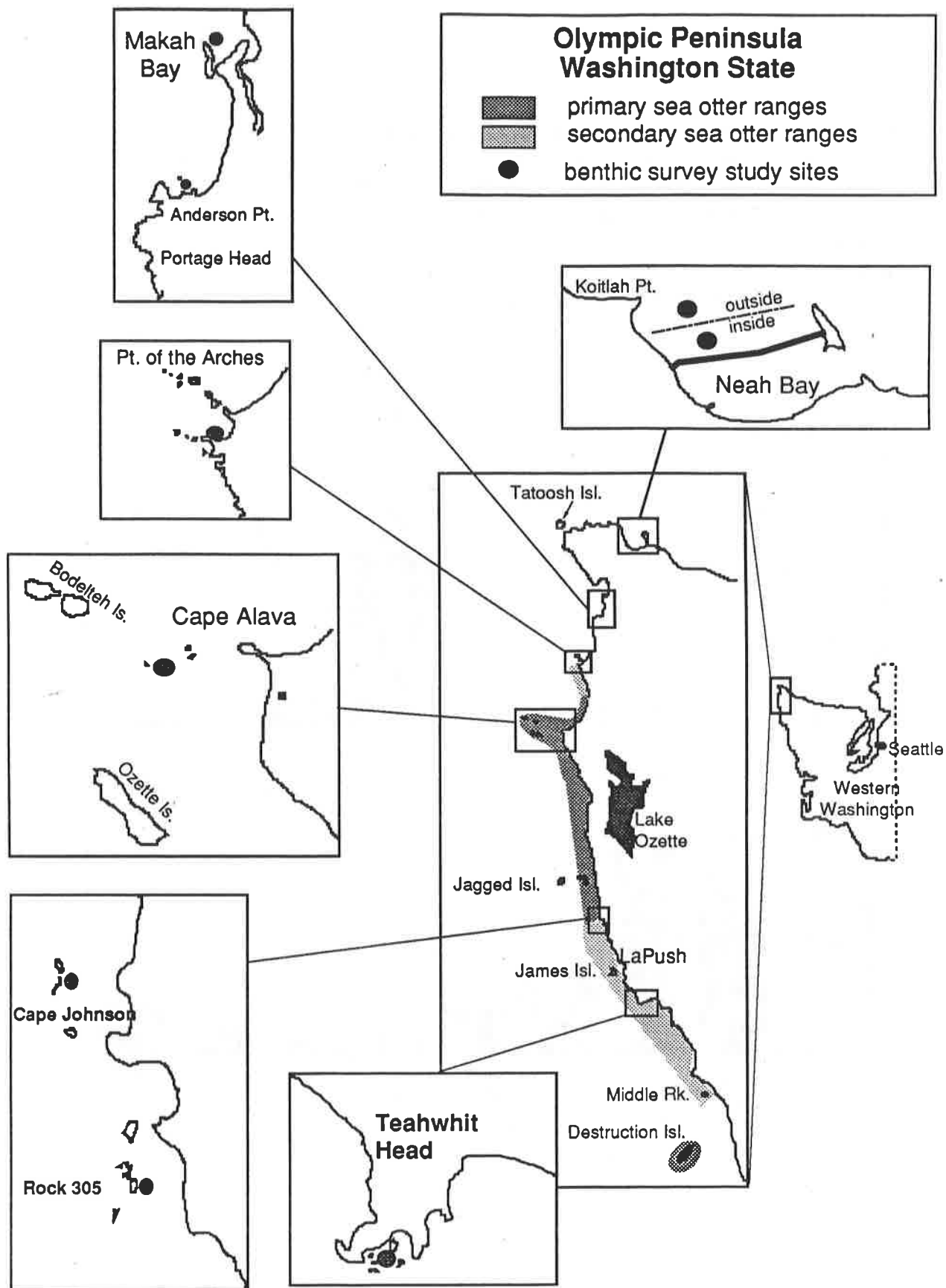
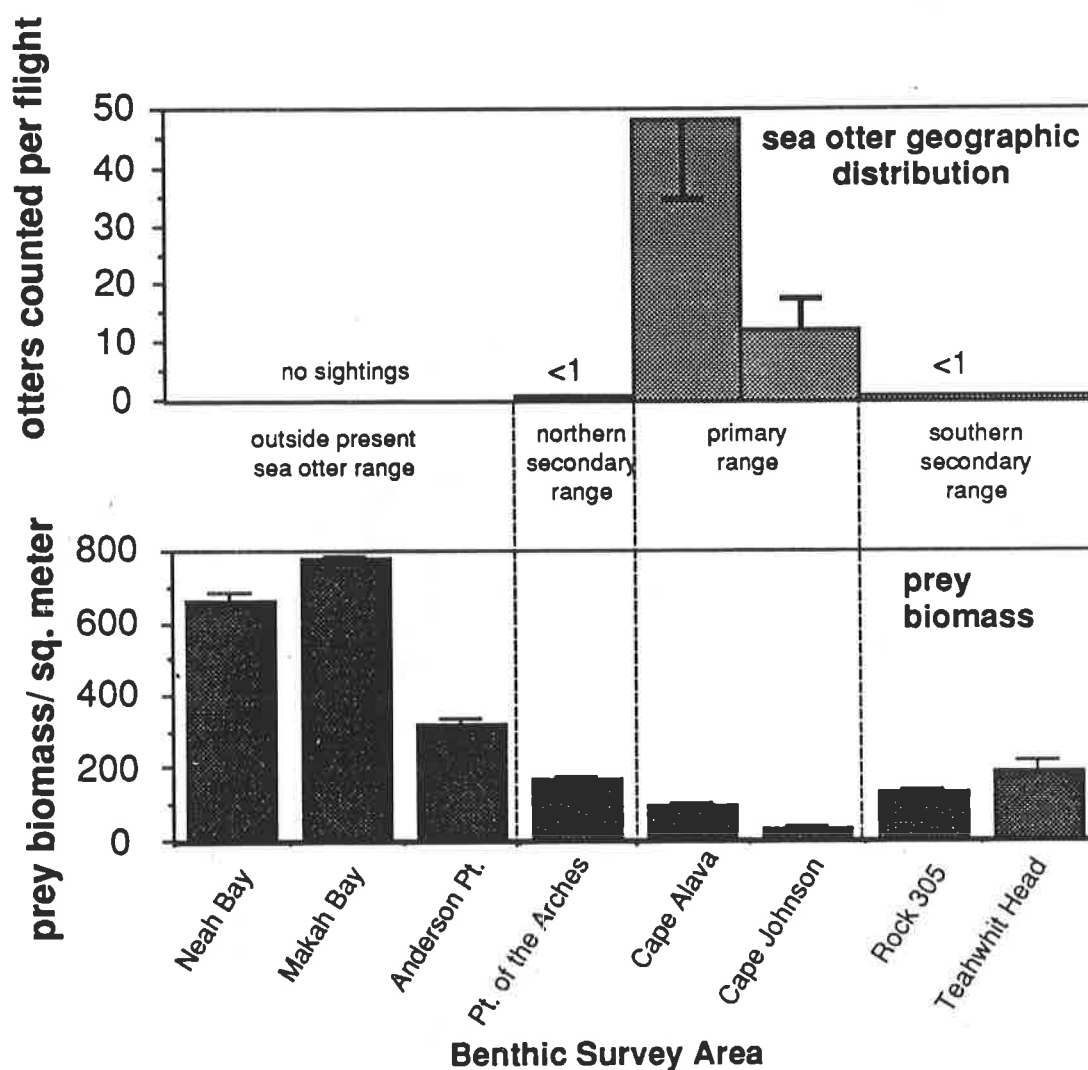


Figure 2. Prey biomass was lowest at sites within the sea otters' primary range (the region in which sea otters were most frequently observed on 7 monthly survey flights between March - Oct 1987, Bowlby and Troutman Washington State Dept. of Wildlife unpublished data). Prey biomass was intermediate at sites within the secondary range (areas with < 1 sighting/flight) and was highest outside the sea otters' range. Mean otter counts (error bars = se) are for geographic areas which include the corresponding benthic study sites.



Sites outside the primary range of otters were selected based on the following criteria: protection from swell via head lands or offshore islands, water depth and substrata similar to within range sites, highest concentrations of prey locatable given the first two constraints. The southern secondary range sites (Figure 1) were placed at Teahwhit Head and rock # 305 (United States Fish and Wildlife Service coastal inventory designation). Sites to the north were placed at Point of the Arches, Anderson Point, Makah Bay and Neah Bay (Figure 1). Two sites were used at Neah Bay, one inside an area in which commercial urchin fishing is prohibited by the Makah Nation, and one outside. Urchins were actively being harvested from Neah Bay in November when our sampling was done at this site. 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 (~ 5) is known to occupy Destruction Island (Figure 1) (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data), 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 principle study sites; Anderson Pt. 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. These were chosen as type communities and were more thoroughly sampled than the other sites.

2.2. Transect Layout and Installation

To promote the comparison of our results with those of researchers in other geographic areas and hence improve our ability to generalize about the impact of sea otters on their prey communities, transect layout and data collection procedures followed the protocol used by USFWS in their monitoring of sea otter habitats (USFWS 1986) whenever possible.

All field work was conducted during the last two weeks of August 1987 with the exception of Neah Bay which was sampled on November 4th. Zodiaks, a 19 ft Glasply skiff and a commercial urchin harvester were variously used as diving platforms.

Two types of transect layouts were employed, permanent and temporary. Permanent transect markers were installed at Cape Alava and Teahwhit Head. These consisted of a 50 m baseline with 5 - 14 m transect lines projecting from alternating sides every 10 m. The end of each line was marked with a stainless steel 1/4 x 4" eye-bolt and numbered stainless steel tag. The bolts were screwed into 7/16" plastic Curtis Industries wall anchors inserted into the rock. A Chicago Pneumatic air hammer, modified to operate off of a scuba tank, was used to drill the 1/2" holes required for installation. Temporary 1/4" nylon transect lines marked at 1 meter intervals could then be clipped to the eye-bolts and data collected.

At all other sites temporary transects were deployed and their positions well noted with surface line-ups such that they could be relocated within at least 10 m. These transects generally consisted of one or more series of 25 or 50 1m² quadrat counts placed end to end.

2.3. Data Collection

2.3.1. quadrat counts

At the permanent transect sites, 10 - 1m² 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.

Invertebrate and brown algal individuals were counted by species within each quadrat. Species deemed to be either potential otter prey, important or conspicuous community members (with the exception of clonal organisms) were sampled at most sites (see appendix tables 1,2 and 3 and for complete list of species monitored).

2.3.2. point contact

Point contact methods were 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.

2.3.2.1. biotic cover

Biotic cover was determined along each transect line by noting substratum cover under each of 5 predetermined points per meter. Substratum types were classified as; folios red algae, coralline algal crust, brown algae, sessile invertebrate, or bare rock. Percent cover of each type was calculated for each of the primary 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.

2.3.2.2. site physical characteristics

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.

2.3.3. species collections

2.3.3.1. species list

In addition to the quantitative sampling, a general list of species observed throughout the course of the study and the relative abundances of invertebrate species was also compiled (appendix tables 2 and 3).

2.3.3.2. 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 meat weights were obtained for likely sea otter prey species. These measurements were then used to calculate size/weight regressions whenever possible (appendix table 6) and combined with density data to compute sea otter prey biomass concentration at each site.

2.3.4. fin fish transects

Sea otters have been shown to feed on fish in habitats where invertebrate prey is scarce (Estes et al. 1981). For this reason, fish abundance was quantified as a potential alternate prey resource at Anderson Pt., Cape Alava and Cape Johnson. Fish counts by species were made along 3 mid-water (2 x 2 x 50 m) and 3 benthic (1 x 2 x 50 m) swimming transects at each of these sites. The fish transects were run off of the ends of the quadrat transects; first the mid-water counts, then the benthic counts on the return. Fish abundance was qualitatively noted at Neah Bay and Teahwhit Head.

2.3.5. aerial kelp canopy survey

The ability of sea otters to limit the densities of macro-grazers, particularly sea urchins is well accepted, and the ability of urchins to greatly reduce kelp canopy cover is also generally acknowledged. As a test of the applicability of this paradigm to the coast of the Olympic Peninsula, contemporary and historic kelp cover comparisons were made of areas with otters vs those without or at a pre-otter time. Cover of the annual kelp species *Nereocystis luetkeana* was measured from aerial photographs taken of the transect sites at Cape Alava from 500 ft on September 17, 1987, and at Neah Bay on November 14, 1987 from a high vantage point. Percent cover was computed by projecting the photographs onto a pattern of random dots divided into quadrats and counting the proportion of dots contacting kelp plants. No winter storms had struck the coast prior to taking the photographs, and the kelp beds were fully intact. As a measure of within site variability of *Nereocystis* percent cover, annual photographs (courtesy of R.T. Paine, Zoology Dept. Univ. of Washington) taken every September from 1976-1986 of a *Nereocystis* patch on Tatoosh Island (Figure 1) were analyzed in the same manner.

Similarly, a July 13, 1959 aerial photograph taken at 500 ft of Ozette Island at Cape Alava by Vic Scheffer, was compared to a June 11, 1986 aerial photograph of the same area taken at the same altitude and angle (Ed Bowby, Washington Dept. Wildlife).

3. Results

3.1. Invertebrate Prey

3.1.1. abundance

At sites north of the sea otter range, overall invertebrate prey abundances 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. From Cape Alava south, urchin densities were very low (0.02 - 0.22) and although more were found south of the otter range, this difference was not significant at the $p = 0.05$ level (Table 1). Within and south of the sea otter range, prey items were generally smaller species, with gastropods, limpets, small chitons and sea cucumbers (the only large prey) the most abundant species found (Table 1). Cape Alava had the highest overall prey concentration of the four southern sites, but gastropods accounted for ~ 75% of the prey (Table 1).

Faunal and algal species sampled but not included as prey are listed with their abundances (when available) in the appendix (tables 2-5).

Table 1. Sea otter prey abundances (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. Alpha superscripts indicate ANOVA and Fisher PLSD multiple range test groupings at $p \leq 0.05$.

Sea Otter Invertebrate Prey Abundance (ind/m²)

Site	<i>Strongylocentrotus franciscanus</i>	sea cucumbers	<i>Cryptochiton stelleri</i>	<i>Minnitiles giganteus</i>	gastropods	limpets	small chitons	crabs	Total Prey	N
sites north of primary sea otter range										
Neah Bay	21.1^a	0.24^c	0.04^b	0^b	0.70^c	0.24^b	ns	0^b	22.4^a	50
inside Makah reserve	(9.36)	(0.59)	(0.20)	(0)	(2.17)	(0.59)		(0)	(10.16)	
Neah Bay	12.3^b	0.36^{t^c}	0.04^b	0^b	0.56^c	0.40^b	ns	0^b	13.5^b	50
outside Makah reserve	(9.66)	(0.66)	(0.20)	(0)	(1.07)	(0.86)		(0)	(9.91)	
Makah Bay	6.69^c	0.10^{t^c}	0.06^b	0.02^b	0.59^c	0.67^a	0.33^b	0^b	8.5^c	49
	(3.63)	(0.31)	(0.24)	(0.14)	(1.72)	(1.01)	(0.46)	(0)	(4.45)	
Anderson Pt.	3.33^d	0.27^{t^c}	0.02^b	0^b	0.29^c	0.06^c	0.04^c	0^b	4.0^e	99
	(2.61)	(0.59)	(0.14)	(0)	(0.70)	(0.31)	(0.20)	(0)	(2.99)	
Pt. of Arches	4.42^d	0^{t^c}	0.11^b	0^b	ns	0^c	0^c	0^b	4.5^e	35
	5.02	(0)	(0.32)	(0)		(0)	(0)	(0)	(5.07)	
sites within primary sea otter range										
Cape Alava	0.02^e	0.93^{t^b}	0^b	0.03^b	3.95^a	0.65^a	0.59^a	0.18^a	6.4^d	100
	(0.14)	(1.65)	(0)	(0.22)	(4.79)	(1.18)	(0.85)	(0.50)	(5.81)	
Cape Johnson	0.0^e	0.22^{t^c}	0.02^b	0.14^a	0.32^c	0.16^b	0.20^b	0^b	1.1^f	50
	(0.0)	(0.82)	(0.14)	(0.76)	(0.55)	(0.47)	(0.25)	(0)	(1.54)	
sites south of primary sea otter range										
Rock 305	0.10^e	1.06^{t^b}	0.1^b	0.1^a	1.18^b	0.96^a	0.30^b	0.02^b	3.8^e	50
	(0.30)	(1.82)	(0.3)	(0.36)	(1.79)	(1.84)	(0.43)	(0.14)	(3.18)	
Teahwhit Hd.	0.22^e	1.31^{t^a}	0.26^a	0.19^a	2.01^b	0.06^c	0.10^b	0.15^a	4.3^e	100
	(0.61)	(2.21)	(0.5)	(0.46)	(3.77)	(0.28)	(0.27)	(0.5)	(4.67)	

ns not sampled

^t *Stichopus californicus*

^{tt} *Cucumaria minata*

3.1.2. prey biomass and size distributions

The highest concentrations of large prey items and total prey biomass were found outside the primary and especially north of the sea otter range (Table 2 and Figure 2). North of Cape Alava total prey biomass was much higher, and prey individuals > 5 cm in size represented > 80% of the prey sampled. South of Cape Johnson, 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 was found at Cape Alava (77% of the items < 5 cm) and the lowest biomass was found at Cape Johnson.

3.2. Fin Fish

Unlike invertebrate biomass, fin fish abundance was not always reduced within the sea otter range (Table 3). Of the three sites quantitatively sampled, significantly more fish and suitable prey species were counted at Cape Alava. Only at Neah Bay were more fish observed.

3.3. Biotic Cover

Folios 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 4). No pattern was found in the distribution of brown algal or sessile invertebrate substratum cover between sites.

3.4. Kelp Canopy Cover

Nereocystis cover at the site with the highest urchin density and no sea otters (Neah Bay) was not found to be significantly different than that found in the middle of the sea otter range (Cape Alava) (Table 5). *Macrocystis* cover, however, was found to be significantly less at Cape Alava ten years before the introduction of sea otters (1959) than 17 years following the introduction (Table 5).

3.5. Physical Characteristics

The three principle study sites (those sampled most intensively) were similar in water depths (4.0 - 4.8 m MLW) (Table 6) 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 6). 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.

Table 2. Total prey biomass (means and SD) and size distributions increase greatly north of the sea otter range, were generally lower within the secondary ranges and lowest within the primary range. Percentages of prey items larger than 5 cm observed consumed by feeding sea otters (Bowby and Troutman Washington State Dept. of Wildlife unpublished) reflect the reduce prey sizes found at sites within the primary range and the otters' preference for larger prey items.

Sea Otter Prey Biomass & Size Distributions

Site	Biomass	Size	
	total biomass g/m ²	benthic survey percent prey ind. >5 cm	feeding otters percent prey ind. >5 cm
sites north and outside of the sea otter range.			
Neah Bay inside Makah reserve	661 (158.6)	83 %	
Neah Bay outside Makah reserve	664 (451.0)	66 %	
Makah Bay	776 (58.1)	87 %	
Anderson Pt.	318 (134.4)	89 %	
northern secondary sea otter range			
Pt. of the Arches	165 (71.1)	92 %	
sites within primary sea otter range			
Cape Alava	98 (42.0)	23 %	45 % n=139
Cape Johnson	31 (42.0)	44 %	73 % n=135
southern secondary sea otter range			
Rock 305	128 (57.6)	43 %	
Teahwhit Head	191 (237.1)	51 %	

Table 3. Significantly more fish were counted along midwater (2x2x50 m) and benthic (2x1x50 m) swimming transects at Cape Alava than either of the other two sites quantitatively sampled (ANOVA and Fisher PLSD multiple range test $p \leq 0.01$, means and (SD), $n = 3$). Qualitative observations indicated high fish densities at Neah Bay and very low numbers at Teahwhit Hd.

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Fin Fish Abundance

Site	black rockfish	striped surfperch	painter greenling	kelp greenling	lingcod	cabezon	kelpfish	total fish	Grand Totals
Neah Bay									abundant
sites north of sea otter range									
very abundant									
Anderson Pt.									
midwater	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0.5 ^b (0.8)
benthic	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.3 (0.6)	1.0 (1.0)	
Cape Alava									
sites within primary sea otter range									
midwater	2.3 (2.1)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2.3 (2.1)	4.8 ^a (3.2)
benthic	3.7 (1.5)	2.3 (1.2)	0.7 (0.6)	0.0 (0.0)	0.3 (0.6)	0.3 (0.6)	0.0 (0.0)	7.3 (1.5)	
Cape Johnson									
midwater	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0.2 ^b (0.4)
benthic	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.3 (0.6)	0.3 (0.6)	0.0 (0.0)	0.0 (0.0)	0.3 (0.6)	
Teahwhit Hd.									
southern secondary range sea otter range									
	rate	rate			rate	rate			rare

Table 4. Folios red algal cover varied inversely with urchin density where as crustose coralline and bare rock percent cover was positively related to urchin abundance. No relationship was found between urchin densities and brown understory algae or invertebrate cover. Algal and invertebrate cover as determined by point contacts ($n = 250$ per station) at the three principle 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. Superscripts indicate results of ANOVA and Fisher PLSD multiple range test groupings at $p \leq 0.05$ (** = $p \leq 0.01$).

Biotic Cover (percent) at the Principle Study Sites

Site	folios red algae	coralline crust	brown algae	Invertebrates	bare rock
high urchin density (21 ind/m²)					
Neah Bay (inside Makah reserve)	0%	100%	nr	nr	nr
moderate urchin density (3 ind/m²)					
Anderson Pt. (north of otter range)	27% ^{b**}	18% ^{a**}	25% ^a	11% ^a	24% ^{a**}
low urchin densities (< 0.2 ind/m²)					
Cape Alava (within otter range)	73% ^a	5% ^b	14% ^b	8% ^a	10% ^b
Teahwhit Hd. (south of otter range)	66% ^a	9% ^b	34% ^a	4% ^b	13% ^b

nr = not recorded

Table 5. There was no significant difference in percent cover of the annual kelp species *Nereocystis* found in the benthic transect areas at Neah Bay (a site with no otters and high sea urchin densities) and Cape Alava (the site with the highest sea otter numbers and lowest urchin densities) (t-test $p = 0.76$). September photographs taken annually at the same site on Tatoosh Island were used as a measure of between year variation in *Nereocystis* cover. The percent cover of the perennial kelp species *Macrocystis* was significantly less in an aerial photograph taken at Cape Alava before the introduction of sea otters than in an aerial photograph of the same site taken in 1986, 17 years after the introduction of sea otters to the Washington coast (t-test $p = 0.014$). (N = number of subsamples taken from each photograph).

Kelp Percent Cover from Aerial Photographs

	<i>Nereocystis</i>			<i>Macrocystis</i>	
	Neah Bay Nov 14 1987	Cape Alava Sept 17 1987	Tatoosh Sept 1976-1986	Cape Alava July 13, 1959 (pre-otter)	Cape Alava June 11 1986
mean	31.8%	34.0%	14.4%	31.5%	58.7%
(SD)	(0.5)	(8.8)	(8.6)	(8.8)	(3.2)
N	4	6	6	4	3

Table 6. Depths (means and SD, n = 50 point contacts per site) and substrata distributions (n = 250 point contacts per site) are given for transects at the three principle 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.

Physical Characteristics of the Principle Study Sites

Site	depth (m)	rugosity Index	Substrata (percent cover)					bed rock
			sand & gravel	cobble (5-10 cm)	small rocks (10-50 cm)	large rocks (50-150 cm)	boulders (>150 cm)	
Anderson Pt. north of otter range	4.0 (0.43)	1.2 (0.08)	6%	18%	22%	16%	6%	28%
Cape Alava within otter range	4.8 (0.52)	1.4 (0.14)	0%	14%	10%	28%	44%	4%
Teahwhit Hd. south of otter range	4.4 (0.44)	1.4 (0.09)	0%	4%	4%	8%	38%	42%

4. Discussion

4.1. Prey Abundance

As in other studies comparing areas with and without sea otters (Estes and Palmisano 1974, Estes et al. 1978, Stewart et al. 1982, Kvitek et al. in review) results of this survey suggest that sea otters have greatly reduced their prey within their present range (Figure 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 (in review) survey of the Washington otter population and habitat in 1985 described the Cape Alava area as the primary range of the population with characteristically low prey densities. 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 reclassified Cape Johnson as a primary otter area and indicate that the bulk of the otter population now moves seasonally between Cape Johnson in the summer and Cape Alava during the winter (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data). Our benthic prey survey results at Cape Johnson are consistent with this hypothesis; unlike Jameson et al.'s earlier qualitative findings, we found Cape Johnson to have the lowest prey numbers and biomass of any site surveyed. Indeed, no red urchins were seen anywhere in the area. The few urchins (greens, purples and reds) that were found at otter sites were always in crevices or within rock burrows and thus inaccessible to sea otters. This is in stark contrast to areas outside the otters' range where the great majority of urchins of all species were sufficiently exposed to be accessible to otters.

The relatively greater abundance of small sized prey at primary range sites was reflected in the observed diets of the feeding otters (Table 2). At Cape Alava where only 23% of the prey sampled was greater than 5cm in length, 55% of prey items observed being consumed by otters were less than 5 cm (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data). At Cape Johnson where the proportion of prey larger than 5 cm was 62% higher than at Cape Alava, the proportion of prey larger than 5cm consumed by otters was also higher (91%) than at Cape Alava. The fact that at both primary otter sites the proportion of consumed items larger than 5 cm was higher than the proportion of this size range found in the available prey indicates that the otters were preferentially selecting larger prey sizes.

4.2. Community Structure

The sea otter's ability to greatly reduce densities of invertebrate grazers, especially sea urchins, has long been implicated as an important factor in determining the structure of nearshore algal communities (Estes and Palmisano 1974, Estes et al. 1978, Stewart et al. 1982). 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 (Duggins 1980, Dayton 1975). Our results both support and contradict this generalized view. As described above and in the other studies mentioned, sea urchin densities varied inversely with otter

presence. Consistent with the otter/urchin/algal paradigm we found a negative relationship between urchin densities and folios red algal cover and a positive one between urchins and coralline crust cover (Table 4). This is understandable given the relative susceptibility of these two algal groups to urchin grazing. However, with respect to kelps the pattern was not as clear cut. Although comparisons of *Macrocystis* cover at Cape Alava before and after the introduction of sea otters to the area indicates a significant increase in percent cover, no difference was found in *Nereocystis* cover between Neah Bay, which had the highest concentrations of urchins found and Cape Alava, the longest occupied otter site and having virtually no urchins.

There are several possible explanations for this apparent contradiction. *Nereocystis* is known to be able to achieve a size refuge from urchin grazing (Duggins 1981); urchins avoid adult *Nereocystis* stipes and hold fasts in preference to young plants and other species. This is not the case with *Macrocystis*; urchins have been known to mow down large stands of adult plants. Thus, on an exposed coast such as the Olympic Peninsula, if surge conditions in spring prevent urchins from foraging during the time of *Nereocystis* recruitment and early growth, this annual plant may gain enough of a head start to out-grow the urchins by the time conditions are calm enough for the grazers to begin foraging. This would explain why *Nereocystis* is so abundant at Neah Bay while folios reds are scarce. Even if the urchins are restricted from foraging until summer, they can always graze down the reds, but not the bull kelp.

Another possible explanation for the seemingly anomalous presence of dense *Nereocystis* at Neah Bay, is that 1987 was an extremely good year for this species. Although there are no hard data to support this claim, urchin fishermen at Neah Bay and Washington State Dept. of Fisheries surveyors (Alex Bradbury, Brinnin Shellfish lab) have commented on the unusually dense cover of *Nereocystis* in 1987. In addition, we have shown *Nereocystis* cover to be quite variable at a site on Tatoosh Island not far from Neah Bay (Table 5). It is therefore possible that kelp recruitment and growth overwhelmed the urchins in 1987, particularly if extensive urchin movement is restricted to the calmer months of summer.

Evidence suggesting a new mechanism by which sea otters may significantly alter the structure of their prey communities was observed during this study. At Cape Alava, considerable numbers of the large rocks in the area had sessile invertebrates (normally found on the undersurfaces) growing on the tops and folios red algal species attached to the undersides. Due to the distribution of available prey, it appears as though the otters were turning over very large rocks to obtain hidden food items (e.g. crabs, octopus, *Cucumaria*). Rock rolling by waves in both the intertidal (Sousa 1979) and subtidal 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 they are mostly likely to occur at opposite times of the year, i.e. otters of the Washington coast appear to shift their range seasonally to avoid exposure to the prevailing swell (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data).

4.3. The Sea Otters' Future on the Washington Coast

The comparison of otter distribution versus their prey along the outer coast (Figure 2) poses two questions. 1) If there is several times the amount of available food present at sites north of the sea otters' range, why do they remain at sites where prey is small and scarce; Cape Alava in the winter and Cape Johnson during the summer? 2) Given that the size of the otter population has been increasing and that their prey resources have been and will continue to decrease, what changes might we expect to see in the future?

Firstly, although prey may be scarce at the two otter sites, both afford protection from swell due to the presence of off-shore islands and rocks. Inspection of the Washington coastline shows Cape Alava to be the best protect site in any swell condition. The Bodeltah Islands and Ozette Island are able to provide shelter both from the sw swells of winter and the nw seas of summer. During the Olympic National Parks 1986 New Years aerial bald eagle count most of the otters seen were in the lee of Ozette Island (Ed Whitaker, Park Ranger, Mora, ONP, pers. com.). This protection combined with a very extensive, shallow subtidal boulder field providing ideal habitat for prey organisms, made Cape Alava the most likely place on the coast to be colonized by the translocated sea otters, and this is apparently what happened (Jameson et al. 1982, Jameson et al. in review). Cape Johnson, on the other hand is protected only from nw swell. This may explain why it has only been recently invaded by otters and used primarily as a summer area. In addition to protection and prey habitat, both these sites are as isolate from boat traffic and human contact as possible on the coast. A shift either north or south would take them closer to the fishing ports of Neah Bay and LaPush respectively where native Americans maintain an active set-net fishery. Gill net fishing has been implicated in restricting the growth of the California otter population (USFWS 1986).

Another possible but unlikely explanation for why otters have remained at these two sites, is that they may be relying on large but more mobile and cryptic prey than we observed in our survey, such as octopus, large crab, clams or fish. However, surface observations at both these sites indicate that the first three categories, while present in the otters' diets, represented a minority of the prey items and fish were never eaten (Bowlby and Troutman, Washington State Dept. of Wildlife unpublished data). Furthermore, in our initial survey of each of these sites, we covered a very large area looking in many crevices and other likely places for these species and found none. This was not true outside the otter range, where even though octopus and crab were not found along the transect lines, they were encountered relatively frequently in the general survey of the sites.

Notwithstanding the otters' apparent reluctance to move, what alternatives are available given their diminishing prey resources? There are several. Some or all of the otters may continue to use Cape Alava under at least the following conditions. If the entire population remains it will probably be at a reduce population growth rate unless they are able to exploit a previously untapped and abundant prey resource. It is believed that some Aleutian otter populations switched to eating fish as their invertebrate prey became scarce and fish numbers increased along with the kelp cover (Estes et al. 1981). This

may occur at Cape Alava where we found several species of large fish to be very abundant and easily approachable (Table 3). Otters may also continue to use Cape Alava as strictly a winter site or a female site as other populations have done with long occupied areas (Garshelis 1983) while the bulk of the population moves to one of the richer prey areas to the north either permanently or seasonally.

If the otters shift their range, they will not be passive participants in the communities they invade, and it is therefore worth considering where they may go and what the consequences might be. A move south would appear to gain them very little; more people, more boats, more nets, generally less protection from swell, and not much more food until they get all the way down into the clam beds of Grays Harbor and Willapa Bay. Sites to the north, however seem more promising on the surface; much more food, large easily caught prey, fairly good protection from swell once inside Anderson Point, and especially inside the Strait of Juan de Fuca. However, the intense native American set-net fishery operating out of Neah Bay, and the new and growing sea urchin fishery developing in the Strait may present a barrier to the otters.

Given all these factors; an expanding otter population, diminished prey within the otters' range, a gradient of both prey abundance and human fishing activity increasing to the north, and the tendency for otters and man to compete for the same resources, the stage appears set for a new round of man/otter conflicts. Because we have seen such interactions raise hot blood on both sides in the past (see Estes and VanBlaricom 1985 for review), perhaps now is the time to plan for the future management of these potential conflicts.

Appendix

Table 1. Taxonomic abbreviation codes for species names listed in the appendix tables.

Group	Code	Species
brown algae	Ld	<i>Laminaria dentigera</i>
	Lg	<i>Laminaria groenlandica</i>
	Mi	<i>Macrocystis integrifolia</i>
	Nl	<i>Nereocystis lutkeana</i>
	Pc	<i>Pterygophora californica</i>
crabs	C sp	<i>Cancer</i> sp.
	Sa	<i>Scyra acutifrons</i>
tunicate	Sm	<i>Styela montereyensis</i>
sea stars	Di	<i>Dermasterias imbricata</i>
	Et	<i>Evasterias troschelii</i>
	Hl	<i>Henricia leviuscula</i>
	Lh	<i>Leptasteria hexactis</i>
	Ok	<i>Orthasterias koehleri</i>
	Ph	<i>Pycnopodia helianthoides</i>
	Po	<i>Pisaster ochraceus</i>
	So d	<i>Solaster dawsoni</i>
	Ss	<i>Solaster stimpsoni</i>
	Sd	<i>Strongylocentrotus droebachiensis</i>
urchins	Sf	<i>Strongylocentrotus franciscanus</i>
	Sp	<i>Strongylocentrotus purpuratus</i>
cucumbers	Cm	<i>Cucumaria miniata</i>
	Eq	<i>Eupentacta quinquesemita</i>
gastropods	Tb	<i>Tegula brunnea</i>
	Cl	<i>Calliostoma ligatum</i>
	Cf	<i>Ceratostoma foliatum</i>
limpets	Ol	<i>Ocenebra lurida</i>
	Am	<i>Acmaea mitra</i>
	Ci	<i>Collisella instabilis</i>
chitons	Da	<i>Diodora aspera</i>
	Cs	<i>Cryptochiton stellarii</i>
	Ml	<i>Mopalia lignosa</i>
	Pv	<i>Placiphorella velata</i>
bivalves	Tl	<i>Tonicella lineata</i>
	Hg	<i>Hinnites giganteus</i>

Appendix

Table 2. Invertebrate abundances measured along transects at Olympic Peninsula study sites (means and SD's). (N = number of square meter quadrats, ns = not sampled). See taxonomic abbreviation key for species names (appendix table 1).

Invertebrate Species Abundances (Ind/m ²)													
		crab		tunicate		sea stars							
	N	Sc	C sp	Sm	Di	Et	Hi	Lh	Ok	Ph	Po	So	Ss
Neah Bay (inside) mean SD	50	0 (0.0)	0 (0.0)	0 (0.0)	0.06 (0.2)	0 (0.0)	0.24 (0.5)	0 (0.0)	0.14 (0.4)	0.22 (0.5)	0.02 (0.1)	0 (0.0)	0 (0.0)
Neah Bay (outside) mean SD	50	0 (0.0)	0 (0.0)	0 (0.0)	0.10 (0.3)	0 (0.0)	0.20 (0.5)	0 (0.0)	0.12 (0.4)	0.28 (0.6)	0.04 (0.3)	0.02 (0.1)	0 (0.0)
Makah Bay mean SD	49	0 (0.0)	0 (0.0)	0.1 (0.4)	0 (0.0)	0 (0.0)	0.18 (0.4)	0.04 (0.2)	0 (0.0)	0.02 (0.1)	0.06 (0.2)	0 (0.0)	0 (0.0)
Anderson Pt. mean SD	99	0 (0.0)	0 (0.0)	0.47 (0.9)	0.08 (0.3)	0.01 (0.1)	0.21 (0.5)	0.04 (0.2)	0 (0.0)	0.11 (0.3)	0.01 (0.1)	0 (0.0)	0 (0.0)
Pl. of Arches mean SD	35	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0.1 (0.3)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Cape Alava mean SD	100	0.17 (0.5)	0.01 (0.1)	0.39 (0.6)	0 (0.0)	0.16 (0.5)	0.35 (0.7)	0.56 (1.2)	0 (0.0)	0.05 (0.2)	0.1 (0.4)	0 (0.0)	0 (0.0)
Cape Johnson mean SD	50	0 (0.0)	0 (0.0)	0.52 (1.0)	0.02 (0.1)	0.06 (0.2)	0.14 (0.4)	0.02 (0.1)	0 (0.0)	0.06 (0.2)	0 (0.0)	0 (0.0)	0.02 (0.1)
Rock 305 mean SD	50	0.02 (0.1)	0 (0.0)	1.96 (2.3)	0 (0.0)	0.08 (0.3)	0.36 (0.7)	0.1 (0.6)	0 (0.0)	0.02 (0.1)	0.04 (0.2)	0.02 (0.1)	0 (0.0)
Teahwhit Head mean SD	100	0.14 (0.5)	0.01 (0.1)	0.56 (0.9)	0.03 (0.2)	0.07 (0.3)	0.51 (0.9)	0.12 (0.6)	0 (0.0)	0.01 (0.1)	0.13 (0.4)	0.01 (0.1)	0 (0.0)

Invertebrate Species Abundances (Ind/m²)

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Appendix

Table 3. Brown algal species abundances (means and SD's) measured along transects at study sites along the outer coast of the Olympic Peninsula. (N = number of meter square quadrats sampled). See taxonomic abbreviation key (appendix table 1) for species names.

Brown Algae Abundances (Ind/m ²)						
Sites	N	Ld	Lg	MI	NI	Pc
north of present sea otter range						
Makah Bay	49					
mean		0.1	0.92	0	0.16	0.04
SD		(0.5)	(4.6)	(0.0)	(0.9)	(0.2)
Anderson Pt.	99					
mean		0	2.0	0	0.34	0.45
SD		(0.0)	(10.5)	(0.0)	(1.0)	(2.3)
northern secondary sea otter range						
Pt. of Arches	35					
mean		0.22	0.08	0	0.06	0
SD		(1.3)	(0.5)	(0.0)	(0.2)	(0.0)
within primary sea otter range						
Cape Alava	100					
mean		2.34	1.09	0.06	0.1	0.54
SD		(4.9)	(3.8)	(0.6)	(0.4)	(1.0)
Cape Johnson	50					
mean		0.12	0.04	0.28	0.04	0.54
SD		(0.4)	(0.3)	(0.7)	(0.2)	(1.6)
southern secondary sea otter range						
Rock 305	50					
mean		0.94	0.14	0	0.52	1.34
SD		(1.3)	(0.5)	(0.0)	(1.2)	(2.7)
Teahwhit Head	100					
mean		2.06	0.23	0	0.09	2.43
SD		(3.5)	(0.9)	(0.0)	(0.5)	(5.4)

Appendix

Table 4. All species listed below were observed at least once during the subtidal survey between Teahwhit Head to the south and Makah Bay to the north. Relative abundances are based on the following rankings of encounters per dive: r = rare (< 1/dive); p = present (1-5/dive); c = common (5-50/dive); a = abundant (50-100/dive); very abundant (>100/dive).

Faunal Species Observed and their Relative Abundances

species	relative abundance	notes
Brachiopods		
<i>Terebratalia transversa</i>	r	
Bryozoans		
<i>Aglaoephenia</i> spp.	p	
Cnidarians		
Anthozoans		
<i>Anthopleura elegantissima</i>	p	
<i>Anthopleura xanthogrammica</i>	c	
<i>Balanophyllia elegans</i>	c	
<i>Corynactis californica</i>	r	
<i>Epiactis proliferata</i>	p	
<i>Gersemia rubiformis</i>	p	
<i>Metridium senile</i>	r	
<i>Urticina crassicornis</i>	p	
<i>Urticina lofotensis</i>	r	
Scyphozoans		
<i>Thaumatoscyphus hexaradiatus</i>	p	
Crustaceans		
<i>Amphithoe</i> sp.	r	
<i>Balanus</i> sp.	p	
<i>Cancer oregonensis</i>	c	(generally found only in rock burrow holes inaccessible to sea otters)
<i>Cryptolithodes</i> spp.	r	
Hermit crabs	c	
<i>Idotea resicata</i>	r	
<i>Mimulus foliatus</i>	r	
<i>Pandalus</i> sp.	r	
<i>Scyra acutifrons</i>	p-c	
Echinoderms		
Asteroids		
<i>Dermasterias imbricata</i>	p	
<i>Evasterias troschelii</i>	c	
<i>Henricia leviuscula</i>	c	
<i>Leptasterias hexactis</i>	c	
<i>Orthasterias koehleri</i>	r	
<i>Patiria miniata</i>	r	
<i>Pisaster ochraceus</i>	p	

Appendix

Table 4. (continued)

species	relative abundance	notes
<i>Pycnopodia helianthoides</i>	p	
<i>Solaster dawsoni</i>	r	
<i>Solaster stimpsoni</i>	p	
Sea Urchins		
<i>Strongylocentrotus drobachiensis</i>	p	
<i>Strongylocentrotus franciscanus</i>	r-v	
<i>Strongylocentrotus purpuratus</i>	p	(generally found only in rock burrow holes inaccessible to sea otters)
Sea Cucumbers		
<i>Cucumaria miniata</i>	a	
<i>Eupentacta quinquesemita</i>	p	
<i>Stichopus californicus</i>	r-c	
Ophiuroids	p	
Hydrozoans		
<i>Allepore porphyra</i>	r	
<i>Tubularia crocea</i>	p	
Molluscs		
Gastropods		
<i>Amphissa columbiana</i>	p	
<i>Calliostoma ligatum</i>	c	
<i>Ceratostoma foliatum</i>	c	
<i>Crepidula adunca</i>	p	
<i>Ocenebra lurida</i>	p	
<i>Opalia chacei</i>	p	
<i>Searlesia dira</i>	r	
<i>Tegula brunnea</i>	p	
Chitons		
<i>Cryptochiton stelleri</i>	p	
<i>Mopalia lignosa</i>	p-c	
<i>Placiphorella velata</i>	p	
<i>Tonicella lineata</i>	p	
Limpets		
<i>Acmaea mitra</i>	c	
<i>Colisella instabilis</i>	c	
<i>Diodora aspera</i>	c	
Nudibranchs		
<i>Anisidoris nobilis</i>	p	
<i>Antiopella barbarensis</i>	p	
<i>Archidoris montereyensis</i>	c	
<i>Archidoris odhneri</i>	p	
<i>Dirona albolineata</i>	p	
<i>Laila cockerelli</i>	p	
<i>Triopha catalinae</i>	c	
<i>Tritonia festiva</i>	p	

Appendix

Table 4. (continued)

species	relative abundance	notes
Bivalves		
<i>Hinnites giganteus</i>	p	
Nemerteans spp.	p	
Polychaetes		
<i>Dodecaceria fewkesi</i>	p	
<i>Eudistyllia</i> spp.	p	
<i>Myxicola infundibulum</i>	p	
<i>Phragmatopoma californica</i>	p	
Sponges		
<i>Tetilla arb</i>	p	
<i>Isodictya quatsinoensis</i>	p	
Tunicates		
<i>Styela montereyensis</i>	a	
<i>Perophora annectens</i>	p	
<i>Metanfrocampa taylori</i>	p	
Fish		
<i>Damalichthys vacca</i>	r	
<i>Embiotica lateralis</i>	p	
<i>Gibbonsia</i> spp.	r	
<i>Gobieosox</i> spp.	r	
<i>Hexagrammos decagrammus</i>	c	
<i>Ophiodon elongatus</i>	p	
<i>Oxylebius pictus</i>	r	
<i>Scorpaenichthys marmoratus</i>	p	
<i>Sebastes auriculatus</i>	r	
<i>S. caurinus</i>	r	
<i>S. melanops</i>	c	
<i>S. nebulosus</i>	p	

Appendix

Table 5. All species listed below were observed at least once during the subtidal survey along the outer coast of the Olympic Peninsula between Teahwhit Head to the south and Makah Bay to the north.

Algal Species Observed

species

brown algae

Alaria marginata
Costaria costata
Desmarestia ligulata var. *ligulata*
Egregia menziesii
Laminaria dentigera
Laminaria groenlandica
Macrocystis integrifolia
Nereocystis luetkeana
Pleurophycus gardneri
Pterygophora californica

green algae

Derbesia marina
Ulva spp.

red algae

Botryoglossum falowianum
B. ruprechtianum
Erythrophyllum delesseriodes
Iridea spp.
Odonthalia washingtoniensis
Plocamium cartilagineum
Prionitis lanceolata
Rhodomenia californica
R. spp.
 articulated coralline algae
 encrusting coralline algae

Appendix

Table 6. The regression equations relate wet meat weight (grams) to size (maximum linear dimension unless otherwise stated) for spp. collected along the outer coast of the Olympic Peninsula between Teahwhit Head to the south and Makah Bay to the north.

Faunal Species Size and Weight Regressions			
species	regression	r	N length range
<i>Acmaea mitra</i>	$wt = 4.827 \times 10^{-6} \times \text{shell length (mm)}^{3.9}$	1.0	5 13-32 mm
<i>Calliostoma liniaia</i>	$wt = 0.0038 \times 10^0.1273 \times \text{shell length (mm)}$	1.0	4 11-19 mm
<i>Ceratosstoma foliatum</i>	$wt = 5.313 \times 10^{-6} \times \text{shell length (mm)}^{3.313}$	0.98	3 31-71 mm
<i>Cucumaria miniata</i>	$wt = 0.036 \times 10^{-6} \times \text{contracted body length (mm)}^{1.694}$	0.86	5 71-115 mm
<i>Diadora aspera</i>	$wt = 0.1486 \times 10^{0.0359} \times \text{shell length (mm)}$	1.0	5 22-67 mm
<i>Mopalia lignosa</i>	$wt = 2.6 \times 10^{-6} \times \text{shell length (mm)}^{3.86}$	0.98	5 22-49 mm
<i>Tegula brunnea</i>	$wt = 2.8 \times 10^{-6} \times \text{shell length (mm)}^{4.077}$	1.0	5 17-33 mm
<i>Strongylocentrotus franciscanus</i>	$wt = 1.49 \times 10^{0.014} \times \text{test diameter (mm)}$	(Bernard and Miller, 1973)	

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