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CHARACTERIZING THE BENTHIC INVERTEBRATE COMMUNITIES OF THE
MIXED-COARSE INTERTIDAL HABITAT IN BOSTON HARBOR

BY

ELIZABETH N. EDDY

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
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IN
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UNIVERSITY OF RHODE ISLAND

2013

MASTER OF SCIENCE THESIS

OF

ELIZABETH N. EDDY

APPROVED:

Thesis Committee:

Major Professor: Charles T. Roman

Candace A. Oviatt

Carol S. Thornber

Nasser H. Zawia

DEAN OF THE GRADUATE SCHOOL

UNIVERSITY OF RHODE ISLAND

2013

ABSTRACT

The Boston Harbor Islands National Recreation Area (BOHA) has an extensive intertidal zone, with 47% of the area composed of mixed-coarse substrate. Given anticipated climate change impacts such as sea level rise and ocean warming, and other stressors associated with the urban environment, the critical ecosystem functions provided by the dominant yet largely understudied mixed-coarse habitat are likely to be altered. To evaluate the benthic invertebrate communities of BOHA and to determine what environmental factors of the mixed-coarse substrate affect community structure, 87 sampling sites were distributed between wave-exposed and wave-protected shorelines between mean higher high water and mean lower low water. A series of physical and environmental data was collected from each site to describe the intertidal habitat, and the epifaunal macroinvertebrate (>1 mm) communities were sampled. We found that benthic epifaunal community structure and diversity differed significantly between wave-exposed and wave-protected sites based on a wave energy model that reflects storm events in the harbor, where diversity was higher at protected sites. We also found that environmental variables collectively explained up to 67% of the variation in community characteristics, with elevation, organic content, water content, and soil skewness individually explaining up to 56%, 30%, 42%, and 33% of the variation, respectively. Other variables also made significant but smaller contributions. Infaunal data analysis was inconclusive, likely as a result of ineffective sampling methods. Differences in crab and periwinkle sizes between wave-exposed and wave-protected groups were also inconclusive with the exception of *Hemigrapsus sanguineus* which had a larger carapace width on wave-exposed shores based on a wave energy model that reflects storm events. Together, these results illustrate

the importance of analyzing multiple measures of community characteristics since community structure, density, richness, diversity, and size may respond differently to wave energy and other environmental factors. This study in its entirety also serves as an inventory for the National Park Service and as a baseline for on-going monitoring efforts in response to climate change, invasive species, or other natural or anthropogenic disturbances.

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PREFACE

This thesis is presented in manuscript format, intended for publication in *Marine Ecology Progress Series* with Charles T. Roman as co-author.

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MANUSCRIPT 1: Characterizing the Benthic Invertebrate Communities of the Mixed-Coarse Intertidal Habitat in Boston Harbor

ABSTRACT

The Boston Harbor Islands National Recreation Area (BOHA) has an extensive intertidal zone, with 47% of the area composed of mixed-coarse substrate. Given anticipated climate change impacts such as sea level rise and ocean warming, and other stressors associated with the urban environment, the critical ecosystem functions provided by the dominant yet largely understudied mixed-coarse habitat are likely to be altered. To evaluate the benthic invertebrate communities of BOHA and to determine what environmental factors of the mixed-coarse substrate affect community structure, 87 sampling sites were distributed between wave-exposed and wave-protected shorelines between mean higher high water and mean lower low water. A series of physical and environmental data was collected from each site to describe the intertidal habitat, and the epifaunal macroinvertebrate (>1 mm) communities were sampled. We found that benthic epifaunal community structure and diversity differed significantly between wave-exposed and wave-protected sites based on a wave energy model that reflects storm events in the harbor, where diversity was higher on protected sites. We also found that environmental variables collectively explained up to 67% of the variation in community characteristics, with elevation, organic content, water content, and soil skewness individually explaining up to 56%, 30%, 42%, and 33% of the variation, respectively. Other variables also made significant but smaller contributions. This study also illustrates the importance of analyzing multiple measures of community characteristics since community structure,

density, richness, and diversity respond differently to wave energy and other environmental factors.

INTRODUCTION

Ecological studies characterizing rocky intertidal habitats in the New England region and elsewhere are extensive (Menge 1976, Bustamante & Branch 1996, Schoch & Dethier 1996, Zacharias & Roff 2001, Bertness et al. 2006, Scrosati & Heaven 2007), but other common intertidal shoreline habitat types are largely understudied. For example, at the Boston Harbor Islands National Recreation Area (BOHA), a long-term monitoring protocol has been established for the rocky intertidal habitats (Long & Mitchell 2010), though this habitat only represents 3% of the park's intertidal substrate. The dominant shoreline type, representing 47% of the intertidal area, is mixed-coarse substrate, defined as cobbles, gravel, shell and sand, each not exceeding 75% cover and rock or boulder each not exceeding 50% cover (Bell et al. 2004, 2005). However, characterization of this habitat is limited aside from qualitative species inventories (Bell et al. 2004, 2005, Matassa 2009). It is important to understand and document the structure of the biotic communities in the mixed-coarse intertidal zone since they may be threatened by global climate change or degradation by shoreline modification or other anthropogenic factors.

Factors driving species diversity or other characteristics of community structure are commonly studied in terms of climate change, temporal or spatial heterogeneity, or biological interactions such as competition and predation (Menge 1976, Bertness & Leonard 1997, Stachowicz 2001, Silva et al. 2006), though the role of physical or environmental factors in influencing marine intertidal biological community structure has

recently been emphasized (McQuaid & Branch 1984, Oak 1984, Dethier & Schoch 2000, Covich et al. 2004).

The purpose of this study was to determine a) if epifaunal community structure, species richness, density, and diversity differ between wave-exposed and wave-protected intertidal environments and b) what environmental variables best explain the variation in the epifaunal community structure, species richness, density, and diversity. Though this study was restricted to the Boston Harbor Islands National Recreation Area, it may prove to be relevant to other coastal communities with similar habitats, such as Narragansett Bay, Rhode Island where cobble shorelines are a major component of the intertidal zone (Schwartz 2009), Buzzards Bay, Massachusetts where boulder fields and coarse sediment are common (Hough 1940), and areas of the Gulf of Maine where unconsolidated shores dominate over rocky shores (Foulis et al. 1994, Foulis & Tiner 1994).

METHODS

Study Area

The Boston Harbor Islands National Recreation Area consists of 34 islands and peninsulas nested within Boston Harbor at approximately 42.3186° N, 70.9458° W. This area is unique as the only drowned drumlin field in the United States (Himmelstoss et al. 2006), formed by a series of glacial till deposits. Additionally, several of the outer islands on the edge of the Boston Basin are composed primarily of exposed bedrock (Rosen & Leach 1987, FitzGerald et al. 2011).

Total land area of the park ranges between 6 km² to 12.4 km² from high tide to low tide, with a mean tidal range of approximately 2.9 meters (Bell et al. 2005). The park

area includes 56 kilometers of shoreline, 30% of which are lined with coastal structures such as seawalls, and 40% lined with glacial bluffs (FitzGerald et al. 2011). This shoreline marks the upper boundary of the park's intertidal zone, which is composed of a range of habitats including rocky or gravel beaches, mud flats, and salt marshes.

Site Selection

Eight islands (Bumpkin, Georges, Grape, Little Brewster, Lovells, Peddocks, Spectacle, and Thompson) of the 34 in the Boston Harbor Islands National Recreation Area were selected for this study. These islands were chosen based on public ferry accessibility. The remaining islands have restricted public access or would have required the rental of a specialized water craft for landing. Detrended correspondence analysis (DCA) plots provided by Bell et al. (2005) show that the eight selected islands are representative of all the other islands not included in this study, in terms of both substrate type and biotic assemblages.

On each of these eight islands, all mixed-coarse habitat was identified from a GIS-based inventory of intertidal habitats (Bell et al. 2004, 2005). The entire mixed-coarse habitat was then categorized into two strata based on wave exposure, as determined by the segment's orientation with respect to the predominant swell direction, similar to the methods of McQuaid & Branch (1984). Based on the direction of mean modal energy data obtained from FitzGerald et al. (2011), the two strata were defined as follows: wave-exposed (wave energy propagates onto the shoreline), or wave-protected (wave energy propagates away from the shoreline).

Nine locations were randomly chosen from each stratum, for a total of eighteen transect sites. Due to this random selection method, only six islands (Bumpkin, Grape, Lovells, Peddocks, Spectacle, and Thompson) were actually represented. Each of the eighteen transect sites were also re-stratified post-hoc into wave-exposed and wave-protected based on the maximum wave energy model obtained from FitzGerald et al. (2011), again resulting in nine transect sites for each stratum. The two wave energy models were selected to determine if intertidal benthic community characteristics were predominantly associated with the prevailing westerly winds (modal energy) or high energy storm events (maximum energy). Due to variations in each wave energy model, several transects were exposed or protected under both models while others were exposed under one model and protected under another model (Table 1-1).

When field sampling at each selected site, a transect tape was placed perpendicular to the shoreline from approximately mean lower low water (MLLW) to the upland boundary at mean higher high water (MHHW). Five 0.25 m² quadrats were placed along each transect using Generalized Random Tessellation Stratified (GRTS) sampling, which randomly selects quadrat locations while ensuring that each quadrat is an independent sample and that the entire elevation gradient along the transect was included in sampling (Steven & Olsen 2004). This method was performed by using the Snapping Measure Tool in ArcGIS to estimate the distance between the upper and lower boundaries of the mixed-coarse intertidal zone according to the data obtained from Bell et al. (2004), dividing that distance into five equal segments, and randomly selecting one quadrat location from each segment.

Some sites had fewer than five quadrats due to either the Bell et al. (2004) intertidal data overestimating the actual extent of the intertidal zone, or sampling was conducted during neap tides when lower elevation quadrats were submerged. A total of 87 independent random quadrats were sampled.

Data Collection

Macroinvertebrate Sampling

All epifaunal macroinvertebrate species, defined for this study as species 1 mm in size or greater, were identified and quantified by overturning all rocks within each quadrat and quickly collecting mobile species by hand. In a similar study, this method has proven to be 100% effective in capturing crabs regardless of cobble size (McClintock et al. 2007). For colonizing sessile species such as tunicates and bryozoans, each colony was counted as one individual.

Barnacle density was often too high to record individual counts in the field, so aerial, plan-view photos were taken of each quadrat, i.e. photoplots, and barnacle counts were estimated by counting individuals in each photoplot in the lab. Barnacle quantification methods likely resulted in an underestimate of total barnacle density since the photoplots are only a two dimensional representation of the quadrat and barnacles may have been present in contours unseen in the photos.

When the surface layer of rock and cobble was cleared, a single core (10 cm diameter, 5 cm depth) was taken from within each quadrat to collect smaller organisms which were otherwise too difficult to detect or collect by hand. The contents of the core were rinsed through a 1 mm mesh sieve, and all amphipods and other epifaunal

organisms were extracted. These species were preserved in 10% buffered formalin for storage, and transferred to 70% ethanol in the lab prior to identification.

All macroinvertebrate data were collected during July 2012 and August 2012. Species identification was aided by various field guides and taxonomic keys (Bousfield 1973, Gosner 1978, Weiss 1995). Count data from the quadrats and cores were scaled up to a surface area of 1 m² for data analysis.

Environmental Variables

Latitude and Longitude

Latitude and longitude of each quadrat was collected with a GPS unit to assess how epifaunal communities varied over the geographical range of the harbor, since physical factors vary between the inner harbor near downtown Boston and the outer harbor extending into Massachusetts Bay.

Date

Date of sampling was included as a variable in the environmental data analysis due to the likelihood that benthic communities could vary throughout the two month data collection process according to natural changes in individual species life histories, and whether a species is in the juvenile or adult stage at the time of sampling can affect whether or not it is identified and quantified. For analysis purposes, date was recorded as Day 1 through Day 57, where Day 1 corresponds to the first sampling date on July 2, 2012.

Elevation, Slope, and Aspect

Elevation, recorded as height in meters relative to MLLW, was determined for each quadrat using a Real Time Kinematic GPS. Elevation data were collected on September 18-20, 2012. Elevation was recorded for each corner of each quadrat, and all values were averaged to obtain a quadrat elevation. Slope was obtained by averaging the upper corners and lower corners of each quadrat separately and using the following equation, where 0.5 is the quadrat length:

$$\text{Percent Grade} = \frac{(\text{average upper quadrat elevation} - \text{average lower quadrat elevation})}{\sqrt{(0.5)^2 - (\text{average upper quadrat elevation} - \text{average lower quadrat elevation})^2}} \times 100$$

Aspect, or the direction the shoreline slope faces, was determined using the Snapping Measure Tool in ArcGIS to record the compass direction in degrees of each transect. This value was assigned to each quadrat on that transect.

Rugosity

Rugosity, representing surface complexity of a substrate, was determined prior to macrofaunal sampling using the methods in Matassa (2009). A string was laid over all the contours of both quadrat diagonals, and the average length, in cm, was recorded. The following equation was then used to determine rugosity, where 71 cm represents the length of a completely flat diagonal surface for a 0.25 m² quadrat:

$$\text{Rugosity} = \frac{\text{Average diagonal length, cm}}{71\text{cm}}$$

A higher rugosity corresponds to an area composed of boulder substrate, while a lower rugosity corresponds to quadrats dominated by gravel or pebbles.

Algae Cover

The 100 point-intercept method was used to determine percent cover of red, green and brown macro-algae using photoplots, or aerial, plan-view images of each quadrat, where a grid containing 100 evenly distributed points was projected onto each photoplot. Algae were identified beneath each point-intercept, where each point-intercept represents 1% cover. This method was adapted from Hutchinson & Williams (2003). Cover was estimated by algal group (red, green, and brown) and total algal coverage rather than by species since identification to the species level was limited in the photoplots. Encrusting algae were also omitted from the analysis due to identification restraints associated with photoplots.

Water and Organic Content

Single sediment samples of approximately 100 cm³ were also taken from the top 5 cm of each quadrat. In the lab, the collected sediment samples were thoroughly mixed by hand with a spatula, and 2 cm³ were removed. These samples were weighed (initial weight), then placed in a muffle furnace at 100°C for 24 hours to determine the dry weight (DW₁₀₀) and again at 550°C for 24 hours to determine organic content (i.e. loss on ignition method, DW₅₅₀). Percent of water and total organic content in each sample were then determined with the following equations adapted from Dean (1974):

$$\text{Percent of water} = \frac{\text{Initial weight} - \text{DW}_{100}}{\text{Initial weight}} \times 100$$

$$\text{Percent of total organic content} = \frac{\text{DW}_{100} - \text{DW}_{550}}{\text{DW}_{100}} \times 100$$

Soil Skewness

After determining water content and organic content of each soil sample, the dried samples were analyzed for grain size using a Ro-Tap sieve shaker to sort the sample through a nested series of sieves (4750, 2000, 1700, 850, 425, 250, 160, 75, and 63 μm). The GRADISTAT program was then used to determine the distribution of grain size, in terms of skewness, for each soil sample, where a negative skew represents a soil sample defined by finer grain sizes and positive skew represents a soil sample defined by coarser grain sizes (Blott & Pye 2001).

Porewater Temperature and Salinity

When porewater was present in a quadrat upon removal of the shallow core or sediment sample, an armored thermometer was used to record temperature and a refractometer was used to record salinity. However, because porewater temperature and salinity were not obtained from all quadrats, these data were omitted from the analysis of relationships between environmental variables and benthic communities.

Data Analysis

Variability among Benthic Intertidal Communities

Routines available in the PRIMER 6 software program (Clarke & Warwick 2001) and the PERMANOVA+ add-on package (Anderson et al. 2008) were used to perform multivariate analyses of intertidal benthic community structure and univariate analyses of density, species richness, and Shannon-Weiner diversity.

For multivariate analysis of community structure, we first calculated the Bray-Curtis similarity index on fourth-root transformed species abundances, with a dummy variable of 0.001 added to the dataset where species abundances had a value of zero. Based on the Bray-Curtis similarity measure, differences in community structure between wave-exposed and wave-protected groups were tested with a one-way permutational multivariate analysis of variance (PERMANOVA) separately for both the maximum and modal wave energy models. PERMANOVAs were performed with the wave energy model as a fixed factor and partitioning was done with Type III sums of squares. Differences in community structure were identified by calculating a distance-based *pseudo*-F statistic, where significance was determined by 9999 unrestricted permutations of the raw data. Analysis of the homogeneity of multivariate dispersions (PERMDISP) was also performed separately for each wave energy model using 9999 permutations to generate an F statistic. PERMANOVA and PERMDISP results are interpreted together to identify the source of dissimilarity between groups, since significant PERMANOVA results indicate location effects, dispersion effects, or both, and PERMDISP results indicate only dispersion effects. The similarity percentages (SIMPER) routine was then used to determine the contribution of each species to the average dissimilarity between wave exposure groups for only the wave energy models that were determined to be significant.

For univariate analysis, the DIVERSE function in PRIMER was used to extract species richness, density, and diversity from the original, untransformed data set. The Euclidean similarity measure was used to calculate distances between samples, and

PERMANOVA and PERMDISP analyses were performed using the same techniques described previously for multivariate analysis of community structure.

Relationships between Benthic Intertidal Communities and Environmental Variables

The relationships between environmental variables and benthic intertidal community structure, density, species richness, and diversity (H') were analyzed using distance-based linear models (DISTLM) from the PERMANOVA+ package. DISTLM analyses were performed on the same Bray-Curtis similarity matrices (for community structure) and Euclidean similarity matrices (for species richness, density, and diversity) used for the previously described PERMANOVA and PERMDISP analyses. Marginal tests were used to assess the relationships between each environmental variable and the response variable, ignoring all other variables. Sequential tests were used to determine which combinations of environmental variables best explain variability in the response variable. To determine how the sequential test was performed, the step-wise selection procedure was chosen using Akaike's Information Criteria (AIC). AIC was chosen as the selection criteria for its penalty term, which discourages increases in the number of variables selected for the model. Each DISTLM analysis was performed twice; once with the total algae variable omitted and once with red, green, and brown algae variables omitted. This was done to prevent redundancy in the models since red, green, and brown algae are components of total algae.

RESULTS

Summary of Biotic and Environmental Variables

Table 1-2 presents the mean and maximum abundance values for the 25 epifaunal species detected, with *Balanus balanoides* clearly the dominant. Table 1-3 presents the mean, minimum, and maximum values for the eleven environmental variables measured across all quadrats, including the frequency or percent of quadrats in which algae were detected. Porewater temperature and salinity are included for descriptive purposes, though these variables were not included in the analysis between environmental factors and community characteristics since porewater was not present at all sampling sites. A species list of the algae detected is also available in Table 1-4 for descriptive purposes, though algae were analyzed by class rather than by individual species.

Variability in Community Structure

We found a significant difference in epifaunal community structure between exposed and protected groups, based on the maximum wave energy model (PERMANOVA, $p=0.0098$, Table 1-5). This significant difference is due only to location effects and is not a result of differences in dispersion or variability. The modal wave energy model was insignificant in influencing community structure.

Similarity percentages (SIMPER) analysis indicates that the species which contribute to 92% of the variability between exposed and protected shorelines in the maximum wave energy model are *Balanus balanoides*, *Littorina littorea*, *Hyale plumulosa*, *Anurida maritima*, *Carcinus maenas*, and *Hemigrapsus sanguineus*, where average abundance per m^2 is higher on exposed shores for *Balanus balanoides* and higher on protected shores for *Littorina littorea*, *Hyale plumulosa*, *Anurida maritima*, *Carcinus maenas*, and *Hemigrapsus sanguineus* (Table 1-6).

Variability in Density, Species Richness, and Diversity

We found no significant differences in density and species richness between exposed and protected shorelines for either the maximum or modal wave energy models (Table 1-5). However, diversity analysis indicates a significant difference between exposed and protected groups based on the maximum wave energy model due to differences in location effects only (PERMANOVA, $p=.0119$), whereas the modal wave energy model was not significantly correlated with diversity (Table 1-5). Average diversity was higher in wave-protected sites according to the maximum wave energy model (Table 1-7).

Relationship between Environmental Data and Community Structure

Since PERMANOVA and PERMDISP results indicated significant differences in community structure between exposure groups for the maximum wave energy or storm event model only, we performed DISTLM analysis separately on community structure for exposed and protected groups using the maximum wave energy model.

Marginal tests indicate that elevation, rugosity, water content, organic content, and skewness all contribute significantly to variability in community structure for both exposed and protected groups (Table 1-8). The proportion of variability explained by elevation, rugosity, water content, and organic content is higher in protected sites than in exposed sites, whereas skewness contributes more to variability in exposed sites than protected sites. Green algae also contribute a significant proportion of variability in the protected sites, whereas slope, aspect, brown algae, red algae, and total algae contribute significant proportions of variability in the exposed sites (Table 1-8).

Sequential tests for community structure also showed different combinations of variables in the best-fit models for each exposure group. In protected sites, elevation, longitude, rugosity, water content, day, and green algae together explained approximately 52% of the variation in community structure. Although day and green algae improved the AIC selection criteria in the model development, their contributions to the model were not statistically significant, therefore we chose to accept the model including the first four variables explaining 47% of variation in the community structure. Alternatively, water content, rugosity, skewness, and elevation together explained approximately 49% of the total variation in community structure in exposed sites, where all terms in the model were significant (Table 1-9).

Relationship between Environmental Data and Density, Species Richness, and Diversity

Since PERMANOVA and PERMDISP results indicated significant differences in diversity between wave exposure groups for the maximum wave energy or storm event model only, we performed DISTLM analysis separately on H' for exposed and protected groups based on the maximum wave energy model. DISTLM was performed on the full dataset for density and species richness since no significant differences occurred between wave exposure groups for either energy model.

Marginal tests indicate that elevation has a negative correlation with density, species richness, and diversity, while water content, organic content, and skewness have positive correlations with the univariate measures. Rugosity and red algae also are positively correlated with density and species richness. For density, there is a positive

correlation with aspect and a negative correlation with slope. Brown algal cover is positively correlated with species richness. Day is positively correlated to H' protected but not H' exposed, whereas brown algae, red algae, and total algae are positively correlated to H' protected but not H' exposed (Table 1-8).

Sequential tests indicate that skewness, elevation, rugosity, and latitude together explain approximately 48% of the total variation in density, though only skewness and elevation are significant in this model, explaining only 44% of the variation. For species richness, about 68% of the total variation is explained by elevation, water content, rugosity, red algae, skewness, organic content, water content, day, and brown algae, though only the first five of these variables are significant in the model and together explain 64% of the variation in density. Elevation, rugosity, latitude, and organic content together explain approximately 69% of the total variation in H' protected, though organic content is not significant in this model, resulting in a significant model explaining only 67% of the variation. For H' exposed, water content, rugosity, and total algae together explain 51% of the total variation, though water content is the only significant term in the model, explaining 43% of the variation (Table 1-9).

DISCUSSION

Epifaunal Communities and Wave Energy

The maximum wave energy model, or wave activity associated with pulse or storm events, proved to be significantly correlated with epifaunal community structure and diversity in the mixed-coarse intertidal zone of Boston Harbor (Table 1-5). Modal wave energy, or prevailing westerly winds, was not correlated with any aspect of

epifaunal community characteristics. McQuaid & Branch (1984) studied epifaunal species richness on rocky shores using data on predominant swells (i.e. modal energy) to define exposed and protected wave exposures and found no significant differences in richness between exposure groups, consistent with our results. A similar study on epifaunal species in Puget Sound, WA, including benthic invertebrates and algae in the overall community structure, found that epifaunal communities varied by wave exposure as determined by wave fetch and mean maximum wind velocity, where mean maximum wind velocity would correspond with our definition of wave exposure by the maximum energy model (Dethier & Schoch 2000).

However, several studies have found that prevailing winds, as oppose to maximum or storm winds, do have an effect on various elements of community structure. For instance, the recruitment of barnacles and mussels is higher on exposed shores when exposure is defined in terms of the prevailing winds (Bertness et al. 2006). Our study found modal energy to be insignificant but in the SIMPER analysis of community structure based on maximum energy, our results agree with Bertness et al. (2006), with average barnacle density greater on exposed shores (Table 1-6). Although trends in barnacle density across wave exposure groups are the same in both studies, the method of defining exposure varied. Also contrary to our results was a similar study that determined disturbance by storm activity increased species richness (Zacharias & Roff 2001), whereas the maximum wave energy model for our study showed no difference in species richness between protected and exposed sites. Other studies also defined exposure by prevailing winds and found significant correlations between community characteristics and wave energy (Ricciardi & Bourget 1999, Scrosati & Heaven 2007).

No studies that we reviewed considered both modal and maximum wave energies to define wave exposure groups, and so comparisons with our findings must be interpreted carefully. Results from this study clearly demonstrate that intertidal community structure, density, richness, and diversity respond differently to the definitions of wave energy. It is also difficult to compare results across different studies where relative exposure groups were used in analysis because the actual energy associated with prevailing or storm winds may vary by geographic region.

Significant wave height and energy density associated with each model may also impact our interpretations. The modal or prevailing wind energy in Boston Harbor is associated with significant mean wave heights ranging between 0 and 0.8 meters, whereas in the maximum energy model significant wave height varies between 0 and 1.5 meters. Also, energy density according to the modal model ranges between 0 and 0.65 J/m², while in the maximum model energy density reaches 3 J/m² (FitzGerald et al. 2011). Although the direction of modal energy with respect to the shoreline may vary, the actual energies associated with the model are minimal and likely do not have a large effect on the intertidal communities. However, the energies associated with the maximum energy model are higher and shoreline orientation to the direction of maximum wave energy likely has a greater effect on the intertidal community.

According to the SIMPER analysis, of the species significantly contributing to community structure differences between wave-protected and wave-exposed sites according to maximum wave energy, only the barnacle *Balanus balanoides* had a higher average abundance in the exposed sites than in the protected sites (Table 1-6). This is consistent with studies demonstrating that filter feeders have a higher abundance on

exposed shores since water movement enhances food supply and alleviates thermal stress (Bustamante & Branch 1996, Harley & Helmuth 2003, Hammond & Griffiths 2004).

However, Bustamante & Branch (1996) also determined that invertebrate predators are more abundant on exposed shores, which was not the case in this study where the crabs *Hemigrapsus sanguineus* and *Carcinus maenas* were more abundant on protected shores.

Grazers such as *Littorina littorea* and the amphipod *Hyale plumulosa* were more abundant on the maximum energy wave-protected shores than wave-exposed shores, and all other amphipods were found exclusively on wave-protected beaches. This is consistent with grazer distribution by wave energies observed in other regions (Bertness 1984, Bustamante & Branch 1996). Elsewhere, higher densities of *Littorina littorea* were associated with a lower abundance of barnacles as the periwinkle interferes with barnacle settlement (Petraitis 1983). This was consistent with our study as SIMPER analysis indicated that periwinkle density was higher on the maximum energy wave-protected shores where barnacle density was lower (Table 1-6).

Wave action tends to extend biological zones of sessile species vertically upshore by increasing food supply and duration of immersion (Ricciardi & Bourget 1999, Harley & Helmuth 2003) while desiccation in protected sites limits vertical ranges (Bertness et al. 2006). Meanwhile, heightened wave energy tends to constrain distribution of mobile organisms (Menge & Olson 1990, Hammond & Griffiths 2004). These trends help to explain why the sessile barnacle had a higher abundance in the maximum energy wave-exposed shores while the other five species contributing to differences between exposure sites were all mobile species and were all more abundant in the maximum energy wave-protected sites.

Exposed shores have been found to have lower richness and diversity (Bustamante & Branch 1996, Scrosati & Heaven 2007), consistent with our results in which the maximum energy wave-exposed shores had lower diversity, though richness did not significantly differ (Table 1-7). It is likely that richness, and also density, were not significant since major differences between wave exposures were dependent on the types of species present. The maximum energy wave-exposed shores were devoid of *Littorina obtusata*, *Diadumene lineata*, *Microdeutopus gryllotalpa*, *Gammarus oceanicus*, *Corophium volutator*, and an unidentified amphipod, while wave-protected shores were devoid of *Styela clava*, *Styela partita*, *Ilyanassa trivittata* and an unidentified insect larva. Together, these results indicate that wave energy primarily affects species composition and species distributions, rather than the absolute number of species and individuals present.

Although diversity was higher in the protected shores than the exposed shores according to a wave energy model that reflects storm events, we cannot definitively say that diversity is negatively correlated with wave exposure because there were only two exposure groups defined in this study. Instead, the intermediate disturbance hypothesis could be relevant, in which diversity would be highest at an intermediate wave energy (Connell 1978, Sousa 1979, Sousa 1984). However, the intermediate disturbance hypothesis could not be tested with our data, since establishing a third exposure group was not possible given the methods used to define wave-exposed and wave-protected sites.

Epifaunal Communities and Environmental Variables

Elevation explained up to 56% of the variation in community characteristics (Table 1-8), consistent with similar studies in which elevation plays a primary role in biomass, species richness, abundance, and diversity across a variety of benthic intertidal communities (Davidson et al. 2004, Davidson 2005, Wallenstein & Neto 2006, Scrosati & Heaven 2007). The percent of variation explained by elevation was about twice as high in protected sites than exposed sites, for community structure and diversity, where site exposure is based on the maximum energy or storm event model. This is expected, as desiccation stress on protected shores limits distribution of particular species whereas higher elevations on exposed shores are less affected by this stress due to increased immersion time.

Soil skewness, organic content, and water content each explained up to 33%, 30%, and 43%, respectively, of the total variation in epifaunal community characteristics (Table 1-8). Little information is available for the expected effect of soil grain size on epifaunal communities since it is mostly studied in the context of infaunal communities (Dethier & Schoch 2000, Ysebaert et al. 2002, Ysebaert & Herman 2002, Martin et al. 2005, Rodil et al. 2007). However, the three variables are typically closely related as grain size affects permeability and the storage of water and organic matter (Masch & Denny 1966, Bergamaschi et al. 1997, Szarek-Gwiazda 2010), and both water and organic matter are essential in sustaining benthic intertidal communities (Levinton et al. 1984).

Up to 23% of the variation in epifaunal communities can be explained by algae, where red algae, brown algae, and total algae are significant in community structure and diversity on exposed shores. This is surprising as it was expected that algae would serve a

larger role on protected shores, alleviating biological communities from desiccation stress by providing shade and retaining moisture (Menge 1978, Hay 1981, Leonard 2000), though thermal buffering may not be that significant in temperate climates (Bertness & Leonard 1997). Instead, algae may play a significant role on exposed shores by stabilizing the substrate and buffering mobile species from intense wave energy (Stachowicz 2001). Not surprisingly, red algae were positively associated with species richness and density and brown algae with species richness, indicating that perhaps algae do provide a buffer against stress in the overall community. Uniquely, green algae were significantly associated with community structure on protected shores only, though this is consistent with findings that green macroalgal mats are related to an increase of gammarid amphipods (Bolam et al. 2000). In Boston Harbor, gammarid amphipod species richness and density were greater on protected shores. These results indicate that the role of algae varies by algal group and by each measure of community characteristics.

Rugosity explained up to only 15% of total variation in community structure, density, and richness, and was not significant in explaining diversity. Surprisingly, rugosity had a negative relationship with richness and density. It was expected that a higher rugosity or surface complexity would be associated with more crevices and areas in or under which organisms could rest to escape thermal stress or predation and with a larger surface area for sessile organisms to colonize (Kostylev et al. 2005).

Aspect and slope each explained up to 9% of the total variation in community structure on exposed shores and density, and day sampled explained up to 9% of the total variation in diversity. Aspect is also related in many cases to wave exposure since the direction of the slope also determines a shore's relation to wind and wave directions, but

aspect also determines solar insolation, or thermal exposure and shading effects in the intertidal zone (Schoch & Dethier 1996). Slope plays a role in determining the reflection or dissipation of wave energy and retention of organic matter since shallower slopes dissipate energy and increase the settling of organic matter while steeper slopes reflect energy and organic matter and as such, typically result in fewer species (McLachlan 1996). However, this negative relationship between slope and species richness was not supported in this study.

Latitude and longitude explained up to only 4% of variation in epifaunal community structure, density, richness, and diversity but the correlations were not significant. We expected that these variables would play a significant role due to the varying physical conditions throughout the harbor. Matassa (2009) noted a slight increase in species richness in Boston Harbor with latitude or with distance from the mainland but this trend was not necessarily significant and included algae, infauna, and other taxa in defining species richness.

Sequential tests indicate that the environmental variables analyzed in this study collectively explain between 44% and 67% of the variation in community characteristics when considering only the significant terms in the models (Table 1-9). Other variables that may have added additional variation are the porewater temperature and salinity which could not be included in analysis due to insufficient data. Precipitation or freshwater input may also be an important variable, as heavy rainfall may later result in an increase in amphipod abundance (Silva et al. 2006). Additionally, biological effects such as predation or facilitation may play important roles in structuring the intertidal communities (Menge 1976, Stachowicz 2001).

The models presented in this study are meant to represent variability in epifaunal community characteristics as a function of environmental variables. Though many of these variables may in fact have a direct effect on the benthic intertidal macroinvertebrate communities, this study is not meant to imply that these environmental variables necessarily have a direct effect on the community as they instead may act as surrogates for other physical (e.g. temperature), chemical (e.g. salinity), or biological (e.g. predation) factors.

Management Implications

Cobble or mixed-coarse beaches, such as those found throughout Boston Harbor's intertidal zones, are confronted with many natural and human-induced disturbances, such as climate change, storms, invasive species, shoreline protection structures, contaminant spills, nutrient enrichment, and boat wakes. An initial step to protecting these habitats and their essential food web support functions for foraging shorebirds (Evans 1988, Hori & Noda 2001) and pelagic communities (Grossman 1986) is to quantify community structure. The findings of this study provide a baseline for long-term monitoring aimed at understanding the response of cobble and mixed-coarse intertidal communities to multiple disturbances and provide a foundation to support habitat restoration actions, if warranted.

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Table 1-1. Location of each transect and its wave exposure strata based on both the modal and maximum wave energy models from FitzGerald et al. (2011).

Transect	Island	Modal	Maximum
A	Thompson	Protected	Exposed
B	Thompson	Protected	Exposed
C	Spectacle	Protected	Protected
D	Peddocks	Protected	Exposed
E	Peddocks	Protected	Exposed
F	Lovells	Protected	Exposed
G	Peddocks	Protected	Protected
H	Thompson	Protected	Exposed
I	Grape	Protected	Protected
J	Thompson	Exposed	Protected
K	Grape	Exposed	Exposed
L	Lovells	Exposed	Protected
M	Lovells	Exposed	Protected
N	Thompson	Exposed	Exposed
O	Peddocks	Exposed	Protected
P	Grape	Exposed	Exposed
Q	Thompson	Exposed	Protected
R	Bumpkin	Exposed	Protected

Table 1-2. Summary of epifaunal species present in the 87 sampling sites in the intertidal mixed-coarse habitat. Mean and maximum values represent abundance per m². The minimum value detected was zero for all species. Frequency indicates the percent of sampling sites that species were observed.

Phylum	Species	Mean	Maximum	Frequency(%)
Arthropoda	<i>Anurida maritima</i>	39.5	1401	5.8
	<i>Balanus balanoides</i>	263.3	4136	48.3
	<i>Carcinus maenas</i>	7.0	64	40.2
	<i>Corophium volutator</i>	1.5	127	1.2
	<i>Gammarus oceanicus</i>	1.5	127	1.2
	<i>Hemigrapsus sanguineus</i>	6.2	104	35.6
	<i>Hyale plumulosa</i>	52.7	764	13.8
	<i>Microdeutopus gryllotalpa</i>	1.5	127	1.2
	<i>Pagurus acadianus</i>	1.5	36	9.2
	<i>Pagurus longicarpus</i>	1.0	40	4.6
	Unidentified amphipod	1.5	127	1.2
	Unidentified insect larva	1.5	127	1.2
Bryozoa	<i>Membranipora membranacea</i>	0.1	4	3.5
Cnidaria	<i>Diadumene lineata</i>	0.5	24	3.5
Chordata	<i>Botrylloides violaceus</i>	0.7	28	5.8
	<i>Styela clava</i>	0.1	4	1.2
	<i>Styela partita</i>	1.3	108	2.3
Mollusca	<i>Crepidula fornicata</i>	1.7	72	6.9
	<i>Crepidula plana</i>	5.2	108	12.6
	<i>Littorina littorea</i>	11.1	728	51.7
	<i>Littorina saxatilis</i>	0.8	16	11.5
	<i>Littorina obtusata</i>	0.3	24	2.3
	<i>Mytilus edulis</i>	1.0	20	12.6
	<i>Ilyanassa trivittata</i>	0.1	4	1.2
	<i>Ilyanassa obsoleta</i>	0.1	8	1.2

Table 1-3. Summary of environmental variables characterizing the 87 sampling sites in the intertidal mixed-coarse habitat, where frequency indicates the percent of sampling sites that algae were observed or porewater temperature and salinity were recorded.

* denotes variables that were not included in further analysis due to insufficient data.

Variable	Mean	Minimum	Maximum	Frequency (%)
Slope (%)	5.85	-4.84	16.83	
Rugosity	1.18	1.01	1.53	
Soil Water Content (%)	13.72	2.09	35.14	
Soil Organic Content (%)	1.48	0.34	4.14	
Soil Skewness	0.17	-0.29	0.70	
Brown Algal Cover (%)	1.75	0	56	9.2
Green Algal Cover (%)	2.80	0	59	14.9
Red Algal Cover (%)	1.16	0	24	57.6
Total Algal Cover (%)	5.71	0	59	37.9
Porewater Temperature (°C)*	23.75	19	29	63.2
Porewater Salinity (ppt)*	29.80	10	33	63.2

Table 1-4. Species list of algae detected in sampling sites. * denotes a crustose algae which was not included in percent cover data due to difficulty observing the algae in each photoplot.

Red Algae

Agardhiella spp.
Chondrus crispus
Gracilaria spp.
Hildenbrandia rubra*
Mastocarpus spp.
Porphyra spp.

Green Algae

Codium fragile
Ulva spp.

Brown Algae

Fucus distichus
Fucus spiralis
Fucus vesiculosus

Table 1-5. Summary of PERMANOVA (pseudo-F statistic) and PERMDISP (F statistic) analyses between wave-exposed and wave-protected sites for epifaunal data, with bold type indicating significant results at $p < 0.05$. PERMANOVAs were performed as a one-way analysis independently for the maximum and modal wave energy models.

	PERMANOVA		PERMDISP		Inference
	Pseudo-F	p-value	F	p-value	
Community Structure					
Maximum	4.4275	0.0098	0.67451	0.4277	Location effect only
Modal	1.3315	0.2287	0.9156	0.3806	No location or dispersion effects
Density					
Maximum	0.19702	0.6773	1.9041	0.3587	No location or dispersion effects
Modal	1.1014	0.3044	3.495	0.1993	No location or dispersion effects
Species Richness					
Maximum	1.36	0.2507	1.919	0.2054	No location or dispersion effects
Modal	.00026	1	1.4897	0.2467	No location or dispersion effects
Diversity					
Maximum	6.6272	0.0119	0.29144	0.5893	Location effect only
Modal	0.87312	0.3542	0.05941	0.807	No location or dispersion effects

Table 1-6. Similarity percentage (SIMPER) analysis, identifying species contributing to the discrimination in epifaunal community structure between wave-exposed and wave-protected shorelines in the maximum wave energy or storm event model. Average abundances presented in individuals per m².

Average dissimilarity between exposure groups = 89.97

Species	Exposed Average Abundance	Protected Average Abundance	Cumulative%
<i>Balanus balanoides</i>	355.0	177.7	35.9
<i>Littorina littorea</i>	69.2	150.1	63.0
<i>Hyale plumulosa</i>	51.5	53.8	76.5
<i>Anurida maritima</i>	30.3	48.1	85.4
<i>Carcinus maenas</i>	5.7	8.2	88.8
<i>Hemigrapsus sanguineus</i>	4.7	7.6	92.2

Table 1-7. Average density, species richness, and diversity of epifaunal species in wave-exposed and wave-protected sites as determined by the maximum wave energy or storm event model. Average values are per m². Only differences in diversity between exposure groups were significant based on PERMANOVA and PERMDISP analysis.

	Density	Species Richness	Diversity
Wave-Exposed	538.2	2.4	0.3
Wave-Protected	467.0	3.1	0.6

Table 1-8. Summary of marginal tests, obtained from distance-based linear models (DISTLM), for epifaunal data. Protected and exposed refer to shoreline stratification based on the maximum wave energy or storm event model. Bold type indicates values significant at $p < 0.05$, and +/- indicate positive or negative correlations. *ln(x), **ln(x+1), [†] 1/x transformed, [‡] sqrt(x) transformed.

Variables	Community Structure		Density	Species Richness	Diversity				
	Protected	Exposed			Protected	Exposed			
Latitude	2.56E-02	4.41E-02	4.74E-03	-	6.22E-04	-	1.26E-03	-	8.35E-03
Longitude	2.80E-02	1.13E-02	5.84E-04	+	5.02E-03	-	7.23E-03	-	2.12E-02
Date	1.83E-02	5.31E-02	7.05E-04	+	3.34E-02	+	9.07E-02	+	3.46E-02
Slope	4.31E-02	8.88E-02	4.51E-02	-	4.38E-02	-	1.38E-03	-	2.97E-02
Aspect	1.69E-02	8.82E-02	7.35E-02	+	2.69E-02	+	1.45E-02	-	6.73E-02
Elevation	3.07E-01	1.83E-01	2.49E-01	-	4.46E-01	-	5.64E-01	-	2.63E-01
Rugosity	6.63E-02	1.51E-01	4.51E-02 [†]	-	5.91E-02 [†]	-	7.69E-02	+	7.69E-02
Water Content	3.07E-01	2.86E-01	1.62E-01	+	4.11E-01	+	3.08E-01	+	4.28E-01
Organic Content	1.83E-01	1.70E-01*	6.81E-02 [‡]	+	2.62E-01 [‡]	+	3.01E-01	+	2.49E-01*
Skewness	9.68E-02	2.06E-01**	3.31E-01	+	2.48E-01	+	8.70E-02	+	8.30E-02**
Brown Algae	1.62E-02	7.52E-02	2.15E-02	+	6.76E-02	+	2.04E-02	+	2.35E-01
Green Algae	6.86E-02	3.63E-02	1.08E-02	-	3.13E-02	-	7.46E-02	-	3.85E-02
Red Algae	2.72E-02	1.49E-01	1.09E-01	+	2.27E-01	+	2.06E-04	+	2.25E-01
Total Algae	4.51E-02	1.42E-01	1.01 E-02	+	2.33E-02	+	2.63E-02	-	1.94E-01

Table 1-9. Summary of sequential tests, obtained from distance-based linear models (DISTLM), for epifaunal data. Protected and exposed refer to shoreline stratification based on the maximum wave energy or storm event model. Bold type indicates values significant at $p < 0.05$. +/- indicate additions to or subtractions from the model. ** $\ln(x+1)$, $^{\dagger} 1/x$ transformed, $^{\ddagger} \sqrt{x}$ transformed.

	Variables	Proportion	Cumulative
Community Structure			
Protected	+Elevation	0.30684	0.30684
	+Longitude	6.76E-02	0.37447
	+Rugosity	6.82E-02	0.44269
	+Water Content	3.09E-02	0.47362
	+Date	2.37E-02	0.49729
	+Green Algae	2.25E-02	0.51978
Exposed	+Water Content	0.28557	0.28557
	+Rugosity	1.19E-01	0.40446
	+Skewness**	4.46E-02	0.4491
	+Elevation	4.41E-02	0.49322
Density	+Skewness	0.33115	0.33115
	+Elevation	1.05E-01	0.43662
	+Rugosity †	2.51E-02	0.46176
	+Latitude	1.95E-02	0.48124
Species Richness	+Elevation	0.44567	0.44567
	+Water Content	8.57E-02	0.5314
	+Rugosity †	4.03E-02	0.57171
	+Red Algae	4.51E-02	0.61677
	+Skewness	2.28E-02	0.63954
	+Organic Content ‡	1.57E-02	0.6552
	-Water Content	9.93E-04	0.65421
	+Date	1.37E-02	0.66792
	+Brown Algae	7.98E-03	0.6759
Diversity			
Protected	+Elevation	0.56446	0.56446
	+Rugosity	6.50E-02	0.62946
	+Latitude	4.13E-02	0.67079
	+Organic Content	1.63E-02	0.68711
Exposed	+Water Content	0.4282	0.4282
	+Rugosity	4.40E-02	0.4722
	+Total Algae	3.93E-02	0.51152

APPENDIX A: Detailed Description of Methods

STUDY AREA

The Boston Harbor Islands National Recreation Area consists of 34 islands and peninsulas nested within Boston Harbor (Figure A-1). This area is unique in that it is the only drowned drumlin field in the United States (Himmelstoss et al. 2006). The islands were formed primarily by two glacial till deposits, starting with a drumlin till deposited by the Wisconsin glaciation approximately 800,000 to 300,000 years before present, and ending with a surface till deposited by the Illinoian glaciation which occurred approximately 15,000 years before present. Additionally, several of the outer islands on the edge of the Boston Basin are composed primarily of exposed bedrock. The glacially formed islands experience a higher degree of transformation by erosion through time as wave and wind energy vary through the harbor and sea level changes, whereas the bedrock islands remain stable. Islands situated within the inner harbor are more protected and typically experience lower wave energy than the outer harbor islands, which open towards Massachusetts Bay and are more exposed to higher levels of wave energy (Rosen & Leach 1987, FitzGerald et al. 2011).

Total land area of the park ranges between 6 km² to 12.4 km² from high tide to low tide, with a mean tidal range of approximately 2.9 meters (Bell et al. 2005). There are about 56 kilometers of shoreline in the park, 30% of which are lined with coastal structures such as seawalls, and about 40% lined with glacial bluffs (FitzGerald et al. 2011). This shoreline marks the upper boundary of the park's intertidal zone, which is composed of a range of substrates in addition to the mixed-coarse habitat including

mixed coarse and fine, reef, mud, peat, boulders, rock, cobble, gravel, shells, and sand. These habitats support a variety of species assemblages, such as *Mytilus* reef, *Spartina alterniflora*, *Semibalanus*, mixed macroalgae, tidepools, marshes, and related assemblages. However, 'no macrobiota' is notably the second most dominant species assemblage type (Bell et al. 2005).

HABITAT DISTRIBUTION AND SITE SELECTION

The following pages show the original wave energy models obtained from FitzGerald et al. (2011; Figure A-2), detailed graphs of the distribution of mixed-coarse intertidal habitat on each of the eight islands selected for this study, as well as the wave-exposed and wave-protected strata based on the modal and maximum wave energy models and transect locations where applicable (Figures A-3 to A-10). Also included is a figure of all transect locations in Boston Harbor (Figure A-11) and a summary table detailing the locations and exposure status of each transect (Table A-1).

Figure A-2. Maximum and modal wave energy models obtained from FitzGerald et al. (2011).

Figure A-3. Mixed-coarse intertidal zone of Bumpkin Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-4. Mixed-coarse intertidal zone of Georges Island and wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models. No transect sites were located on this island. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-5. Mixed-coarse intertidal zone of Grape Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-6. Mixed-coarse intertidal zone of Little Brewster Island and wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models. No transect sites were located on this island. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-7. Mixed-coarse intertidal zone of Lovells Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-8. Mixed-coarse intertidal zone of Peddocks Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-9. Mixed-coarse intertidal zone of Spectacle Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Figure A-10. Mixed-coarse intertidal zone of Thompson Island, wave-exposed and wave-protected strata based on the FitzGerald et al. (2011) wave energy models, and transect site locations. (A) modal wave energy model, (B) maximum wave energy model.

Table A-1. Location of each transect and its wave exposure strata based on both the modal and maximum wave energy models from FitzGerald et al. (2011). Latitude and longitude are presented in 19N UTM.

Transect	Date Sampled	Island	Latitude	Longitude	Modal	Maximum
A	2013-07-25	Thompson	0334777	4687032	Protected	Exposed
B	2013-07-26	Thompson	0334778	4687362	Protected	Exposed
C	2013-08-13	Spectacle	0336547	4688032	Protected	Protected
D	2013-07-31	Peddocks	0340944	4684597	Protected	Exposed
E	2013-07-29	Peddocks	0339804	4683736	Protected	Exposed
F	2013-07-17	Lovells	0341361	4688007	Protected	Exposed
G	2013-07-15	Peddocks	0339463	4683944	Protected	Protected
H	2013-08-25	Thompson	0334278	4686212	Protected	Exposed
I	2013-08-08	Grape	0341484	4681262	Protected	Protected
J	2013-07-13	Thompson	0333795	4686393	Exposed	Protected
K	2013-08-06	Grape	0341619	4681634	Exposed	Exposed
L	2013-07-02	Lovells	0340956	4688440	Exposed	Protected
M	2013-07-16	Lovells	0340941	4688472	Exposed	Protected
N	2013-07-14	Thompson	0334103	4686731	Exposed	Exposed
O	2013-07-30	Peddocks	0340129	4683353	Exposed	Protected
P	2013-08-07	Grape	0341735	4681710	Exposed	Exposed
Q	2013-08-27	Thompson	0333792	4686356	Exposed	Protected
R	2013-08-09	Bumpkin	0343068	4682769	Exposed	Protected

Figure A-11. Location of transect sites throughout the Boston Harbor Islands National Recreation Area.

PHOTOQUADRAT STAND AND PHOTOPLOTS

A photoquadrat stand (Figure A-12) was constructed using a similar design described in Long et al. (2010) for rocky intertidal monitoring. The stand, made of PVC pipe, consists of a 50x50 cm base and two vertical legs approximately 65 cm in length attaching the 10x25 cm camera rest to the quadrat base. It is necessary to make sure that when assembled, the camera rest is directly centered over the base of the photoquadrat for consistent results. The bottom portion of the photoquadrat stand is spray painted black to eliminate glare while taking a photo. To take a photo, a digital camera is placed flat on top of the camera rest and the use of an umbrella is recommended to provide even shading over the quadrat. This method provides uniform aerial, plan-view images of each quadrat for further analysis in the lab.

In the lab, the photoplots were analyzed for barnacle density and algae cover. Each photo was uploaded to Microsoft Office PowerPoint, where a 100-point intercept grid was projected over the photoplot (Figure A-13). For barnacle density analysis, the grid simply served as a tool to divide the photoplot into small portions for counting individual barnacles and ensuring that portions of the photoplots were not omitted or double counted.

The 100-point intercept grid was also used to estimate brown, red, green, and total algae coverage by projecting the grid over a photoplot (Figure A-14) and identifying the algae group present at each point intercept, where each point intercept corresponds to 1% coverage. This method was adapted from Hutchinson & Williams (2003).

Figure A-12. Assembled photoquadrat.

Figure A-13. Photoplot of barnacles with 100 point-intercept grid.

Figure A-14. Photoplot of algae with 100 point-intercept grid.

GRAIN SIZE ANALYSIS

The dry-sieving methods employed for grain size analysis, where a Ro-Tap sieve shaker sorted soil through a series of nested sieves, were efficient in retaining soil from the original sample throughout the process. Only $0.44\% \pm 0.19\%$ of each sample was lost during sieving, based on 85 out of the 87 (the original weight of two of the samples was not obtained). The grain size data was then entered into GRADISTAT (Blott & Pye 2001) for further analysis. A summary of the GRADISTAT output describing grain sizes for each soil sample is included in Table A-2.

GRADISTAT is a computer program run in Excel that analyzes grain sizes of soil samples. The program was used to generate a value for skewness, a univariate measure for the distribution of grain sizes in each sample, where a negative skew represents a soil sample defined by finer grain sizes and positive skew represents a soil sample defined by coarser grain sizes.

The widely used Folk and Ward method was used, which has reduced errors for samples with small portions of undetermined grain size (Blott & Pye 2001). For all samples, the maximum grain size was assumed to be 4.8 cm, which was the largest measured cobble obtained from the soil samples. However, soils that accumulated in the pan during sieving were of undetermined size. The pan fraction could have been analyzed further with laser granulometry, though this method produces results for grain size in percent by volume, rather than the sieve method which produces results in percent by weight. Grain size by weight can be calculated from the granulometry results, but the GRADISTAT guide advises against using multiple techniques of grain sizing in the analysis. Instead, minimum grain size in the pan fraction was assumed to be 1 micron.

For the Folk and Ward method, only samples with more than 5% of the sample in the pan fraction produce significant errors. This occurred in 20 out of the 87 samples. Thus, skewness results should be interpreted with some caution, though a majority of the samples are without error.

Table A-2. Descriptive details of each soil sample as determined by GRADISTAT. A-R refers to each transect, and 1-5 refers to each quadrat on the transect from higher to lower elevation.

Sample	Sieving Error	Textural Group	Mean (mm)	Sorting	Skewness	Kurtosis	% Gravel	% Sand	% Mud
A1		Gravelly Muddy Sand	412.4	8.485	0.146	1.534	20.8%	68.2%	11.0%
A2	8.20%	Sandy Gravel	1006.1	4.113	0.183	0.956	30.5%	68.5%	1.0%
A3		Sandy Gravel	2318.5	5.937	-0.024	0.925	55.3%	44.4%	0.3%
A4	-0.50%	Sandy Gravel	906.5	7.469	0.653	0.678	35.6%	61.1%	3.2%
A5	0.30%	Gravelly Muddy Sand	417.6	5.039	-0.038	1.420	12.6%	77.0%	10.3%
B1	0.50%	Muddy Sandy Gravel	1072.1	11.56	0.054	0.882	38.9%	53.0%	8.0%
B2	0.30%	Sandy Gravel	2291.3	6.057	0.029	0.666	52.3%	46.3%	1.5%
B3	2.70%	Gravelly Sand	386.3	6.872	0.186	1.412	18.1%	74.9%	7.0%
B4	0.30%	Sandy Gravel	996.0	5.889	0.639	0.725	37.1%	61.6%	1.3%
B5	0.30%	Gravelly Sand	610.0	4.481	0.697	1.031	22.8%	75.2%	2.0%
C1	0.80%	Gravelly Muddy Sand	383.4	12.46	0.205	1.186	23.1%	59.8%	17.1%
C2	1.80%	Gravelly Muddy Sand	396.2	11.09	0.114	1.290	21.9%	61.5%	16.6%
C3	0.50%	Gravelly Muddy Sand	543.1	10.57	-0.059	1.364	26.0%	59.4%	14.6%
C4	0.60%	Gravelly Muddy Sand	396.1	7.341	-0.087	1.621	16.1%	72.6%	11.3%
C5	-0.20%	Gravelly Sand	483.8	3.174	0.473	1.178	15.1%	82.1%	2.8%
D1	0.10%	Sandy Gravel	3408.9	5.235	-0.011	0.829	59.5%	39.2%	1.3%
D2	0.10%	Sandy Gravel	1920.2	4.321	0.085	1.098	47.2%	52.0%	0.8%
D3	0.00%	Sandy Gravel	1891.3	4.338	0.230	1.029	41.2%	57.8%	0.9%
D4	1.80%	Gravelly Muddy Sand	819.6	6.599	0.152	1.327	28.4%	64.4%	7.3%
D5	1.00%	Gravelly Muddy Sand	523.5	5.976	0.229	1.493	21.5%	67.7%	10.8%
E1	-0.20%	Sandy Gravel	2561.1	4.452	0.250	0.882	48.9%	50.9%	0.1%
E2	0.00%	Sandy Gravel	3462.8	4.460	0.067	0.923	63.9%	35.9%	0.2%
E3	0.40%	Sandy Gravel	3967.1	3.776	0.151	0.995	70.2%	29.8%	0.1%
E4	0.00%	Sandy Gravel	3078.9	4.370	0.109	0.895	59.6%	40.2%	0.2%
E5	0.10%	Sandy Gravel	3718.4	4.898	-0.028	0.789	65.3%	34.5%	0.2%

Table A-2 (Continued).

Sample	Sieving Error	Textural Group	Mean (mm)	Sorting	Skewness	Kurtosis	% Gravel	% Sand	% Mud
F1	0.20%	Sandy Gravel	3728.3	5.677	-0.200	0.613	58.3%	41.6%	0.1%
F2	-0.10%	Sandy Gravel	4231.3	4.846	-0.122	0.658	66.2%	33.7%	0.0%
F3	2.00%	Sandy Gravel	5036.5	4.867	-0.233	0.755	71.3%	28.7%	0.0%
F4	0.60%	Sandy Gravel	3651.1	5.101	-0.048	0.690	60.4%	39.5%	0.0%
F5	0.40%	Gravel	9804.3	3.150	-0.182	1.031	92.2%	7.7%	0.1%
G1	0.10%	Sandy Gravel	3903.9	5.127	-0.102	0.886	71.1%	28.4%	0.5%
G2	1.30%	Muddy Sandy Gravel	676.6	11.67	0.141	1.067	31.5%	58.6%	9.9%
G3	0.20%	Sandy Gravel	1130.6	5.345	0.585	0.818	32.4%	65.5%	2.0%
G4	0.10%	Gravelly Sand	923.4	3.958	0.290	0.962	29.2%	68.8%	1.9%
G5	-0.30%	Sandy Gravel	803.1	5.087	0.513	0.887	32.0%	65.1%	2.9%
H1	-0.20%	Sandy Gravel	2686.5	4.451	0.151	1.093	52.3%	47.5%	0.2%
H2	-0.10%	Sandy Gravel	4381.5	4.315	0.060	1.042	68.4%	31.4%	0.3%
H3	-0.30%	Sandy Gravel	2450.2	5.536	0.122	0.708	50.8%	48.8%	0.4%
H4	-0.20%	Sandy Gravel	2462.9	6.064	0.032	0.684	52.6%	46.5%	0.9%
H5	0.20%	Gravelly Sand	291.5	3.522	0.337	3.405	10.4%	82.1%	7.5%
I1	-0.10%	Sandy Gravel	1901.7	3.598	0.078	1.359	46.9%	52.8%	0.2%
I2	0.00%	Sandy Gravel	4246.1	5.899	-0.293	0.885	71.8%	27.7%	0.5%
I3	0.00%	Sandy Gravel	2027.3	5.039	-0.043	1.061	54.4%	44.5%	1.0%
I4	0.10%	Sandy Gravel	2352.0	5.456	-0.012	0.840	56.0%	43.0%	1.0%
I5	0.20%	Muddy Sandy Gravel	1922.8	10.41	-0.174	0.891	50.8%	41.1%	8.1%
J1	-0.30%	Sandy Gravel	6337.2	3.862	-0.123	0.825	78.2%	21.7%	0.1%
J2	-0.30%	Sandy Gravel	5517.3	4.203	-0.125	0.788	73.2%	26.5%	0.2%
J3	-0.30%	Sandy Gravel	2789.7	4.337	0.229	0.768	52.4%	47.3%	0.2%
J4	-0.10%	Sandy Gravel	4286.2	3.944	0.112	0.889	70.5%	29.3%	0.2%
J5	2.90%	Sandy Gravel	2588.9	4.120	0.249	1.137	48.3%	50.8%	1.0%

Table A-2 (Continued).

Sample	Sieving Error	Textural Group	Mean (mm)	Sorting	Skewness	Kurtosis	% Gravel	% Sand	% Mud
K1	0.10%	Sandy Gravel	3073.1	4.723	0.084	0.863	58.2%	41.7%	0.1%
K2	0.90%	Gravelly Muddy Sand	431.7	9.770	0.062	1.330	24.2%	60.9%	14.9%
K3	8.70%	Sandy Gravel	1034.6	3.765	0.421	0.970	32.0%	67.0%	1.0%
K4	-0.20%	Gravelly Sand	857.7	4.435	0.633	1.250	22.9%	76.0%	1.1%
K5	-7.90%	Sandy Gravel	1300.2	6.470	0.583	0.622	42.0%	56.9%	1.1%
L1	-0.50%	Gravelly Sand	325.8	2.146	0.439	1.878	6.4%	92.5%	1.1%
L2	-0.10%	Sandy Gravel	2443.0	6.279	-0.018	0.645	54.1%	45.3%	0.6%
L3	-0.10%	Sandy Gravel	1614.4	4.987	0.214	0.869	41.9%	57.3%	0.8%
L4	0.20%	Sandy Gravel	1559.0	4.659	0.129	0.908	43.5%	55.8%	0.7%
L5	0.20%	Gravelly Sand	977.3	3.750	0.460	1.199	23.6%	75.8%	0.6%
M1	6.00%	Sandy Gravel	1551.0	4.325	0.216	0.919	42.2%	57.7%	0.1%
M2	0.20%	Sandy Gravel	1680.9	5.341	0.456	0.700	41.3%	58.4%	0.3%
M3	-0.10%	Sandy Gravel	1511.4	4.148	0.301	0.991	35.1%	64.8%	0.1%
M4	0.10%	Sandy Gravel	1614.5	5.340	0.349	0.748	41.7%	57.7%	0.6%
M5	0.10%	Sandy Gravel	1111.5	5.012	0.477	0.856	33.1%	66.2%	0.6%
N1	0.30%	Sandy Gravel	1616.1	3.826	0.376	0.996	37.0%	63.0%	0.1%
N2	-0.30%	Sandy Gravel	2025.0	4.263	0.291	1.007	41.3%	58.3%	0.4%
N3	0.10%	Gravelly Sand	899.6	3.913	0.504	0.962	27.7%	71.1%	1.2%
N4	0.20%	Gravelly Muddy Sand	384.9	4.724	0.108	2.895	11.3%	77.3%	11.4%
O1	0.10%	Sandy Gravel	3310.5	4.838	0.016	0.861	63.7%	35.8%	0.5%
O2	1.40%	Gravelly Sand	283.4	5.186	0.082	1.277	11.6%	80.2%	8.3%
O3	0.90%	Gravelly Sand	646.2	5.510	0.311	1.070	26.9%	67.4%	5.8%
O4	0.40%	Sandy Gravel	1083.2	6.723	0.314	0.815	36.5%	59.5%	4.1%
O5	0.80%	Gravelly Sand	516.7	3.013	0.328	1.020	14.6%	82.7%	2.7%

Table A-2 (Continued).

Sample	Sieving Error	Textural Group	Mean (mm)	Sorting	Skewness	Kurtosis	% Gravel	% Sand	% Mud
P1	1.10%	Muddy Sandy Gravel	1076.9	12.45	0.005	0.935	39.1%	50.8%	10.1%
P2	1.90%	Gravelly Muddy Sand	578.8	11.12	-0.113	1.229	28.7%	55.6%	15.7%
P3	0.90%	Gravelly Muddy Sand	461.5	5.671	0.295	2.863	12.8%	78.3%	8.8%
Q1	-0.10%	Sandy Gravel	2594.0	5.129	0.179	0.738	50.5%	49.1%	0.4%
Q2	-0.20%	Sandy Gravel	2480.3	5.035	0.162	0.829	50.1%	49.2%	0.8%
Q3	-0.20%	Sandy Gravel	1621.6	4.403	0.272	0.949	39.7%	59.5%	0.8%
Q4	0.00%	Sandy Gravel	2936.0	4.836	0.076	0.795	57.5%	42.0%	0.5%
Q5	-0.40%	Sandy Gravel	3394.3	5.262	-0.035	0.701	59.7%	40.0%	0.4%
R1	-1.40%	Sandy Gravel	3275.8	4.590	0.070	0.883	61.2%	38.3%	0.5%
R2	-0.10%	Sandy Gravel	3701.5	4.436	0.054	0.865	66.2%	33.5%	0.3%
R3	0.00%	Sandy Gravel	1666.4	3.884	0.221	1.109	38.5%	60.2%	1.3%
R4	0.10%	Gravelly Sand	828.2	4.018	0.442	1.145	23.0%	75.2%	1.9%
R5	-0.10%	Sandy Gravel	1034.0	6.275	0.546	0.735	35.0%	62.8%	2.2%

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APPENDIX B: Infaunal Macroinvertebrates in the Mixed-Coarse Intertidal Zone of Boston Harbor

INTRODUCTION

In addition to epifaunal species, infaunal species were also collected while sampling for macroinvertebrates in the intertidal zone of Boston Harbor, in order to determine how infaunal community structure, richness, density, and diversity responded to wave energy and additional environmental variables.

METHODS

Infaunal species were collected after the surface layer of rock and cobble was cleared from each of the 87 quadrats using a single core (10 cm diameter, 5 cm depth) taken from within each quadrat, and the contents were rinsed over a 1 mm mesh sieve. All infaunal invertebrates from within each core were preserved in 10% buffered formalin for storage, and transferred to 70% ethanol in the lab prior to identification. Identification was aided with various taxonomic keys (Cook & Brinkhurst 1973, Cutler 1977, Pettibone 1963). After identification, all abundances were scaled up to a surface area of 1 m².

Data analysis was performed using the same PERMANOVA, PERMDISP, and DISTLM methods described for the analysis of epifaunal species in Manuscript 1.

RESULTS

Table B-1 presents the mean and maximum abundance values for the sixteen infaunal species detected in the study. The minimum value detected was zero for all

species. Frequency, or percent of quadrats in which species were detected, is also included.

Our results indicate that infaunal community structure, richness, density, and diversity were not significantly different between wave-protected and wave-exposed groups for either the modal or maximum wave energy models (Table B-1).

DISTLM analysis was performed using the entire community structure, density, richness, and diversity datasets since there were no significant location effects between wave exposure groups for either the maximum or modal wave energy models. Marginal tests indicate that water content, skewness, and brown algae independently explain small but statistically significant proportions of variation in infaunal community structure (Table B-2). According to the sequential test, skewness and brown algae together explain 9% of the total variation in community structure (Table B-3).

Marginal tests indicate that skewness explains significant proportions of the variation in richness, density, and diversity, with a positive correlation between skewness and each univariate measure. Water content also significantly explains a small portion of the variation in species richness with a positive correlation (Table B-2).

Sequential tests indicate that skewness, rugosity, and slope together explain approximately 13% of the total variation in density. Skewness and red algae together explain about 15% of the total variation in richness, and skewness alone represents the best fit model for diversity, explaining approximately 6% of the total variation (Table B-3).

In all models for community structure, density, richness, and diversity, only skewness made a significant contribution and so we may therefore chose to accept that

only 6% of variation in these infaunal community characteristics is explained by environmental variables.

DISCUSSION

Results indicate that infaunal community structure, density, species richness, and diversity are not influenced by either high energy pulse events or prevailing winds, as there were no significant differences among wave exposure sites for either wave energy model. However, evidence exists to indicate that infaunal communities in other intertidal regions do in fact respond to wave energy (Ricciardi & Bourget 1999, Hammons & Griffiths 2004, Rodil et al. 2007). The fact that wave energy is significant in several studies is likely due not to wave energy directly but the effect it has on soil structure and the distribution of organic matter.

Soil skewness was observed to be a contributing factor to variations in the infaunal community structure, density, richness, and diversity. This was not surprising considering the amount of evidence which supports the role that grain size or soil structure plays as the habitat for infaunal communities (McLachlan 1996, Ricciardi and Bourget 1999, Dethier and Schoch 2000, Ysebaert and Herman 2002), where increased grain size typically results in reduced diversity or richness. Water content was also important in influencing community structure and diversity, which is unsurprising considering the need of moisture in the soil to prevent desiccation.

Several environmental variables did not come up as significant though evidence is available to suggest they play important roles in infaunal community characteristics. For examples, several studies have determined that infaunal density, richness, and community

structure are closely related to elevation (Ysebaert & Herman 2002, Edgar et al. 2006). Diversity, richness, and biomass have also been proven to be highly correlated with organic content (Fujii 2007, Rodil et al. 2007). Macrophyte abundance may also be correlated with infaunal density and richness (Edgar et al. 2006), though in this particular study, only brown algae was correlated with community structure and no algae groups were correlated with any of the univariate measure of community characteristics. Additionally, Ricciardi & Bourget (1999) demonstrated a relationship between slope and infaunal biomass, likely due to the effect of slope on the dissipation of wave energy, though slope was not significant in this study. Additional studies indicate that variables such as salinity and chlorophyll a content are also important in determining community structure, richness, density, diversity, and biomass (Dethier & Schoch 2000, Ysebaert & Herman 2002, , Edgar et al. 2006, Fujii 2007) but these environmental variables were not included in our infaunal analysis.

One of the reasons we did not see significant results between wave-exposure groups and weak correlations between environmental variables and infaunal characteristics was likely that the sampling for infaunal species was not very robust. Similar studies that analyzed infaunal invertebrate communities used sediment cores with depths ranging between 5 centimeters and 25 centimeters and mesh sizes between .5 mm and 2 mm to define macrofauna (McLachlan 1996, Cusson & Bourget 1997, Dethier & Schoch 2000, Edgar & Barrett 2002, Ysebaert & Herman 2002, Silva et al. 2006, Fujii 2007, Rodil et al. 2007). The chosen infaunal core dimensions and sieve size used in this study were likely insufficient at adequately describing the true infaunal composition of our study site. However, the use of deeper core was not possible given the difficulty in

penetrating the gravelly soil beyond a depth of 5 cm. Additionally, the use of a deeper core and a smaller sieve size would have greatly increased identification effort in the lab. The results of this study are therefore inconclusive as we likely failed to adequately sample the infaunal community; however, these data do contribute to the National Park Service's efforts to assemble species inventories.

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Table B-1. Summary of infaunal species present in the 87 sampling sites in the intertidal mixed-coarse habitat. The mean and maximum values represent abundance per m². Frequency indicates the percent of sampling sites in which species were observed.

Phylum	Species	Mean	Maximum	Frequency(%)
Annelida	<i>Clitellio arenarius</i>	16.1	636.62	5.75
	<i>Nephtys caeca</i>	1.46	127.32	1.15
	<i>Nereis virens</i>	4.39	254.65	2.3
	<i>Polydora cornuta</i>	1.46	127.32	1.15
	<i>Scoloplos fragilis</i>	19.03	381.97	9.2
	<i>Spiophanes bombyx</i>	1.46	127.32	1.15
	<i>Tubificoides benedii</i>	42.44	2673.8	6.9
	Unidentified cirratulid	1.46	127.32	1.15
	Unidentified oligochaete 1	5.85	381.97	2.3
	Unidentified oligochaete 2	7.32	381.97	2.3
	Unidentified oligochaete 3	4.39	381.97	1.15
	Unidentified polychaete	4.39	127.32	3.45
	Unidentified <i>Polycirrus</i>	7.32	636.62	1.15
	Unidentified <i>Tubificoides</i>	23.42	763.94	8.05
Mollusca	<i>Mya arenaria</i>	0.05	4	1.15
Sipuncula	<i>Phascolopsis gouldii</i>	2.93	127.32	2.3

Table B-2. Summary of PERMANOVA (pseudo-F statistic) and PERMDISP (F statistic) analyses between wave-exposed and wave-protected sites for infaunal data, with bold face indicating significant results at $p < 0.05$. PERMANOVAs were performed as a one-way analysis independently for the maximum and modal wave energy models.

	PERMANOVA		PERMDISP		Inference
	Pseudo-F	p-value	F	p-value	
Community Structure					
Maximum	1.8886	0.1016	6.6153	0.1129	No location or dispersion effects
Modal	1.3946	0.2077	3.3003	0.2589	No location or dispersion effects
Density					
Maximum	2.4455	0.1077	5.4765	0.137	No location or dispersion effects
Modal	0.33912	0.6695	0.59171	0.7763	No location or dispersion effects
Species Richness					
Maximum	2.1788	0.1654	2.6208	0.2832	No location or dispersion effects
Modal	0.031397	0.9119	0.28245	0.7732	No location or dispersion effects
Diversity					
Maximum	0.36047	0.5907	1.5691	0.5637	No location or dispersion effects
Modal	0.33912	0.5991	1.4703	0.5765	No location or dispersion effects

Table B-3. Summary of marginal tests, obtained from distance-based linear models (DISTLM), for infaunal data. Bold type indicates values significant at $p < 0.05$, and +/- indicate positive or negative correlations. [†] 1/x transformed, [‡] sqrt(x) transformed.

Variables	Community						Diversity
	Structure	Density		Species Richness			
Latitude	7.75E-03	1.55E-02	+	8.19E-03	+	1.03E-02	+
Longitude	3.46E-03	9.70E-03	-	2.20E-03	-	5.35E-03	-
Date	1.33E-02	5.91E-03	+	8.92E-05	+	1.58E-02	+
Slope	2.06E-02	2.47E-03	+	1.01E-02	-	1.06E-03	-
Aspect	2.11E-02	2.58E-02	+	4.31E-02	+	1.93E-02	+
Elevation	2.53E-02	1.55E-02	-	3.58E-02	-	1.11E-02	-
Rugosity [†]	1.09E-02	4.16E-02	-	6.59E-03	-	4.52E-03	-
Water Content	5.23E-02	1.65E-02	+	5.43E-02	+	1.02E-02	+
Organic Content [‡]	2.13E-02	2.55E-03	+	1.07E-02	+	1.20E-04	+
Skewness	6.17E-02	7.23E-02	+	1.24E-01	+	7.01E-02	+
Brown Algae	3.56E-02	8.54E-04	-	1.91E-02	+	8.12E-03	+
Green Algae	9.28E-03	2.24E-04	+	1.11E-04	-	7.45E-03	-
Red Algae	3.92E-03	5.05E-03	-	1.98E-03	-	2.00E-03	-
Total Algae	2.05E-02	6.69E-04	-	3.73E-03	+	6.41E-04	-

Table B-4. Summary of sequential tests, obtained from distance-based linear models (DISTLM), for infaunal data. Bold type indicates values significant at $p < 0.05$. +/- indicate additions to or subtractions from the model. [†] 1/x transformed

	Variables	Proportion	Cumulative
Community Structure	+Skewness	6.17E-02	6.17E-02
	+Brown Algae	2.77E-02	8.94E-02
Density	+Skewness	7.23E-02	7.23E-02
	+Rugosity [†]	3.19E-02	1.04E-01
	+Slope	2.14E-02	0.12563
Species Richness	+Skewness	1.24E-01	1.24E-01
	+Red Algae	2.55E-02	1.50E-01
Diversity	+Skewness	7.01E-02	7.01E-02

APPENDIX C: Variability among Species Sizes in the Mixed-Coarse Intertidal Zone of Boston Harbor

INTRODUCTION

In addition to collecting abundance data for *Hemigrapsus sanguineus*, *Carcinus maenas*, and *Littorina littorea* for each of the 87 quadrats sampled from Boston Harbor, widths and shell lengths were also recorded to determine if species sizes differed between wave-exposed and wave-protected groups for either the modal or maximum wave energy models.

METHODS

Measurements of *Hemigrapsus sanguineus* and *Carcinus maenas* carapace widths were recorded in the field to the nearest whole millimeter using a standard ruler. *Littorina littorea* were collected from the field and brought to the lab where shell lengths were measured to the nearest one hundredth of a millimeter using digital calipers.

Analyses were performed on width and length data separately for maximum and modal wave energy models using the same methods described in Manuscript 1 for PERMANOVA and PERMDISP analyses. Euclidean similarity matrices on untransformed data were used as the basis for each analysis.

RESULTS

The carapace width of green crab *Carcinus maenas* did not differ significantly between wave-protected and wave-exposed sites for either the modal or maximum wave energy model (Table C-1). The carapace width of the Asian shore crab *Hemigrapsus*

sanguineus differed significantly between exposure groups for both wave energy models, though the difference was due exclusively to location effects (i.e. differences between groups) in the maximum model and to dispersion (i.e. variability within groups) and perhaps location effects in the modal model (Table C-1). The periwinkle *Littorina littorea* had significantly different shell length between wave-exposed and wave-protected sites for both energy models, but in neither model was the result due exclusively to location effects (C-1).

DISCUSSION

The difference in shell lengths for *Littorina littorea* between exposure groups are certainly a result of dispersion, but not necessarily location. Since this is true for both wave energy models, a definitive conclusion about periwinkle shell lengths in response to wave energy cannot be drawn with the given data. For *Hemigrapsus sanguineus*, we can conclude that carapace width does differ significantly between wave-exposed and wave-protected sites based on storm activities, but the response to wave energies associated with the modal model, or prevailing winds, are inconclusive. Additionally, it can be determined that *Carcinus maenas* carapace width is not affected by exposure to either prevailing winds or pulse storm events.

Although the source of the difference in shell length for *Littorina littorea* cannot be determined, evidence does suggest that location effects would be likely in this environment, particularly with the higher energy associated with the maximum wave model. Shell sizes of *Littorina* and other gastropods are recorded to be significantly smaller on wave-exposed sites, in order to reduce drag and likelihood of dislodgement

(Brown & Quinn 1988, Trussell et al. 1993). This is consistent with our results for the modal wave energy model but not the maximum wave energy model (Table C-2), though neither model is conclusive (Table C-1). In other cases, predation by shore crabs also plays a major role in shell size and shell thickness (Reimchen 1982, Boulding and Van Alstyne 1993, Boulding et al. 1999).

Little information is available on the effect of wave exposure on carapace width of crabs, but a similar study has found that the crab *Eriphia verrucosa* had a larger carapace width on exposed shores than protected shores (Silva et al. 2010). This is consistent with our findings that *Hemigrapsus sanguineus* had a larger carapace width on the exposed shores according to the maximum wave energy model. The fact that carapace width is larger on exposed shores than protected shores may tie in with the relationship between density and biomass, where epifaunal density typically decreases with increased wave exposure but biomass increases (Bustamante & Branch 1996, Ricciardi & Bourget 1999, McLintock et al. 2007). In our study, crab density decreased with wave exposure (Manuscript 1) and carapace width, which may correspond to biomass, increased with wave exposure.

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Table C-1. Summary of PERMANOVA (pseudo-F statistic) and PERMDISP (F statistic) analyses between wave-exposed and wave-protected sites for species size data, with bold face indicating significant results at $p < 0.05$. PERMANOVAs were performed as a one-way analysis independently for the maximum and modal wave energy models.

	PERMANOVA		PERMDISP		Inference
	Pseudo-F	p-value	F	p-value	
<i>Carcinus maenas</i>					
Maximum	2.2112	0.1354	1.4516	0.4473	No location or dispersion effects
Modal	0.9125	0.3525	6.9598	0.0934	No location or dispersion effects
<i>Hemigrapsus sanguineus</i>					
Maximum	5.1521	0.0269	0.11367	0.7626	Location effects only
Modal	4.7868	0.0306	7.0957	0.0119	Dispersion effect and perhaps (though not necessarily) a location effect as well.
<i>Littorina littorea</i>					
Maximum	166.4	0.0001	161.45	0.0001	Dispersion effect and perhaps (though not necessarily) a location effect as well.
Modal	55.939	0.0001	8.959	0.004	Dispersion effect and perhaps (though not necessarily) a location effect as well.

Table C-2. Average shell length and carapace width by wave-exposure groups for both the maximum and modal wave energy models. Sizes presented in millimeters. Only the maximum model for *Hemigrapsus sanguineus* was significant for location effects based on the maximum wave energy or storm event model.

	Exposed	Protected
<i>Hemigrapsus sanguineus</i>		
Maximum	15.04	12.6
Modal	12.39	14.66
<i>Littorina littorea</i>		
Maximum	13.04	11.05
Modal	11.21	12.31

APPENDIX D: Raw Data and Detailed Outputs

The following pages include original raw data for species abundances at each quadrat for both epifaunal (Tables D-1) and infaunal (Tables D-2) species, measurements for environmental variables (Tables D-3), as well as the detailed outputs from PRIMER and PERMANOVA+ for all analyses related to epifaunal species (Tables D-4 to D-7), infaunal species (Tables D-8 to D-11), and species sizes (Tables D-12 to D-14). Also included are detailed DISTLM results for analysis between environmental variables and epifaunal (Tables D-15 to D-20) and infaunal (Tables D-21 to D-24) data.

Table D-1. Raw abundance data per m² for all epifaunal species in each quadrat. A-R refers to each transect, and 1-5 refers to each quadrat on the transect from higher (1) to lower (5) elevation.

Species	A1	A2	A3	A4	A5	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
<i>Anurida maritima</i>	0	0	0	0	0	763.94	0	0	0	0	0	0	0	0	0
<i>Balanus balanoides</i>	0	0	0	1296	456	0	0	2288	2140	4136	20	4	28	272	1440
<i>Botrylloides violaceus</i>	0	0	0	4	0	8	0	0	0	4	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	0	8	4	0	0	16	0	4	0	4	16	4	32
<i>Corophium volutators</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula formicata</i>	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0
<i>Crepidula plana</i>	0	0	0	0	44	0	0	0	4	48	0	0	0	0	0
<i>Diadumene lineata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	24	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemigrapsus sanguineus</i>	0	0	0	0	0	0	104	4	0	0	8	4	24	4	4
<i>Hyale plumulosa</i>	0	0	0	0	0	0	381.97	0	0	0	0	127.32	0	0	0
<i>Littorina littorea</i>	0	0	0	76	44	0	140	132	236	236	0	76	112	252	472
<i>Littorina obtusata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	0	0	0	0	0	0	0	0	4	0	0	4
<i>Membranipora membranacea</i>	0	0	0	4	0	0	0	0	0	4	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	12	0	0	0	4	4	4	0	0	0	0	4
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	4	0	0	0	0	28	0	0	0	0	4
<i>Pagurus longicarpus</i>	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela partita</i>	0	0	0	108	4	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Inset Larva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-1 (Continued).

Species	D1	D2	D3	D4	D5	E1	E2	E3	E4	E5	F1	F2	F3	F4	F5
<i>Anurida maritima</i>	0	509.3	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Balanus balanoides</i>	0	0	76	184	1596	0	0	0	0	0	0	0	0	0	0
<i>Botrylloides violaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	0	16	20	0	0	0	0	0	0	0	0	0	0
<i>Corophium volutators</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula fornicata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula plana</i>	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0
<i>Diadumene lineata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemigrapsus sanguineus</i>	0	4	4	24	4	0	0	0	0	0	0	0	0	0	0
<i>Hyale plumulosa</i>	0	127.32	254.65	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littorina littorea</i>	0	0	4	240	252	0	0	0	0	0	0	0	0	0	0
<i>Littorina obtusata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Membranipora membranacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus longicarpus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela partita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Inset Larva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-1 (Continued).

Species	G1	G2	G3	G4	G5	H1	H2	H3	H4	H5	I1	I2	I3	I4	I5
<i>Anurida maritima</i>	0	381.97	0	0	0	0	0	0	0	0	0	0	381.97	0	0
<i>Balanus balanoides</i>	0	0	296	400	1200	0	0	0	48	264	0	0	0	12	300
<i>Botrylloides violaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	20
<i>Carcinus maenas</i>	0	0	4	16	44	0	0	32	48	8	0	0	0	8	4
<i>Corophium volutators</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula fornicata</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	24
<i>Crepidula plana</i>	0	0	0	0	0	0	0	0	0	84	0	0	0	0	92
<i>Diadumene lineata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemigrapsus sanguineus</i>	0	8	16	36	8	0	0	0	0	0	0	0	0	0	4
<i>Hyale plumulosa</i>	0	254.65	0	0	0	0	0	381.97	763.94	0	0	0	0	0	0
<i>Littorina littorea</i>	0	0	192	424	588	0	0	0	208	20	0	0	0	24	200
<i>Littorina obtusata</i>	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	4	0	0	0	0	4	0	0	0	0	0	0
<i>Membranipora membranacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	12
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	16	0	0	0	0	8	0	0	0	0	0
<i>Pagurus longicarpus</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
<i>Styela partita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Inset Larva	0	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0

Table D-1 (Continued).

Species	J1	J2	J3	J4	J5	K1	K2	K3	K4	K5	L1	L2	L3	L4	L5
<i>Anurida maritima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Balanus balanoides</i>	0	0	0	0	24	0	0	276	864	916	0	12	440	28	240
<i>Botrylloides violaceus</i>	0	0	0	0	0	0	0	0	0	28	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	0	0	40	0	0	24	12	16	8	0	0	16	0
<i>Corophium volutators</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula fornicata</i>	0	0	0	0	0	0	0	0	0	72	0	0	0	0	0
<i>Crepidula plana</i>	0	0	0	0	0	0	0	0	8	108	0	0	0	0	0
<i>Diadumene lineata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemigrapsus sanguineus</i>	0	0	0	0	0	0	0	8	32	0	0	0	12	8	0
<i>Hyale plumulosa</i>	0	0	0	0	763.94	0	0	0	0	0	0	0	0	0	0
<i>Littorina littorea</i>	0	0	0	0	376	0	0	200	312	152	0	512	44	184	164
<i>Littorina obtusata</i>	0	0	0	0	24	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	0	8	0	0	0	0	0	0	8	16	4	0
<i>Membranipora membranacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	0	4	0	0	0	0	20	0	0	0	0	0
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	0	0	0	0	0	36	0	0	0	0	0
<i>Pagurus longicarpus</i>	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela partita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Inset Larva	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-1 (Continued).

Species	M1	M2	M3	M4	M5	N1	N2	N3	N4	O1	O2	O3	O4	O5
<i>Anurida maritima</i>	0	1400.56	0	0	0	0	0	0	0	0	0	0	0	0
<i>Balanus balanoides</i>	0	0	0	40	72	0	0	60	84	0	20	580	476	664
<i>Botrylloides violaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	0	0	0	0	0	4	16	0	0	12	16	28
<i>Corophium volutators</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Crepidula fornicata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	8
<i>Crepidula plana</i>	0	0	0	0	0	0	0	0	0	0	0	0	16	0
<i>Diadumene lineata</i>	0	0	12	0	0	0	0	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	127.32
<i>Hemigrapsus sanguineus</i>	0	0	4	40	0	0	0	0	0	0	8	20	4	24
<i>Hyale plumulosa</i>	0	0	0	0	0	0	0	254.65	0	0	763.94	127.32	0	0
<i>Littorina littorea</i>	0	0	0	204	268	0	0	92	292	0	160	240	288	316
<i>Littorina obtusata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	4	0	0	0	0	0	0	0	0	0	0
<i>Membranipora membranacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	0	0	0	0	0	16	0	0	0	0	0
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	8	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	28
<i>Pagurus longicarpus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	40
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela partita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Inset Larva	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-1 (Continued).

Species	P1	P2	P3	Q1	Q2	Q3	Q4	Q5	R1	R2	R3	R4	R5
<i>Anurida maritima</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Balanus balanoides</i>	0	0	224	0	0	32	24	16	0	0	8	1176	172
<i>Botrylloides violaceus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carcinus maenas</i>	0	0	12	0	8	0	0	0	0	8	4	32	64
<i>Corophium volutators</i>	0	0	0	0	0	127.32	0	0	0	0	0	0	0
<i>Crepidula fornicata</i>	0	0	0	0	0	0	0	0	0	0	0	0	16
<i>Crepidula plana</i>	0	0	4	0	0	0	0	0	0	0	0	0	20
<i>Diadumene lineata</i>	0	0	0	0	0	8	0	0	0	0	0	0	0
<i>Gammarus oceanicus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Hemigrapsus sanguineus</i>	0	8	4	0	0	0	0	0	0	16	52	36	0
<i>Hyale plumulosa</i>	0	0	0	0	0	0	0	0	0	381.97	0	0	0
<i>Littorina littorea</i>	0	0	272	4	4	36	72	24	0	0	160	728	632
<i>Littorina obtusata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Littorina saxatilis</i>	0	0	0	0	12	0	0	0	0	0	0	0	0
<i>Membranipora membranacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Microdeutopus gryllotalpa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mytilus edulis</i>	0	0	0	0	0	0	0	0	0	0	0	4	0
<i>Ilyanassa obsoleta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ilyanassa trivittata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pagurus acadianus</i>	0	0	0	0	0	0	0	0	0	0	0	0	8
<i>Pagurus longicarpus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela clava</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Styela partita</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified Amphipod	0	0	0	0	0	0	0	0	0	0	0	0	127.32
Unidentified Inset Larva	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-2. Raw abundance data per m² for all infaunal species in each quadrat. A-R refers to each transect, and 1-5 refers to each quadrat on the transect from higher (1) to lower (5) elevation.

Species	A1	A2	A3	A4	A5	B1	B2	B3	B4	B5	C1	C2	C3	C4	C5
<i>Clitellio arenarius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phascolopsis gouldii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	127.32	0	0	254.65	0	127.32	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified cirratulid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	381.97	0	0
Unidentified oligochaete 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaete	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-2(Continued).

Species	D1	D2	D3	D4	D5	E1	E2	E3	E4	E5	F1	F2	F3	F4	F5
<i>Clitellio arenarius</i>	0	127.32	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phascolopsis gouldii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	0	254.65	0	0	0	0	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified cirratulid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaeta	0	0	0	0	0	0	0	127.32	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table D-2(Continued).

Species	G1	G2	G3	G4	G5	H1	H2	H3	H4	H5	I1	I2	I3	I4	I5
<i>Clitellio arenarius</i>	0	0	0	254.65	0	254.65	636.62	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phascolopsis gouldii</i>	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	0	0	127.32	0	0	0	0	0	0	0	254.65	0
<i>Spiophanes bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	381.97	0	254.65	0	0	0	0	0	0	0	0	0	0
Unidentified cirratulid	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaeta	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	636.62	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	381.97	0	0	0	127.32	0	0	0	0	0	0	0	0

Table D-2(Continued).

Species	J1	J2	J3	J4	J5	K1	K2	K3	K4	K5	L1	L2	L3	L4	L5
<i>Clitellio arenarius</i>	0	0	0	127.32	0	0	0	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Phascolopsis gouldii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	0	0	0	0	0	381.97	0	0	0	0	127.32	0
<i>Spiophanes bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	0	0	0	0	0	0	0	0	0	0	127.32	0	0
Unidentified cirratulid	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	127.32
Unidentified oligochaete 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	381.97	0	0
Unidentified polychaeta	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	763.94	0	0	0	0	0	0	0	0	127.32	0	0	381.97

Table D-2(Continued).

Species	M1	M2	M3	M4	M5	N1	N2	N3	N4	O1	O2	O3	O4	O5
<i>Clitellio arenarius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	0	127.32	0
<i>Phascolopsis gouldii</i>	0	0	0	0	0	0	0	0	127.32	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	0	0	0	0	0	0	0	0	127.32	0	0	0
Unidentified cirratulid	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 2	0	254.65	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaeta	0	0	0	0	127.32	0	0	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	0	0	0	0	0	0	0	0	0	127.32	0	0

Table D-2(Continued).

Species	P1	P2	P3	Q1	Q2	Q3	Q4	Q5	R1	R2	R3	R4	R5
<i>Clitellio arenarius</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Mya arenaria</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Nephtys caeca</i>	0	0	0	0	0	0	0	0	0	0	0	0	127.32
<i>Nereis virens</i>	0	0	0	0	0	0	0	0	0	0	0	254.65	0
<i>Phascolopsis gouldii</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Polydora cornuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Scoloplos fragilis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Spiophanes bombyx</i>	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Tubificoides benedii</i>	0	0	127.32	0	0	0	0	0	0	0	0	2673.8	0
Unidentified cirratulid	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 1	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified oligochaete 2	0	0	0	0	0	0	0	0	0	0	0	381.97	0
Unidentified oligochaete 3	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polychaeta	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified polycirrus	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified tubificoides	0	0	127.32	0	0	0	0	0	0	0	0	0	0

Table D-3. Environmental variables for each quadrat sampled in Boston Harbor. Latitude and longitude are presented in 19N UTM. A-R refers to each transect, and 1-5 refers to each quadrat on the transect from higher (1) to lower (5) elevation.

Sample	Latitude	Longitude	Day	Slope (%)	Aspect	Elevation (m)	Rugosity	Soil					Total Algae (%)	Soil Skewness
								Water Content (%)	Organic Content (%)	Brown Algae (%)	Green Algae (%)	Red Algae (%)		
A1	334783	4687031	23	8.33	115	2.39	1.06	12.99	1.32	0	0	0	0	0.146
A2	334783	4687030	23	8.33	115	1.92	1.04	18.52	1.82	0	0	3	3	0.183
A3	334791	4687026	23	7.32	115	1.27	1.13	15.00	1.33	0	0	0	0	-0.024
A4	334806	4687021	23	5.91	115	0.43	1.11	21.29	1.64	28	1	17	46	0.653
A5	334811	4687016	23	6.11	115	0.18	1.12	20.26	2.39	7	0	10	17	-0.038
B1	334783	4687367	24	6.41	343	2.96	1.20	11.71	1.52	0	0	0	0	0.054
B2	334782	4687374	24	13.01	343	2.17	1.32	12.27	1.40	0	0	0	0	0.029
B3	334779	4687386	24	4.81	343	0.91	1.20	14.59	1.62	0	0	0	0	0.186
B4	334776	4687395	24	0.90	343	0.67	1.23	16.75	1.49	0	0	1	1	0.639
B5	334775	4687402	24	1.40	343	0.32	1.27	18.90	1.51	0	0	12	12	0.697
C1	336558	4688024	42	-4.81	130	2.27	1.53	13.20	1.56	0	0	0	0	0.205
C2	336557	4688021	42	2.40	130	2.31	1.38	13.55	1.56	0	0	0	0	0.114
C3	336566	4688014	42	8.73	130	1.55	1.30	13.84	1.79	0	0	0	0	-0.059
C4	336570	4688012	42	5.41	130	1.30	1.23	13.78	1.76	0	0	0	0	-0.087
C5	336577	4688006	42	5.71	130	0.82	1.11	23.62	2.18	0	0	1	1	0.473
D1	340946	4684603	29	11.88	138	2.85	1.10	9.47	1.24	0	0	0	0	-0.011
D2	340955	4684594	29	11.27	138	2.10	1.25	15.89	1.60	0	0	0	0	0.085
D3	340958	4684589	29	9.75	138	1.43	1.25	16.39	1.94	0	0	0	0	0.23
D4	340962	4684584	29	12.09	138	0.69	1.26	11.95	1.39	0	0	0	0	0.152
D5	340965	4684579	29	5.71	138	0.39	1.22	14.03	1.38	0	0	3	3	0.229

Table D-3 (Continued).

Sample	Latitude	Longitude	Day	Slope (%)	Aspect	Elevation (m)	Rugosity	Soil Water Content (%)	Soil Organic Content (%)	Brown Algae (%)	Green Algae (%)	Red Algae (%)	Total Algae (%)	Soil Skewness
E1	339805	4683731	27	12.29	160	2.43	1.07	5.17	1.12	0	0	0	0	0.25
E2	339813	4683724	27	6.61	160	1.49	1.13	7.13	1.39	0	0	0	0	0.067
E3	339811	4683716	27	6.51	160	1.37	1.01	16.51	1.54	0	0	0	0	0.151
E4	339815	4683708	27	6.41	160	0.53	1.11	15.48	1.37	0	0	1	1	0.109
E5	339818	4683698	27	2.20	160	0.17	1.10	17.70	1.22	0	0	0	0	-0.028
F1	341379	4688018	15	6.51	46	2.17	1.11	3.29	0.63	0	1	0	1	-0.2
F2	341382	4688024	15	5.71	46	1.84	1.10	4.39	0.80	0	1	0	1	-0.122
F3	341384	4688020	15	6.41	46	1.55	1.06	4.86	1.24	0	0	0	0	-0.233
F4	341388	4688023	15	9.04	46	1.11	1.07	2.90	0.82	0	1	0	1	-0.048
F5	341392	4688028	15	4.50	46	0.71	1.11	5.34	0.74	0	1	0	1	-0.182
G1	339473	4683946	44	9.64	357	2.96	1.20	13.42	1.29	0	0	2	2	-0.102
G2	339472	4683946	44	1.90	357	2.62	1.32	11.33	1.30	0	0	0	0	0.141
G3	339473	4683960	44	8.83	357	1.58	1.37	19.31	1.81	0	0	0	0	0.585
G4	339472	4683972	44	8.43	357	1.13	1.23	17.45	2.04	0	0	0	0	0.29
G5	339473	4683982	44	4.00	357	0.62	1.14	16.62	1.56	0	0	0	0	0.513
H1	334279	4686216	57	8.94	122	3.54	1.07	7.34	1.04	0	0	0	0	0.151
H2	334281	4686213	57	16.83	122	3.26	1.15	8.63	1.22	0	0	0	0	0.06
H3	334291	4686205	57	10.36	122	2.04	1.25	15.77	1.44	11	0	0	11	0.122
H4	334294	4686205	57	9.24	122	1.78	1.30	15.66	1.63	8	0	0	8	0.032
H5	334302	4686200	57	3.00	122	0.52	1.12	26.14	2.22	0	0	24	24	0.337

Table D-3 (Continued).

Sample	Latitude	Longitude	Day	Slope (%)	Aspect	Elevation (m)	Rugosity	Soil Water Content (%)	Soil Organic Content (%)	Brown Algae (%)	Green Algae (%)	Red Algae (%)	Total Algae (%)	Soil Skewness
I1	341488	4681259	37	9.95	176	2.58	1.06	5.10	0.96	0	0	0	0	0.078
I2	341488	4681255	37	13.21	176	2.02	1.15	11.32	1.25	0	0	0	0	-0.293
I3	341489	4681252	37	10.36	176	1.67	1.23	12.38	1.30	0	0	0	0	-0.043
I4	341489	4681246	37	13.93	176	0.88	1.33	14.46	1.26	0	0	0	0	-0.012
I5	341489	4681242	37	12.50	176	0.43	1.17	13.94	1.34	0	0	0	0	-0.174
J1	333799	4686397	11	3.80	297	3.23	1.13	3.85	1.26	0	0	0	0	-0.123
J2	333789	4686404	11	2.20	297	2.80	1.11	5.16	1.62	0	10	2	12	-0.125
J3	333773	4686415	11	3.80	297	2.31	1.15	6.30	1.36	0	33	0	33	0.229
J4	333764	4686419	11	2.60	297	2.04	1.10	8.40	0.34	0	44	0	44	0.112
J5	333743	4686428	11	2.60	297	1.29	1.11	17.83	2.67	56	0	1	57	0.249
K1	341617	4681640	35	12.09	325	2.80	1.20	4.66	1.21	0	0	0	0	0.084
K2	341615	4681644	35	12.80	325	2.22	1.25	10.82	1.44	0	0	0	0	0.062
K3	341608	4681654	35	6.82	325	1.30	1.21	18.43	1.39	0	0	1	1	0.421
K4	341604	4681660	35	2.80	325	0.83	1.24	21.13	1.41	0	0	0	0	0.633
K5	341596	4681673	35	5.81	325	0.08	1.12	20.61	1.34	0	0	12	12	0.583
L1	340944	4688442	0	3.80	253	1.87	1.05	23.01	1.29	0	0	0	0	0.439
L2	340917	4688433	0	-3.20	253	1.64	1.09	21.87	1.67	0	0	0	0	-0.018
L3	340904	4688430	0	-2.90	253	1.63	1.30	17.00	1.60	0	0	0	0	0.214
L4	340898	4688429	0	5.91	253	1.58	1.14	15.67	1.60	0	0	0	0	0.129
L5	340871	4688421	0	-4.20	253	1.45	1.20	17.42	1.35	0	0	0	0	0.46

Table D-3 (Continued).

Sample	Latitude	Longitude	Day	Slope (%)	Aspect	Elevation (m)	Rugosity	Soil Water Content (%)	Soil Organic Content (%)	Brown Algae (%)	Green Algae (%)	Red Algae (%)	Total Algae (%)	Soil Skewness
M1	340932	4688464	14	0.00	240	2.41	1.29	6.56	1.36	0	17	0	17	0.216
M2	340920	4688458	14	-0.50	240	2.22	1.13	8.87	1.19	0	37	0	37	0.456
M3	340912	4688454	14	1.20	240	2.06	1.14	7.03	1.34	0	4	0	4	0.301
M4	340890	4688447	14	0.40	240	1.74	1.34	17.40	1.40	0	0	0	0	0.349
M5	340879	4688436	14	1.20	240	1.41	1.13	21.03	1.24	0	0	0	0	0.477
N1	334104	4686736	12	13.73	330	3.50	1.06	2.10	1.14	0	0	0	0	0.376
N2	334097	4686750	12	8.23	330	1.80	1.32	10.36	1.98	0	0	0	0	0.291
N3	334094	4686755	12	7.72	330	1.12	1.18	18.13	1.80	0	0	0	0	0.504
N4	334092	4686759	12	5.41	330	0.88	1.12	35.14	4.14	4	0	5	9	0.108
O1	340129	4683351	28	10.46	239	2.83	1.08	3.18	0.35	0	0	0	0	0.016
O2	340110	4683341	28	2.00	239	1.31	1.34	16.10	1.36	0	0	0	0	0.082
O3	340103	4683338	28	-3.60	239	0.77	1.28	14.73	1.50	0	0	1	1	0.311
O4	340095	4683331	28	2.10	239	0.43	1.16	17.81	2.06	0	0	0	0	0.314
O5	340080	4683323	28	1.90	239	0.42	1.18	18.31	1.92	0	0	1	1	0.328
P1	341736	4681715	36	5.41	328	1.99	1.27	10.87	1.34	0	0	0	0	0.005
P2	341731	4681719	36	9.34	328	1.69	1.38	11.20	1.14	0	0	0	0	-0.113
P3	341719	4681736	36	4.60	328	0.23	1.11	18.81	1.46	37	0	3	40	0.295

Table D-3 (Continued).

Sample	Latitude	Longitude	Day	Slope (%)	Aspect	Elevation (m)	Rugosity	Soil Water Content (%)	Soil Organic Content (%)	Brown Algae (%)	Green Algae (%)	Red Algae (%)	Total Algae (%)	Soil Skewness
Q1	333786	4686350	56	1.40	246	2.24	1.09	13.73	1.83	0	35	0	35	0.179
Q2	333774	4686343	56	5.71	246	1.78	1.08	16.91	1.81	0	59	0	59	0.162
Q3	333767	4686341	56	2.10	246	1.61	1.08	17.93	1.72	1	0	0	1	0.272
Q4	333745	4686332	56	-4.60	246	1.05	1.08	16.70	1.71	0	0	0	0	0.076
Q5	333730	4686327	56	5.71	246	1.04	1.08	10.76	1.46	0	0	0	0	-0.035
R1	343069	4682768	38	7.72	288	2.72	1.25	7.10	1.11	0	0	0	0	0.07
R2	343067	4682773	38	12.60	288	1.78	1.20	8.42	1.31	0	0	0	0	0.054
R3	343058	4682776	38	3.90	288	1.29	1.39	13.43	1.34	0	0	0	0	0.221
R4	343053	4682777	38	9.54	288	0.66	1.36	18.44	1.58	0	0	0	0	0.442
R5	343045	4682781	38	2.60	288	0.44	1.12	21.06	1.86	0	0	1	1	0.546

Table D-4. Detailed PERMANOVA and PERMDISP results for epifaunal community structure in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA					PERMDISP				
	RESULTS TABLE					DEVIATIONS FROM CENTROID				
	Source	df	SS	MS	Pseudo-F	P(perm)	F: 0.67451	df1: 1	df2: 85	
	Ma	1	13763	13763	4.4275	0.0098	P(perm): 0.4277			
	Res	85	2.64E+05	3108.6						
	Total	86	2.78E+05							
	ESTIMATES OF COMPONENTS OF VARIATION						MEANS AND STANDARD ERRORS			
	Source	Estimate	Sq.root				Group	Size	Average	SE
	S(Ma)	245.23	15.66				E	42	54.787	1.5538
	V(Res)	3108.6	55.755				P	45	52.524	2.2321
b)	PERMANOVA					PERMDISP				
	RESULTS TABLE					DEVIATIONS FROM CENTROID				
	Source	df	SS	MS	Pseudo-F	P(perm)	F: 0.9156	df1: 1	df2: 85	
	Mo	1	4287.5	4287.5	1.3315	0.2287	P(perm): 0.3806			
	Res	85	2.74E+05	3220.1						
	Total	86	2.78E+05							
	ESTIMATES OF COMPONENTS OF VARIATION						MEANS AND STANDARD ERRORS			
	Source	Estimate	Sq.root				Group	Size	Average	SE
	S(Mo)	24.568	4.9566				P	45	56.207	1.1
	V(Res)	3220.1	56.746				E	42	54.191	1.8362

Table D-5. Detailed PERMANOVA and PERMDISP results for epifaunal density in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Ma	1	1.10E+05	1.10E+05	0.19702	0.6773	F:	1.9041	df1: 1	df2: 85
	Res	85	4.75E+07	5.59E+05			P(pern):	0.3587		
	Total	86	4.76E+07				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	597.71	103.13
	S(Ma)	-10323	-101.6				P	45	441.36	52.183
	V(Res)	5.59E+05	747.36							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Mo	1	6.09E+05	6.09E+05	1.1014	0.3044	F:	3.495	df1: 1	df2: 85
	Res	85	4.70E+07	5.53E+05			P(pern):	0.1993		
	Total	86	4.76E+07				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	45	613.84	98.544
	S(Mo)	1290.3	35.921				E	42	404.52	47.721
	V(Res)	5.53E+05	743.43							

Table D-6. Detailed PERMANOVA and PERMDISP results for epifaunal species richness in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Ma	1	1.01E+01	1.01E+01	1.36	0.2507	F: 1.919	df1: 1	df2: 85	
	Res	85	6.30E+02	7.41E+00			P(pern): 0.2054			
	Total	86	6.40E+02				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	2.517	0.21864
	S(Ma)	6.14E-02	0.24772				P	45	2.1037	0.20357
	V(Res)	7.41E+00	2.7216							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Mo	1	1.97E-03	1.97E-03	2.62E-04	1	F: 1.4897	df1: 1	df2: 85	
	Res	85	6.40E+02	7.53E+00			P(pern): 0.2467			
	Total	86	6.40E+02				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	45	2.5067	0.20895
	S(Mo)	-0.17316	-0.41613				E	42	2.1429	0.21231
	V(Res)	7.53E+00	2.7433							

Table D-7. Detailed PERMANOVA and PERMDISP results for epifaunal diversity in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Ma	1	1.21E+00	1.21E+00	6.6272	0.0119	F: 0.29144	df1: 1	df2: 85	
	Res	85	1.56E+01	1.83E-01			P(perm): 0.5893			
	Total	86	1.68E+01				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	0.36289	2.77E-02
	S(Ma)	2.37E-02	0.15407				P	45	0.38588	3.20E-02
	V(Res)	1.83E-01	0.42813							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Mo	1	1.71E-01	1.71E-01	8.73E-01	0.3542	F: 5.9414E-2	df1: 1	df2: 85	
	Res	85	1.66E+01	1.96E-01			P(perm): 0.807			
	Total	86	1.68E+01				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	45	0.39545	2.59E-02
	S(Mo)	-5.71E-04	-2.39E-02				E	42	0.40478	2.82E-02
	V(Res)	1.96E-01	0.44224							

Table D-8. Detailed PERMANOVA and PERMDISP results for infaunal community structure in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Ma	1	5.19E+03	5.19E+03	1.8886	0.1016	F:	6.6153	df1: 1	df2: 85
	Res	85	2.34E+05	2.75E+03			P(pern):	0.1129		
	Total	86	2.39E+05				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	37.687	4.21E+00
	S(Ma)	5.62E+01	7.4987				P	45	51.617	3.45E+00
	V(Res)	2.75E+03	52.436							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(pern)	DEVIATIONS FROM CENTROID			
	Mo	1	3.86E+03	3.86E+03	1.39E+00	0.2077	F:	3.3003	df1: 1	df2: 85
	Res	85	2.35E+05	2.77E+03			P(pern):	0.2589		
	Total	86	2.39E+05				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	45	40.368	4.01E+00
	S(Mo)	2.51E+01	5.01E+00				E	42	50.317	3.70E+00
	V(Res)	2.77E+03	52.586							

Table D-9. Detailed PERMANOVA and PERMDISP results for infaunal density in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Ma	1	4.06E+05	4.06E+05	2.4455	0.1077	F: 5.4765	df1: 1	df2: 85	
	Res	85	1.41E+07	1.66E+05			P(perm): 0.137			
	Total	86	1.45E+07				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	107.4	1.75E+01
	S(Ma)	5.52E+03	74.32				P	45	280.39	6.95E+01
	V(Res)	1.66E+05	407.46							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Mo	1	5.66E+04	5.66E+04	3.32E-01	0.6695	F: 0.59171	df1: 1	df2: 85	
	Res	85	1.45E+07	1.70E+05			P(perm): 0.7763			
	Total	86	1.45E+07				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	45	169.01	3.10E+01
	S(Mo)	-2.61E+03	-5.11E+01				E	42	228.34	7.26E+01
	V(Res)	1.70E+05	412.47							

Table D-10. Detailed PERMANOVA and PERMDISP results for infaunal species richness in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Ma	1	1.79E+00	1.79E+00	2.1788	0.1654	F: 2.6208	df1: 1	df2: 85	
	Res	85	7.00E+01	8.23E-01			P(perm): 0.2832			
	Total	86	7.17E+01				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	0.52721	5.89E-02
	S(Ma)	2.23E-02	0.14943				P	45	0.74469	1.18E-01
	V(Res)	8.23E-01	0.90719							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Mo	1	2.65E-02	2.65E-02	3.14E-02	0.9119	F: 0.28245	df1: 1	df2: 85	
	Res	85	7.17E+01	8.44E-01			P(perm): 0.7732			
	Total	86	7.17E+01				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	42	0.52721	5.89E-02
	S(Mo)	-1.88E-02	-1.37E-01				P	45	0.74469	1.18E-01
	V(Res)	8.44E-01	0.91857							

Table D-11. Detailed PERMANOVA and PERMDISP results for infaunal diversity in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA										PERMDISP									
	RESULTS TABLE										DEVIATIONS FROM CENTROID									
	Source	df		SS		MS		Pseudo-F		P(perm)		F: 1.5691	df1: 1	df2: 85						
	Ma	1		2.07E-02		2.07E-02		0.36047		0.5907										
	Res	85		4.87E+00		5.73E-02														
	Total	86		4.89E+00																
	ESTIMATES OF COMPONENTS OF VARIATION										MEANS AND STANDARD ERRORS									
	Source	Estimate		Sq.root							Group	Size		Average		SE				
	S(Ma)	-8.44E-04		-2.90E-02							E	42		0.10412		2.29E-02				
	V(Res)	5.73E-02		0.2394							P	45		0.15712		3.49E-02				
b)	PERMANOVA										PERMDISP									
	RESULTS TABLE										DEVIATIONS FROM CENTROID									
	Source	df		SS		MS		Pseudo-F		P(perm)		F: 1.4703	df1: 1	df2: 85						
	Mo	1		1.94E-02		1.94E-02		3.39E-01		0.5991										
	Res	85		4.87E+00		5.73E-02														
	Total	86		4.89E+00																
	ESTIMATES OF COMPONENTS OF VARIATION										MEANS AND STANDARD ERRORS									
	Source	Estimate		Sq.root							Group	Size		Average		SE				
	S(Mo)	-8.72E-04		-2.95E-02							P	4.50E+01		1.56E-01		3.50E-02				
	V(Res)	5.73E-02		0.23943							E	4.20E+01		0.10499		2.28E-02				

Table D-12. Detailed PERMANOVA and PERMDISP results for *Hemigrapsus sanguineus* size data in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(permutation)	DEVIATIONS FROM CENTROID			
	Ma	1	1.85E+02	1.85E+02	5.1521	0.0269	F: 0.11367	df1: 1	df2: 132	
	Res	132	4.74E+03	3.59E+01			P(permutation): 0.7626			
	Total	133	4.93E+03				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	49	4.5589	5.55E-01
	S(Ma)	2.40E+00	1.55E+00				P	85	4.7812	3.85E-01
	V(Res)	3.59E+01	5.9951							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(permutation)	DEVIATIONS FROM CENTROID			
	Mo	1	1.73E+02	1.73E+02	4.7868	0.0306	F: 7.0957	df1: 1	df2: 132	
	Res	132	4.76E+03	3.60E+01			P(permutation): 0.0119			
	Total	133	4.93E+03				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	6.50E+01	4.07E+00	3.58E-01
	S(Mo)	2.04E+00	1.43E+00				E	6.90E+01	5.6207	4.54E-01
	V(Res)	3.60E+01	6.0031							

Table D-13. Detailed PERMANOVA and PERMDISP results for *Carcinus maenas* size data in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Ma	1	4.20E+01	4.20E+01	2.2112	0.1354	F: 1.4516	df1: 1	df2: 150	
	Res	150	2.85E+03	1.90E+01			P(perm): 0.4473			
	Total	151	2.89E+03				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				E	60	3.32	4.63E-01
	S(Ma)	3.17E-01	5.63E-01				P	92	2.6824	3.03E-01
	V(Res)	1.90E+01	4.358							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(perm)	DEVIATIONS FROM CENTROID			
	Mo	1	1.75E+01	1.75E+01	0.9125	0.3525	F: 6.9598	df1: 1	df2: 150	
	Res	150	2.87E+03	1.92E+01			P(perm): 0.0934			
	Total	151	2.89E+03				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root				P	7.20E+01	2.27E+00	3.09E-01
	S(Mo)	-2.21E-02	-1.49E-01				E	8.00E+01	3.6097	3.92E-01
	V(Res)	1.92E+01	4.3767							

Table D-14. Detailed PERMANOVA and PERMDISP results for *Littorina littorea* size data in maximum (a) and modal (b) wave energy models. df: degrees of freedom, SS: sum of squares, MS: mean square, SE: standard error.

a)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(permutation)	DEVIATIONS FROM CENTROID			
	Wa	1	2.05E+03	2.05E+03	166.4	0.0001	F: 161.45	df1: 1	df2: 2440	
	Res	2440	3.01E+04	1.23E+01			P(permutation):	0.0001		
	Total	2441	3.21E+04				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root	ESTIMATES OF COMPONENTS OF VARIATION			P	1690	2.6351	4.14E-02
	S(Ma)	1.96E+00	1.40E+00				E	752	3.6594	7.72E-02
	V(Res)	1.23E+01	3.5097							
b)	PERMANOVA									
	RESULTS TABLE					PERMDISP				
	Source	df	SS	MS	Pseudo-F	P(permutation)	DEVIATIONS FROM CENTROID			
	Mo	1	7.20E+02	7.20E+02	55.939	0.0001	F: 8.9595	df1: 1	df2: 2440	
	Res	2440	3.14E+04	1.29E+01			P(permutation):	0.004		
	Total	2441	3.21E+04				MEANS AND STANDARD ERRORS			
							Group	Size	Average	SE
	Source	Estimate	Sq.root	ESTIMATES OF COMPONENTS OF VARIATION			E	1.43E+03	2.90E+00	4.69E-02
	S(Mo)	5.97E-01	7.73E-01				P	1.01E+03	3.1434	6.90E-02
	V(Res)	1.29E+01	3.5865							

Table D-15. Distance-based linear models (DISTLM) of the epifaunal community structure on protected shorelines, based on the maximum wave energy model. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df		
Latitude (La)	3435.3	1.1313	0.3098	2.56E-02	43		
Longitude (Lo)	3745.7	1.2365	0.263	2.80E-02	43		
Date (Da)	2457.9	0.80343	0.5039	1.83E-02	43		
Slope (Sl)	5770.3	1.9349	0.1055	4.31E-02	43		
Aspect (As)	2262.9	0.73858	0.5442	1.69E-02	43		
Elevation (El)	41118	19.034	0.0001	0.30684	43		
Rugosity (Ru)	8882.2	3.0524	0.0253	6.63E-02	43		
Water Content (WC)	41085	19.012	0.0001	0.30659	43		
Organic Content (OC)	24596	9.6667	0.0001	0.18354	43		
Skewness (Sk)	12977	4.6105	0.0057	9.68E-02	43		
Brown Algae (BA)	2164.4	0.70591	0.5506	1.62E-02	43		
Green Algae (GA)	9192.3	3.1668	0.0168	6.86E-02	43		
Red Algae (RA)	3641.1	1.201	0.293	2.72E-02	43		
Total Algae (TA)	6037.9	2.0288	0.0826	4.51E-02	43		
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+El	347.46	41118	19.034	0.0001	0.30684	0.30684	43
+Lo	344.84	9063.9	4.5414	0.0007	6.76E-02	0.37447	42
+Ru	341.65	9142	5.0188	0.0002	6.82E-02	0.44269	41
+WC	341.08	4144.8	2.3504	0.0312	3.09E-02	0.47362	40
+Da	341.01	3172	1.8364	0.0929	2.37E-02	0.49729	39
+GA	340.95	3013.7	1.7795	0.1091	2.25E-02	0.51978	38
BEST SOLUTION							
AIC	R ²	RSS	Variables				
340.95	0.51978	64353	El, Lo, Ru, WC, Da, GA				

Table D-16. Distance-based linear models (DISTLM) of epifaunal community structure on exposed shorelines, based on the maximum wave energy model. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, *ln(x) transformed, **ln(x+1) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df		
Latitude (La)	5738.4	1.8439	0.1415	4.41E-02	40		
Longitude (Lo)	1477.8	0.45913	0.6912	1.13E-02	40		
Date (Da)	6920.2	2.2449	0.0934	5.31E-02	40		
Slope (Sl)	11567	3.8991	0.0214	8.88E-02	40		
Aspect (As)	11484	3.8687	0.0259	8.82E-02	40		
Elevation (El)	23947	9.013	0.0007	0.18389	40		
Rugosity (Ru)	19682	7.122	0.0018	0.15114	40		
Water Content (WC)	37188	15.989	0.0001	0.28557	40		
Organic Content (OC)*	22148	8.1971	0.0004	0.17007	40		
Skewness (Sk)**	26872	10.4	0.0001	0.20635	40		
Brown Algae (BA)	9791.8	3.2522	0.0079	7.52E-02	40		
Green Algae (GA)	4722.5	1.5052	0.2184	3.63E-02	40		
Red Algae (RA)	19455	7.0255	0.0001	0.1494	40		
Total Algae (TA)	18478	6.6143	0.0003	1.42E-01	40		
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+WC	327.53	37188	15.989	0.0001	0.28557	0.28557	40
+Ru	321.88	15483	7.7861	0.0005	1.19E-01	0.40446	39
+Sk**	320.61	5813.2	3.0792	0.0277	4.46E-02	0.4491	38
+El	319.11	5744.4	3.2206	0.0198	4.41E-02	0.49322	37
BEST SOLUTION							
AIC	R ²	RSS	Variables				
319.11	0.49322	65995	WC, Ru, Sk**, El				

Table D-17. Distance-based linear models (DISTLM) of epifaunal density. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, [†]1/(x) transformed, [‡]sqrt(x) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	2.25E+05	0.40456	0.5402	4.74E-03	85	-	
Longitude (Lo)	27785	4.97E-02	0.832	5.84E-04	85	+	
Date (Da)	33533	5.99E-02	0.805	7.05E-04	85	+	
Slope (Sl)	2.14E+06	4.0103	0.0497	4.51E-02	85	-	
Aspect (As)	3.50E+06	6.7475	0.0098	7.35E-02	85	+	
Elevation (El)	1.19E+07	28.27	0.0001	0.24958	85	-	
Rugosity (Ru) [†]	2.15E+06	4.0172	0.048	4.51E-02	85	-	
Water Content (WC)	7.71E+06	16.433	0.0001	0.16201	85	+	
Organic Content (OC) [‡]	3.24E+06	6.2109	0.0207	6.81E-02	85	+	
Skewness (Sk)	1.58E+07	42.083	0.0001	0.33115	85	+	
Brown Algae (BA)	1.03E+06	1.8716	0.0983	2.15E-02	85	+	
Green Algae (GA)	5.15E+05	0.92927	0.3044	1.08E-02	85	-	
Red Algae (RA)	5.22E+06	10.467	0.0132	0.10964	85	+	
Total Algae (TA)	4.82E+05	0.86976	0.3497	1.01E-02	85	+	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Sk	1118.5	1.58E+07	42.083	0.0001	0.33115	0.33115	85
+El	1105.5	5.02E+06	15.726	0.0002	1.05E-01	0.43662	84
+Ru [†]	1103.6	1.20E+06	3.8762	0.0521	2.51E-02	0.46176	83
+La	1102.4	9.27E+05	3.0799	0.0797	1.95E-02	0.48124	82
BEST SOLUTION							
AIC	R ²	RSS	Variables				
1102.4	0.48124	2.47E+07	Sk, El, Ru [†] , La				

Table D-18. Distance-based linear models (DISTLM) of epifaunal species richness. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, [†]1/(x) transformed, [‡]sqrt(x) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	3.98E-01	5.29E-02	0.8231	6.22E-04	85	-	
Longitude (Lo)	3.214	4.29E-01	0.511	5.02E-03	85	-	
Date (Da)	21.36	2.94E+00	0.0922	3.34E-02	85	+	
Slope (Sl)	2.80E+01	3.8978	0.0505	4.38E-02	85	-	
Aspect (As)	1.72E+01	2.3482	0.1381	2.69E-02	85	+	
Elevation (El)	2.85E+02	68.34	0.0001	0.44567	85	-	
Rugosity (Ru) [†]	3.78E+01	5.3426	0.0216	5.91E-02	85	-	
Water Content (WC)	2.63E+02	59.421	0.0001	0.41144	85	+	
Organic Content (OC) [‡]	1.67E+02	30.137	0.0001	2.62E-01	85	+	
Skewness (Sk)	1.59E+02	28.026	0.0001	0.24796	85	+	
Brown Algae (BA)	4.33E+01	6.1661	0.0133	6.76E-02	85	+	
Green Algae (GA)	2.00E+01	2.7459	0.0952	3.13E-02	85	-	
Red Algae (RA)	1.45E+02	24.908	0.0001	2.27E-01	85	+	
Total Algae (TA)	1.49E+01	2.0302	0.157	2.33E-02	85	+	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+El	126.24	2.85E+02	68.34	0.0001	0.44567	0.44567	85
+WC	113.62	5.48E+01	15.366	0.0002	8.57E-02	0.5314	84
+Ru [†]	107.8	2.58E+01	7.8133	0.0065	4.03E-02	0.57171	83
+RA	100.13	2.88E+01	9.641	0.0022	4.51E-02	0.61677	82
+Sk	96.798	1.46E+01	5.1158	0.0246	2.28E-02	0.63954	81
+OC [‡]	94.932	1.00E+01	3.6353	0.0603	1.57E-02	0.6552	80
-WC	93.182	6.35E-01	0.23034	0.6361	9.93E-04	0.65421	81
+Da	91.663	8.7678	3.302	0.072	1.37E-02	0.66792	80
+BA	91.546	5.1063	1.9458	0.1599	7.98E-03	0.6759	79
BEST SOLUTION							
AIC	R ²	RSS	Variables				
91.546	0.6759	2.07E+02	El, Ru [†] , RA, Sk, OC [‡] , Da, BA				

Table D-19. Distance-based linear models (DISTLM) of epifaunal diversity on protected shorelines, based on the maximum wave energy model. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	1.10E-02	5.42E-02	0.8133	1.26E-03	43	-	
Longitude (Lo)	6.31E-02	3.13E-01	0.5775	7.23E-03	43	-	
Date (Da)	7.92E-01	4.2887	0.0467	9.07E-02	43	+	
Slope (Sl)	1.21E-02	5.96E-02	0.8066	1.38E-03	43	-	
Aspect (As)	1.27E-01	0.63325	0.4292	1.45E-02	43	-	
Elevation (El)	4.93E+00	55.727	0.0001	5.64E-01	43	-	
Rugosity (Ru)	6.72E-01	3.5841	0.0654	7.69E-02	43	+	
Water Content (WC)	2.69E+00	19.141	0.0001	3.08E-01	43	+	
Organic Content (OC)	2.63E+00	18.501	0.0001	0.30083	43	+	
Skewness (Sk)	0.75901	4.095	0.0499	8.70E-02	43	+	
Brown Algae (BA)	1.78E-01	0.89663	0.5119	2.04E-02	43	+	
Green Algae (GA)	6.51E-01	3.4644	0.0693	7.46E-02	43	-	
Red Algae (RA)	1.80E-03	8.87E-03	0.9247	2.06E-04	43	+	
Total Algae (TA)	2.30E-01	1.1633	0.2864	2.63E-02	43	-	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+El	-107.2	4.93E+00	55.727	0.0001	0.56446	0.56446	43
+Ru	-112.48	5.67E-01	7.3679	0.009	6.50E-02	0.62946	42
+La	-115.8	3.61E-01	5.1469	0.0251	4.13E-02	0.67079	41
+OC	-116.09	1.42E-01	2.0863	0.1562	1.63E-02	0.68711	40
BEST SOLUTION							
AIC	R2	RSS	Variables				
-116.09	0.68711	2.73E+00	El, Ru, La, OC				

Table D-20. Distance-based linear models (DISTLM) of epifaunal diversity on exposed shorelines, based on the maximum wave energy model. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom. *ln(x) transformed, **ln(x+1) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	5.72E-02	3.37E-01	0.5699	8.35E-03	40	-	
Longitude (Lo)	1.45E-01	8.68E-01	0.3527	2.12E-02	40	-	
Date (Da)	2.37E-01	1.44E+00	0.2383	3.46E-02	40	+	
Slope (Sl)	2.04E-01	1.2256	0.2706	2.97E-02	40	-	
Aspect (As)	4.61E-01	2.89E+00	0.0947	6.73E-02	40	+	
Elevation (El)	1.80E+00	14.242	0.0004	2.63E-01	40	-	
Rugosity (Ru)	5.27E-01	3.3333	0.0732	7.69E-02	40	+	
Water Content (WC)	2.93E+00	29.955	0.0001	4.28E-01	40	+	
Organic Content (OC)*	1.71E+00	13.283	0.0006	2.49E-01	40	+	
Skewness (Sk)**	5.69E-01	3.6208	0.0488	8.30E-02	40	+	
Brown Algae (BA)	1.61E+00	1.23E+01	0.0021	2.35E-01	40	+	
Green Algae (GA)	0.26355	1.6003	0.2265	3.85E-02	40	-	
Red Algae (RA)	1.54E+00	11.614	0.0011	2.25E-01	40	+	
Total Algae (TA)	1.33E+00	9.6456	0.0039	1.94E-01	40	+	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+WC	-95.636	2.93E+00	29.955	0.0001	0.4282	0.4282	40
+Ru	-96.998	3.01E-01	3.2509	0.0756	4.40E-02	0.4722	39
+TA	-98.25	2.69E-01	3.0591	0.087	3.93E-02	0.51152	38
BEST SOLUTION							
AIC	R ²	RSS	Variables				
-98.25	0.51152	3.35E+00	WC, Ru, TA				

Table D-21. Distance-based linear models (DISTLM) of infaunal community structure. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, [†]1/(x) transformed, [‡]sqrt(x) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df		
Latitude (La)	1.85E+03	6.64E-01	0.6067	7.75E-03	85		
Longitude (Lo)	8.28E+02	2.96E-01	0.9449	3.46E-03	85		
Date (Da)	3.18E+03	1.14E+00	0.2897	1.33E-02	85		
Slope (Sl)	4.92E+03	1.789	0.1168	2.06E-02	85		
Aspect (As)	5.05E+03	1.84E+00	0.1041	2.11E-02	85		
Elevation (El)	6.05E+03	2.21	0.0698	2.53E-02	85		
Rugosity (Ru) [†]	2.61E+03	0.93758	0.4087	1.09E-02	85		
Water Content (WC)	1.25E+04	4.6922	0.0034	5.23E-02	85		
Organic Content (OC) [‡]	5.09E+03	1.8505	0.1137	2.13E-02	85		
Skewness (Sk)	1.48E+04	5.5931	0.0015	6.17E-02	85		
Brown Algae (BA)	8.50E+03	3.1376	0.043	3.56E-02	85		
Green Algae (GA)	2.22E+03	7.96E-01	0.4613	9.28E-03	85		
Red Algae (RA)	937.63	0.33492	0.9005	3.92E-03	85		
Total Algae (TA)	4.90E+03	1.7799	0.116	2.05E-02	85		
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Sk	687.31	1.48E+04	5.5931	0.0016	6.17E-02	6.17E-02	85
+BA	686.71	6.62E+03	2.5558	0.0663	2.77E-02	8.94E-02	84
BEST SOLUTION							
AIC	R ²	RSS	Variables				
686.71	8.94E-02	2.18E+05	Sk, BA				

Table D-22. Distance-based linear models (DISTLM) of infaunal density. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, $\dagger 1/(x)$ transformed, $\ddagger \sqrt{x}$ transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	2.24E+05	1.33E+00	0.2741	1.55E-02	85	+	
Longitude (Lo)	1.41E+05	8.32E-01	0.4081	9.70E-03	85	-	
Date (Da)	8.58E+04	0.50528	0.4883	5.91E-03	85	+	
Slope (Sl)	3.58E+04	2.10E-01	0.6535	2.47E-03	85	+	
Aspect (As)	3.75E+05	2.2515	0.1357	2.58E-02	85	+	
Elevation (El)	2.24E+05	1.3349	0.2636	1.55E-02	85	-	
Rugosity (Ru) [†]	6.03E+05	3.6865	0.0501	4.16E-02	85	-	
Water Content (WC)	2.40E+05	1.4272	0.2292	1.65E-02	85	+	
Organic Content (OC) [‡]	3.70E+04	0.21719	0.5496	2.55E-03	85	+	
Skewness (Sk)	1.05E+06	6.6267	0.0073	7.23E-02	85	+	
Brown Algae (BA)	1.24E+04	7.27E-02	0.733	8.54E-04	85	-	
Green Algae (GA)	3.25E+03	1.90E-02	0.8683	2.24E-04	85	+	
Red Algae (RA)	73300	0.43134	0.3426	5.05E-03	85	-	
Total Algae (TA)	9.72E+03	5.69E-02	0.7951	6.69E-04	85	-	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Sk	1043.6	1.05E+06	6.6267	0.0082	7.23E-02	7.23E-02	85
+Ru [†]	1042.6	4.63E+05	2.9936	0.0811	3.19E-02	1.04E-01	84
+Sl	1042.5	3.10E+05	2.0301	0.16	2.14E-02	0.12563	83
BEST SOLUTION							
AIC	R ²	RSS	Variables				
1042.5	1.26E-01	1.27E+07	Sk, Ru [†] , Sl				

Table D-23. Distance-based linear models (DISTLM) of infaunal species richness. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, [†]1/(x) transformed, [‡]sqrt(x) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	5.88E-01	7.02E-01	0.4199	8.19E-03	85	+	
Longitude (Lo)	1.58E-01	1.87E-01	0.6784	2.20E-03	85	-	
Date (Da)	6.40E-03	7.58E-03	0.9346	8.92E-05	85	+	
Slope (Sl)	7.23E-01	8.65E-01	0.3605	1.01E-02	85	-	
Aspect (As)	3.09E+00	3.8267	0.052	4.31E-02	85	+	
Elevation (El)	2.57E+00	3.1554	0.0808	3.58E-02	85	-	
Rugosity (Ru) [†]	4.73E-01	0.5638	0.4595	6.59E-03	85	-	
Water Content (WC)	3.90E+00	4.8836	0.0302	5.43E-02	85	+	
Organic Content (OC) [‡]	7.65E-01	0.91561	0.3088	1.07E-02	85	+	
Skewness (Sk)	8.92E+00	1.21E+01	0.0004	1.24E-01	85	+	
Brown Algae (BA)	1.37E+00	1.6595	0.0836	1.91E-02	85	+	
Green Algae (GA)	8.00E-03	9.48E-03	0.9219	1.11E-04	85	-	
Red Algae (RA)	1.42E-01	1.69E-01	0.6687	1.98E-03	85	-	
Total Algae (TA)	0.26775	0.3184	0.5572	3.73E-03	85	+	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
+Sk	-24.314	8.92E+00	12.061	0.0006	1.24E-01	1.24E-01	85
+RA	-24.883	1.83E+00	2.518	0.0859	2.55E-02	1.50E-01	84
BEST SOLUTION							
AIC	R ²	RSS	Variables				
-24.883	1.50E-01	6.10E+01	Sk, RA				

Table D-24. Distance-based linear models (DISTLM) on infaunal diversity. +/- indicate additions to or subtractions from the model. AIC: Akaike Information Criteria, SS: sum of squares, RSS: residual sum of squares, res.df: residual degrees of freedom, [†]1/(x) transformed, [‡]sqrt(x) transformed.

MARGINAL TESTS							
Variables	SS(trace)	Pseudo-F	P	Prop.	res.df	Trend	
Latitude (La)	5.06E-02	8.88E-01	0.3762	1.03E-02	85	+	
Longitude (Lo)	2.62E-02	4.57E-01	0.5179	5.35E-03	85	-	
Date (Da)	7.73E-02	1.37E+00	0.252	1.58E-02	85	+	
Slope (Sl)	5.18E-03	9.01E-02	0.7609	1.06E-03	85	-	
Aspect (As)	9.43E-02	1.6704	0.2049	1.93E-02	85	+	
Elevation (El)	5.44E-02	0.95635	0.3449	1.11E-02	85	-	
Rugosity (Ru) [†]	2.21E-02	0.38595	0.5449	4.52E-03	85	-	
Water Content (WC)	5.00E-02	0.87768	0.3545	1.02E-02	85	+	
Organic Content (OC) [‡]	5.89E-04	1.02E-02	0.9132	1.20E-04	85	+	
Skewness (Sk)	0.34307	6.41	0.0117	7.01E-02	85	+	
Brown Algae (BA)	3.97E-02	6.96E-01	0.1643	8.12E-03	85	+	
Green Algae (GA)	3.64E-02	0.63776	0.3937	7.45E-03	85	-	
Red Algae (RA)	9.79E-03	1.71E-01	0.7347	2.00E-03	85	-	
Total Algae (TA)	3.14E-03	5.46E-02	0.808	6.41E-04	85	-	
SEQUENTIAL TESTS							
Variables	AIC	SS(trace)	Pseudo-F	P	Prop.	Cumul.	res.df
Sk	-252.73	3.43E-01	6.41	0.0121	7.01E-02	7.01E-02	85
BEST SOLUTION							
AIC	R ²	RSS	Variables				
-252.73	1.01E-02	4.55E+00	Sk				

APPENDIX E: Data Maps

The following pages include maps of Boston Harbor with bubble plots representing selected species abundances, as well as epifaunal diversity, richness, and density. These plots show graphical representations of the spatial variation in species abundances and community characteristics, highlighting locations of “hot spots” throughout the harbor.

Bubble plots are only shown for the six species selected by SIMPER analysis which contribute to the separation between exposed and protected shorelines based on the maximum wave energy model: *Balanus balanoides*, *Littorina littorea*, *Hyale plumulosa*, *Anurida maritima*, *Carcinus maenas*, and *Hemigrapsus sanguineus*.

Figure E-1. Bubble plot of *Balanus balanoides* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-2. Bubble plot of *Littorina littorea* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-3. Bubble plot of *Hyale plumulosa* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-4. Bubble plot of *Anurida maritima* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-5. Bubble plot of *Carcinus maenas* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-6. Bubble plot of *Hemigrapsus sanguineus* abundance across Boston Harbor. Only data from the quadrat with the highest abundance at each transect is represented.

Figure E-7. Bubble plot of diversity across Boston Harbor. Only data from the quadrat with the highest diversity at each transect is represented.

Figure E-8. Bubble plot of species richness across Boston Harbor. Only data from the quadrat with the highest species richness at each transect is represented.

Figure E-9. Bubble plot of density (total individuals per m^2) across Boston Harbor. Only data from the quadrat with the highest density at each transect is represented.