Local- and regional-scale effects of wave exposure, thermal stress, and absolute versus effective shore level on patterns of intertidal zonation

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Abstract

Rocky intertidal ecosystems are characterized by marked zonation patterns in which species replace one another along the vertical gradient of emersion time. Yet, we still do not fully understand the reasons that zonation patterns are variable in space and time. Here, we use effective shore level (ESL), a metric that incorporates the modifying influence of wave splash, to describe the relationship between uninterrupted emersion time and the zonation patterns of two ecologically important species: the mussel *Mytilus californianus* and the barnacle *Balanus glandula*. At the local scale (10s to 100s of meters) on Tatoosh Island, the upper limits of both species are closely related to ESL, regardless of substrate aspect or maximum temperature. At larger spatial scales (10s to 100s of kilometers), the upper limit of *Balanus* is related to ESL at cool sites but not at hotter sites. Thus, although ESL explains most of the local-scale variation in zonation at a cool site, other factors (temperature, desiccation) likely become important as spatial scale increases to incorporate warmer sites. Our results emphasize that an understanding of where and when specific ecological factors are limiting is crucial for our ability to explain and predict large-scale biological patterns in space and time.

Recent advances in physiology, ecology, and biological oceanography have considerably improved our understanding of the environmental factors that generate and maintain biological pattern in the marine environment (Bertness et al. 2001; Dahlhoff et al. 2001; Helmuth and Hofmann 2001). Emerging from this recent work is the realization that the importance of any given environmental driver may vary tremendously through space and time (e.g., Bertness and Ewanchuk 2002). The present challenge for ecologists is to understand when and where organisms respond to specific drivers in their environment. Only with such an understanding will we be able to predict the ecological outcomes of perturbations resulting from resource extraction, changes in species composition (e.g., species introductions and extinctions), and changes in climate.

In intertidal systems, environmental conditions range from fully aquatic to fully terrestrial over the space of a few vertical meters. The resultant patterns of biological zonation are

striking and have been documented worldwide (see, e.g., Knox 2001). The positions of the upper and lower limits of biological zones provide easily quantifiable biological benchmarks for ecological comparisons through space (between sites separated by centimeters to hundreds of kilometers) and time (between seasons, years, decades). Intertidal zonation is influenced by a variety of factors, including wave exposure (Evans 1947; Stephenson and Stephenson 1961; Lewis 1964), temperature (Wethey 1983), salinity (Druehl 1967), substrate orientation and composition (Raimondi 1988; Harley in press), and tidal dynamics (Denny and Paine 1998). Owing to this complexity, variation in one factor often masks the effects of another. Wave exposure in particular has such a dramatic local effect on zonation patterns that it is often difficult to identify the impacts of other variables.

Because intertidal zonation patterns are driven, directly or indirectly, by emersion time, wave action tends to extend biological zones vertically (upshore) by effectively reducing the duration of emersion at any given shore level. Early workers recognized this phenomenon and attempted to standardize zonation patterns across exposure regimes by using the concept of an "effective" position on the shore (Evans 1947; Lawson 1957; Glynn 1965). For the purposes of this paper, we define the effective shore level (ESL) of a given point in the intertidal zone to be equal to the absolute shore level (i.e., the vertical distance above still-water chart datum) with equivalent emersion characteristics (timing and duration) in the absence of waves. We describe the practical measurement of ESL and relate ESL to offshore wave conditions through time. We then examine patterns of ESL through space at multiple sites in northern Washington, U.S.A. Specifically, we explore the relationship between ESL and the

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upper limits of mussels and barnacles with respect to local (10s to 100s of meters) scale variation in wave action and substrate aspect, as well as the upper limit of barnacles with respect to regional (10s to 100s of kilometers) scale variation in thermal stress.

Methods

Study sites-This research was conducted in the Northwest Straits of Washington State (Fig. 1A), which extend from the Pacific Ocean, through the Strait of Juan de Fuca and the San Juan Islands, and into Puget Sound. The primary field site was Tatoosh Island (Fig. 1B), which lies approximately 0.6 km off the NW tip of the Olympic Peninsula. Tatoosh is typified by cool air temperatures, frequent cloud cover, and fog. Wave exposure ranges from moderately protected in sheltered coves to extreme on exposed benches. As a result of this broad range of wave exposures, the upper limits of bed-forming species are highly variable from site to site around the island (Suchanek 1978; Leigh et al. 1987). Additional field sites included Slip Point (48°15.8'N, 124°15.2'W) and Observatory Point (48°09.2'N, 123° 38.5'W) on the Olympic coast, Colin's Cove (48°32.9'N, 123°00.4'W) on San Juan Island, and Saddlebag Island (48° 32.2'N, 122°33.5'W) in northern Puget Sound. Generally speaking, this west-to-east longitudinal gradient is accompanied by decreasing wave action, increasing insolation, and moderately variable tidal amplitude (Table 1), as well as increased frequency of midday lower low tides in summer (Helmuth 1999; Helmuth et al. 2002), all of which may alter physiological stress at a given height on the shore.

Measurement of effective shore level-Estimating effective shore level requires a way to measure emersion characteristics through time. One means of estimating the ESL of a given point is to record the time at which that point is first wetted by the incoming tide; the ESL is equal to the predicted still tide level at this time. For example, consider a point on the shore 3 m above chart datum. The absolute shore level (ASL) of this point is mean lower low water (MLLW) + 3 m. If this point is just wetted by waves when the still tide level is 1 m below this point, then the ESL for that tidal cycle is equal to ASL minus 1 m, or MLLW +2m. Note that the point of interest at +3 m ASL/+2 m ESLwill be fully submersed for slightly less time than a point of +2 m ASL/+2 m ESL (at a site with no wave action). However, the duration of uninterrupted emersion during low tide will be equivalent at the two points (despite a meter difference in absolute shore level), and factors that depend on the duration of emersion, such as desiccation and thermal stresses, are expected to be comparable at these two points.

Because effective shore level varies through time with the wave regime, ESL should be viewed as a probabilistic distribution rather than as a constant. Extensive observations are thus required before reliable estimates of mean ESL can be made. For this reason, ESL has seldom been used in a quantitative fashion (but *see* Glynn 1965; Druehl and Green 1982). However, recent technological advances allow these measurements to be made easily and inexpensively via the use of serially recording temperature loggers. Conveniently,



Fig. 1. (A) Map of the Strait of Juan de Fuca region. Study sites, indicated by stars, are Tatoosh Island (TI), Slip Point (SP), Observatory Point (OP), Colin's Cove (CC), and Saddlebag Island (SI). (B) Map of Tatoosh Island. The asterisk indicates the location of the six TidbiT logger deployment microsites. Closed wedges and open wedges indicate the locations of the north-facing and southfacing iButton mussel-mimic deployment microsites, respectively.

the return of the tide is often marked by a sharp thermal discontinuity, which is measurable with such loggers (Fig. 2). Temperature loggers also provide quantitative information on the thermal characteristics of the habitat, which can

Table 1. Abiotic conditions at the regional scale. Wave exposure rankings (1 = most exposed) were made using observations of breaking wave heights and species composition (Harley 2001). Sunny days are defined as those with >50% sunshine during low tide. Wave and atmospheric data represent summer (April–September) conditions only. Tidal amplitude, defined here as the difference (in centimeters) between mean higher high water and mean lower low water, was calculated for May–August 2000 using HarborMaster software (version 5.2).

Site	Wave exposure rank	% sunny days (n)	Tidal amplitude
Tatoosh Island	1	30 (40)	237
Slip Point	3*	47 (15)	221
Observatory Point	2	38 (16)	212
Colin's Cove	5	69 (16)	239
Saddlebag Island	4	52 (25)	262

* Although much of Slip Point is more exposed than Observatory Point, areas of high intertidal bedrock with extensive *Balanus glandula* populations investigated here are relatively protected.

in turn be used to estimate frequency of cellular damage due to thermal stress (Hofmann and Somero 1995; Helmuth and Hofmann 2001; Helmuth et al. 2002).

To obtain long time series of ESL and temperature, we used TidbiT[®] loggers (Onset Computer Corporation) embedded in epoxy that was then shaped to resemble an 8-cm mussel (Mytilus californianus). The size, shape, color, and thermal inertia (mass \times specific heat) of these mussel mimics were designed to approximate the thermal characteristics of live mussels of similar size (Helmuth and Hofmann 2001; Helmuth et al. 2002). The TidbiTTM mussel mimics were deployed at a nearly uniform absolute shore level (MLLW + 1.5-1.7 m) at six microsites along a 50-m transect in Strawberry Draw on Tatoosh Island (see Fig. 1). The location of each logger varied slightly between deployment periods (loggers were relocated following disturbance events in the mussel bed) but remained within this 20-cm tidal range. Tidal heights were verified using a laser level, relative to a benchmark where still tide height had been measured repeatedly (C.H. unpubl. data). Mussel mimics were attached to the shore using epoxy (Z-spar splash zone epoxy, Kopcoat Corporation) and maintained lateral contact with the surrounding mussels in the mussel bed matrix. Temperature data, with a resolution of 0.3°C, were collected nearly continuously from June 2000 to August 2002 at sampling intervals of 10-15 min.

ESL for an individual rising tide was defined as the predicted still-water tide height (Xtides, http://tbone.geol.sc. edu/tide, or equivalently HarborMaster 5.2, Zihua Software) at the time of first wetting upon the tide's return. We estimated the time of the tide's return based on temperature decreases $\geq 3.0^{\circ}$ C over 20 min (or, $>2.25^{\circ}$ C per 15 min) during rising tides. Data from a fully terrestrial logger indicate that climate-driven (tide independent) temperature drops of this magnitude were rare, and preliminary analyses indicated that increasing this threshold from 3°C to 5°C, while potentially reducing false positives, incurred a substantial cost in sample size.



Fig. 2. Data from a mussel-mimic logger showing the sharp decline in temperature as waves first begin to hit the instrument. The time of this first drop (of at least 3°C in 20 min) is then matched against predicted still tide height level to yield the ESL for that day.

To determine the relationship between offshore wave climate and temporal patterns of ESL, we used maximum daily significant wave height and median wave direction recorded at the nearest available buoy (Cape Elizabeth, National Data Buoy Center buoy 46041; 47°20.4'N, 124°45.0'W). Wave height data were ln x transformed to improve normality. Because the nonnormal nature of the ESL data could not be improved with standard transformations, we used ln (ASL – ESL) for the purposes of these regression analyses. ESL data were normalized to a fixed ASL of MLLW +1.7 m.

ESL, temperature, and the upper limits of sessile invertebrates—We addressed the thermal and emersion environment as applied to the upper limits of two species of intertidal invertebrates: the mussel Mytilus californianus and the barnacle Balanus glandula. M. californianus is common on Tatoosh, where it forms extensive midintertidal beds. Although it is a community dominant at coastal sites from Alaska to Baja (Morris et al. 1980), M. californianus is rare or absent at most sites in the San Juan Islands and Puget Sound (Kozloff 1993; pers. obs.). B. glandula is the dominant barnacle in high intertidal habitats in the Northeast Pacific (Morris et al. 1980), where it forms extensive beds in a discrete zone. It occurs at all sites surveyed in this study.

To obtain thermal time series that approximated mussel body temperatures at the upper range of their intertidal distribution, iButton⁽¹⁾ temperature loggers (Dallas Semiconductor) were embedded in *M. californianus* shells using silicone rubber sealant. These mussel mimics were also attached using Z-spar. This design has been shown to approximate the body temperatures of live mussels measured in the field to within a few degrees Celsius (Helmuth and Hofmann 2001). Additional iButtons were used to estimate the thermal and emersion conditions experienced by the barnacle *B. glandula.* To this end, iButtons were wrapped in aluminum foil and epoxied (Sea Goin' Poxy Putty, Permalite Plastics) into shallow depressions chiseled into the substrate. Small grain (~1 mm) rock fragments were pressed into the setting epoxy to mimic the surface albedo of the surrounding rock. Rock temperatures, as measured with iButtons as described above, are excellent predictors of barnacle body temperatures ($T_{\text{barnacle}} = 0.866T_{\text{substrate}} + 2.36$, $r^2 = .981$, data in degrees Celsius; Harley and Lopez 2003).

The iButton mussel mimics were deployed along the upper limit of the mussel bed at eight north- and eight southfacing sites on Tatoosh (Fig. 1). These loggers recorded temperatures (with a resolution of 0.5°C) once every 20 min from 14 July to 11 August 2000. The rock-embedded barnacle mimics were deployed at two different scales. At the local scale, these loggers were deployed at three north-facing and three south-facing sites at the upper limit of B. glandula on Tatoosh. These loggers recorded temperatures at 20-min intervals from 17 July through 13 August 2000. At the regional scale, rock-embedded iButtons were deployed at five localities in the Northwest Straits (see above) at two shore levels: a standard 1.5 m (ASL) above MLLW and at the top of the Balanus glandula zone. These iButtons recorded temperatures once every 20 min for the month of July 2000 (the month shown by the TidbiT loggers to be one of the hottest months of the year on Tatoosh). Three iButtons were deployed at both heights at each site, but many of these malfunctioned or were lost. The remaining sample sizes, for [+1.5 m, top of zone], were Tatoosh [3,3], Slip Point [2,2], Observatory Point [2,2], Colin's Cove [3,3], and Saddlebag Island [1,3].

As with the TidbiT⁽³⁾ data, ESL was determined by identifying the still-water level associated with temperature decreases $\geq 3.0^{\circ}$ C over 20 min on rising tides. Exceptions to these sorting rules were made for the upper limit of barnacles on Tatoosh, where the rarity of immersion and the frequency of stochastic 3°C temperature drops made the identification of the emersion/immersion transition difficult to pinpoint. For these loggers, the temperature threshold was set to 4°C during the day and 2°C during the night to maximize the available estimates of ESL and minimize error. Because maximum ESL approximates absolute shore level, we use the average ESL to describe the emersion characteristics of each site as distinct from ASL.

The thermal characteristics of each sampling location were described using several metrics. The first and simplest of these was the absolute maximum temperature recorded over the sampling interval. The second was the mean of all the daily maxima over the same period. Finally we calculated total degree hours above a fixed threshold temperature. Total degree hours was the sum of all recorded temperatures above a given threshold minus that threshold, divided by three to adjust the 20 min sampling interval to units of hours. For loggers that represented mussels, the temperature threshold was set to 25°C, a temperature shown to inhibit the synthesis of those proteins not involved in the heat shock response in M. californianus (Roberts et al. 1997). For B. glandula, the inhibition of protein synthesis, while highly variable between individuals, becomes most obvious at body temperatures of 33°C (M. Berger pers. comm.). Therefore, we set the threshold rock surface temperature to 35°C, which corresponds to predicted barnacle temperatures of 32.7°C (*see* Harley and Lopez 2003).

For the purposes of interpretation, it is of interest to know which metric (ASL, ESL, or some aspect of temperature) is least spatially variable at the upper limit of mussels or barnacles and thus the most likely to be causally linked to the vertical distributional limits of these invertebrates. This is a difficult comparison to make, since the five variables differ in units and in range relative to the mean. To standardize across variables, we divided values in each data series by the maximum range of that series. Because we were interested in whether or not each variable was related to the extreme tolerance limit of intertidal organisms, we set the upper limit of the potential range equal to the highest value recorded in the field. The lower limit of the potential range was determined by a biologically relevant minimum: extreme lower low water for ASL and ESL, and the average temperature of sea water for the temperature-based metrics. The amount of variation in these standardized data was compared using F tests. All statistics were performed in JMP 3.2.6 (SAS Institute).

Results

Temporal patterns in wave height, ESL, and mussel temperature-Because of instrument loss, the number of loggers used to record temporal patterns of mussel body temperature at midlevel heights on Tatoosh Island ranged from three to five. Both the extreme monthly maximum temperature (a metric of rare events, or acute stress, Helmuth and Hofmann 2001) and the average daily maximum (a measure of chronic high temperature stress) occurred in June at this site, but the month of July was nearly as hot as this peak month (Fig. 3A). Monthly high extrema varied from a low of 10°C in January to over 30°C in June, and considerable variability (i.e., a high standard deviation) often occurred among microsites. Variability in the average daily maximum temperature was lower and was almost negligible for metrics of monthly average, average daily minimum, and monthly minimum temperatures (Fig. 3A).

ESL varied seasonally, with a peak in late summer (Fig. 3B). ESL was calculated only for the months of April-September, as emersion times during cooler times of the year were difficult to discern. Seasonal dips in ESL correspond to larger waves measured offshore (Fig. 3C). The difference between ASL and ESL (a measure of wave run-up) was positively related to offshore wave height, varied with median wave direction (southwest swell > northwest swell), and differed between microsites (analysis of covariance [ANCOVA]: wave height $F_{1,739} = 404$, $p \ll 0.001$; median wave direction $F_{1,739} = 28.1, p \ll 0.001$; microsite $F_{5,739} =$ 22.6, $p \ll 0.001$). Wave height, wave direction, and microsite explained 30.3%, 1.9%, and 8.5% of the variation in the data, respectively. Offshore wave height alone explained between 19.6% and 38.7% of the variability at individual microsites (data not shown).

Local-scale patterns: upper limits of mussels and barnacles—The upper limit of Mytilus californianus occurred at



Fig. 3. Seasonal variation in (A) mussel-mimic temperature, (B) average effective shore level of mussel mimics, and (C) average daily maximum significant wave height measured at Cape Elizabeth. Temperatures are too cool to discern ESL in the months of October–March. Wave data are missing for January–February 2001 and March–May 2002.

similar shore levels on north- and south-facing surfaces, both in terms of absolute shore level and effective shore level (Fig. 4A, Table 2). The temperature characteristics of mussel mimics at the upper limit of the mussel bed did not differ with substrate aspect, whether measured as absolute maximum temperature, average daily maximum temperature, or total degree hours above 25°C (Fig. 4A, Table 2). The vertical position of the upper limit of *Balanus* was also aspect invariant; neither ASL nor average ESL differed between aspects. Rock temperatures at the upper limit tended to be cooler on north-facing surfaces, particularly in terms of maximum temperatures and total degree hours >35°C (Fig. 4B). However, these differences were not statistically significant following a Bonferroni correction of α to 0.01 to adjust for the multiple tests (Table 2). It should be noted that sample sizes were minimal (n = 3), and the power to detect differences at $\alpha = 0.01$ was low (0.22 and 0.18 for maximum temperature and degree hours, respectively).

Regional-scale patterns: upper limit of barnacles-Average daily maximum rock temperatures at midtidal shore levels (MLLW + 1.5 m) varied at the regional scale, ranging from $<20^{\circ}$ C on Tatoosh to $>30^{\circ}$ C at Colin's Cove. The absolute shore level of the upper limit of Balanus glandula, after correcting for local variation in tidal amplitude, declined with increasing midtidal substrate temperatures (Fig. 5A). On cool, wave-swept shores (e.g., Tatoosh Island and Observatory Point), barnacles occurred well above predicted mean higher high water (MHHW). At hotter protected sites (e.g., Colin's Cove and Saddlebag Island), barnacles were restricted to shore levels well below MHHW. As a result, standardized ASL was strongly negatively correlated with midtidal rock temperature ($F_{1,9} = 67.5$, $p \ll 0.001$, Bonferroni sequentially corrected $\alpha = 0.01$, $r^2 = 0.869$). Average ESL, similarly standardized to tidal range, was also negatively related to midtidal rock temperature, although the nature of this pattern was distinctly different. At cooler sites, the upper limit of barnacles occurred at a nearly uniform average ESL near MHHW despite >10°C differences in midtidal substrate temperatures. Above a threshold of approximately 26°C, however, average ESL declined sharply with increasing midtidal temperatures (Fig. 5B). A second degree polynomial provided the best fit to the data: ([ESL] = 28.92 + 6.34[temperature] - 0.159[temperature]²; $F_{2.8} =$ 18.9, p < 0.001, Bonferroni sequentially corrected α = 0.0125, $r^2 = 0.781$). Maximum temperature, average daily maximum temperature, and total degree hours above 35°C at the upper limit of the barnacle zone were positively (but weakly) related to midtidal rock temperatures (Fig. 5C-E), but none of these correlations were significant after sequential Bonferroni correction of α to 0.017 (maximum temperature: $F_{1,9} = 5.92$, p = 0.038, $r^2 = 0.330$; average daily maximum temperature: $F_{1,9} = 6.89$, p = 0.028, $r^2 = 0.371$; log (total degree hours): $F_{1,9} = 5.38$, p = 0.046, $r^2 = 0.305$).

Environmental variability along the upper limits—The average ESL of the upper limit of the mussel bed on Tatoosh is much less variable than the ASL (see Fig. 4); the total range of the former is 28 cm, as compared to a range of 142 cm for the latter. Once ESL, ASL, and the three temperature metrics were normalized by their possible range of variation, average ESL was least variable of all measured parameters, followed by average daily maximum temperature, ASL, absolute maximum temperature, and total degree hours (Table 3A). *F* tests reveal that average ESL is significantly less variable, and total degree hours above 25° C significantly more variable, than ASL and metrics of maximum temperature. We acknowledge that these analyses hinge on the values chosen as potential ranges and that arguments could be



Fig. 4. Box and whisker diagrams of environmental variables on north- versus south-facing surfaces at the upper limits of (A) *Mytilus californianus*, and (B) *Balanus glandula*. Data from the upper limit of *Mytilus* were derived from mussel mimics (n = 8 per aspect). Data from the upper limit of *Balanus* are based on rock temperatures (n = 3 per aspect). The lower whisker, lower box boundary, midline, upper box boundary, and upper whisker correspond to the 10th, 25th, 50th, 75th, and 90th percentiles, respectively. The filled diamonds are arithmetic means. Note the differences in *y*-axis scaling between ASL, which is highly variable in both cases, and average ESL, which is not.

made for the use of alternative range values. Therefore, we conducted additional analyses to gauge the sensitivity of our results to the range values used. The statistically significant differences between total degree hours above 25°C and maximum and average maximum temperatures are sensitive to changes of <10% of the range; we thus recommend that these results be interpreted with caution. The results obtained for all comparisons involving average ESL were robust to simultaneous, independent alterations of range values by >25% in either direction, which supports the hypothesis that ESL is indeed less variable than ASL or any temperature-based metric.

The average ESL of the upper limit of *Balanus* was the least variable environmental correlate at the local scale, being significantly less variable than ASL and the three temperature metrics (Table 3B). As was seen with the upper limit of *Mytilus*, degree hours were significantly more variable than all other metrics. These statistical differences were robust to the simultaneous variation of range estimates by 25% in either direction.

At the regional scale, ASL, average ESL, and temperature characteristics of the upper limit of *Balanus* showed moderately high variability relative to their potential range. Total degree hours above 35°C was the most variable, being sig-

Variable	Upper limit of Mytilus californianus		Upper limit of <i>Balanus glandula</i>	
	${F}_{1,14}$	р	${F}_{\scriptscriptstyle 1,4}$	р
ASL	0.51	0.487	0.22	0.667
ESL	0.32	0.581	2.12	0.220
Maximum temperature	2.25	0.155	8.20	0.046
temperature	2.89	0.111	1.23	0.330
Total degree hours	2.58	0.130	6.88	0.059

Table 2. Statistical comparisons (ANOVA) of environmental variables on north- versus south-facing surfaces at the upper limits of *Mytilus californianus* and *Balanus glandula*. Data from the upper limit of *M. californianus* were collected using mussel mimics (n = 8 per aspect). Data from the upper limit of *B. glandula* are based on rock temperatures (n = 3 per aspect). Total degree hours (*see text for explanation*) were ln (x + 1) transformed to meet the assumption of normality.

nificantly more variable than absolute maximum temperature, ESL, and average daily maximum temperature (Table 3C). These statistical differences hold up even when the potential range values are allowed to vary independently by $\pm 25\%$. All other metrics exhibited statistically similar levels of variability.

Discussion

Intertidal height is correlated with many physical and biological parameters that are relevant to littoral species. The long emersion times associated with higher positions on the shore result in a variety of potential stresses, including extremes in temperature (Roberts et al. 1997; Tomanek and Somero 1999; Stillman and Somero 2000) and osmotic stress/desiccation (Lent 1968), as well as reductions in oxygen availability (Lent 1968; Bayne et al. 1976; Shick et al. 1986) and feeding time (Bayne et al. 1988). Nonetheless, intertidal height (i.e., absolute shore level) is not always an effective means of comparing communities at different sites (e.g., Benedetti-Cecchi 2001). In this paper, we focus on the potentially confounding effects of wave splash and intertidal height on physiological stress, and specifically on emersion time and high temperature. An ability to quantitatively measure these variables is key if we are to interpret the potential role of physiological stress in setting the upper distributional limits of intertidal species and is especially crucial if we are to quantify and predict the effects of climate change on intertidal communities (e.g., Lubchenco et al. 1993; Barry et al. 1995; Helmuth et al. 2002).

Table 3. Variance of the five metrics relating to the upper limit of (A) *Mytilus californianus* on Tatoosh Island (local scale), (B) *Balanus glandula* on Tatoosh Island (local scale), and (C) *Balanus glandula* through the Strait of Juan de Fuca (regional scale). Maximum values were taken as the maxima determined in the field. Minimum values reflect the lowest value that is biologically realistic (extreme lower low water in the case of ASL and ESL, and the mean temperature of seawater in the case of absolute maximum and average daily maximum temperatures). Total degree hours were ln (x + 1) transformed to meet the assumption of normality. Normalized variance among metrics within the three species and scale categories were compared using *F* tests. Different letters in the final column refer to those groups that are significantly different from one another using sequentially Bonferroni corrected alpha values for the 10 possible comparisons.

					Statistical			
	Maximum value	Minimum value	Range	SD/range	group			
(A) Mytilus californianus (local scale)								
ASL	324 cm	-61 cm	385 cm	0.106	b			
ESL	175 cm	-61 cm	236 cm	0.034	а			
Absolute max	34.0°C	10.7°C	23.3°C	0.130	b			
Average daily max	26.1°C	10.7°C	15.4°C	0.132	b			
$\ln (\text{degree hours} + 1)$	6.02	0	6.02	0.283	с			
(B) Balanus glandula (local s	cale)							
ASL	347 cm	-61 cm	435 cm	0.102	b			
ESL	219 cm	-61 cm	280 cm	0.011	а			
Absolute max	41.5°C	10.7°C	30.8°C	0.080	b			
Average daily max	28.5°C	10.7°C	17.8°C	0.076	b			
$\ln (\text{degree hours} + 1)$	4.45	0	4.45	0.251	b			
(C) Balanus glandula (regional scale)								
Relative ASL	158%	0%	158%	0.194	a,b			
Relative ESL	100%	0%	100%	0.098	а			
Absolute max	46.5°C	10.7°C	35.8°C	0.091	а			
Average daily max	36.8°C	10.7°C	26.1°C	0.101	а			
$\ln (\text{degree hours} + 1)$	5.68	0	5.68	0.339	b			



Average daily maximum midtidal rock temperature (°C)

Fig. 5. Relationships between average daily maximum substrate temperature at +1.5 m and the following characteristics at the top of the barnacle zone: (A) ASL, (B) average ESL, (C) maximum substrate temperature, (D) average daily maximum substrate temperature, and (E) total degree hours (above 35°C). Owing to slight variation in tidal amplitude at the regional scale (*see Table 1*), ASL and average ESL have been standardized relative to tidal range at each site so that, on the *y*-axes in panels A and B, 0 = MLLW, 0.5 is approximately mean tide level, and 1.0 = MHHW. Site codes as in Fig. 1.

ESL and wave exposure-Descriptive accounts of zonation shifts in response to wave action have a long history (e.g., Shelford et al. 1935; Evans 1947; Burrows et al. 1954). It is generally assumed that waves elevate the vertical distributions of littoral organisms by decreasing the effective duration of emersion. We were able to quantify this relationship by measuring the effective time of the tide's return, and to some extent this was related to offshore wave height. It should be noted that the wave climate recorded at the buoy is an imperfect indicator of the wave conditions at Tatoosh, and it is not unreasonable to expect that the relationship between daily ESL and wave height might be higher given local measurements of wave direction and wave height. Regardless, the highly significant relationship between offshore wave height and ESL verifies that ESL is indeed tied to the wave environment through time. This pattern would presumably be even more striking if winter data were included. Although temperature-based measurements of ESL are ineffective in winter, alternative techniques (Venegas et al. 2002; M. O'Donnell unpubl. data) hold great promise for future studies.

ESL and species' upper limits—The upper limits of intertidal invertebrates have been associated with abiotic stressors resulting from aerial exposure. Mussels and barnacles have been shown to experience subcellular thermal stress at realistic field temperatures (Hofmann and Somero 1995; Roberts et al. 1997; Buckley et al. 2001; M. Berger pers.

comm.). Experimental work in New England has demonstrated that abiotic stress results in mortality of high-shore mussels (Mytilus edulis) and barnacles (Semibalanus balanoides) when individuals are not buffered by neighbors or protected by experimental shades (Bertness and Leonard 1997; Bertness et al. 1999). High-shore die offs of Mytilus trossulus (reported as M. edulis) have been documented (Suchanek 1978; Tsuchiya 1983) and have been associated with extreme high temperatures (Tsuchiya 1983). Decadal-scale fluctuations in tidal emersion patterns may be associated with vertical shifts in the upper limit of *M. californianus* on Tatoosh Island (Denny and Paine 1998). The upper limits of barnacles have been attributed to a variety of abiotic factors, including temperature and desiccation (Foster 1971a,b; Raimondi 1988). Additional factors related to the duration of emersion, including food availability (Dahlhoff and Menge 1996; Roberts et al. 1997; Dahlhoff et al. 2001) and hypoxia (Shick et al. 1986) may also operate to set the upper limits of intertidal invertebrates at any given site.

At the local scale, we sought to determine the relationship between emersion time and the upper limits of invertebrates across a gradient of substrate aspect, which is known to alter vertical zonation patterns (Wethey 1983). Previous work at the same 16 Tatoosh study sites used in this study revealed a strong effect of aspect on substrate temperatures and the distribution of the algal turf communities (Harley in press). To our surprise, however, substrate aspect was unrelated to both mussel-mimic temperature and the position of mussel upper limits. Earlier work with *Mytilus californianus* demonstrated clear temperature differences between horizontal and north-facing vertical surfaces (Helmuth and Hofmann 2001). The microsites investigated in the present study sloped approximately 30° from horizontal. Because mussels extend several centimeters above the substrate, the surface area of shell exposed to solar radiation for individuals at the upper limit of the bed may be roughly equivalent on gently sloping north- and south-facing surfaces. This may explain why mussel-mimic temperatures did not vary with aspect.

The upper limits of *Balanus glandula* were also aspect invariant on Tatoosh Island (*see also* Harley in press). We were not able to detect any aspect-related differences in substrate temperature at the upper limit of *Balanus*, although there were trends for south-facing surfaces to be warmer than north-facing surfaces. It is likely that such a difference exists and that our sample sizes were simply insufficient to detect it.

Although the temperatures of north- versus south-facing loggers were statistically indistinguishable at the upper limits of mussels and barnacles, high temperature alone does not appear to set their upper limits on Tatoosh. In retrospect, this result is not surprising given that Tatoosh is among the least thermally stressful sites measured in a recent latitudinal survey of the Pacific coast of the U.S. (Helmuth et al. 2002). The maximum temperatures of mussel mimics at the upper limit of *M. californianus* ranged from 23.5°C to 34.0°C, and the maximum rock temperatures, which are tightly linked to barnacle tissue temperatures (Harley and Lopez 2003), ranged from 35.0°C to 41.5°C at the upper limit of B. glandula. Maximum temperatures are thus not tightly linked to the upper limit of either species on Tatoosh Island. It is possible that the distributions of sessile invertebrates on Tatoosh are restricted by some other component of temperature stress, but in ways not addressed here (e.g., midwinter freeze events, some aspect of thermal history [Buckley et al. 2001], etc.). Freezes are extremely rare on Tatoosh (none were recorded during the course of this study; Fig. 3A), although one such event did lower the upper limit of mussels in 1989 (R. T. Paine pers. comm.). Regardless, the fact that we did not observe any upward shift in invertebrate upper limits (C.H. pers. obs.) during the 2 years of our study suggests that the distributional patterns under study were not in the process of recovering from an extreme temperature event in the recent past.

Although we found little evidence for a relationship between high temperature and upper limits on Tatoosh Island, effective shore level, which serves as a proxy for emersion time, is an excellent predictor of the position of the upper limits of both *M. californianus* and *B. glandula*. At the upper limits of these two species, average ESL was the least spatially variable environmental correlate that we measured. Emersion time may set upper limits of invertebrates via a complex interaction with temperature and/or desiccation (*see*, e.g., Dahlhoff and Menge 1996; Dahlhoff et al. 2001). Desiccation stress, however, is modified by patterns and timing of thermal conditions, and there is little evidence that degree hours above a physiologically relevant threshold temperature exhibit any relationship with the position of the upper limit of mussels or barnacles on Tatoosh. Alternatively, emersion time may influence the distribution of intertidal organisms via restricted feeding time (Bayne et al. 1988). Sessile invertebrates on Tatoosh may occur up to a vertical position on the shore above which maintenance costs exceed energy intake and growth is not possible. Thus, although a position higher on the shore may not be stressful in the sense of producing acute mortality, organismal energy budgets may preclude the occupation of such a shore level.

The consistent relationship between ESL and the upper limits of sessile invertebrates on Tatoosh Island did not hold at the regional scale. At the two coolest sites, the upper limit of Balanus glandula occurs at a fairly constant average ESL. However, at progressively warmer sites, the upper limit of B. glandula occurred at lower and lower average ESLs. This suggests a link with temperature, although the upper limit was no more closely tied to any of the measured temperature characteristics than it was to ESL. It appears likely that, at the regional scale, additional factors such as desiccation or thermal time history remain unaccounted for. It is further possible that local adaptation, both phenotypic and genotypic, may be operating at the regional scale. Thermal acclimation of individuals has been shown to be important in other intertidal invertebrates (Buckley et al. 2001). Genotypic variation in adult B. glandula has been demonstrated across gradients of intertidal height and latitude (Hedgecock 1986), and postsettlement selection for thermal tolerance occurs in barnacles in New England (Schmidt and Rand 1999; Schmidt et al. 2000). Finally, it is probable that our limited, 1-month sampling period was insufficient to identify important abiotic signals at the regional scale and that biologically important thermal stress may have occurred during times other than July (Helmuth 1999). Nevertheless, there is an important shift from emersion time to some other factor or suite of factors once some abiotic threshold is surpassed. Thus, in the Strait of Juan de Fuca, the factors that set the upper limit of Balanus glandula at one site (Tatoosh) are not necessarily representative of the factors that set the upper limit at all sites.

There has been a recent emphasis on the interplay between the physiological tolerances of individual organisms and small- to large-scale variability in the biotic and abiotic environment, particularly in coastal ecosystems (e.g., Tomanek and Somero 1999; Stillman and Somero 2000; Helmuth and Hofmann 2001). Much of this research involves measuring a selected number of abiotic parameters and attempting to correlate these parameters with biological responses from subcellular processes up to community interactions. Our data suggest that tight correlations with a single parameter should not necessarily be expected, especially across large spatial scales. An understanding of how the importance of any given parameter, such as temperature or emersion time, varies from site to site will be central to our ability to interpret large-scale variability in benthic organismal physiology, population biology, and community dynamics.

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