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

**Ontogeny of trophic cascades…**

**Beyond trophic cascade theory…**

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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, “keystone” species 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 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 et al., 2011) found that wave disturbance overwhelmed the effect of herbivory and nutrient availability in determining kelp forest dynamics in central and southern California. 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).

Coastal kelp forests of Washington help support recreational and commercial fisheries on nearshore fishes and invertebrates and provide additional ecosystem services from nearshore habitats such as rocky reefs and kelp forests (Kvitek et al. 1989, Steneck et al. 2002). Our study falls entirely within the Olympic Coast National Marine Sanctuary (OCNMS, designated in 1994; Fig. 1a) which includes high native biodiversity and healthy populations of keystone species among its key objectives (Office of National Marine Sanctuaries 2008).

Sea otters are native to the coast of the Olympic Penninsula 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)(; Fig. 1b). 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 increased kelp canopy cover and yet the total kelp canopy area has declined since roughly 2005 (Fig. 1c). These The decoupling of sea otter and kelp changes warrant renewed research to understand patterns of nearshore community change at the regional and landscape scales. An intriguing possibility is that the decoupling of sea otters and kelp indicates a recovery of benthic grazers in OCNMS.

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 scales. 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 at 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 the invertebrate community dynamics that requires invoking additional environmental influences. MORE HERE.

**Materials and Methods**

*Study locations*

We focus on ten kelp forest sites located within the OCNMS (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. Canopy forming kelp forests occupy depths of up to approximately 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 frequently in time. 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.

For analysis, we divided our sites into three geographic groupings (Fig. 1a): Northern (Neah Bay, Chibadehl Rocks, and Tatoosh Island), Central (Andersen Point, Point of the Arches, and Cape Alava) and Southern (Rock 305, Cape Johnson, Teahwhit Head, and Destruction Island). These groupings reflect the areas used to describe sea otter trends historically (REF) and reflect geographic pattern in kelp and sea otter trend (see Results). We also use these grouping to avoid pseuo-replication in analysesand to allow for regional difference in biological relationships.

*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). 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. Available evidence does not suggest that summer and winter distributions of sea otters are substantially different in this region (Laidre et al. 2009), but information on seasonal patterns is notably uncertain.

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 pattern of results did not change with alternate bandwidths.

We estimated the temporal trend in sea otter abundance at each site and coastwide 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 become 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 are exponential changes in area), and allows for sites across a large range of abundance 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 described 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, 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). The strata used by WDNR are substantially larger than the area surveyed during invertebrate surveys (see below). 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 northern Olympic Coast coastwide estimate of kelp area (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 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 average kelp area observed during the first three years of the survey (1989-91)*,* , for site *j* and taking the natural logarithm of the ratio:.

*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.

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 year, and some taxonomic groups of interest were not identified in available reports (e.g. seastars were not listed in the results for 1995, gastropod densities were only available for 1987 and 2015). 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 time-series of abundance for six species groups that are common important members of the Olympic coast nearshore invertebrate community: sea urchins (genus *Mesocentrotus*), sea cucumbers (genera *Cucumaria, Parastichopus)*, crab (primarily genera *Pugettia, Cancer)*, bivalves (primarily rock scallops, *Crassadoma gigantea*), 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, snails, and limpets as common prey items; crabs as occasional prey items; chitons, sea stars, and sea cucumbers as rare prey items; and, anemones, tunicates, and nudibranchs as not prey items.

*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 ask if the relationship between sea otters and kelp shifted between periods.

To assess the effect of otter abundance on the variability of kelp, we used the difference in CV at each site between periods as the response variable and Region, difference in otter abundance at each site, and CV of kelp area in the 1989-2001 period as predictors. We explored only additive main effects due to a sample size of 10 and selected among models using AIC corrected for small sample sized (AICc).

Invertebrate methods:

1. calculating proportional declines in each species (paired t-tests 1987 v. 2015),
2. calculating SD among sites 1987 v. 2015
3. Multivariate stuff.

To examine changes in the abundance of sea urchins, bivalves, crabs, sea stars, and sea cucumbers over time, we used permutational analysis of variance (PERMANOVA) to compare community structure across three time periods (1987, 1995, 2015) or three regions (northern, central, and southern) using the adonis function in R. The taxa-specific average densities (individuals m-2) for each site-year-region were used as the dependent variables, and converted to dissimilarity matrices using Manhattan log(*x* + 1) distances. We performed randomizations within strata based on regions or time periods. We also tested whether community composition was more variable in some regions than others an in some time periods rather than others by examining multivariate dispersion in community composition using the betadisper function in R. To visualize differences among time periods or regions in invertebrate community structure, we used non-metric multidimensional scaling (nMDS) based on the nmds function and plotted vectors explaining how variation in the densities of individual taxa related to community dissimilarity using the envfit function. Because information about gastropod densities was not collected at some sites in 1995, we repeated all of the above analyses for 1987 and 2015 data only to determine if doing so modified our inferences about changes in the mean or variability in community composition. All multivariate analyses and visualizations were conducted in the R package vegan. We also calculated proportional declines in mean abundance and used paired *t*-tests to evaluate their significance.

**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). In most cases, the local trend in sea otters differ substantially from the coastwide sea otter trend. Near 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 at densities just above those observed in 1990 (Fig. 2c, dashed line). This represents a longer period of increasing otter densities than the northernmost region. The increase in sea otter density 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. 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 kernel bandwidth used for home range estimation; see Eq. 1.]

Further analysis of sea otter observations data shows that 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 for much of the 1980s and 1990s. Starting in the late 1990s, the center of gravity rapidly shifted south to near Destruction Island, where it has remained. In recent years sea otter observations are rare inside the Strait of Juan de Fuca (Fig. 3, above dashed line) and rare near Point Grenville in the far south but common at most point in between (Fig. 3).

Overstory kelp canopy area exhibited spatiotemporally distinct patterns in the three regions of the study area from 1989-2015 (Fig. 2b,d,f). Kelp area showed substantial interannual variation both at the individual sites and the coastwide scale. 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 furthest north sites, kelp area indices showed no clear long-term trends but with notably higher interannual variability at Tatoosh Island than Neah Bay and Chibadehl Rocks inside the Strait of Juan de Fuca (Fig. 2b; note that Neah Bay and Chibadehl Rocks are in the same kelp monitoring strata (Fig. 1a), and thus share a single kelp time-series). The central region had 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. 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 (average 161 ha) whereas the other two sites are on the order of 10 ha (Table XXX). The index of canopy area at Cape Alava was far less variable than the other two central sites. At the southerly 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.

*Connections between sea otters, invertebrates, and kelp*

We detected differences in the kelp growth rate between periods with 2002-15 having approximately 5% reduced growth rate from the 1989-2002 period (difference between periods of 0.053, p =0.012; Fig. 3). While the temporal effect is intruiging, more interesting is the interaction between sea otter growth rate, with both an estimated positive effect of sea otter growth rate on kelp during the earlier period (point estimate of slope = 0.285) and a negative effect of sea otters during the later period (point estimate = -0.507; interaction term *p* = 0.045). There was no support for regional variation in kelp growth after accounting for the effect of sea otters (*p* = 0.128). The model considering a single period found no effect of sea otters on kelp (*p =* 0.40) but differences in kelp growth rate among regions (*p =* 0.024*).* This result shows how the temporal context substantively alters the interpretation of mechanisms driving kelp growth.

After accounting for changes in kelp growth rates, the variability in kelp area declined at most sites between the two time periods (Fig. 5). Specifically, bootstrapped estimates of CV showed all sites but one (Tatoosh Is.) declined between the two time periods, though the magnitude of decline varied substantially by region. The three northern sites had virtually no change in CV (changes of less than 0.05 for all sites), the southern sites showed substantial declines in CV (declines of 0.175 to 0.694), and the central region also showed declines in CV but with differences among sites (declines of 0.033, 0.343, and 0.351, for Cape Alava, Anderson Point, and Point of the Arches, respectively). For most sites, these are large, biologically significant, changes in kelp variability. Linear models showed that including kelp CV in 1989-2001 alone best predicted the change in CV between periods ( adj. *R2* = 0.54). Sites with high CV in the first time period reduced CV in the second. The only other model with a small amount of statistical support included both kelp CV in 1989-2001 and the change in the number of otters ( adj. *R2* = 0.64). In this model coefficient for the change in otters was negative, indicating increased sea otter abundance was associated with reduced kelp CV (point estimates correspond to an increase of approximately 13 otters leading to a decrease of 0.01 in CV). As we only have 10 sites for comparison, our statistical power and precision of these estimates is low. NEED TO ADD AVAILABLE EXPOSURE INFORMATION TO ANAYLSES IN HERE. THEY EXPLAIN NOTHING BUT I NEED TO TALK ABOUT THEM.

The mechanistic link between sea otters and kelp is through the benthic invertebrates that comprise sea otter prey and the major grazers of kelp. While we lack continuous time-series for invertebrates at OCNMS, available information shows significant variation in the benthic invertebrate community over time but not across regions (Fig. 7, Ax; Tables 4, Ax). Not only was there a shift in mean community composition between 1987 and the two later survey years, but community composition became less variable after 1987 (Tables 5, Ay). The differences in community composition among years reflected substantial declines reduction in all 5 taxonomic groups from 1987-2015 (Figs. 6-7). The iconic prey of sea otters, sea urchins, declined precipitously with the across site mean falling by more than 99% between 1987 to 2015 (from 3.7 m-2 to 0.01 m-2). While the other five species groups did not decline as dramatically as urchins, they all showed substantial declines from 1987 to 2015: bivalves (decline of 90%), sea cucumbers (86%), crabs (84%), and sea stars (70%) [gastropods show 98% decline but were only sampled in 87 and 2015]. All of these declines are strongly significant (paired t-tests, *p*<0.01 for all species groups). Only sea urchins showed a pattern in which the highest density occurred in the three sites defined by Kvitek et al. (1989) as outside of the range of sea otters (Neah Bay, Anderson Point, Point of the Arches; Fig. 6a). For all four (five w/ gastropods) other species groups, densities were not notably different between sites inside and outside of the otter range in 1987. This suggests that the dramatic and immediate effect of otters are limited to a few species or species groups, even if over time there are substantial but gradual changes in invertebrate community. Beyond declines in mean densities, all five species also show notable declines in the among site variation in density; the among site standard deviation among site means fell by 75 to 99% for our six species groups (SIGNIFICANCE=?). This indicates that the spatial variability in invertebrate densities has become lower over the past 30 years.

**Discussion**

Sea otters are iconic keystone predators in coastal ecosystems of the northeastern Pacific whose presence radically affects invertebrate and algal communities (Estes and Duggins 1995, Steneck et al. 2002). Here we revisit a series of historical invertebrate surveys and complement these surveys with independent spatio-temporal data on kelp and sea otters. We show that while kelp and sea otter abundance are statistically decoupled when viewed coastwide and over the entirety of the 30 year period, there is strong evidence for regional connections between sea otters and kelp. When viewed regionally, the relationship between kelp and sea otter growth rates has shifted from positive during the 1990s to neutral or possibly slightly negative post-2000. We show that in addition to the immediate and large effects of sea otter invasion on preferred prey items like sea urchins, there are gradual consequences of changes in otter abundance for both invertebrate and kelp communities. This suggests the consequences of sea otter populations for kelp abundance are not exclusively an immediate shift in state, but can manifest gradually over the span of roughly a decade. However, we show that this deline in kelp growth rates is not mediated by increased invertebrate abundance; in recent years as all major invertebrate groups remain far below historical densities (Fig. 6).

Our data does not enable examining year to year changes in the linkages between sea otters, benthic invertebrates, and kelp, opening the possibility that invertebrate communities substantially shifted during the years between surveys in a way that can explain kelp variation. While there is abundant evidence of other factors have affected the abundance of some invertebrate groups (e.g. sea star wasting disease outbreak between XXX and YYY), there is no suggestion of dramatic changes. Personal observations and communications of one of the authors (AOS) between 2003 and 2009 at Tatoosh Island do not support radical changes in invertebrate abundances during the longest gap in our invertebrate time-series (pers. comm. C. Pfister?). So while we cannot exclude the possibility of strong variability in invertebrate communities driving these pattern, we find that to be an unlikely driver of kelp populations.

Overall, recent years have seen kelp abundance plateau or slightly decline (Fig 1, 2). Notably, kelp area fell dramatically in 2014 to levels that had not been seen in at least 15 years when sea otter population were less than half current abundance. Possible speculative story: decline in CV coastwise, more similarity among sites, stronger links to oceanographic conditions? We speculate….

**Other Points:**

CV of kelp is interesting.

Looks like otters have stabilized around their carrying capacity at local sites (e.g. Cape Alava) if not coastwide. Suggest that we can revisit estimates of coastwide carrying capacity for sea otters which are already above the very high estimates produced by (Laidre et al., 2002) (for areas between Neah Bay-ish to Point Grenville, carrying capacity estimates range from 922-1189… current pop is >1400). Also point out that Laidre’s work was based on pre 2000 otter and food densities. We know from our work that food availability has continued to fall.

**Open question:** If there are functionally no inverts present, what are these stable populations of sea otters eating? Shifting to smaller prey that we are not counting well? Moving to deeper or shallower habitats?

**Notes from Chris.**

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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Invertebrate Survey description in table form.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Survey |  | Area surveyed per site (m2) |
| 1987 | 1.0m2 quadrat by SCUBA | 100 per site. Not randomly placed locations | 100 |
|  | All counts conducted *in situ* |  |  |
| 1995 | 0.25m2 quadrat by SCUBA using video | 14-35 per site | 3.5-8.75 |
|  | Counts done by post-processing video. Most of the locations with video collected were not actually processed. |  |  |
| 1999 | 0.25m2 quadrat by SCUBA using video | 30 per site | 7.5 |
|  | 25 x 1m video transects | 3-4 per site | 75-100 |
| 2015 | 30 x 2m transects by SCUBA | 4 per site | 240 |
|  |  |  |  |

Sites and the years they were sampled.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | 1987 | 1995 | 1999 | | 2015 |
| **Sites** | Quadrats | Quadrats | Quadrats | Transects | Transects |
| Neah Bay | X (2 Sites) | X | X |  | X |
| Chibahdel Rocks |  |  | X |  | X |
| Cape Flattery |  | X | X | X |  |
| Tatoosh Island |  | X | X | X | X |
| Makah Bay | X | X | X | X |  |
| Anderson Point | X | X | X | X | X |
| Point of the Arches | X | X | X | X | X |
| Cape Alava | X | X | X | X | X |
| Cape Johnson | X | X | X | X | X |
| Rock #305 | X | X | X | X | X |
| Teahwhit Head | X | X | X | X | X |
| Destruction Island |  |  | X |  | X |
|  |  |  |  |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |
|  |  |  |  |  |  |

Table of Kelp areas.

|  |  |
| --- | --- |
| Site Name | Average Area 1989-2015 (ha) |
| Neah Bay, Chibadehl Rocks | 97.5 |
| Tatoosh Island | 10.9 |
| Anderson Point | 14.5 |
| Point of the Arches | 5.3 |
| Cape Alava | 161.9 |
| Cape Johnson | 6.9 |
| Rock 305 | 8.1 |
| Teahwhit Head | 9.5 |
| Destruction Island | 9.3 |
|  |  |

Table 4. PERMANOVA partitioning of benthic invertebrate assemblages on the basis of Manhattan log(*x*+1) dissimilarities in densities in response to (a) Year (fixed, 3 levels 1987, 1999, 2015) or (b) Region (fixed, 3 levels) using sequential sums of squares.

(a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Year | 1 | 1.208 | 8.298 | 0.001 |
| Residuals | 25 | 0.146 |  |  |
| Total | 26 |  |  |  |

(b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Region | 2 | 0.169 | 0.899 | 0.326 |
| Residuals | 24 | 0.188 |  |  |
| Total | 26 |  |  |  |

Table 5. Multivariate test of dispersion for benthic invertebrate assemblages on the basis of Manhattan log(*x*+1) dissimilarities in densities in response to (a) Year (fixed, 3 levels 1987, 1999, 2015) or (b) Region (fixed, 3 levels).

(a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Year | 2 | 0.571 | 17.120 | 0.001 |
| Residual | 24 | 0.033 |  |  |
| Total | 26 |  |  |  |

(b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Region | 2 | 0.024 | 0.194 | 0.860 |
| Residual | 24 | 0.121 |  |  |
| Total | 26 |  |  |  |

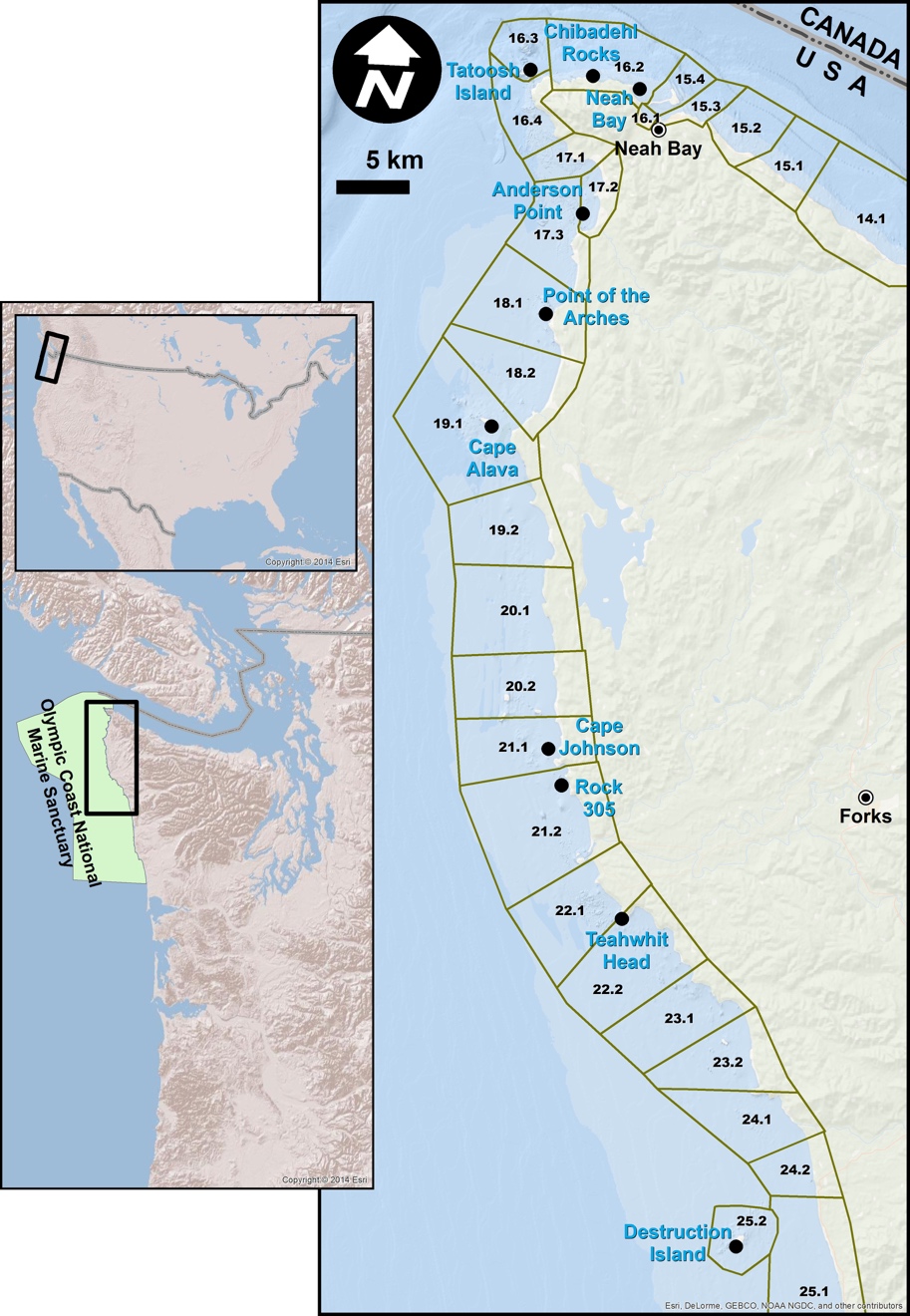


Figure 1. Sites (map will be updated; otter figure needs to be revised so that the three regions are separate, stacked lines)

OLE TO DO: MAKE UPPER RIGHT PLOT FOR OTTERS STACKED BY REGION. Ole is not sure that this is necessary any more…. But could be convinced otherwise.



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). Line is coastwise trend indexed to 1990



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 using the starting number of otters of each period (top) or the mean of each time period (bottom panel).



Figure 6. Inverts through time.

Note that data on seastars are not available for 1995

../Plots/Invertebrate%20panels%20v1%20+%20Gastro.pdf

Figure 6 alternate. Inverts through time.

Note that data on seastars are not available for 1995, gastropods are not available in 95 or 99.

Figure 7. Non-metric multidimensional scaling

../Plots/_Multivariate/MDS%20invert%20community%201987-1995-2015%20Manhattan%20for%20pub.pdf

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**Appendix**

Table x. PERMANOVA partitioning of benthic invertebrate assemblages on the basis of Manhattan log(*x*+1)dissimilarities in densities in response to (a) Year (fixed, 2 levels 1987 and 2015) or (b) Region (fixed, 3 levels) using sequential sums of squares.

(a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Year | 1 | 2.318 | 8.172 | 0.002 |
| Residuals | 15 | 0.284 |  |  |
| Total | 16 |  |  |  |

(b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Region | 2 | 0.279 | 0.649 | 0.494 |
| Residuals | 14 | 0.430 |  |  |
| Total | 16 |  |  |  |

Table y. Multivariate test of dispersion for benthic invertebrate assemblages on the basis of Manhattan log(*x*+1)dissimilarities in densities in response to (a) Year (fixed, 2 levels 1987 and 2015) or (b) Region (fixed, 3 levels).

(a)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Year | 1 | 1.684 | 39.875 | 0.001 |
| Residual | 15 | 0.042 |  |  |
| Total | 16 |  |  |  |

(b)

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Source | df | MS | Pseudo-*F* | *P* |
| Region | 2 | 0.033 | 0.119 | 0.897 |
| Residual | 14 | 0.278 |  |  |
| Total | 16 |  |  |  |

Fig. xx. MDS plots for 1987 vs 2015 only, so as to include gastropods.

../Plots/_Multivariate/MDS%20invert%20community%201987-2015%20Manhattan%20for%20pub.pdf