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Evaluation of effective shore level as a method of characterizing intertidal wave exposure regimes

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Abstract

Wave splash modifies the duration and timing of aerial exposure of intertidal organisms, influencing patterns of vertical zonation, thermal stress, and the consequences of climate change. Harley and Helmuth (Limnol. Oceanogr. 48:1498-1508, 2003) described a method for measuring effective shore level (ESL), a metric that combines the influence of wave splash and tidal regime on patterns of emersion and immersion. They identified immersion events as sharp drops in temperature recorded by submersible dataloggers and compared the tide height at the time of the temperature drop to the wave height recorded by an offshore buoy. Here we explore the generality of this method at 10 sites along the Pacific coast of North America spanning 14° of latitude. We deployed miniature temperature loggers at fixed intertidal heights at each site and recorded temperatures at intervals of 5 to 15 min for periods of up to 5 years. We use these data to explore the effects of different approaches to calculating temperature drops and wave heights, as well as variation in the buoy location, on ESL calculations. We present a software program (SiteParser) that can be used to identify temperature drops in a datalogger time series and also calculate daily and monthly summary statistics of temperature. We show that ESL parameters provide a useful metric for comparing the effects of wave action on immersion patterns within sites. We also introduce a metric of average wave run-up that can be used to compare the effect of wave action on immersion patterns among more distant locations.

Introduction

Zonation, the clustering of organisms into distinct horizontal belts, is a common phenomenon of intertidal habitats worldwide (Stephenson and Stephenson 1972, Ricketts et al. 1985). The position of the upper and lower edges of these intertidal zones have long intrigued ecologists (Connell 1961, Paine 1966, Stephenson and Stephenson 1972), and intertidal zones are frequently used in ecological studies as indicators of comparable environmental conditions across locations or over time (e.g., Johannesson et al. 1995, Gilman 2005). Zonation is thought to reflect changes in patterns of emersion and immersion with vertical position on the shore. The timing and duration of emersion modulate the degrees of desiccation, temperature, and salinity stress an organism experiences (Wolcott 1973, Stillman and Somero 1996, Wethey 2002, Dahlhoff 2004); conversely, the duration of immersion regulates feeding time, photosynthesis, and in some cases susceptibility to predation (Connell 1961, Paine 1966, Bell 1993). Thus zonation is thought to reflect species-specific physiological and ecological tolerance of immersion and emersion patterns. Many schemes have been proposed over the years to associate intertidal zonation patterns in particular locations with fixed tidal elevations or tidal regime statistics (Doty 1946, Ricketts et al. 1985). Yet attempts to generalize such local zonation schemes to larger regions are frequently unsuccessful (Stephenson and Stephenson 1972). There is often great disparity in zonation patterns among locations or within a location over time (Lawson 1957, Paine 1966, Leigh et al. 1987, Foster 1990).

Wave action alters patterns of zonation (Evans 1947, Lewis 1964, Stephenson and Stephenson 1972, Lindegarth and Gam-

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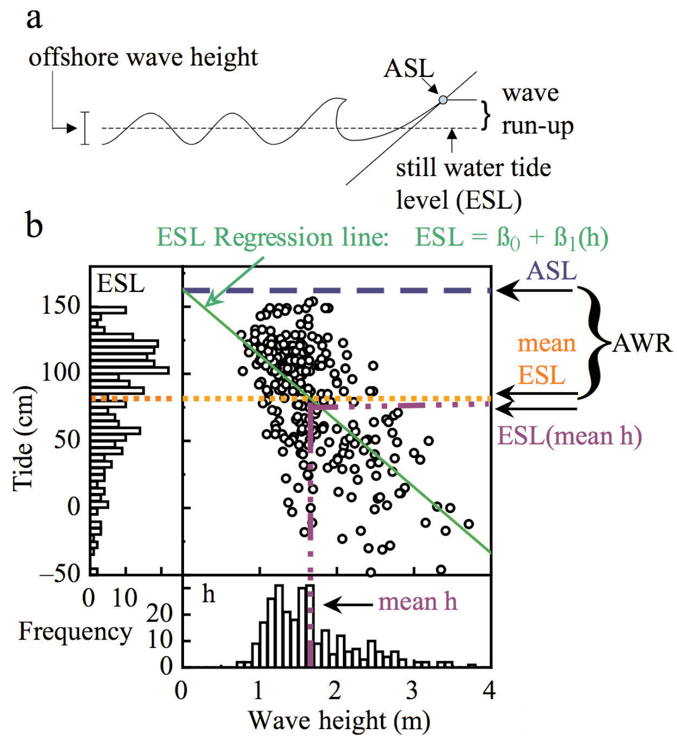

Fig. 1. (a) Schematic showing the effect of wave action on ESL. On a calm day, a point on the shore (circle) would not be immersed until the still tide height exceeded its absolute shore level (ASL). The run-up of waves onshore lifts the effective water level, causing immersion at a lower tide height, and depressing the point's effective shore level (ESL). (b) Sample ESL regression illustrating terminology used in this paper. In the main plot, the observed tidal height at the time of each temperature drop (ESL) is plotted against the significant wave height (h), and a linear regression is calculated. The left and lower plots show the frequency distribution of ESL and h, respectively. The ASL is calculated by surveying the location relative to a known benchmark or estimated from the intercept of the ESL regression line (β_0). The average wave run-up (AWR) is calculated as the difference between ASL and the mean observed ESL, or between β_0 and the ESL predicted from the regression equation for an average-sized wave. In this example, ASL and β_0 differ by less than 5 cm, but larger differences are more common (e.g., Figure 4).

feldt 2005). In some cases, lack of tolerance to high wave forces may limit local species composition in wave-exposed areas (Menge and Sutherland 1976). Waves may also increase the height of water on the shore, effectively decreasing the frequency and duration of emersion and concomitant thermal and desiccation stresses (Stephenson and Stephenson 1972, Ricketts et al. 1985). Specifically, high wave action will cause a point on the shore to behave as if it is effectively lower than its actual still-water tide height (Figure 1a). By comparing the observed timing of immersion for a point at a known tide height to its predicted immersion pattern, based on a tide table, it is possible to estimate the point's effective shore level. Such calculations have been made only occasionally (e.g., Glynn 1965, Druehl and Green 1970), presumably because they are tedious and difficult to conduct comparatively for multiple locations.

Harley and Helmuth (2003) described a method for identifying immersion events from time series of intertidal temperature. Their method relied on miniature submersible temperature dataloggers that store high-frequency (twice an hour or faster) time series of temperature data for periods of 1 to 6 months. Harley and Helmuth (2003) used a sudden sharp drop in temperature (3°C over 20 min) on a rising tide to identify immersion events during the daytime, when cooler seawater engulfs a temperature logger that has previously been warming from exposure to terrestrial climate. Once the tide height and wave height at the time of the immersion event are identified for many such events, regression can be used to calculate the effect of wave action on the tidal height of immersion (Figure 1b). The effective shore level (ESL) of a given point in the intertidal zone is equal to the absolute shore level (ASL), the vertical distance above still-water chart datum, with equivalent emersion characteristics (timing and duration) in the absence of waves (Figure 1a; see also Harley and Helmuth 2003). This method should apply similarly to regions with little or no tidal fluctuation, although we have not tested it in these situations.

The mean of all observed ESLs for a location describes the average tide height at which the location will transition from emersed to immersed. The difference between the location's mean ESL and its ASL can be used as a measure of its average wave run-up (AWR), literally an estimate of how far the location's effective shore level is depressed by wave action (Figure 1b). AWR depends on both wave height and local shoreline topography and is a very different measure of wave exposure than wave force. Although both wave splash and wave force should increase with increasing wave height, they need not be strongly correlated. For example, a site with a gently sloping shoreline may experience a fairly low AWR because of the large distance that the waves need to travel in the horizontal plane before moving very far in the vertical direction. In contrast, a steeply-sloped site may experience high AWR at even fairly low wave heights because all points on the shore are never far from the still-water tide line. Thus spatial patterns of AWR (and ESL), may not be correlated with patterns of wave force.

In their introduction of the ESL technique, Harley and Helmuth (2003) conducted only a modest examination of the robustness of the ESL metric to changes in the temperature threshold used to identify drops. Here we examine more fully the uses and limitations of the ESL approach. We first present a software program (SiteParser) that automates the process of identifying temperature drops of a user-specified threshold. The program also calculates daily and monthly temperature summary statistics. We use data sets of rapid temperature drops generated by SiteParser to explore the ESL methodology in more detail. Specifically, we compare the effect of changes in the magnitude of temperature drop threshold, in the measurement of wave height, and in the source of wave data on the number and reliability of calculated temperature drops and on the robustness of the wave height—immersion relationship. We introduce a modification to the calculation of AWR for locations where ASL is not available. Finally, we apply the technique to quantitatively describe the wave splash regimes of multiple sites along the Pacific coast of the continental United States. We show that ESL is a useful technique for comparing the effect of waves on immersion patterns within a site, and that AWR can be used to make comparisons among more distant locations.

Materials and procedures

Materials—Three time series are necessary to calculate a wave height–immersion relationship: a temperature time series for the specific location of interest, an observed or predicted tide height time series, and a concomitant time series of significant wave height. The temperature and tidal height time series must be of fairly high temporal resolution (< 30 min between samples); the temporal resolution of the wave height data set should be at least every 6 hours. Temperature time series may be collected using miniature, submersible temperature dataloggers with a reasonably fast (< 5 min) thermal equilibration time, such as TidbiTs (Onset Computer, Pocahassett, MA, USA) or iButtons (Maxim Integrated Products, Sunnyvale, CA, USA). Fitzhenry et al. (2004) and Helmuth (2002) discuss such loggers in the context of intertidal thermal physiological studies. Computer programs such as Tides and Currents (Nobeltec, Portland, OR, USA) or Xtide (www.flaterco.com) can be used to generate detailed tidal predictions for locations worldwide. The U.S. National Ocean Service's Center for Operational Oceanographic Products and Services (NOS, tidesandcurrents.noaa.gov) also collects tidal observations and constructs predictions for many coastal locations in the United States. The U.S. National Data Buoy Center (NDBC, www.ndbc.noaa.gov) reports wave data from many U.S. and international locations. In this article, we also use wave height data from buoys maintained by the Scripps Institution of Oceanography's Coastal Data Information Program (CDIP, cdip.ucsd.edu).

SiteParser—Temperature drop events may be calculated by any of a number of mathematical or spreadsheet computer programs (e.g., Excel, Matlab, SAS). Calculations require one or more temperature time series for locations of interest and a predicted or observed time series of still-water tide height. A drop is identified as a decrease in temperature greater than or equal to a specified threshold, within a fixed time interval (usually 20 min), and during an incoming tide (Harley and Helmuth 2003).

To facilitate such drop calculations, we developed the SiteParser program (Appendix 1), a stand-alone application that runs on Windows systems. SiteParser requires a text file as input, each line of which consists of the date and time, the predicted or observed tidal height, and the observed temperature of one or more loggers. An unlimited number of temperature time series may be included in the same input file. Once the user specifies the minimum magnitude of temperature drop to count, the program will output as separate files the time and tide height of all such temperature drops observed on an incoming tide. In addition to identifying temperature drops, SiteParser also automatically calculates daily and monthly temperature averages, maxima, minima, 97.9th percentile and 2.08th percentile (the maximum and minimum temperature that loggers are exposed to for at least half an hour; Fitzhenry et al. 2004), and percentile ranges. SiteParser will also calculate average temperature when the still-water tide height is above a user-specified level; this can be used to estimate water temperature during periods of logger immersion.

ESL regression calculation—The ESL regression equation is calculated by regressing the tide height at the time of the temperature drop onto a measure of significant wave height for the same time interval. The wave metric is usually the maximum significant wave height observed over a period of 1 to 24 h preceding the temperature drop event. Longer time windows are necessary when wave data are collected from a distant buoy because there may be a time lag before the wave height recorded by the offshore buoy reaches the temperature logger onshore. We discuss more fully in the assessment section the effect of buoy distance and wave time interval on the ESL regression function.

Standard least-squares linear regression is used to calculate the relationship between wave height and the tide at the time of the drop. Any number of statistical software packages (e.g., SAS, JMP, R, Statview, but not Microsoft Excel, cf McCullough and Wilson 2002) can be used to calculate the regression function. The regression equation is of the form: ESL = $\beta_0 + \beta_1 h$, where ESL is the tide height at immersion and h is a measure of significant wave height preceding the immersion. The slope of this equation (β_1) usually has units of centimeters of tidal height per meter of wave height and represents the reduction effective in tidal height to the logger location of a 1-m increase in wave height. In other words, it estimates the number of centimeters below a point's ASL that the threshold for submergence will occur for each 1-m increase in wave height. The intercept (β_0) could be interpreted as an estimate of the absolute shore level (ASL); we test this assumption below. Harley and Helmuth (2003) used a log transformation of both dependent and independent variables prior to regression; however, we have not found that such a transformation improves either the regression fit or the normality of errors.

Harley and Helmuth (2003) define the average wave run-up as the difference between a location's ASL and the mean observed ESL. We suggest a slight modification: replacing the mean ESL with the predicted ESL from the regression equation evaluated at the mean wave height of the buoy. AWR can be used to compare the relative effect of wave action among different locations within a site or among different sites. Where the ASL of a location is unknown, it can be estimated by β_0 (see discussion below). We refer to both calculations interchangeably as average wave run-up (AWR).

Table 1. Study sites and summary of ESL regression results.

Group	Location	Buoy name	Buoy distance, km	Loggers, no.	Wave period, h	Threshold, °C/20 min	R^2	n	AWR
Alegria, CA	34.50 N,120.50 W	cdip107	46.45	3	9	5	0.193–0.367	19–59	27.588–36.686
Lompoc, CA	34.72 N,120.61 W	cdip076	58.85	4	12	4	0.033–0.221	24–164	16.588–58.193
Piedras, CA	35.67 N,121.29 W	ndbc46028	54.69	4	3	5	0.350–0.410	37–60	62.534–81.843
Monterey, CA (exposed)	36.62 N,121.90 W	ndbc46042	48.54	4	6	5	0.300–0.424	12–171	53.056–94.332
Monterey, CA (protected)	36.62 N,121.90 W	ndbc46042	48.54	2	6	6	0.377–0.582	199–229	28.408–44.260
Strawberry Hill, OR (exposed)	44.25 N,124.12 W	ndbc46050	52.46	5	3	5	0.124–0.547	32–97	22.739–47.394
Strawberry Hill, OR (protected)	44.25 N,124.12 W	ndbc46050	52.46	5	3	5	0.070–0.226	83–378	24.206–27.497
Boiler Bay, OR	44.83 N,124.05 W	ndbc46050	44.51	7	1	6	0.226–0.434	89–209	28.493–66.100
Colin's Cove, WA	48.55 N,123.00 W	ndbc46088	27.47	3	12	7	0.023–0.054	19–27	3.201–6.156
Tatoosh, WA	48.39 N,124.74 W	ndbc46041	116.68	6	1	6	0.056–0.503	27–78	10.069–67.924

Assessment

Data collection—All assessments were conducted from multiyear intertidal temperature time series collected from 10 sites along the Pacific Coast of the United States (Table 1) as part of a long-term study of intertidal mussel temperatures (Helmuth and Hofmann 2001, Helmuth et al. 2002, Fitzhenry et al. 2004). Each instrument recorded average temperatures at 10- to 15-min intervals. Three to seven instruments were deployed at each site. Most instruments were placed at the approximate vertical center (mid) of the mussel bed at each site. At some sites, instruments were placed in up to four additional positions within the mussel bed: the upper (upper) or lower (low) edge of the bed, or halfway between the center and either the upper limit (midupper) or lower limit (midlow).

For most sites, we used tidal prediction time series generated at 10-min intervals from the Xtide Program. For some analyses at Monterey, California, we used observed tidal heights reported by the NOS tide station in Monterey Bay (NOS9413450). Offshore wave height data were obtained from the nearest NDBC or CDIP buoys (Table 1). At Monterey, nearshore wave data were also collected from a Seabird pressure transducer (Sea-Bird 26-03 Seagauge) located approximately 125 m offshore of the site (Helmuth and Denny 2003).

Accuracy testing of the SiteParser program—We compared the statistics calculated by SiteParser for data from two sites in southern California (Alegria and Jalama, 34.47°N,120.28°W and 34.50°N, 120.50°W) to calculations done by hand for each site using the Microsoft Excel spreadsheet program. These summaries were in agreement. Additional testing was performed on other rocky intertidal data sets and from other types of environments, including salt marsh and shallow coral reef habitats (B. Helmuth, K. Schneider, J. Jost, and K. Castillo, unpublished data).

Effect of temperature threshold on the number and accuracy of drops—Fluctuations in terrestrial climate, such as sunset, clouds, or fog, may also produce sudden drops in temperature when loggers are exposed at low tide. Such fluctuations may be excluded by increasing the magnitude of the temperature drop threshold; however, increasing the drop magnitude may also exclude valid immersion events and reduce the total number of events available for regression. Figure 2 shows the total number of drops and reliability, over 1 year, at multiple

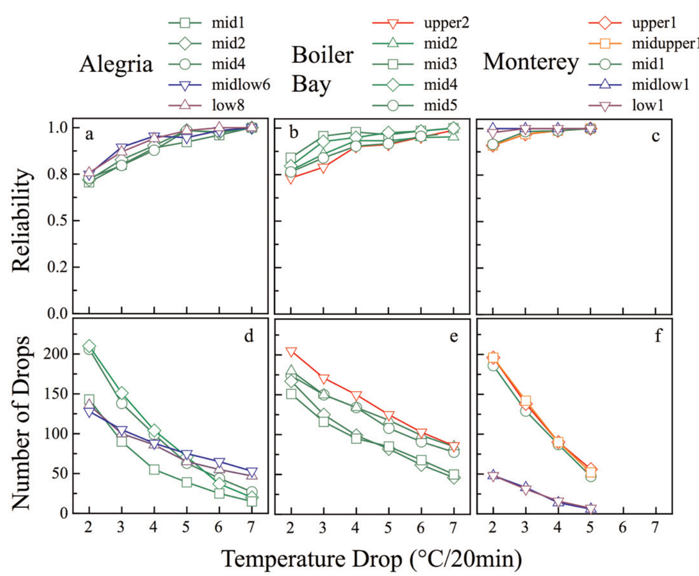

Fig. 2. (a-c) Drop reliability (proportion of temperature drops not coincident with a temperature drop in a terrestrial datalogger). (d-f) Total number of drops identified over a year for a range of temperature drop thresholds at three sites. See Table 1 for site information. Loggers were placed at one of five vertical positions within mussel beds, ordered from highest to lowest as upper, midupper, mid, midlow, low. Logger locations used in more than one figure retain the same symbol throughout.

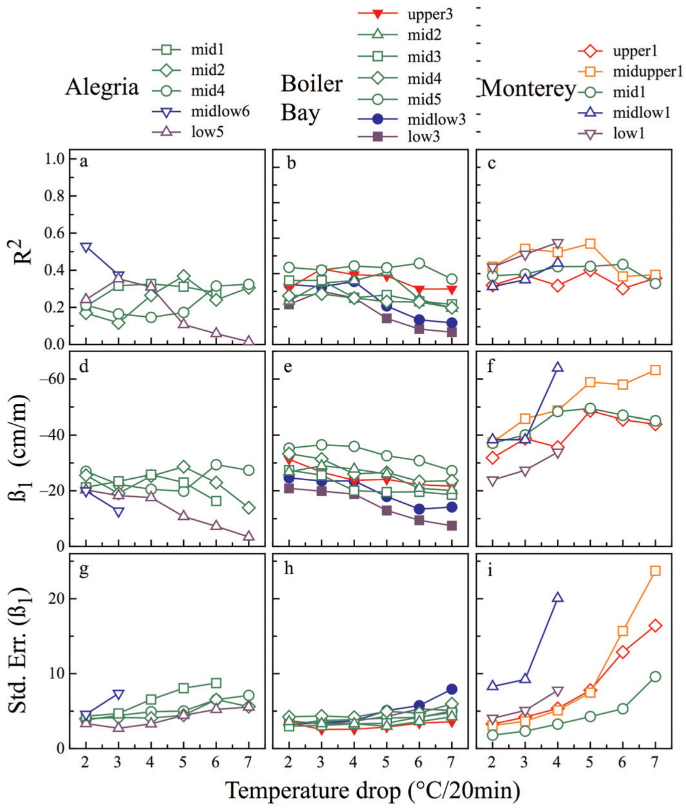

Fig. 3. (a-c) R^2; (d-f) slope; and (g-i) standard error of the slope calculated for the same range of drop thresholds and sites examined in Figure 2. Regressions for Alegria and Boiler Bay used a 1-h wave window; for Monterey, a 6-h window. Any regression with less than 10 data points was excluded. Data for Alegria and Boiler Bay are from a slightly different time interval than those presented in Figure 2, but all regressions used a single year of data. Logger locations used in more than one figure retain the same symbol throughout.

datalogger locations at three of the sites listed in Table 1. Monterey is the only site with data for all five vertical positions within the mussel bed. To assess reliability we used a "terrestrial" datalogger, placed well above the highest tide line at each location. An observed temperature drop at an intertidal logger was considered to be false if it occurred within 30 min of an observed drop at the terrestrial logger. This provides an estimate of the frequency of false temperature drops in the data set, but may not identify all such drops.

The three sites show slight differences in the fraction of drops considered reliable (i.e., not coincident with an event in the terrestrial logger) as a function of temperature threshold (Figure 2a-c), presumably reflecting local differences in the temporal dynamics of terrestrial climate. Greater temperature thresholds generally increased reliability and decreased the total number of drops. Low and midlow vertical positions also showed greater reliability and fewer drops than higher locations (Figure 2). Loggers at lower-shore positions spend less time overall exposed to air and experience lower maximum temperatures, which reduces the likelihood of experiencing spurious temperature drops relative to loggers higher in the intertidal zone. At all sites, temperature thresholds of around 4° to 5°C were usually associated with ≥ 90% reliability and ≥ 100 drops/year for mid and upper sites. Because of the overall fewer number of drops and higher reliability, a lower temperature threshold may be preferred for lower intertidal locations.

Effect of temperature threshold on the estimation of ESL parameters—Increasing the temperature threshold generally increases the R^2 value of the ESL regression (Figure 3a-c), with one clear exception. At lower intertidal positions, particularly at Alegria, CA (Figure 3a), and Boiler Bay, OR (Figure 3b), R^2 decreases at the highest threshold levels. This presumably reflects a loss of information from the exclusion of reliable data points by the high temperature threshold. Except for the lower intertidal loggers, the ESL slopes estimated for Alegria, CA (Figure 3d), and Boiler Bay, OR (Figure 3e), were relatively insensitive to changes in the temperature threshold, with variation of less than 10 cm height/m wave common. Standard errors of the slope estimates were relatively small (< 10 cm) at the two sites (Figure 3g-h). In contrast, all logger locations at Monterey (Figure 3f) showed consistent declines in slope, even when R^2 values were relatively constant. The standard errors of the Monterey slopes (Figure 3i) were also higher than at the other two sites. We cannot explain these observations.

The intercept of the ESL regression equation (β_0) predicts the effective shore level under a wave height of zero, and may be useful as an estimate of a location's surveyed, or absolute, tidal height (ASL). To test this hypothesis, we compared estimates of β_0 to ASL values for 10 logger locations within the Monterey site. Surveyed tidal heights were measured with an Ashtech Z-extreme GPS system (Thales Navigation, Santa Clara, CA, USA). The difference between ASL and β_0 ranged from less than 5 cm in the best case to more than 50 cm in the worst (Figure 4a). β_0 tended to underestimate the actual ASL of the logger locations at Monterey, but improved at higher drop thresholds. The difference was generally greatest for high intertidal locations and probably reflects the lower reliability of drops (Figure 2a-c) at these locations. Standard errors of β_0 were generally less than 25 cm (Figure 4b). This seems high, but may reflect idiosyncrasies of the Monterey site that are also apparent in the high standard errors of β_1 (Figure 3i). Unfortunately, ASL values were not available for any of the other study sites. Heights estimated by β_0 were positively correlated with observed ASL ($r = 0.6972–0.9004$, $P < 0.05$ for all thresholds), suggesting that β_0 may be a useful measure of relative tidal height even where it underestimates ASL. More stringent drop threshold may improve the accuracy of β_0 as an estimate of ASL, but will require a longer temperature time series to generate enough data points.

Effect of wave time interval—Generally, the more distant an offshore buoy is from the intertidal shore, the longer time it will take for a wave recorded at the buoy to reach the shore and the greater the difference in wave environments between the two. Increasing the time window over which the wave

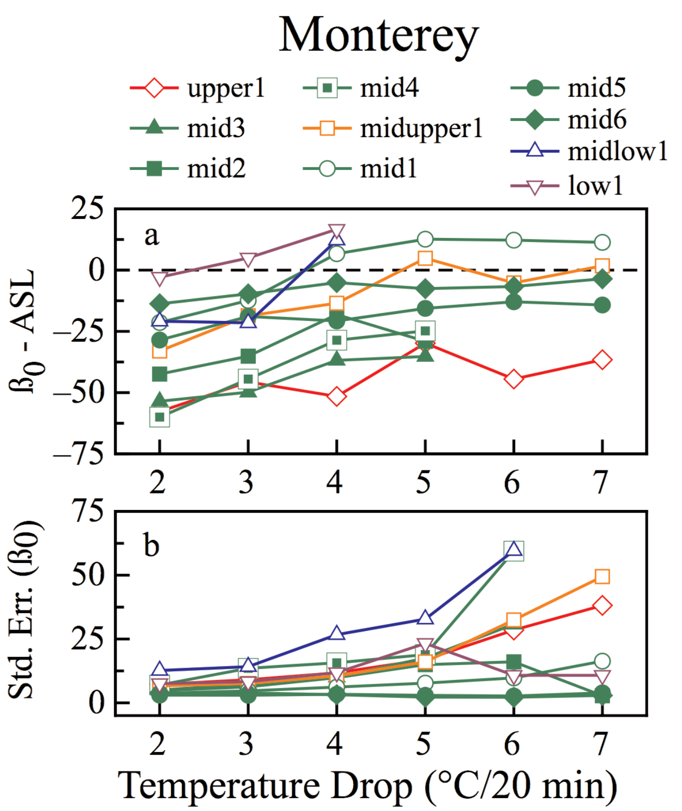

Fig. 4. (a) Difference between the predicted ESL intercept and measured ASL as a function of temperature drop threshold for 10 logger locations at Monterey. (b) Standard error of the ESL intercept. All regressions were done using wave data from NDBC46042 with a 6-h time window. Symbols that match those used in Figures 1 and 2 indicate the same logger locations. ASL values (in cm): upper1 = 195.1, mid3 = 185.02, mid2 = 181.24, mid4 = 172.83, midupper1 = 171.05, mid1 = 162.10, mid5 = 138.98, mid6 = 130.33, midlow1 = 110.98, low1 = 71.02.

metric is calculated may mitigate at least the first of these two problems. Harley and Helmuth (2003) only used the maximum wave for the calendar day. We compared the maximum wave calculated for windows of 1, 3, 6, 12, and 24 h before the observed temperature drop for seven logger locations at the Boiler Bay site (Figure 5). The R^2 of the ESL regression showed only moderate variation in response to the wave time window, but there was a clear decline in R^2 at the longest time window (24 h). Slopes also tended to flatten at longer time windows. This probably reflects the overall decline in the regression fit, as maximum wave heights at the buoy become a progressively poorer metric of onshore wave action at the time of a temperature drop at the longer time intervals. Longer time intervals should be associated with larger maximum waves, because of the larger number of wave heights sampled, and this may also explain some of the slope change. Average wave run-up tended to decrease slightly at higher time windows, but run-up was generally less sensitive to time window than slope. Overall there was little effect of the time window on ESL parameters, particularly in comparison to the effect of changing the drop

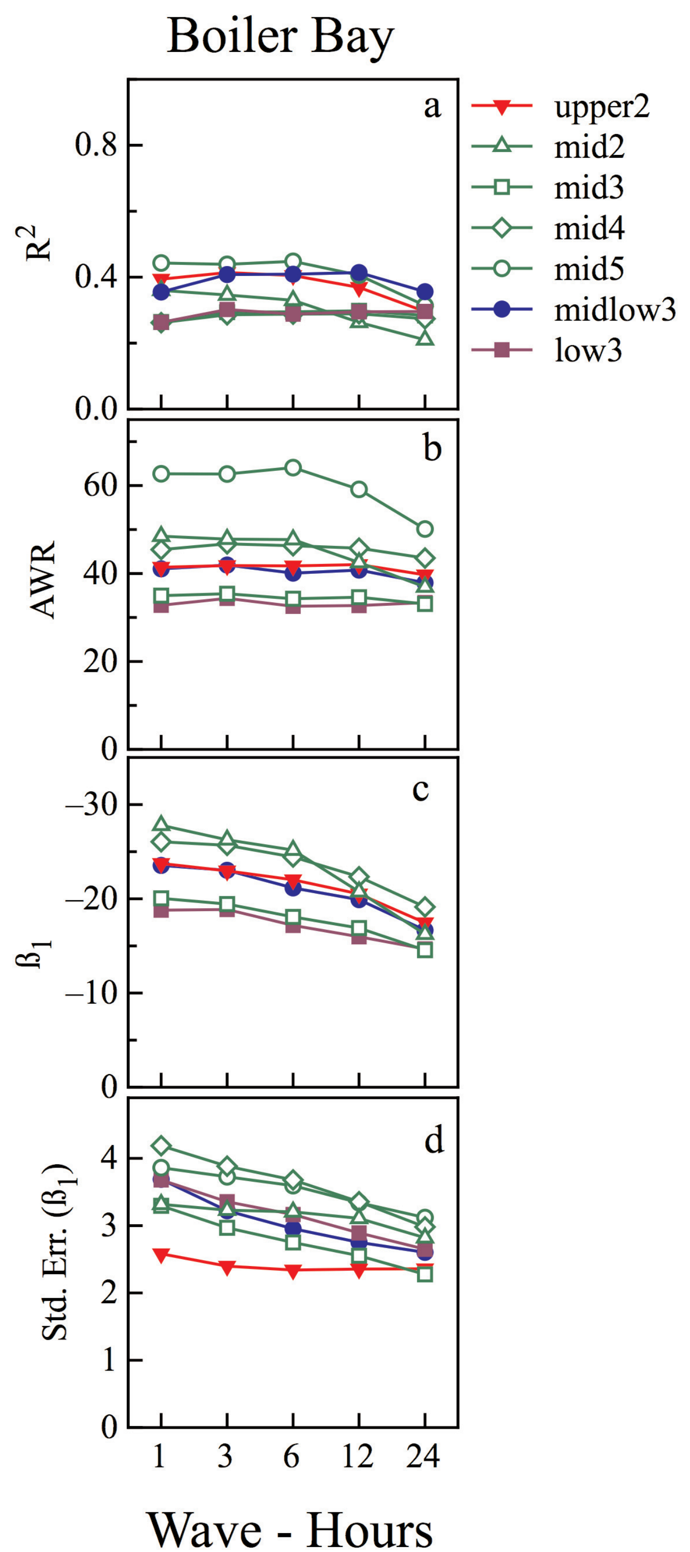

Fig. 5. (a) R^2; (b) average wave run-up; (c) slope; and (d) standard error of the slope calculated for ESL regressions under varying time windows of wave data for logger locations at Boiler Bay. A 4°C temperature drop was used in all calculations.

threshold (Figure 5 vs. Figure 3). Because both ESL parameters and the run-up statistic appear robust to changes in the wave metric, we recommend using the wave-time interval that maximizes the R^2 of the ESL regression.

Effect of buoy distance on ESL regression—In most cases, the ESL regression uses wave data collected from an offshore buoy located far from the intertidal site. The success of the ESL regression approach depends on such wave data accurately reflecting onshore wave dynamics. In particular, a large distance between the wave buoy and the shore may decrease the correlation between the buoy observations and actual onshore wave dynamics. We compared the effect of buoy distance on the ESL regression equation and calculation of average wave run-up for two sites. At Monterey, CA, we compared ESL regressions calculated using wave height data from the NDBC46042 buoy (36.75°N,122.42°W), which is approximately 48 km away, to those calculated using wave height data collected using a Seabird wave gauge located 125 m away. The close distance of this wave gauge should represent a best-case scenario for measuring onshore wave height. For this analysis, we also used observed tidal heights reported for the NOS site in Monterey Bay (NOS9413450). We conducted a second analysis using data from three buoys located close to the Alegria, CA, site: NDBC46054 (34.27°N,122.42°W), NDBC46053 (34.24°N,119.85°W), and CDIP107 (34.44°N,119.803°W) which are 27.15, 47.00, and 46.45 km away, respectively. All regressions were done on 1 year of data, using only logger locations with 20 or more observations.

A shorter distance between the buoy and the intertidal site did not lead to a better overall model fit. At Alegria, the nearest buoy, NDBC46054, showed the lowest R^2 values (Figure 6a), perhaps because the shoreline faces south to southeast and NDBC46054 is west to northwest of the site. At Monterey, the local wave gauge had slightly lower R^2 values at nearly all locations, and this may be because the gauge samples less frequently than the offshore buoy (every 6 hours vs. hourly).

At both sites, the slopes calculated from the different buoys for the same logger location were also markedly different (Figure 6c,d). In particular at Monterey, the slopes were twice as large for the local wave gauge as the offshore buoy. This is because each buoy experiences a slightly different wave regime and thus there is a unique relationship between the magnitude of a wave recorded by the buoy and the size of the wave that reaches the intertidal shore. Importantly, interbuoy variation in the AWR (Figure 6e,f) is much smaller than the slope variation. In all but one case, average wave run-ups differed by less than 15 cm between regressions. Thus the AWR may be a useful statistic for comparing effects of wave splash that is less sensitive to the idiosyncrasies of specific buoys than ESL parameters. The AWR may be particularly useful for comparisons across sites, when all locations cannot be compared to a single source of wave height data.

Comparison of wave exposure regimes—When ESL regression parameters are calculated for multiple locations within a site,

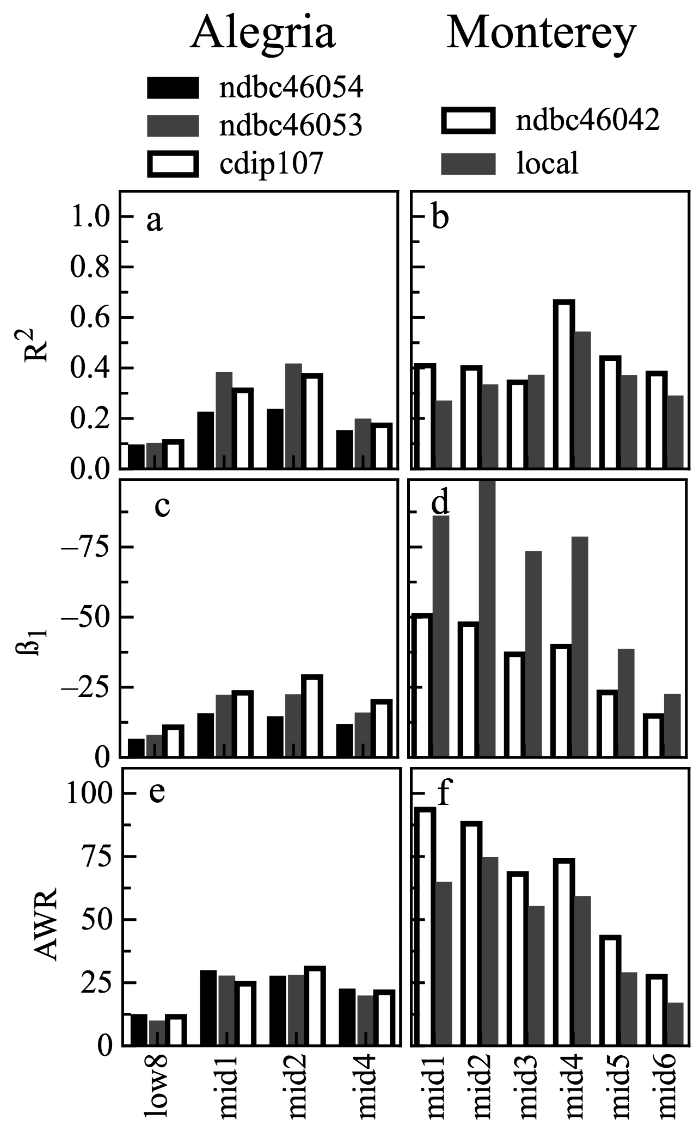

Fig. 6. (a-b) R^2; (c-d) slope; and (e-f) average wave run-up compared among multiple sources of wave data for loggers locations at the Alegria and Monterey sites. Regressions were calculated for a 1-h wave window and 5°C drop for Alegria and for a 6-h wave window and 5°C drop for Monterey. All regressions shown have at least 10 data points.

from a single source of wave data, they may be used to compare wave exposure. For example, two of the six mid locations within the Monterey site (mid5 and mid6) are located within a sheltered cove (Agassiz Beach) that receives less direct wave action (B.H., personal observation). Figure 6d shows the slope (β_1) estimates for all six mid loggers at Monterey. Regardless of which wave data are used to calculate β_1, the slopes for mid5 and mid6 are consistently lower than those of the other four locations. Similarly, the average wave run-ups (Figure 6f) are also lower for mid5 and mid6. These results indicate that, consistent with their placement, mid5 and mid6 have a lower overall wave exposure than the other locations. Thus these two locations should experience longer and more frequent

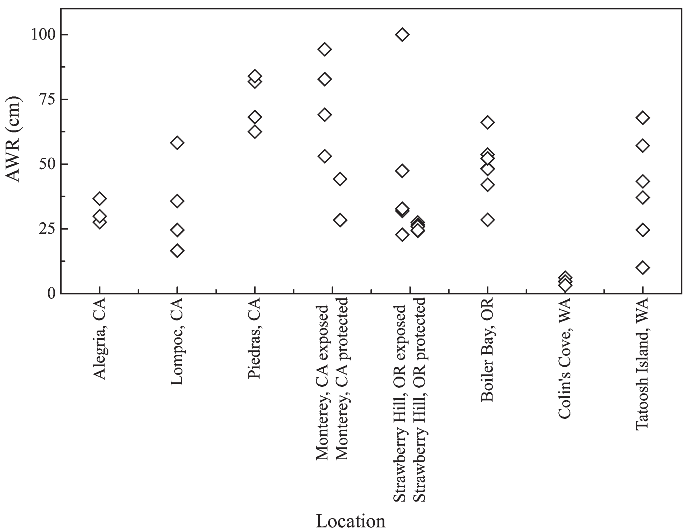

Fig. 7. Average wave run-up (AWR) for the center of the mussel bed at 11 sites along the U.S. Pacific coast. AWR was calculated for all available mid temperature loggers, for the combination of temperature threshold and wave time window that maximized R^2 values within each site (Table 1). The total length of shoreline sampled at each site ranged from 25 to 500 m. Sites are arranged from south to north along the *x*-axis; exact latitude and longitude are listed in Table 1.

periods of aerial exposure than locations of equivalent ASL near the other four loggers.

To compare overall patterns of wave exposure across the Pacific coast of the United States, we calculated ESL regressions and average wave run-ups for 10 sites using a range of drop thresholds (3° to 7°C per 20 min) and wave time lag intervals (from 1 to 24 h). ESL regressions were calculated separately for up to seven replicate logger locations within the center of the mussel bed at each site, and the best overall combination of wave time window and temperature drop threshold was chosen from the resulting R^2 values (Table 1). The regression fit (R^2) varied markedly among sites, and was particularly poor at the most wave-protected sites (Table 1). For example, R^2 values at Colin's Cove, WA, were always below 0.1. This is likely both because the site occurs in a highly wave-sheltered portion of the coast (inside the Strait of Juan de Fuca), and because the nearest available buoy is west of the island whereas Colin's Cove is on the eastern shore. A low R^2 implies there is little relationship between offshore wave and data and onshore immersion patterns, and should be expected for a wave-sheltered site. In contrast, at three sites (Monterey, CA; Strawberry Hill, OR; and Tatoosh, WA) R^2 values exceeded 0.5.

Differences in AWR among sites (Figure 7) reflect known differences in wave exposure, indicating that AWR is a reasonable method of quantifying large-scale variation in wave exposure. For example, two of the 10 sites, Alegria, CA, and Colin's Cove, WA, are highly wave sheltered, occurring within the Southern California Bight and Strait of Juan de Fuca, respectively. As expected, these two sites showed the lowest overall AWR values, indicating that wave action has little effect on immersion patterns. Similarly, when wave-exposed and wave-protected locations were identified a priori within both the Monterey, CA, and Strawberry Hill, OR, sites, the AWR values were generally lower at the wave-protected locations.

Average wave run-up varies considerably both among and within sites. Among the four California sites, there is a trend of increasing AWR with latitude. But no such trend is apparent in Oregon or Washington. This may be due in part to the specific locations selected for logger deployment within each site. For instance, the Tatoosh Island loggers were deployed in a south-facing cove that was moderately protected from the predominantly west to northwesterly swell (see map in Harley and Helmuth 2003). Indeed, our calculations of AWR revealed sizeable variation in wave exposure within locations. For example, the range of AWR values exceeds 50 cm within the Monterey, CA, wave-exposed location, the Strawberry Hill, OR, wave-exposed location, and the Tatoosh Island, WA, location. This variation is not correlated with the length of shoreline sampled, which ranges from 25 to 500 m, depending on the site. This suggests that wave exposure can be quite variable within sites, even among locations that appear superficially quite similar. Similarly, Denny et al. (2004) and Helmuth and Denny (2003) found greater than 5-fold variation in wave forces along a 300-m transect within the Monterey site.

Discussion and recommendations

Understanding the processes that control the distribution and abundance of species is a fundamental goal of ecology. Few patterns of distribution and abundance are as striking as the bands of intertidal zonation common to shores worldwide (Evans 1947, Lawson 1957, Connell 1961, Lewis 1964, Paine 1966, Stephenson and Stephenson 1972, Leonard et al. 1999). Wave exposure, through both wave force and changes in immersion patterns, has long been known to alter patterns of abundance and zonation (Stephenson and Stephenson 1972, Druehl and Green 1982, Ricketts et al. 1985, Denny and Paine 1998, Lindegarth and Gamfeldt 2005), yet few studies have quantitatively described spatial differences in wave action or the consequences for species distributions (Lindegarth and Gamfeldt 2005). Our analysis of the ESL regression method, originally presented by Harley and Helmuth (2003), demonstrates the usefulness of ESL regression parameters for characterizing differences in both tidal height and wave splash among neighboring points along a shore. Our analyses also suggest that average wave run-up is a useful metric for comparing wave exposure among more distant locations.

When ESL parameters for all locations can be calculated from a single source of wave data, such as when all measured points lie along a single shoreline, the parameters of the ESL regression equation can be used to estimate differences in both wave exposure and absolute shore level. The ESL intercept (β_0) may be used as an estimate of absolute shore level (ASL), although we found that β_0 frequently underestimated the true ASL. We recommend that β_0 be considered primarily a relative index of ASL, suitable for comparisons within locations. The slope of the ESL regression (β_1) is an estimate of the decrease in effective shore level as wave height increases. It may be used for direct comparison of wave splash among locations. Greater values of β_1 indicate greater relative wave splash and a reduction in the frequency and duration of immersion. However, because the magnitude of β_1 depends on the relationship between onshore and offshore wave heights, values of β_1 have no literal meaning outside a single study area.

All calculations for within-location comparisons must also be done using identical temperature thresholds, tidal data, and wave height metrics. Care must be taken in choosing a temperature threshold that will exclude false temperature drops during aerial exposure, while minimizing the loss of valid data. False drops occur during low tide under sudden changes in terrestrial climate such as fog, rain, or sunset. They are most common at locations with long aerial exposures, mainly high intertidal or highly wave-protected sites. Because the mussel beds used for analyses in this article occur relatively high in the intertidal zone (approximately the top quartile of tidal range at most locations) our sites should have a large frequency of false drops relative to other parts of the intertidal zone and thus present a conservative test of the ESL approach. At lower intertidal locations, we found that high temperature drop thresholds may decrease R^2 by excluding valid data points. Thus we recommend screening a large range of temperature drop thresholds and wave time windows to find one that maximizes R^2 values across all sites of interest. Appendix 2 contains sample SAS code for conducting such screenings; other statistical programs can also be used.

Because ESL regression parameters are highly sensitive to the choice of wave height data, they are not directly comparable among locations that differ in their source of wave height measurements. Instead, we propose the average wave run-up (AWR) as a metric for comparing wave exposure among distant locations. The AWR is the average change in tidal height of immersion due to wave action. If a site's ASL is known or can be measured against a surveyed benchmark, the AWR can be calculated as the difference between ASL and the mean tide height of observed temperature drops. When ASL is unknown, AWR may be calculated from the ESL regression as the mean wave height multiplied by the absolute value of β_1. Our analyses suggest that AWR calculated in this way is relatively robust to variation in the source of wave height data. In particular, we found that estimates of AWR calculated from different sources of wave data usually differed by less than 15 cm, and we suggest a threshold of 25 to 30 cm be used before considering two AWR values to be different. Comparison of AWR values among 11 sites spanning ~1400 km demonstrated that AWR successfully predicted relative rankings of wave exposure based on a priori knowledge of wave action or coastal morphology.

Overall our analyses suggest that effective shore level regression is a useful and robust method for local estimates of tidal height and wave exposure regime and for calculating average wave run-ups, which may be used to compare wave exposures at larger spatial scales. A number of other techniques exist for quantifying wave exposure as discrete or continuous values. Categorical definitions based on a location's biological or physical properties are frequently used in the published literature, but may be subject to idiosyncrasies of the researcher (Lindegarth and Gamfeldt 2005). One common quantitative approach is based on the measurement of dissolution of plaster, but its interpretation is complicated by differences in temperature and other conditions among sites (Muus 1968, Doty 1971, Porter et al. 2000). A number of techniques for quantifying maximum wave force exist (Denny 1985, Bell and Denny 1994); however, the relationship between wave force and changes to immersion/emersion patterns is unknown. Local wave height can be measured directly by sensors (e.g., Helmuth and Denny 2003), but such sensors may be costly. A number of schemes also exist to estimate local wave height from coastal morphology and wind data (Ruuskanen et al. 1999, Lindegarth and Gamfeldt 2005). The ESL regression method relies on relatively low-cost temperature dataloggers that may already be in place for other reasons. Our analyses suggest that ESL and AWR provide an accurate, quantitative measurement of the thermal aspects of wave exposure that can be compared both locally and among geographically distant sites. Such measurements should prove useful to intertidal ecology for studies of the effects of wave splash on species interactions, intraspecific variation in growth and morphology, patterns of intertidal zonation, and spatial variation in thermal stress.

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