**Big ol’ title: otters and kelp and prey and stuff**

Chris J. Harvey1, Kelly S. Andrews1, Kinsey E. Frick1, Jameal F. Samhouri1, Andrew O. Shelton1, Nick Tolimieri1, Gregory D. Williams2, Jessica R. Hale3, and Liam D. Antrim4

1Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E, Seattle, WA 98112 USA

2Pacific States Marine Fisheries Commission, under contract to Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 2725 Montlake Blvd E, Seattle, WA 98112 USA

3School of Aquatic and Fisheries Sciences, University of Washington, PO Box 355020, Seattle, WA 98195-5020 USA

4Olympic Coast National Marine Sanctuary, National Ocean Service, National Oceanic and Atmospheric Administration, 115 E. Railroad Ave. Suite #301, Port Angeles, WA 98362 USA

**Abstract**

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**Keywords**

Sea otters, sea urchins, kelp forests, keystone predator hypothesis, nearshore ecology, community ecology, spatial management

**Introduction**

Sustainable management and conservation of marine ecosystems hinges, in part, on understanding pressures that act on system stability (Knowlton 2004). Important structural forces include both natural and anthropogenic factors; many coastal zones are contending with marine resource and ecosystem service issues related to climate variability and human activities like fishing, nutrient loading and habitat alteration (e.g., Sherman and Duda 1999, Möllmann et al. 2009). Marine ecosystems also may be strongly influenced by species interactions. For example, so-called keystone predators affect marine community structure and function to an extent that is highly disproportionate to their biomass (Paine 1969, Power et al. 1996). A classic example is the seastar *Pisaster ochraceus*, which can dramatically alter the community composition of rocky intertidal regions of the northeast Pacific Ocean by preying upon mussels *Mytilus* spp. that otherwise outcompete other benthic invertebrates for space (Paine 1966, 1974).

Another well-known keystone species is the sea otter *Enhydra lutris*, which is capable of fundamentally altering the structure of subtidal rocky habitats in the north Pacific (Estes and Palmisano 1974, Estes and Duggins 1995, Steneck et al. 2002). Sea otters impose heavy predation pressure upon and reduce populations of benthic grazing invertebrates, such as sea urchins; the resulting decrease in grazing pressure allows kelp canopies to develop (Fig. 1). Through provision of habitat structure and production, kelp forests are further expected to promote differences in fish biomass, species composition and trophic ecology relative to urchin-dominated habitats (Fig. 1; see Duggins 1988, Ebeling and Laur 1988, Reisewitz et al. 2006, Markel and Shurin 2015).

Although sea otters are native to the Olympic Coast of Washington State, USA (Fig. 2), they were hunted to extirpation in this area by the early 20th Century (Lance et al. 2004). In 1969-1970, 59 sea otters were translocated from Amchitka Island, Alaska to the Olympic Coast in an attempt to reestablish a local population (Jameson et al. 1982). Although translocated otters experienced high initial mortality in the 1970s, the population eventually began to grow, and surpassed 200 individuals by 1989 (Jameson 1993). Kvitek et al. (1989) hypothesized that the sea otters’ keystone effect would lead to increased coverage of canopy-forming kelps, based on findings from other Northeast Pacific systems (e.g., Estes and Palmisano 1974, Dayton 1975, Duggins 1980, Breen et al. 1982, VanBlaricom and Estes 1988). Scuba-based surveys of nearshore community structure in 1987 showed that otter densities were indeed negatively correlated with abundance and size of benthic invertebrates including red sea urchins *Strongylocentrotus franciscanus*, while coverage of foliose and canopy-forming kelps increased (Kvitek et al. 1989). By the late 1990s, the sea otter population had increased to ~600 individuals and expanded its spatial range to the south and north (Jameson and Jeffries 1999). Subtidal community surveys in 1995 and 1999 indicated that keystone effects on benthic invertebrates and algae had expanded into previously otter-free areas of the coast (Kvitek et al. 2000). Since those last community surveys, the Olympic Coast sea otter population has more than doubled, with most of the population in the south of the region, and small numbers extending north to Tatoosh Island and the mouth of the Strait of Juan de Fuca (Fig. 2; Jeffries and Jameson 2014).

Here, we update the condition of kelp forest communities along the Olympic Coast that were previously surveyed in 1987, 1995 and 1999 (Kvitek et al. 1989, Kvitek et al. 2000), and assess the long-term effect of sea otter presence at these sites. We do using scuba-based surveys and both qualitative and quantitative methods to analyze temporal and spatial effects of sea otter presence on the algal and invertebrate communities. We also add new information on the species composition and abundance of non-cryptic fishes in these same habitats. We hypothesized that the otter-invertebrate grazer-kelp keystone relationships summarized in Figure 1 would have been maintained and potentially even more broadly distributed, consistent with the increase and spatial expansion of the sea otter population. Additionally, we anticipated that there would be greater biomass and diversity of fishes at sites with historically greater influence of sea otters on kelp community structure (Fig. 1, bottom). These issues are of potential value to coastal human communities, fisheries that target nearshore fishes or sea urchins, visitors to the adjacent Olympic Coast National Park, and other groups who derive ecosystem services from nearshore habitats such as rocky reefs and kelp forests (Kvitek et al. 1989, Steneck et al. 2002). These questions are also relevant to the Olympic Coast National Marine Sanctuary (OCNMS; Fig. 2), which was designated in 1994 and includes high native biodiversity and healthy populations of keystone species among its key objectives (Office of National Marine Sanctuaries 2008).

**Materials and Methods**

*Study location*.—Our study took place at ten kelp forest sites located in or adjacent to OCNMS boundaries (Fig. 2). At eight of these sites, sea otters have become reestablished since 1969: Destruction Island, Teahwhit Head, Rock 305, Cape Johnson, Cape Alava, Point of the Arches, Anderson Point, and Tatoosh Island. Sea otters make occasional forays to the remaining two sites, Chibadehl Rocks and Neah Bay, both inside the Strait of Juan de Fuca. All ten sites have been previously examined at least once (Kvitek et al. 1989, Kvitek et al. 2000), including six sites (Teahwhit Head, Rock 305, Cape Johnson, Cape Alava, Anderson Point, and Neah Bay) that have been studied in each of the four years of monitoring (1987, 1995, 1999 and 2015). All sites feature subtidal rocky reef habitats with dense stands of canopy-forming kelp (bull kelp *Nereocystis luetkeana* and giant kelp *Macrocystis pyrifera*), along with diverse communities of understory red, brown, green and coralline algae. These kelp forests are generally found in depths up to X m in the OCNMS (REF?).

*Field surveys*.—Between 3-7 August 2015, we sampled the ten sites at depths between 5-10 m. At each site divers surveyed benthic communities along visual transects (30 m x 2 m, n = 4 transects site-1) and within focal quadrats along each transect (0.25 m2, n = 8 transect-1). This approach mirrors that of the PISCO/CRANE surveys, the Channel Islands Kelp Forest Monitoring survey, and others (CITES). Transect surveys provided data on kelp stipe densities and the abundance and size distributions of large, non-cryptic invertebrates and fishes. On each transect, one diver recorded the number of canopy-forming kelp stipes encountered (primarily *Nereocystis*, *Macrocystis* and *Pterygophora*), while the other diver counted and estimated sizes of larger invertebrates (>5 cm diameter) and fishes (>5 cm TL). Common invertebrate and fish taxa included sea stars, tunicates, anemones, sea cucumbers, sculpins (Cottidae), rockfishes (Sebastidae), and greenlings (Hexagrammidae). Quadrat surveys assayed the percent cover of understory algae and non-living substrates such as rock, gravel, sand, pavement, and shell hash. In addition, divers counted and estimated sizes of smaller invertebrates (≤5 cm diameter) and fishes (≤5 cm TL) that were within the quadrats; common taxa included gastropods, crabs, nudibranchs, limpets, chitons, arthropods, smaller sculpins, surfperches (Embiotocidae), and gobies (Gobiidae).

At one site (Destruction Island SW), visibility was sufficiently poor that it was not possible to follow the more quantitative methods described above. Instead, we assumed the convention of Kvitek (1987) and recorded the categorical abundances of taxa immediately following our dives. The categories included rare (<1 individual per dive), present (1-5 individuals per dive), common (5-50 individuals per dive), abundant (51-100 individuals per dive), and very abundant (≥101 individuals per dive). This type of logarithmic scale has been effective for discerning broad scale spatial variability in abundance in other visual survey contexts (CITE REEF citizen science stuff, including Thorson’s paper).

*Data analysis*.—blah blah blah…TILE PLOTS ARE QUADRATS, OTHER STUFF IS TRANSECTS

(Jaccard Matrix? nMDS plots through time---1987 vs 2015—are sites more similar now than they used to be? For similarities)

Ole’s analyses

This will include some math gymnastics to account for spatiotemporal changes in otters, mismatch in time periods of when otters were counted and when inverts and kelps were surveyed

**Results**

*Presence/absence of species at study sites*.—FOR TILE PLOTS: REMEMBER TO STICK TO SIMPLE HYPOTHESES, MAYBE GROUP THE TILE PLOTS BY THE MAJOR TROPHIC CASCADE GROUPS FROM FIG 1.

All sites contained canopies of *Macrocystis*, *Nereocystis*, or a mix of both, while common understory algae included *Pterygophora californica*, *Laminaria* *spp.*, *Desmarestia*, *Pleurophycus gardneri*, and various types of low, foliose red algae (Fig. 3). Corraline algae were ubiquitous. Other algae and the seagrass *Phyllospadix* occurred at one or more sites.

The benthic invertebrates that Kvitek et al. (1989) identified as potential sea otter prey (urchins, crabs, mollusks, sea cucumbers) were more likely to be absent than present along transects in the ten sites. We observed no red urchins *Strongylocentrotus franciscanus* along any transects at any site (Fig. 4), which is notable because they are a preferred sea otter prey that also exerts strong grazing pressure on kelp (Dean et al. 1984, Estes and Duggins 1995). We did, however, observe purple urchins *S. purpuratus* at several of the northernmost sites. Of the other potential prey items, only the snail *Ceratostoma* and the sea cucumber *Cucumaria* were present at a majority of sites. Gumboot chitons *Cryptochiton stelleri* were found at half of the sites. Other prey items were only present along transects at a minority of sites. In contrast, several seastars (*Pisaster sp*, *Dermasterias sp*, *Henricia leviuscula*) were present in transects at half or more of the sites.

Among fishes, kelp greenling *Hexagrammos decagrammus* were observed along transects at nine out of the ten sites (Fig. 5). Black rockfish *Sebastes melanops* were observed at five out of ten sites, but no other fish species was observed at more than three sites. ANYTHING ELSE?

*Comparison to 1980s and 1990s*.—Our ? analysis of KELP DATA… (Fig. 6).

Macroinvertebrate densities showed little change in the 16 years since the previous surveys by Kvitek et al. (2000). Sea urchin biomass remained close to zero at all ten sites (Fig. 6), even the two sites in the Strait of Juan de Fuca (Chibadehl Rocks, Neah Bay) where sea otters are rarely observed (REF). Sea cucumber biomass also remained close to zero at all sites, although two sites (Teawhit Head in the south of the range, Neah Bay in the north) did show slight increases relative to 1999. SPECIES? WAS PARASTICHOPUS PART OF THIS? Scallop densities remained far below the maximum values observed in 1987, although scallop densities did increase slightly at Anderson Point and Tatoosh Island from 1999 to 2015 (Fig. 6). There were no significant changes in densities of crabs, limpets, or other gastropods from 1999 to 2015, with all at very low densities.

ADD A SEASTAR FIGURE

**Discussion**

General segue paragraph

Invert abundance and distributions, relative to otter distributions and what are otters feeding on…Kvitek et al proposed cryptic prey like crabs and octopuses that we may not have been able to observe in our scuba transects. Or they’re feeding predominately outside of where we were, outside of kelp beds…they must be doing something because their numbers have more than doubled and yet there is no evidence from our sites that prey numbers have been going up to sustain a larger population. Observations of prey items from Jessie?

Seastars? Any predatory influence? Any effect of seastar wasting disease?

Kelp… Densities of stipes, etc. Can we propose anything about this being a climax forest?

Fishes

Management relevance, if any; relate to the mission of the OCNMS; concerns related to urchin fishing; any others?

Future studies that derive from this—improvements, hypotheses, etc.

Conclusion

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Abundance



Time

Figure 1. Keystone hypotheses



Figure 2. Sites

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