**Success and succession in species recovery: kelp forest community dynamics following decades of sea otter reestablishment**

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**Abstract**

Blah blah blah sea otter *Enhydra lutris* canopy-forming kelps *Nereocystis luetkeana* and *Macrocystis pyrifera*

**Keywords**

Sea otters, sea urchins, kelp forests, top-down control, predator-prey interactions, keystone predator hypothesis, nearshore ecology, community ecology, spatial ecology, marine ecosystems

**Introduction**

Sustainable management and conservation of marine ecosystems hinges on understanding natural and anthropogenic pressures and structural forces that act on system stability (Knowlton 2004). Marine resources and ecosystem services in coastal zones contend with climate and environmental variability as well as human activities like fishing, nutrient loading and habitat alteration (e.g., Sherman and Duda 1999, Möllmann et al. 2009). Species interactions also play an important role in marine ecosystem dynamics. 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 sea otter *Enhydra lutris* in coastal waters of the North Pacific Ocean. Researchers from Alaska to California have found that sea otter predation can severely reduce local densities of benthic grazing invertebrates such as sea urchins, thereby allowing kelp canopies to develop and expand (Estes and Palmisano 1974, Breen et al. 1982, Estes and Duggins 1995, Steneck et al. 2002). The effects of sea otters may extend beyond just sea urchins and kelp: kelp canopies support distinct fish and invertebrate communities (Duggins 1988, Ebeling and Laur 1988, Reisewitz et al. 2006, Markel and Shurin 2015) and perform ecosystem roles such as wave energy attenuation (Pinsky et al. 2013).

While sea otters are generally assumed to play a strong top-down role in shifting North Pacific coastal ecosystems from herbivore-dominated to algae-dominated (Soulé et al. 2003), this generality has been both affirmed and challenged over the past 40 years. Numerous examples exist in which eastern Pacific coastal systems are not uniformly herbivore-dominated in the absence of sea otters (Foster 1990, Lafferty 2004, Carter et al. 2007, Reed et al. 2011). For example, {Reed:2011ef} found that wave disturbance overwhelmed the effect of herbivory and nutrient availability in determining kelp forest dynamics. This highlights the importance of other physical and biological interactions for structuring coastal habitats in the absence of otters, and encourages an explicit consideration of the spatiotemporal heterogeneity of coastal kelp systems. Such a landscape perspective on the drivers of heterogeneity and complexity has been used to improve understanding of kelp forest dynamics (Bell et al. 2015).

Sea otters are native to the Olympic Coast of Washington State, USA (Fig. 1a), but were hunted to extirpation by the early 20th Century (Lance et al. 2004). Reestablishment efforts began in 1969-1970, when 59 sea otters were translocated to Washington from Amchitka Island (Jameson et al. 1982). Despite high mortality in the early 1970s, the population eventually began to grow (Fig. 1b), surpassing 200 individuals by 1989 (Jameson 1993) and 600 by the late 1990s (Jameson and Jeffries 1999). Scuba surveys at multiple sites (Fig. 1a) in 1987 indicated that otter densities were correlated with increased coverage of foliose and canopy-forming kelps, and reduced abundance and size of benthic invertebrates, including the kelp-grazing red sea urchin *Mesocentrotus franciscanus* (Kvitek et al. 1989). Subsequent surveys in 1995 and 1999 indicated that the expanding sea otter population had brought these keystone predator effects on invertebrates and kelp to recently otter-free areas of the coast (Kvitek et al. 2000). Around this time, the kelp canopy reached peak surface coverage at the scale of the Olympic Coast (Fig. 1c; Washington Department of Natural Resources kelp monitoring program; https://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/kelp-monitoring; Pfister et al. in review. )

Since the last subtidal community surveys in 1999, the Olympic Coast sea otter population has more than doubled (Fig. 1b; Jeffries and Jameson 2014). According to the keystone hypothesis, this increase in otters should have further suppressed benthic macroinvertebrates and enhanced kelp canopy cover. However, total kelp canopy area has declined since roughly 2005 (Fig. 1c). The past 15 years have seen a spatial diversification of sea otter densities: the greatest increase in sea otters has occurred at southerly sites (Fig. 1b), especially Destruction Island, while smaller numbers have extended north to Tatoosh Island and the mouth of the Strait of Juan de Fuca (Jeffries and Jameson 2014). These changes warrant renewed research to understand patterns of nearshore community change at the regional and landscape scales.

The overall condition of these coastal kelp forests is of value to fisheries that target nearshore fishes and sea urchins, and to others who live in or visit this region and 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), 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).

Here we combine available information on sea otters, kelp, and benthic invertebrates along the Olympic coast over the past 30 years to understand nearshore community dynamics at regional and landscape scale. We conduct spatial and temporal analyses on sea otters and kelp data available from publically available surveys and extend previous kelp forest invertebrate surveys conducted a focal sites by Kvitek et al. (1989, 2000). Together these data demonstrate that coastwide trends in sea otter, kelp, and benthic invertebrate abundance are not necessarily emblematic of trends at smaller spatial scales. In addition, they suggest that while an otter-induced trophic cascade explained changes in the nearshore community along the Washington coast initially, more recent years have seen a fundamental shift in community dynamics that requires invoking additional environmental influences.

We hypothesized that sea otter keystone effects (negative effects on invertebrate grazers, positive effects on kelp) previously observed by Kvitek et al. (1989, 2000) would have been maintained, but that the magnitude of the otter effect would be proportional to otter densities at the different survey sites.

**Materials and Methods**

*Study locations*

We focus on ten kelp forest sites located in or adjacent to OCNMS boundaries (Fig. 1a). Most of the sites are on the outer coast, while two sites, Chibadehl Rocks and Neah Bay, are fully inside the Strait of Juan de Fuca (Fig 1a). All sites feature subtidal rocky reef habitat with dense stands of *Nereocystis luetkeana* and/or *Macrocystis pyrifera*), along with diverse communities of understory red, brown, green and coralline algae. These kelp forests generally occupy depths of up to ~10 m in the OCNMS. Each site was surveyed for benthic invertebrates using SCUBA in 2015 (see methods below) and in at least two of three survey years of Kvitek and colleagues (1987, 1995, and 1999; Kvitek et al. 1989, Kvitek et al. 2000). Six sites (Teahwhit Head, Rock 305, Cape Johnson, Cape Alava, Anderson Point, and Neah Bay) were surveyed in all four years of monitoring (1987, 1995, 1999, and 2015).

Data for sea otters and kelp were derived from long term monitoring surveys conducted on larger spatial scales but more frequent temporally. Below we describe these data sources and detail how we connect these coastwide surveys to provide sea otter and kelp abundance at our ten focal sites.

*Invertebrate SCUBA surveys*

We conducted SCUBA surveys between 3-7 August 2015, and gathered historical survey information collected by Kvitek and colleagues in 1987, 1995, and 1995. During 2015, SCUBA divers surveyed benthic communities in kelp beds at each site (Fig. 1a) at depths between 5-10 m, along visual transects (30 m x 2 m, *n* = 4 transects per site). On each transect, one diver recorded the species and number of canopy-forming kelp stipes encountered (primarily bull kelp *Nereocystis* *luetkeana*,giant kelp *Macrocystis pyrifera* and stalked kelp *Pterygophora californica*), while the other diver counted and estimated sizes of large, non-cryptic invertebrates >5 cm diameter (sea urchins, sea stars, sea cucumbers, crabs, scallops, anemones, chitons, tunicates, etc.). Also in each transect, divers randomly placed PVC quadrats (0.25 m2, *n* = 8 quadrats per transect) and estimated the percent cover of understory algae and non-living substrates such as rock, gravel, sand, pavement, and shell hash within each quadrat. At one site (Destruction Island), visibility was sufficiently poor in 2015 that divers could not follow the quantitative methods described above. Instead, we assumed the convention of Kvitek (1987) and recorded the abundances of taxa immediately following our dives, into one of five categories: rare (<1 individual per dive), present (1-5 individuals per dive), common (5-50 per dive), abundant (51-100 per dive) or very abundant (≥101 per dive).

For the 1987, 1995, and 1999 subtidal surveys, we extracted summary statistics on benthic invertebrate densities from literature (Kvitek et al. 1989, Kvitek et al. 2000). Raw data were not available from these reports nor from the original authors (L. Antrim pers. comm.). We include surveys that occurred at the same sites and comparable depths (5-10m). All surveys use standard quadrat and transect sampling methods, though the sample sizes vary among years. For the sake of comparison, we converted data from all subtidal surveys into units of countsm-2. Not all sites were sampled in each years, and some taxonomic groups of interest were not identified in available reports (e.g. seastars were not listed in the results for 1995). We used all available data for each site and year. When necessary, we combined quadrat and transect data using a weighted average with weights corresponding to the area surveyed by each type (see Supplement S1 for additional details). We include only species that are large and readily identifiable, to avoid concerns about among diver variation in detection of cryptic species (e.g. chitons; class *Polyplacophora*). We focus on the abundance of six species groups that are common important members of the Olympic coast nearshore invertebrate community: sea urchins, sea cucumbers, crab (primarily genera *Pugettia, Cancer)*, bivalve (primarily rock scallops, *Crassadoma gigantea*), large gastropods (*Triton, Caliostoma)*, and seastars (including genera *Pisaster, Orthaster, Dermasterias, Henricia, Pychnopodia)*. Based on sea otter diet information provided by Jesse, we classified these groups based on their frequency of occurrence in otter diets. We identified urchins and gastropods as COMMON, crab and bivalve as XXXX, and sea cucumber and sea stars as YYY prey (check categories).

ADDITIONAL STATS USED: Jameal/Ole; trends, nMDS.

ALSO: reread to be sure it’s clear what invert info is from quadrat data, what is from transect data, etc., and how it was all compiled so that it’s more or less apples to apples.

*Sea otter abundance and distribution*

We extracted sea otter location and abundance information from research reports and literature (see e.g. Lance et al. 2004, Jefferies and Jameson 2014) to examine shifts in otter abundance and distribution over the past several decades. Sea otter surveys along the Olympic Coast have been conducted by a mix of aerial surveys and land-based observations since 1977. Surveys were approximately biennial through the 1980s (no data in 1979, 1980, 1982, 1984, 1986, or 1988), and annual from 1989-2015 (but no surveys in 2009 or 2014). As with the kelp canopy data, the sea otter surveys were conducted in summer and thus reflect summer distribution and abundance (Laidre et al. 2009). Sea otters are highly mobile predators with substantial home ranges, although anecdotal evidence does not suggest that summer and winter distributions of sea otters are substantially different in this region (Laidre et al. 2009).

To estimate trends in sea otter abundance at each focal site, we developed a kernel-smoothed distribution of otters along the coast to incorporate uncertainty about how snapshot surveys translate to effective numbers of otters present at a given location. We first developed a one-dimensional coastline for the Olympic Peninsula and identified the position of each WDNR survey location along this coastline. We generated a smooth density of otters along the coastline using kernel density estimates which approximate the observed otter data using a mixture of Normal (Gaussian) distributions. Specifically, we placed a Gaussian distribution centered at each survey location and used a standard deviation *h* (the bandwidth) that corresponds to the home-range size of sea otters of 40 km for the Washington coast (*h* = 10.2; Laidre et al. 2009, their Fig. 3). The normal kernel at location *i* in year *t* received a weight, corresponding to proportion of total sea otters observed at each location: , where is the number of sea otters observed during the survey and is the total number of otters observed. The probability density function for otters along coastal position *X* in year *t* is

(1)

where integrates to 1. We let be the coastline position of the *j*th focal site and used the density from Equation (1) to calculate the number of sea otters within a 10-km shoreline radius of each of our ten survey sites in each year, as

(2)

Due to uncertainty in the effective home range size of sea otters, we performed sensitivity analyses using a range of bandwidths (*h* between 5 and 15). The qualitative results did not change with alternate bandwidths.

We estimated the temporal trend in sea otter abundance at each site by regressing the natural logarithm of sea otter abundance against time. We performed this analysis on the entire time series (1989-2015), and separately for the two halves of the time-series (1989-2001, 2002-2015) to assess changes if trends shifted over time. As estimates of trends became progressively less precise with less data, we elected not to further subdivide the time series. To facilitate comparison among sites that vary substantially in the sea otter abundance, we constructing a log-index of sea otter abundance; we standardized the number of sea otters by dividing the sea otter numbers observed during the first three years of the kelp surveys (1989-91,) and taking a natural logarithm of this ratio:. Using such an index provides a graphical interpretation (linear trends indicate exponential changes in area), and allows for sites across a large range of areas to be visualized on the same axes.

*Kelp canopy area*

To describe kelp abundance at each site, we used publicly available data from aerial overflight surveys of algae from the Washington Department of Natural Resources (WDNR; survey methods provided in Pfister et al. in review). Surveys were conducted annually between 1989 and 2015 (no data available for 1993) during peak kelp abundance for the region (late July or early August of each year). Surface canopies in this region consist of a mix of *Macrocystis* and *Nereocystis*. While overflight surveys differentiate between the two species (REF), we are primarily interested in the canopy habitat kelps provided, and thus we focus on the total surface coverage provided by the two species; additionally, the two species’ abundances are strongly positively correlated in this region (Pfister et al., in review). We examined kelp abundance at two scales. First, we used kelp area within discrete strata along the coast to provide estimates of local kelp surface coverage, , for the strata containing each of our ten sites, *j*, in each year, *t* (see Fig. 1a). Note that strata used by WDNR are substantially larger than the area surveyed during invertebrate surveys – shorlines on the order of kilometers whereas invertebrate surveys span the order of 0.1 kilometers. Unfortunately, these strata are the smallest spatial unit for which it is appropriate to generate kelp area estimates (H. Barry pers. Comm., OTHER?). Second, we summed kelp surface coverage in all strata between Neah Bay and Destruction Island to provide a coastwide for the northern Olympic Coast (Fig. 1c). (see Supplement for more?).

We estimated the temporal trend in kelp canopy coverage at each site and coastwide by regressing the natural logarithm of kelp area against time. We also calculated the standard deviation (SD) and coefficient of variation (CV = SD / mean) of observations around each trend. We performed this analysis on the entire time series (1989-2015), and separately for the two halves of the time-series (1989-2001, 2002-2015) in order to determine if trends shifted over time. As estimates of kelp coverage trends became progressively less precise with less data, we elected not to further subdivide the time series. As with sea otter data, to facilitate comparison among sites that vary substantially in the kelp area, we constructed a log-index of kelp area; we standardized the area of kelp by dividing the kelp area observed during the first three years (1989-91) of the survey at site *j,* , and taking the natural logarithm of the ratio:.

*Statistical analyses*

To ask if local changes in sea otter abundance resulted in subsequent changes in kelp area among the 10 focal sites, we regressed exponential trends in sea otter abundance against kelp area. We performed this analysis for the entire time-series (1989-2015) and separately for each half of the study period (1989-2001 and 2002-2015), using region and otter growth rate as fixed effects. In the model with two time periods we allowed for a period otter growth rate interaction.

To assess the effect of otter abundance on the variability of kelp, we used a GLM with

**Results**

*Spatiotemporal trends of sea otters and kelp*

Sea otter density trends have followed three spatially distinct patterns along the Olympic Coast since the 1970s (Fig. 2a,c,e; for all species, we roughly follow spatial grouping used for sea otters; see Lance et al. 2004). At the most northerly study sites, sea otter densities showed the greatest increase from the mid-1980s until the early 1990s before declining slightly and then remaining stable from the mid-1990s to present (Fig. 2a). Sea otter densities in the central region of the study area including Anderson Point, Point of the Arches, and Cape Alava experienced exponential growth from the late 1970s until the mid-1990s, but have remained largely stable in recent years at densities just above those observed in 1990 (Fig. 2c). This represents a longer period of increasing otter densities than the northernmost region. The increase in sea otters has been strongest and most consistent in the southern region of the study area (Fig. 2e). Sea otter densities near the southern sites have increased exponentially since the late 1970s; since roughly 2000, the rate of increase in the Destruction Island area has outpaced rates of increase near Teahwhit Head and Cape Johnson / Rock 305; note that due to proximity and the width of the smoothing kernel used (see Methods), Cape Johnoson and Rock 305 have indistinguishable sea otter trends (Fig. 2c). The absolute abundance of sea otters is also greater in this portion of the coast than in the central region, while sea otter abundances in the northern region are the lowest by at least an order of magnitude (Fig. 1b). [Cape Johnson and Rock 305 have essentially the same trend in Figure 2e due to their close proximity (Fig. 1a) relative to the value of *h* in Equation (1).]

As a consequence of variation in local trends, the distribution of the Olympic Coast population has shifted over time (see also Jeffereies and Jameson 2014). The population has had a bimodal or multimodal distribution for much of the study period, with the most significant modes in the area between Cape Alava and Cape Johnson, and another further south near Destruction Island (Fig. 3). The center of gravity of the population was in the vicinity of Teahwit Head in the late 1970s, but then shifted north to the area around Cape Alava throughout much of the 1980s and 1990s. From the late 1990s to the early 2000s, the center of gravity rapidly shifted south to near Destruction Island, where it has remained. Sea otter observations presently span from rare sightings inside the Strait of Juan de Fuca (Fig. 3, above dashed line) to comparably rare sightings in the far south at Point Grenville, where they had essentially not been observed prior to 2010.

Similar to sea otters, kelp canopy area exhibited spatiotemporally distinct patterns in the three regions of the study area from 1989-2015 (Fig. 2b,d,f). While the area of kelp in absolute terms varied substantially among sites within a region (Table XXX), kelp trends varied predominantly by region within the Olympic coast. At the northern sites, kelp indices showed no clear long-term trends. However, Tatoosh Is. showed notably more variability than Neah Bay/Chibadehl Rocks which are in the Strait of Juan de Fuca (Fig. 2b). Note that Neah Bay and Chibadehl Rocks are in the same kelp monitoring polygon (Fig. 1a), and thus have the same kelp index. The central region had noteworthy differences between sites (Fig. 2d) with canopy area at Cape Alava increasing from 1989 to 2000 before stabilizing and possibly declining in recent years, while Point of the Arches and Anderson Point experienced decreases in the early 1990s before following a qualitative pattern similar to Cape Alava. The index of canopy area at Cape Alava was far less variable than the other two central sites. This is likely in part due to and interaction between total kelp area are each site and measurement error – Cape Alava is a very large kelp bed (~100s of ha) whereas the other two sites are on the order of 10s of ha (Table XXX). At the southern sites, canopy area generally increased until the early 2000s before stabilizing or declining slightly (Fig. 2f); as with the central region (Fig. 2d), there were some differences in the signs of short-term trends across the four southern sites early in the time series, although the degree of interannual variability was fairly consistent across the sites. In addition, there is little resemblance between the coastwide trend in kelp (Fig. 1c) and the trend at a given site (Fig. 2).

*Spatiotemporal correlations between sea otters and kelp coverage*

ANALYSIS of whole time-period kelp trend vs. otter trend.

In contrast, separating the time series in half reveals two distinct interactions between kelp and otters. During the first time period

Statistically, there is a negative period by otter growth rate interaction

Descriptive text for Fig. 4: positive correlation between site-specific otter pop growth rate and kelp growth rate prior to 2001. No correlation between 2002-2015, and otter growth rates generally slower, kelp growth rates slower, generally around zero or slightly negative. BUT, variability from 2002-2015 is far lower than 1989-2001, for both metrics.

*Spatiotemporal trends of benthic macroinvertebrates*

Insert info here from new invert analyses related to time series and/or nmds plots.

**Discussion**

General segue paragraph…otters otters, yayyyyyyyyyy

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?

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

**Acknowledgments**

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Table of Kelp areas.

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| Site Name | Average Area 1989-2001 | 2002-2015 | Kelp Strata. |  |
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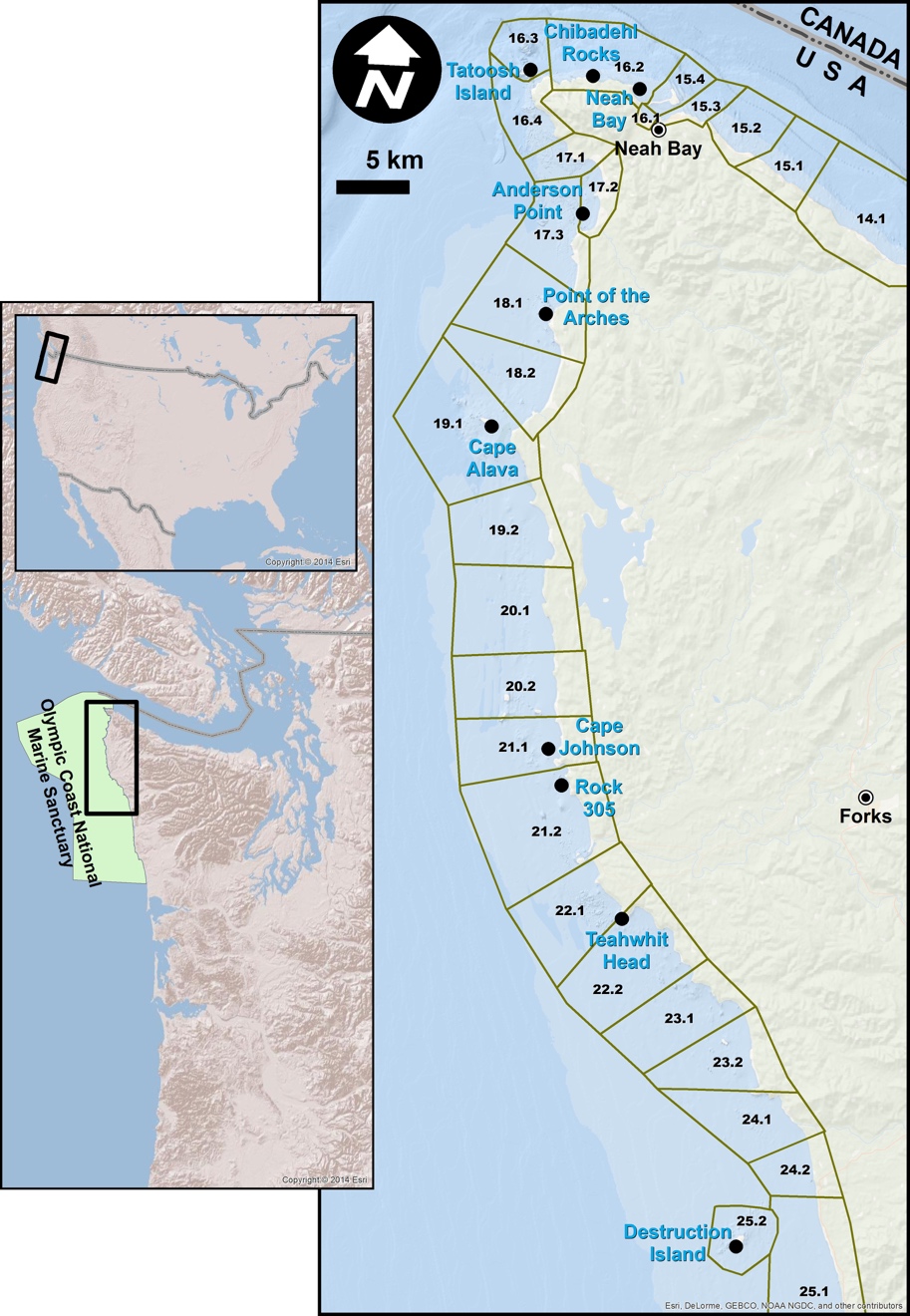


Figure 1. Sites (map will be updated; otter figure needs to be revised so that the three regions are separate, stacked lines)

OLE TO DO: MAKE UPPER RIGHT PLOT FOR OTTERS STACKED BY REGION.



Fig. 2 (to better link to text, suggest we label each panel so it’s a-f; otters are a, c, e and kelp is b, d, f)



Figure 3. Otter Distribution. Grey shows kernel smoothed density, dots show center of gravity of the distribution (median). Dashed line shows smoothed trend in the center of gravity (loess)



Figure 4. Otter and Kelp exponential growth rates by site & region and the number of otters present at each site in 1990. (Fix the color legend for the top panel?)



Figure 5. CV between periods.



Figure 6. Inverts through time.

Note that data on seastars and gastropods are not available for 1995





Insert NMDS plots

Insert Tables

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