



Padilla Bay

National Estuarine Research Reserve

Technical Report No. 23

**SPECIES-SPECIFIC RESPONSES TO ENVIRONMENTAL
GRADIENTS DETERMINE REGIONAL SCALE PATTERN
IN AN INTERTIDAL COMMUNITY**

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December 1998

Publication No. 00-06-019

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Padilla Bay National Estuarine Research Reserve is managed by the Shorelands and Environmental Assistance Program, Washington State Department of Ecology, in cooperation with the Estuarine Reserves Division, National Oceanic and Atmospheric Administration (NOAA), U.S. Department of Commerce. The preparation of this document was financially aided through a grant to the Washington State Department of Ecology with funds obtained from NOAA/Office of Ocean and Coastal Resource Management, and appropriated for Section 306 or 315 of the Coastal Zone Management Act of 1972, as amended.



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Bibliographic Citation: Harley, C.D.G. 1998. Species-specific responses to environmental gradients determine regional scale pattern in an intertidal community. Final report Washington State Department of Ecology, Contract No. C9800053. Padilla Bay National Estuarine Research Reserve Technical Report No. 23, Mount Vernon, Washington.

Final Report
Agreement Number C9800053
20 December 1998

Abstract

Although the factors that control the local patterns of distribution and abundance of species are well studied, their relative influences on regional patterns remain poorly understood. In this study, I manipulated a biological interaction (predation) at either end of a regional scale environmental gradient in the Strait of Juan de Fuca. From west to east, wave action decreases, air temperature increases, and the upper limits of intertidal organisms retreat down the shore. Because of this redistribution of sessile species, a larger percent of their intertidal range becomes vulnerable to intertidal predators, such as the sea star *Pisaster ochraceus*, that are able to track the tide. Thus, at the west entrance of the Strait, the barnacle *Balanus glandula* is rarely encountered by *Pisaster*. However, at the eastern terminus of the Strait, the effective vertical ranges of *Pisaster* and *Balanus* overlap almost completely, and barnacle populations are restricted to refuge habitats such as crevices. It is the differential impact of the environmental gradient on the vertical ranges of predator and prey that creates the dramatic differences in assemblage structure seen on a regional scale. An understanding of ecological pattern over multiple spatial gradients will aid in our ability to predict the outcome of temporal changes over an environmental gradient.

"When we travel from south to north, or from a damp region to a dry, we invariably see some species gradually getting rarer and rarer, and finally disappearing; and the change of climate being conspicuous, we are tempted to attribute the whole effect to its direct action. But this is a very false view: we forget that each species, even where it most abounds, is constantly suffering enormous destruction at some period of its life, from enemies or from competitors for the same place and food; and if these enemies or competitors be in the least degree favoured by any slight change of climate, they will increase in numbers, and, as each area is already fully stocked with inhabitants, the other species will decrease."

- Charles Darwin (1859, p. 69)

Introduction

Ecologists' interest in the influence of environmental gradients on species distributions and abundances goes back at least as far as Darwin. The mechanisms limiting the spatial extent of any given species across a particular gradient are likely to be a complex interplay of environmental and biological interactions. However, if our goal is to manage large, economically important populations, or to predict the outcome of climate change for conservation purposes, an understanding of these mechanisms is crucial.

One ecologically obvious, and experimentally tractable, environmental gradient exists on rocky shores between the high and low water marks. This steep vertical gradient creates dramatic biological pattern (Lewis 1964), which has received a great deal of attention from ecologists. The distinctive vertical zonation of species may be created directly by physical variables (Hawkins 1985), or indirectly by competition (Connell 1961a, b), herbivory (Santelices 1990, Underwood 1990), predation (Paine 1966, 1974), and facilitation (Bertness & Leonard 1997). Despite extensive investigation of the dramatic vertical patterns, larger scale horizontal patterns in the intertidal are poorly understood at best. The study of large-scale pattern in the intertidal, or any other system, is complicated by non-parallel environmental gradients. The vertical gradient in thermal and desiccation stress is superimposed on horizontal patterns in a variety of environmental variables, such as wave action, air temperature, salinity, and exposure to solar radiation.

In an effort to understand the ecological consequences of multiple environmental gradients, I have undertaken a large scale study of rocky intertidal community pattern in Washington, USA. Vertical zonation is pronounced in this region, and its causes are well studied (e.g. Paine 1966, 1974, Connell 1970, Dayton 1971, Wootton 1993). This elevational gradient is superimposed upon an east-west gradient in environmental harshness. On the outer coast, wave splash and cooler air temperatures reduce desiccation stress on the essentially marine intertidal flora and fauna. Further east through the Strait of Juan de Fuca and into the San Juan Islands, reduced wave action and higher air temperatures create less favorable conditions for intertidal organisms. I conducted experiments at either end of this regional gradient to determine the factors that limit the distribution and abundance of the barnacle *Balanus glandula*. I demonstrate that 1) the upper limit of *Balanus*

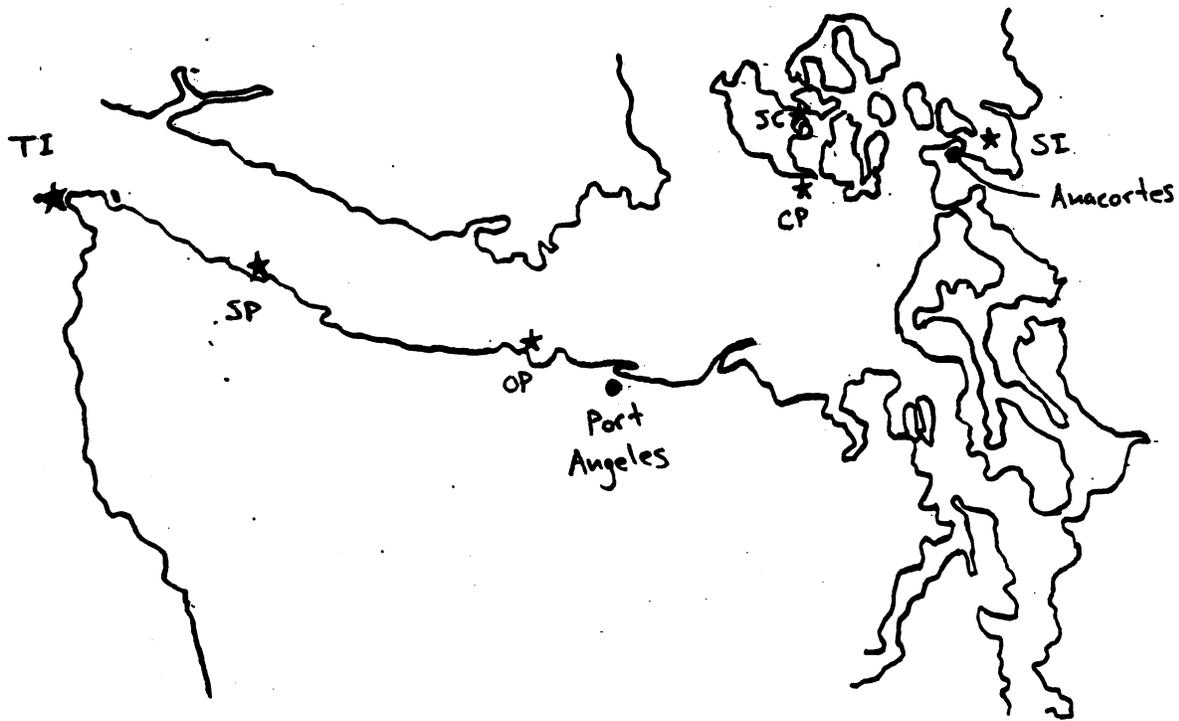


Figure 1. Locations of the study sites (stars) and weather stations (circles). TI = Tatoosh Island, SP = Slip Point, OP = Observatory Point, CP = Cattle Point, SC = Shady Cove, SI = Saddlebag Island.

descends from west to east, 2) the upper foraging limit of the predatory sea star *Pisaster ochraceus* does not vary systematically along the same west-east gradient, and 3) this differential response strongly impacts the regional pattern of *Balanus* abundance.

Methods

Study sites

Six study sites were chosen between the western entrance of the Strait of Juan de Fuca and the eastern terminus of the Fuca-Georgia-Puget Basin (Figure 1). All sites were typified by extensive rock benches extending from the high tide mark to at least several meters below MLLW. The western-most site, Tatoosh Island, is situated just off the tip of Cape Flattery, where it is exposed to the full brunt of ocean swells. Heavy waves impose impressive forces on intertidal organisms (Denny 1987), and extend intertidal zones upward by constant wave swash (Lewis

1964, Leigh et al. 1987). Tatoosh features extensive sessile invertebrate assemblages, particularly barnacles and mussels in the high- and mid-intertidal, respectively. Further east along the Olympic coast are Slip Point, at the eastern end of Clallam Bay, and Observatory Point, at the west end of Freshwater Bay. These two sites are similar to Tatoosh in that the high-intertidal is dominated by barnacles and the mid-intertidal by mussels. Wave exposure is lower at these two sites, and intertidal organisms do not extend as far up the shore. Cattle Point and Shady Cove are located on opposite sides of San Juan Island. Cattle Point is moderately exposed, and is biologically similar to the more westerly sites, although mussels are less abundant. Shady Cove is extremely protected; barnacles are uncommon, and mussels are extremely rare. The eastern-most site, Saddlebag Island, sits at the seaward edge of Padilla Bay. Like Shady Cove, it is very protected, with few *Balanus glandula* or mussels. The shore is dominated by *Fucus* spp., and *Pisaster* is extremely abundant.

Air temperature

Long term records of air temperatures for western Washington are available from the Western Regional Climate Center <<http://www.wrcc.dri.edu/index.html>>. I downloaded the average and extreme daily maxima and minima for Tatoosh Island (period of observation: 1931-1966), Port Angeles (~15 km east of Observatory Point, period of observation: 1948-1998), and Anacortes (~5 km west of Saddlebag Island, period of observation: 1931-1998). The locations of these weather stations are included in Figure 1.

Hydrodynamic variables

Wave exposure was quantified by direct measurement of breaking wave heights (for small shorebreaks), or by comparing the heights of breaking waves with fixed objects (e.g. boulders) of known dimensions. Wave height measurements were taken at approximately mid-tide once per day on each visit to each site. At hydrodynamically complex sites, such as Tatoosh, measurements from several locations were averaged. For more uniform sites such as Shady Cove, one or two locations were used to measure breaking wave height. Because I recorded the heights of the highest waves, but over a brief time interval (1-2 minutes), my measurements are roughly comparable to significant wave heights (see Denny 1995 for details).

Total water flux (surge plus currents) was estimated with plaster dissolution blocks. Dissolution blocks were created by pouring a modeling plaster (Lightweight Hydrocal) into film canisters containing a 3 inch, #12 stainless steel screw. When the plaster had set, the resulting cylinder could be screwed into wall anchors set into holes drilled in the intertidal. Plaster dissolves away at a rate proportional to water flow (Thompson & Glenn 1994), and thus represents a qualitative estimate of water flux. Dissolution rate is thus a reasonable approximation of the volume of water that a filter feeding organism, such as a barnacle, is likely to encounter.

Vertical zonation patterns

The relative upper limits of *Balanus glandula* and *Mytilus californianus* were measured using surveying equipment. The relative heights in the intertidal were converted to absolute heights by including measurements of the time and height of the tide, which were then standardized to predicted tide levels calculated by Harbor Master (Zihua Software, Marlborough, CT). Total tidal amplitude is similar across the region.

Regional scale biological pattern

The community structure in the high intertidal at each of the six sites was followed in permanent 100 cm² quadrats (n = 5 per site). Quadrats were chosen to reflect typical conditions across a variety of aspects and slopes. In each quadrat, percent cover was estimated for all sessile species. For invertebrates, the number of individuals was also recorded. *Pisaster* abundances were recorded along unmanipulated stretches of shoreline. All censuses took place periodically between September 1997 and December 1998.

Balanus recruitment and growth were followed in 100 cm² quadrats which were scraped down to bare rock in the fall of 1997 (Shady Cove: n = 4; Cattle Point: n = 12; all other sites: n = 15). The total number of new recruits was sampled on a monthly basis to gauge larval supply to each site. Recruited barnacle diameters were measured in September 1998 to provide an estimate of growth rates during the first several months of life.

Experimental manipulations - Tatoosh Island

The manipulations on Tatoosh were initiated in May of 1996 as a part of a separate experiment. Four 25 x 30 cm plots were scraped bare, and caged with inverted wire letter baskets to exclude large-bodied predators. Each cage was

paired with an open area that was also scraped and served as a control. Within each treatment, percent cover of all species was estimated by counting the number of "hits" on a 50 point (10 x 20 cm) grid held over the central section of the plot.

Experimental manipulations - Saddlebag Island

On 12 June, 1998, large-bodied predators were excluded from twenty 25 x 30 cm plots on the west side of Saddlebag with inverted wire letter baskets. Unlike Tatoosh, small crabs and small *Pisaster* were common, necessitating a lining of vexar (mesh size = 6mm) along the sides of the letter baskets.

Each exclusion was paired with an uncaged control area. Half of these pairs were haphazardly assigned to *Pisaster* removal areas. In these areas, all *Pisaster* were removed by hand every 1 - 2 weeks. This design controlled for any cage effects other than the exclusion of *Pisaster*. Unfortunately, *Pisaster* overran the manual exclusion areas within about six weeks, necessitating an alternate control for cage effects. Therefore, half (N = 10) of the exclusion cages were converted into cage controls by removing the central portion of the roof. This allowed access to predators, but mimicked any influence that full cages would have on potentially confounding factors such as water movement and shading.

Statistical analysis

Statistical analyses were performed in Splus (MathSoft Inc, 1996). Percent cover data was arcsine square root transformed for analysis purposes, but untransformed data is used in all figures. Specific statistical tests are described in the figure legends. All post-hoc tests were performed in SuperANOVA; only significant comparisons are listed in statistical description of the data. All error bars are standard errors.

Results

Environmental variables

Figure 2 is a histogram of the number of days, in an average year, that reach or exceed the temperature listed on the X axis. The "average year" is a series of "average days" determined by averaging the maximum temperatures for a particular date over the span of the data set. In an average year, Anacortes has

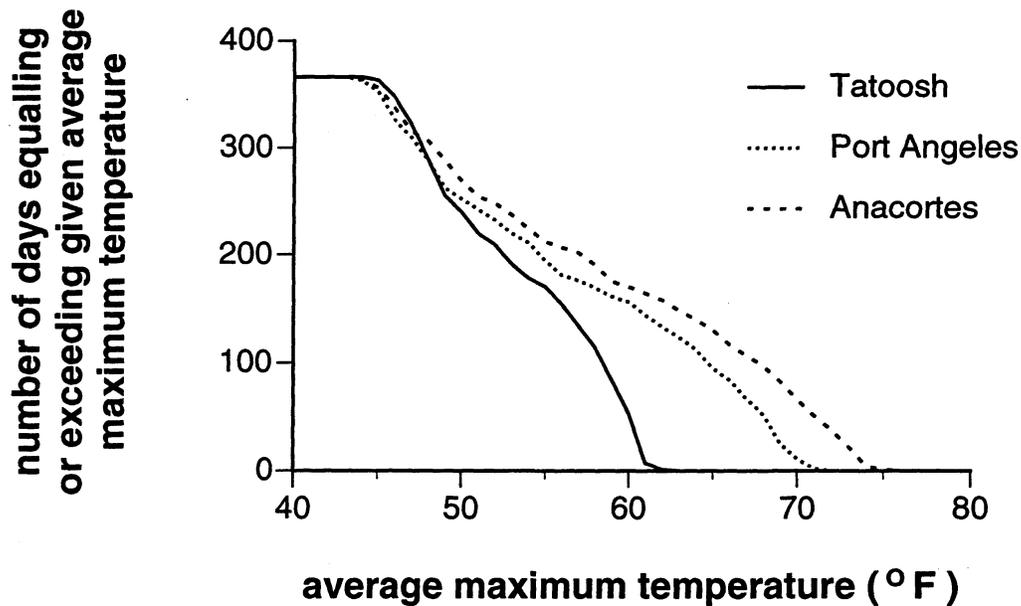


Figure 2. Histogram of average maximum daily temperatures for an average year (see text for details) at Tatoosh Island, Port Angeles, and Anacortes.

more "hot" days (which could be defined arbitrarily as days exceeding 65 ° F, 70 ° F, etc.) than does Port Angeles, which in turn has more hot days than Tatoosh. Thus, air temperatures increase from west to east as the moderating effect of the Pacific becomes less important with distance (Figure 2).

Wave heights vary seasonally, and decline predictably from west to east (Figure 3). Winter conditions at Cattle Point are rougher than would be predicted from distance to the open ocean alone, but Cattle Point faces out along the long axis of the Strait, and is thus subject to considerable fetch for wind-driven waves.

Although water flux is positively correlated with wave height on Tatoosh ($r^2 = .92$, $p = .0002$, $n = 8$), the monotonic decline in wave height from west to east does not translate into a similar decline in water flux (Figure 4). Other variables, such as current velocity and submersion time, most likely play a larger role in water flux at more easterly sites. For example, current velocities past Cattle Point are typically extreme, which may explain the high dissolution rates there.

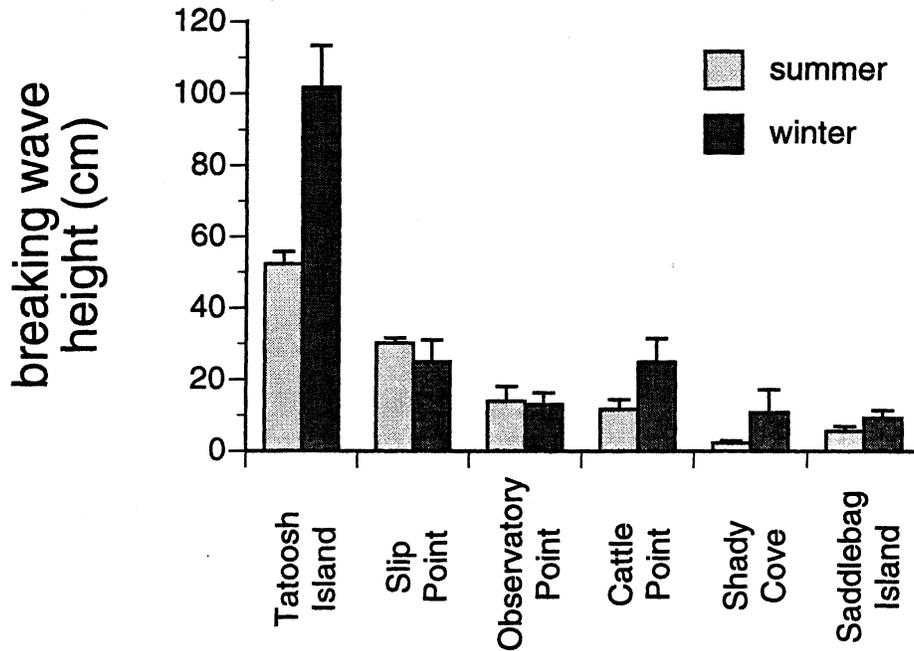


Figure 3. Regional variation in wave exposure. 2 factor ANOVA results: site ($p < .001$), season ($p = .012$), site x season ($p = .001$). In general, wave heights decrease from west to east, and from winter to summer.

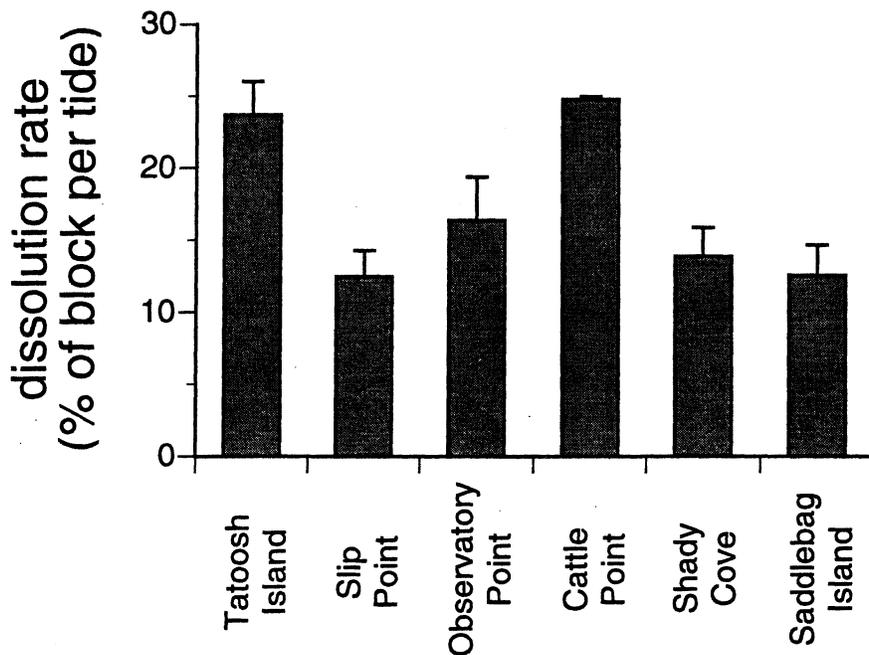


Figure 4. Regional variation in water flux, as measured by plaster dissolution rates. 1-factor ANOVA, Tukey (TI>SI, $p < .001$).

Regional scale biological pattern

Perhaps the most obvious biological change along the regional environmental gradient is the change in species composition. Table 1 gives an overview of the presence, absence, and rough abundance of some of the more common species of intertidal algae and invertebrates. In general, the number and abundance of sessile species declines from west to east, although a few species (e.g. *Fucus*, *Chthamalus*) are more common further east. The trend is less clear with mobile invertebrates, since these animals are generally able to retreat into less physically harsh habitats, such as crevices, tide pools, or the subtidal, when harsh conditions prevail at low tide.

Another biological change along the environmental gradient is the depression of the upper limits of sessile species. I measured the upper limits of *Balanus glandula* and *Mytilus californianus* on Tatoosh, at Observatory Point, and on Saddlebag (Figure 5). The upper limit of *Balanus* decreases from Tatoosh to Observatory Point, but does not decline further to Saddlebag. This may be an artifact of the sampling, as I was unable to survey the more exposed portions of Observatory Point, where upper limits would presumably be higher. Alternately, this similarity may turn out to be real. Note that in Figure 2 the temperature maxima for Anacortes, while higher than those for Port Angeles, are nonetheless much more similar to Port Angeles than to Tatoosh. *Mytilus californianus* also declines significantly from Tatoosh to Observatory Point. *M. californianus* does not occur on Saddlebag Island, so a comparison between Saddlebag and the more westerly sites cannot be made. (It should be noted that tidal amplitude actually increases slightly from west to east).

High intertidal community structure throughout the region is summarized in Figure 6. Note the scarcity of *Balanus glandula* east of Cattle Point, and the high percent cover of *Chthamalus dalli* on Saddlebag Island. At Shady Cove, where neither species is abundant, approximately 70% of the available space is bare rock.

Population dynamics of Balanus glandula

The lower abundance of *Balanus* on Saddlebag relative to the other sites could be caused by a number of factors: lower recruitment, slower growth, or increased mortality due to predators and/or environmental stress. Recruitment is

Table 1. Species distributions across the regional gradient. Species are subjectively ranked as common (+ +), rare (+), or absent (-). These species were chosen because they are dominant members of the intertidal community at at least one of the six sites studied.

| | TI | SP | OP | CP | SC | SI |
|--------------------------------------|----|----|----|----|----|----|
| algae | | | | | | |
| <i>Corallina vancouveriensis</i> | ++ | ++ | + | ++ | - | - |
| <i>Fucus gardneri</i> | + | + | + | + | ++ | ++ |
| <i>Hedophyllum sessile</i> | ++ | ++ | + | + | - | - |
| <i>Laminaria digitata</i> | ++ | ++ | - | - | - | - |
| <i>Mazzaella cornucopia</i> | ++ | + | ++ | - | - | - |
| <i>Postelsia palmaeformis</i> | ++ | - | - | - | - | - |
| invertebrates | | | | | | |
| sessile species | | | | | | |
| <i>Anthopleura elegantissima</i> | ++ | ++ | ++ | ++ | + | + |
| <i>Balanus glandula</i> | ++ | ++ | ++ | ++ | + | + |
| <i>Chthamalus dalli</i> | + | + | + | + | + | ++ |
| <i>Mytilus californianus</i> | ++ | ++ | ++ | + | - | - |
| <i>Mytilus trossulus</i> | ++ | ++ | + | + | + | + |
| <i>Pollicipes polymerus</i> | ++ | ++ | ++ | + | - | - |
| <i>Semibalanus cariosus</i> | ++ | ++ | ++ | ++ | + | + |
| mobile herbivores | | | | | | |
| <i>Littorina scutulata</i> | + | + | ++ | ++ | + | ++ |
| <i>Littorina sitkana</i> | ++ | ++ | ++ | + | + | + |
| <i>Strongylocentrotus purpuratus</i> | ++ | ++ | ++ | + | - | - |
| <i>Tegula funebris</i> | ++ | + | + | - | - | - |
| mobile predators | | | | | | |
| <i>Hemigrapsus nudus</i> | + | ++ | + | + | + | ++ |
| <i>Nucella emarginata</i> | ++ | + | + | + | ++ | + |
| <i>Pisaster ochraceus</i> | ++ | ++ | ++ | - | ++ | ++ |

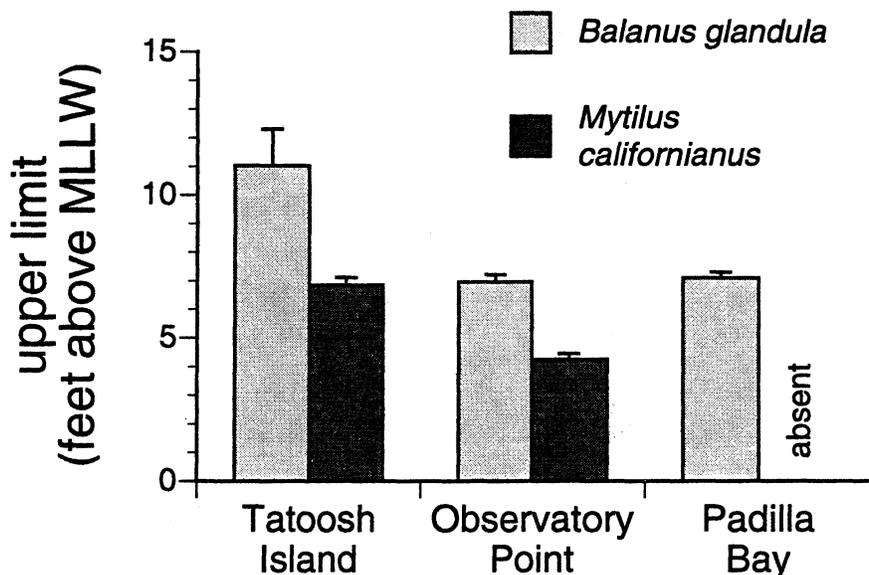


Figure 5. Upper limits of *Balanus glandula* and *Mytilus californianus* for Tatoosh (n=10), Observatory Point (n=4), and Padilla Bay (Saddlebag Island: n=4; Dot Island: n=2). Separate 1-factor ANOVAS were performed for each species: *Balanus* ($p < .001$, Tukey: TI>OP,PB); *Mytilus* ($p < .001$).

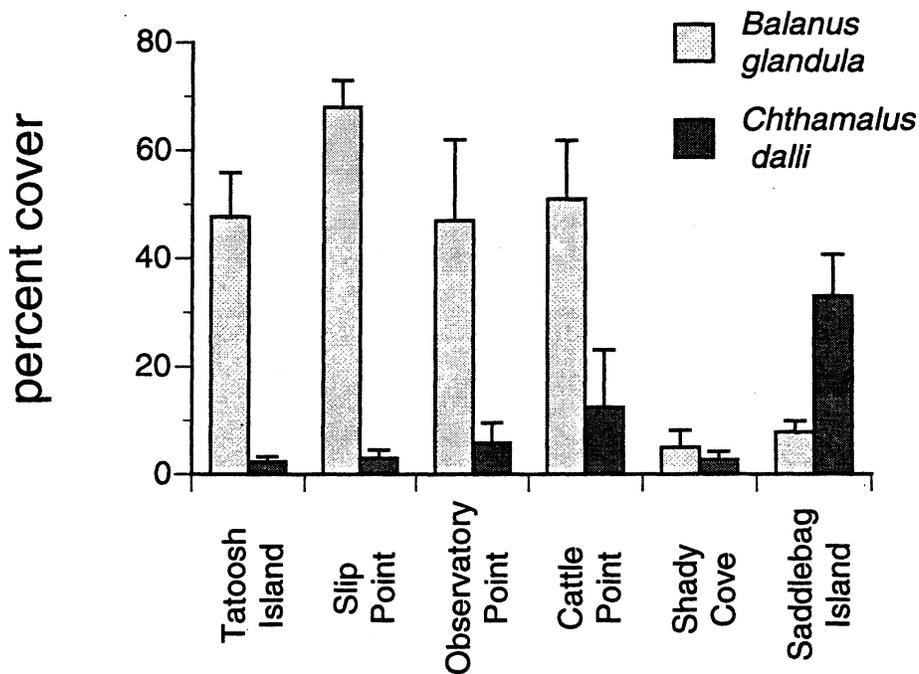


Figure 6. Regional variation in barnacle abundance. *Balanus*: 1-factor ANOVA, Tukey (TI,SP,OP,CP > SC,SI, $p < .001$); *Chthamalus*: 1-factor ANOVA, Tukey (TI,SP,OP,CP,SC < SI, $p = .004$).

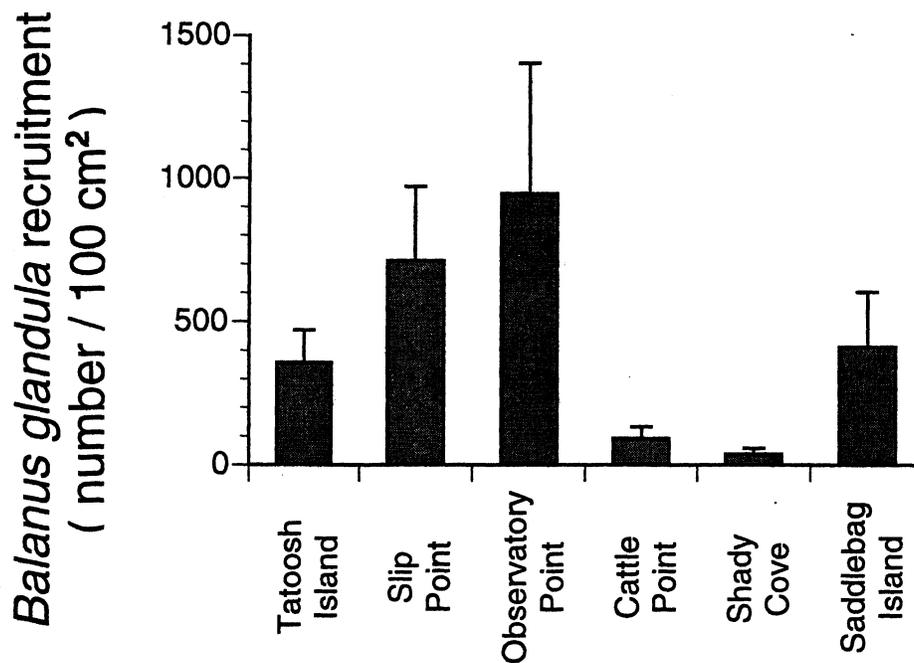


Figure 7. Regional variation in *Balanus glandula* recruitment. 1-factor ANOVA on log-transformed data, Tukey (TI,SP,OP,SI > SC, $p = .018$).

clearly not limiting on Saddlebag (Figure 7). In fact, Saddlebag recruitment rates are extremely similar to Tatoosh, and considerably greater than Cattle Point, both of which have more extensive adult barnacle populations. *Balanus* abundance patterns do not appear to be dictated by regionally variable growth conditions either (Figure 8). In fact, barnacle growth increases dramatically from west to east. The fact that the growth rates are high, but similar, at Cattle Point, Shady Cove, and Saddlebag, despite differences in flow regime (see Figure 4), suggests that ~1.5 mm/month may be a physiologically determined maximum growth rate.

Abundance, intertidal range, and diet of Pisaster

Pisaster abundance does not vary monotonically with the environmental gradient (Figure 9). From a numerical standpoint, *Pisaster* are extremely abundant on Saddlebag, fairly abundant on the Olympic Peninsula, less abundant at Shady Cove and on Tatoosh, and absent at Cattle Point. (Large site-to-site variation in *Pisaster* has been described before, but its causes are not readily apparent [Paine

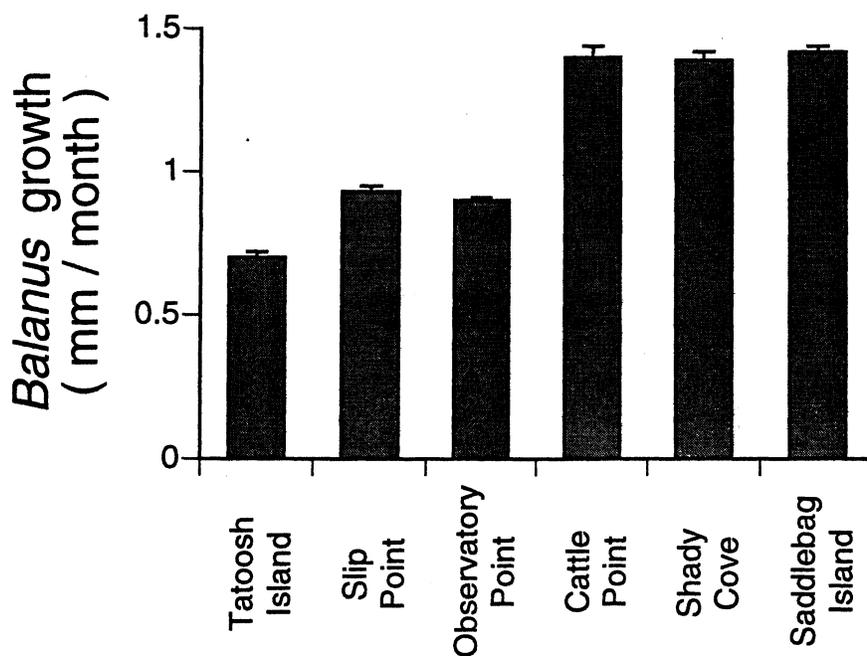


Figure 8. Regional variation in *Balanus* growth. 1-factor ANOVA, Tukey (TI<SP,OP<CP,SC,SI, $p < .001$).

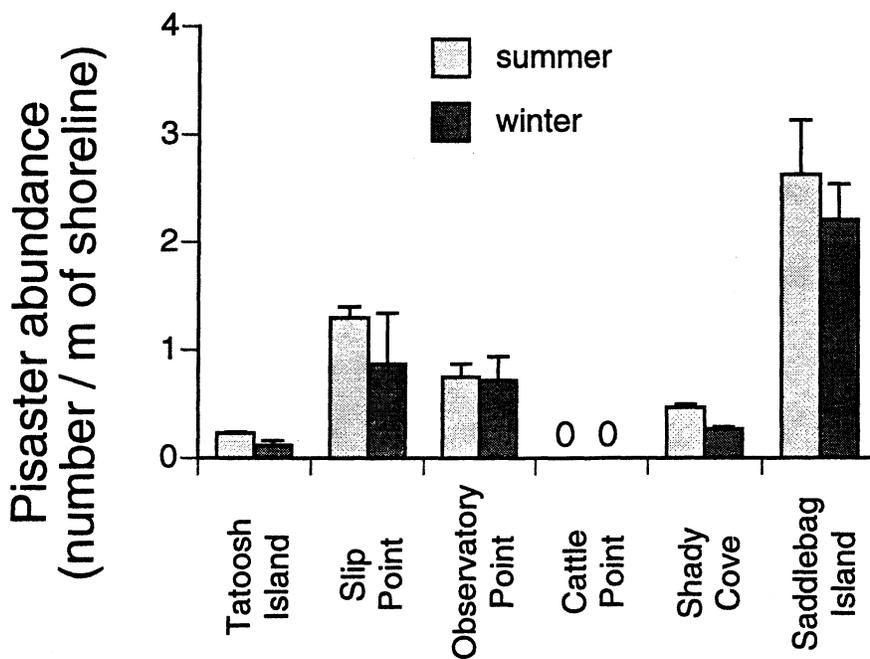


Figure 9. Regional pattern of *Pisaster* abundance. 2-factor ANOVA on log-transformed data: site ($p < .001$), season ($p = .006$), site x season ($p = .42$).

1976].) *Pisaster* are less abundant intertidally in the winter, possibly due to seasonality in feeding and reproduction (Mauzey 1966, Paine 1974).

Pisaster size varies from site to site as well (see Table 2). Although sea star wet weight was not measured in this study, size can be converted to mass with a simple regression equation (Paine 1976). Because the relationship is non-linear, the between-site differences in individual mass are even more pronounced than size differences (Table 2). In terms of total biomass, Tatoosh, Cattle Point, and Shady Cove are still on the low end of the scale. Because of small starfish size, Saddlebag actually has less *Pisaster* biomass per meter of shoreline than the Olympic Peninsula sites despite much greater sea star densities (Figure 10).

Table 2. Regional variation in *Pisaster* size and mass (mean \pm s.e.). Ray length is the distance between the mouth and the tip of a representative ray. Masses were determined by doubling the ray length to approximate diameter, and then inserting diameter into the pre-spawning diameter to mass regression equation provided by Paine (1976). 1-factor (site) ANOVA results for both ray length and mass: OP > TI = SP = SC > SI, $p < .001$. There were no *Pisaster* at Cattle Point.

| Site | ray length (cm) | mass (g) |
|-------------------|--------------------|---------------|
| Tatoosh Island | 13.7 \pm .5 | 864 \pm 75 |
| Slip Point | 14.9 \pm .3 | 910 \pm 40 |
| Observatory Point | 16.6 \pm .5 | 1290 \pm 86 |
| Cattle Point | NA | NA |
| Shady Cove | 14.0 \pm .3 | 767 \pm 28 |
| Saddlebag Island | 9.1 \pm .2 | 287 \pm 13 |

Pisaster positions at low tide were categorized as low (within 50 cm of MLLW), medium (50 - 100 cm above MLLW), and high (> 100 cm above MLLW). The percentage of the total *Pisaster* population foraging at different intertidal elevations on Tatoosh and Saddlebag are very similar (Figure 11).

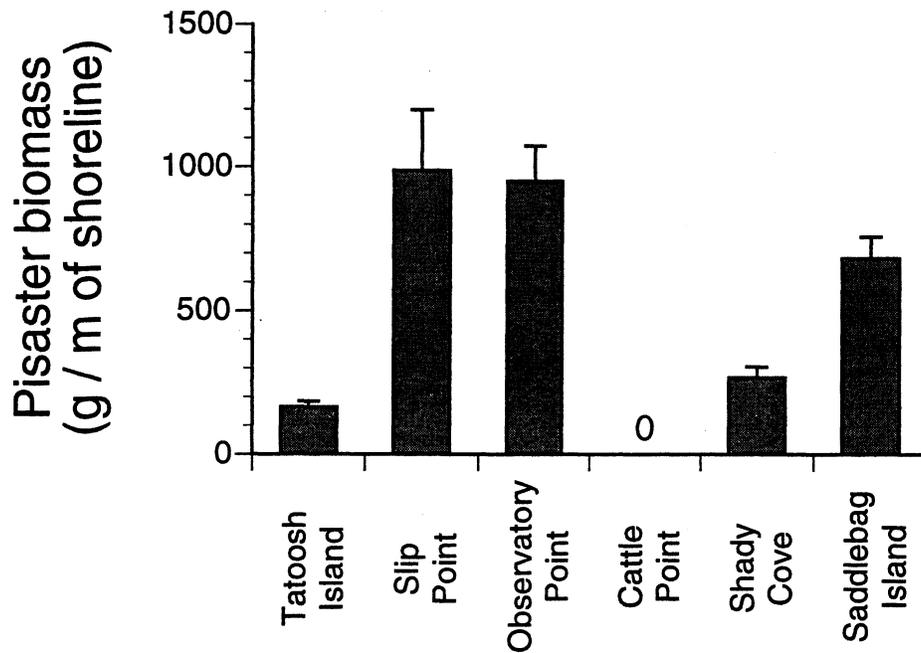


Figure 10. Regional distribution of *Pisaster* biomass per meter of shore. 1-factor ANOVA, Tukey (exclusive of CP data - TI,SC<SP,OP,SI, $p < .001$).

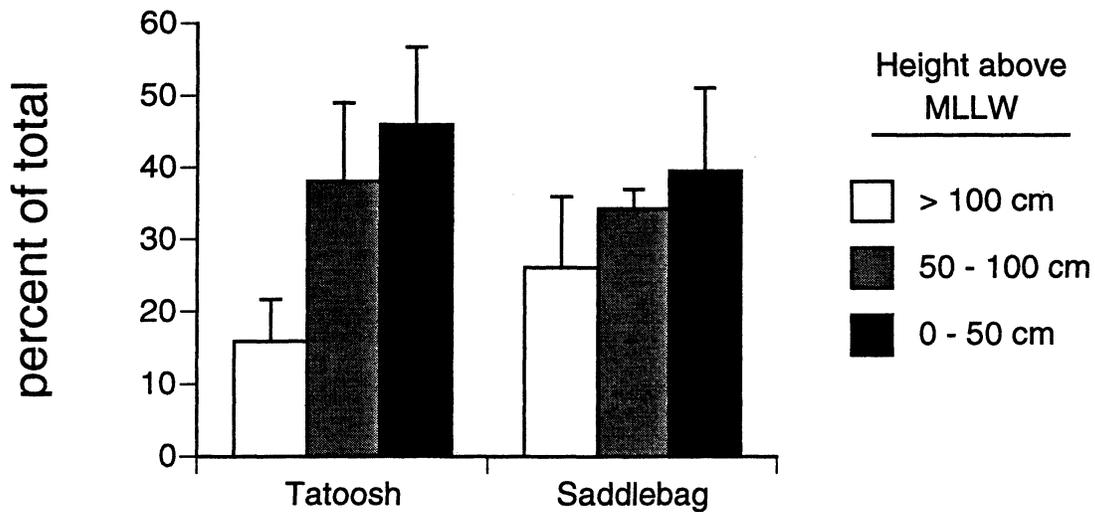


Figure 11. Vertical distribution of *Pisaster*. The percent of the local *Pisaster* population at various heights did not vary between Tatoosh and Saddlebag (1-factor ANOVAs on individual height categories: $p > .5$ in all cases).

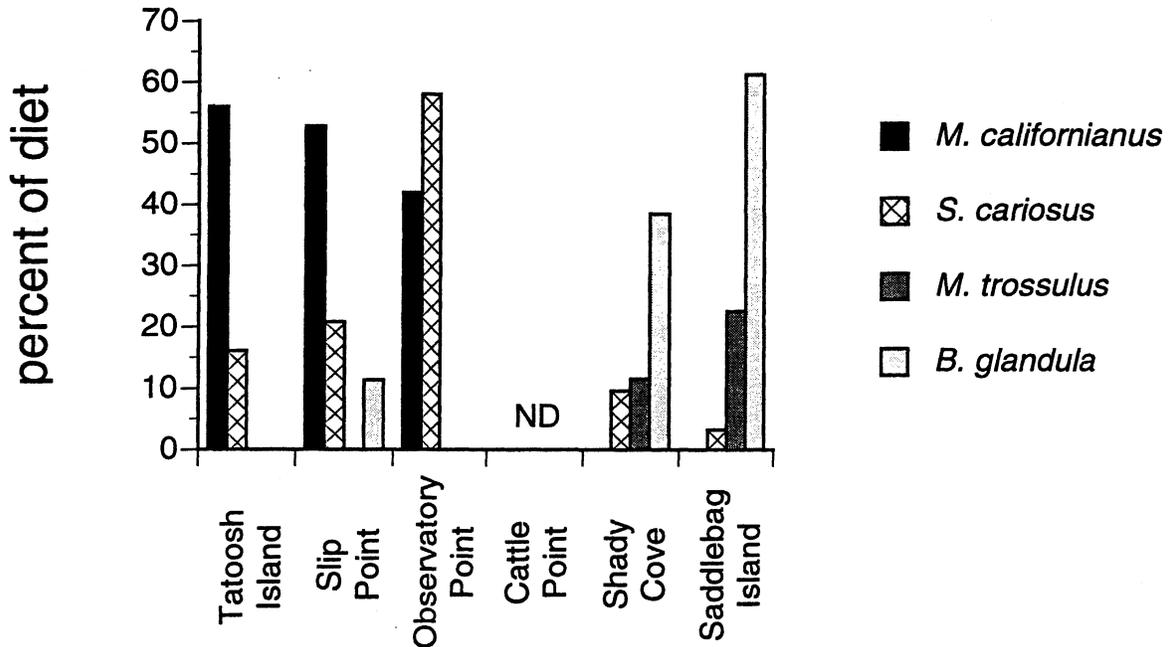


Figure 12. Regional variation in *Pisaster* diet, on a prey item (not total caloric value) basis. *Mytilus californianus* composes the majority of prey items in the west, while *Balanus glandula* forms is the most common prey item in the east.

Pisaster diet varied on the regional scale (Figure 12) in accordance with prey availability. Where *Pisaster*'s preferred prey, *Mytilus californianus* (Landenberger 1968), is abundant (Tatoosh, Slip Point, Observatory Point), it forms the bulk of *Pisaster*'s diet. Where *M. californianus* is absent (Shady Cove, Saddlebag), *Pisaster* must resort to less preferred prey items, such as *Balanus glandula*.

Predator manipulations

Sessile invertebrates responded dramatically to predator removals on Saddlebag Island (Figure 13a, c, e). Within the first two months, the percent cover of *Balanus glandula* rose slightly in the predator exclusion cages, but dropped significantly in the open areas. In the cage controls, which were created from full cages after the August census, *Balanus* cover declined through the fall, but have yet to reach the low levels seen in the open areas. *Mytilus trossulus* on Saddlebag followed the same general pattern (Figure 13c). By November, *Mytilus* was more abundant in predator exclusions than in open areas or cage controls. As *Balanus*

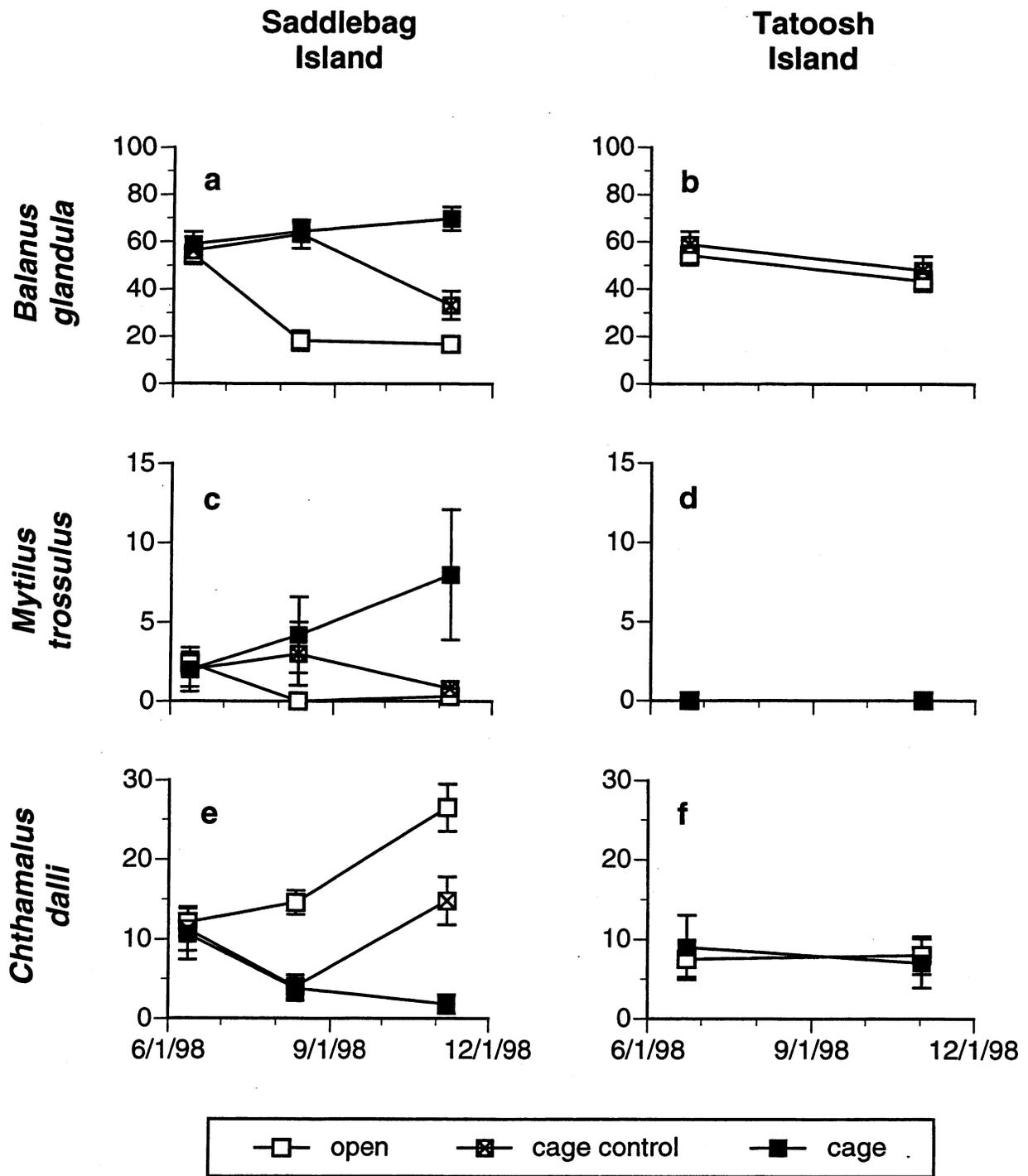


Figure 13. The effects of predator exclusion on sessile invertebrates on Saddlebag and Tatoosh Islands. Statistics are presented in Table 3.

and *Mytilus* increased in areas protected from predators, *Chthamalus dalli* cover decreased (Figure 13e).

On Tatoosh, where experimental plots had been scraped clear in the spring of 1996, the sessile invertebrate community had reached levels similar to undisturbed areas (compare Figure 13 to Figure 6). Despite an experimental duration of over two years, there was no difference in barnacle or mussel cover between open and cage treatments (Figure 13b, d, f).

Since invertebrate herbivores are smaller-bodied than *Pisaster*, the experimental cages did not influence the densities of the three most common herbivores: *Lottia strigatella*, *Lottia digitalis*, and *Littorina scutulata* ($p > .05$ for all three species at all three sampling dates, data not shown). Thus, caging probably did not significantly alter rates of herbivory.

Despite the similarity of herbivore densities between treatments, certain algae did differ between treatments. Both *Endocladia muricata* (Figure 14a) and ulvoids (Figure 14c) increase significantly in caged treatments on Saddlebag. These algae grow on barnacle tests, which likely retain some moisture during low tide. Fleshy red crusts, by comparison, grow predominantly on rock surfaces and are rare on barnacles. Not surprisingly, then, fleshy crust abundance declines in cages where barnacle abundance increases (Figure 14e). Finally, *Fucus gardneri* and *Mastocarpus papillatus* do not respond to predator exclusion. The high abundance of *Fucus* in cage controls in August is not a true treatment effect, since the cage vs. cage control distinction was randomly assigned after that data was collected. As with sessile invertebrates, algae were unaffected by predator exclusion on Tatoosh (Figure 14b, d, f, h, j). Table 3 provides post-hoc comparisons for any species exhibiting significant treatment effects.

Discussion

The influence of predators on Saddlebag Island

Predators clearly have a strong impact on sessile invertebrates on Saddlebag Island (Figure 13a, c, e). Prior to the recruitment of *Balanus* in May, *Chthamalus* was the dominant space occupier (personal observation). Although the magnitude of *Balanus* recruitment was great enough to temporarily swamp predators (the percent cover of rapidly growing *Balanus* was almost 60% in June, Figure 13a), the

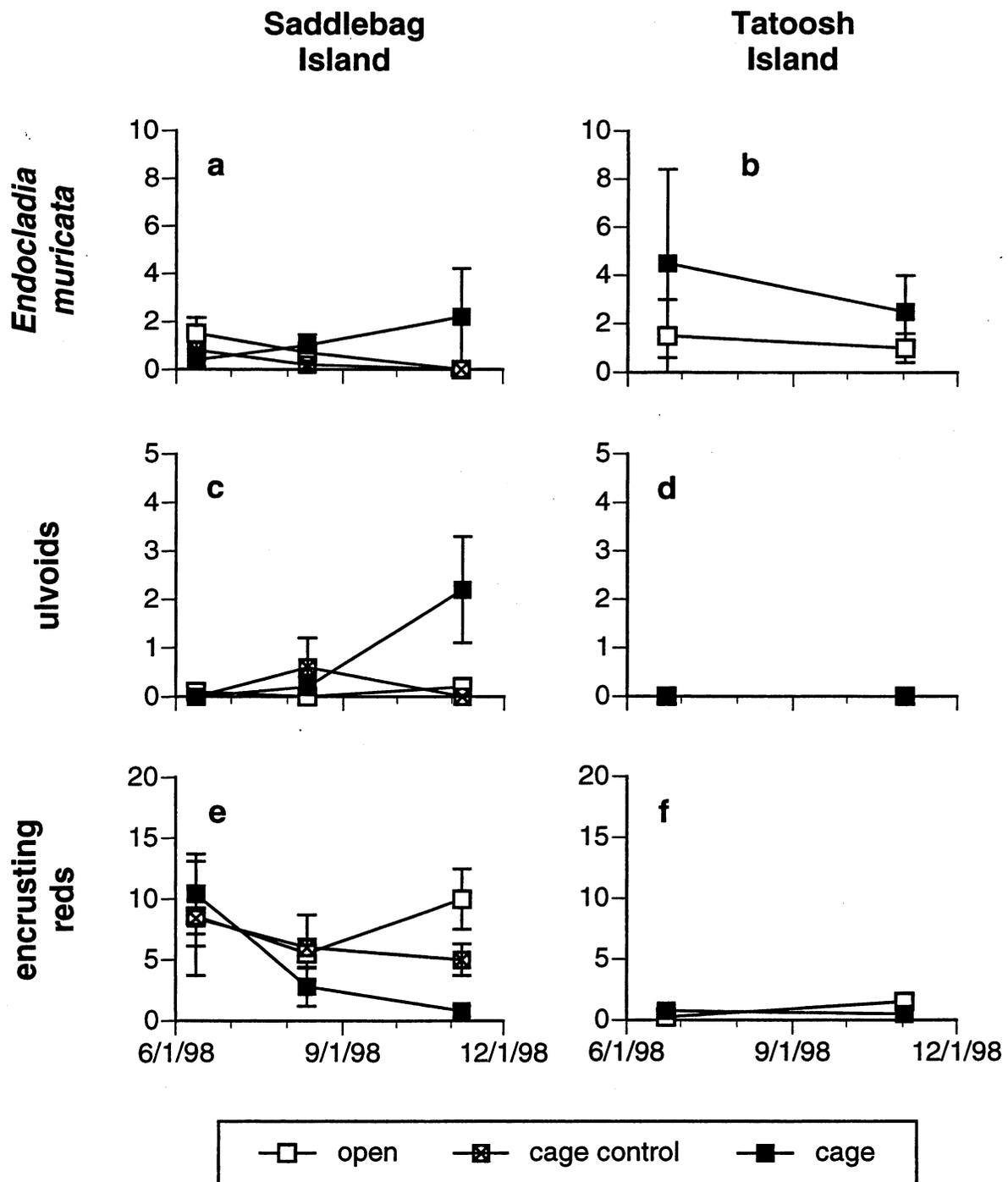


Figure 14. The effects of predator exclusion on algae on Saddlebag and Tatoosh Islands. Statistics are presented in Table 3.

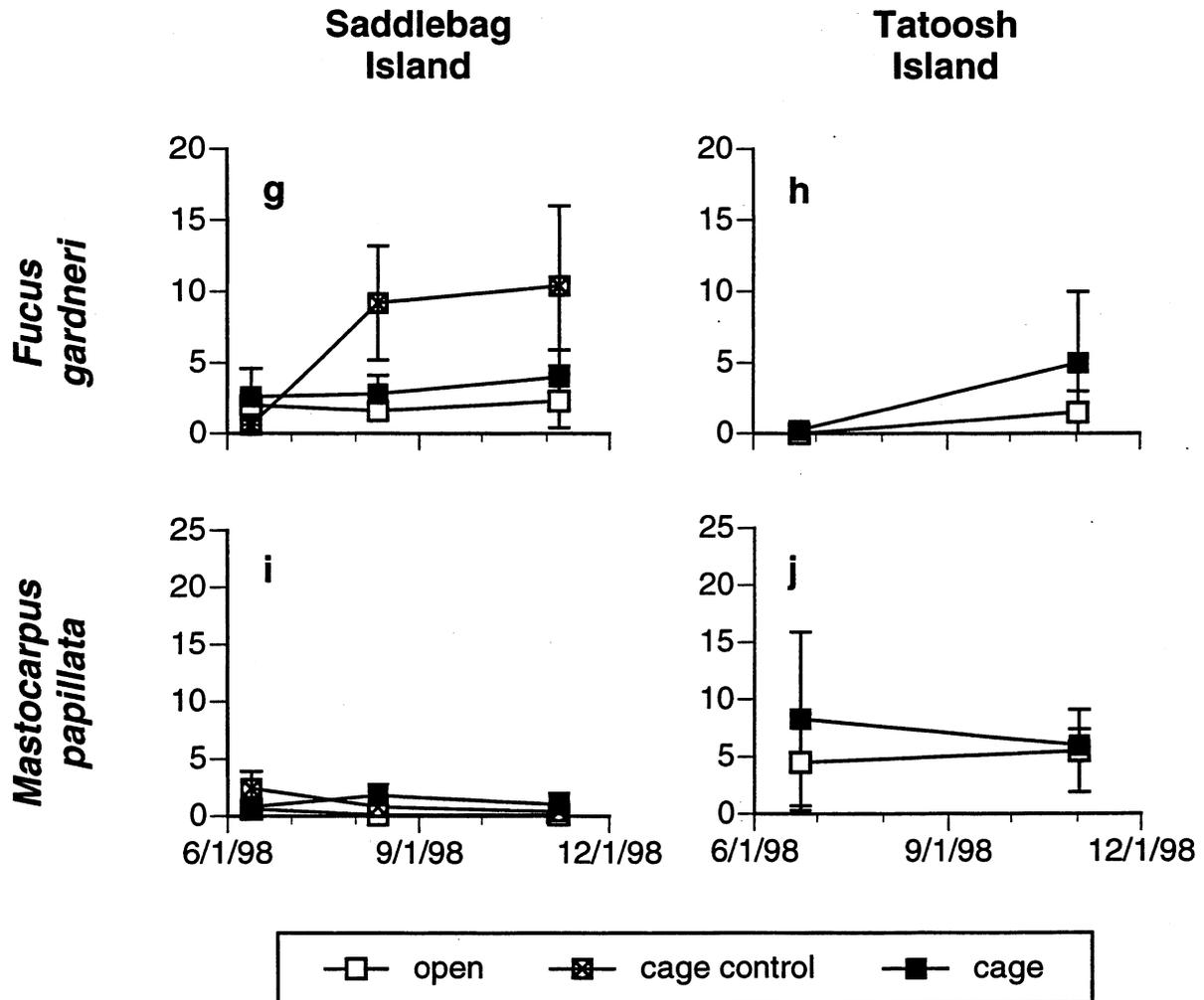


Figure 14 (continued).

community quickly returned to one dominated by *Chthamalus* in unmanipulated plots (Figure 13b).

In plots where predators were excluded, *Balanus* continued to increase its spatial coverage, and *Chthamalus* was gradually squeezed out. *Balanus glandula*'s competitive superiority over *Chthamalus dalli* is well established, and chthamalids are known to be favored by differential predation on competitively superior balanids (Dayton 1971, Paine 1981, Farrell 1991). Although *Balanus glandula* has been shown to compose a portion of *Pisaster*'s diet at other sites in the San Juan Islands (Mauzey 1966, Menge 1972), this is the first demonstration of *Pisaster* predation leading to increased *Chthamalus* abundance at a community-wide level.

Table 3. Post-hoc (Tukey) comparisons for all site-date combinations yielding a significant treatment effect (1 factor ANOVA) for a given species. O = open, C = cage, CC = cage control. The number below in parentheses is the p value; ns = non-significant. There were no significant ($p < .05$) treatment differences for any species on any date on Tatoosh Island.

| | 12 Jun 1998 | 12 Aug 1998 | 7 Nov 1998 |
|-------------------------------|-------------|------------------------|------------------------|
| <u>Saddlebag Island</u> | | | |
| <i>Balanus glandula</i> | ns | C=CC,O ($< .001$) | C>CC,O ($< .001$) |
| <i>Mytilus trossulus</i> | ns | C,CC>O (.024) | C>CC,O (.008) |
| <i>Chthamalus dalli</i> | ns | O>C,CC ($< .001$) | O>CC>C ($< .001$) |
| <i>Endocladia muricata</i> | ns | ns | C>CC,O (.013) |
| <i>ulvoids</i> | ns | ns | C>CC,O (.008) |
| <i>fleshy red crusts</i> | ns | ns | O>C (.006) |
| <i>Fucus gardneri</i> | ns | CC>C,O (.039) | ns |
| <i>Mastocarpus papillatus</i> | ns | ns | ns |

Predator exclusion also led to the appearance of *Mytilus trossulus*, which is exceptionally rare on Saddlebag except for certain refuge habitats. While barnacles are known to facilitate mussel recruitment in some situations (Petraitis 1987), this does not appear to be necessary in this instance as mussels recruited to irregularities in the rock in addition to areas dominated by barnacles (personal observation). The persistence of mussels, on the other hand, is almost certainly due to predator exclusion. Whereas barnacles are heavily preyed upon by sea stars,

mussels are vulnerable to both sea stars and cancrivorous crabs, which have been observed consuming mussels on Saddlebag (personal observation). Because the experimental cages excluded both crabs and *Pisaster*, it is impossible to know which type of predator limits mussel populations on Saddlebag, but it is likely that either sea stars or crabs would be sufficient in the absence of the other. (Barnacles, by comparison, are most likely limited predominantly by *Pisaster*. I have not seen crabs feeding on barnacles, although my intertidal observations at high tide are limited.)

Predator exclusion led to some interesting indirect effects on the algal components of the community, depending on how *Balanus* interacted with particular algal species. In the case of fleshy red crusts, which compete with barnacles for space, predator exclusion led to a significant decline (Figure 14e). For *Endocladia muricata* and ulvoids, which occur predominantly *Balanus* tests, predator exclusion led to significant increases (Figure 14a, c). Thus, the exclusion of *Pisaster* dramatically altered species abundances, both directly in the cases of *Mytilus* and *Balanus*, and indirectly in the cases of certain algae. The Saddlebag Island interaction web is summarized in Figure 15.

Regional scale pattern

In the Strait of Juan de Fuca, the regional gradient in environmental conditions is pronounced (Figures 2 and 3). These physical trends are accompanied by an alteration in species composition (Table I) from west to east. If species were to be adversely affected by increasing desiccation stress from west to east, they should be expected to shift their distribution down in the intertidal. This does in fact happen; the upper limits of *Balanus glandula* and *Mytilus californianus* descend from west to east. (Figure 5). However, the west-east pattern is more than a simple compression of intertidal zonation. Note that in Table 1, seven out of thirteen sessile species present at the western sites are absent on Saddlebag Island. Unlike sessile species, *Pisaster* moves up the shore when the tide is in and can retreat from potentially hazardous desiccating conditions by moving down as the tide ebbs. Perhaps because of this mobility, the upper range of *Pisaster* foraging is not greatly affected by the regional gradient in environmental factors (Figure 11), since these factors only impact the intertidal when the tide is out.

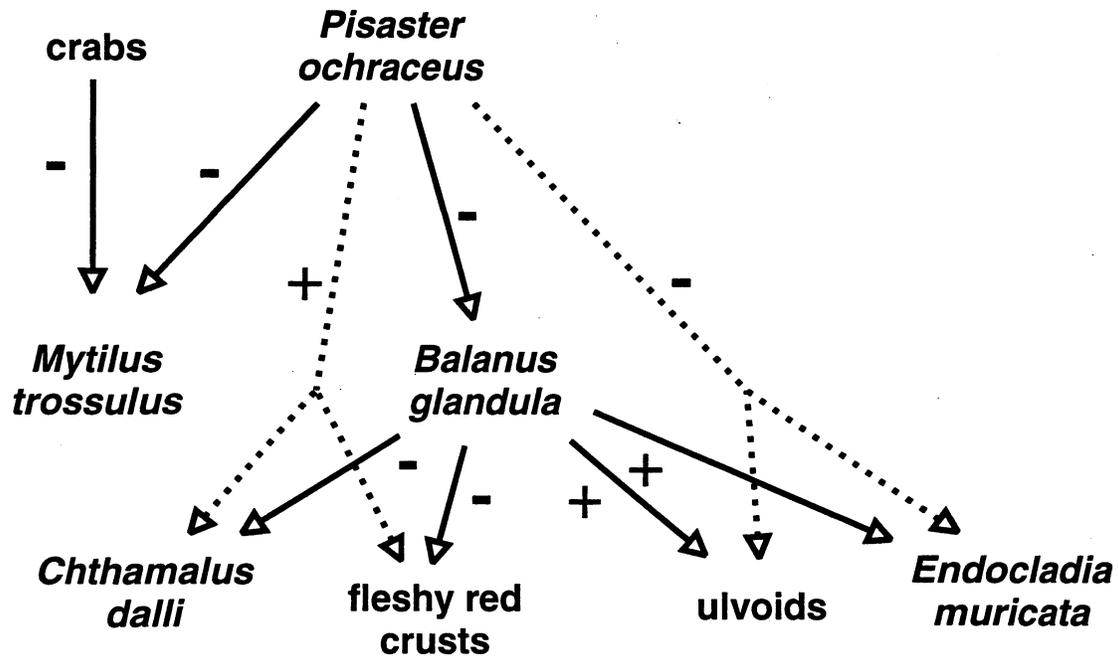


Figure 15. Interaction web for Saddlebag Island. Solid arrows are direct interactions; dashed lines are indirect interactions. "+" and "-" indicate positive and negative interactions, respectively.

As a result of species specific responses to the environmental gradient, invertebrates that can persist above *Pisaster's* effective foraging range on Tatoosh (i.e. *Mytilus* spp., *Semibalanus cariosus*, *Balanus glandula*) have their upper limits moved down to within reach of tide-tracking sea stars as one moves from west to east (see Figure 16). Any individuals of these species present on Saddlebag Island, where the entire intertidal is essentially available to *Pisaster*, may owe their existence to recruitment that can temporarily swamp predators. Otherwise, the only mussels and most of the barnacles are found in refuge habitats such as crevices where *Pisaster* cannot forage.

Implications

Differential responses to spatial or temporal environmental gradients are not new to ecologists. Plant species shifted their ranges at different rates and in different directions in response to the retreat of the North American ice sheet (e.g. Webb 1987). Because of species-specific responses to this temporal "gradient", entire communities (e.g. parklands) that were present 12,000 years ago no longer

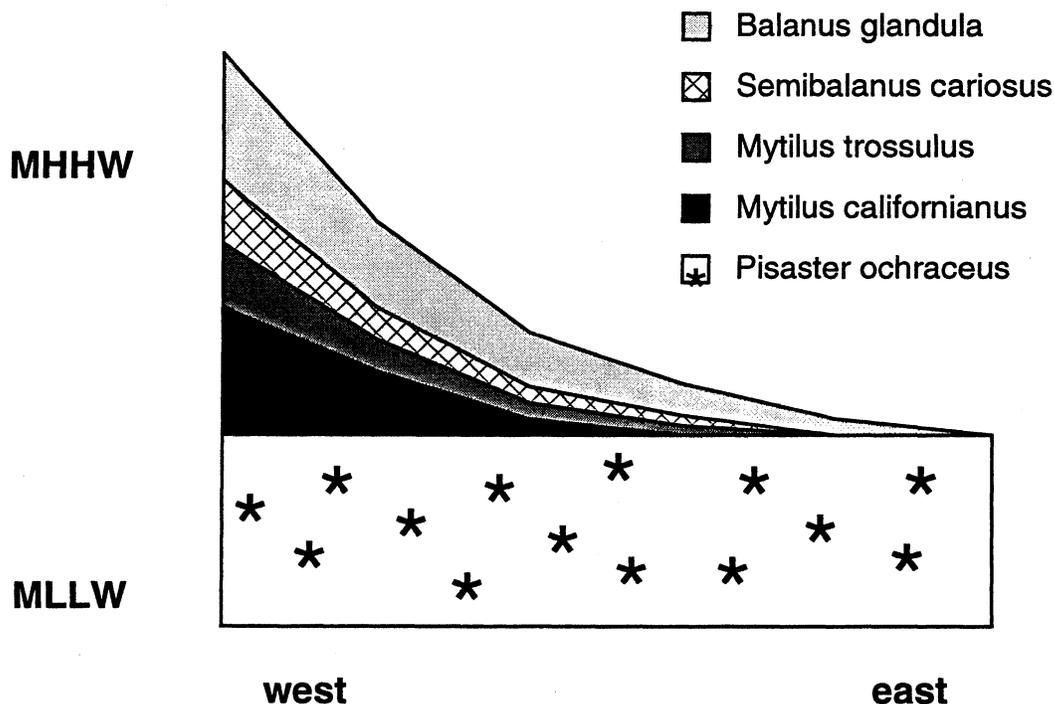


Figure 16. A simplified model of regional determination of community structure. Moving from west to east, the upper limits of sessile species descend until they intersect the upper foraging limit of *Pisaster*, which does not vary predictably from east to west. Sessile species gradually drop out towards the eastern end of the regional gradient as *Pisaster* is able to eliminate them or restrict them to refuge habitats.

exist in North America (Webb 1987, Overpeck et al. 1992). Ongoing range shifts occurring in response to climate change are also influenced by non-parallel environmental gradients (e.g. Parmesan 1996, Iverson & Prasad 1998). For example, Parmesan (1996) has shown that Edith's checkerspot butterfly populations are more likely to become extinct at low latitudes and low elevations as climate has warmed over the last century. What remains unknown is the nature of the butterfly's physiological tolerances relative to the tolerances of its host plants or potential predators. If the upper limit of the butterfly's range is determined by a physical or biological variable that does not move northward or upslope as quickly as the butterfly's lower limit, it is possible that the butterfly will be squeezed out

through time (i.e. become extinct) in much the same way that *Balanus* and *Mytilus* are squeezed out in space.

All ecosystems display spatial and temporal variability in environmental conditions, and few species, if any, have such restricted ranges that they are not distributed over multiple environmental gradients. Because potentially interacting species respond individualistically to various environmental gradients, predicting distributions over large spatial or temporal scales becomes a considerable challenge. Nevertheless, this is a challenge that ecologists must face if we are to understand the ways in which communities are structured in space and time. This knowledge will play a crucial role in our efforts to manage and conserve species now, and will be fundamental to our ability to predict the ecological consequences of future environmental change.

Conclusions

This study demonstrates that a conspicuous, regional scale biological pattern, i.e. the west-to-east decrease of *Balanus glandula* (Figure 6a), is only indirectly maintained by regional patterns in environmental variables. Previous work (e.g. Menge & Olson 1990) suggests that single large scale environmental gradients may alter the strength of interspecific interactions. This study emphasizes the importance of multiple, non-parallel gradients in determining not just the strength of interactions, but the spatial overlap of potentially interacting species. In this case, it is the differential vertical response of predator and prey across a large scale horizontal gradient that creates the observed regional scale biological pattern.

Acknowledgments

The staff at the Padilla Bay National Estuarine Research Reserve, particularly Mark Olson, were indispensable for the completion of this research. Their patience with my unorthodox schedule and less-than-skookum boat karma is gratefully acknowledged. The Pfaff family generously granted me access to their property at Observatory Point, and supplied me with much appreciated culinary treats. The Makah Tribe and the U.S. Coast Guard granted permission to work on Tatoosh Island. The manuscript benefited from the comments of Doug Bulthuis, Bob Paine, Sharon Riggs, Adrian Sun, and Marjorie Wonham. Support was

provided by an assistantship from the Padilla Bay NERR, and an NSF predoctoral fellowship.

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