Longstanding signals of marine community structuring by winter storm wave-base

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ABSTRACT: Coastal marine communities face both physical oceanographic changes and altered ecological relationships due to indirect human activities, such as climate-related changes, and direct human activities, such as extraction of wave energy as a renewable resource. Often single physical oceanographic changes and altered ecological relationships are investigated, rather than multiple potential drivers. Here we investigated the links between the structure of offshore benthic bivalve communities to multiple physical drivers including wave-base, and more traditional drivers of marine soft sediment community structure (e.g. temperature, pH, dissolved oxygen, salinity, and nutrients). Our benthic bivalve community data (both modern and historical) were collected from bulk sediment box-core samples taken over a depth range of 20–70 m on the continental shelf of Newport, Oregon, USA. Environmental data were collected through CTD casts at sampling locations and through NOAA Buoy Station 46094. We used a non-linear hierarchical regression approach to look for a systematic response in the benthos. Subtidal bivalve communities structured themselves along a depth gradient with a distinct shift in species' rank abundance at 50 m, and this shift was most strongly associated with storm wave-base. This distinct wave-driven community structure was present in both modern-day bivalve communities and century-scale historical communities, suggesting both the importance of waves and the longstanding nature of their impacts on biological communities in this system. These results emphasize potential consequences of changing wave-base on this shelf, which could occur indirectly through changing storm regimes due to anthropogenic climate change or directly through large-scale wave energy harvest.

KEY WORDS: Benthic fauna · Community structure · Wave energy · Bivalves

INTRODUCTION

Anthropogenic activities may impact coastal shelf communities through multiple mechanisms of action. Changes in atmospheric CO_2, for example, are expected to cause rising water temperatures and changing chemistry of the inorganic carbon system, leading to declining pH and ocean acidification (Orr et al. 2005, Harris et al. 2013). There is increasing evidence of rapid pH decline and biological impacts along the coastal waters of the eastern Pacific (Grantham et al. 2004, Orr et al. 2005, Wootton et al. 2008, Barton et al. 2012, Harris et al. 2013, Wald-

busser et al. 2013). While these expected changes arising from anthropogenic CO_2 release have received much recent attention, changes in factors associated with altered storm frequency and intensity may also affect coastal ecosystems through changes in wave impact on the ocean floor (Knutson et al. 2010). Furthermore, methods to counteract CO_2 release, such as wave energy extraction for renewable energy power production, may have their own environmental impacts that need to be incorporated into policy planning (Boehlert & Gill 2010). Anthropogenic change may also affect other drivers including altered phytoplankon abundance and hypoxia

from eutrophication and changing upwelling (Chan et al. 2008), and shifts in water column fish communities from overharvesting (Jackson et al. 2001, Myers & Worm 2003). Hence, identifying and teasing apart the roles of multiple potential drivers on coastal shelf communities is important to inform coastal management plans.

Currently, we lack a thorough understanding of the ecological implications on benthic subtidal marine communities for changing wave regimes and wave energy extraction (Shields et al. 2011). Waves can both directly and indirectly affect benthic marine communities through physical disturbance or by mixing resources like oxygen and nutrients throughout the water column (Denny 1988, Shields et al. 2011). Specifically, high shear forces from waves impact the seafloor at the sediment–water interface (Shields et al. 2011), depending on wave size in relation to bottom depth, and we refer to this as wave-base. Organisms must resist the mechanical failure that can result from these hydrodynamic forces of wave-base or face damage or dislodgment from the substratum (Gaylord et al. 2001). Indirectly, water flow is affected by wave energy and is important for the transport of gasses, nutrients, sediments, and food while also facilitating the dispersal of propagules and waste products (Shields et al. 2011). Wave impacts have primarily received attention in intertidal habitats where breaking waves impart focused energy release along the shore. Subtidal soft-sediment communities have received less attention regarding wave energy impacts than intertidal and surf zone shores (but see Armonies et al. 2014). Do benthic subtidal communities reflect effects of wave energy through spatial structure or ecological characteristics? If so, how might nearshore communities respond to anthropogenic impacts on wave regime arising from climate change or wave energy extraction? Linking these physical wave energy characteristics with biological community responses is critical for understanding the potential ecological impact of altered wave regimes and to accurately predict the magnitude of effects from wave energy extraction (Shields et al. 2011).

Many biologists and ecological assessments have attempted to answer questions about community structure by collecting richness, relative abundance, and biomass data during rapid short-term biodiversity studies of geographically dispersed sites (Lie 1974, Gray 1979, Sagarin et al. 1999, Hewitt et al. 2005, Smith 2005, Schoch et al. 2006, Blanchette et al. 2008). These studies often include seasonal and annual variation with their time series data (>10 yr)

and a potentially unknown degree of human alteration (Lie 1974, Gray 1979, Swartz et al. 1986, Ferraro et al. 1991, Sagarin et al. 1999). In contrast, paleoecologists eliminate seasonal and annual variation by working at a coarser scale of decades to centuries and using paleoenvironmental proxies, death assemblages (the dead remains of previously living communities that persist in the environment), and even fossil assemblages (centuries to millennial time scales) (Dietl & Flessa 2011, Lötze & McClenachan 2014). Here we examined both live samples and death assemblages for a different perspective of impacts on the continental shelf of Newport, Oregon (USA). We thus build on other historical studies that have used these alternative resources of data to provide baselines of comparisons with modern data and reconstruct the transformation of marine ecosystems by humans through impacts on top consumers, expose unprecedented rates of rapid, anthropogenically driven ocean acidification, and even track overfishing (Lötze et al. 2006, McClenachan 2009, Pfister et al. 2011). By developing these approaches to using non-traditional historical (>50 yr) data, we can test the robustness of apparent ecological relationships with environmental drivers.

Previously, we developed a death assemblage data set for the continental shelf of Newport, Oregon, to verify the historical structure of soft-sediment bivalve communities of the Oregon coastal shelf (Voorhies 2015). The estimated temporal window for death assemblages in Newport can be determined from the analysis of age-frequency distributions of bivalves in similar environments (siliciclastic shelf in southern California) that were dominated by individuals from the most recent decades (Kidwell 2013). These younger, more recently dead shells, dominate the community characteristics of death assemblages and the only observed deviations from counterpart living assemblages occurred when human disturbance was present (rather than other taphonomic drivers) (Kidwell 2007). Both our modern and historical data from Newport documented distinct spatial patterns in community structure that were coherent across timescales. Here we examined relationships between these patterns and key ecological parameters to elucidate the potential ecological drivers contributing to soft sediment benthic community structure and potential links to anthropogenic change. In particular, we found evidence for a strong non-linear effect of wave-base on ecological composition of the coastal shelf, with weaker signals of ocean pH, which may be altered by future anthropogenic impacts.

MATERIALS AND METHODS

Biological data

Benthic community data were obtained from bulk sediment samples collected from the continental shelf of Newport, Oregon, from June 2010 to August 2012 using a 0.1 m^2 box core and sieved through a 1 mm mesh. This high-energy open coast setting was sampled with a grid of sampling stations (Fig. 1) arrayed at 10 m depth contours from 20 to 70 m water depth and spaced 1 km or more from each other. Sampling stations 1 km or more apart are reasonably treated as independent for low-mobility bivalve species that were the response variables in this study (Somerfield & Gage 2000). Modern (living assemblages) and historical (death assemblages) were both obtained through sieving box core samples on-board the sampling vessel, with death assemblages retained from 2011 only. Benthic assemblages were washed into a sample jar where they were treated with 5% buffered formalin and Rose-Bengal to stain living organisms. After 72 h, the sample was rinsed and transferred into 70% ethanol. A dissecting microscope was used to separate live organisms from the death assemblage at this stage. Bivalve death assemblages were given a freshwater rinse and allowed to air-dry before being sorted and individuals identified. Identifications for the live bivalves were done in the Henkel lab, and K. Voorhies identified the dead shells. Validation and cross-checking of identifications were done using photos and reference collections. More details on identification of the death assemblage can be found in Voorhies (2015).

Environmental data

We focused our analysis on potential mechanistic drivers of changes connected directly to demographic and physiological rates in benthic communities. The environmental variables we included in our analyses were temperature, pH, dissolved oxygen, salinity, sediment type (median grain size and percent silt), and chlorophyll, which were all independently estimated and varied spatially as well as with depth. We chose not to include depth as a predictor variable because depth is not a mechanistic variable that would directly affect community demographics. Environmental variables of temperature, pH, dissolved oxygen, and salinity were collected from CTD casts completed during the sampling of benthic communities from 2010–2012. At each station, vertical water column profiles of conductivity (salinity), temperature, dissolved oxygen, pH, and depth were obtained with a Sea-Bird Electronics CTD unit with additional sensors. Median grain size and percent silt/clay were determined from sediment samples taken from the box core using a laser diffraction particle size analyzer. The study area was mostly sand with mean silt content of less than 1%. Coarser-grained sand and a slightly greater fraction of silt characterize shallower stations when compared to deep stations. No grain size differences were found from the top and middle of the box core, and the entire box core was processed as a single sample for live and dead individuals. We estimated phytoplankton availability from surface water chlorophyll *a* (chl *a*) content reported by
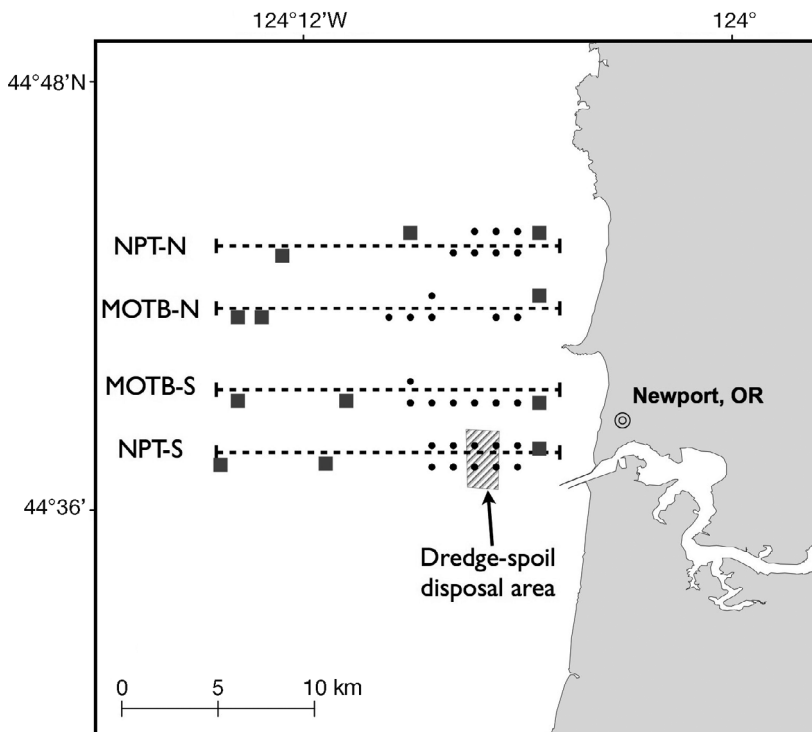

Fig. 1. Sampling sites off the coast of Newport, Oregon (USA), using grid of Henkel (2011). Four bathymetric transects (NPT-N, MOTB-N, MOTB-S, NPT-S) arrayed along the coast with stations at 30, 40, and 50 m water depth were sampled multiple times a year from 2010–2012 (black circles). Stations at 20, 60, and 70 m were sampled only once, in June 2011 (gray squares). The dredge-material disposal area was not used in the analyses

the National Oceanic Atmospheric Administration (NOAA). Specifically, we downloaded monthly averages of chlorophyll fluorescence as calculated from the Aqua/MODIS satellite platform from the Coast-Watch West Coast Node site that corresponded to the same years as our benthic sampling (2010–2012) and used the specific latitude and longitude coordinates of our stations to cover the same spatial area. We then aggregated the chl *a* data to a yearly estimate to compare with other environmental drivers on an annual basis.

We also considered the physical environmental factor of wave energy through wave-bases interacting with the seafloor. Our analysis focused on cumulative wave-base distributions, because wave-base directly impacts the benthic bivalves and their environment. Wave-base describes the wave energy regime most relevant to our study questions rather than other often used characterizations of waves at the surface, such as significant wave height (e.g. Armonies et al. 2014). We calculated wave-base distributions using wave period data from 2011 integrated across 20 min intervals from NOAA Buoy Station 46094 off of Newport, Oregon. NOAA provides 'average' wave periods that are the mean wave period over a window of 20 min and 'dominant' wave periods, which are the wave periods with the maximum energy in each 20 min window. Wave period data were converted into wave-base values using a widget to calculate shallow-water wavelengths through the University Corporation for Atmospheric Research Meted marine resources website (www.meted.ucar.edu/marine/widgets/). The equation used was:

$$\text{Wavelength} = 1.56 \times (\text{Wave period})^2 \quad (1)$$

The wave-base is 1/2 of the wavelength. Another approach (Denny 1988) uses shallow-water celerity (the speed of the wave) in the equation for shallow-water waves:

$$\text{Wave-base} = (\text{Period} \times \text{Celerity})/2 \quad (2)$$

Both approaches yielded similar results, so we used the UCAR widget to calculate wave-bases.

We log-transformed the calculated wave-bases from each 20 min period to generate a cumulative frequency distribution and then used a LOESS curve fit ('loess' function in the R Stats package, R Core Team 2013) of this distribution to calculate the proportion of wave observations in which the bottom was impacted by wave energy (wave-base > station depth), which we used as our wave-base metric. We calculated wave-base using both 'average' and 'do-

minant' wave periods under 3 seasonal wave-regime scenarios: year-round wave energy continuously measured throughout the year, wave energy during summer months (April–September), and wave energy during winter months (October–March).

Analysis

We averaged all samples collected at different times at each station to avoid non-independence of temporal replicates in the analyses. To reduce the complexity of the benthic bivalve community and to facilitate statistical analysis in the face of co-varying species abundances, we converted biological community data into aggregate variables using ordination, with non-metric multidimensional scaling (MDS). Our MDS analyzed a Bray-Curtis distance matrix of square-root transformed community data using the metaMDS procedure in the package 've-gan' in R (R Core Team 2013).

Potential relationships between community composition and potential environmental drivers are not necessarily linear. Therefore, we first probed for candidate driver variables by testing for associations between physical variables and community composition using Spearman's rank correlations (r_s), which test for monotonic, but not necessarily linear, associations. Where multiple years of *in situ* physical measurements were made, we explored a full range of descriptors including means, maxima, minima, and temporal variance of environmental variables in our analyses, as extreme values or variability might have stronger effects on community structure than simple mean values. We then used a hierarchical non-linear regression approach to develop a model that best explained the distribution of benthic species while minimizing the chances of over-fitting, starting with the physical variable with the highest magnitude significant pairwise r_s. Because we suspected distinctly different relationships in communities regularly impacted by wave energy compared with those minimally affected by wave energy, we used breakpoint (piecewise) regression assuming a simple non-linear (exponential) function for each segment:

$$Y = \begin{cases} a_1(1 + b_1 X^{c_1}) & X \le d \\ a_1(1 + b_1 d^{c_1} + b_2(X - d)^{c_2}) & X > d \end{cases} \quad (3)$$

where Y is community composition and X is a physical driver of interest. Note that this model generates a continuous function with a very flexible form, which can include a single relationship across all values of the dependent variable, constant values, linear

relationships, and various sigmoidal, unimodal, accelerating, and decelerating relationships. We used the nonlinear regression procedure in SPSS to find parameter values that minimized the sum of the squared residual (SSR) across all data points. Parameters that did not contribute significantly to model fit as assessed by comparing the difference in SSR between full and nested parameter values using an F-test, were not included. Residuals from this model were then tested for the strongest association (r_s) to the remaining potential driver variables, and the model was refit after adding the variable with the highest $|r_s|$ to it using the same non-linear form and parameter removal procedure. The process was repeated until adding potential drivers did not significantly improve model fit. In our model exploration, we did not restrict parameter values that would give rise to a simpler linear or constant model (i.e. $c = 1$ or $b = 0$) that would have been chosen when the more complex forms failed to generate better fit. This approach was adopted because clear non-linear relationships were present, precluding the use of standard multiple linear regression methods.

RESULTS

Bivalve communities as a whole separated along an apparent depth gradient shown in both proportional and sample-standardized raw abundances (Fig. 2). Sample-standardized raw abundances showed a difference in number of individuals sampled between shallower and deeper water depths due to the numerically abundant families of Veneridae and Thyasiridae increasing with water depth (Fig. 2b). The increase in numbers of individuals sampled with depth occurred in both living and death assemblages. The shift in bivalve community composition with depth was also captured by MDS axis 1 (Fig. 3, stress = 0.119, 2 axes). The families Tellinidae, Pharidae, and Mytilidae drove the variation in multidimensional space, corresponding to negative values along MDS axis 1 (Fig. 4) whereas the families Veneridae and Thyasiridae and, to a lesser degree, Pandoridae and Nuculidae contributed positively (Fig. 4). Ordinated community data have less spread along the second axis. Negative values along the second axis were driven by the families Hiatellidae, Lasaeidae, and Thyasiridae, whereas the positive values were driven by Veneridae (Fig. 4). Ordinations also showed that modern living and historical death assemblages are not significantly different when plotted in correlation space along the first
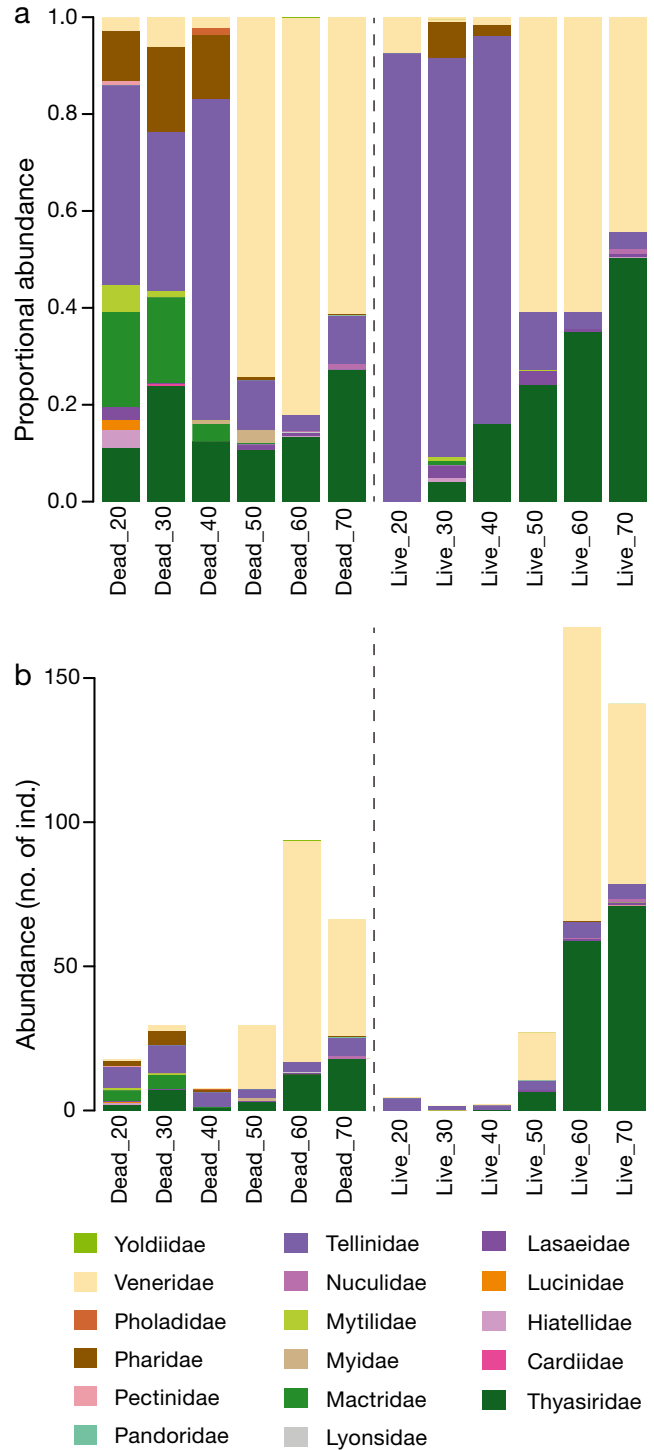

Fig. 2. Infaunal bivalve families across water depths from all samples. Dashed line separates death assemblage data from living assemblages sampled across the same water depths. (a) Proportional abundances show the shallow to deep shift at 40–50 m water depth in both living and dead compositional abundance. (b) Raw abundances (no. of ind.) show the same shift but also show the shift to the more numerically abundant families of Veneridae and Thyasiridae at 50, 60, and 70 m water depth. Data from Voorhies (2015)
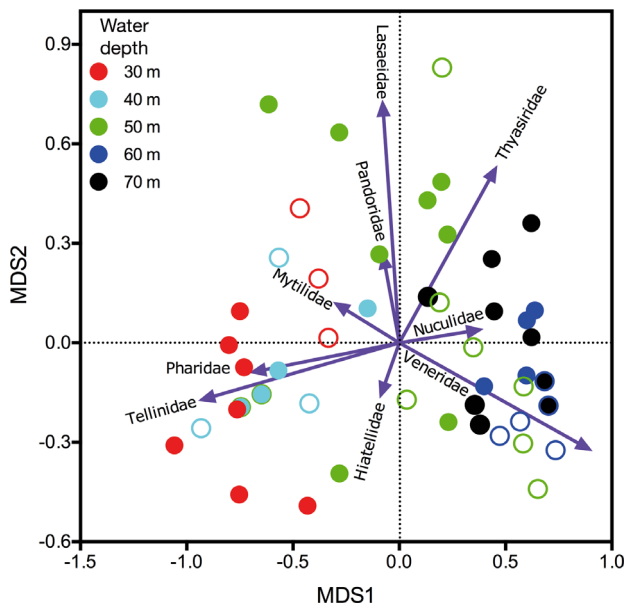
Fig. 3. Relationship of multi-dimensional scaling (MDS) axes derived from species composition data in pooled samples from each site and family composition. Vectors show molluscan bivalve families associated with ordinated community data. Length of family vectors represents the strength (r) of the correlation with each MDS axis. Solid circles are living assemblages and open circles are dead assemblages
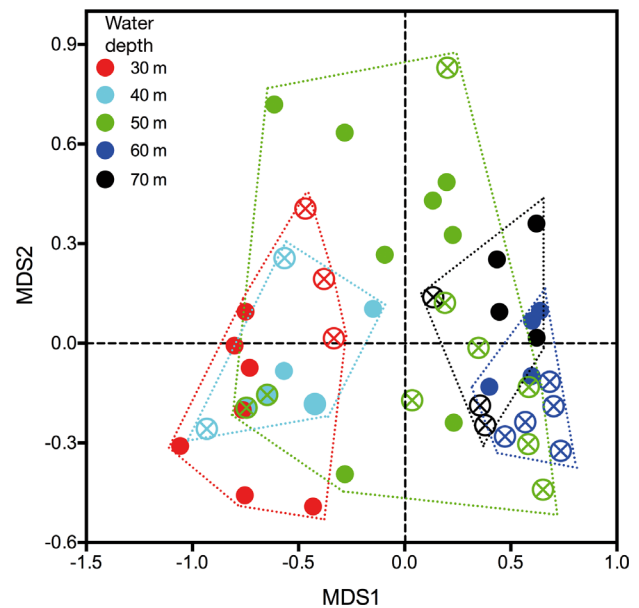

Fig. 4. Benthic communities described by non-metric multi-dimensional scaling (MDS) ordination space for both modern (solid circles = live) or historical samples (open circle with X = dead) across an onshore–offshore depth gradient (p = 0.281 for differences between live and dead data). Solid circles with overlapping X are samples where live and dead values were equal. Ordination results are based on Jaccard-Chao dissimilarity scores of square-root transformed abundances

axis (Fig. 3; MDS axis 1 ~ Live or Dead, F = 1.193, p = 0.281). The dominant MDS axis was significantly correlated with most environmental variables (Table 1) but associated most strongly with calculated winter wave energy expressed as wave-base (r_s = −0.92, p < 0.0001). The along-shore variability in all of the environmental variables except waves reduced the possible correlations with wave-base and allowed the discrimination of relationships to benthic community structure in our analyses. In contrast to

the dominant axis, MDS axis 2 was not significantly correlated with any of the environmental variables that we studied (all p > 0.15).

The relationship of the dominant MDS axis with wave-base (wave-base index, WBI) was distinctly non-linear, exhibiting a constant value at low energies, and then a sharp exponentially decaying shift at high wave energies (r^2 = 0.905; Fig. 5). This simplified relationship fit similarly to the full non-linear function we explored ($F_{2,24}$ = 1.83, p = 0.190). Mini-

Table 1. Spearman rank correlation coefficients among physical properties of sampling sites and community composition, summarized by multi-dimensional scaling axis 1 (MDS1). MDS2 (not shown) did not correlate with any physical property (p > 0.05). Correlations of physical properties with residuals from hierarchical non-linear (piecewise exponential) models including winter wave-base index (WBI) and minimum pH are also presented. Significant correlations (p < 0.05) are indicated in **bold**. DO: dissolved oxygen

|	% sand	Min. salinity	Min. % silt & clay	Med. chl a	Temperature	Min. DO	Min. pH	MDS1	Residual (WBI)	Residual (WBI, pH)
Winter wave-base	**−0.843**	**−0.813**	**0.754**	**0.766**	**0.778**	**0.523**	**0.401**	**−0.919**	–	–
% sand		**0.761**	**−0.824**	**−0.631**	**−0.748**	**−0.623**	−0.247	**0.766**	−0.010	0.025
Min. salinity			**−0.620**	**−0.581**	**−0.977**	**−0.436**	−0.100	**0.746**	0.073	0.115
Min. % silt & clay				**0.566**	**0.578**	**0.750**	0.255	**−0.707**	−0.067	−0.125
Med. chl a					**0.534**	**0.570**	**0.627**	**−0.701**	−0.262	−0.089
Temperature						0.342	−0.016	**−0.690**	−0.028	−0.120
Min. DO							0.332	**−0.504**	−0.017	0.037
Min. pH								**−0.448**	**−0.491**	–
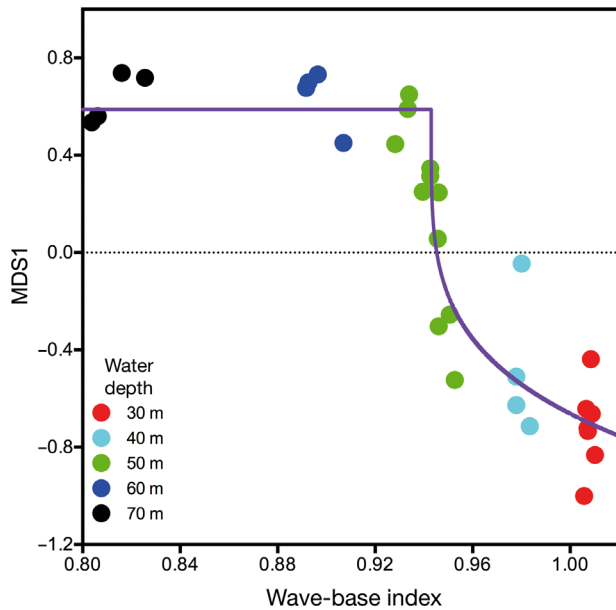
Fig. 5. Results of a break-point regression analysis exploring the relationship between community structure described as multi-dimensional scaling axis 1 (MDS1), and wave-base impact. Curve derived from least-squares, piece-wise, non-linear regression in the form of Eq. (3), following removal of uninformative terms
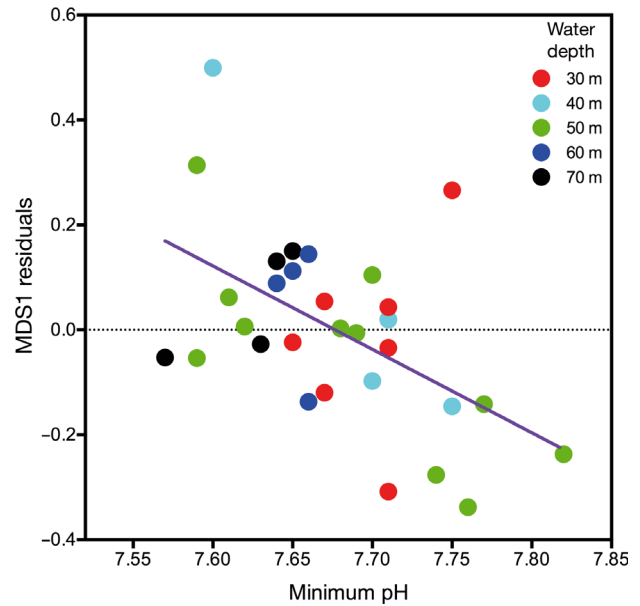

Fig. 6. Residual plot of minimum pH values versus the residual from the piece-wise non-linear regression with winter dominant waves (Fig. 5). Curve from least-squares non-linear regression is shown, which was parsimoniously described by a linear relationship. MDS1: multi-dimensional scaling axis 1

mum pH was most strongly associated with residual variation after accounting for the relationship with wave energy (Table 1, $r_s = -0.491$, Fig. 6), and a linear relationship with minimum pH was retained in the regression model ($r^2 = 0.927$, $F_{1,25} = 10.60$, p = 0.003). The model with a simple linear relationship to minimum pH fit as well as a model with a fully non-linear functional form ($F_{4,21} = 0.11$, p = 0.980). No further relationships with MDS axis 1 and the other environmental variables (temperature, dissolved oxygen, salinity, mean grain size, and percent silt/clay) were observed after accounting for wave energy and minimum pH. Hence our final relationship was:

$$Y = \begin{cases} 13.683 - 1.71\text{pH}_{min} & \text{WBI} \leq 0.943 \\ 13.683 - 2.353(\text{WBI} - 0.943)^{0.238} & \\ \quad - 1.71\text{pH}_{min} & \text{WBI} > 0.943 \end{cases} \quad (4)$$

DISCUSSION

Wave-base structuring of communities

We believe the results of our study point to a longstanding and persistent biological community structure characterized by the distinct separation of bivalve communities (both modern [living] and historical [dead]) at high and low wave energies. The longstanding nature of the shallow–deep pattern is

reflected by the death assemblages which we can reliably estimate to represent the natural baseline for living assemblages within the last century. Using death assemblages as a reliable source for this historical information is confirmed in our study by the lack of significant difference between the living and dead assemblages in our ordinations. Therefore, the shallow-deep pattern represented in this study is a key component of the environmental regime of the subtidal benthic community within the last century off Newport, Oregon.

Our results point to wave energy, particularly wave-base, as the strongest likely driver of community structure for infaunal bivalves both historically and in modern environmental regimes in this area. The relationships between benthic communities and temperature, dissolved oxygen, salinity, and percent silt/clay were significant but not as strongly associated with benthic community structure as wave-base (Table 1). These variables are all correlated with wave-base, and largely became non-significant once wave-base was accounted for using non-linear breakpoint regression.

In a high-energy environment like the shelf of Newport, Oregon, there is little fine sediment, a result of winnowing of small particles by wave energy. The organisms living in this environment of coarse shifting sand have to adapt to survival through either

rapid burial, if they are uprooted, or shell thickening to help prevent being uprooted in the first place (Stanley 1970a, Gaylord et al. 2001). Wave energy separates marine communities better adapted to higher energetic environments according to burial ability, shell thickness, and body size. Biological information from families associated with MDS axis 1 support the wave-base interpretation (Fig. 5). Above the wave-base, mixed deposit feeders of the family Tellinidae and sub-surface deposit feeders of the family Pharidae strongly drive ordinated marine community data (Fig. 5). The family Tellinidae has a characteristic elongated shape and long siphons that support the ability to rapidly re-bury after the possible disturbance events caused by winter storm wave-base (Stanley 1970b). Additionally, the family Pharidae is represented by the razor clam *Siliqua patula*, which can bury itself quickly. The family Mytilidae is also associated with the shallow-water communities and has the distinctly wave-related functional characteristic of uniquely evolved byssal threads that are strong enough to resist wave shear (Qin & Buehler 2013, Carrington et al. 2015). The shallow-water community above the wave-base may also experience different dissolved oxygen and nutrient conditions than deep-water communities due to wave-driven vertical mixing (Shields et al. 2011). Deeper communities experiencing low wave energy were driven in ordination space by the smaller-bodied and thin-shelled *Axinopsida serricata* (Thyasiridae) and *Nutricola lordi* (Veneridae). These deeper communities consisted of suspension feeders that live just below the surface. In contrast, in higher-energy shallow-water communities, suspension feeders and deposit feeders live deeper in the more unstable and shifting sediment (Stanley 1970a). These life positional patterns were also reflected in methodological issues that arose while sampling these assemblages: shallow-water species were difficult to sample because of speed of burial or depth at which they existed in the substratum (the sampling device penetrates only 6–10 cm, whereas deposit feeders easily exist as deep as 20–30 cm; see Voorhies 2015). Deep-water communities were sampled in high abundances because their life position was so close to the surface (Stanley 1970a,b).

The pattern of zonation reported here is similar to results observed in the North Sea. Armonies et al. (2014) analyzed species composition from a time series of benthic samples spanning 2 to 40 m depth, noted a distinct break in abundance and taxon richness between 20 and 30 m, and found that annual variation in the depth of this break correlated with variation in the frequency of waves >3 m. Our study extends these results by explicitly modeling species composition patterns as a non-linear function of the distribution of winter wave forces expected to directly interact with the benthos, which did not require an arbitrary cutoff choice of a particular critical surface wave size. Additionally, we considered multiple potential drivers for the patterns we observed and identified a parsimonious multi-driver model that was most consistent with the patterns while taking steps to avoid over-fitting. The difference in the location of the break between communities with depth between the 2 studies could be explained by several factors. First, the studies differ in the range of depths surveyed, such that a 50 m break could not be observed by Armonies et al. (2014), and a 20 m break could not be detected in our sampling. Taken together, these studies may argue for extended sampling from the surf zone to depths regularly below the dominant winter wave-base. Second, the criteria for identifying a break differed between studies: breaks in abundance versus in taxon composition may not necessarily correspond to each other. Third, the differences might largely arise because of differences in wave energy impacting the locales, with larger, longer-period waves more regularly generated in the North Pacific compared to the North Sea.

The structuring of soft-sediment subtidal communities by wave energy indicated in this study has parallels to studies that show the effects of waves on intertidal species (Dayton 1971, Paine & Levin 1981) and in areas impacted directly by surf (McLachlan et al. 1984, Defeo & McLachlan 2005), but wave-base is usually not emphasized as a structuring force in off-shore subtidal soft-sediment communities. On rocky shores, species traits are clearly shaped by wave energy. Many biomechanical studies of macroalgae constantly reveal an ability to both resist the damage caused by wave impingement and stretch/move in response to changing wave energy (Harder et al. 2006, Gaylord et al. 2008). Sea star morphology responds to high or low wave energy environments that affect the ability to hold on and resist damage or removal from their position (Hayne & Palmer 2013). Sea urchins reduce the chronic stress of wave energy in an exposed environment by being physically adapted to resist dislodgment even for lower thresholds for wave action than theoretically expected in an exposed environment, meaning they are prepared to hold on before the higher wave action starts (Siddon & Witman 2003, Tuya et al. 2007). There is even evidence for optimal sizes for invertebrates existing under different wave energy regimes in the intertidal

to maximize their ability to withstand the physical environment and their opportunity to achieve greater reproductive potential at larger sizes (Sebens 2002). Intertidal sponges vary the production of energetically costly stiffer and stronger tissues based on the wave energy of their environment even when moved to an environment with a different wave regime (Palumbi 1984). The bivalves studied here appear to have partitioned their habitat in a similar way to the previously observed adaptations of other groups, albeit in the intertidal.

Harvesting is a ubiquitous and intensifying feature of marine ecosystems that has clear impacts on the assemblage of fish species in the water column and can also impact benthic invertebrate communities in many cases (Durán & Castilla 1989, Jackson et al. 2001, Myers & Worm 2003). Although our analysis did not directly assess harvesting, we do not believe that it is a driver of the spatial patterns we documented for several reasons. First, our study was focused on the relative taxonomic composition of benthic bivalves in subtidal habitats. Although there is selective harvesting of some bivalves in intertidal habitats, large-scale commercial harvest of bivalves does not occur in our study area, so direct impacts of harvesting are unlikely. Second, it is possible that intensified harvesting of finfish has indirect effects on the benthic community through food web changes or the physical effects of some fishing methods (Hiddink et al. 2017). By incorporating death assemblage analysis in the study, we can more carefully probe the possibility of indirect fishing effects. As fishing intensifies through time, we would expect strongly divergent signals on currently living assemblages and the death assemblages that include communities less impacted by fishing in the past. Instead we find similar spatial patterns in taxonomic composition in both living and dead assemblages of bivalves, indicating that the process generating spatial variation in relative species composition has been a consistent feature of this system through time.

Possible connections to anthropogenic change

Potential structuring of subtidal benthic communities through wave-base is notable because of the proposed human harvest of wave energy. Emerging marine renewable energy initiatives (MREIs) seek to collect energy from waves in high-energy environments like the Oregon coast. There are a variety of proposed wave energy converters (WECs), but the actual biological and ecological impacts of wave energy withdrawal have not been clearly demonstrated (Shields et al. 2011). In classifying the wave resources in Oregon and southwest Washington, García-Medina et al. (2014) used numerical models to characterize the greatest areas of wave energy based on wave characteristics measured by wave buoys. Off the coast of Newport, using the same NOAA buoy used in our study, García-Medina et al. (2014) identified the greatest concentration of energy at the 50 m water depth contour and in the winter months. This abundant resource derives from the same factor that we have identified as a potentially major driving factor for subtidal benthic communities off Newport.

The data from our study suggest that the 2 standing communities on subtidal benthos of the Oregon coast could represent before and after scenarios for the removal of wave energy from the noted 50 m depth contour. Before wave energy is removed, we have the shallow-water community, a biologically and functionally diverse fauna relative to that which exists below the winter storm wave-base. The removal of energy would be predicted to facilitate migration of the deep-water communities shoreward as the wave-base becomes shallower and no longer imposes disturbance on to the depths it did previously. The biological relationships that we found (Fig. 5) could foreshadow the degree and direction of faunal change that would occur with a specified degree of wave energy withdrawal from the system. The direct measurement of the change in wave period lengths caused by WECs could be translated into wave-base changes over seasons and years.

While extraction effects will depend on designs and deployment densities that are developed in the future, WECs are expected to reduce wave heights because they are 'tuned' to extract energy from swell or low-frequency wind waves, so the energy, and thus the height, of these long waves will be reduced (Shields et al. 2011). A technical memorandum by Pacific Gas and Electric (PG&E) suggests that wave heights in northern California will only change by 5–12 cm (Kingery 2009), but changes in the wave period length are more important than changes in wave height in determining energy delivery to the benthos. The preferred extraction choice for power and efficiency is from waves of period length 7.5 s and heights of up to 3.8 m (Kingery 2009), resulting in a wavelength of 87.75 m and a wave-base of 43.88 m, very similar to the breakpoint identified in our study. Lenee-Bluhm et al. (2011) also calculated sea state changes for wave energy extraction in Oregon, and identified the greatest contribution of wave

energy to arise from wave periods between 8 and 12 s, a range very close to the one we identified here as important for structuring benthic communities (range 3.85–21.05 s, median 12.12 s). Lenee-Bluhm et al. (2011) emphasized that these sea states are not the most common for the Oregon coast, but they are key for understanding the best wave energy available and need to be considered for the survival and reliability of wave energy buoys. If wave-base changes are tracked, WEC's can be tuned to maintain sufficient wave energy in the environment to minimize impacts to biological communities (Shields et al. 2011). Furthermore, the possibility of WECs going into self-protection mode during storms means that the most important sources of benthic wave energy input, winter storms, might not be affected (Lenee-Bluhm et al. 2011). The data presented in this study indicate possible mechanisms for impact on marine benthic communities that should be considered when developing or deploying WECs that will result in changes to the local wave energy regime.

The only other significant relationship between benthic community structure and an environmental variable was a weak one with minimum pH. Data suggesting that minimum pH is a secondary driver of subtidal marine bivalve communities is noteworthy in the context of ongoing observations of changing carbonate chemistry in the oceans due to increasing atmospheric carbon dioxide (CO_2) levels (Orr et al. 2005, Kelypas et al. 2006, Wootton et al. 2008, Doney et al. 2009, Feely et al. 2009). Ocean acidification occurs when rising atmospheric CO_2 causes wholesale shifts in seawater carbonate chemistry resulting in reduced ocean pH. In the eastern Pacific in particular, pH has dropped unexpectedly rapidly in the past decade and a half (Wootton et al. 2008, Feely et al. 2009, Pfister et al. 2011, Wootton & Pfister 2012), and this decline has been linked to shifts in benthic organism performance (Wootton et al. 2008, Barton et al. 2012). There is an urgent need for data on biological sensitivity to pH changes to predict species responses to ocean acidification (Kroeker et al. 2011, Kelly & Hofmann 2013). Minimum pH is relevant because previous studies have shown reduced growth rates, reduced calcification rates, and changes in protein synthesis for mollusks when elevated levels of CO_2 occur in the environment (Widdicombe & Spicer 2008, Doney et al. 2009, Kroeker et al. 2011). Our data are consistent with these observations in that community structure shifted toward species with lower calcification requirements as minimum pH declined. Shell thickness was also linked to wave energy, however, raising the possibility that declin-

ing pH will negatively affect performance under more turbulent conditions if shell calcification is compromised.

CONCLUSIONS

Investigating the relationship between benthic communities and environmental conditions leads to insights about the potential role of wave energy as a dominant physical driver of community structure in offshore benthic soft sediments. Biological communities have adjusted to the physical disturbances, water flow, and sediment transport caused by winter storm wave-base in both modern and historical settings. However, minimum pH may be a secondary driver of benthic community structure and is important to note due to increased threats from ocean acidification. Our data suggest that the current development of offshore wave energy extraction may affect benthic communities through numerous mechanisms. Therefore, these potential effects merit further study. Extracting wave energy may disturb sediment transport, larval fertilization and dispersal, feeding behaviors and predatory behaviors throughout the benthic ecosystem. Fortunately, the potential effects of wave energy extraction can be measured and possibly mitigated using the data developed by this study. By considering shallower and deeper communities as a before and after scenario of wave energy input into the ecosystem, a theoretical relationship between the amount of wave energy extracted and possible spatial shifts in the marine benthic community can be developed. The exact mechanics of this theoretical relationship will require further work and information on wave energy extraction systems as they develop, but could provide useful predictions about how to design and deploy wave energy devices.

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