A LONG TERM COMPARISON OF ROCKY INTERTIDAL COMMUNITIES IN REDWOOD NATIONAL AND STATE PARKS

By

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We certify that we have read this study and that it conforms to acceptable standards of scholarly presentation and is fully acceptable, in scope and quality, as a thesis for the degree of Master of Arts.

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ABSTRACT

Long term comparisons are important for understanding intertidal community dynamics and documenting response to environmental pressures. This study compares the historical abundance of high intertidal sessile organisms at two rocky intertidal sites within Redwood National and State Parks shortly after the park was established (“historical”:1974-1976) to the present community (2004-2005) at the same locations. Percent cover of ephemeral, early successional species was higher in historical assessments, whereas percent cover and magnitude of seasonal variation in perennial, late successional organisms increased in assessments of the present community. The long term successional shift is likely a result of decreased disturbance severity between the mid 1970’s to present. Severe historical disturbance is linked to increased sedimentation and frequent driftwood battering associated with logging. Conservation and rehabilitation strategies in the adjacent terrestrial landscape since 1978 may have resulted in spatial dominance by mid to late successional species at these two sites. Several alternative causal hypotheses regarding long term climate change, El Niño Southern Oscillation, upwelling intensity, and species interactions are evaluated, but not supported by the results of this study.

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Rebecca Degan (far left), Wendell Wood (third from right), and Katherine Hedges (far right) with invertebrate zoology students at Enderts Beach Cove.

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Melissa Miner, Karah Cox, Maya George, and Erin Maloney at Damnation Creek Trailhead

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INTRODUCTION

The rocky intertidal has long been a preferred experimental area because of accessibility, and the small scale over which interactions and processes occur (Underwood 1992). More recently, the susceptibility of intertidal systems to anthropogenic effects from a vast array of terrestrial and oceanic sources has been recognized. Understanding and monitoring mechanisms underlying ecological change in the rocky intertidal has become a priority for managers, conservation biologists, and ecologists. For conservationists, it is important to determine biological responses to natural pressures and disturbances (desiccation, sedimentation, salinity changes, wave stress, predation, competition etc.), as well as to anthropogenic pressures (changes due to global warming, pollution, etc). Assessments of community organization and dynamics are also important for making before-after comparisons and for tracking recovery when anthropogenic disturbances occur (Underwood 1992, 1994, Crowe et al. 2000), or to measure the effectiveness of a change in management strategies (Murray 1998).

Short term variation in intertidal assemblages is generally attributed to physical stress, disturbance, or biotic interactions (Dayton 1971, McQuaid 1985, Foster et al.1988, Connolly and Roughgarden 1999, Bertness et al. 1999, Menge and Branch 2000, Harley and Helmuth 2003, but see Menge et al. 1999). Similarly, most long term investigations have linked change in intertidal communities to climate or oceanographic changes (Lubchenco et al. 1993, Navarrete and Lubchenco 1993, Barry et al 1995, Sagarin et al. 1999), or to ocean-transported pollutants (Kussakin and Tsurpalo 1999, Driskell et al.

2001). Long term changes in intertidal communities have also been attributed to a variety of factors, especially oil spills (Carls 2001, Peterson 2001) and thermal discharge from nuclear power plants (Lardicci 2001).

The rocky intertidal areas within Redwood National and State Parks have remained relatively pristine. Their remote location ensures protection from most human exploitation and pollution, with the exception of perturbations resulting from logging activities. Studies of ecological change at sites within Redwood National and State Parks provides a unique chance to examine long term trends in rocky intertidal communities without the confounding factors of adjacent urban development and trampling by visitors.

The primary purpose of this investigation is to assess long term changes in composition and percent cover of sessile species in the rocky intertidal communities at two sites within Redwood National Park. Data collected between June 2004 and June 2005 are compared to data analyzed from photographs taken by Boyd and DeMartini (1977) from July 1974 to June 1976 (herein referred to as “historical data”). Data for both time periods were collected at False Klamath Cove and Enderts Beach Cove. I also consider the possible factors driving long- term change in the abundance and seasonal variation (in percent cover) of sessile algae and invertebrates at these two sites. Comparisons are made at the decadal (1974-1976 vs. 2004-2005) and inter-annual (1974/1975 vs. 1975/1976) scale. I evaluate several hypotheses relating to long term change in rocky intertidal communities as set forth by Sagarin et al. (1999), and one additional hypothesis regarding a change in disturbance regime. These hypotheses are as follows:

Community shifts are due to short term inter-annual population variation. Sampling was limited to two historical years in the 1970's and one recent year (2005) in this study. Data were compared between the two historical years to determine if community changes were a result of random inter-annual changes rather than actual long term differences. To reject this hypothesis, percent cover of sessile species should be more similar between the two historical years (1974/1975 vs. 1975/1976) than between recent and historical years (1974/75 vs. 2004/2005 or 1975/1976 vs. 2004/2005). To prevent possible effects of seasonal variability, percent cover data were compared for the same month between years only.

Long term community shifts are a result of a change in the magnitude of seasonal variation. A change in the disturbance regime could result from changes in a variety of physical factors. However, a shift in disturbance regime would be manifest in the biological community by a change in species composition and in the magnitude of seasonal variation. The effects of disturbance have been studied extensively with respect to biodiversity (Connell 1978, Sousa 1984 and1985, Connell et al. 1997). Connell (1978) hypothesized that biodiversity is highest in areas where disturbance (resulting in patchy loss of individuals) is intermediate in both frequency and severity. Disturbances can also effect community composition and species abundances. In areas with frequent/severe disturbances, ephemeral, early successional species dominate. In areas with low or infrequent disturbance, perennial, late successional organisms are more abundant. By recording changes in the percent cover of sessile organisms from one sampling event to the next, it is possible to determine the magnitude of seasonal variation and the relative degree of disturbance at a given site. When disturbance is frequent and severe, both percent cover of early successional species and the coefficient of variation (CV) in percent cover of sessile organisms should be low. Severe and frequent disturbance would continually limit the percent cover of sessile organisms by complete removal or removal of vegetative parts, such that their percent cover should remain low (close to zero) and variation in percent cover (CV) should be small (Paine 1979). When disturbance is severe, but infrequent, the percent cover of sessile organisms should be highly variable (CV value high). Under relatively stable conditions, sessile organisms would be able to establish high percent cover but severe “unpredictable” disturbance events would cause drastic changes in cover yielding a high CV (Paine 1979). If disturbance is frequent but of minor impact, sessile organisms would be expected to establish at a relatively high percent cover, but the CV should be low.

Life history traits correspond with community shifts. Changes occurring disproportionately in groups of organisms sharing a particular life history trait (dispersal or successional category), or geographic range, could lend insight to the nature of the factors driving long term change. For example, a simultaneous increase in percent cover of algae and a decrease in percent cover of sessile animals could be an indication that some factor is promoting primary productivity (e.g. an increase in upwelling intensity). Long term changed could occur disproportionately in species belonging to a successional group (early, mid, late) if changes in a site’s disturbance regime were to occur. Similarly, long term environmental changes could promote the dominance of unrelated species that share a certain life history trait. For example, if percent cover increased disproportionately in organisms with a prolonged planktonic larval stage, it would suggest that a change transport processes caused a shift in community composition (Sagarin et al. 1999).

Anthropogenic environmental changes have resulted in community shifts. Trampling and harvesting by humans can have adverse impacts, especially in high intertidal areas where access is more frequent (Beauchamp and Gowing 1982, Brown and Taylor 1999, Schiel and Taylor 1999, Crowe et al. 2000, Jenkins et al. 2002). Because of the remote location and low human population surrounding these sites, sessile organisms in these intertidal communities are probably not strongly affected by direct human exploitation, however. Pollution from industrial sources is also unlikely adjacent to the coastline because there has been very little industrial activity in this area, with the exception of logging activities. There are three river mouths (Smith River, Klamath River, and Redwood Creek) within 25 miles of both intertidal sites. Output from these rivers and other smaller tributaries is likely the source of any pollution, sediment, and other debris that might be delivered to these sites. It is difficult to predict the effects of agricultural runoff from these watersheds on rocky intertidal communities, so these impacts are not be evaluated in this retrospective study. Rivers and other small watercourses probably contribute to variation in salinity at adjacent rocky intertidal sites. Freshwater contributions are highly episodic and seasonal, but it is unknown how changes in salinity affect rocky intertidal communities in this region.

Effects of sedimentation and battering by large woody debris are more predictable and are considered here as possible drivers of community change. Sediment and driftwood levels, entering the rocky intertidal from these watersheds, were likely to have been extremely high between 1950 and 1978 when up to 85% of the land in these watersheds was logged by clear-cutting (Janda 1975). Historically, sedimentation occurred at higher levels than today because of an unfortunate combination of unstable slopes, poorly built roads, and clear cut hillsides (Janda 1975, 1977, Kelsey et al. 1981, Pitlick 1982, Best 1984, Madej 1984, Madej 1992). Large drift logs were also more abundant at these intertidal sites historically (Boyd, pers. comm. 2004).

Possible anthropogenic effects on intertidal communities indirectly resulting from logging activities are discussed mostly from historical records. Increased sediment loads probably caused sand scour. If sand scour and battering by drift logs contributed to higher levels of disturbance to sessile organisms in the rocky intertidal, historical data should reflect a higher abundance of early successional species and those better able to survive scour/sedimentation relative to present assessments.

Sand scour and burial can affect the community composition depending on the duration, intensity, and frequency of sand burial/scour. A change in the abundance of sand tolerant species, such as *Anthopleura elegantissima* (Raimondi et al. 1999), would suggest a change in the amount of sand present at a site. Battering by drift logs would result in patchy rock clearings, especially on exposed rocky substrates, such as the tops of rocks. Sedimentation and frequent battering of logs would likely result in the removal of erect algal thali and smashing of mussels and barnacles. Differences in percent cover for sessile organisms and the variability in the maximum percent cover might indicate a change in the disturbance regime between these two time periods as well.

Climate-related change drives community shifts. Sagarin et al. (1999) found that a shift in the abundance of certain macro-invertebrate species was correlated with an increase in shoreline ocean temperature resulting from long term climate change. Species whose published northern range limit was close to their study site increased in abundance, while species whose southern range limit was close to their study site decreased in abundance. Changes in the abundance of central species were non-directional. To accept this hypothesis in my study, I would expect the mean, minimum or maximum shoreline ocean temperature to be significantly higher in recent years, and for percent cover to increase in sessile species whose northern range limit is near my study sites.

ENSO-related events caused the observed community shifts. El Niño-Southern Oscillation events usually impact the California coast by increasing the flow of warm surface water northward. This anomalous current promotes the transport of southern species and inhibits southern dispersal of species from north to south. To accept this hypothesis, ENSO would have to be stronger or more frequent in the years preceding recent surveys. Long term changes in the biological community should include a higher abundance of southern species and a decrease in the abundance of northern species, particularly in species with planktonic larvae (Sagarin et al. 1999).

Community shifts are related to changes in upwelling intensity. Upwelling intensity/frequency is known to affect the abundance and distribution of intertidal organisms. Increased upwelling intensity occurring in nutrient limited environments can cause higher algal productivity (due to increased nutrient availability) and increased herbivore biomass (Bosman et al. 1987). Upwelling events have also been linked to reduced delivery of planktonic larvae (Shanks 1983, Roughgarden et al. 1988 and 1991, Sanford 1999). To support this hypothesis, upwelling intensity would have to have changed in the time periods leading up to both sampling periods. The biological community should reveal *both* an increase in the percent cover of algae and a decrease in the percent cover of organisms with planktonic larvae, in periods of high upwelling intensity.

Patterns of community changes have arisen from species interactions. Changes in the abundance of sessile organisms could be a direct effect of interactions between sessile organisms and their associated motile invertebrates (usually grazers or predators), or an indirect effect resulting from interactions between an associated predator/grazer and environmental factors (Bertness et al. 2004, Nielsen and Navarrette 2004). Unfortunately there are no data available regarding the abundance of motile invertebrates in historical plots. So this possibility can only be explored in recent data.

To evaluate the hypothesis that changes in the sessile community have arisen from biological interactions, the seasonal variation in percent cover of sessile species is compared against variation in the abundance of motile invertebrates occurring in within the same plots and against variation in physical factors including upwelling, near shore ocean temperature, air temperature, precipitation, and wave height. Although this comparison is not at the long term scale, it is an indication of the relative strength of interactions between sessile organisms with higher trophic levels versus oceanographic processes. Results will suggest whether or not biological interactions are affecting the abundance of sessile species more than physical processes. To accept this hypothesis, seasonal variation in sessile species should be best predicted by variation in the abundance or size distribution of motile invertebrates rather than variation in physical factors.

METHODS

Study Sites

Historical comparisons took place at two rocky intertidal sites within Redwood National and State Parks (Fig. 1): (1) False Klamath Cove and (2) Enderts Beach Cove, which are two rocky intertidal sites on the Northern California coast (Figs. 2 and 3). The intertidal community at both sites was originally monitored bi-monthly by Boyd and DeMartini (1977) from June 1974 to July 1976. I revisited and assessed (June 20 and 21, 2005) these sites for a "snap-shot" comparison of percent cover in high intertidal sessile species with historic levels of abundance (also assessed in mid summer). I also monitored seasonal variation in sessile organisms and associated motile invertebrates at these two sites, and a third, called Damnation Creek, to determine if changes in the magnitude of seasonal variation occurred. Recent data were collected approximately bi-monthly at each of these three sites from May 2004 through June 2005.

Enderts Beach Cove (N 41.69592, W 124.14245, Fig. 2) is the northern-most site, located just south of the rocks jutting out of the point at the south end of Crescent Beach. The site is comprised of a large, gently sloping bench (approx. 100 m wide) and a series of three smaller out-cropping benches separated by rocky trenches and cobble beds. Sampling was conducted on the larger bench and the three smaller benches.

False Klamath Cove (N 41.59377, W 124. 10773, Fig. 3) is the southern-most site in the national park. It is located about 5 miles north of the current Klamath River mouth. The intertidal site at False Klamath Cove is peninsula-like with ocean on both sides, and a sea stack (approx. 75 m tall and 100 m wide) at the seaward end. It is a gently sloping field of boulders and small rock benches. Sampling was restricted to large sedentary boulders and small rocky benches.

Damnation Creek (N 41.65249, 124.12784, Fig. 4) is 6.5 kilometers north of False Klamath Cove and 5 kilometers south of Enderts Beach Cove. It is an extensive rocky bench cut by channels, but also has a few large sedentary boulders at its seaward edge. The landward edge of the bench has an accumulation of smooth cobble. The site is near the mouth of Damnation Creek, but monitoring plots were established on either side of the creek’s outflow, far enough away to avoid brackish water input (salinity was checked in tide pools close to the plots).

Figure 1 Map of northern Redwood National and State Parks showing locations of False Klamath Cove (low center), Enderts Beach Cove (upper center), and Damnation Creek (approximately half-way between the other two sites). This is a modification of the Redwood National and State Parks Map available from the national parks website: www.nps.gov/redw/pphtml/maps.html.

Figure 2 Enderts Beach Cove is a rocky bench cut by channels. It is the northernmost rocky intertidal bench in Redwood National and State Parks, located about five miles south of Crescent City.

Figure 3 False Klamath Cove is a field of giant sedentary boulders and rocky benches with varying amounts of coarse sand and cobble settled between boulders. The site is about 10 miles south of Enderts Beach Cove and 5 miles north of the mouth of the Klamath River.

Figure 4 Damnation Creek is a series of rocky benches cut by channels with some large boulders and large cobble near the high tide limit. The site is about 5 miles south of Enderts Beach Cove and 10 miles north of the mouth of the Klamath River.

Survey Methods

To determine if there have been significant increases or decreases in the abundance and diversity of sessile species/groups present in the high intertidal of False Klamath Cove and Enderts Beach Cove, the percent cover of sessile organisms (in permanent "photo plots") was compared over short- (1975 vs. 1976) and long term (1975 vs. 2005 and 1976 vs. 2005). Seasonality can have profound effects on percent cover of sessile species (Raimondi et al. 1999), so comparisons were made on data collected in mid summer of each year (as close to the same dates as tides and historical sample availability would permit). Mid summer data were used because Boyd and DeMartini (1977) found that the algal communities at these two sites reached maximum diversity in July.

Historical Plots

Boyd and DeMartini photographed three high intertidal photo plots at Enderts Beach Cove on July 22, 1975 and June 13 1976. At False Klamath Cove, they photographed 6 high intertidal plots on July 21, 1975 and June 11, 1976. Percent cover in these plots was predominantly bare rock, barnacles (*Balanus glandula/Chthamalus dalli*), *Pelvetiopsis limitata*, *Mastocarpus* sporophyte, and *Porphyra* spp. (I did not attempt to distinguish between *Porphyra* species for this study; I will refer to members of this genus as "*Porphyra* spp." throughout). Historical plots had lettered plastic strip markers (attached with Z-Spar marine epoxy) in the center of each permanent plot. Unfortunately these markers did not persist, and I was not able to relocate the exact plots used by Boyd and DeMartini. Hence recent plots are not re-assessments of the same historical plots.

I scored historical photographs for percent cover digitally (see "Photo Plot Scoring" below for methods). Considerable preparation was necessary to digitize and unify the scale of photographs taken by Boyd and DeMartini (1977). Historic photos were originally developed on slide film. I digitized these slides on an Epson slide scanner. Boyd and DeMartini (1977) did not use quadrats or a photo framer to standardize the size of monitoring plots. I standardized the scale of their photos such that monthly replicates of a plot were of the same scale and comparable with one another. This was done by scaling the letters on the plot labels to a metric grid in Adobe Photoshop, then adjusting and cropping the picture accordingly. Their photographic replicates varied in scale from about 40 x 60 cm to 20 x 30 cm. These plots were scored for percent cover of sessile taxa for comparison with percent cover for these same taxa in recent (2004/2005) photo plots.

Recent Plots

Recent photo plots were located in very close proximity to historical photo plots, as determined by historical maps and site overview photos. They are not replicates of the historical plots, which could not be relocated due to marker loss. Recent plots were randomly selected within the high intertidal zone (characterized by prevalence of the same species that Boyd and DeMartini (1977) found). I photographed 34 plots at Enderts Beach Cove on June 21, 2005, and 30 plots at False Klamath Cove on June 20, 2005. This number of replicates was necessary to exceed 70% statistical power for most taxonomic comparisons. These plots are meant to represent to high intertidal community at large, to facilitate comparison with historical plots, because spatial replication was not possible. Recent plots were photographed with an Olympus 560 digital camera mounted on a 50 x 75 cm PVC photo framer (Fig. 5), to ensure equal scale among plots. Digital photographs were scored for percent cover in the laboratory (see below).

Figure 5 PVC photo framer for photographing permanent 50 x 75 cm plots. A camera (not shown here) is mounted to the top brackets to ensure accurate replicate size. Three corners of the framer's base are aligned with three stainless steel bolts that are permanently fixed in the rock. One of the three bolts is notched with the plot number, and indicates the orientation of the plot.

Photo Plot Scoring

I scored all photos for percent cover of sessile species using a rectangular grid (10 x 10 units) of one-hundred evenly-spaced points created on an LCD computer monitor using Adobe Photoshop. This grid was overlaid on the digital photos, and was switched on and off to determine what taxon was below each point. Different layers of algae were not scored separately, so the total percent cover was constrained to 100%. The top-most layer that was attached to the substrate (not an obvious epibiont) was always scored. Limpets, chitons, and sea stars were scored, but for other motile invertebrates, whatever was beneath the motile species was scored if possible; otherwise, the point was scored as “unidentified”. This photo plot scoring technique was adopted from the Multi- Agency Rocky Intertidal Network (MARINe) monitoring group (Engle 2005). Data were entered into Microsoft Excel for organization and descriptive statistics. NCSS was used for statistical analysis.

Biological Comparisons

The species used for short- and long term comparison of abundance include: *A. elegantissima,* barnacles (*C. dalli* and *B. glandula*), *Endocladia muricata, Fucus gardneri*, limpets, *Mastocarpus* spp. *(jardinii* and *papillatus), Mastocarpus* sporophyte, *Mazzaella parksii, Mytilus californianus, P. limitata*, *Porphyra* spp., and rock (Tables 1A and 1B). Three other species (*Ulva californica*, *Semibalanus cariosus*, and *Cladophora columbiana*) were present in recent plots, but not included in the analysis. Their occurrence was rare and their percent cover was never higher than 5% in any plot. The area sampled in the recent survey was far greater than that of the historical plots, so it is likely that these species were found in recent plots, despite their relative rarity, due to the increased sampling area. Boyd and DeMartini (1977) did record *Ulva* sp. and *C. columbiana* in their inventory lists for these sites, but no barnacles were included on the list. It is unknown if *S. cariosus* was absent at these sites in Boyd and DeMartini’s study, or if it was simply overlooked.

One-sample t-tests were used to compare recent (2005) percent cover values to mean percent cover values (as the null hypothesis value: H_o) from historical photographs (Tables 1A and1B). Historical means were used as the value for the null hypothesis because sample sizes (plots) in Boyd and DeMartini (1977) were too low to meet 70% statistical power in two-sample t-tests. Recent data were compared to both historical years (1975 and 1976) separately. When percent cover data could not be transformed to meet the normality assumption, results from Wilcoxon signed-rank tests were reported instead.

Short term changes in percent cover (1975 vs. 1976) were compared using a paired t-test, because historical plots were exact replicates of one another (Zar 1999). For each species compared, the null hypothesis states that the difference in percent cover between years was zero. Significance was assessed at alpha = 0.05 (Table 2).

To assess the possibility that changes in relative abundance were related to biogeography, reproductive strategy, or successional level, I assigned each sessile species to categories based on published information (Tables 3A and 3B). To test for biogeographic trends, species were categorized based on their published range relative to the study sites. Range categories are northern (N) for species whose distribution was Cape Mendocino and north. Species whose distribution extended from central California to localities north of the Oregon border were considered central (C). Southern (S) species were considered to be those with ranges extending from below the Oregon border southward to localities south of central California. Range descriptions from Morris et al. (1980) were used for invertebrates. Algal range distributions were referenced from Abbott and Hollenberg (1987).

Reproductive categories for invertebrates are defined as (1) brooder/short distance disperser, (2) larvae less than 10 days in plankton or dispersal range of 100’s of meters for algae, (3) larvae more than 10 days in plankton for invertebrates (invertebrate categories from Sagarin et al. 1999). Little is known about the dispersal range of the algae in this study. Categories are based on reproductive method, spore morphology, and growth habit. (Shaughnessy pers. comm. 2005).

Successional categories were based on the amount of time required for each species to establish in cleared space after complete removal. Factors affecting recovery in succession studies are varied and complex (Farrell 1991, Berlow 1997, Kim 1997, Wootton 2002, Petraitis et al. 2003). Values here are based on the relative amount of time it took for each species to recover from complete removal. Early successional organisms (E) are considered to be the first colonizers that establish within one year of initial disturbance. Intermediate level (I) organisms are considered to be those that re-establish within one to three years after disturbance. Late successional organisms (L) are those that establish late in the successional regime and persist under relatively stable conditions. Vesco and Gillard (1980), Kinetics (1991), Scrosati (1998), Raimondi et al. (1999), and McKindsey and Bourget (2001) were consulted for deciding upon successional ranking.

Seasonal Variation

Long term changes in the magnitude of seasonal variation in sessile species were assessed from historical and recent photo plots sampled approximately every two months. Historical plots were photographed monthly by Boyd and DeMartini (see “Historical Plots” above) at False Klamath Cove and bi-monthly at Enderts Beach Cove from September 1974 to June 1976. (see Appendix A for actual sampling days). Recent photo plots are not replicates of historical plots. Rather, they were set up to specifically target certain sessile groups/taxa. The recent monitoring plots used for this comparison target barnacle (*C. dalli* and *B. glandula*) and rockweed *P. limitata* populations. They also indicate levels of seasonal variance in associated sessile taxa and in the percent cover of rock (bare space). Comparisons of seasonal variation are restricted to barnacles, rockweed (False Klamath Cove only), *Mastocarpus* sporophyte, and rock because these cover types were spatially dominant in the high intertidal during both time periods. Historical and recent monitoring photos were located in close proximity to one another as determined from historical maps and overview photographs.

Protocols for establishment and monitoring of recent plots were adopted from the Multi-Agency Rocky Intertidal Network monitoring group (Engle 2005). Recent photo plots were marked with 3/8 x 4 inch stainless bolts in three corners of a 50 x 75 cm rectangular plot. The bolt in the upper left corner had the plot number etched into the top. Plots were relocated at each sampling event with the aid of plot markers, plot to plot direction and distance measurements, site maps, and site photographs (Appendix B). Plots were photographed bi-monthly with an Olympus 560 digital camera mounted on a PVC photo framer (Fig. 5). The base of the photo framer was a 50 x 75 cm quadrat that was aligned with the three marker bolts to assure accurate replication of photos. Plot sketches were also made in the field to aid with identification of sessile taxa in photo analysis.

Historical and recent photos were digitally analyzed for percent cover of sessile organisms (see above for photo plot analysis protocol). From this data, I have calculated the mean percent cover and coefficient of variation for each taxa occurring in the photo plots (Table 4). These values were calculated for each plot-year separately so that they reflect the mean, variance, and coefficient of variation of a species in a single plot through five sampling events (= 1 year of sampling).

To test the hypothesis that the magnitude of seasonal variation had changed since the mid 1970's, two-sample t-tests were used to determine if coefficients of variation (as a measure of seasonal variation in sessile taxa) were significantly different among years (Table 4). The coefficient of variation is a measure of variability relative to the mean of the data set. Variance is a similar measure, but it is strongly affected by abundance. The coefficient of variation allows me to compare seasonal variation in plots despite significantly different means (Zar 1999). Data were log-transformed if the normality assumption was not met. For comparisons where equal variance was rejected, results from the Aspin-Welch Unequal-Variance test are reported

Physical Factors

Unfortunately, there are no sedimentation records for the small tributaries emptying directly into the study sites, such as Wilson Creek (at False Klamath Cove) and Nickle Creek (at Enderts Beach Cove), so inputs from these sources are speculative based upon the well-studied Redwood Creek watershed. Sedimentation data from the mouth of the Klamath River (less than 5 miles/8km south of False Klamath Cove) only goes back to the fall of 2004. Lack of long term sediment data makes it difficult to consider the impact of output from the Klamath River on nearby rocky intertidal areas, but freshwater input, nutrients, and sedimentation from this river is likely to have significant impacts, an issue which merits further investigation, but is not discussed here.

The mouth of Redwood Creek is about 15 miles (25 km) south of False Klamath Cove, so output from this river may not impact the study sites as much as output from the Klamath River, but sediments from Redwood Creek are known to travel up to 25 km/day when northward currents are strong, usually in late fall/early winter (Carlson and Harden 1975, Ricks 1985). Redwood Creek is very well studied, and there are substantial data on flow and sedimentation between the time periods in this study. It is the only watershed in close proximity to the study sites that has been continuously monitored. Yearly sediment load (suspended sediment and bedload) and flow data (in cubic feet per second “cfs”) from 1954 to 2003 are presented from Redwood Creek (Figs. 6 A-D). Measurements were recorded at a gauging station in Redwood Creek, 3.7 miles (6.15 km) upstream from its mouth. Data are from the Humboldt County Hydrology and United States Geologic Service, Arcata Ca. Here, Redwood Creek is discussed as both a source of sediment and drift logs, and as a model for how other watersheds may have been affected by terrestrial activities over the past 50 years.

Local near shore ocean temperature data collected at the end of the Coast Guard Pier in Crescent City Harbor (41°44.7´N, 124°11.8´W) were used to compare long term changes in the maximum, mean, and minimum annual water temperatures between 1955 and 2005 (Fig. 7). These data were also used to determine if there have been significant changes in water temperature between the periods preceding and including the two study periods (Fig. 7). Monthly mean and maximum values (from daily measurements) were compared for the 15 years preceding each study, such that average (or maximum) water temperatures recorded in the month of January from 1961 to 1976 were compared with the average (or maximum) water temperatures measured in the month of January from 1990 to 2005. Mean and maximum values for June and October were compared in the same manner (Fig. 8). Data were assessed using a two-sample t-test (n = 15). Daily near shore ocean temperature data were compiled by the Shore Station Project at Scripps Institute of Oceanography. Historical data (1933-2000) are accessible at ftp://ccsweb1.ucsd.edu/shore/old_data/combined_years/. Recent near shore temperature data are available from the National Oceanic and Atmospheric Administration/National Ocean Service at: http://140.90.121.76/data_options.shtml?stn=9419750+Crescent+City,+CA.

Air temperature and precipitation measurements from Crescent City weather station (41°48.0´N, 124°13´W, Co-op ID 042147) were used to generate yearly means of maximum, minimum, and mean daily air temperature measurements from 1961 to 2005 (Figs. 9and10). Data are available from the National Climatic Data Center at http://cdo.ncdc.noaa.gov/CDO/cdo. The monthly mean and maximum air temperature measurements and monthly total precipitation measurements were compared to determine if long term shifts had occurred in these environmental factors. Air temperature and precipitation measurements for January, June, and October of the 15 years preceding and including each study period were compared using two-sample t-tests.

Potential changes in the strength of El Niño- Southern Oscillation (ENSO) events were evaluated using the Southern Oscillation Index (SOI, Figs. 11A and11B). This index is a measurement of fluctuations in the air pressure gradient between Tahiti and Darwin, NT, Australia. Negative values of the SOI generally indicate El Niño episodes.

These episodes are usually accompanied by a sustained increase in sea surface temperatures in the eastern Pacific Ocean, and a decrease in the strength of the Pacific Trade Winds. Positive values of the SOI, popularly known as La Niña episodes, are associated with cooler sea surface temperatures in the eastern Pacific (Australian Bureau of Meteorology http://www.bom.gov.au/climate/glossary/soi.shtml). Monthly SOI measurements from the 10 years preceding both study periods (Figs. 11A and11B) are compared using a paired T-test to determine if there are differences in the ENSO regime between study periods.

Upwelling indices from Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/products) were used to evaluate long term differences in the magnitude of upwelling between study periods (Figs. 12A and12B). These upwelling indices are calculated from Ekman’s theory of wind-driven mass transport of sea surface water. On the California coast, warm, nutrient poor surface water (50-100 m depth) is transported offshore, and is replaced by water that upwells from depths greater than 50-100 meters. Upwelled water is typically cooler, and more nutrient rich. Positive upwelling values are indicative of the amount of water being upwelled, while negative values imply downwelling, the shoreward transport of surface water accompanied by downward displacement of water (www.pfeg.noaa.gov). T-tests were used to compare the annual maximum upwelling and downwelling strengths in both of the study periods plus three years preceding each study period. This time span was used because it includes the lifespan of most intertidal organisms. Longer time spans could include upwelling events that occurred too early to have a marked effect on the current community, and could be misleading. Shorter spans could underestimate nutrient contributions from earlier events whose effects are sustained in the present community.

Species Interactions

Seasonal data from recent monitoring plots were used to determine if the percent cover of sessile taxa co-vary with variation in the abundance of associated motile invertebrates. Sessile organisms monitored included: mussels (*M. californianus*), barnacles (*B. glandula/C. dalli*), and three algal species (*E. muricata*, *P. limitata*, and *F. gardneri*). These five species were chosen for monitoring because they are conspicuous, bed-forming, abundant, and ecologically important species. Protocols for plot establishment and assessment were the same as those described above (“Seasonal Variation” paragraph two). Surveys were conducted at Enderts Beach Cove, False Klamath Cove, and Damnation Creek. Unfortunately, *Fucus* was not dense and continuous enough at Enderts Beach Cove, nor was there dense enough *P. limitata* at Damnation Creek when the study was initiated, to merit plot establishment for those species at those sites. Otherwise, each species type was monitored in five replicate plots at each site (Table 1).

Table 1 This table shows the type of photo-plot and number of replicates at each site. There was not enough *P. limitata* present (NP=not present) at Damnation Creek for photo plots, nor was there enough *Fucus* at Enderts Beach Cove when we set up the study.

Site	Mussels	Barnacles	*Pelvetiopsis limitata*	*Endocladia muricata*	*Fucus gardneri*
Damnation Creek	5 plots	5 plots	NP	5 plots	5 plots
False Klamath Cove	5 plots	5 plots	5 plots	5 plots	5 plots
Enderts Beach Cove	5 plots	5 plots	5 plots	5 plots	NP

All plots were sampled and photographed every two to three months from June 2004 though June 2005 (see Appendix A for actual dates). Usually sampling was done for all three sites within six days. In January 2005, Damnation Creek was sampled two weeks later than the other two sites because of frozen rain and road closures on the scheduled sampling day that prevented travel to the site.

In addition to percent cover measurements; motile invertebrates were counted within each photo plot area. With the exception of burrowing organisms and amphipods, all motile invertebrates were counted in the field within a 50 x 75 cm PVC quadrat. The quadrat was aligned with the three plot marker bolts to ensure accurate replication. Algal over-story was gently moved so that hidden invertebrates could be located. For select species, such as *Tegula funebralis*, *Nucella ostrina*, the length of the shell (measured at its longest axis) was recorded to determine the size distribution of individuals present. This was done for the first 10 individuals recovered from each plot only (unless fewer were present). In mussel beds, tweezers and forceps were used to remove *N. ostrina*, *T. funebralis*, and other species that were partially hidden in between mussels. Extremely abundant motile invertebrates, such as limpets (smaller than 15 mm) and littorines (*Littorina* spp.), were sub-sampled using a smaller quadrat. Limpets larger than 15 mm were counted in the entire 50 x 75 cm plot. Small (0-15 cm) limpets were counted in two size categories (< 5 mm and 5-15 cm) within three 20 x 20 cm quadrats laid diagonally through the larger quadrat. Limpets occurring on rocky or other substrata (including barnacle tests) were recorded separately from those occurring on mussel valves.

Littorines were counted in three 10 x 10 cm quadrats placed diagonally through the larger quadrat. Data were entered into a Microsoft Excel spreadsheet for analysis.

To test the hypothesis that variation in sessile species is correlated with changes in the abundance or size distribution of associated motile invertebrates, it was necessary to first determine which species are positively correlated with the each sessile species. I ran two correlation analyses on percent cover data and motile invertebrate counts (with all three sites combined). Data from June of 2004 and June 2005 were run separately to ensure that associations are consistent between years. The correlation tables (Table 2) show Spearman rank values, because data were non-normal for most taxa. However equal variance assumptions were met. Results in the correlation table for June 2004 are generally consistent with results from 2005, indicating that associations continued from one year to the next. I consider Spearman correlation values of 0.3 and greater to indicate an association. In both years, *T. funebralis* was associated with the rock weed *F. gardneri*, small limpets (less than 5 mm) with *E. muricata*, limpets (5-15 mm) with *P. limitata*, *N. ostrina* with mussels and *Pollicipes polymerus*, and littorines with barnacles and rock. Both limpet size classes were counted on mussels separately, so their association is a given. *N. ostrina*, and both limpet size classes on mussel classes are positively associated with *P. polymerus*, but these barnacles are only found in mussel plots, so it is difficult to determine if this is a direct or indirect association. The percent cover of *P. polymerus* is low in all plots, so further correlative analysis is not included in this report. Littorines were positively correlated with *P. limitata* in 2004, but not the following year. The association between *N. ostrina* and *P. polymerus* was still present in

2005, but it was weaker than in the previous year. The association between small limpets (< 5 mm) and the rock class was weaker in 2004 than in 2005. I ran a linear regression on each correlated pair to test for positive relationships. In each case the slope of the linear relationship was positive and significantly greater than zero.

Table 2 Correlation matrix shows associations between motile invertebrates and sessile taxa. I consider Spearman correlation values of 0.3 and greater to indicate an association. These associations are generally consistent between the matrices for (A) June 2004 and (B) June 2005.

A

Motile Invertebrate	***Fucus gardneri***	***Endocladia muricata***	***Pelvetiopsis limitata***	**Mussel**	**Barnacles**	***Pollicipes polymerus***	**Rock**
Nucella ostrina	0.073	-0.268	0.057	0.454*	-0.276	0.398*	-0.528
Tegula funebralis	0.387*	-0.018	-0.013	0.113	-0.387	-0.001	-0.438
Limpets < 5 mm	0.031	0.517*	0.123	-0.475	0.046	-0.143	0.266
Limpets < 5 mm on mussel	-0.327	-0.458	-0.060	0.667*	-0.137	0.520*	-0.332
Limpets 5-15 mm	0.156	0.030	0.308*	-0.397	0.252	-0.225	0.377*
Limpets 5-15 mm on mussel	-0.317	-0.461	-0.198	0.731*	-0.142	0.409*	-0.365
Littorina spp.	0.106	-0.104	0.338*	-0.431	0.571*	-0.342	0.502*

B

Motile Invertebrate	***Fucus gardneri***	***Endocladia muricata***	***Pelvetiopsis limitata***	**Mussel**	**Barnacles**	***Pollicipes polymerus***	**Rock**
Nucella ostrina	-0.012	-0.151	-0.275	0.513*	-0.162	0.268	-0.377
Tegula funebralis	0.428*	-0.170	-0.304	0.088	-0.343	-0.133	-0.106
Limpets < 5 mm	0.132	0.644*	0.135	-0.633	0.269	-0.345	0.450*
Limpets < 5 mm on mussel	-0.311	-0.396	-0.210	0.888*	-0.348	0.593*	-0.648
Limpets 5-15 mm	0.150	0.027	0.521*	-0.528	0.701*	-0.330	0.429*
Limpets 5-15 mm on mussel	-0.310	-0.402	-0.208	0.888*	-0.354	0.469*	-0.593
Littorina spp.	0.133	-0.015	-0.026	-0.302	0.519*	-0.207	0.516*

*Strong positive correlations

To determine whether physical factors or species associations best described variation in the percent cover of sessile organisms, I used variable selection routines (All Possible, Forward Stepwise and Backward Stepwise). Dependent variables used included the abundance and size distribution of associated motile invertebrates, near shore ocean temperature (measured at Crescent City Harbor), upwelling indices, precipitation, wave height, or air temperature. A multiple regression was run on each set of variables selected by the different selection routines, to determine the best variables, and to check for multi-colinearity.

RESULTS

Long Term Comparison

Historically, the intertidal community at Enderts Beach Cove was characterized by higher percent cover of *Mastocarpus* sporophyte, *Porphyra* spp., and *A. elegantissima*. Mean percent cover of *Mastocarpus* sporophyte was 15.33% in 1975 and 11.50% in 1976 vs. 6.44% in 2005. (1975: p<<0.001, 1976: p<<0.001). Mean percent cover of *Porphyra* spp. was 42.33% in 1975 and 39% in 1976 vs. 3.53% in 2005 (1975 and 1976: p<<0.001). Percent cover of *A. elegantissima* reduced from 1.33% in 1975 and 0.75% in 1976 to 0.53% in 2005 (both 1975 and 1976: p<<0.001). Percent cover of bare rock was higher in plots measured in 1975 (26%) and 1976 (36.25%) than in 2005 (21.94%), but this trend was only significant in 1976 (p<<0.001, 1975: p=0.180). Percent cover of *P. limitata* at Enderts Beach Cove was significantly higher in 2005 (39.88%) than in historical plots where it was absent both years (1975 and 1976: p <<0.001). *E. muricata* percent cover was 2.12% in 2005, but this alga was not present in plots in both 1975 and 1976 (1975 and 1976: p<<0.001). Similarly, *M. parksii* reached a mean percent cover of 6.91% in 2005, but was absent from plots in both 1975 and 1976 (1975 and 1976: p<<0.001). Mean percent cover of *M. californianus* was 1.94% in 2005 but absent in 1975 and 1976 assessments (1975 and 1976: p=0.003). Barnacle mean percent coverage was also higher in 2005 plots (12.70%), but this trend was only significant when compared with 1975's mean of 5% (p=0.003). In 1976, mean barnacle percent cover was 10.25% (p=0.316 Table 3A).

The high intertidal zone at False Klamath Cove had changes in the sessile community similar to those at Enderts Beach Cove (Table 3B), except that *Porphyra* spp. was absent from recent and historical monitoring plots. The mean percent cover of bare rock was significantly higher in 1975 (42.67%) and 1976 (42.2%) than in 2005 (11.9%, p<<0.001 both comparisons). Mean percent cover of barnacles was also significantly higher in both 1975 (33%, p<<0.001) and 1976 (27.2%, p<<0.001) than in 2005 (17.9%). Recent plots contained significantly higher percent cover of *F. gardneri, P. limitata, E. muricata*, *Mastocarpus* spp., *M. parksii,* and *M. californianus.* Mean percent cover of *F. gardneri* was 1.83% in recent plots, but absent in 1975 and 1976 (both years: p<<0.001). Mean percent cover of *P. limitata* was 40.97% in 2005 vs. 13.83% in 1975 and 21.2% in 1976 (1975: p<<0.001, 1976: p<<0.001). Average *E. muricata* percent cover was 2.53% in 2005, vs. 0.33% in 1975 and 0% in 1976 (1975: p<<0.001, 1976: p<<0.001). Mean percent cover of *Mastocarpus* spp. was 5.57% in 2005 vs. 0.17% in 1975 and 0% in 1976 (1975: p=0.167, 1976: p<<0.001). Percent cover of *M. parksii* reached an average of 3.17% in plots assessed in 2005, but this alga was absent from plots in both historical years (1975 and 1976: p=0.014). Mean percent cover of *M. californianus* was 6.5% in 2005 compared to 0.33% in 1975 and 0% in 1976 (1975: p=0.001, 1976: p<<0.001). The percent cover of *Mastocarpus* sporophyte did not change significantly in either comparison. In 2005, mean percent cover was 6.27% vs. 5.67% in 1975 and 7% in 1976 (1975: p=0.117, 1976: p=0.080).

Table 3 Mean percent cover values calculated from historical photographs (Boyd and DeMartini 1977) taken in July 1975 and June 1976 at (A) Enderts Beach Cove (3 plots) and (B) False Klamath Cove (6 plots). These values were used as the hypothesized percent cover value (H_o) in one-sample t-tests with percent cover data from photographs taken in June 2005 in close proximity to the historical plots. * significant at alpha = 0.05

A

Sessile taxa	2005 Mean	1975 Mean (H_o)	1975:2005 P	1976 Mean (H_o)	1976:2005 P
Pelvetiopsis limitata	39.9	0	<0.001*	0	<0.001*
Endocladia muricata	2.1	0	<0.001*	0	<0.001*
Mazzaella parksii	6.9	0	<0.001*	0	<0.001*
Porphyra spp.	3.5	42.3	<0.001*	39	<0.001*
Mastocarpus sporophyte	6.4	15.3	<0.001*	11.5	<0.001*
Anthopleura elegantissima	0.5	1.3	<0.001*	0.75	<0.001*
Mytilus californianus	1.9	0	0.003*	0	0.003*
Limpets	0.5	0	0.001*	0.75	0.038*
Barnacles	12.7	5	0.003*	10.25	0.316
Rock	21.9	26	0.180	36.25	<0.001*

B

Sessile taxa	2005 Mean	1975 Mean (Ho)	1975:2005 P	1976 Mean (Ho)	1976:2005 P
Fucus gardneri	1.8	0	<0.001*	0	<0.001*
Pelvetiopsis limitata	40.9	13.8	<0.001*	21.2	<0.001*
Endocladia muricata	2.5	0.3	<0.001*	0	<0.001*
Mastocarpus spp.	5.6	0.2	0.001*	0	<0.001*
Mazzaella parksii	3.2	0	0.014*	0	0.014*
Mastocarpus sporophyte	6.3	5.7	0.117	7	0.08
Mytilus californianus	6.5	0.3	0.001*	0	<0.001*
Barnacles	17.8	33	<0.001*	27.2	<0.001*
Rock	11.9	42.7	<0.001*	42.2	<0.001*

Inter-Annual Comparison

There were no significant differences in the mean percent cover of *F. gardneri*, *Mastocarpus* sporophyte, *Mastocarpus* spp., *P. limitata, Porphyra* spp., *A. elegantissima,* barnacles, *M. californianus,* or rock measured in replicate plots compared between the summers of 1975 and 1976, indicating that inter-annual change in percent cover is minor compared to long term changes (Table 4). Inter-annual comparisons or percent cover at Enderts Beach Cove indicate that barnacles and *Porphyra* spp. both had low P-values in comparisons between 1975 and 1976, which indicates that these two species changed more, relative to other species, over the short term. In contrast, the inter-annual comparison of barnacle percent cover at False Klamath Cove showed greater stability, having a higher p-value. This result could be a due to differences in the *B. glandula* -to-*C. dalli* ratio between sites, or to actual differences in the magnitude of variation characteristic of the two sites. Unfortunately, it was not possible to accurately distinguish between *B. glandula* and *C. dalli* in photo plots where juveniles dominated.

Table 4 Mean percent cover values calculated from historical photographs (Boyd and DeMartini 1977) taken in July 1975 and June 1976 at Enderts Beach Cove (3 plots) and False Klamath Cove (6 plots). P-values indicate inter-annual differences in mean percent cover values (* significant at alpha = 0.05).

	Enderts Beach Cove					False Klamath Cove				
	1975		1976		1975:1976	1975		1976		1975:1976
Species	Mean	SD	Mean	SD	P-value	Mean	SD	Mean	SD	P-value
Fucus gardneri	0	0	1.67	1.53	0.193	0	0	0	0	-
Mastocarpus sporophyte	15.33	24.01	15	19.08	0.366	6.6	6.27	7	8.94	0.389
Mastocarpus spp.	0	0	0	0	-	0.2	0.45	0	0	0.375
Pelvetiopsis limitata	0	0	0	0	-	15.2	15.51	21.2	19.83	0.252
Porphyra spp.	42.33	37.81	52	34.77	0.151	0	0	0	0	-
Anthopleura elegantissima	1.33	2.31	1	1	0.655	0	0	1	2.24	0.377
Barnacles	5	7.81	0.67	1.15	0.183	29.4	12.5	27.2	7.66	0.714
Mytilus californianus	0	0	0	0	-	0.4	0.89	0	0	0.375
Rock	26	26.96	29.33	20.82	0.728	44.6	13.13	42.2	9.93	0.830

Categorical Changes

The published geographical range of species was not correlated with changes in percent cover of sessile organisms between the two study periods. Most of the species in this study are categorized as central (Table 5). The two northern species (*M. parksii and C. dalli)* increased significantly in recent percent cover measurements at Enderts Beach Cove. At False Klamath Cove, *M. parksii* increased in percent cover, but barnacles declined in 2005 relative to both 1975 and 1976 levels. An increase in percent cover of northern species is contrary to what would be expected if warmer ocean temperatures alone were driving community change.

Changes in relative percent cover do not seem to be linked to dispersal ability. An equal number of short and long distance dispersers increased in percent cover over the comparison period at Enderts Beach Cove. Species that declined at Enderts Beach Cove belonged to all three dispersal categories. At False Klamath Cove, increases in percent cover are associated with short distance dispersers, while only long distance dispersers declined. Mussels, the only species in the intermediate dispersal category, increased in percent cover over the comparison period (Table 5). These changes are inconsistent with what would be expected if large scale physical transport processes (possibly associated with upwelling intensity) had been altered at these sites.

Long term changes did occur disproportionately in among successional categories. All taxa in the late successional category reached a higher percent cover in the 2005 assessment, a trend that is consistent at both study sites. Early and intermediate successional species declined consistently in recent plots compared to historical plots, at Enderts Beach Cove (Table 5A). At False Klamath Cove, early successional organisms declined between historical and recent assessments, but percent cover of *Mastocarpus* sporophyte (intermediate succession) did not change significantly over the study period (Table 3B). Changes in barnacle percent cover show opposite trends at the two sites.

Percent cover changes in invertebrate species were inconsistent between sites (Tables 5). At Enderts Beach Cove, three algal species increased, while the other two declined. Similarly, one invertebrate species declined while the others increased. At False Klamath Cove, most algae and mussels increased while barnacles decreased in percent cover (Table 5). These changes in the biological community are not supportive of changes in physical processes that would alter nutrient availability and alter the amount of algal biomass.

Table 5 Categorical rankings and mean percent cover measurements for the species compared between Boyd and DeMartini (1977) and the present study. (A) Enderts Beach Cove (3 plots), (B) False Klamath Cove (6 plots). Range categories are northern (N: Cape Mendocino and north), central (C: central California to localities north of the Oregon border), and southern (S: below the Oregon border southward to localities south of Point Conception. Dispersal categories for invertebrates are defined as (1) brooder/short distance disperser, (2) dispersal range ~100-200 m or <10 days in plankton, and (3) >200 m or > 10 days in plankton. Early successional organisms (E) establish within one year of initial disturbance. Intermediate level (I) re-establish within one to three years after disturbance. Late successional organisms (L) are those that establish later than three years after disturbance (* differences significant at alpha = 0.05).

A

Species	Range	Dispersal ability	Succession Category	Change	Sig.	Historical Mean		Recent Mean
						1975	1976	2005
Pelvetiopsis limitata	C	1	L	+	*	0	0	39.88
Endocladia muricata	C	1	L	+	*	0	0	2.12
Mazzaella parksii	N	1	L	+	*	0	0	6.91
Porphyra spp.	C	2	E	-	*	42.33	39	3.53
Mastocarpus sporophyte	C	1	I	-	*	15.33	11.5	6.44
Anthopleura elegantissima	C	3	I	-	*	1.33	0.75	0.53
Mytilus californianus	C	2	L	+	*	0	0	1.94
Chthamalus dalli	N	3	E	+	#	5	10.25	12.71
Balanus glandula	C	3	L	+	#	5	10.25	12.71
Rock (free space)	-	-	E	-	%	26	36.25	21.94

B

Species	Range	Dispersal ability	Succession Category	Change	Sig.	Historical Mean		Recent Mean
						1975	1976	2005
Fucus gardneri	C	1	L	+	*	0	0	1.83
Pelvetiopsis limitata	C	1	L	+	*	13.83	21.2	40.97
Endocladia muricata	C	1	L	+	*	0	0	2.53
Mazzaella parksii	N	1	L	+	*	0	0	3.17
Mastocarpus spp.	C	1	I	+	*	0.17	0	5.57
Mastocarpus sporophyte	C	1	I	0		5.7	7	6.27
Mytilus californianus	C	2	L	+	*	0.3	0	6.5
Chthamalus dalli	N	3	E	-	*	33	27.2	17.8
Balanus glandula	C	3	L	-	*	29.4	27.2	17.8
Rock (free space)	-	-	E	-	*	42.67	42.2	11.9

Change in percent cover significantly different in 1975:2005 comparisons, but not in 1976:2005.

% Change in percent cover significantly different in 1976:2005 comparisons, but not in 1975:2005.

Seasonal Variation

At Enderts Beach Cove, seasonal variation (coefficient of variation) in percent cover was higher historically for bare rock, barnacles and *Mastocarpus* sporophyte (Table 6A). This difference was significant for comparisons of barnacles in 1974/75:2004/05 and 1975/76:2004/05 comparisons (1974/75: p=0.046, 1975/76: p=0.009). Variation in the percent cover of bare rock were significantly different in 1974/75 versus 2004/05 (p=0.032), but not when 1975/76 was compared to 2004/05.

Contrary to the results at Enderts Beach Cove, seasonal variation (coefficient of variation) in percent cover at False Klamath Cove was significantly higher in the present study for barnacles (1974/75: p=0.017, 1975/76: p=0.001) and bare rock (1974/75: and 1975/76: p<0.001). Percent cover of *Mastocarpus* sporophyte was more variable in the recent assessment as well, but this trend was not significant in comparisons with either historical year (1974/75: p=0.122, 1975/76: p=0.290. Seasonal variation in *P. limitata* was higher historically, but this trend was only significant in 1976 (p=0.014, Table 6B).

Table 6 Plot means, and coefficient of variation (C.V.) values from permanent monitoring plots at (A) Enderts Beach Cove and (B) False Klamath Cove. C.V. values reflect the magnitude of seasonal variation over one year. Plots assessed from 2004/2005 were not replicates of those sampled in 1974-1976, but were located in close proximity to historical plots within the same biological zone.

A

Year/Plot #	Barnacles		Rock		*Mastocarpus* sporophyte	
2004/2005	Mean	Coefficient of Variation	Mean	Coefficient of Variation	Mean	Coefficient of Variation
1	33.8	0.57	13	0.54	0.8	2.24
2	54.6	0.08	26.4	0.38	5.2	0.61
3	55.8	0.3	27	0.49	8	0.35
4	67.2	0.12	20.6	0.47	0.6	1.49
5	53	0.29	29.4	0.51	2	0.94
6	6	0.68	16.6	0.47	8.4	0.92
7	12.2	0.37	20	0.4	4.8	0.58
8	18.2	0.38	24	0.24	5.4	0.82
9	2.8	1.3	13.6	0.48	0.6	0.91
10	7	0.42	21.8	0.32	0.6	0.91
Site Mean	31.06	0.45	21.24	0.43	3.64	0.98
1974/1975						
1	3.25	1.21	46.25	0.49	13	0.96
2	3.8	0.58	65.2	0.58	2.4	1.25
3	13.2	1.09	39.6	0.65	17.8	0.99
Site Mean	6.75	0.96	50.35	0.57	11.07	1.07
1975/1976						
1	4.75	1.02	67.25	0.31	1	1.41
2	2	1.08	50.5	0.39	16.5	0.92
3	4.5	1.21	32.25	0.91	9.25	0.94
Site Mean	3.75	1.1	50	0.53	8.92	1.09

B

Year/Plot #	Barnacles		Rock		*Pelvetiopsis limitata*		*Mastocarpus* sporophyte	
2004/2005	Plot mean	Coefficient of Variation	Plot mean	Coefficient of Variation	Plot mean	Coefficient of Variation	Plot mean	Coefficient of Variation
1	62.2	0.5	30.4	0.97	0	0	0	0
2	57	0.71	38	1.07	0	0	1.4	0.39
3	67	0.35	32	0.74	0	0	3.2	0.81
4	63.4	0.61	35.6	1.07	0	0	0.4	2.24
5	59.8	0.58	33.6	1.01	0	0	4.8	0.5
6	10.2	0.53	5.4	0.38	67.6	0.16	9.2	0.54
7	10.6	0.55	8.2	1.16	71.4	0.15	1.4	1.48
8	24.4	0.19	5.2	0.79	65.4	0.12	3.6	0.72
9	18	0.44	12.2	0.51	66	0.16	1.8	0.72
10	16	0.37	5	0.55	68.4	0.1	4.6	0.63
Site Mean	38.86	0.48	20.56	0.82	67.76	0.14	3.38	0.89
1974/1975								
1	43	0.12	49.67	0.11	0	0	0	0
2	34	0.14	43.8	0.08	11.6	0.65	2	0.5
3	32.75	0.12	33	0.35	4	0.25	25.5	0.16
4	17.4	0.52	51.4	0.12	26.4	0.34	3.4	0.45
5	14	0.42	30.75	0.07	41.5	0.2	12.25	0.24
6	41	0.25	51	0.13	0.8	1.05	4.8	0.77
Site Mean	30.36	0.26	43.27	0.14	16.86	0.5	9.59	0.42
1975/1976								
1	41.33	0.15	40.33	0.21	0	0	0	0
2	38	0.29	29.67	0.19	10	0.24	1.25	1.01
3	25	0.3	43.25	0.34	29.75	0.35	25.67	0.13
4	18.25	0.24	39.5	0.1	36.75	0.14	4.75	0.47
5	32.5	0.23	61	0.07	3	0.24	1.25	0.29
6	24.8	0.05	43	0.06	20.8	0.54	10.4	1.01
Site Mean	29.98	0.21	42.79	0.16	20.06	0.3	8.66	0.58

Seasonal variation is inconsistent between the two sites and among years (Tables 5and6). In 2004/2005, the percent cover of rock was significantly more variable at False Klamath Cove (p=0.001), and *P. limitata* was significantly more variable at Enderts Beach Cove (p=0.043), but recent mean percent cover values for these species are not significantly different between sites in 2004/2005.

Historically, seasonal variation in all taxa is higher at Enderts Beach Cove, regardless of relative percent cover. This trend is significant for barnacle percent cover in both 1974/75 and 1975/76 (p=0.004 and p<0.001 respectively). Seasonal variation in rock and *Mastocarpus* sporophyte percent cover was also greater at Enderts Beach Cove, but these trends were only significant in 1974/75 (p<0.001 and 0.007 respectively). Percent cover values for *Mastocarpus* sporophyte and bare rock were only slightly higher at Enderts Beach Cove than at False Klamath Cove in historical plots, while Barnacle percent cover was considerably lower at Enderts Beach Cove than at False Klamath Cove. This could be an indication that disturbances were more frequent at Enderts Beach Cove historically, but this trend is not present in recent site: site comparisons.

Table 7 Table Results from two-sample t-tests comparing differences in seasonal variation (measured as the coefficient of variation) values between False Klamath Cove and Enderts Beach Cove. Plots compared were sampled in the same year. Alpha = 0.05*

Year	Barnacles	Rock	*Mastocarpus* sporophyte	*Pelvetiopsis limitata*
2004/05	0.290	0.001*	0.307	0.043*
1974/75	0.004*	<0.001*	0.007*	NA
1975/76	<0.001*	0.180	0.109	NA

Sediment and Flow in Redwood Creek

There have been significant decreases in both suspended sediment and bedload levels measured near the mouth of Redwood Creek from the mid 1970’s to the present. Suspended sediment levels (Fig. 6A) decreased at an average rate of 48356 cfs/yr. between 1971 and 2001 (p=0.005). Bedload (Fig. 6B) has decreased at the average rate of 9375 cfs/yr between 1974 and 1992 (p=0.036). Total sediment (combined bedload and suspended sediment) levels decreased at the average rate of 76420 cfs/yr between 1974 and 1992 (p=0.005). Reductions in sediment load are not coupled with reductions in flow, however. There have been no significant trends in total annual flow/day measurements (p=0.276, Fig. 6C) or total winter-spring flow/day measurements (p=0.081, Fig. 6D) at Redwood Creek between 1971 and 2003.

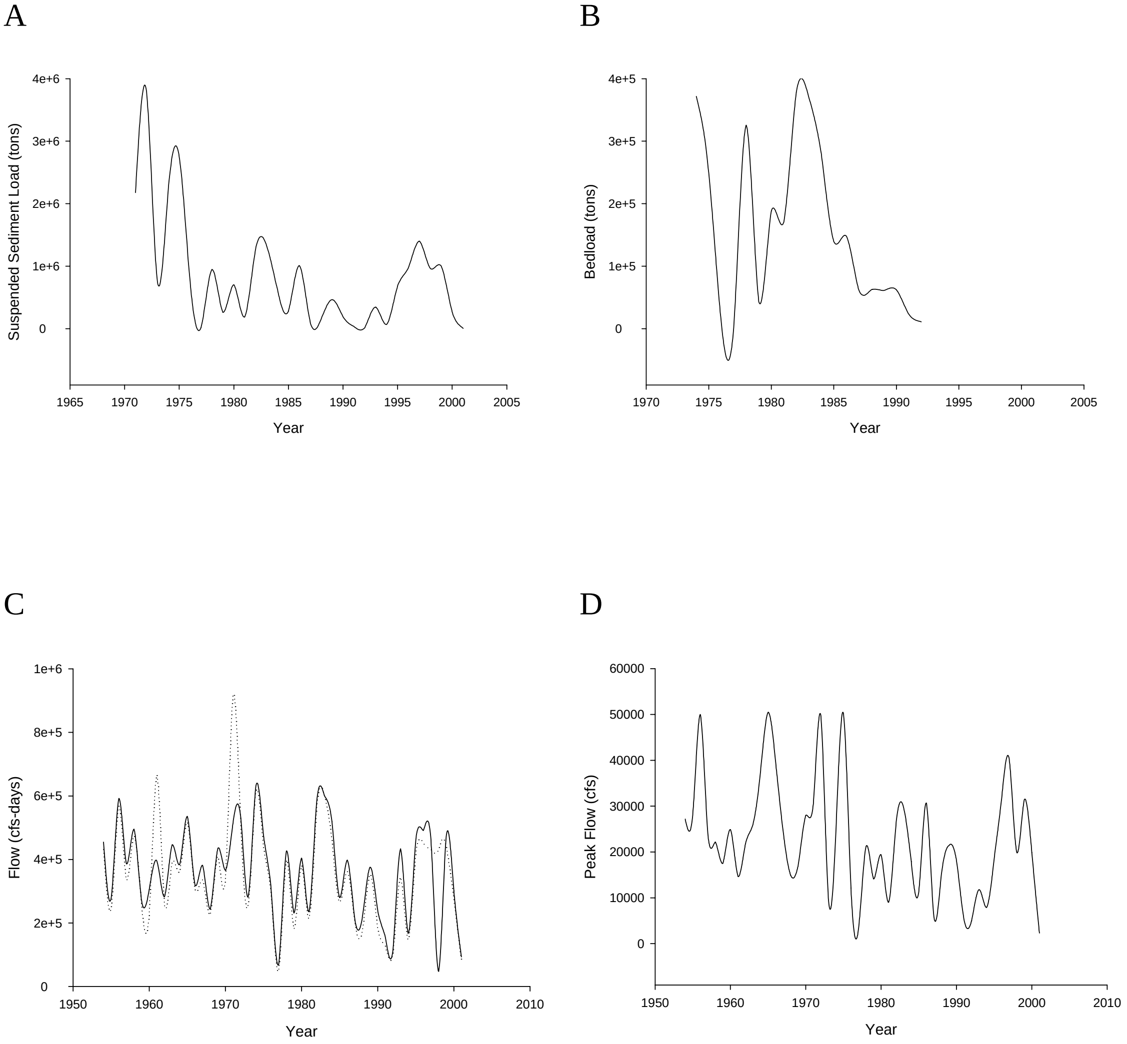


Figure 6 October to April from 1971 to 2001 by USGS, (B) Annual spring-winter bedload (tons) measured from October to April from 1974 to 1992 by USGS, (C) Total annual (dotted line), and total winter-spring (October to April, solid line) flow/day measurements (cfs-days), (D) Peak flow measurements (in cfs) from a gauging station 3.7 mi. (6.15 km) from the mouth of Redwood Creek. Maximum flow reached or exceeded 50,000 cfs in 1956, 1964, 1972, and 1975. All measurements were recorded at a USGS gauging station in Orick, Ca. approximately 3.7 mi. (6.15 km) from the mouth of the river.

Near Shore Ocean Temperature

Long term trends in the annual mean, minimum, or maximum near shore ocean temperatures from 1955 and 2005 are not apparent (Fig. 7). Results from t-tests comparing monthly mean and maximum near shore ocean temperatures measured in January of the 15 years prior to and including each study period, indicate that mean and maximum ocean temperatures were significantly warmer in measurements from 1990–2005 than in January 1961–1976 ($p_{\text{January mean}}<0.001$, $p_{\text{January max}}=0.039$). However, mean water temperatures measured in June and October of 1961–1976 were not significantly different than measurements from those months in 1990–2005 ($p_{\text{June}}=0.296$, $p_{\text{October}}=0.343$). Similarly, maximum temperature measurements from the same period were not significantly different ($p_{\text{June}}=0.202$, $p_{\text{October}}=0.228$). Differences in near shore ocean temperatures seem to be stronger in winter and early spring months (Fig. 8).

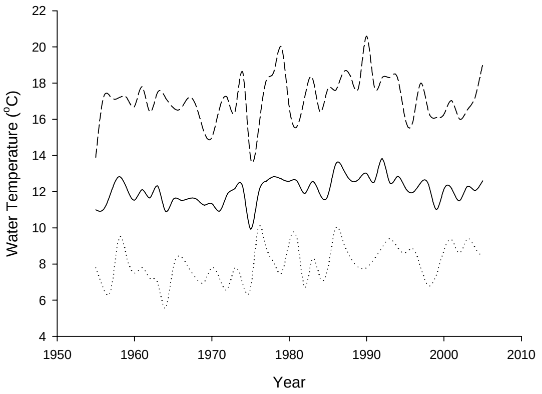


Figure 7 Plot of annual maximum, mean, and minimum near shore ocean temperature measured at Crescent City’s Coast Guard Pier (41°44.7´N, 124°11.8´W) from 1961 to 2005. Daily mean temperature data were compiled by the Shore Station Project at Scripps Institute of Oceanography (historical data 1933-2000). Recent near shore temperature data were downloaded from the National Oceanic and Atmospheric Administration/National Ocean Service (NOAA/NOS).

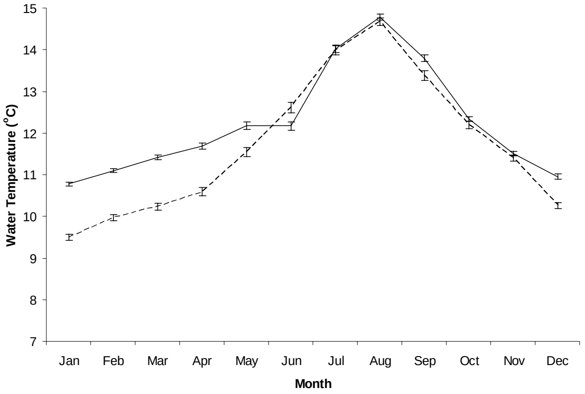


Figure 8 Plot of monthly mean near shore ocean temperature from the 15 years preceding and including each study period. Historical means were calculated from 1961 to 1976 (dotted line). Recent means were calculated from 1990 to 2005 (solid line). Temperature was measured at Crescent City's Coast Guard Pier (41°44.7´N, 124°11.8´W). Daily mean temperature data were compiled by the Shore Station Project at Scripps Institute of Oceanography (historical data, 1933-2000). Recent near shore temperature data are from the NOAA/NOS. According to a t-test, near shore ocean temperature was significantly warmer in January 1990 – 2005 ($p<0.001$), but there were no significant differences in water temperature measurements for June and October ($p=0.296$ and 0.343 respectively)

Air Temperature and Precipitation

Annual means of daily maximum, minimum, and mean air temperature measurements (Fig. 9) show numerous undulations, but no consistent increases or decreases in temperature between 1961 and 2005. Mean temperatures measured in January, June, and October for 1961 – 1976 were not significantly different from mean temperatures measured in those same months from 1990 to 2005 ($p_{January}=0.140$, $p_{June}=0.945$, $p_{October}=0.575$). Similarly, maximum temperatures measured in these months were not significantly different in comparisons between 1961–1976 and 1990–2005 ($p_{January}=0.922$, $p_{June}=0.132$, $p_{October}=0.467$).

Annual precipitation levels indicate no strong directional changes between 1961 and 2005, although undulations have occurred. Annual rainfall levels were similar in the two study periods (Fig. 10). Total monthly precipitation levels measured in January, June, and October 1961–1976 were not significantly different from precipitation levels measured in the same months in 1990–2005 according to two-sample t-tests ($p_{January}$=0.754, p_{June}=0.124, $p_{October}$=0.525)

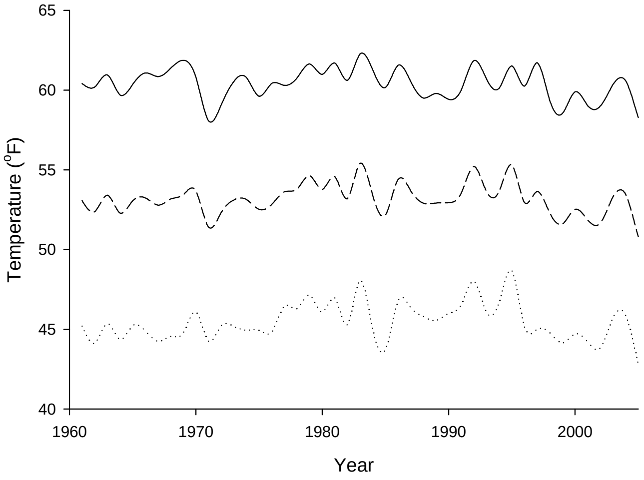


Figure 9 Plot of yearly averages for maximum, mean, and minimum, air temperature measured at Crescent City weather station (41°48.0´N, 124°13´W, Co-op ID 042147) from 1961 to 2005 (do from top to bottom again-see comments on other graph). Data are available from the National Climatic Data Center at http://cdo.ncdc.noaa.gov/CDO/cdo. There have been no significant trends in air temperature over this period.

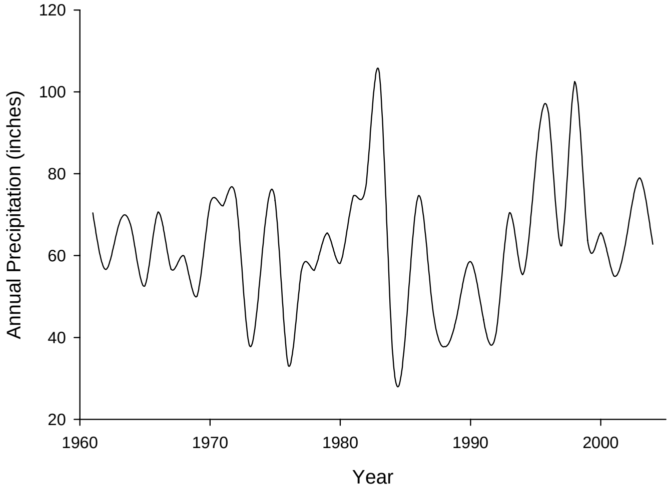
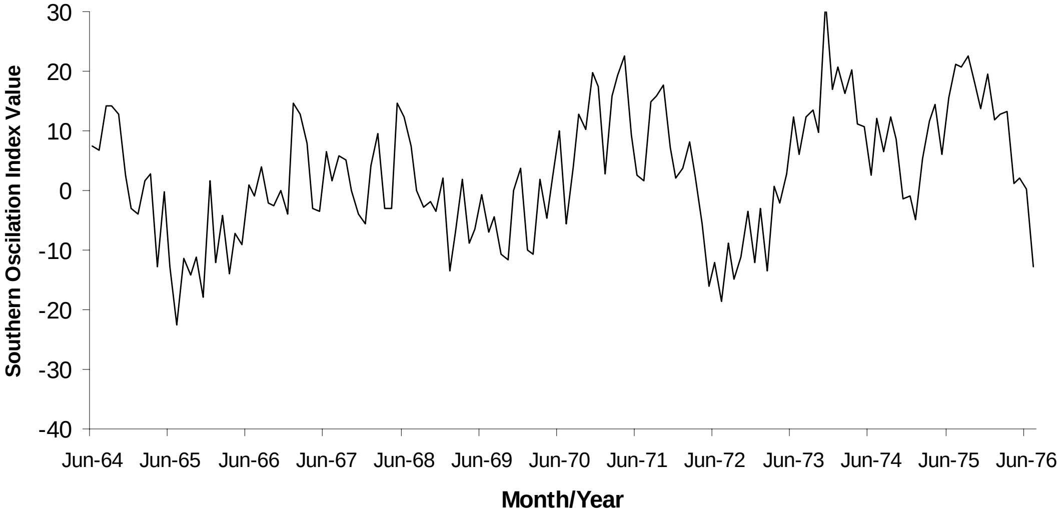


Figure 10 Total annual precipitation values measured at Crescent City weather station (41°48.0´N, 124°13´W, Co-op ID 042147) from 1961 and 2005. Data are available from the National Climatic Data Center at http://cdo.ncdc.noaa.gov/CDO/cdo.

El Niño-Southern Oscillation (ENSO)

T-tests of the Southern Oscillation index indicate that El Niño events have been stronger in recent years (p=0.011), but La Niña events were stronger historically (p=0.016416). Strong El Niño events occurred in 1972-1973 and in 1997-1998. Moderate events occurred in 1965, 1976, 1994, and 2004 (Figs. 11A and 11B, classifications based on Quinn et al. 1987). The 1997-1998 El Niño was very strong, and long-lasting. This event may be primarily responsible for significant differences in the strength of El Niño events between time periods. Despite significant differences in strength, the number and ranking of events were similar in the 10-year periods preceding each study.

A



B

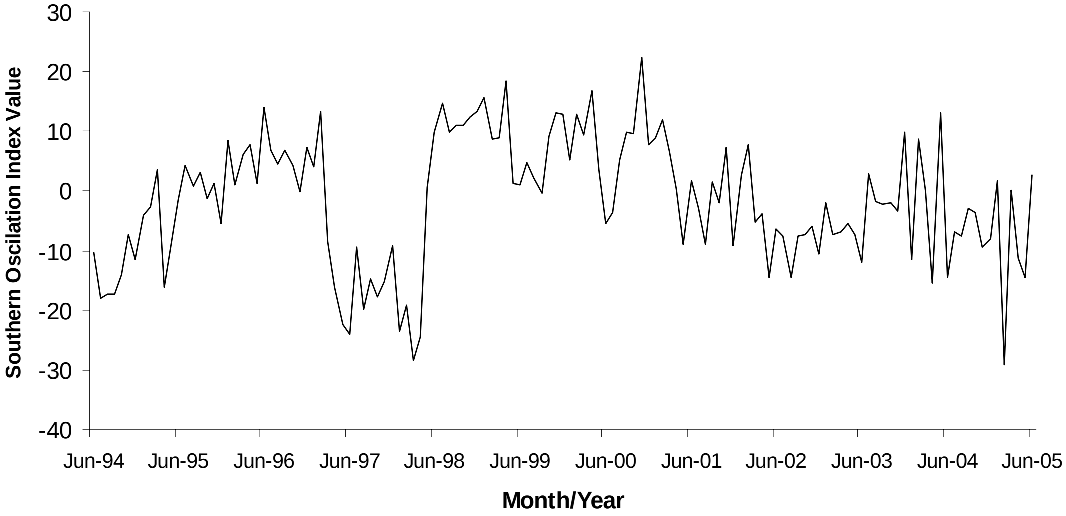


Figure 11 Southern Oscillation Index values from (A) June 1964 - June 1976 and (B) June 1994 - June 2005. These values indicate changes in the strength of El Niño-Southern Oscillation (ENSO). Negative values of the SOI generally indicate El Niño episodes, while positive SOI values generally indicate La Niña episodes (Australian Bureau of Meteorology http://www.bom.gov.au/climate/glossary/soi.shtml). Moderate El Niño events occurred in 1965, 1976, 1994, and 2004. Strong events occurred in 1972-1973 and 1997-1998. Classifications are based on Quinn et al. (1987). (A) SOI June 1964-June 1976. (B) SOI June 1994-June 2005.

Upwelling

Upwelling events (generally in summer months) have been stronger in recent years, but this trend is not significant (p=0.095). Downwelling events have become significantly stronger recently (p=0.006). However, it appears that downwelling and upwelling greatly decreased in the summers of 2004 and 2005 (Fig. 12B). Upwelling and downwelling alternations remained stable throughout the historical study period (Fig. 12A).

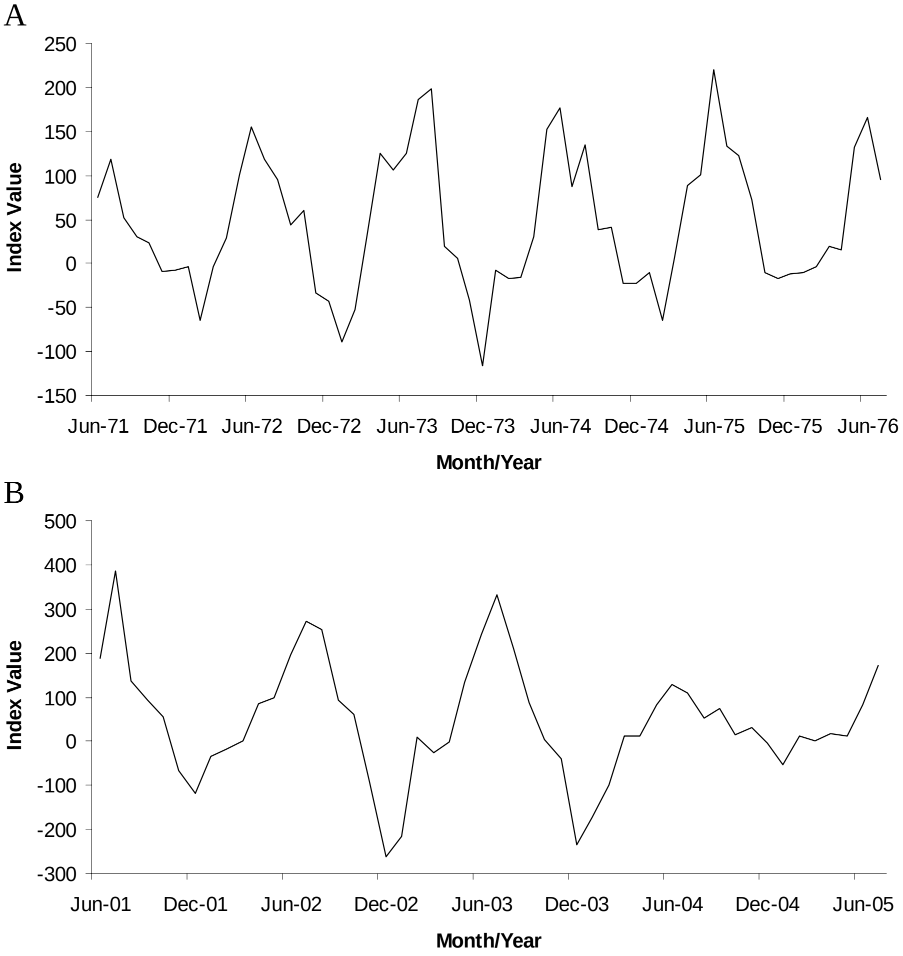


Figure 12 Upwelling indices from Pacific Fisheries Environmental Laboratory (http://www.pfeg.noaa.gov/products) depict the strength of upwelling and downwelling events in (A) June 1971 - June 1976 and (B) June 2001 - June 2005.

Species interactions

According to multivariate selection routines, physical factors were appropriate predictors of variation in *E. muricata* and *Fucus* cover, but motile invertebrate counts best predicted percent cover changes in mussel percent cover. Percent cover of barnacles and *P. limitata* were predicted with a combination of biological and physical variables. Precipitation, near shore ocean temperature, wind speed, and air temperature were selected for predicting seasonal changes in the percent cover of *E. muricata* (p=0.001). Precipitation alone was sufficient for predicting percent cover variation in *F. gardneri* (p=0.001). Variation in the percent cover of *P. limitata* was predicted by upwelling, near shore ocean temperature, and barometric pressure (p=0.003). *Nucella ostrina* abundance was the only variable selected for prediction of mussel percent cover (p=0.050). Barnacle percent cover was best predicted by a combination of upwelling, barometric pressure, air temperature, and littorine counts (p<0.001). Size distributions of motile invertebrates were not important predictors of variation in percent cover for any sessile group.

DISCUSSION

The high intertidal communities at both Enderts Beach Cove and False Klamath Cove have undergone significant changes in the percent cover of sessile organisms from the mid 1970's to the present. These changes are consistent within successional categories and support the notion that the disturbance regime at these two sites has changed over the last 30 years (Table 5). The groups with higher historical percent cover at both sites are characteristic of early to mid succession and would be expected at a site with frequent and/or recent disturbance. The higher percent cover of bare rock is another indication that the amount of free space in the intertidal was higher historically.

Porphyra spp. are early successional algae known to colonize in disturbed areas. *Porphyra* spp. are spring annual red algae that capitalize on free space and are commonly found where disturbance is frequent or severe (Vesco and Gillard 1980, Raimondi et al. 1999). *Porphyra* spp. cover was significantly higher at Enderts Beach Cove in 1975-76 than in 2005; however it was scarce in photo plots at False Klamath Cove in both study periods.

Mastocarpus sporophyte is an intermediate successional algal stage (Vesco and Gillard 1980). It is a fairly poor competitor with other algae, and requires free space for recruitment (Foster et al. 2003). *Mastocarpus* sporophyte was historically more abundant at Enderts Beach Cove, but percent cover did not change significantly between study periods at False Klamath Cove, perhaps because changes in the disturbance regime were more severe at Enderts Beach Cove than at False Klamath Cove, such that this mid-successional organism occurred at intermediate abundance in both study periods at False Klamath Cove.

Barnacles were more abundant historically at False Klamath Cove and at Enderts Beach Cove in 1975, but barnacles had a significantly lower percent cover in the 1976 comparison at Enderts Beach Cove. There are two possible explanations for this inconsistent outcome. Recent barnacle percent cover measurements may have been underestimated in *P. limitata* plots, because the actual percent cover of these taxa may have been obstructed by a thicker canopy of algae in recent photos. Barnacles are extremely common under *P. limitata* in recent plots (personal observation), but the historical percent cover of this alga was low at False Klamath, and *P. limitata* was not present in any of the historical plots at Enderts Beach Cove.

The second possible cause of this inconsistency could relate to the successional categories of the two barnacle species that were lumped together. *C. dalli* generally occurs early in succession, whereas *B. glandula* occurs later in succession (Vesco and Gillard 1980, Raimondi et al. 1999). Because these species were lumped together when data were collected, it is impossible to tell if the proportion of these species changed over the course of the studies such that early photos were dominated by *C. dalli*, and recent plots by *B. glandula*, as would be consistent with the successional shifts in all other sessile groups.

Anthopleura elegantissima (the aggregating anemone) is characterized as an intermediate successional species (Vesco and Gillard 1980), most commonly found in areas with heavy sand movement. This anemone is resistant to sand scour (Raimondi et al. 1999) and can withstand up to three months of burial (Sebens 1980). The presence of this species at both Enderts Beach Cove and False Klamath Cove historically (Table 4) is a likely indication that sand scour was more severe. It is possible that scour and sedimentation were components of the historical disturbance regime. Unfortunately it is difficult to measure sand scour on rock surfaces and sand was extremely scarce in photo plots. Photographing rock surfaces is not ideal for monitoring the presences of sand. Rather this plot location is best for avoiding sand burial, which would obstruct sessile organisms from view in photo plot analysis. However, these anemones are known to dominate on hard substrate where sand is present (Sebens 1980 and Raimondi et al. 1999) and anemones in historical photographs were coated with course sediment.

Increased percent cover of late successional, long lived species (*F. gardneri, P. limitata, E. muricata, M. parksii, and M. californianus,* Table 5) at both Enderts Beach Cove and False Klamath Cove in recent monitoring data indicate that disturbance may have decreased in either frequency or severity at these sites. Succession would not proceed to late stages if disturbance events, severe enough to cause rock clearing or removal of vegetative parts, were frequent.

The biological community has undergone both a change in species composition and a change in the magnitude of seasonal variation (coefficient of variation for seasonal measurements of percent cover), indicating a change in the intensity and frequency of disturbance between studies. In Boyd and DeMartini’s (1977) study at Enderts Beach Cove, disturbance was both frequent and very severe. The percent cover of barnacles and *Mastocarpus* sporophyte remained low, but the coefficient of variation was also low. This is an indication that disturbance events were severe enough to prevent extensive growth (high percent cover), but frequent enough to prevent high variation levels (CV), such that the standing stock remained consistently low.

In the present study at Enderts Beach Cove percent cover of barnacles has increased significantly, but the coefficient of variation has decreased since the historical study. The percent cover of *Mastocarpus* sporophyte has decreased from the mid 1970's to the present, but this is probably due to its inability to compete for space with other sessile species rather than removal by disturbance events. The significant decrease in bare rock in recent plots also indicates a decrease in the occurrence of space-clearing disturbance events. Higher mean percent cover of barnacles and low CV values indicate that disturbance at Enderts Beach Cove is frequent but less severe than in the historical regime.

At False Klamath Cove historically, disturbance was frequent, but of moderate severity. Barnacles maintained a percent cover similar to recent measurements, but variation was slightly higher. *P. limitata* percent cover was lower in historical plots and variation was higher than in recent plots. This may be an indication that the historical disturbance type particularly affected this late successional alga. *Mastocarpus* sporophyte had a higher mean percent cover historically, but a lower coefficient of variation. Disturbance events resulting in patch clearings seem to have decreased in the recent community, as is evident by the decrease in percent cover of bare rock and *Mastocarpus* sporophyte, and the increase in percent cover of *P. limitata,* a late successional alga.

It appears that disturbance regimes may have differed between the two sites historically, but this does not seem to hold true in recent assessments, where percent cover measurements and coefficients of variation are similar between sites. Historically, percent cover measurements varied between sites for each cover type, but variation was always higher at Enderts Beach Cove. Percent cover of rock and *Mastocarpus* sporophyte were similar at both sites, but barnacles were far more abundant at False Klamath Cove. This is likely an indication that disturbance at Enderts Beach Cove was more severe than at False Klamath Cove. What caused this site-to-site difference is unknown, but it is most likely a result of differences in temporary local conditions. It is possible that the morphology or transport processes at Enderts Beach Cove made the site more susceptible to certain types of disturbance. It is unlikely that localized sediment inputs from Nickel Creek caused the differences, as Wilson Creek at False Klamath Cove is similar in size and proximity.

Mean percent cover values and CVs are similar between sites in the current community, indicating that they are both experiencing similar disturbance regimes. Disturbance in the present study probably results from storm events and seasonal changes in wave exposure that effect both sites similarly. There is no reason to assume that wave and storm disturbance patterns are dissimilar between historical and recent studies, unfortunately buoy data are not available prior to 1980.

Alternative Hypotheses

Community shifts are due to short term inter-annual population variation. Percent cover comparisons between the mid summers of 1975 and 1976 indicate no significant inter-annual differences. Decadal differences were far stronger than inter-annual changes. What inter-annual changes did occur were slight, and did not occur disproportionately in any category of organisms. This result is important, because it indicates that the successional changes are not likely to represent short term fluctuations and because between-year variation is weak enough to allow detection of long term trends in the intertidal community. Inter-annual variation is likely a result of the community’s response to short term fluctuations in physical factors such as the upwelling and temperature. Nevertheless, the long term trend corresponding with successional categories was strong enough not to be masked by the culmination of these short term factors.

Life history traits correspond with community shifts. Long term changes in the two high intertidal communities did not occur disproportionately in algae or sessile invertebrates. Nor did changes occur consistently in species with a certain reproductive strategy. These findings support the idea that percent cover shifts due to changes in the disturbance regime rather than changes in nutrient availability or physical transport processes, as would be expected if community change were driven by long term changes in the upwelling regime or ENSO events (Sagarin et al. 1999).

Climate-related change drives community shifts. Contrary to the findings of Sagarin et al. (1999) in Monterey, California, changes in the percent cover of sessile species at Enderts Beach Cove and False Klamath Cove do not correspond with a trend of increasing near shore ocean temperature. Trends in near shore ocean temperature in the years proceeding each study period were similar (Figs. 7and8). Near shore ocean temperature was significantly warmer in the winter months of years proceeding and including the recent study, but this difference was not maintained throughout the year. Also, community changes did not occur as would be expected if increased water temperature was driving community change. Changes in percent cover of sessile organism did not occur disproportionately in any published range distribution. If an increase in ocean temperature were driving community change, species with a northern distribution (Table 5) should have decreased, while species with a central distribution should have maintained approximately the same mean percent cover.

ENSO-related events caused the observed community shifts. It is unlikely that ENSO events, or change in the intensity thereof, were responsible for the changes in these two intertidal communities in RWNSP. El Niño-Southern Oscillation events were similar in frequency and severity in the years preceding sampling events. El Niño events have been stronger and La Nina events weaker in recent years, but changes in the biological community do not follow expected patterns as set forth by Sagarin et al. (1999). ENSO events usually impact the California coast by increasing the flow of warm surface water northward. This anomalous current promotes the transport of southern species and inhibits southern dispersal of species from north to south. This should result in increased percent cover for southern species with larvae capable of long-distance dispersal (Pearcy and Schoener 1987, Lenarz et al. 1995; see Table 5 for dispersal and range categories). There were no “southern” species in this study, but results among “central” species with planktonic larvae were inconsistent with this hypothesis. Moreover, range shifts resulting from ENSO events usually occur in pelagic and subtidal species (Pearcy and Schoener 1987, Sagarin et al. 1999). The effects of ENSO events are poorly understood for intertidal species. Changes in intertidal communities during ENSO events have been attributed to severe storms rather than oceanographic processes (Gunnill 1985, Dayton and Tegner 1990). Nevertheless, ENSO related changes are generally short lived (Dayton and Tegner 1990), so any shifts that did occur probably did not persist into the study years. While ENSO was unlikely to have caused these long term changes at the intertidal sites in RWNSP, the effects of ENSO events on intertidal organisms are poorly understood and this possibility cannot be ruled out without further investigation.

Community shifts are related to changes in upwelling intensity. Upwelling intensity has not increased significantly between study periods. Downwelling events were stronger in recent years. Nevertheless, changes in the upwelling intensity do not seem to be driving the observed percent cover changes. Upwelling events have been shown to cause increased algal productivity at intertidal sites because of increased nutrient availability (Bosman et al. 1987, Wootton et al. 1996, Bracken 2004). If a change in downwelling intensity was responsible for observed changes, percent cover of algae should be lower in the present study, but the opposite result actually occurred (Table 3). It is possible, but unlikely, that algal biomass was actually higher in the historical study even though the percent cover was lower.

Upwelling intensity has also been linked to an increase in the abundance of late successional, corticated algae (Nielsen and Navarrette 2004). If changes in upwelling were driving community change, the recent community should have a higher abundance of early successional species or no change in species composition at all. The actual results indicate community trends opposing this hypothesis. Upwelling is known to affect larval transport because of changes in physical transport processes. Upwelling can inhibit onshore transport of planktonic larvae (Roughgarden et al. 1988, 1991), but, again, there were no shifts in percent cover consistent among dispersal categories (Table 5).

Patterns of community changes have arisen from species interactions. Species interactions do now seem to be driving changes in the high intertidal communities at Enderts Beach Cove and False Klamath Cove. *Nucella ostrina* abundance predicts variation in mussels plots (which is slight), and littorines are partial contributors to prediction of percent cover variation in barnacles and *P. limitata,* but these results were not consistent in other sessile species. Since variation in the abundance and size distribution of motile invertebrates is not an important factor in predicting percent cover changes for a majority of sessile species, it is unlikely that these herbivores/predators are driving community change at least in the short term. The correlation of *Nucella* abundance and mussel percent cover is probably a result of a predator-prey relationship or congruent response to similar physical conditions (Dahlhoff et al. 2001). The relationship between littorine abundance and percent cover of barnacles and *P. limitata* is probably not an indication of direct species interactions. Littorines are not known to affect the barnacles or *P. limitata* assumably because of differences in size. This correlation is probably an indication that these sessile species provide shelter or other resources which promote a higher abundance of littorines. The association could be sustained through differential recruitment, survival, or behavioral habitat selection (Crowe and Underwood 1998). In any case, it is more likely that these sessile species are affecting littorine abundance than vice versa.

Mechanisms of Change

Increases in the percent cover of late successional species and changes in the magnitude of variation in percent cover both indicate that disturbance was more severe and possibly more frequent historically. Results are not consistent with long term climate change or changes in oceanographic processes. Natural and human-caused alterations to nearby terrestrial systems have been the most drastic changes on this coast line. Dense driftwood deposits were present at both Enderts Beach Cove and False Klamath Cove in the early 1970's (Figs. 13 and 14). It is probable that bashing by logs (Fig. 15) and scour from increased sediment loads were the primary sources this severe historical disturbance regime. There have been no other documented changes in physical factors at these sites that were severe enough to account for such a change in the disturbance regime. Increase in sand scour probably resulted from increased sediment loads entering the intertidal from the mouths of Smith River, Klamath River, Redwood Creek, and numerous other creeks and tributaries. Terrestrial activities, such as logging and mining, heightened the amount of sediment and logs being delivered to intertidal areas, especially between 1950 and 1978 when clear cutting was most severe (Janda 1975). Bashing by drift logs is known to remove sessile species and open up patches of free space in rocky intertidal habitats

(Dayton 1971, Maser et al. 1988), unfortunately there is no record of the amount of drift wood delivered to rocky intertidal sites in Redwood National Park.

There are no quantitative records of sediment discharge from the tributaries nearest Enderts Beach Cove (Nickle Creek, < 1km north) and False Klamath Cove, (Wilson Creek <0.5 km north) so sediment discussion is restricted to anecdotal evidence for these sites and discussion of sedimentation from the nearby Klamath River and Redwood Creek basin (6 km and 29 km south of False Klamath Cove respectively). It is probable that these two rivers provide a significant amount of sediment to both study sites. Northward currents dominate in October-December at peak flow of 25 km/day from Redwood Creek north to the Crescent City (Carlson and Harden 1975, Ricks 1985). The Klamath River plume was discernable 50 km (30 mi) offshore (Ricks 1985).

Redwood Creek's sediment load was probably higher than that of the Klamath River because its watershed has been logged more extensively since the 1950's, but it is the best studied waterway in the area. Sediment load from Redwood Creek alone may have had considerable impacts on the study sites in the historical study. Sediment accumulation increased extensively at the mouth of Redwood Creek between the 1950's through the 1980's. Sediment discharge at the mouth was altered by channeling of the mouth in 1966-1968 and heightened sediment loads that were linked to both natural and anthropogenic pressures. Channeling the mouth increased the flow and shunted sediment (62-81% sand) further from shore, promoting wave transport (Ricks 1985).

Peak logging pressures in the 1950's and 1960's, poor road construction and logging practices, and unstable slopes coupled with exceptionally severe storm events

(1953, 1955, 1964, 1972, and 1975), particularly the Christmas Flood of 1964, drastically increased the sediment load in the Redwood Creek catchment (Janda 1975, 1977, Kelsey et al. 1981, Pitlick 1982, Best 1984, Madej 1984, Madej 1992). Increased intensity and frequency of bedload transport, channel aggradation, and a decrease in stream bottom particle size were documented in the 1970s (Janda 1975, Kelsey et al. 1981). Pool fills along the main channel contained up to 4 meters of sediment. While quantitative data before 1972 are scarce, this sediment load is thought to be far higher than any previous levels (Kelsey et al. 1981). The resulting sediment discharge was thought to be 7.5 times the typical pre-flood levels (Janda 1977).

Floods of equal or greater magnitude had occurred between 1860 and 1940, but sediments loads were far lower (Coghlan 1984). Increased sedimentation is associated with an increase in clear-cut acreage (Best 1984). In catchments where tractor-yarded, clear-cut timber harvest techniques had been used, tributaries were more drastically modified than intact catchments. Sedimentation in these catchments was also higher. In addition to sediment increase, logging activities caused a dramatic increase in the deposition of sawed logs, and logging cables (Janda 1975, 1977). Sediment contributions from land-based human activities upstream, beyond the park boundary were considered severe enough that an act of Congress expanded the park boundary to include an additional 119 square miles (6545 m^2) of the lower Redwood Creek basin (Kelsey et al. 1981).

Sediment loads (suspended and bedload) in Redwood Creek have decreased significantly between the historical and recent study periods (Fig. 6B). By 1980, Redwood Creek’s bed load had begun decreasing compared to 1964 levels (Potter et al. 1987 and Madej 1992). Based on bedload changes, stored sediment will continue to decrease slowly, but it is expected to take until at least 2013 for Redwood Creek’s sediment budget to return to background levels (Kelsey et al. 1981, Madej 1992). This decrease in sediment load is associated with changes in logging practices, a decrease in annual acreage cut, and a decreased in maximum cut plot area (Best 1984). In general, scour from river based sediment and bashing by driftwood in the near shore environments of Redwood National and State Parks has probably decreased since the 1970’s. Variability in sessile organisms seems to have stabilized, and drift wood levels have decreased considerably (Figs. 13 and 14).

This study highlights a need for ecologists and managers to understand the nature of terrestrial inputs in intertidal ecosystems. Terrestrial degradation in areas adjacent to the intertidal can modify the dynamics and composition of intertidal communities. Long term monitoring of both biological communities and physical factors such as salinity, sedimentation, and debris levels should be considered for determining and documenting the response of intertidal communities to terrestrial inputs.

A

B

C

Figure 13 Aerial overview of Enderts Beach Cove large deposits of driftwood in 1972 (A), reducing in 1979 (B) and 1989 (B). Copyright © 2002-2005 Kenneth & Gabrielle Adelman, California Coastal Records Project, www.Californiacoastline.org

A

B

C

Figure 14 Aerial overview of False Klamath Cove large deposits of driftwood in 1972 (top), reducing in 1979 (center) and 1989 (bottom). Copyright © 2002-2005 Kenneth & Gabrielle Adelman, California Coastal Records Project, www.Californiacoastline.org

Figure 15 Large log in the rocky intertidal at Enderts Beach Cove ca. 1975. Driftwood was more abundant at rocky intertidal sites in the 1970’s from logging efforts directly, and the erosion of water courses as a result of logging. Photo by Milt Boyd.

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APPENDIX A

Photographs of permanent plots (n = 6) were taken by Boyd and DeMartini (1977) at False Klamath Cove on 08/01/74, 10/15/74, 01/25/75, 03/28/75, 05/25/76, 09/04/75, 11/03/75, 01/76 (actual day not recorded), 04/18/76, and 6/11/76. At Enderts Beach Cove, they photographed plots (n = 3) on 09/17/74, 11/16/74, 09/05/75, 11/2/74, 1/24/75, 01/76 (actual day not recorded). For comparison with these historical plots, recent photo plots (n = 10) were photographed in 2004/2005 at the same two sites on June 1 and 7, 2004; July 31 and August 2, 2004; October 28-29 2004; January 9 and 10, 2005; April 2 and 3, 2005; and June 4 and 5, 2005.

Assessments made to test for species interactions were conducted at False Klamath Cove, Damnation Creek, and Enderts Beach Cove on June 1, 5, and 7, 2004; July 29, 31 and August 2, 2004; October 27-29 2004; January 9, 10 and 23, 2005; March 31 and April 2, 3, 2005; June 4, 5, and 8, 2005.

APPENDIX B

Recent monitoring plots were set up and sampled using the MARINe protocol (Engle 2005). Five replicate plots were set up for each target species. Target species include mussels (*Mytilus californianus*), barnacles (*Balanus glandula*/*Chthamalus dalli*), and three algal species (*Fucus gardneri*, *Pelvetiopsis limitata*, and *Endocladia muricata*). All five target species were monitored at False Klamath Cove (25 plots total, Table 1). Mussels (M), barnacles (B), *F. gardneri* (F), and *E. muricata* (E) were monitored at Damnation Creek (20 plots, Table 1). Five additional mussel plots (Mf, 25 total plots) are located near the mouth of Damnation Creek where salinity is frequently lower than at mussel plots farther up-coast from the mouth. At Enderts Beach Cove, mussels, barnacles, *P. limitata* (P), and *E. muricata* were monitored (20 plots, Table 1). Because of insufficient percent cover, *P. limitata* was not monitored at Damnation Creek, nor was *F. gardneri* monitored at Enderts Beach Cove. Permanent monitoring plots (50 x 75 cm) were set up where the percent cover of a particular target species is approximately 80%. These plots marked on three corners with stainless steel bolts (5/16 or 3/8 in. diameter, 3 to 6 in. length) to ensure precise plot relocation for repeated sampling events. Longer bolts were used for mussel plots because of overgrowth. In some plots, a metal detector should be used to relocate bolts. Plot to plot direction and distance measurements, site maps, and site photographs are included here to assist in relocation of monitoring plots.

False Klamath Cove

GPS Coordinates

Up-coast site boundary: N 41.59377, W 124.10773

Site center: N 41.59476, W 124.10643

Down-coast site boundary: N 41.59526, W 124.10513

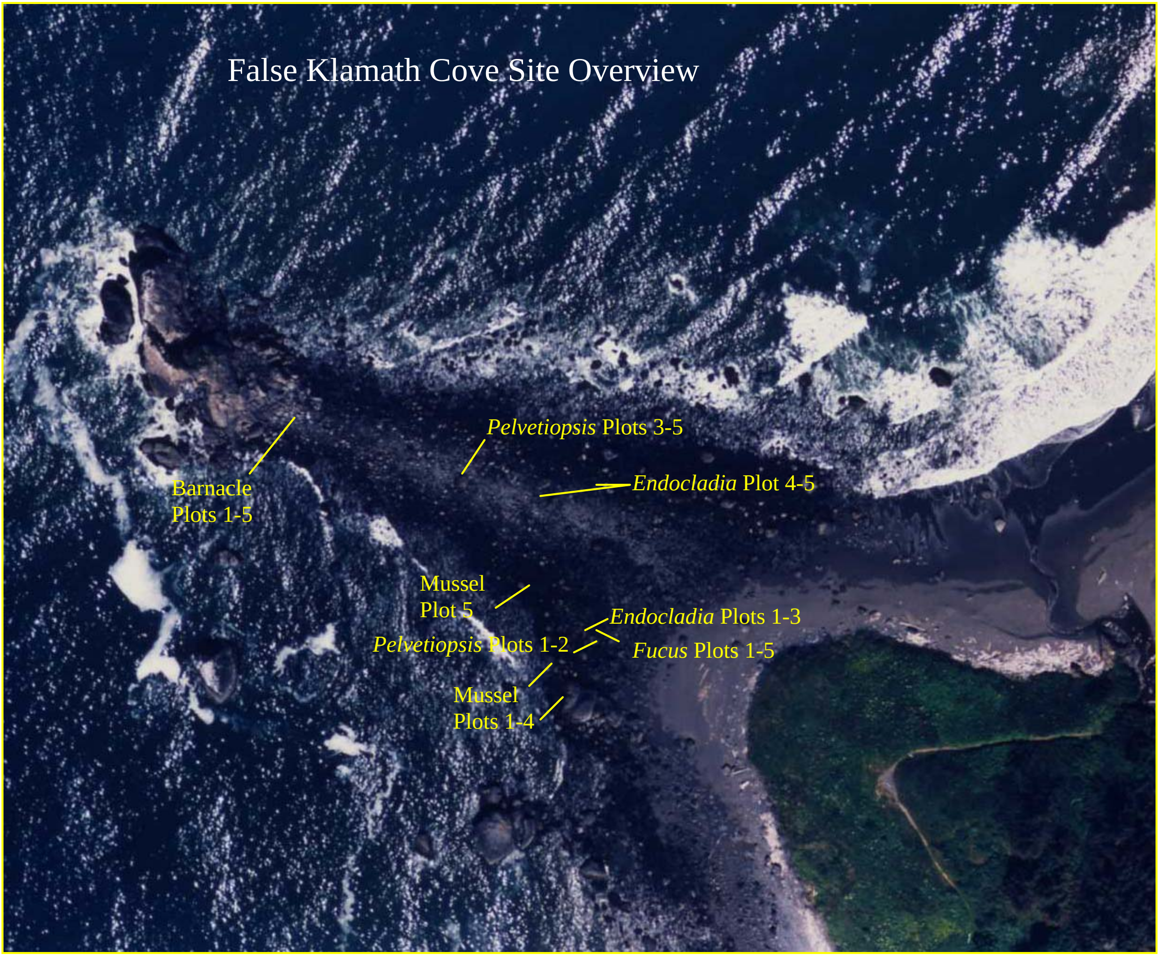
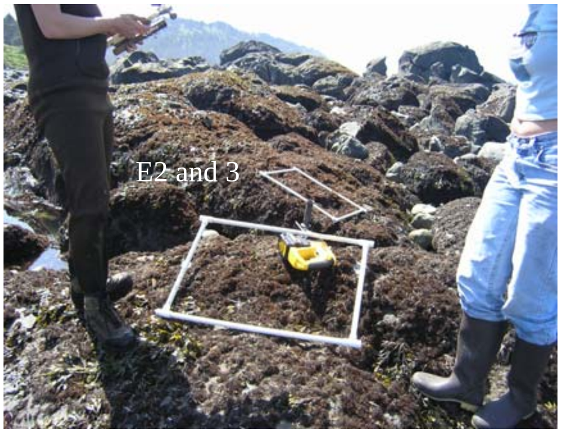


Photo courtesy of Redwood National Park

False Klamath Cove Barnacles Plots

From	To	Distance (m)	Bearing (degrees)
B1	B2	12.1	21 NE
B2	B3	4.8	272 NW
B3	B4	9.3	314 NW
B3	B5	9.8	306 NW
B4	B5	1.1	330 NW

False Klamath Cove *Endocladia* Plots



From	To	Distance (m)	Bearing (degrees)
E1	E2	0.9	329 NW
E2	E3	1.9	339 NW
E3	E4	43.9	12 NNE
E3	E5	49.6	4 NNE
E4	E5	13.8	55 NE
E1	M5	32.7	280 NW

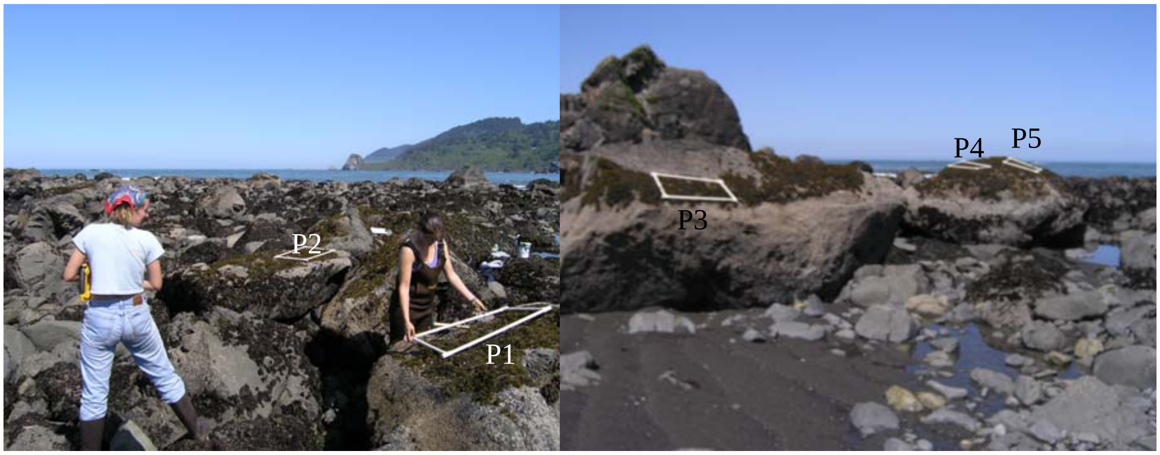
False Klamath Cove *Fucus* Plots

From	To	Distance (m)	Bearing (degrees)
F1	F2	1.2	249 WSW
F2	F3	1.5	350 NW
F3	F4	1.0	260 W
F4	F5	0.8	340 NW
F1	M3	21.3	200 SW
F1	P2	4.8	210 SW

False Klamath Cove Mussel Plots

From	To	Distance (m)	Bearing (degrees)
M1	M2	2.9	300 NW
M2	M3	17.6	305 NW
M3	M4	1.1	315 NW
M4	M5	42.7	305 NW

False Klamath Cove *Pelvetiopsis* Plots



From	To	Distance (m)	Bearing (degrees)
P1	P2	4.7	304 NW
P2	P3	47.5	310 NW
P3	P4	9.3	330 NW
P4	P5	1.1	15 NE

Enderts Beach Cove

GPS Coordinates

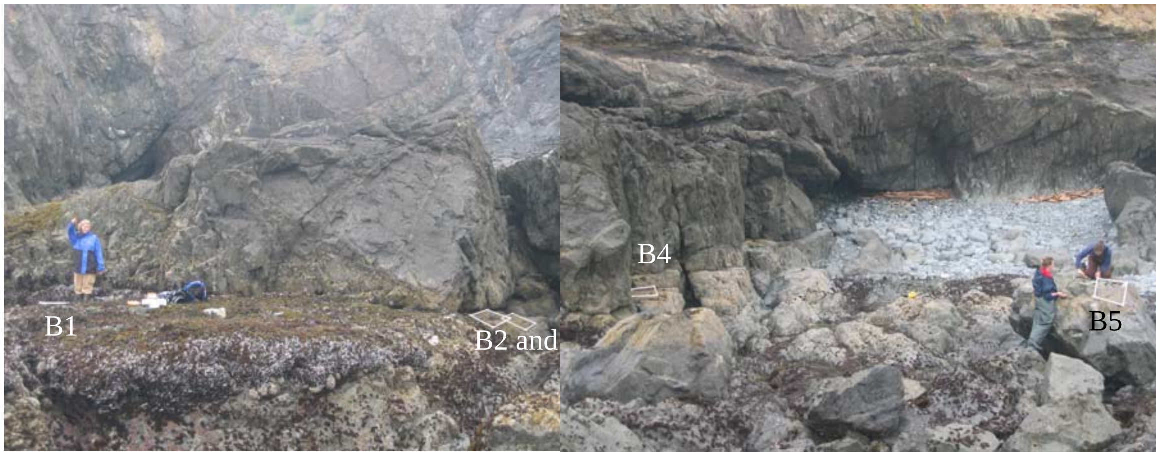
Up-coast site boundary: N 41.69592, W 124.14245

Site center: N 41.69590, W 124.14257

Down-coast site boundary: N 41.69526, W 124.14255

Photo courtesy of Redwood National Park

Enderts Beach Cove Barnacle Plots

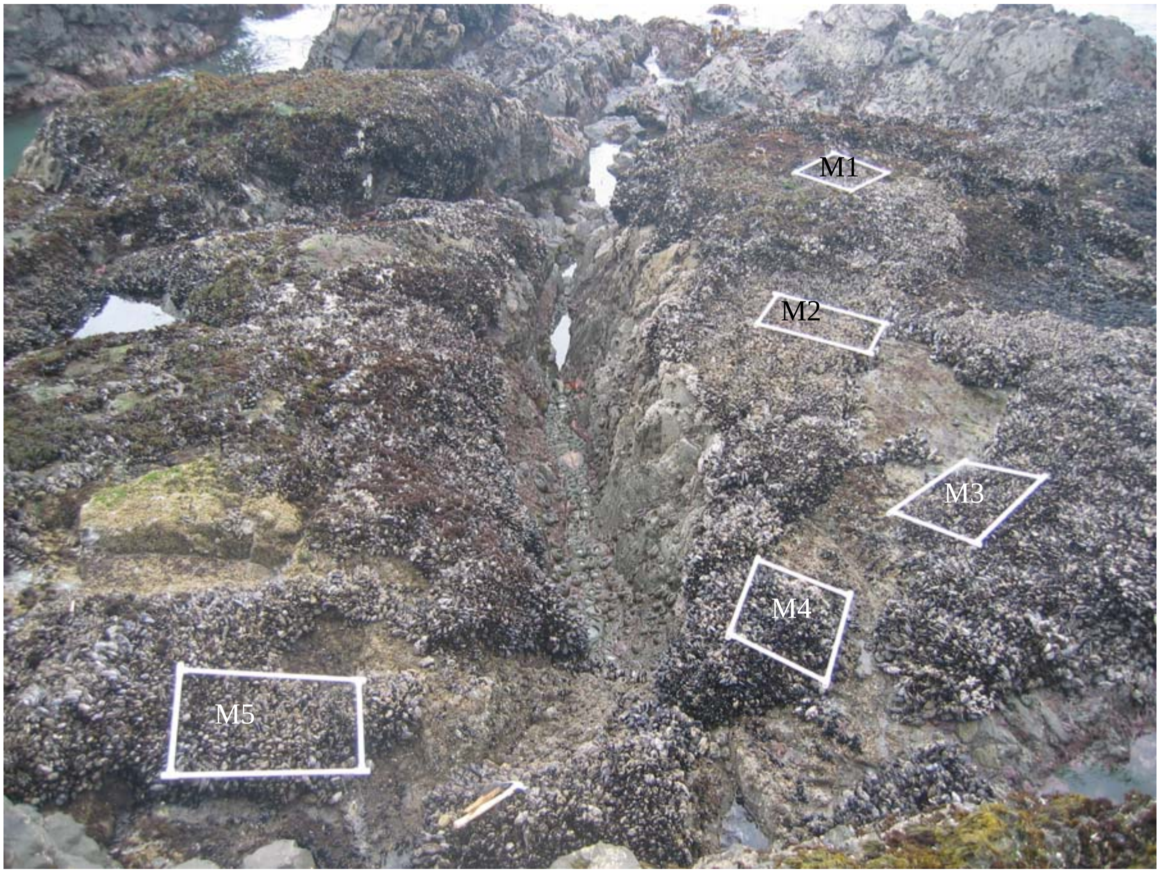


From	To	Distance (m)	Bearing (degrees)
B1	B2	8.0	110 W
B2	B3	1.08	268 W
B3	B4	7.4	146 S
B4	B5	9.2	178 SW
B1	M5	2.5	0 N

Enderts Beach Cove *Endocladia* Plots

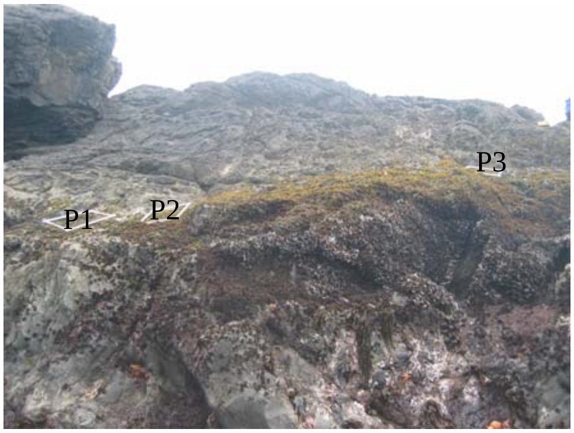
From	To	Distance (m)	Bearing (degrees)
E1	E2	2.8	144 SE
E2	E3	6.6	138 SE
E3	E4	7.4	327 NW
E4	E5	5.9	154 SE
E3	P4	18.6	164 SE

Enderts Beach Cove Mussel Plots



From	To	Distance (m)	Bearing (degrees)
M1	M2	2.9	50 NE
M2	M3	1.5	30 NE
M3	M4	1.4	60 NE
M4	M5	2.8	100 SE

Enderts Beach Cove *Pelvetiopsis* Plots



From	To	Distance (m)	Bearing (degrees)
P1	P2	5.0	80 E
P2	P3	2.2	92 E
P4	P5	6.9	118 E
P1	B1	8.6	224 SW

Damnation Creek

GPS Coordinates

Up-coast site boundary: N 41.65301, W 124.12907

Site center: N 41.65249, W 124.12784

Down-coast site boundary: N 41.65168, W 124.12696

Photo courtesy of Redwood National Park

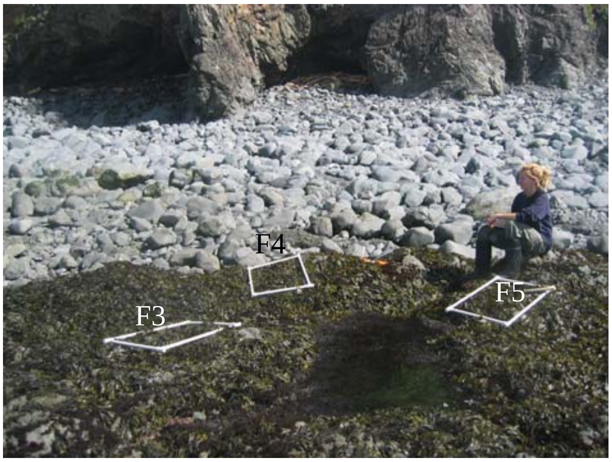
Damnation Creek Barnacle Plots

From	To	Distance (m)	Bearing (degrees)
B1	B2	1.2	98 SE
B2	B3	1.3	32 NE
B3	B4	17.4	108 SE
B4	B5	7.3	200 SW

Damnation Creek *Endocladia* Plots

From	To	Distance (m)	Bearing (degrees)
E1	E2	5.5	140 SE
E2	E3	3.8	215 SW
E3	E4	42.6	118 SE
E4	E5	6.4	42 NE
E4	B5	17.5	120 SE

Damnation Creek *Fucus* Plots



From	To	Distance (m)	Bearing (degrees)
F1	F2	1.7	91 NE
F2	F3	27.5	125 SE
F3	F4	2.8	30 NE
F4	F5	1.9	180 S
F1	M1	111.0	280 NW

Damnation Creek Mussel Plots

From	To	Distance (m)	Bearing (degrees)
M1	M2	1.3	232 SW
M2	M3	1.2	233 SW
M3	M4	2.1	245 W
M4	M5	1.7	0 N

Damnation Creek Freshwater Mussel Plots

From	To	Distance (m)	Bearing (degrees)
MFW1	MFW2	6.2	30 NE
MFW2	MFW3	7.9	180 S
MFW3	MFW4	3.7	80 NE
MFW4	MFW5	9.1	230 SW
MFW1	F5	8.3	90 E