OCNMS Kelp-Invert-Otter Paper

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Introduction

Otter- Kelp-Invertebrate interactions are a classic example of a trophic cascade (PAINE 1966, others) in which the (re-)introduction of a top predator shifts the ecosystem from one with abundant urchins and minimal kelp to one with few urchins and dense algae {Estes:1998hr, Estes:1995hv, Estes:1974tk}. Over the past 40 years, the generality of the importance of top down control on kelp forests has been both affirmed (Otters in the Aleutians, Konar, others; Otters in the Monterey area) and challenged from a variety of perspectives {Carter:2007en, Lafferty:2004dn, Reed:2011ef}. Otters can play a strong role in shifting coastal ecosystems from herbivore dominated to algae dominated {Soule:2003fb} which can have substantial indirect consequences for other species {e.g. fish, Markel:2015kv}. But importantly, there are numerous examples in which coastal systems are not uniformly herbivore dominated in the absence of otters {Lafferty:2004dn, Foster:1990kc, Carter:2007en, Reed:2011ef}. 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 spatio-temporal heterogeneity of coastal kelp systems. Such a landscape perspective on the drivers of heterogeneity and complexity have been used to improve understanding of kelp forest dynamics {Bell:2015ei}.

are both among the most compelling aspects of coastal kelp forest systems and an important factor that may inhibit predictability of coastal systems.

Historically, examination

1) Spatial comparisons, where areas with otters are compared to areas without otters; 2) Temporal comparisons, where the change in herbivores respond

Here we combine nearly 30 years of spatial data on benthic invertebrates, algae, and sea otters from the coast of Washington state to examine the dynamics of this tri-trophic system during periods of otter expansion and eventual population stabilization. We leverage spatial information from 10 sites spanning approximately 100km of shoreline to link otters to invertebrates and algae and show how the predictive subsequent patterns .

By utilizing spatial time-series, we avoid some of the troubles with space for time substitutions.

We suggest some general patterns of communities

Something about time-series approaches like ives being about the deviations from equilibrium…

Simply put, the quest to identify a single most important factor structuring coastal systems is flawed and futile

Studies of coastal

Other species may play a vital role controlling herbivores {Lafferty:2004dn}

Though the

{Bell:2015ei}

{Soule:2003fb}

There have been a wide

Classical

Mixture of patterns for kelps –

* Bottom up driven dynamics over relatively short time-periods (Dan Reed and friends).
* Other species are performing top down control in the absence of otters but this is disputed by some
* {Graham:2007wp}

**Pfister et al. In review:**

Reference Pfister et al. In review for WDNR methods description. Also,

(http://www.dnr.wa.gov/programs-and- services/aquatics/aquatic-science/kelp-monitoring)

There was no evidence of negatively correlated dynamics that are associated with competition (Rees *et al.*, 1996). Instead, both species appeared to covary through time, suggesting that conditions favorable to one species were also favorable to the other.

**Methods**

Data

*Invertebrate surveys*

We combined multiple SCUBA surveys conducted along the Olympic coast to characterize the benthic invertebrate fauna over time at 10 focal sites (Fig. 1). We extracted survey data from surveys conducted in 1987 (Kvitek et al. 1989, REF), 1995 (REF), and 1999 (REF) and conducted SCUBA surveys in August 2015 (see below). Unfortunately, not all sites were visited in all years (see Table 1) and the survey methodologies varied among surveys but all involved a mix of quadrat and transect sampling conducted at shallow depths (5-12m). Survey locations and survey depths were consistent over time. We have estimates of mean density and standard deviation in units m-2 from the years 1987, 1995, and 1999, but we lack the raw data at the quadrat or transect level. Importantly, the sampling design from 1987 – in which many quadrats were placed directly adjacent to one another – means that the number of independent replicates are far less than the number of quadrats sampled (100; i.e. the quadrats are pseudo-replicated). In the absence of the information to empirically estimate the effective sample size, we used a sample size of 20 for the 1987 data to better reflect this uncertainty. For 1999 we had both quadrat and transect information. We combined the quadrat and transect data by first calculating the mean and SE for each data independently and combining the information using a weighted mean and weighted standard deviation. We used the inverse of SE2 as weights. Similarly, in 1995 and 1999 surveys were conducted at two depths at each site (6m and 12m). We elected to combine information from both depths, again weighting the different depths by SE2.

DESCRIPTION OF INVERT SURVEYS IN 2015.

*Red Urchin Fishery closed in Neah Bay region (#5) in 1995*

*Kelp*

We used publically available aerial surveys of algae from the Washington Department of Natural Resources (WDNR) to document changes in canopy forming brown algae (REF). We used the mostly annual surveys between 1989 and 2015 to examine changes in kelp area (no data were available for 1993). Coastal kelp forests of the Olympic coast consist of a mix of giant kelp (*Macrocystis pyrifera)* and bull kelp*(Nereocystis luetkeana).* While overflight surveys differentiate between the two species (REF), we are primarily interested in the canopy habitat kelps provided and so we focus on the total surface area provided by the two species. Additionally, the two species abundance are strongly positively correlated in the data (Pfister et al. In Review). We examine kelp abundance at two scales. We use estimates of kelp area within discrete strata along the coast to provide estimates of local kelp area trends for each of our 10 focal study sites (see Fig. Supplement X). Additionally, we summed the area of kelp present in all strata between Neah Bay and Destruction Island (Fig. 1) to provide a coastwide estimate kelp along the northern Olympic coast (see Supplement for list of survey strata used for each area and areas used to derive a total kelp area metric). Surveys were conducted during peak kelp abundance in Washington (late summer: late July or early August). BLAKE: add detailed methods if needed.

We calculated several metrics to quantify the trend and variability of kelp at each focal site. First we calculated the trend in kelp at each site be regressing the natural logarithm of kelp area against time. This produces an estimate of the exponential trend in kelp area. 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). Splitting the time series allowed us to explore how trends have shifted over time. As estimates of population growth become progressively less precise with less data, we elected not to subdivide the time-series further. ARBITRARY-NESS CRITIQUE.

After we estimated the trend in kelp, we calculated the standard deviation of observations around the estimated trend for each site and calculated the coefficient of variation (CV; CV= standard deviation / mean) for each site. We used the average kelp area for the mean abundance at each site. Again we calculated these metrics for both the entire time-series and separately for the two halves of the time-series.

*Sea Otter*

We extracted otter location and abundance information from publicly available research reports and published literature. Sea otters were reestablished along the Olympic Penninsula in 1969 and 70 with the translocation of 59 otters captured at Amchitka Island, Alaska {Jameson:1982bu}. Otter surveys have been conducted by a mix of aerial survey and land-based observations since 1977 (see e.g. THESE REPORTS), biennial surveys through the 1980s (no data in 1979, 80, 82, 84, 86, or 88), and mostly annually surveys from 1989-2015 (no data in 2009 or 2014). We mapped the location of otter observations from WDFW reports to examine shifts in otter abundance and distribution over the time-series. We used total otter counts for all of our analyses. Similar to the kelp data, otter surveys reflect summer distribution and abundance (REF). As otters are highly mobile predators with substantial home-ranges and the potential to have distinct seasonal distributions {Laidre:2009td}, our data only allow us to discuss summer distributions. However, anecdotal evidence does not suggest that winter distribution of otters are substantially different {Laidre:2009td}.

As we were interested in estimates of otter abundance at each survey site, we developed a kernel smoothed distribution of otters along the coast to incorporate uncertainty about how snapshot surveys from WDNR translate to the effective numbers of otters present at a given location. We first developed a one dimensional coastline for the Olympic Penninsula and identified the position along this coastline for each listed WDNR survey location. Kernel distributions generate a density of otters along the Olympic coastline by approximating the observed otter surveys as a mixture distribution. We used normal kernels for our mixture components, placing a normal distribution centered at each survey location and used a standard deviation *h* (the bandwidth) that corresponds to the home-range size of otters of 40 km for the Washington coast ({Laidre:2009tda}; *h* = 10.2). The normal kernel at location *i* in year *t* received a weight, corresponding to proportion of total otters observed at each location: , where is the number of otters observed during the survey and is the total number of otters observed. Then the probability density function for otters along coastal position *X* in year *t* is

(1)

and integrates to 1. We let be the shoreline position of the *j*th focal site and used the density from eqn. to calculate the number of sea otters within a 10km shoreline radius of our focal sites in each year, is

This provides estimated abundance of otters in each year over a standardized shoreline length and enables comparisons among sites and across time at a given site. Due to uncertainty in the effective home-range size of sea otters, we performed sensitivity analyses using a range of alternative bandwidths (*h* between 5 and 15). The qualitative results did not change with alternate bandwidths.

As with the kelp data, we calculated an exponential rate of increase for each site by regressing log-abundance against time for the period 1989-2015 – coincident with the available data for kelp - and period divided into two halves, 1989-2001 and 2002-2015.

Analyses for each type

Kelp:

* Area
  + Total
  + By each strata associated with invertebrate surveys
* Trend since 1990
  + Regression to estimate exponential change in area since 1990 by region

Otters:

* Total Coastwide
* Kernel density smoothed onto 1D shoreline for each focal area using a kernel of 10km or so corresponding to a 95% home range of 40km.
  + Center of gravity
* Local population trend
  + Regression to estimate exponential change in area since 1990.

Invertebrates:

* Patterns for major herbivores (urchins)
* Sea stars
* Cucs

Comparisons:

* Local otter growth explain local kelp growth at local scales
  + Two periods 1989-2001,2002-2015.
* Kelp CV vs. otters.

**Results**

Sea otters, kelp, and invertebrates all show large changes in abundance in the Olympic coast over the study period. On a coast-wide basis, sea otters increase nearly exponentially from the first surveys 1977(Fig. 1). Kelps were largely stable between 1989 and 1998 averaging 385 ha, nearly doubling in area during the last years of the 1990s to an average of near 679 ha after 2000, though with a notable decline recently (2013-14; Fig. 1). Invertebrate abundance showed XYZ(FIG. 2).

However, the patterns of each sat the coastwide scale are not reflected at the individual site scale (Fig. 2). As the overall abundance of sea otters and kelp varied substantially among sites, we constructed an index of abundance (otters) or area (kelp) to the average value at each site in during the period 1989-91, the first three years of the kelp survey. This allow us to compare changes relative to a reference date and compare changes in populations on shared, logarithmic axes (Fig. 2). We identified geographically distinct patterns in sea otter and kelp trends, with the three northern, three central, and four southern sites showing similar patterns. In the north, sea otter abundances peak in the early 1990s and decline to approximately 1990 levels by 2000; kelp abundances fluctuate but are generally stable. Centrally, populations increase slightly from 1990 levels, before stabilizing around 2000; kelp generally show an increasing trend with variability. In the south sea otter populations show sustained increases throughout the time series, with Destruction Island outpacing the other sites; kelps show an accompanying increase. Together, these patterns result in an overall southerly shift in the distribution of otters beginning around 1997 with the midpoint of the otter distribution shifting ~45 km south from near Cape Alava to just north of Destruction Island (Fig YY).

Dividing the post-1989 time-series in two show two different relationships between changes in otter abundance and kelp area. Specifically, there is a strong positive relationship between otter and kelp trends for 1989-2002 (Pearson’s product-moment correlation; ), but not for 2002-15 (; Fig X). This suggests….

While otter trends do not result in continued increases in kelp, changes in the local abundance of sea otters do translate into changes in the variability of kelp. At both central and southern sites increases in sea otters corresponded to declines in kelp variability (Fig. ZZ). In contrast, the three northern sites show no changes in otter abundance and kelp CV was unchanged as well.

For the three northern sites, there was virtually

1. **Substantial temporal variation in kelp & otters at the outer coast scale.**
   1. Otter exponentially increase (Fig.1)
   2. Kelp rapidly increases before falling in recent years (Figure 1).
2. **Coastwide patterns obscure patterns at the landscape scale**
   1. Three regional patterns in otter and kelp trends are suggested by the data
   2. Non-uniform patterns in overall kelp abundance and habitat availability (some sites have a lot of kelp, some have little)
   3. Local trends in kelp are strongly related to otters during the invasion and increase in otters but are unrelated after otter numbers have stabilized (Figure).
   4. Decline in kelp variability is associated with increases in otters. (need to do bootstrapping for confidence bounds on Fig).
3. **Invertebrate assemblages**

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Description of what Ole did to the OCNMS data to massage and poke the data to make it comparable.

Raw data from Kvitek’s 1987, 1995, and 1999 are generally not available, so we extracted summary statistics about density of benthic invertebrates from project reports for each year. However, the methods for estimating the density of benthic invertebrates varied substantially among years (See TABLE) and we needed to convert data from each survey year into common units for comparison. We elected to translate all of the different surveys into units of countsm-2. We have estimates of mean density and standard deviation in unit m-2 from the years 1987, 1995, and 1999, but we lack the raw data at the quadrat data. Importantly, the sampling design from 1987 – in which many quadrats were placed directly adjacent to one another – means that the number of independent replicates are far less than the number of quadrats samples (i.e. the quadrats are pseudo-replicated). In the absence of the information to estimate the effective sample size, we used a sample size of 20 for the 1987 data to better reflect the uncertainty.

For 1999 we had both quadrat and transect information. We combined the quadrat and transect data by first calculating the mean and se for each data independently and combining the information using a weighted mean and weighted standard deviation. We used the inverse of SE2 as weights. Similarly, in 1995 and 1999 surveys were conducted at two depths at each site (6 an 12m). We elected to combine information from both depths, again weighting the different depths by SE2.

Weirdness: No seastar info from 1995.

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 |
| Tatoosh Island |  | 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 |
|  |  |  |  |  |  |
|  |  |  |  |  |  |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | Year Otters Exceed Number | | | |
| **Sites** | **2** | **5** | **10** | **25** |
| Neah Bay | 1988 | 1991 | 1991 | - |
| Chibahdel Rocks | 1988 | 1990 | 1991 | 1991 |
| Tatoosh Island | 1987 | 1988 | 1990 | 1991 |
| Anderson Point | 1977 | 1981 | 1983 | 1988 |
| Point of the Arches | 1977 | 1980 | 1981 | 1987 |
| Cape Alava | 1977 | 1977 | 1981 | 1984 |
| Cape Johnson | 1977 | 1979 | 1983 | 1987 |
| Rock 305 | 1977 | 1979 | 1983 | 1987 |
| Teahwhit Head | 1977 | 1981 | 1986 | 1991 |
| Destruction Island | 1977 | 1984 | 1988 | 1994 |

Figure 1 Map and Coastwide trends in otters and kelp area.



Figure 2:



Figure X Essentially a summary of Figure 2. Otter and Kelp exponential growth rates by site & region and the number of otters present at each site in 1990.



Fig. ZZ. Kelp CV in two periods ( after accounting for trend in abundance. Make bootstrapped confidence intervals.



Figure YY 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)



