**Success and succession in response to sea otter recovery: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion**

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**Abstract**

The recovery of predators has the potential to restore ecosystems and fundamentally alter the services they provide. One of the most iconic examples of this potential comes from keystone predation by sea otters in nearshore habitats of the Northeast Pacific. Here we combine spatial time-series of sea otter abundance, canopy kelp area, and benthic invertebrate abundance from Washington state, USA, to examine the shifting consequences of sea otter introduction for kelp and kelp forest communities. We leverage the spatial variation in timing and speed of sea otter recovery to understand connections between sea otters and the kelp forest community. A small population of sea otters was re-introduced to the Washington coast in 1969-70 that by 2015 had grown to more than 1,400 individuals. This population increase created a pronounced decline in sea otter prey - particularly kelp-grazing sea urchins – and led to an expansion of canopy kelps until roughly 2000. However, while sea otter and kelp population growth rates were positively correlated prior to 2000, this association disappeared over the last two decades. This occurred despite the fact that surveys of benthic invertebrates show that sea otter prey have continued to decline. Kelp area trends appear to be largely decoupled from both sea otter and benthic invertebrate abundance at current densities. However, variability in kelp abundance has declined in the most recent 15 years of the time series. Altogether these results suggest that initial nearshore community responses to sea otter population expansion follow predictably from trophic cascade theory, but now other factors may be as or more important in influencing community dynamics. Thus, the role of sea otter predation may be context-dependent with shifting environmental conditions strongly affecting their utility in ecosystem restoration.

**Keywords**

Sea otters, sea urchins, kelp forests, top-down control, predator-prey interactions, keystone predator hypothesis, nearshore ecology, community ecology, spatial ecology, marine ecosystems, *Enhydra lutris,* *Nereocystis luetkeana,* *Macrocystis pyrifera*

**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 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).(Watson & Estes 2011) The effects of sea otters extend beyond just sea urchin abundance and kelp coverage: kelp canopies support distinct fish, invertebrate, and understory algal communities (Duggins 1988, Ebeling and Laur 1988, Reisewitz et al. 2006, Markel and Shurin 2015) (Watson & Estes 2011) and perform ecosystem roles such as wave energy attenuation (Pinsky et al. 2013) and carbon storage (Wilmers et al. 2012). Similar community and ecosystem level consequences of sea otters have been noted in other coastal habitats as well {e.g. seagrass communities; Hughes:2013gk}.

Sea otters are native to the coast of the Olympic Peninsula of Washington state, USA (Fig. 1), 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, AK (Jameson et al. 1982). Despite high mortality in the early 1970s, the population eventually began to grow (Fig. 1), surpassing 200 individuals by 1989 (Jameson 1993) and 600 by the late 1990s (Jameson and Jeffries 1999)(; Fig. 1). SCUBA surveys at multiple sites (Fig. 1) 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 produced these keystone predator effects on invertebrates and kelp to additional areas of the coast (Kvitek et al. 2000) (Kvitek et al. 1998). Around this time, the kelp canopy reached peak surface coverage at the scale of the Olympic Coast (Fig. 1; Washington Department of Natural Resources kelp monitoring program; https://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/kelp-monitoring; (Pfister et al. 2017))

Since the subtidal community surveys in 1999, the Olympic Coast sea otter population has more than doubled (Fig. 1; Jeffries and Jameson 2014). We expect that increased top down predation by sea otters might have further suppressed benthic macroinvertebrates and increased kelp canopy cover; however, the total kelp canopy area has declined from a peak abundance in roughly 2005 (Fig. 1). 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 on the Olympic Coast.

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 (Watson & Estes 2011). Numerous examples exist in which 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, 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).

Here we combine available information on sea otters, kelp, and benthic invertebrates along the Olympic Coast over the past 30 years in order to better understand nearshore community dynamics at regional and landscape scales. We conduct spatial and temporal analyses on sea otter and kelp data available from publically available surveys and extend previous kelp forest invertebrate surveys conducted at focal sites by Kvitek et al. (1989, 1998, 2000). Together our analyses 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 early in the time series, more recent years have seen a fundamental shift in invertebrate community dynamics that requires invoking additional influences. Our ability to understand the dynamics between habitat, predators and prey is essential for proper management and conservation of coastal species, habitats, ecosystems and services, particularly in this area where maintaining high native biodiversity and keystone species populations are explicit management objectives (Office of National Marine Sanctuaries 2008).

**Materials and Methods**

*Study locations*

Our study sites fall within the Olympic Coast National Marine Sanctuary (OCNMS, designated in 1994). Analyses are both large scale (sea otter abundance and kelp coverage for the entire coastwide region) and fine scale (sea otter, kelp and invertebrate abundance by region and by site). For the large-scale analysis, data for sea otters and total kelp canopy surface coverage were derived from long-term coastwide monitoring surveys conducted in most years. Below we describe these data sources and detail how we connect these coastwide surveys to provide sea otter and kelp abundance at our focal sites.

For finer-scale analyses, we focus on ten kelp forest sites located within the range of coastwide surveys for sea otters and kelp canopies (Fig. 1). Most of the sites are on the outer coast, while two sites, Chibadehl Rocks and Neah Bay, are inside the Strait of Juan de Fuca (Fig 1). 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 generally occupy depths of ≤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 years (1987, 1995, and 1999) by Kvitek and colleagues (Kvitek et al. 1989, Kvitek et al. 2000) (add 1998). Six sites (Teahwhit Head, Rock 305, Cape Johnson, Cape Alava, Anderson Point, and Neah Bay; Fig. 1) were surveyed in all four years monitoring was conducted.

For regional comparisons, we divided the ten sites into three geographic groupings: Northern (Neah Bay, Chibadehl Rocks, and Tatoosh Island), Central (Andersen Point, Point of the Arches, and Cape Alava) and Southern (Cape Johnson, Rock 305, Teahwhit Head, and Destruction Island). These groupings approximately reflect the areas used to describe sea otter trends within OCNMS historically (Lance et al. 2004) and reflect distinct geographic patterns in kelp and sea otter trends (see Results). We also use these grouping to reduce pseudo-replication in statistical analyses and to allow for regional differences in biological relationships.

Finally, we calculated an exposure metric for each site to use as an explanatory variable in statistical models. These metrics of wave exposure … [BLAKE INSERT METHODS HERE FOR ANALYSES]

*Sea otter abundance and distribution*

We extracted sea otter location and abundance information from research reports and peer-reviewed literature (see e.g. Lance et al. 2004, Jeffries 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 estimated home-range size of sea otters of 40 km for the Washington coast (*h* = 10.2; Laidre et al. 2009, their Fig. 3). After calculating the smoothed kernel probability density, we calculated the proportion of the total sea otter population that was present within a radius of 10 km of each focal site by integrating the probability density and multiplying by the total sea otter population size to arrive at an estimate of sea otters at each site. Due to uncertainty in the effective home range size of sea otters, we performed sensitivity analyses using a range of bandwidths (*h* = 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 and 2002-2015) to assess 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 sea otter abundance, we constructed a log-index of sea otter abundance. We standardized the number of sea otters by dividing by the average number of sea otters estimated at each site during the first three years of the kelp surveys (1989-91;) and taking a natural logarithm of this ratio:. Using such an index allows for sites across a large range of abundance to be visualized on the same axes and provides a graphical interpretation of sea otter trend (linear trends are exponential changes in abundance).

*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. 2017)). 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). Kelp 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 total canopy habitat 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 (Pearson’s *r = 0.689;* (Pfister et al. 2017)). 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. 1). 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. Or cite for DNR DOCUMENTATION?). 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. 1).

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. Thus, our measures of CV represent variability after accounting for the overall trend in area. We performed this analysis on the entire time series (1989-2015), and separately for the two halves of the time-series (1989-2001 and 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 by 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 1999 (Kvitek et al. 1989, 1998, 2000). During 2015, SCUBA divers surveyed benthic communities in kelp beds at each site (Fig. 1) at depths between 5-10 m, along visual transects (30 m x 2 m, *n* = 4 transects per site). On each transect, divers counted and estimated sizes of large, non-cryptic invertebrates >5 cm diameter (sea urchins, sea stars, sea cucumbers, crabs, bivalves, gastropods, anemones, chitons, tunicates, etc.).

For the 1987, 1995, and 1999 subtidal surveys, we extracted summary statistics on benthic invertebrate densities from Kvitek and colleagues (1989, 1998, 2000) (Kvitek et al. 1989, Kvitek et al. 2000). (Kvitek et al. 1998) Raw data were not available from these reports nor from the original authors. 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 (Table 1). 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. sea stars 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. 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* and *Cancer)*, bivalves (primarily rock scallops, *Crassadoma gigantea*), and sea stars (including genera *Pisaster, Orthaster, Dermasterias, Henricia, Pycnopodia)*. Consistent with previous research, we identified sea urchins as the dominant invertebrate grazer in this system and contrast the trends in sea urchin abundance with the other invertebrate groups. Based on sea otter diet information provided by Jesse, we classified these groups based on their frequency of occurrence in otter diets. We identified sea urchins, scallops (bivalves), 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 non-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. We also included our measure of wave exposure as a potential covariate in all models.

To assess the effect of otter abundance on the variability of kelp, we used the difference in CV of kelp area (yes?) at each site between periods as the response variable and region, wave exposure, difference in otter abundance between periods 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 sizes (AICc).

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, 1999, 2015) or three regions (northern, central, and southern) using the adonis function in R. We exclude data from 1995 because sea star data were absent. 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 or in some time periods 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 1999, 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). In general, local trends in sea otters differ substantially from the coastwide 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. 2b). 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. 2c). 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 greatest in the southern region; sea otter abundances in the northern region are the lowest by at least an order of magnitude (estimated 2015 sea otter abundance of 439, 207, and 18 for Destruction Island (Southern region), Cape Alava (Central), and Tatoosh Island (Northern), respectively). Cape Johnson and Rock 305 have essentially the same trend in Fig. 2c due to their proximity relative to the kernel bandwidth used for home range estimation (Fig. 1; see Methods).

Further analysis of sea otter observations data shows that the distribution of the Olympic Coast population has shifted over time (see also Jefferies 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 points in between (Fig. 3).

Canopy kelp area exhibited spatiotemporally distinct patterns in the three regions of the study area from 1989-2015 (Fig. 2d-f). Kelp area showed substantial interannual variation both at the individual sites and the coastwide scale (Fig. 1; see also (Pfister et al. 2017)). While the area of kelp in absolute terms varied substantially among sites within a region (Table 3; Pfister et al. 2017), 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. 2d; note that Neah Bay and Chibadehl Rocks are in the same kelp monitoring strata (Fig. 1), and thus share a single kelp time-series). The central region also showed within-region differences among sites (Fig. 2e). Canopy area at Cape Alava increased from 1989 to 2000 before stabilizing and possibly declining in recent years, while Point of the Arches and Anderson Point decreased 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. 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. 2e), 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 canopy growth rate between periods with 2002-15 having approximately 5% reduced annual growth rate from the 1989-2002 period (difference between periods of 0.053, *p* =0.012; Fig. 4). While the temporal effect is intriguing, more interesting is the interaction between sea otter population growth rate and time period, 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 of slope (yes?)= -0.507; interaction term *p* = 0.045). There was no support for regional variation in kelp growth after accounting for other factors (*p* = 0.128). The model considering only a single time 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 can substantively alter the interpretation of mechanisms driving kelp growth.

After accounting for 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, 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 variability 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 and 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 half of the period showed 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, the coefficient for 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. Estimates of wave exposure were not a significant explanatory variable for any aspect of kelp CV.

Benthic invertebrates are the mechanistic link between sea otters and kelp, comprising both sea otter prey and the major grazers of kelp in the system. While we lack continuous time-series for invertebrates at OCNMS, available information shows significant variation in the benthic invertebrate community over years but not across regions (Fig. 6; Table 2). Not only was there a shift in mean community composition between 1987 and the two later survey years, but community composition among sites became less variable after 1987 (Table 3). The differences in community composition among years reflected substantial declines in all 5 major taxonomic groups from 1987-2015 (Fig. 7). Sea urchins, the iconic prey of sea otters, declined precipitously with the across-site mean density 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%). 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 densities 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. 7a). For the four 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 communities. 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. By all measures, the spatial variability in invertebrate densities has declined 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 (Watson & Estes 2011) Estes and Duggins 1995, Steneck et al. 2002) (Breen et al. 1982). Here, we revisit a series of historical invertebrate surveys and complement these surveys with independent spatio-temporal data on kelp and sea otters in Washington’s OCNMS since 1987 along with new *in situ* invertebrate surveys. Our analyses reveal a strong correlation between sea otter abundance and kelp population growth at the local scale, despite local variability in the trajectories of sea otters and kelp. However, there is a temporal component to these associations: the relationship between kelp and sea otter growth rates shifted from positive during the 1990s to neutral or possibly slightly negative post-2000 (Fig. 4). In addition, contrary to predictions from trophic cascade theory (Estes et al. 2011), kelp and sea otter abundance are statistically decoupled when viewed coastwide and over the entirety of the 30-year period. The decoupling of otter and kelp abundance in more recent years, and the disconnect between coastwide versus local scale spatial patterns, may provide insight into appropriate theoretical expectations for short- vs long-term dynamics following the reintroduction of predators more generally (Ritchie papers, Stier et al. 2016 Science Advances), and sparks intriguing hypotheses about the relative influence of top-down and bottom-up forcing factors in temperate coastal habitats.

Classic trophic cascade theory predicts that increased sea otter abundance should reduce the abundance of their prey, including functionally important invertebrate grazers such as sea urchins. In turn, reduced grazer abundance should release kelp and other algae from top-down control and lead to increases in their abundance. Our results echo those of Kvitek et al. (1989, 1998, 2000) and demonstrate large, immediate, and persistent effects of sea otter expansion on the main invertebrate kelp-grazer and a preferred prey, sea urchins. We also show that increases in otter abundance lead to declines for a broad suite of invertebrate species. These reductions suggest the consequences of sea otter populations for kelp forest community composition are not exclusively an immediate shift in state, but can manifest gradually over the span of decades (other REFS THAT SHOW THIS?). Furthermore, because invertebrate densities remain far below historical levels and those associated with shifts to non-kelp dominated states (CITE), the observed decline in kelp growth rates (Fig. 4) and total area (Fig.1) in OCNMS since 2000 is unlikely to be caused by increased invertebrate grazing pressure. Rather, these results suggest that forces unrelated to otter abundance may also contribute to kelp forest community dynamics and composition.

One hypothesis for the decoupling of kelp and otter growth rates since 2000 is an increase in the influence of abiotic factors. Oceanographic dynamics in the late 1990s and early 2000s in the Northeast Pacific have been the subject of intense study because they were characterized by major El Nino and La Nina events and a shift in productivity regimes (PDO; {Mantua:1997tv, Mantua:2002jp}). It is possible that at that time the vast majority of changes in invertebrate grazer abundance due to otter predation had already occurred, and at that point kelp dynamics became more strongly influenced by sea surface temperature, upwelling, nutrient availability and other bottom-up forces (Pfister et al. 2017). For kelp in particular, we expected that the variability in kelp area would be strongly related to exposure at a given site (Reed et al. 2011, Bell et al. 2015). While kelp CV varied substantially among sites (Fig. S1), it was unrelated to calculated wave exposure values. Surprisingly, post-2002 Neah Bay had nearly equivalent kelp CVs as five of the other locations on the outer coast including Cape Alava and Destruction Island (Fig. 5; detrended CV of approximately 0.2). We speculate that this may be driven predominantly by the fact that we only have information about kelp area during the summer during which wave energy on the coast is relatively low. An alternative prediction is that kelp CV in Neah Bay would decline if sea otters invaded Neah Bay, as kelp CV appears to be potentially related to the number of otters present at each site (Fig. 5). While we cannot identify definitively what caused the decoupling of otter and kelp dynamics in OCNMS, shifts in factors controlling alternate states within ecological communities are not without precedent in other systems (Petraitis intertidal stuff, Bellwood et al. sleeping functional group on coral reefs). Our study adds richness and complexity to the classic trophic cascade explanation for the dynamics of kelp forest communities in the presence of sea otters.

Beyond the mean effects of sea otters on kelp and invertebrates, both kelp area and the benthic invertebrate community showed reduced variability as sea otter abundance increased. We know of no other study that has examined the interaction between otter abundance and kelp variability, but suggest this is a particularly interesting avenue of future research due to the connection between canopy kelps, benthic community structure {Arkema:2009to}, and various ecosystem services (Wilmers et al. 2012, Pinsky & Fogarty 2012). For benthic invertebrates, both multivariate and univariate analyses show that invertebrate communities cluster by year rather than spatial region, suggesting the primary driver of communities is a temporal rather than a spatial process (Fig. 6, 7). Thus both kelp and invertebrates show evidence of homogenization in concert with the expansion of sea otters, which aligns with previous suggestions that sea urchin dominated habitats may show more variability than sea otter controlled habitats (Watson & Estes 2011). We acknowledge that there are potentially many consequences for other groups including understory algae (Watson & Estes 2011) and fish (Markel & Shurin 2015) that we cannot explore in this manuscript.

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 that other factors have affected the abundance of some invertebrate groups (e.g. sea star wasting disease outbreak in 2013-4; Eisenlord et al. 2016), personal observations of one of the authors (AOS) between 2003 and 2009 at two sites - Tatoosh Island and Pt. of the Arches - do not support radical changes in invertebrate abundances during the 1999 to 2015 gap in our invertebrate time-series. We cannot exclude the possibility of strong variability in invertebrate communities driving these patterns but we suggest that is an unlikely driver of observed kelp patterns.

Looking to the future, sea otter numbers appear to have stabilized in much of the northern and central regions of the OCNMS (Fig. 2) and may be at or near carrying capacity in these regions. Invertebrate densities in these areas are very low, which begs the question of how sea otter populations are maintained with very low prey abundances. Rocky subtidal and kelp forest habitats support higher densities of sea otters in Washington than either sandy bottom or estuarine habitats (Laidre et al. 2001, 2002), suggesting that sea otters are not likely to simply be foraging in nearby sandy habitats, but they may be capturing invertebrates in deeper rocky habitats that were not included in our surveys or historical surveys. Furthermore, we note that the abundance of sea otters in 2015 is substantially above the published estimates of carrying capacity for the Washington outer coast (current population is greater than 1,400, but carrying capacity estimates range from 922 to 1189; Laidre et al. 2002), suggesting that either the carrying capacity of otters needs to be revisited or, if those estimates are correct, the population is predicted to decline in the coming years.

FINAL PARAGRAPH ON FUTURE WORK,

Overall, recent years have seen total kelp area 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 populations were less than half their current abundance. Possible speculative story: decline in CV coastwise, more similarity among sites, stronger links to oceanographic conditions? We speculate….

(Watson & Estes 2011)

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Table 1: Description of benthic invertebrate SCUBA surveys.

|  |  |  |  |
| --- | --- | --- | --- |
|  | Survey methods. | Number of replicates | Area surveyed per site (m2) |
| 1987 | 1.0m2 quadrat by SCUBA, all counts conducted *in situ* | 100 per site. Not randomly placed locations | 100 |
| 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 |

Table 2. 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 3. 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 |  |  |  |

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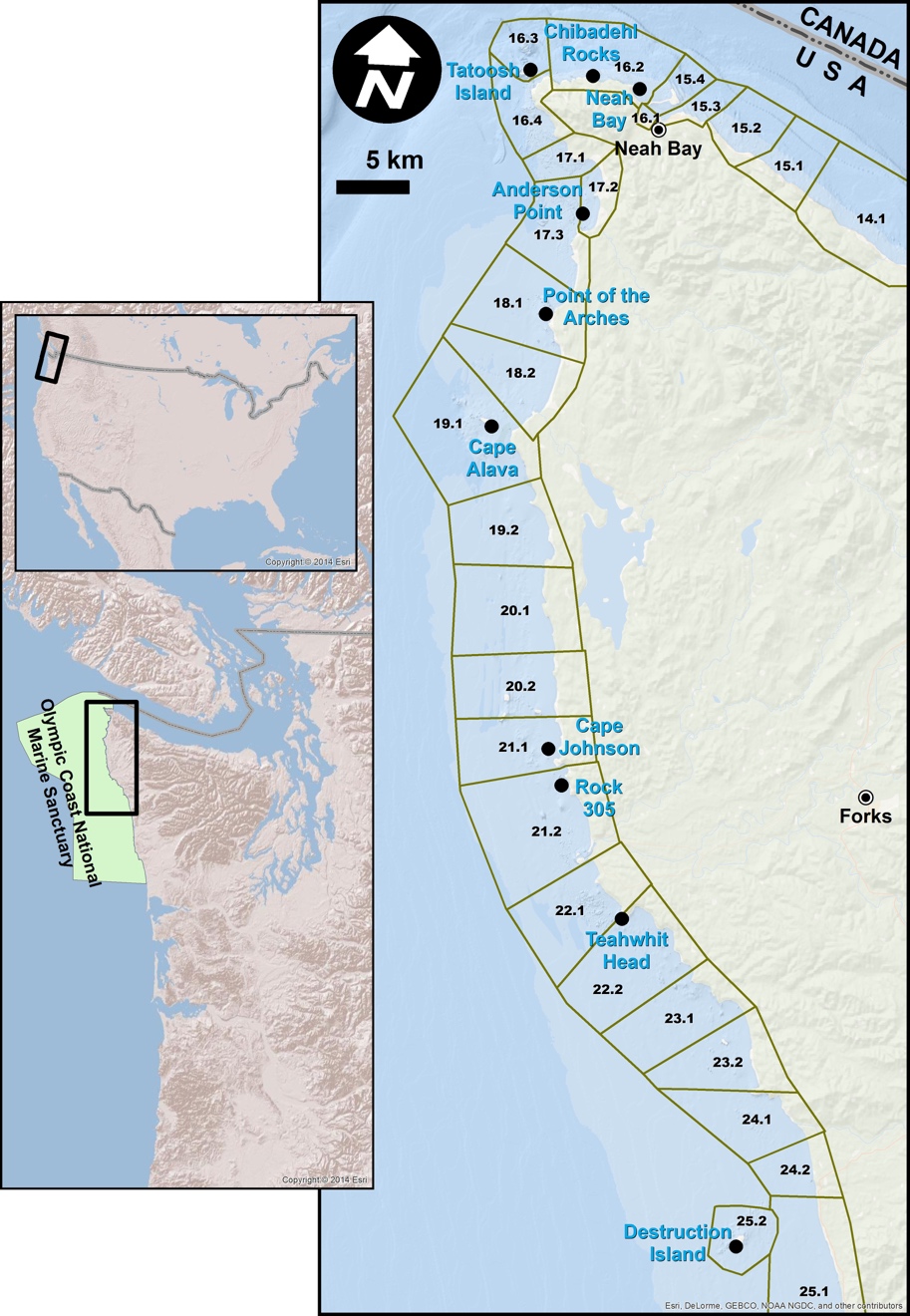


Figure 1: Study area with survey site locations for invertebrate surveys (blue labeled dots). Numbered areas along the coast indicate strata within which WDNR calculates kelp area. *Top right*: Time-series of sea otter abundance on the Washington coast. *Bottom right*: Time-series of total kelp canopy area for kelp strata between 15.1 and 25.2



Figure 2: Time-series for sea otters (left column, *a, b, c*) and kelp area (right column, *d, e, f*) at sites divided into three regions (rows*)* in OCNMS. In all panels, points and dashed lines show log-indices for sea otters and kelp area for individual sites. Both kelp area and sea otters are indexed such that the average values for each site during the 1989 to 1991 period are 0. Solid lines represent the summed coastwide values for otters and kelp area, respectively, indexed to the average value from 1989 to 1991.



Figure 3. Kernel smoothed sea otter distributions for sea otters on the Washington coast. Grey densities show the probability distribution for each year, dots show the annual center of gravity (median) of the distribution, and bold dashed line shows smoothed trend in the center of gravity from a loess smoother. Prominent geographic points and invertebrate survey locations noted on the y-axis. Dashed horizontal line indicates the entrance to the Strait of Juan de Fuca at Tatoosh Island (see Fig. 1).



Figure 4. Sea otter and kelp area exponential growth rates at individual sites for two periods (Mean ± SE; *a:* 1989-2001, *b:* 2002-2015). Shapes correspond to the three regions and shading indicates the number of sea otters estimated to be at each site at the beginning of each time period.



Figure 5. Kelp area CV for two periods (1989-2001 and 2002-2015) as a function of the number of otters at the beginning of each period. Points represent bootstrapped means and 95% intervals. Individual sites are connected with dashed lines.



Figure 6: Non-metric multidimensional scaling results for benthic invertebrate communities at OCNMS sites grouped by year (*a*) or coastal region *(b).*



Figure 7. Time-series of densities of benthic invertebrates. Species are ordered roughly by otter prey diet frequency from common (top row) to rare (bottom row). Graphs show site means and SE. Points have been jittered slightly along x-axis to reduce overlap. Red filled points show sites designated by Kvitek et al. (1989) as outside the primary otter range in 1987. By 1995 all sites were within the otter range. Note that data on seastars are not available for 1995.

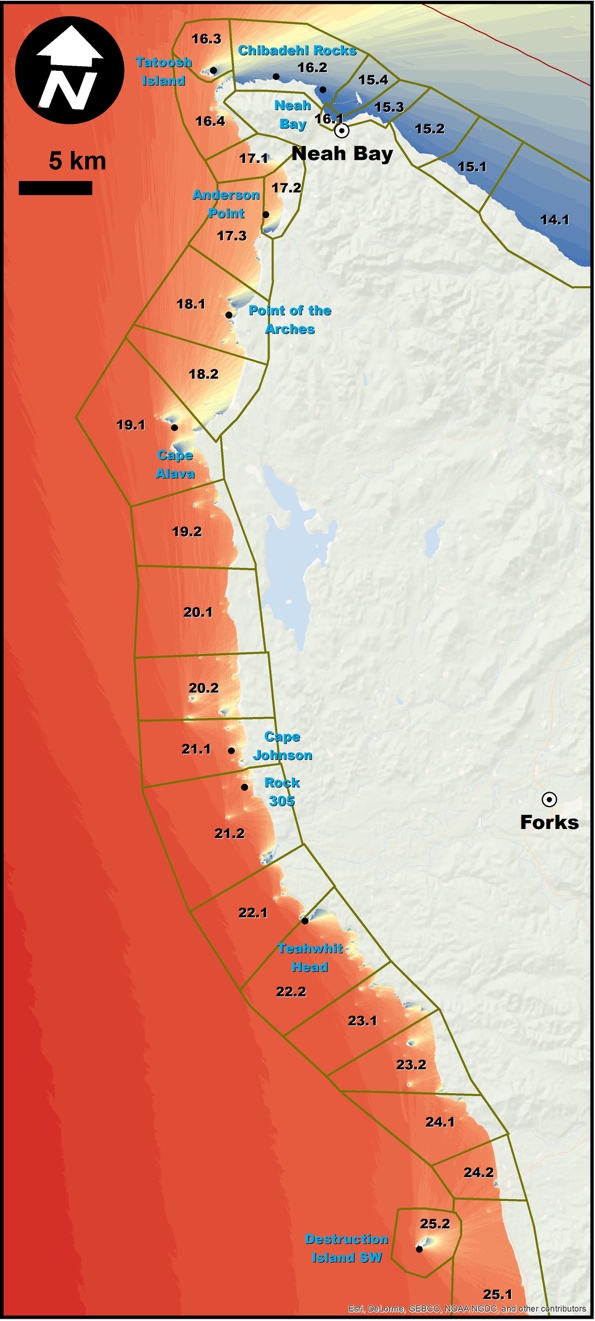
Table S1: Kelp areas.

|  |  |
| --- | --- |
| Site Name | Average Kelp Area (ha) 1989-2015 |
| 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 S1: Sites and the years they were sampled.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
|  | 1987 | 1995 | 1999 | | 2015 |
| **Sites** | Quadrats | Quadrats | Quadrats | Transects | Transects |
| Neah Bay | X (2 distinct 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 |

Figure S1. Estimates of exposure from Blake’s model.



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