

AN ABSTRACT OF THE THESIS OF

Stephanie Grace Labou for the degree of Master of Science in Marine Resource Management presented on August 27, 2013

Title: Physical Factors Affecting the Spatial Distribution of Infaunal Bivalve Assemblages and Species along the Continental Shelf of the Pacific Northwest

Abstract approved:

Sarah K. Henkel

The spatial distribution and abundance patterns of benthic infauna result from interactions with a host of environmental variables including sediment characteristics (percent silt-clay, grain size, total organic carbon), depth, temperature, and dissolved oxygen. This thesis focuses on the association of bivalve assemblages and species with potentially influential environmental variables along the continental shelf of the Pacific Northwest. Data for this research comes from two surveys funded by the Bureau of Ocean Energy Management (BOEM), conducted in 2010 and 2012. Across the six sites from northern California to Washington sampled in 2010, eight distinct bivalve assemblages were identified using non-metric multidimensional scaling and SIMPER analysis from the ecological software PRIMER 6. Environmental characteristics associated with each assemblage were determined. Percent silt-clay was the most useful environmental variable for distinguishing bivalve assemblages by habitat, with major differences between sandy and silty areas. Within predominantly sandy habitats, changes from one bivalve assemblage to another were associated with small differences in the

remaining percentage of silt-clay in the sediment, whereas within predominantly silty habitats, changes in assemblage were associated with changes in depth, rather than exact percent silt-clay. Sediment was also associated, to varying extent, with the distributions of the most abundant bivalve species observed – *Axinopsida serricata*, *Nutricula lordi*, *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis*. While *Axinopsida serricata* was a soft-sediment generalist, *Nutricula lordi* was a specialist, restricted to very sandy (<1-2% silt-clay) sediment. High abundances of *Ennucula tenuis* were associated with specific combinations of depth, sediment type, and DO, while distribution of *Acila castrensis* was most associated with depth, sediment type, and TOC. *Macoma carlottensis*, which can function as either a suspension or deposit feeder, displayed the highest abundances in sediment with an equal mix of silt/sand and high TOC. Except for *Nutricula lordi*, biotic interactions or “missing” environmental variables not assessed here are likely at least as influential in structuring the spatial distribution of these species. These results can be used to inform the selection of appropriate control sites for assessing wave energy device impacts on benthic infauna.

© Copyright by Stephanie Grace Labou

August 27, 2013

All Rights Reserved

Physical Factors Affecting the Spatial Distribution of Infaunal Bivalve Assemblages and
Species along the Continental Shelf of the Pacific Northwest

by

Stephanie Grace Labou

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented August 27, 2013

Commencement June 2014

Master of Science thesis of Stephanie Grace Labou presented on August 27, 2013.

APPROVED:

Major Professor, representing Marine Resource Management

Dean of the College of Earth, Ocean, and Atmospheric Sciences

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Stephanie Grace Labou, Author

ACKNOWLEDGEMENTS

I would like to express my gratitude to my advisor, Dr. Sarah Henkel, my committee members Dr. Walt Nelson and Dr. George Waldbusser, and Dr. Virginia Lesser, who served as my graduate council representative. I would especially like to thank Dr. Nelson for allowing me to use the wonderful resources at the EPA and everyone at the EPA who kindly took the time to meet with me and discuss my data. I would also like to thank the Northwest National Marine Renewable Energy Center (NNMREC) for giving me many opportunities to discuss my work with the public.

I would like to express my sincere appreciation to the Bureau of Ocean Energy Management (BOEM) for funding this research. I was also fortunate to receive the Laurel Scholarship and the Mamie L. Markham First Year Student Award to support my work.

I would like to acknowledge and thank the researchers and crew of the 2010 and 2012 BOEM surveys, as well as everyone in the Henkel lab who pitched in for the 2012 survey. Special thanks to Kristin Politano, lab manager extraordinaire, for all the hard work she put in with the BOEM dataset before I arrived at OSU.

I would be remiss if I did not express my appreciation for the OSU Statistics Consulting program for their advice on my data; Dr. Charlotte Wickham, for her assistance with R coding; and Dr. Yuan Jiang, for his input on negative binomial modeling. Many thanks as well to the CEOAS students who, when they heard I was teaching myself statistical modeling, offered bits of advice and lots of enthusiasm for my work.

I would also like to sincerely thank OSU Libraries. The day I discovered I could request old print articles (not available online) to be scanned and e-mailed to me was the happiest day of my thesis writing process.

Finally, I would like to thank the friends and family members, especially my parents, who provided me with invaluable emotional support (and scientific advice!) during this entire process.

TABLE OF CONTENTS

	<u>Page</u>
1. INTRODUCTION	1
1.1 Background	1
1.2 Research goals	5
2. MATERIALS AND METHODS.....	7
2.1. Data collection.....	7
2.1.1. BOEM 2010 regional survey	7
2.1.2. BOEM 2012 additional survey sites	8
2.2. Data analysis and visualization	9
2.2.1 Comparison among sites.....	9
2.2.2. Comparison among stations.....	10
2.2.3. Dominant bivalve species	11
2.2.3.1. Exploratory analysis.....	11
2.2.3.2. Species' models	12
2.2.3.2.1. Explanatory variables of interest.....	12
2.2.3.2.2. Correlation matrix of explanatory variables.....	13
2.2.3.2.3. Principal component analysis.....	13
2.2.3.2.4. Variance inflation factor.....	15
2.2.3.3. Negative binomial generalized linear models	16
3. RESULTS	24
3.1. Summary of total benthic community of sites	24
3.1.1. North San Andreas Fault (NSAF)	24
3.1.2. Eureka.....	24

TABLE OF CONTENTS (Continued)

	<u>Page</u>
3.1.3. Coquille *	25
3.1.4. Siltcoos	25
3.1.5. Cape Perpetua *	25
3.1.6. Newport	25
3.1.7. Nehalem	26
3.1.8. Grays Harbor	26
3.2. Summary of differences among sites	26
3.2.1. Physical and environmental variables	26
3.2.2. Bivalve assemblages of sites	28
3.3.3. Bivalve relationship with sediment	28
3.3.4. BIO-ENV analysis	29
3.3. Comparison among stations (bivalve assemblages)	29
3.3.1. nMDS and CLUSTER analysis	29
3.3.2. SIMPER analysis	30
3.4. Dominant species	31
3.4.1. Exploratory analysis	31
3.4.1.1. <i>Axinopsida serricata</i>	32
3.4.1.2. <i>Nutricula lordi</i>	33
3.4.1.3. <i>Ennucula tenuis</i>	33
3.4.1.4. <i>Macoma carlottensis</i>	34
3.4.1.5. <i>Acila castrensis</i>	35
3.4.2. Species models	36

TABLE OF CONTENTS (Continued)

	<u>Page</u>
4. DISCUSSION	62
4.1. Sediment type and bivalve assemblages	62
4.2. Latitude and bivalve richness	63
4.4. Dominant bivalve species.....	64
4.4.1. <i>Axinopsida serricata</i>	64
4.4.2. <i>Nutricula lordi</i>	67
4.4.3. <i>Ennucula tenuis</i>	70
4.4.4. <i>Macoma carlottensis</i>	71
4.4.5. <i>Acila castrensis</i>	73
4.3 Variables for individual species versus bivalve assemblages	74
4.5 Limits to models and analysis	76
5. RESEARCH SIGNIFICANCE.....	80
6. CONCLUSION.....	84
BIBLIOGRAPHY	86
APPENDIX.....	95
Results	96
Negative binomial model for <i>Nutricula lordi</i>	96

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1. Map of the 2010 and 2012 BOEM sample stations	18
2. The five most abundant bivalve species from the 2010 BOEM survey	19
3. Scatterplots of selected environmental variables in relation to one another.....	20
4. Proportion of major phyla for the BOEM sites.....	39
5. Proportion of major bivalve species across the BOEM sites	40
6. Boxplots of percent silt-clay of top core sediment of the six sites sampled in 2010....	44
7. Boxplots of percent silt-clay of mid-core sediment by site	45
8. Boxplots of total bivalve abundance by site	46
9. Non-metric multidimensional scaled plot for bivalves from the six 2010 sites	47
10. Dendrogram (from CLUSTER analysis) of stations by bivalve assemblage	48
11. Frequency occurrence histograms of <i>Axinopsida serricata</i> presence based on depth, latitude, and percent silt-clay of sediment	51
12. Scatterplots of <i>Axinopsida serricata</i> abundance in relation to environmental variables.	52
13. Frequency occurrence histograms of <i>Nutricola lordi</i> presence based on depth, latitude, and percent silt-clay of sediment	53
14. Scatterplots of <i>Nutricola lordi</i> abundance in relation to environmental variables	54
15. Frequency occurrence histograms of <i>Ennucula tenuis</i> presence based on depth, latitude, and percent silt-clay of sediment	55
16. Scatterplots of <i>Ennucula tenuis</i> abundance in relation to environmental variables ...	56

LIST OF FIGURES (Continued)

<u>Figure</u>	<u>Page</u>
17. Frequency occurrence histograms of <i>Macoma carlottensis</i> presence based on depth, latitude, and percent silt-clay of sediment	57
18. Scatterplots of <i>Macoma carlottensis</i> abundance in relation to environmental variables	58
19. Frequency occurrence histograms of <i>Acila castrensis</i> presence based on depth, latitude, and percent silt-clay of sediment	59
20. Scatterplots of <i>Acila castrensis</i> abundance in relation to environmental variables....	60

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1. Correlation matrix of environmental variables of interest	21
2. Standard deviation, proportion of variance, and cumulative proportion of variance explained for each of the principal components.	22
3. Coefficients for each environmental variable by principal component.	22
4. Variance inflation factor (VIF) for each variable using negative binomial models for <i>Axinopsida serricata</i>	23
5. Summary of bivalve richness, diversity, and evenness (average with standard deviation where appropriate) across all eight sampled BOEM sites	41
6. Averages and standard deviation of environmental variables for each site.....	42
7. SIMPER analysis results for bivalve groups	49
8. R^2 values for linear and quadratic regression of species abundance (from 2010 sites) on environmental variables	50
9. Negative binomial models for the most abundant bivalve species	61

1. INTRODUCTION

1.1 Background

The life cycle of most benthic invertebrates is comprised of a pelagic larval stage, followed by benthic juvenile and adult stages (Thorson 1950). The importance of sediment for benthic species begins early on in the life cycle. Pelagic larvae use a variety of mechanisms in order to navigate to potentially favorable sediment (whether defined by grain size or surface complexity) for settlement, including negative phototaxis, positive geotaxis, and pressure (depth) sensitivity (Gray 1974).

For larvae which actively select habitat upon which to settle (e.g. Woodin 1986, Butman 1987), larvae may reject the sediment based on negative settlement cues or accept the sediment as suitable habitat based on positive cues (Woodin 1991). Positive settlement cues include: presence of biofilms (Hadfield 2011); presence of certain chemicals (Pawlik 1992, Alfaro et al. 2011), sometimes released by adult conspecifics and dissolved in the water column (Tamburri et al. 1996); and increased carbonate saturation state of surface sediments (Green et al. 2013), among others. While there is a large body of literature supporting active habitat selection by larvae, active selection does not necessarily exclude passive deposition as a common settlement mechanism, albeit one working on a separate spatial and temporal scale (Butman 1987). For instance, active selection can be a function of conditions faced by larvae: Butman et al. (1988) found that the bivalve *Mercenaria mercenaria* displays active substrate selection in still water, but no substrate preference in a flume flow, possibly because larvae were more easily resuspended in the flow and therefore behaved more like passive particles. Furthermore, even if habitat is favorable for bivalve larvae, successful settlement is not guaranteed. As noted, flow conditions can affect larval choice of habitat and settlement (Snelgrove et al. 1993, Abelson and Denny 1997, Snelgrove et al. 1998) and in some cases, larvae may be caught by feeding currents of adult bivalves and filtered from the water column (Troost et al. 2008), which can remove a high percentage of potential recruits (Porri et al. 2008).

Sediment selection, successful settlement, and survival of larvae is also related to species' feeding guild. While suspension feeders filter particulate matter from the water column, deposit feeders ingest sediment and the organic matter it contains (Dame 2011); in general, suspension feeders tend to be found in sandy sediments, while deposit feeders are more abundant in silt/clay/mud sediments (Rhoades and Young 1970). Rhoades and Young (1970) noted that deposit feeders reworked the top centimeters of sediment, producing an unstable, easily resuspended, habitat and hypothesized that the uncompacted surface subsequently inhibited suspension feeders by (1) clogging filtering structures and (2) burying newly settled larvae (Rhoades and Young 1970). While the exclusion of suspension feeders from soft mud areas may be due to the unstable, reworked sediment, Sanders (1958) hypothesized that deposit feeders were most often observed in fine sediments because clay environments tend to be organic-rich and therefore provide a rich food source for deposit feeders.

In addition to being an important settlement factor, sediment type also affects post-settlement activities. For example, Nel et al. (2001) found grain size and sediment sorting affected burrowing time for the bivalves *Donax serra* and *Donax sordidus*, with fastest burrowing time observed in fine/medium sediment and burrowing time of *Donax serra* faster in well-sorted sediments than moderately sorted sediments. The relationship between burrowing and sediment can be size-dependent: Huz et al. (2002) found that for *Donax trunculus*, smaller individuals burrowed faster in medium/coarse sands whereas larger individuals burrowed faster in fine/medium sands. Furthermore, for some species, sediment type and burrowing is related to growth and survival: Huz et al. (2002) found that metabolism and growth rate of *Donax trunculus* were highest in medium/coarse sediment and de Goeij and Luttikhuisen (1998) noted that deeper buried *Macoma balthica* displayed smaller body mass and decreased survival compared to shallower buried individuals.

Although sediment is an important environmental factor associated with bivalve distribution, sediment characteristics are not the only abiotic, environmental factors

encountered by benthic infauna. Bivalves are poikilotherms, or “cold blooded” animals, so their body temperatures are greatly influenced by the temperature of the surrounding environment (Dame 2011) which consists not only of sediment, but also the overlying water column. Most marine bivalves are found within a temperature range of -3°C to 44°C (Vernberg and Vernberg 1972) and can become acclimated to new temperature conditions (Crisp and Ritz 1967), such as those that might occur with seasonal changes (Dame 2011).

In general, larval and reproductive stages tend to be the most sensitive to temperature (Dame 2011). The effect of temperature on growth rate is best represented by a performance curve (Butler 1953, see also Odum et al. 1979): increases in temperature are associated with increased growth up to an optimal temperature, above which decreased growth rate occurs. The same is true for development rate: higher temperatures correspond to quicker development time of planktonic larvae (Hoegh-Guldberg and Pearse 1995), but higher temperatures can also lead to a decline in instantaneous survival rates of larvae (Drent 2002). Once populations are established, temperature can affect further recruitment via decreased reproductive output and an earlier onset of spawning (Philippart et al. 2003).

Stress responses to increased temperature can also be reflected in metabolism (e.g. Anestis et al. 2007) and respiration (e.g. Dye 1979). Responses to heat stress are species-specific. For example, Kennedy and Mihursky (1972) found that among the bivalves *Macoma balthica*, *Mulinia lateralis*, and *Mya arenaria*, respiration rates of *Macoma balthica* were the least impacted by high or low temperature stress. Furthermore, within a species, responses to increased temperature differed between “old” and “young” age classes, with “older” *Mya arenaria* displaying greater sensitivity to increased temperatures (Kennedy and Mihursky 1972). Stress responses can also manifest as changes in behavior such as changes in valve opening and closure (Anestis et al. 2007), burrowing rate (Savage 1976), and lateral cilia beat frequency (Jørgensen and Ockelmann 1991).

Changes in physiological functioning and behavior in bivalves can result from low dissolved oxygen (DO) as well as changes in temperature. The defined threshold for hypoxic conditions is 1.4 ml/L of oxygen (Rabalais et al. 2010), but the exact “low” threshold where effects are observed varies by species (Rosenberg et al. 1991). Early life stages can be affected by low DO (Imabayashi 1986), with effect of DO on survival of settled individuals dependent upon the redox state of the sediment (Nilsson and Rosenberg 1994). Post-settlement, low concentrations of DO are associated with changes in metabolism and decreased burial depth of bivalves (Lee et al. 2012), although some species’ burrowing behavior is quite robust to changes in DO (Savage 1976). For species such as *Macoma balthica*, which manifest behavioral changes in response to low DO, decreased burial depth can result in increased predation pressure (Long et al. 2008). Physiological changes can also occur: shell deformation in *Macoma balthica* is associated with low DO concentrations (Sokołowski et al. 2008).

The environmental variables discussed above – sediment (grain size, percent fine sediment, organic content), temperature, and dissolved oxygen – affect the settlement, growth, and survival of bivalves and therefore influence the spatial distribution and abundance patterns of bivalve species. The same suite of environmental variables is also used to describe and differentiate whole benthic assemblages. For instance, multiple studies (Weston 1988, Hoey et al. 2004, Jayaraj et al. 2008, Labrune et al. 2008) have found significant associations between macrofaunal composition of soft-bottom benthic communities and sediment characteristics (percent silt-clay, organic carbon, grain size). Other studies (Cerame-Vivas and Gray 1966, Cimberg et al. 1993, Carroll and Ambrose 2012) have found that benthic assemblages are associated with water temperature and dissolved oxygen. Still other surveys (Hyland et al. 1991, Oug 1998, Bergen et al. 2001) have noted that differences in benthic assemblages are most related to differences in depth.

As with species and assemblage level analysis, biodiversity and species richness patterns are often discussed in terms of environmental factors. Latitude is often used as

the predictive factor since it incorporates a variety of environmental and physical variables. Latitudinal trends in species diversity (richness) are in general well documented and well accepted, with diversity highest at the tropics and decreasing towards the poles (Fischer 1960, Gaston 1996, Willig et al. 2003, Hillebrand 2004). However, marine infauna present a taxonomic area where this gradient is not as widely described. Thorson (1957) argued that the latitudinal gradient was not reflected in marine infauna because of the burrowing nature of species in soft bottom habitats: unlike epifauna, infauna were sheltered from large scale latitudinal variations in environmental variables and infaunal species richness was therefore independent of latitude. A decade later, Sanders (1968) concluded that species richness in marine soft sediments displayed gradients in relation to both latitude and depth, with greater richness in the tropics and deep-sea areas compared to polar and shallow areas, respectively. More recently, Roy et al. (2000) found that marine bivalves, including infaunal bivalves, display a strong latitudinal gradient in species richness, with greater richness in the tropics.

1.2 Research goals

This thesis seeks to address precisely which physical, environmental factors are most associated with the spatial distribution of infaunal bivalve assemblages and selected individual bivalve species along the continental shelf of the Pacific Northwest. To that end, this research has two main goals: (1) describe the spatial variation of bivalve assemblages along the shelf and define typical habitat associated with the assemblages, and (2) assess species-specific relationships with potentially influential environmental variables and characterize variability in species abundance attributable to environmental factors. Additionally, latitudinal trends in bivalve richness are briefly discussed.

I hypothesize that the observed spatial variation in bivalves – at both the assemblage and species level – along the continental shelf is largely due to differences in sediment characteristics. I anticipate that, on a species level, differences in temperature and DO will assist in explaining differences in abundance not adequately accounted for

by differences in sediment characteristics. Additionally, the amount of variability unexplained by environmental factors should indicate the extent to which biotic factors (not addressed here) play a role. In terms of bivalve richness, some natural variations within the latitudinal range sampled are expected, with diversity of bivalves anticipated to be higher at southern sites than northern sites.

2. MATERIALS AND METHODS

2.1. Data collection

2.1.1. BOEM 2010 regional survey

In 2010, the Bureau of Ocean Energy Management (BOEM) funded benthic surveys conducted by the Northwest National Marine Renewable Energy Center (NNMREC) Benthic Lab at the Oregon State University Hatfield Marine Science Center. The 118 BOEM sample stations were grouped into six distinct sites from northern California to Washington. From south to north, the sites were identified by their closest onshore town or other distinguishing feature: North San Andreas Fault (NSAF, n=21), Eureka (n=20), Siltcoos (n=19), Newport (n=22), Nehalem (n=22), and Grays Harbor (n=14) (Figure 1). Sites were stratified by depth bin and stations were randomly assigned within each depth bin. Therefore, the depth most common across the six sites, based on bathymetry, received the most stations. The sites were sampled between August 24 and October 18, 2010.

At each station, a CTD cast collected data about salinity, fluorescence, temperature, and dissolved oxygen (DO). Although data was collected for the entire water column, only temperature and DO values from as close as possible to the sediment interface were used for further analysis. Benthic cores of 0.1 m² were retrieved using a Gray-O'Hare box core. Two subsamples of sediment – from the top and middle sections of the core – were collected and later used to determine percent silt-clay of sediment and median grain size (MGS). The mid-core sample was also used to determine percent total organic carbon (TOC) and total nitrogen. The remainder of the core was then sieved through a 1.0 mm mesh and retained macrofauna were preserved in 5% formalin. Upon return to the laboratory, fauna were transferred to 70% ethanol. Only organisms which were living at the time of the core (i.e. the live assemblage) were considered for this thesis. In the laboratory, specimens were sorted into live and dead assemblages (whole

organism versus shell hash) and live assemblage specimens were then sorted by phylum, and identified to the lowest possible taxon, which was usually species level.

For grain size analysis, a portion (30 g) of the sediment subsample was washed with a 30% hydrogen peroxide (H_2O_2) solution in order to remove organic material and deflocculated with a 0.05% sodium hexametaphosphate (SHMP) solution. Subsamples were then run through a Beckman Coulter LS 13 320 Laser Diffraction Particle Size Analyzer, using the Fraunhofer optical model. The Wentworth scale (Wentworth 1922) was used when describing grain size categories. A Carlo Erba NA1500 analyzer was used for TOC and nitrogen analysis. Acetanilide was used as the standard reference material with known percentages of carbon and nitrogen (71.09% and 10.34%, respectively). Analysis was conducted following the methods of Verardo et al. (1990). Total nitrogen values were obtained, but were barely above detection levels and so are not discussed further here.

The CTD used during the 2010 BOEM survey was not equipped with a pH meter. In certain cases, pH may be calculated from water column variables; however, there is not currently a robust equation to calculate pH for Pacific Northwest shelf waters without using aragonite saturation data (Laurie Juranek, personal communication). Since the necessary data was not collected, pH values were not calculated for the BOEM stations and pH is not discussed further here.

2.1.2. BOEM 2012 additional survey sites

In 2012, BOEM funded sampling of two additional sites to fill in latitudinal gaps: Coquille (n=15) and Cape Perpetua (n=20) (Figure 1). These sites were sampled using the same methods described above with one difference: in 2012, only one sediment subsample (from the middle of the core) was used to determine percent silt-clay and median grain size. The two sites in 2012 were sampled between August 30 and October 5, which is considered the same sampling “season” as the 2010 survey.

Because there isn't equivalent 2010 data for these two sites, data from Coquille and Cape Perpetua are used here strictly as qualitative checks of conclusions based on the 2010 data. For example, data from these sites was not included in PRIMER analysis or species models (described below) because there was no way to account for the potential temporal change in communities between 2010 and 2012; using the data would have induced uncertainty in the output. However, because Coquille and Cape Perpetua represent sediment types which were undersampled during the 2010 survey, the data are used to qualitatively corroborate observed trends for species found primarily in these habitats. Therefore, taxonomic composition (community level and bivalve level) along with physical dimensions of sites are reported. In results, figures, and tables, Coquille and Cape Perpetua sites are marked with an asterisk (*) to emphasize the temporal difference between these sites and the six sites from 2010.

2.2. Data analysis and visualization

2.2.1 Comparison among sites

Community level taxonomic composition for each site was calculated by summing the number of taxa within major phyla groups and dividing by the total number of taxa, resulting in relative proportion of major phyla. Similarly, the taxonomic composition of bivalves (relative proportions of different bivalve species) was determined by summing the total number of each species and dividing by the total number of bivalves collected at a site. Average bivalve abundance (per 0.1 m²) and total number of bivalve species were noted for each site and the most abundant species were identified. Average bivalve richness (over all stations at a site) was also noted. Shannon's H' diversity index (Shannon 1948) and Pielou's J' evenness index (Pielou 1966) were calculated for each station using the ecological statistical software PRIMER 6 (Clarke and Gorley 2006); averages and standard deviations of each index were reported for each site.

Community-level and bivalve-level taxonomic composition were compared among the eight sites, as was bivalve richness and measures of diversity. Average physical and environmental characteristics were determined for each site. Student's *t*-tests were used to determine whether percent silt-clay differed between top core and mid-core sediment subsamples at each of the six 2010 sites.

2.2.2. Comparison among stations

Comparison of species presence/absence and abundance among stations was used to determine and characterize the relationship between certain bivalve species and assemblages and particular variables, such as depth, latitude, and sediment type. Within a sediment type (i.e. sand, silt), species presence and abundance was also used to assess the degree to which bivalve assemblages in one site were applicable to another site with similar sediment characteristics. The ecological statistical software PRIMER 6 (Clarke and Gorley 2006) was used to conduct analyses on the bivalve data from the six 2010 sample sites. Bivalve abundance data were square root transformed to deal with the skewed nature of biological count data.

BIO-ENV analysis (Clarke and Ainsworth 1993) – also referred to as BEST (Biota and/or Environment Matching) analysis – was used to determine which environmental factors displayed the best correlations with observed abundances for all bivalve species together. The idea behind BIO-ENV is similar to multiple regression, wherein samples with similar environmental variables would be expected to have similar species compositions. Given the biotic data (in this case, bivalve abundances), BIO-ENV examines all possible combinations of abiotic variables to determine which combination has the highest correlation with the biotic data. More specifically: given a biotic matrix (here, a Bray-Curtis similarity resemblance matrix), and an abiotic matrix (using Euclidean distance) the Spearman rank correlation is maximized. The candidate abiotic variables were: latitude, longitude, depth, temperature, DO, salinity, percent silt-clay (mid-core), MGS (mid-core), TOC, total nitrogen, fluorescence, and indices of Pacific

Decadal Oscillation (PDO), Multivariate ENSO Index (MEI), and Northern Oscillation Index (NOI).

The Bray-Curtis similarity resemblance matrix was also used to create a non-metric multi-dimensional scaled (nMDS) plot (Clarke 1993) of significant groups of stations based on bivalve species presence/absence and abundance (i.e. bivalve assemblages). Similarly, CLUSTER analysis (Clarke 1993) used group averages of the resemblance matrix to create clusters represented in a dendrogram, which provided another way to look at the relative similarity between bivalve assemblages at individual stations and between significant groups of stations. The similarity profile (SIMPROF) routine (Clarke and Warwick 2001) was run concurrently with the CLUSTER analysis to identify the significant groups of stations.

In order to determine which bivalve species were most characteristic of the significant groupings (i.e. unique bivalve assemblages), bivalve abundance data were analyzed for similarity/dissimilarity using SIMPER (Clarke 1993) one-way analysis (via the Bray-Curtis resemblance matrix with a cut off of 80% for contributions). The resulting output contained significant groups of stations, average similarity of each group and dissimilarity between groups, and average abundance of species characteristic of each assemblage. Physical variables of stations within significant groups were assessed in order to determine environmental characteristics associated with each unique bivalve assemblage.

2.2.3. Dominant bivalve species

2.2.3.1. Exploratory analysis

The five most abundant bivalve species across the six BOEM 2010 sites were: *Axinopsida serricata*, *Nutricula lordi*, *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis* (Figure 2). Frequency of occurrence histograms – for the 2010 sites only – were used to identify patterns of species presence/absence in regards to fairly permanent

physical characteristics of sites (depth, latitude, and percent silt-clay of sediment¹). Scatterplots of species abundance versus environmental variable of interest (also, using only the 2010 data) were used to identify any patterns in species abundance. Plots were constructed using basic R plotting and the ggplot2 package (Wickham 2009) in the statistical software R (R Core Team 2013). Generalist/specialist tendencies of species were noted. The two additional sites from 2012 were used to check observed trends based on the six 2010 sites.

2.2.3.2. Species' models

For each of the five most abundant species, I wanted to construct abundance models (abundance as response, environmental variables as predictors). In conjunction with the exploratory analysis described above, these models could assist in determining which environmental factors were most associated with species distribution along the continental shelf. Prior to model construction, preliminary analyses, detailed below, were conducted so that models produced later were as robust as possible.

2.2.3.2.1. Explanatory variables of interest

Preliminary analysis identified the following environmental variables² as most associated with species' abundance trends: latitude, longitude, depth, temperature, DO, silt-clay, MGS, and TOC. There was a large amount of missing temperature and DO data for the Nehalem site. Nehalem data were therefore approximated: based on the depth of the station with the missing values, the temperature and DO values from the nearest (depth-wise) station were used in place of the missing values. Longitude was also included as a variable of interest at the species level because preliminary analyses

¹ At the time of this analysis, data from the top-core sediment subsamples were unavailable. Consequently, for this section all references to silt-clay refer to percent silt-clay from the mid-core data. Additionally, TOC data were determined from mid-core samples and in light of the strong correlation between TOC and percent silt-clay, use of the TOC data necessitates the use of the mid-core silt-clay data.

² For this section, all references to silt-clay and TOC refer to the mid-core silt-clay and TOC data.

indicated a strong correlation between longitude and patterns in assemblage distribution. Although longitude can be considered a proxy for depth (i.e. distance offshore), longitude may also provide additional information – about abundance variability in regards to the morphological characteristics of the shelf – in addition to that provided by depth.

The relationship between environmental variables and abundance was not always linear: based on preliminary analyses, species' relationship with individual variables was sometimes better modeled by a quadratic, rather than a linear, equation. Therefore, squared terms were also of interest in order to capture possible optima in environmental variables for species abundance.

2.2.3.2.2. Correlation matrix of explanatory variables

It was anticipated that the variables - latitude, longitude, depth, temperature, DO, silt-clay, MGS, and TOC - could display strong correlations with one another (Figure 3). To assess the potential for multicollinearity, a correlation matrix of the linear terms of these variables was constructed using the statistical software R (R Core Team 2013). Significance of correlations was determined using Pearson's r correlation coefficients, via the "rcorr" routine from the "Hmisc" package (Harrell 2013) in R.

Nearly all variables were significantly correlated with one another (Table 1). Latitude was significantly correlated ($p < 0.01$) with all variables except DO. The sediment variables of silt-clay, MGS, and TOC were each significantly correlated ($p < 0.01$) with all variables except longitude.

2.2.3.2.3. Principal component analysis

Principle component analysis (PCA) was conducted as a potential way to handle the multicollinearity in the dataset. PCA takes a set of correlated variables – here, the explanatory variables – and converts them into a set of new, uncorrelated variables, represented by linear combinations of the original variables (Ramsey and Schafer 2013). PCA was run using the built-in "princomp" routine in R (R Core Team 2013) using only

the linear terms of variables of interest – latitude, longitude, depth, temperature, DO, silt-clay, MGS, and TOC. Prior to analysis, variables were standardized and rows with missing values were removed. Analysis was then run on the remaining 110 samples.

The first three principle components (PCs) explained approximately 94% of the variability observed in the data (Table 2). The three PCs emphasized different explanatory variables (Table 3).

Based on the sign of the PC coefficients, the first PC (PC1) appeared to be a contrast between the weighted average of MGS and latitude and the weighted average of longitude, depth, temperature, DO, silt-clay, and TOC. However, the absolute value of the coefficients for longitude, DO, and depth were smaller than the similarly weighted coefficients for latitude, temperature, silt-clay, MGS and TOC. Therefore, PC1 suggested a contrast between the average of latitude and MGS and the average of temperature, silt-clay, and TOC.

Based on sign of coefficients, PC2 appeared to be a contrast between the weighted average of longitude, depth, and MGS and the weighted average of latitude, temperature, DO, silt-clay, and TOC. For PC2, temperature, MGS, and TOC could potentially be dropped from empirical analysis, based on their relatively small coefficients. Additionally, the coefficients for silt-clay, latitude, and depth were smaller than the more similarly weighted coefficients for longitude and DO. Therefore, based on both sign and weight, PC2 suggested a contrast between longitude and DO.

Finally, PC3 appeared to be a contrast between the weighted average of latitude, depth, silt-clay, and TOC and the weighted average of longitude, temperature, DO, and MGS. For PC3, latitude, DO, silt-clay, MGS, and TOC could be dropped from empirical analysis, due to their relatively small coefficients. The remaining similarly weighted coefficients for PC3 suggested a contrast between depth and the average of longitude and temperature.

Overall, PC1 heavily weighted sediment terms, PC2 most heavily weighted DO, and PC3 emphasized longitude, depth, and temperature. Therefore, PC1 could be considered a sediment component while PC2 and PC3 were physical/water components.

2.2.3.2.4. *Variance inflation factor*

As an alternative to PCA, explanatory variables could be dropped until multicollinearity was no longer a serious problem for the remaining explanatory variables. To quantify multicollinearity, the variance inflation factor (VIF) (Marquardt 1970) was calculated for all variables of interest for inclusion into species' models: latitude, depth, temperature, DO, silt-clay, MGS, and TOC (as well as the squares of each), and longitude. Unlike PCA, VIF takes the response variable into consideration (Ramsey and Schafer 2013).

Prior to analysis, variables were centered in order to reduce correlation between linear and squared terms of the same variable. Negative binomial “full” models were constructed with species abundance as response and all possible environmental variables as explanatory variables. VIF values were then calculated for each variable in the model, via the “vif” function from the “HH” package in R (Heiberger 2013). Although most rules of thumb prefer a VIF cut-off of 10 (e.g. Marquardt 1970), for this dataset, VIF values below 20 were determined to be acceptable (Virginia Lesser, personal communication). Full models displayed VIF values much larger than 20, so variables which were strongly correlated with others (from the correlation matrix) and displayed high VIF values were removed from the model. A new model was constructed using the remaining variables and VIF of those variables was calculated. The process was repeated until all variables displayed acceptable VIF values.

VIF of variables were similar across species, so only results for the *Axinopsida serricata* negative binomial model are reported as an example (Table 4). When all variables were included, silt-clay, MGS, and latitude displayed the largest VIF values, indicating serious multicollinearity. Since latitude was highly correlated with nearly all

other variables (Table 1), it was removed first in order to reduce multicollinearity. With latitude removed, the sediment variables of silt-clay, MGS, and TOC displayed the highest VIF values. Removing TOC alone did not substantially improve the VIF values for silt-clay and MGS. Ultimately, for VIF values to be meet the acceptable threshold, only one sediment characteristic could remain. Using silt-clay as the one sediment variable instead of MGS resulted in slightly better VIF values for all variables (Table 4).

2.2.3.3. Negative binomial generalized linear models

Rather than use the PCs in principal component regression, I decided to use a subset of variables (based on VIF analysis: no latitude or TOC and only one sediment variable) to construct the species abundance models. I chose to use silt-clay as the sediment variable for the models of *Axinopsida serricata*, *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis*. Alternatively, since *Nutricola lordi* was found exclusively in sandy areas, I chose to use MGS as the sediment variable for that species rather than silt-clay.

Since species distribution was overdispersed, a negative binomial distribution was assumed rather than a Poisson distribution. Models were created using untransformed abundance data. Stations with missing values were removed prior to modeling; analysis was conducted on the remaining 110 stations with no missing environmental variables of interest.

Starting with a “full” model including all nine variables – depth, temperature, DO, silt-clay, and their squares, as well as longitude – a stepwise selection procedure in R was used to select a single best model for each species. The selection procedure used was the “stepAIC” function in the MASS package (Venables and Ripley 2002) in R, which tests single term deletions in an automated fashion. For each term in the model, an AIC value is given, corresponding to the AIC the model would have if that term were dropped. This continues automatically until removing no further terms results in a model with the lowest AIC.

Although the default of the “stepAIC” function is to test deletions by AIC, I used BIC as the selection criterion instead of AIC. BIC imposes a stricter penalty for large numbers of variables in a model than AIC: whereas the penalty term for BIC is $p * \log(n)$ (Schwarz 1978) – where p is the number of estimated variables in the model and n is the sample size – the penalty term for AIC is only $2p$ (Akaike 1974). The “stepAIC” function was therefore adjusted (using $k=\log(110)$) rather than the default $k=2$) so that BIC values were used as model selection criteria instead of AIC values.

The function “stepAIC” will remove linear terms while leaving the corresponding squared terms in the model. This was problematic, since it was desired to find a final model in which linear terms were always present if the corresponding squared term was included. In the case where the “stepAIC” function selected a final model which did not meet this criteria, the selection process was conducted by hand, using the “dropterm” function, also from the MASS package (Venables and Ripley 2002) in R. Unlike the “stepAIC” function, which continues running automatically with no further input from the user, the “dropterm” function runs one deletion, then stops. The user then manually creates a new model, by dropping the desired term. In the event that the lowest BIC resulted when a linear term would be dropped but its squared form remained, the next lowest BIC term was dropped instead.

A residual plot was constructed for each species’ final model using the built-in “plot” function in R (R Core Team 2013).

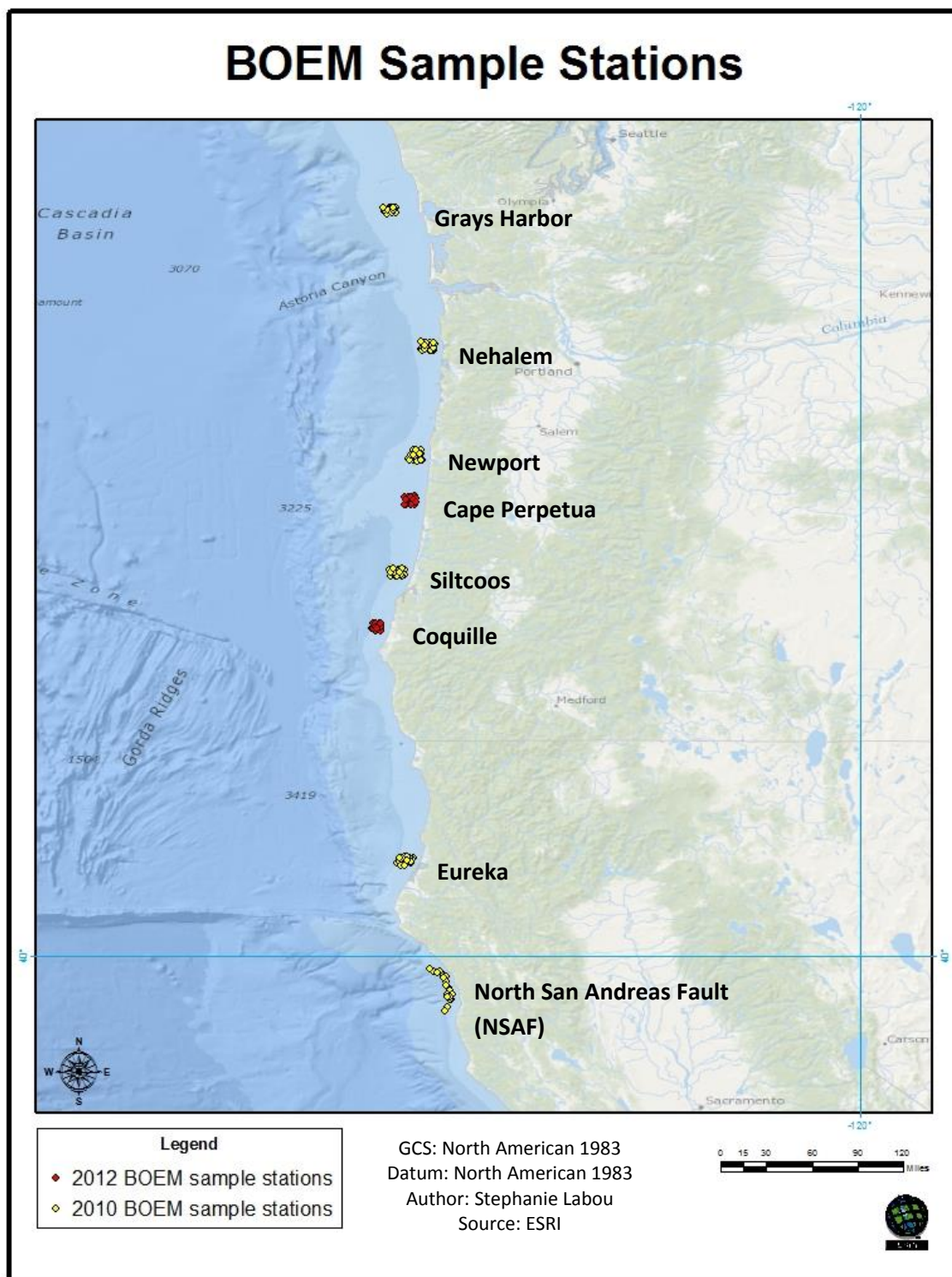


Figure 1. Map of the 2010 and 2012 BOEM sample stations.



Figure 2. The five most abundant bivalve species from the 2010 BOEM survey.

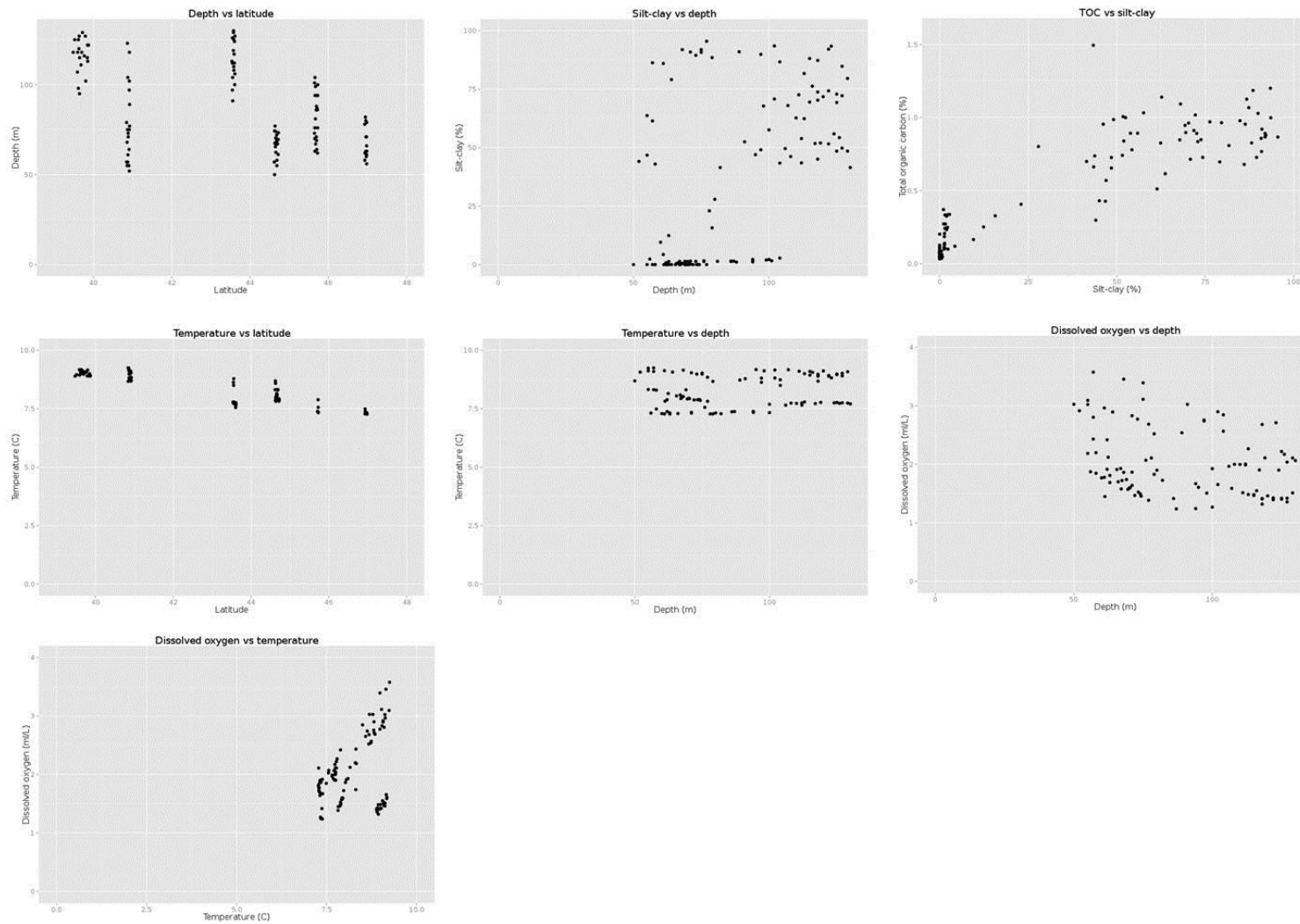


Figure 3. Scatterplots of selected environmental variables in relation to one another.

Table 1. Correlation matrix of environmental variables of interest. Significance is denoted by stars: $p < 0.05$ (*), $p < 0.01$ (**).

	Latitude	Longitude	Depth	Temperature	DO	Silt-clay	Median grain size	TOC
Latitude	1							
Longitude	-0.410**	1						
Depth	-0.476**	0.188*	1					
Temperature	-0.921**	0.406**	0.169	1				
DO	-0.164	-0.429**	-0.348**	0.364**	1			
Silt-clay	-0.862**	0.024	0.511**	0.751**	0.376**	1		
Median grain size	0.780**	-0.033	-0.587**	-0.628**	-0.303**	-0.914**	1	
TOC	-0.711**	-0.041	0.674**	0.555**	0.266**	0.894**	-0.881**	1

Table 2. Standard deviation, proportion of variance, and cumulative proportion of variance explained for each of the principal components.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Standard deviation	2.147	1.303	1.097	0.447	0.371	0.310	0.212	0.114
Proportion of Variance	0.576	0.212	0.150	0.025	0.017	0.012	0.006	0.002
Cumulative Proportion	0.576	0.788	0.939	0.964	0.981	0.993	0.998	1.000

Table 3. Coefficients for each environmental variable by principal component.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8
Latitude	0.427	-0.120	0.252	-0.330	0.155	-0.206	-0.005	0.752
Longitude	-0.087	0.561	-0.517	-0.572	0.176	-0.139	0.182	-0.012
Depth	-0.277	0.396	0.512	-0.275	-0.488	0.412	0.030	0.142
Temperature	-0.378	-0.026	-0.497	0.247	-0.308	0.026	-0.384	0.553
DO	-0.141	-0.703	-0.195	-0.577	-0.228	0.201	0.097	-0.116
Silt-clay	-0.457	-0.115	0.059	0.219	0.125	-0.124	0.792	0.263
MGS	0.431	0.062	-0.169	0.112	-0.732	-0.351	0.324	-0.072
TOC	-0.420	-0.052	0.301	-0.186	-0.091	-0.768	-0.279	-0.145

Table 4. Variance inflation factor (VIF) for each variable using negative binomial models for *Axinopsida serricata*. VIF values and patterns were similar for the other species of interest.

Terms in model	Latitude	Latitude ²	Longitude	Depth	Depth ²	Temp	Temp ²	DO	DO ²	Silt-clay	Silt-clay ²	MGS	MGS ²	TOC	TOC ²
All terms	57.30	4.86	4.70	10.48	1.92	33.02	6.25	7.78	3.55	229.29	6.90	203.49	25.34	36.36	4.01
Latitude removed			4.17	9.85	1.92	11.50	2.69	5.27	2.85	200.48	6.64	188.42	23.65	31.97	3.65
Latitude removed; MGS as sediment variable			3.69	6.30	1.36	9.36	2.15	4.57	2.47			18.02	3.67		
Latitude removed; Silt-clay as sediment variable			3.88	6.28	1.36	10.00	2.34	4.28	2.73	15.53	2.07				

3. RESULTS

3.1. Summary of total benthic community of sites

The two sites sampled in 2012 are denoted with an asterisk (*) after the site name to distinguish them from the six sites sampled in 2010.

3.1.1. North San Andreas Fault (NSAF)

The dominant phylum at NSAF was Annelida, which comprised nearly 41% of the sampled benthic community (Figure 4). Molluscs made up 32.6% of taxa, with bivalves comprising 97% of all molluscs, for a total bivalve percentage of 31.6%. Sixteen bivalve species were observed at NSAF and the site displayed the most even bivalve composition on average (Table 5). The most abundant bivalve species was *Axinopsida serricata*, which made up 49% of all bivalves observed at NSAF stations (Figure 5). *Acila castrensis*, the next most abundant bivalve, comprised nearly 21% of observed bivalves. On average, the site had a bivalve density of 15 bivalves per 0.1 m², the lowest of all sites.

3.1.2. Eureka

The dominant phylum at Eureka was Mollusca (52%), with bivalves comprising over 47% of all taxa (Figure 4). Annelida was the next most abundant phylum, making up 37% of all taxa. For Eureka, 19 species of bivalves were observed. *Axinopsida serricata* was the dominant species, comprising 59% of all observed bivalves (Figure 5). The second most abundant species was *Ennucula tenuis*, which made up 22% of observed bivalves. Eureka had an average bivalve density of approximately 67 bivalves per 0.1 m² (Table 5).

3.1.3. *Coquille**

The dominant phylum at Coquille was Mollusca (69%), followed by Annelida (23%) (Figure 4). Bivalves alone comprised over 65% of all taxa. A total of 15 bivalve species were observed at Coquille, with *Axinopsida serricata* the most abundant (68%), followed by *Acila castrensis* (15%) (Figure 5). Coquille had an average bivalve density of 81 bivalves per 0.1 m² (Table 5).

3.1.4. *Siltcoos*

The dominant phylum at Siltcoos was Mollusca (69%), followed by Annelida (20.5%) (Figure 4). Bivalves comprised 60% of total taxa. Twenty bivalve species were observed across the Siltcoos stations; the site displayed the highest average bivalve diversity (Table 5). The dominant species was *Axinopsida serricata*, which made up 53% of observed bivalves (Figure 5). The next most abundant species were *Macoma carlottensis* (16%) and *Acila castrensis* (12%). Siltcoos had an average bivalve density of just over 88 bivalves per 0.1 m².

3.1.5. *Cape Perpetua**

The dominant phylum at Cape Perpetua was Mollusca (59%), followed by Annelida (30%) (Figure 4). Bivalves made up 54% of all observed taxa. There were 12 bivalve species observed at Cape Perpetua, dominated by *Nutricula lordi* (58%) and *Axinopsida serricata* (27%) (Figure 5). Cape Perpetua had an average bivalve density of 62 bivalves per 0.1 m² (Table 5).

3.1.6. *Newport*

The dominant phylum by far at Newport was Mollusca (almost 79%), with bivalves making up 71% of total taxa (Figure 4). The next most abundant phyla were Annelida (10%) and Crustacea (9%). Although 10 species of bivalves were observed at

Newport – the lowest bivalve richness across all sites – the site was dominated by only two species: *Nutricula lordi* (nearly 63% of bivalves) and *Axinopsida serricata* (34%) (Figure 5). The other 8 species made up less than 3% of all observed bivalves for Newport. Consequently, the site displayed the lowest average bivalve diversity (Table 5). Newport did, however, display the greatest average bivalve density, with approximately 116 bivalves per 0.1 m².

3.1.7. Nehalem

The dominant phylum for Nehalem was Annelida (45%), followed closely by Mollusca (38%) (Figure 4). Bivalves comprised 25% of total observed taxa. Nehalem had a total of 18 bivalve species, dominated by *Axinopsida serricata* (42% of observed bivalves) and *Ennucula tenuis* (24%) (Figure 5). Nehalem had an average of approximately 28 bivalves per 0.1 m² (Table 5).

3.1.8. Grays Harbor

The dominant phylum for Grays Harbor was Annelida (53%) (Figure 4). Molluscs comprised 35% of taxa, with bivalves alone making up nearly 33% of observed taxa. A total of 24 bivalve species were observed across the Grays Harbor stations, the highest bivalve species richness of all the sites; however, the site also displayed the lowest measure of evenness (Table 5). *Axinopsida serricata* comprised nearly 57% of observed bivalves, followed by *Nutricula lordi* (19%) (Figure 5). Grays Harbor had an average bivalve density of nearly 57 bivalves per 0.1 m².

3.2. Summary of differences among sites

3.2.1. Physical and environmental variables

Of the six 2010 sites, NSAF was the site furthest south (northern California) whereas Grays Harbor was the northernmost site (Washington) (Figure 1). NSAF and

Siltcoos were, on average, the deepest sites, while Newport and Grays Harbor were the shallowest sites (Table 6). Average penetration depth of core varied across sites, although all cores captured at least the top seven centimeters of sediment. Since presence of the small infaunal bivalves of interest was deemed unlikely to increase with core depth, no further analysis was conducted regarding penetration depth.

Average temperature and DO did show variations among sites: NSAF was the warmest site while Grays Harbor was the coolest, on average; Eureka had the highest DO while NSAF had the lowest DO of the six 2010 sites. When all eight sites were considered together, Cape Perpetua displayed the lowest DO (below the hypoxic threshold). Although in theory cold water contains higher DO than warm water, the opposite relationship was observed here, with DO increasing with higher temperatures (Figure 3).

Regardless of whether sediment was sampled from the top of the core or the middle of the core, Eureka had the highest percent of silt-clay in the sediment, followed by NSAF (Table 6, Figure 6, 7). In contrast, sediment at Nehalem and Newport was almost entirely sand. Along with filling in latitudinal gaps, Coquille and Cape Perpetua represented further sampling of sediment types: 36% silt-clay and <1% silt-clay, respectively. Coquille and Grays Harbor displayed the greatest interquartile ranges for mid-core percent silt-clay of sediment, due to the presence of gravel at some stations along with sand and silt-clay (Figure 7).

Two of the six 2010 sites displayed significant differences in percent silt-clay between the top core and mid-core sediment subsamples: at Nehalem, there was a significantly smaller percent silt-clay in the mid-core than the top core (*t*-test, $p < 0.0001$); conversely, Eureka had significantly more silt-clay in the mid-core (*t*-test, $p = 0.005$), due primarily to samples at two stations. The other four sites did not display significant differences (NSAF: $p = 0.165$, Siltcoos: $p = 0.505$, Newport: $p = 0.612$, Grays Harbor: $p = 0.122$).

3.2.2. Bivalve assemblages of sites

The six 2010 BOEM sites displayed variations in relative and absolute bivalve abundance as well as particular bivalve species present. Newport contained the greatest relative abundance, compared to other phyla, of molluscs (and bivalves), followed by Siltcoos (Figure 4). Grays Harbor contained the greatest number of bivalve species (richness), while Newport contained the least (Table 5). In general, bivalve assemblages at each site were dominated by a single species, with a large portion of the remaining bivalves split between two or three other species. Beyond these abundant four or so species, other bivalves were present in low abundances, often with only one specimen per species. Newport was the exception to this trend, with 97% of bivalves coming from only two species. Similarly, all sites except Newport displayed a relatively high (compared to other bivalve species for the site) and similar abundance of *Axinopsida serricata*. Although Newport had the lowest number of bivalve species, that site also displayed the greatest average abundance of bivalves (Figure 8).

In regards to the two 2012 sites, the bivalve assemblage at Cape Perpetua was very similar to Newport while the assemblage at Coquille was more similar to those at Siltcoos and Eureka (Figure 5). In terms of total bivalve abundance, Coquille and Cape Perpetua had similar average abundances, although Coquille had a larger range of abundances (Figure 8). Considering all three sand sites (Cape Perpetua, Newport, and Nehalem), Newport displayed the highest average bivalve abundance.

3.3.3. Bivalve relationship with sediment

The average silt-clay percent of mid-core sediment observed for the six 2010 sites ranged from 0.05% (Newport) to 82% (Eureka). The bivalve assemblages from the three southern silty sites (NSAF, Eureka, Siltcoos) were fairly similar to one another (Figure 5), although NSAF contained far fewer total bivalves than Eureka and Siltcoos (Figure 8). There was a large difference in average bivalve abundance observed between sites with similar sediments off Newport (average 0.05% silt-clay top core and mid-core)

and Nehalem (average 3.91% top-core, 1.48% silt-clay mid-core). Not only was there a difference in total bivalve abundance, but there was also a pronounced difference in the bivalve species breakdown between these two sites: Newport was dominated (97% of all bivalves) by only two species, whereas Nehalem was more reflective of the trend observed in the other sites (two species constituting the majority of bivalves, and the remainder split among a host of other species). Despite these differences, both Newport and Nehalem bivalve communities were made up by a large proportion of the species *Axinopsida serricata*.

3.3.4. BIO-ENV analysis

The combination of environmental variables with the best correlation to all observed bivalves consisted of longitude, depth, and MGS (correlation = 0.473). Out of the top ten correlations, depth and MGS were included in all ten and longitude was included in nine.

3.3. Comparison among stations (bivalve assemblages)

3.3.1. nMDS and CLUSTER analysis

Five Grays Harbor stations included gravel in the sediment and contained few, if any, bivalves. Since these stations comprised a unique habitat type, not sampled elsewhere in 2010, they were removed from subsequent analysis, to better facilitate interpretation of the assemblages in soft-sediment habitat ranging from sand to silt.

Based on the nMDS analysis of the remaining 113 stations sampled in 2010 (Figure 9), although most stations grouped with others at their site – i.e. most Eureka stations tended to fall within the same group due to similar abundances of certain bivalves – some stations with similar physical characteristics spawned multiple significant groups. For example, not all Nehalem stations were included in a single group, but showed up in multiple significant groups with dissimilar sediment and latitude. This

can also be observed from the cluster analysis dendrogram (Figure 10), where the y-axis gives a measure of how similar groups are to one another.

3.3.2. *SIMPER analysis*

A total of 113 stations (following removal of five Grays Harbor gravel stations) formed eight distinct groups (i.e. unique bivalve assemblages) (Table 7). Group B (Newport group) contained the most stations, followed closely by Group H (NSAF/Siltcoos group). Conversely, Group A was comprised of a single NSAF station, and was therefore excluded from further similarity/dissimilarity analysis. Even though this NSAF station shared physical characteristics with other stations, it failed to group with any others due to the absence of common bivalve species and the presence of rare bivalve species.

Differences in sediment and depth explain most of the groupings and therefore differences in bivalve assemblages. Within the sandy sites, Newport-dominated Group B had the lowest average percent silt-clay of sediment and was the only group where *Nutricula lordi* was a characteristic species. Approximately half of the Nehalem stations, which were only slightly siltier than the Newport stations, formed a unique group (Group G). Grays Harbor stations grouped with either Newport (Group B), Nehalem (Group G), or by themselves (Group D, with the highest characteristic abundance of *Axinopsida serricata*), depending on percent silt-clay of the sediment at the particular station.

Within the silty sites, the shallow silty stations of Eureka – a depth/sediment combination not observed elsewhere – formed a single group (Group C) characterized by a relatively high abundance of *Axinopsida serricata*. All Siltcoos stations displayed similar sediment types, but differences in depth best explain the grouping: Group E was comprised of shallower Siltcoos stations, while the remaining, deeper, Siltcoos stations grouped with NSAF stations (Group H), which were siltier but of a similar depth. Finally, stations in Group F contained the largest range of sediment types and depths, and the characteristic species were all common, abundant species. The Nehalem stations in this

mixed group tended to be shallower than those in the Nehalem-dominated group (Group G) and contain fewer *Ennucula tenuis* and more *Axinopsida serricata*. As a result, these shallow, sandy Nehalem stations displayed bivalve assemblages more like the deep, silty stations of Eureka and NSAF and were grouped accordingly.

Groups H and B – the NSAF/Siltcoos group and the Newport dominated group – had the largest average dissimilarity (77.5%) due to the near absence of *Nutricola lordi* in Group H as well as a lower average abundance of *Axinopsida serricata* compared to Group B. In fact, the Newport-dominated very sandy Group B was quite dissimilar from all other groups (Figure 9, 10), indicating that >1% silt-clay in sediment was enough to differentiate those bivalve assemblages from the one observed in the <1% silt-clay stations of Newport. In contrast, Groups E and D – which were made up of shallow Siltcoos stations and Grays Harbor stations, respectively – had the smallest (43.2%) average dissimilarity: the two groups displayed the two highest average abundances of *Axinopsida serricata* and somewhat similar abundances of *Acila castrensis* and *Ennucula tenuis*.

3.4. Dominant species

3.4.1. Exploratory analysis

The R^2 values discussed below refer to the relationship of untransformed abundance with the indicated environmental variable.

Shepard's ternary diagram (Shepard 1954) is often used to distinguish and describe types of sand-silt-clay sediment. However, this classical sediment breakdown is less useful here since sediment analysis did not distinguish silt from clay, but rather grouped the two types together, in contrast to sand. Furthermore, based on the sample sites selected, the 118 stations³ sampled in the BOEM 2010 survey fell into five

³ The five gravel Grays Harbor stations were included in analysis, since they contain a percentage of sand and/or silt-clay. Stations with gravel tended to include few, if any, of the species under consideration, but were included for the sake of completeness.

approximate sediment groups (which differ from Shepard's) based on percent silt-clay⁴: very sandy (0-6%), mostly sand (7-39%), an approximate sand/silt split (40-60%), mostly silty (61-80%), and very silty (81-100%) (Figure 11). For the purposes of these results and later discussion, these categories will be referred to, rather than the Shepard's sediment classifications.

3.4.1.1. *Axinopsida serricata*

Out of the 118 stations in the 2010 survey, 109 contained at least one specimen of *Axinopsida serricata*. Although there were some differences in abundance, *Axinopsida serricata* was found at nearly all stations and therefore displayed frequency of occurrences which would be expected of a species with little or no habitat restrictions in regards to depth, latitude, or percent silt-clay of sediment (Figure 11). The highest average abundance was observed at Siltcoos due to stations with over 100 *Axinopsida serricata* per 0.1 m². The species displayed similar abundances across Grays Harbor, Eureka, and Newport; the lowest average abundances were observed in Nehalem and NSAF (Figure 12).

Axinopsida serricata abundance did not display any distinct trends in regards to the individual environmental variables assessed. Although some relationships were significant, all were very weak and explained negligible amounts of variability (Table 8). Abundances were slightly lower below 120 meters (Figure 12); however, given the relatively small number of stations below this depth, and the very weak relationship, this is likely a product of sampling bias. As in the 2010 data, there was no clear trend of *Axinopsida serricata* abundance with environmental variables in the two additional sites sampled in 2012.

In general, the only places *Axinopsida serricata* was not found were the few gravel stations of Grays Harbor and Coquille. However, gravel stations in general

⁴ At the time of this analysis, results from the top-core sediment subsamples were unavailable. Consequently, for this section all sediment discussion refers to the mid-core data.

contained relatively few, if any, bivalves – gravel habitat, unlike soft-sediment habitat, did not support high abundances of bivalves of any species observed in the BOEM surveys.

3.4.1.2. *Nutricula lordi*

Nutricula lordi was present at only 34 stations in the 2010 survey and was therefore underrepresented at deeper (85-135 meters) depths and generally restricted to very sandy stations (Figure 13). These patterns are a reflection of the fact that *Nutricula lordi* was found almost exclusively at the Newport site (Figure 13, 14), which was sandy and shallower than 80 meters (Table 6). Because of its limited distribution, *Nutricula lordi* displayed relatively strong relationships with depth, MGS, percent silt-clay, and TOC (Table 8).

Nutricula lordi was also observed in relatively high abundances at a few (4 in total) stations at Nehalem and Grays Harbor. These stations all fell within the depth range observed at Newport and are only slightly siltier (i.e. >0% silt-clay) than Newport. Aside from a few instances, *Nutricula lordi* was rarely observed at stations with more than 1% silt-clay. This was corroborated by data from the 2012 BOEM sites: like Newport, Cape Perpetua was composed of over 99% sand and *Nutricula lordi* was the dominant bivalve species. *Nutricula lordi* abundance did show variation in regards to MGS between the nearly pure sand sites of Newport and Cape Perpetua: the sand grains at Cape Perpetua were much larger than at Newport (Table 6) and the average abundance of *Nutricula lordi* at Cape Perpetua was approximately half the average abundance at Newport.

3.4.1.3 *Ennucula tenuis*

Ennucula tenuis was present at 65 stations in the 2010 survey. This species was underrepresented in both the shallowest portion of stations and the deepest, as well as very sandy and mostly silty stations (Figure 15). The frequency of occurrence histogram for latitude showed no clear pattern: *Ennucula tenuis* displayed a lower frequency of

occurrence than expected (if there were no latitudinal habitat restrictions) at NSAF, Newport, and Grays Harbor, and it was observed most often at Eureka, Nehalem, and Siltcoos (Figure 15). This pattern, or lack thereof, can be partially explained in terms of sediment and depth, given that Newport was the sandiest site and NSAF was the deepest on average. *Ennucula tenuis* was essentially absent at Newport; conversely, the highest abundances were observed at Eureka (Figure 16).

Although relationships with depth and sediment type were weak (Table 8), some patterns of *Ennucula tenuis* with these variables could be determined: *Ennucula tenuis* was generally found in areas shallower than 110 meters and within that depth range, it was mainly observed in non-sandy areas. More specifically, shallower than 110 meters, *Ennucula tenuis* was observed in sandy (but with >1% silt-clay), sand/silt split, and very silty stations, but was absent in essentially pure sand (<1% silt-clay) or mostly silty stations (Figure 15, 16). Given that only a few stations fall within 4-40% silt-clay, it is difficult to interpret anything useful about *Ennucula tenuis* within this sediment range. The lack of *Ennucula tenuis* observed in mostly silty stations was likely because these stations were often deeper than 110 meters. Conversely, no such depth trend explained the absence in sand stations: stations of a similar depth to Newport (which was <1% silt-clay), but at least 1% silt-clay, tended to contain at least low abundances of *Ennucula tenuis*. The two additional sites sampled in 2012 support these patterns: *Ennucula tenuis* was not present at Cape Perpetua (like Newport, <1% silt-clay) and only rarely present at Coquille (average of 36% silt-clay).

The one exception to the weak relationship of abundance with environmental variables was the relationship with DO (Table 8), where *Ennucula tenuis* abundance tended to increase with increasing DO (Figure 16).

3.4.1.4. *Macoma carlottensis*

A total of 70 stations contained at least one specimen of *Macoma carlottensis*. The frequency of occurrence graphs for *Macoma carlottensis* displayed a similar overall

pattern as would be expected of a species without depth or sediment restriction; however, the species was underrepresented in shallow, very sandy stations (Figure 17). Although *Macoma carlottensis* was found at stations over a wide range of latitudes, the highest abundances were observed at Siltcoos (100-130 meters, sand/silt split) (Figure 18). A few Grays Harbor stations (55-80 meters, very to mostly sandy sediment) also contained high abundances of *Macoma carlottensis*.

In general, the relationships of *Macoma carlottensis* abundance with environmental variables were fairly weak (even significant relationships explained relatively low amounts of variability), with a few exceptions (Table 8). *Macoma carlottensis* displayed the strongest relationship with the square of silt-clay, indicating a possible silt-clay optimum: *Macoma carlottensis* abundance peaked at Siltcoos (average 52% silt-clay), was an order of magnitude lower at Grays Harbor (average 13% silt-clay), was very low at NSAF (average 70% silt-clay), Newport (0.05%), and Nehalem (1.5%), and essentially absent at Eureka (average 82% silt-clay) (Figure 18). This trend of abundance with sediment was also observed in the 2012 data: *Macoma carlottensis* was essentially absent at the sandy Cape Perpetua site but at Coquille, abundance patterns were similar to those observed in the 2010 data (increasing abundance towards mixed sand/silt-clay sediment, then decreasing abundance, with none in very silty sediment).

As noted, *Macoma carlottensis* was observed primarily at Siltcoos, which was a relatively deep site, and was essentially absent at Eureka, which spanned the greatest depth range. However, because *Macoma carlottensis* was found at the same depths as the Eureka stations at other sites, it is unlikely the spatial pattern observed is because the species is depth limited.

3.4.1.5 *Acila castrensis*

A total of 71 stations contained at least one *Acila castrensis*. Compared to the pattern expected of a species with no physical habitat restrictions, *Acila castrensis* was underrepresented at shallow (50-80 meters) stations and therefore Newport and Grays

Harbor stations, which fall primarily in this depth range (Figure 19). These stations were also generally sandier so *Acila castrensis* was also underrepresented in the sandiest stations. Although the highest abundances of this species were observed at the Siltcoos site, it was found in low abundances across a wide range of depth, latitude, and sediment, although it was most rare at Newport (Figure 20).

In general, the relations of abundance of *Acila castrensis* with environmental variables were better explained by quadratic relationships than a linear ones (Table 8); however, with the exception of TOC, relationships were still very weak and failed to explain a high proportion of variability. Some of the lack of fit was due to the large spread of data: a quadratic fit was better than a linear fit for *Acila castrensis* abundance in relation to depth due to half a dozen high abundances, found between 100 and 120 meters depth, which were in contrast to most stations which contained only low abundances of *Acila castrensis* (Figure 20, Table 8). Likewise, the highest abundances of *Acila castrensis* were observed in sand/silt split and mostly silt stations; a curve proved a better fit than a linear relationship (Table 8). The same general sediment trend was observed from the two 2012 sites, with *Acila castrensis* absent or present in only low abundances in sand and higher abundances in sand/silt and mostly silty sediment.

3.4.2. Species models

A negative binomial model could not be developed for *Nutricola lordi* (Appendix). Models were able to be developed for the other four species (Table 9).

The model for *Axinopsida serricata* contained seven terms total, including intercept. All possible terms were included except the square of depth and both DO terms. However, although DO was excluded from the final model, it was correlated with temperature (which was included in the model) so DO cannot entirely be ruled out as a possible variable of influence. Of the variables included in the final model, only the linear forms of temperature and silt-clay were not significant. They were included, however, because squares of both those variables were significant (temperature²: $p=0.008$;

silt-clay²: $p < 0.001$).

The model for *Ennucula tenuis* was the largest, with nine terms total, including intercept. The final model included all possible variables. Only depth was not significant ($p=0.76$), although there was suggestive evidence that longitude was also not significant ($p=0.055$). All other environmental variables were significant (at least $p < 0.01$). There was some suggestion of an optimal depth for *Ennucula tenuis* – although depth alone was not significant, the square of depth was highly significant.

The model for *Macoma carlottensis* contained six terms, including intercept. The model was comprised of: temperature, DO, DO², silt-clay, and silt-clay². Only DO was not significant ($p=0.55$). The square of silt-clay in the *Macoma carlottensis* model ($p=5.87\text{e-}14$) was the most significant variable out of all variables in all models, which corroborates the suggestion of a sediment optimum observed in the scatterplot of *Macoma carlottensis* abundance vs. silt-clay. Although physical variables (longitude, depth) were excluded from the model, longitude and depth could still potentially function as influential factors: although correlations were not strong enough to cause serious multicollinearity, longitude was significantly correlated with both temperature and DO (which were included in the model) and depth was significantly correlated with DO.

Finally, the model for *Acila castrensis* contained only five terms total, including intercept. The included environmental variables were depth, silt-clay, and their squares; all were significant ($p < 0.001$). Longitude was not included in the final model; however, since longitude and depth are themselves significantly correlated, it is not possible to definitely conclude that depth, rather than longitude, is the primary physical variable of importance. Likewise, although the absence of water column variables (temperature, DO) from the model suggests that they are less influential on *Acila castrensis* distribution than depth and silt-clay, DO was significantly correlated with both depth and temperature, so potential water column impacts cannot be entirely ruled out.

Overall, the residual plots (Appendix) suggest that none of the models are a very good fit for their respective species abundance data. The plot for *Axinopsida serricata* is

closest to what would be expected of a well-fitting model, with a random scatter of points; however, the points were not centered around zero. For the other species, the residual plots displayed clustering with some suggestion of heteroscedasticity. For *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis*, abundance data were apparently clustered to such an extent by non-assessed variables as to inhibit the creation of a single model using the variables discussed here. Along with potentially influential “missing” environmental variables, clustering in these species could be due to biotic factors – such as limited dispersal ability or presence of conspecifics as a positive settlement cue – which would manifest as clumped or patchy distribution of adults. That is, species distribution may be non-random not only in terms of the environment (i.e. preference for certain sediment type), but also in terms of biotic interactions. As such, environmental, abiotic models would not be a good fit for the abundance data.

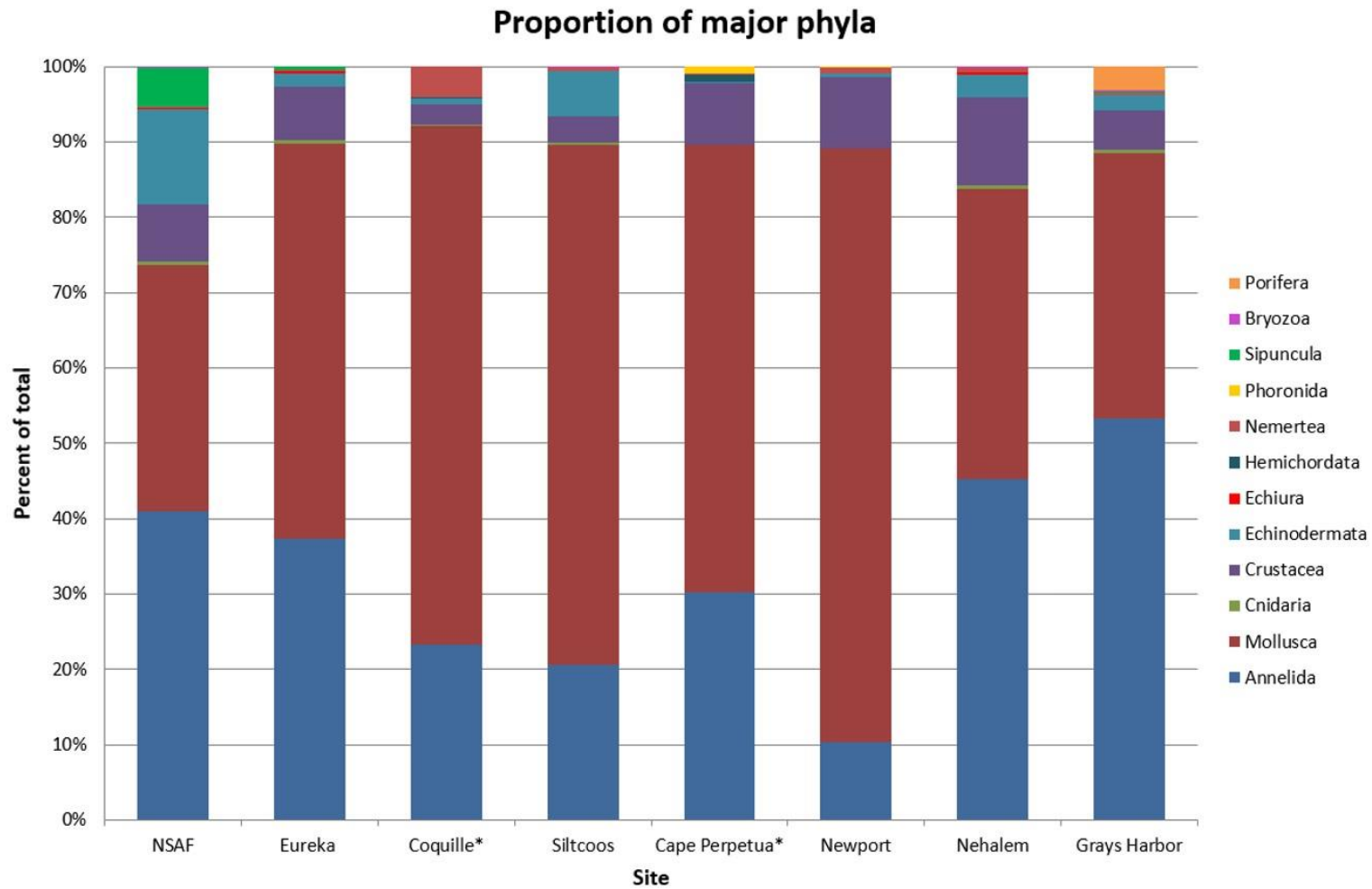


Figure 4. Proportion of major phyla for the BOEM sites. Sites are ordered southernmost to northernmost (left to right). An asterisk (*) denotes the two sites from 2012.

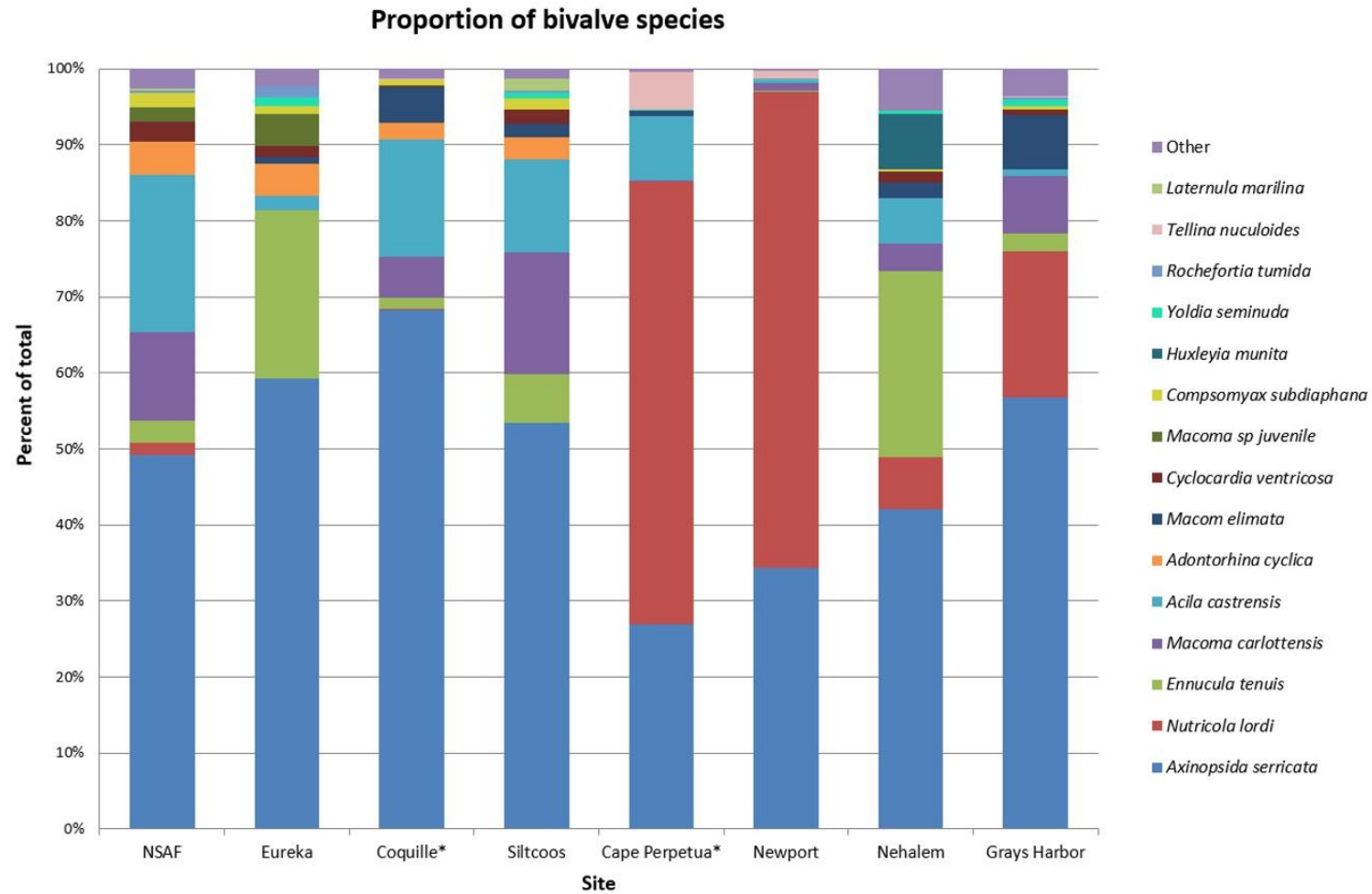


Figure 5. Proportion of major bivalve species across the BOEM sites. The 15 most abundant species are denoted; the rest are grouped into the “other” category. Sites are ordered southernmost to northernmost (left to right). An asterisk (*) denotes the two sites from 2012.

Table 5. Summary of bivalve richness, diversity, and evenness (average with standard deviation where appropriate) across all eight sampled BOEM sites. An asterisk (*) denotes the two sites sampled in 2012.

Site	Total bivalve richness	Average bivalve richness	Shannon's H'	Pielou's J'
NSAF	16	4.1 ± 1.7	1.064 ± 0.392	0.789 ± 0.163
Eureka	19	6.5 ± 2.1	1.183 ± 0.327	0.654 ± 0.158
Coquille*	15	5.1 ± 2.5	0.966 ± 0.468	0.677 ± 0.220
Siltcoos	20	8.1 ± 2.1	1.387 ± 0.232	0.678 ± 0.106
Cape Perpetua*	12	3.7 ± 1.1	0.747 ± 0.247	0.624 ± 0.200
Newport	10	3.5 ± 1.0	0.647 ± 0.164	0.547 ± 0.169
Nehalem	18	5.4 ± 2.3	1.135 ± 0.436	0.695 ± 0.163
Grays Harbor	24	5 ± 3.5	0.809 ± 0.694	0.470 ± 0.317

Table 6. Averages and standard deviation of environmental variables for each site. An asterisk (*) denotes the two sites sampled in 2012. For Grays Harbor, gravel stations were not included in TOC analysis. TOC data was unavailable for Coquille and Cape Perpetua at the time of writing.

Site	NSAF	Eureka	Coquille*	Siltcoos	Cape Perpetua*	Newport	Nehalem	Grays Harbor
Latitude	39.70 ± 0.12	40.89 ± 0.03	43.07 ± 0.02	43.58 ± 0.02	44.25 ± 0.03	44.67 ± 0.03	45.69 ± 0.03	46.96 ± 0.02
Longitude	-123.92 ± 0.06	-124.30 ± 0.04	-124.57 ± 0.03	-124.38 ± 0.05	-124.25 ± 0.04	-124.20 ± 0.04	-124.09 ± 0.04	-124.45 ± 0.04
Depth (m)	116.43 ± 9.44	77.60 ± 21.34	100.83 ± 20.00	114.89 ± 12.10	69.39 ± 7.35	66.52 ± 6.96	82.05 ± 13.59	67.86 ± 8.88
Core depth (cm)	27.32 ± 6.08	20.13 ± 5.93	16.43 ± 7.54	24.50 ± 5.38	10.33 ± 1.52	7.59 ± 1.69	10.11 ± 3.04	7.88 ± 4.42
Temperature (°C)	9.02 ± 0.10	8.96 ± 0.18	8.07 ± 0.08	7.86 ± 0.35	7.84 ± 0.04	8.08 ± 0.25	7.46 ± 0.20	7.32 ± 0.06
DO (ml/L)	1.47 ± 0.08	2.91 ± 0.30	2.46 ± 0.36	2.17 ± 0.33	1.34 ± 0.17	1.85 ± 0.44	1.62 ± 0.46	1.82 ± 0.12
Salinity (psu)	33.94 ± 0.02	33.73 ± 0.11	32.99 ± 2.35	33.90 ± 0.06	33.79 ± 0.02	33.71 ± 0.10	33.77 ± 0.13	33.72 ± 0.05
Fluorescence	-0.03 ± 0.01	0.04 ± 0.05	0.21 ± 0.04	0.06 ± 0.03	0.18 ± 0.02	0.96 ± 0.30	0.88 ± 0.19	0.74 ± 0.06

Table 6 (Continued). Averages and standard deviation of environmental variables for each site. An asterisk (*) denotes the two sites sampled in 2012. For Grays Harbor, gravel stations were not included in TOC analysis. TOC data was unavailable for Coquille and Cape Perpetua at the time of writing.

Site	NSAF	Eureka	Coquille*	Siltcoos	Cape Perpetua*	Newport	Nehalem	Grays Harbor
Top core Silt-Clay (%)	71.99 ± 14.03	78.47 ± 21.61	NA	53.54 ± 12.37	NA	0.04 ± 0.14	3.91 ± 1.78	7.18 ± 8.25
Top core Sand (%)	28.01 ± 14.03	21.53 ± 21.61	NA	46.46 ± 12.37	NA	99.96 ± 0.14	96.09 ± 1.78	77.32 ± 24.66
Top core Gravel (%)	0	0	NA	0	NA	0	0	15.50 ± 26.92
Top core MGS (μm)	40.61 ± 23.27	35.44 ± 25.13	NA	58.26 ± 20.88	NA	273.54 ± 56.15	211.81 ± 30.30	225.11 ± 102.95
Mid-core Silt-Clay (%)	70.25 ± 12.87	82.41 ± 15.50	36.02 ± 26.61	52.18 ± 7.83	0.53 ± 0.45	0.05 ± 0.15	1.48 ± 0.55	12.91 ± 15.35
Mid-core Sand (%)	29.75 ± 12.87	17.59 ± 15.50	57.92 ± 24.75	47.82 ± 7.83	99.47 ± 0.45	99.95 ± 0.15	98.52 ± 0.55	64.22 ± 37.48
Mid-core Gravel (%)	0	0	6.64 ± 9.41	0	0	0	0	22.87 ± 36.56
Mid-core MGS (μm)	40.83 ± 14.76	26.39 ± 17.08	79.43 ± 54.53	60.42 ± 12.55	431.67 ± 80.09	273.44 ± 58.59	217.28 ± 26.83	223.69 ± 102.40
Mid-core TOC (%)	0.84 ± 0.16	0.83 ± 0.25	NA	0.91 ± 0.20	NA	0.07 ± 0.04	0.21 ± 0.10	0.26 ± 0.23

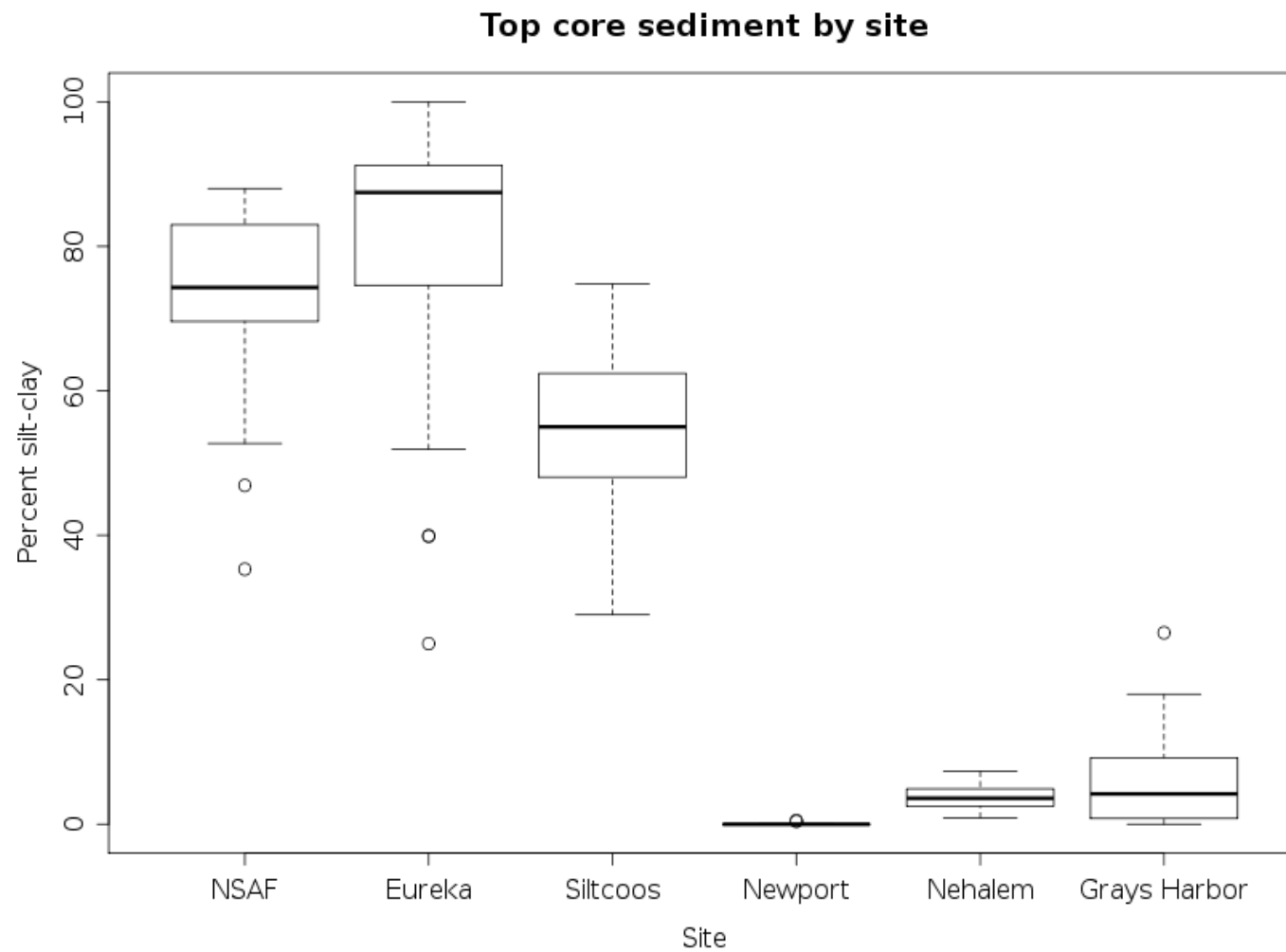


Figure 6. Boxplots of percent silt-clay of top core sediment of the six sites sampled in 2010.

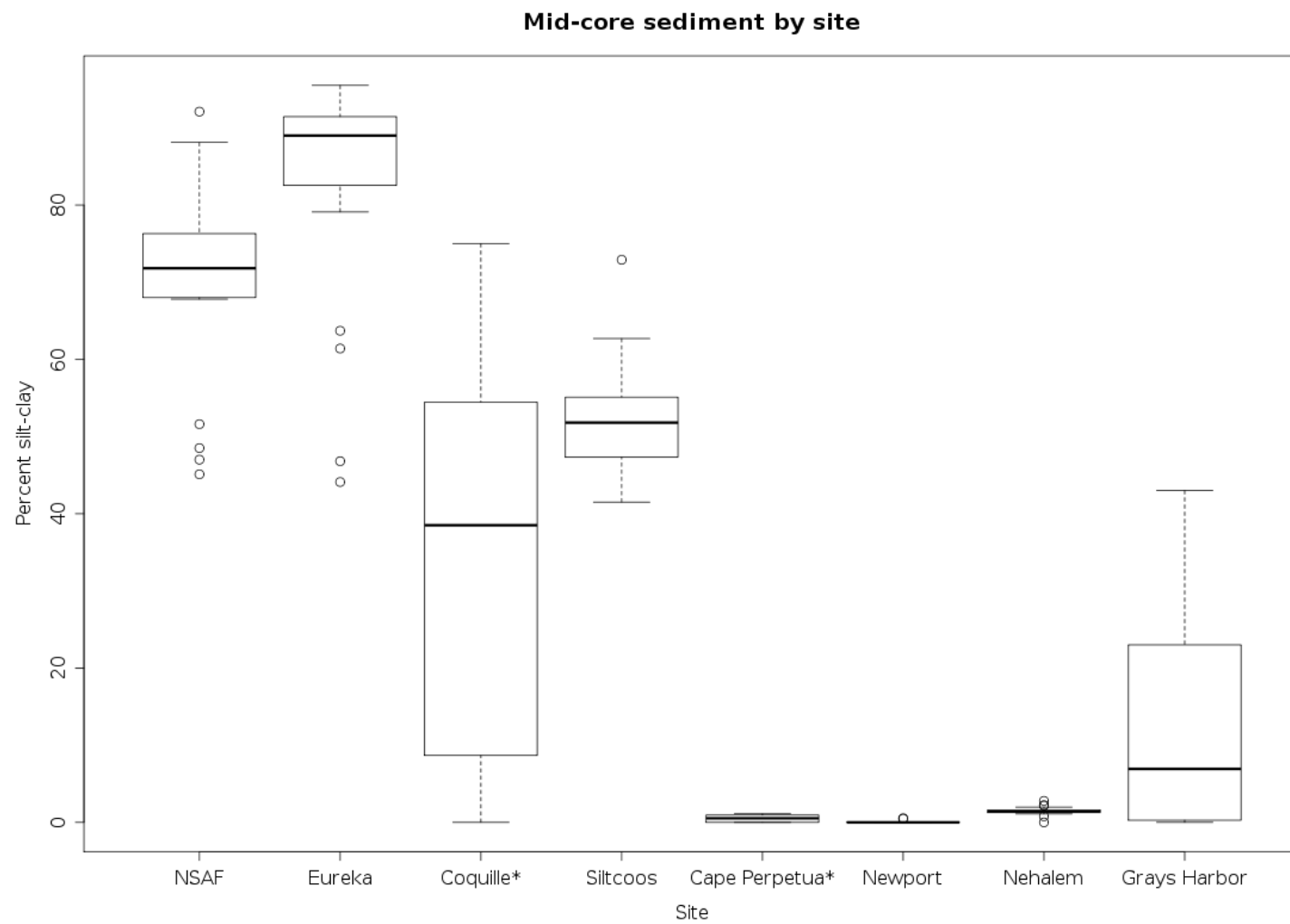


Figure 7. Boxplots of percent silt-clay of mid-core sediment by site. An asterisk (*) denotes the two sites sampled in 2012.

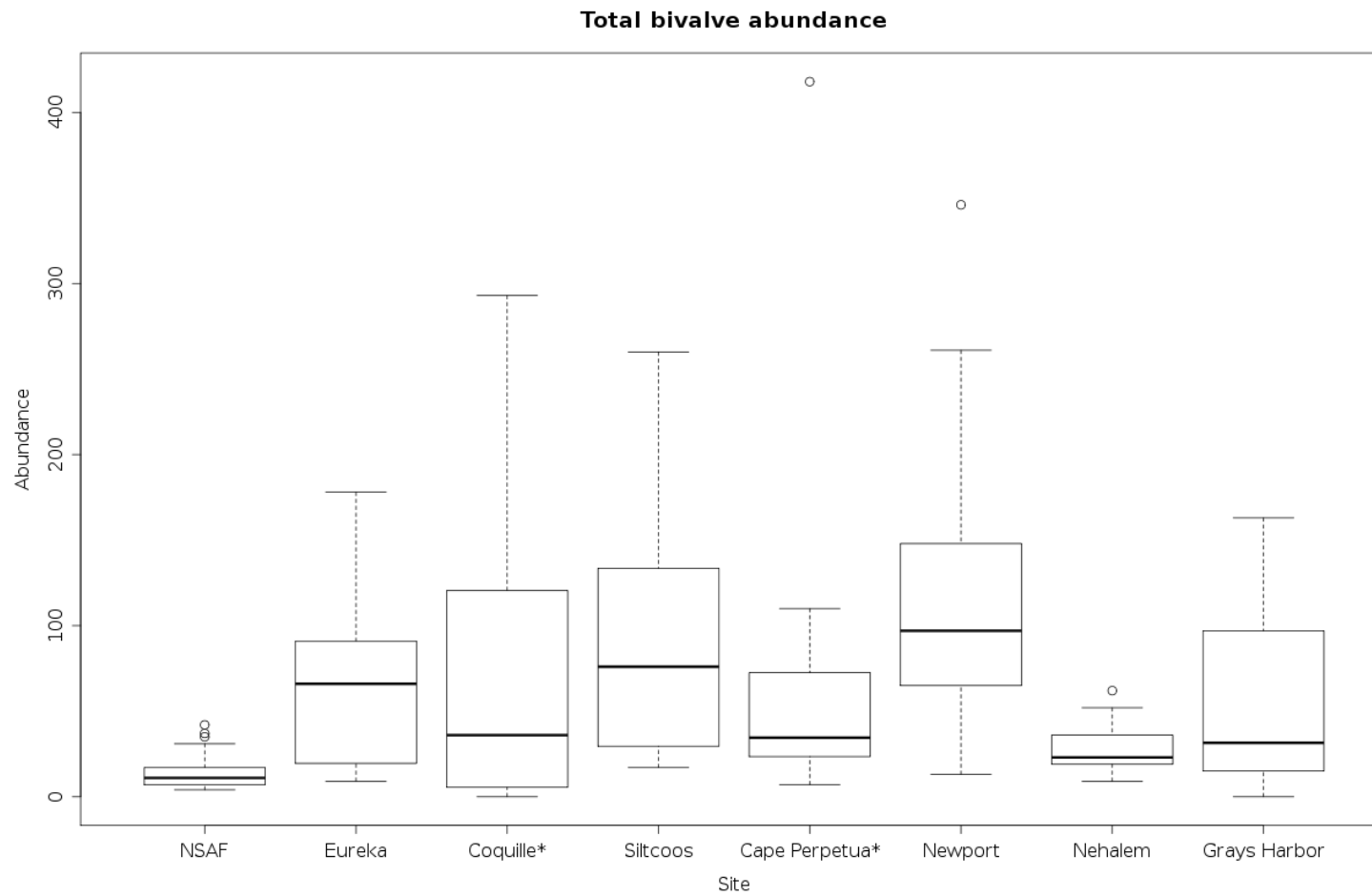


Figure 8. Boxplots of total bivalve abundance by site. An asterisk (*) denotes the two sites sampled in 2012.

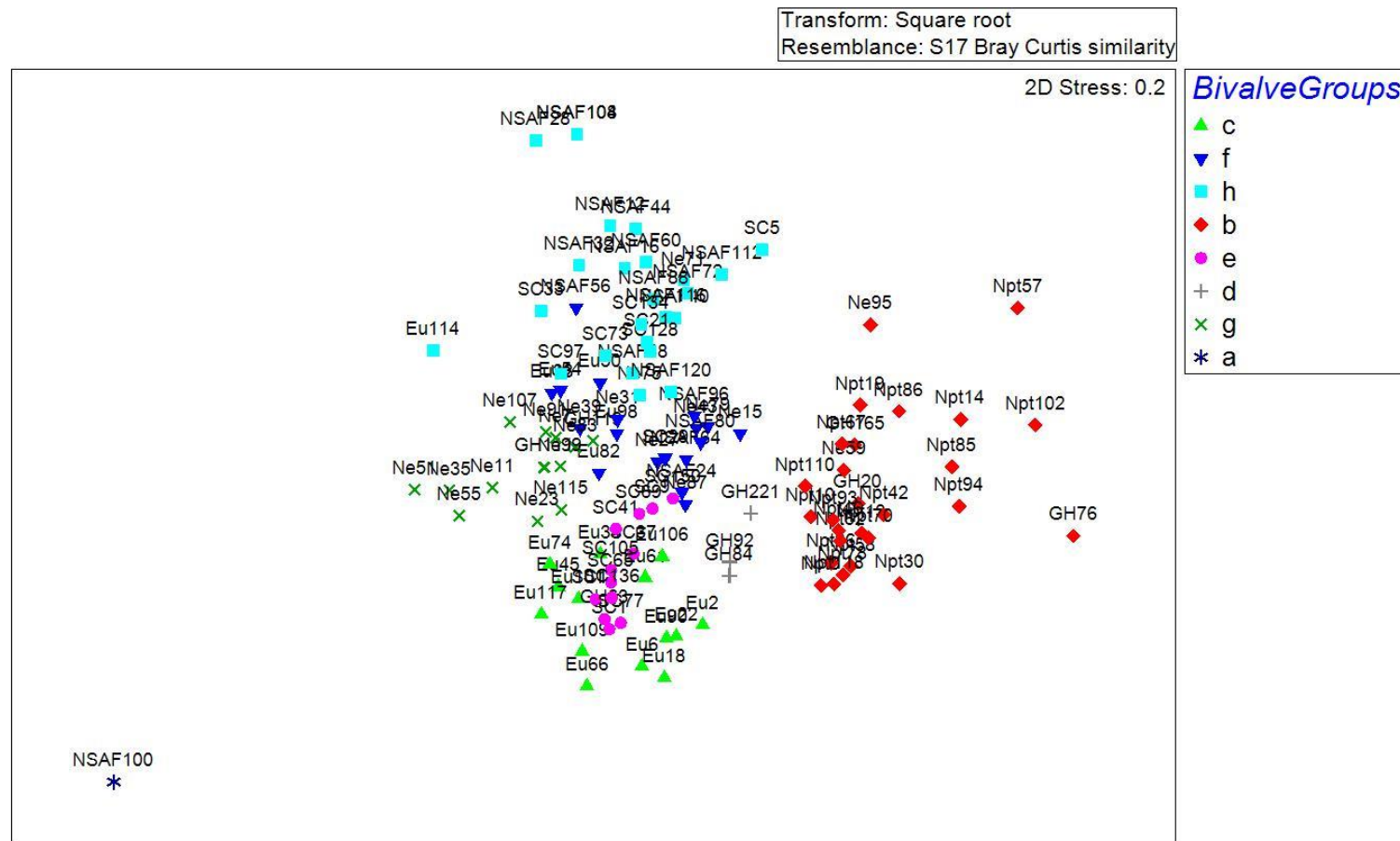


Figure 9. Non-metric multidimensional scaled plot for bivalves from the six 2010 sites. Site codes: NSAF = North San Andreas Fault, Eu = Eureka, SC = Siltcoos, Npt = Newport, Ne = Nehalem, GH = Grays Harbor. Color codes for significant groups are listed in “BivalveGroups” box.

Table 7. SIMPER analysis results for bivalve groups. Group designations are the same as in Figures 9 and 10.

Group	Site (number of stations in group)	Average similarity	Characteristic species (abundance per 0.1 m ²)	Depth (m) Range (average ± standard deviation)	Mid core silt-clay (%) Range (average ± standard deviation)	Top core silt-clay (%) Range (average ± standard deviation)
C	Eureka (14)	62.86%	<i>Axinopsida serricata</i> (7.02) <i>Ennucula tenuis</i> (4.20) juvenile <i>Macoma</i> species (1.70)	52 - 70 (65.6 ± 9.43)	44 - 95.5 (79.0 ± 17.5)	25 - 93.8 (72.7 ± 23.6)
F	Eureka (5) Nehalem (7) NSAF (5) Siltcoos (1)	61.83%	<i>Axinopsida serricata</i> (3.95) <i>Ennucula tenuis</i> (1.36) <i>Acila castrensis</i> (1.01)	63 - 127 (95.4 ± 23.0)	1.28 - 93.5 (45.6 ± 39.2)	2.5 - 100 (48.0 ± 38.5)
H	Eureka (1) Nehalem (2) NSAF (15) Siltcoos (7)	49.88%	<i>Axinopsida serricata</i> (1.89) <i>Acila castrensis</i> (1.40) <i>Macoma carlottensis</i> (1.67)	73 - 133 (115.3 ± 14.9)	1.34 - 88.1 (61.6 ± 4.49)	3.4 - 90.8 (61.8 ± 24.7)
B	Grays Harbor (3) Nehalem (2) Newport (22)	61.08%	<i>Nutricula lordi</i> (7.30) <i>Axinopsida serricata</i> (5.15)	50 - 77 (65.7 ± 6.64)	0 - 2.35 (0.176 ± 0.488)	0 - 2.20 (0.287 ± 0.587)
E	Grays Harbor (1) Siltcoos (11)	68.84%	<i>Axinopsida serricata</i> (8.46) <i>Macoma carlottensis</i> (3.81) <i>Acila castrensis</i> (3.58) <i>Ennucula tenuis</i> (2.80)	78 - 127 (105.3 ± 12.8)	23 - 62.7 (49.3 ± 3.02)	26.5 - 74.8 (54.9 ± 14.9)
D	Grays Harbor (3)	77.19%	<i>Axinopsida serricata</i> (10.49) <i>Macoma carlottensis</i> (2.73)	60 - 63 (61.3 ± 1.53)	4.31 - 12.4 (8.75 ± 4.10)	4.20 - 9.20 (7.08 ± 2.60)
G	Grays Harbor (2) Nehalem (11)	59.13%	<i>Ennucula tenuis</i> (3.11) <i>Axinopsida serricata</i> (2.74) <i>Macoma carlottensis</i> (1.03) <i>Acila castrensis</i> (1.15)	79 - 104 (91.7 ± 8.04)	1.08 - 27.9 (4.84 ± 7.94)	1.50 - 18.0 (5.85 ± 5.01)
A	NSAF station 100	Only one station, so no similarity		122	92.1	80.2

Table 8. R^2 values for linear and quadratic regression of species abundance (from 2010 sites) on environmental variables. Significance for whole equation is denoted by stars: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

Parameter	Fit	<i>Axinopsida serricata</i>	<i>Nutricola lordi</i>	<i>Ennucula tenuis</i>	<i>Macoma carlottensis</i>	<i>Acila castrensis</i>
Latitude	Linear	0.007	0.044*	0.021	0.012	0.005
	Quadratic	0.086**	0.084**	0.055*	0.106**	0.054*
Depth (m)	Linear	0.082**	0.128***	0.034*	0.139***	0.057**
	Quadratic	0.082**	0.158***	0.065*	0.146***	0.116***
MGS (μm)	Linear	0.003	0.204***	0.071	0.049*	0.043*
	Quadratic	0.062*	0.204***	0.072*	0.069*	0.046
Mid-core silt-clay (%)	Linear	0.002	0.139***	0.072**	0.009	0.019
	Quadratic	0.037	0.172***	0.080**	0.329***	0.128***
TOC %)	Linear	0.0000	0.185***	0.041*	0.097***	0.167***
	Quadratic	0.079*	0.255***	0.095**	0.106**	0.432***
Temperature (°C)	Linear	0.004	0.019	0.059*	0.127***	0
	Quadratic	0.02	0.171***	0.121**	0.149***	0.017
DO (ml/L)	Linear	0.083**	0.019	0.286***	0.0000	0.005
	Quadratic	0.092**	0.028	0.348***	0.168***	0.014

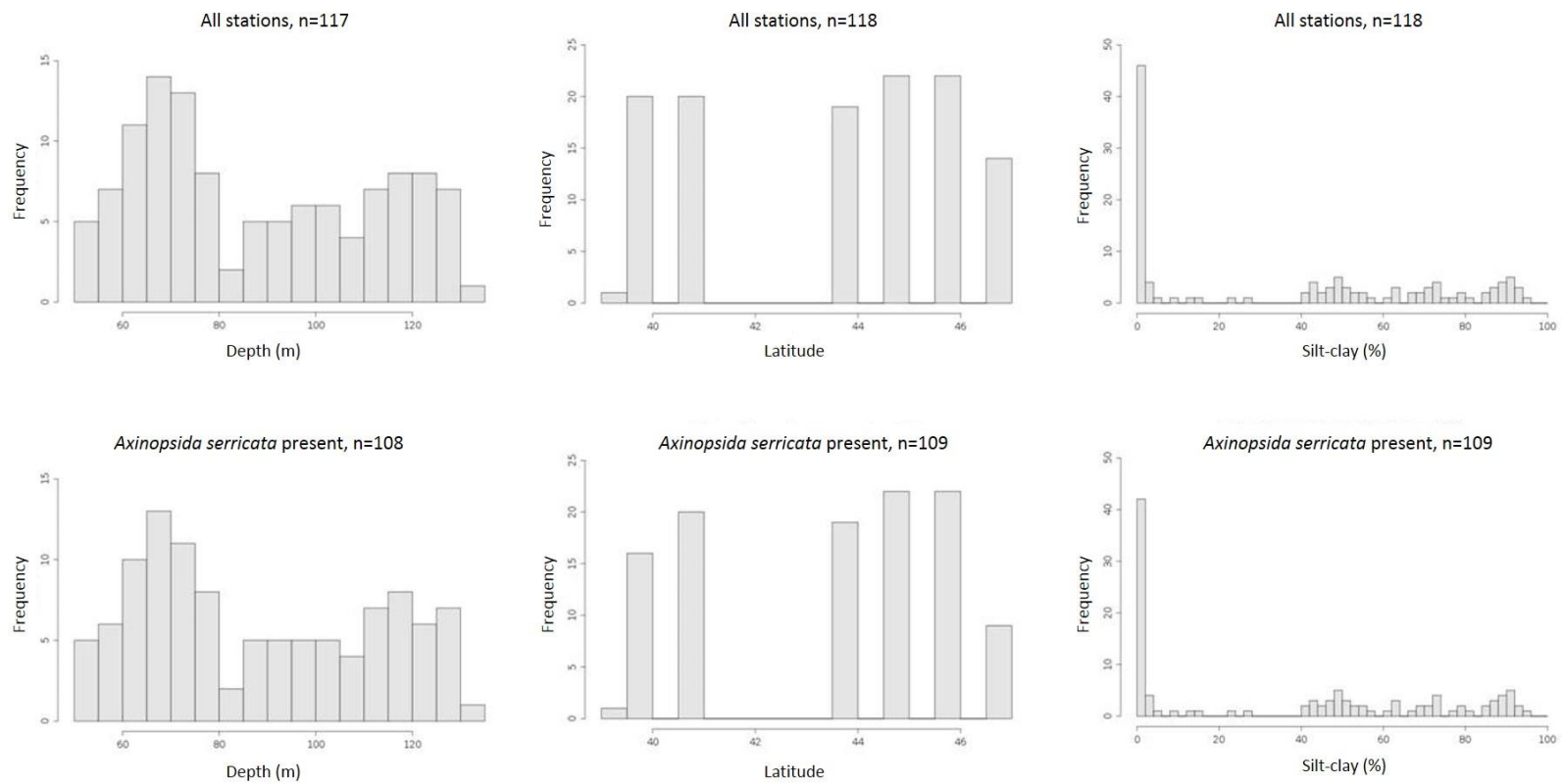


Figure 11. Frequency occurrence histograms of *Axinopsida serricata* presence based on depth, latitude, and percent silt-clay of sediment. One Newport station, where depth was not recorded, was removed from total stations for the depth histogram.

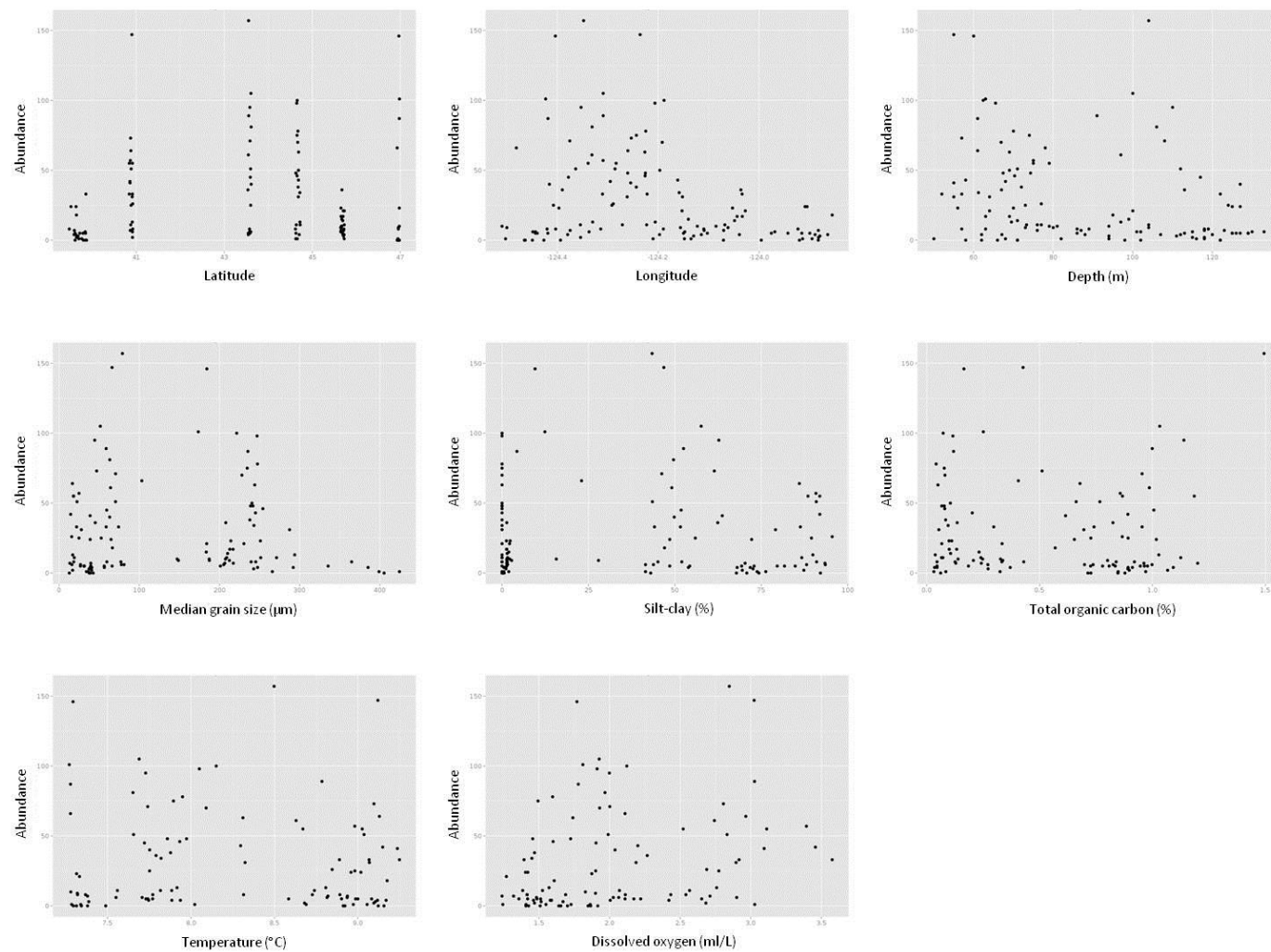


Figure 12. Scatterplots of *Axinopsida serricata* abundance in relation to environmental variables.

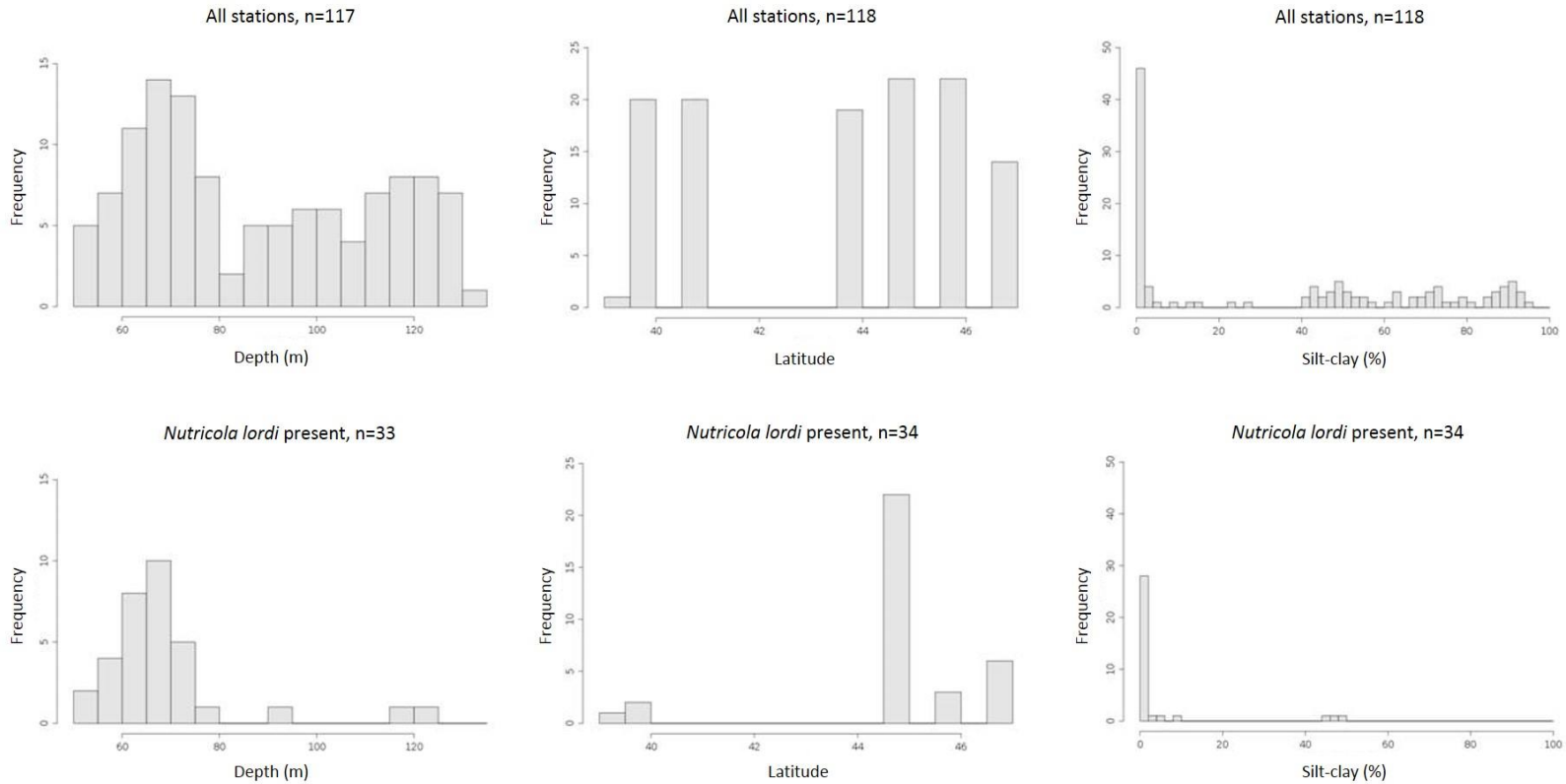


Figure 13. Frequency occurrence histograms of *Nutricola lordi* presence based on depth, latitude, and percent silt-clay of sediment. One Newport station, where depth was not recorded, was removed from total stations for the depth histogram.

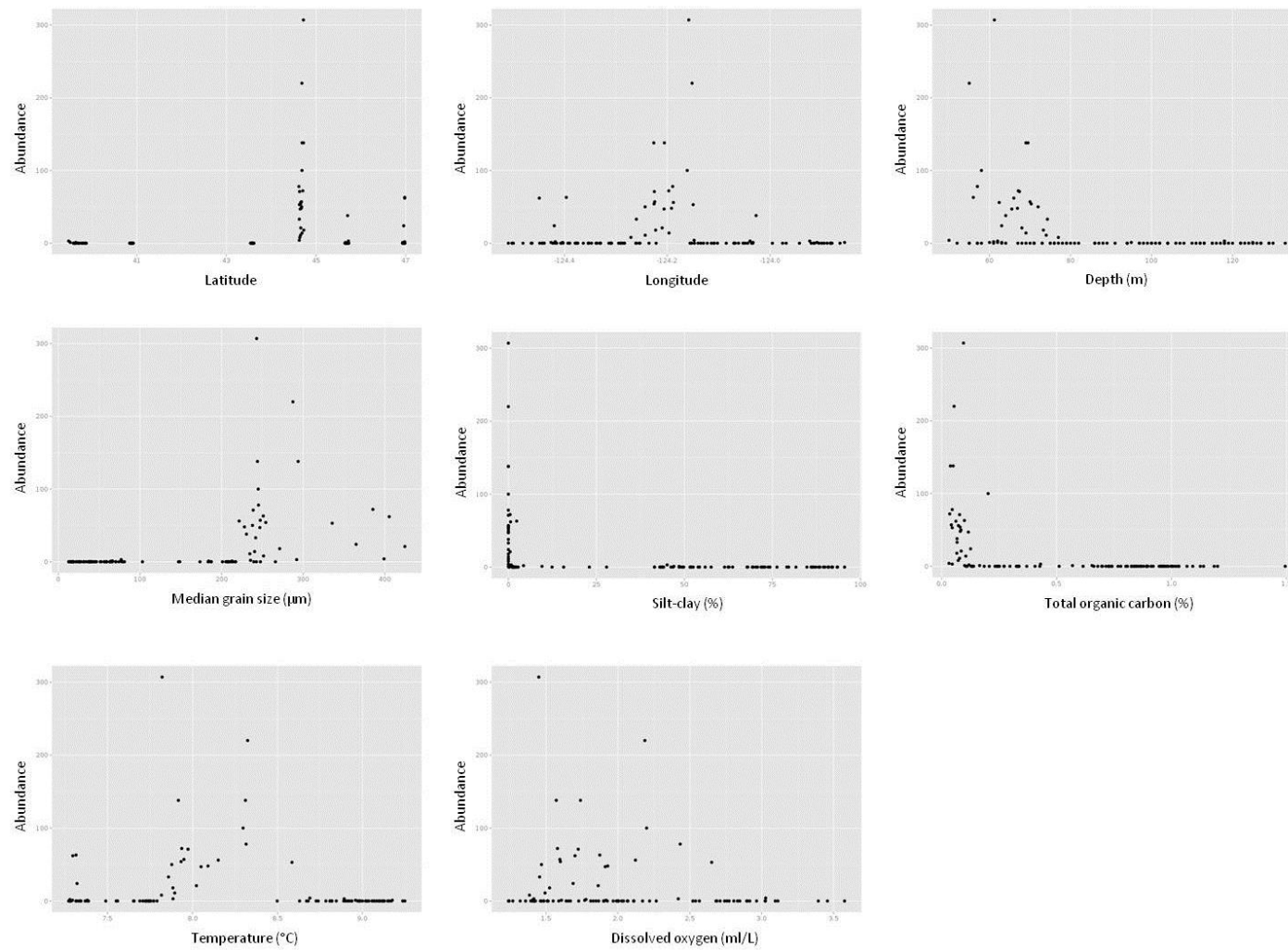


Figure 14. Scatterplots of *Nutricola lordi* abundance in relation to environmental variables.

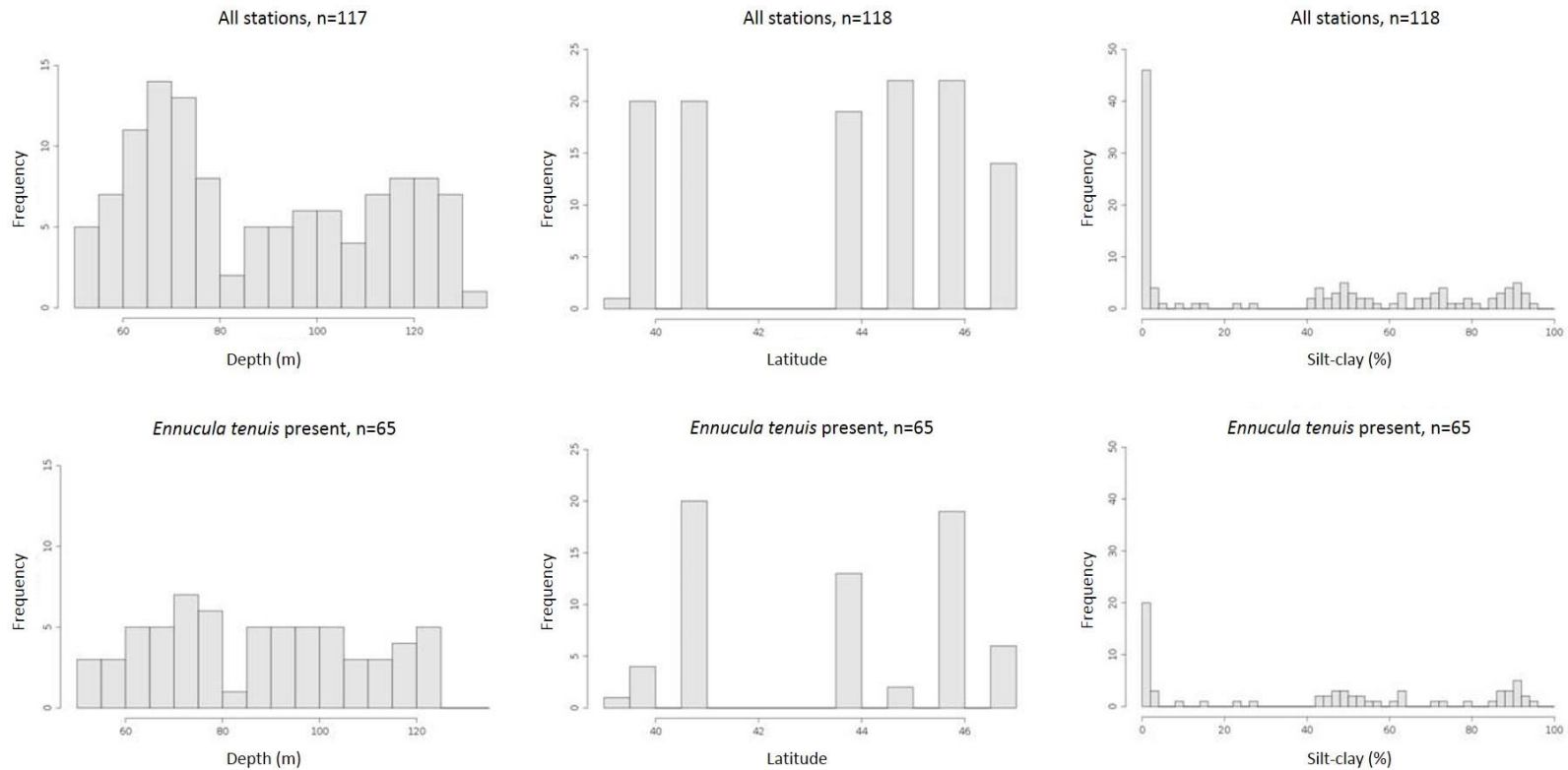


Figure 15. Frequency occurrence histograms of *Ennucula tenuis* presence based on depth, latitude, and percent silt-clay of sediment. One Newport station, where depth was not recorded, was removed from total stations for the depth histogram.

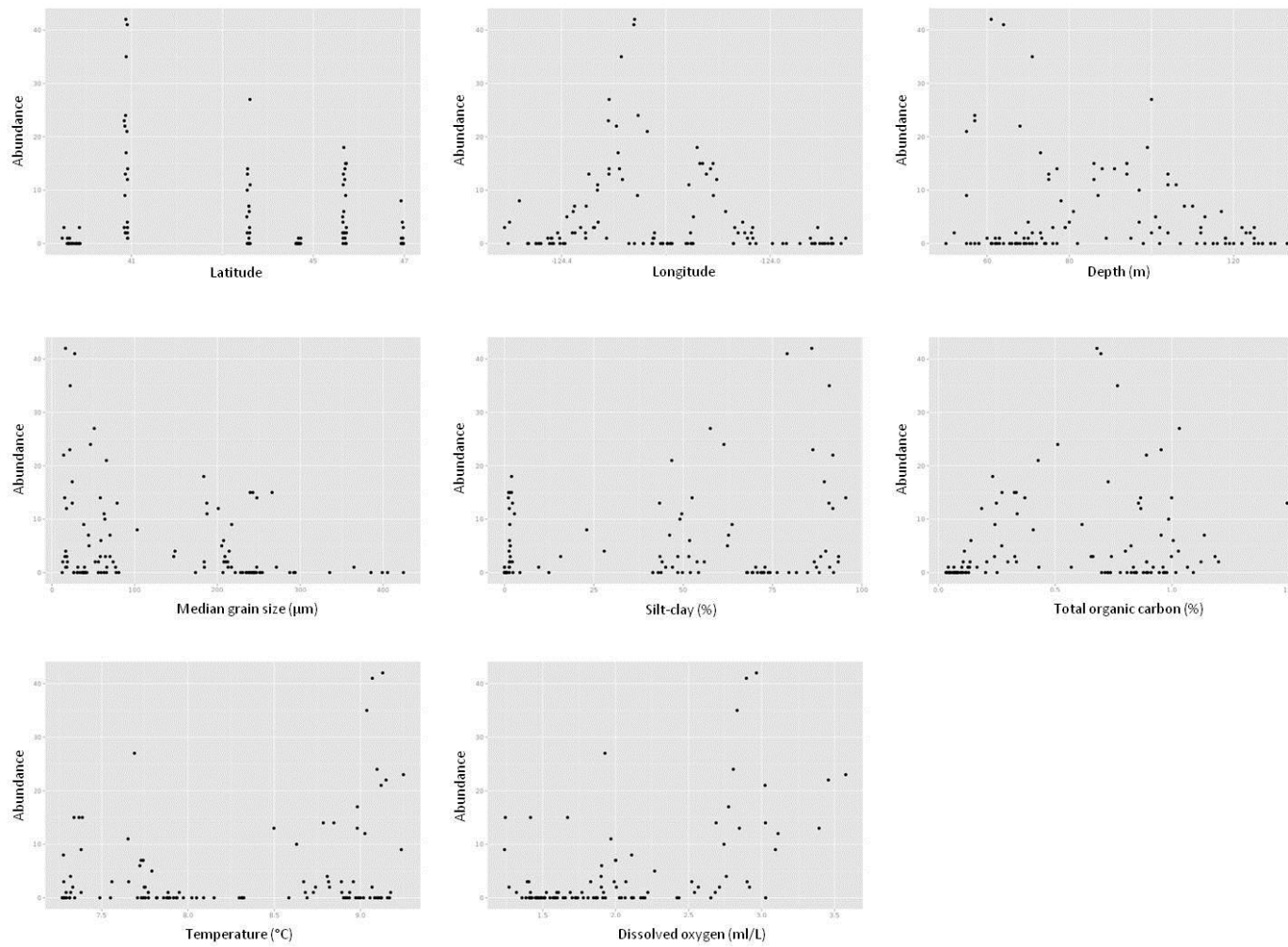


Figure 16. Scatterplots of *Ennucula tenuis* abundance in relation to environmental variables.

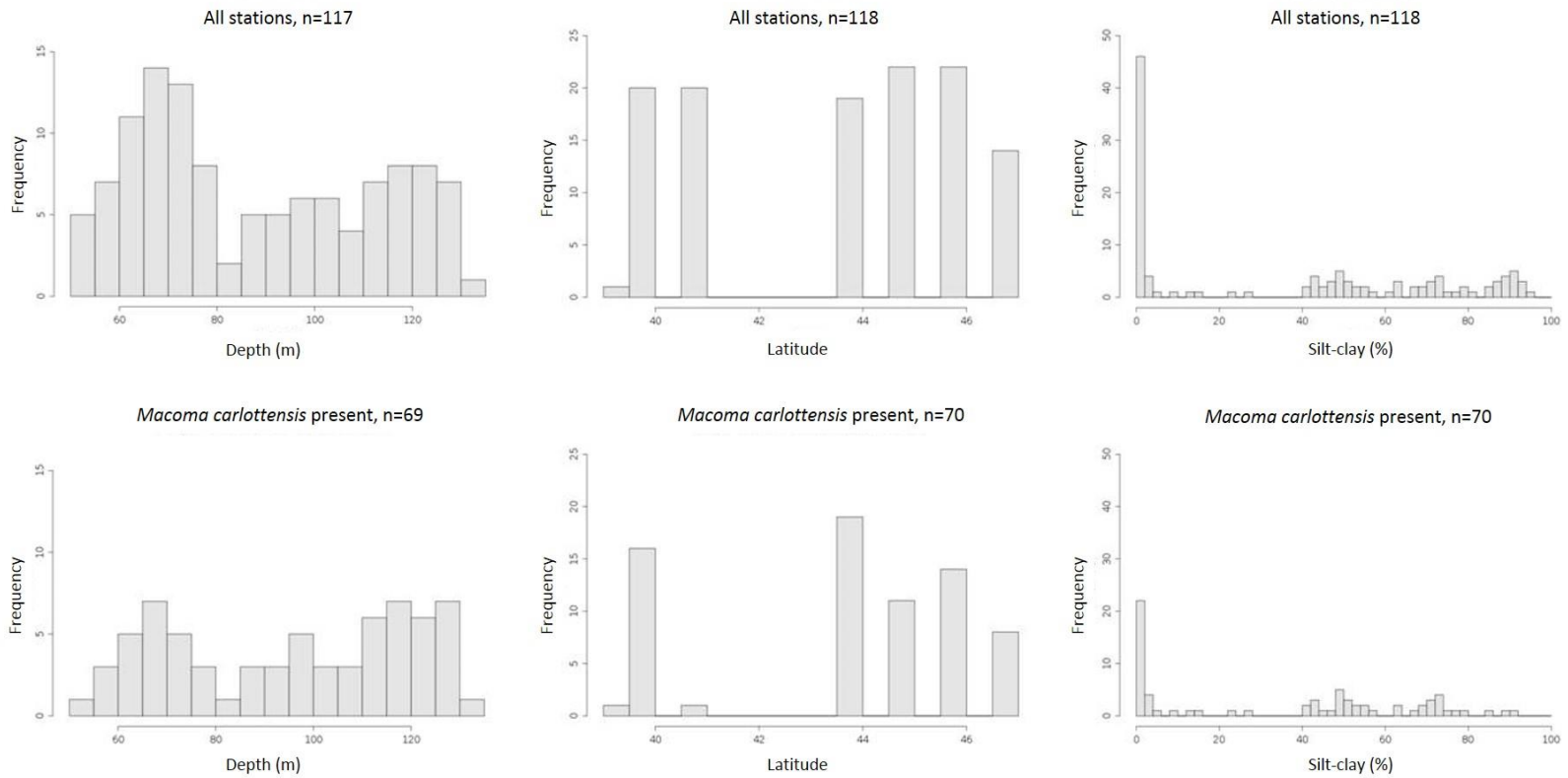


Figure 17. Frequency occurrence histograms of *Macoma carlottensis* presence based on depth, latitude, and percent silt-clay of sediment. One Newport station, where depth was not recorded, was removed from total stations for the depth histogram.

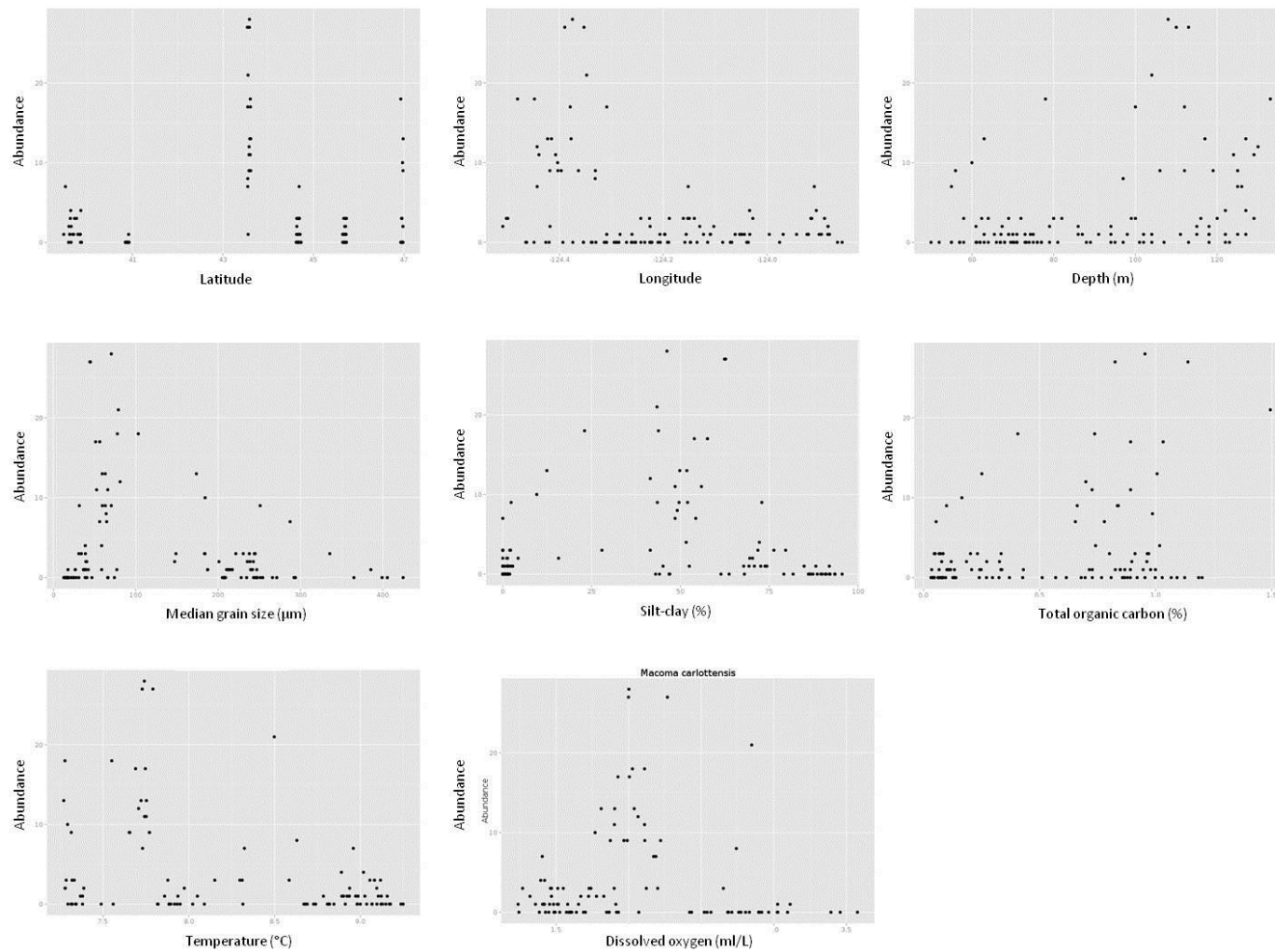


Figure 18. Scatterplots of *Macoma carlottensis* abundance in relation to environmental variables.

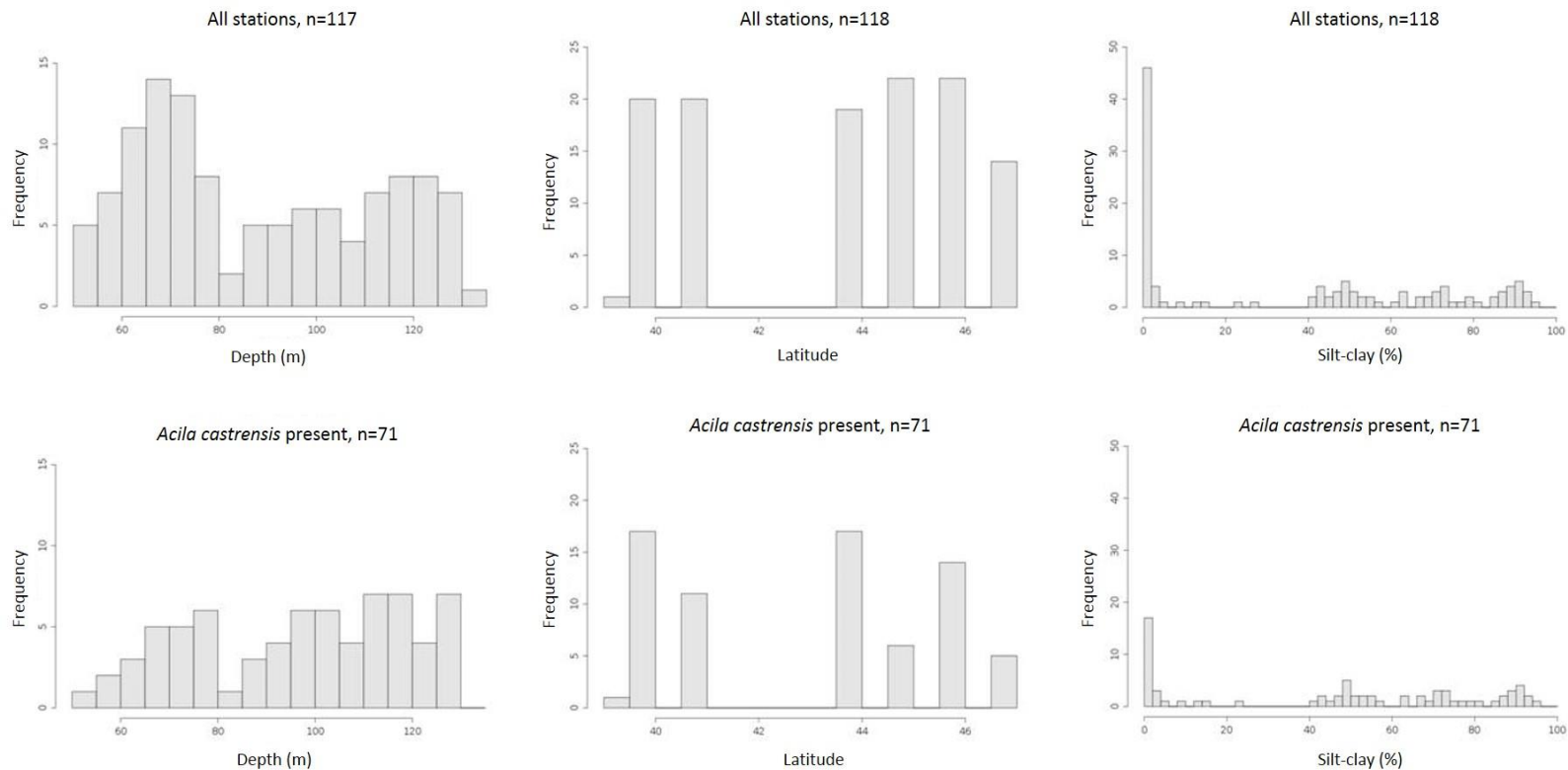


Figure 19. Frequency occurrence histograms of *Acila castrensis* presence based on depth, latitude, and percent silt-clay of sediment. One Newport station, where depth was not recorded, was removed from total stations for the depth histogram.

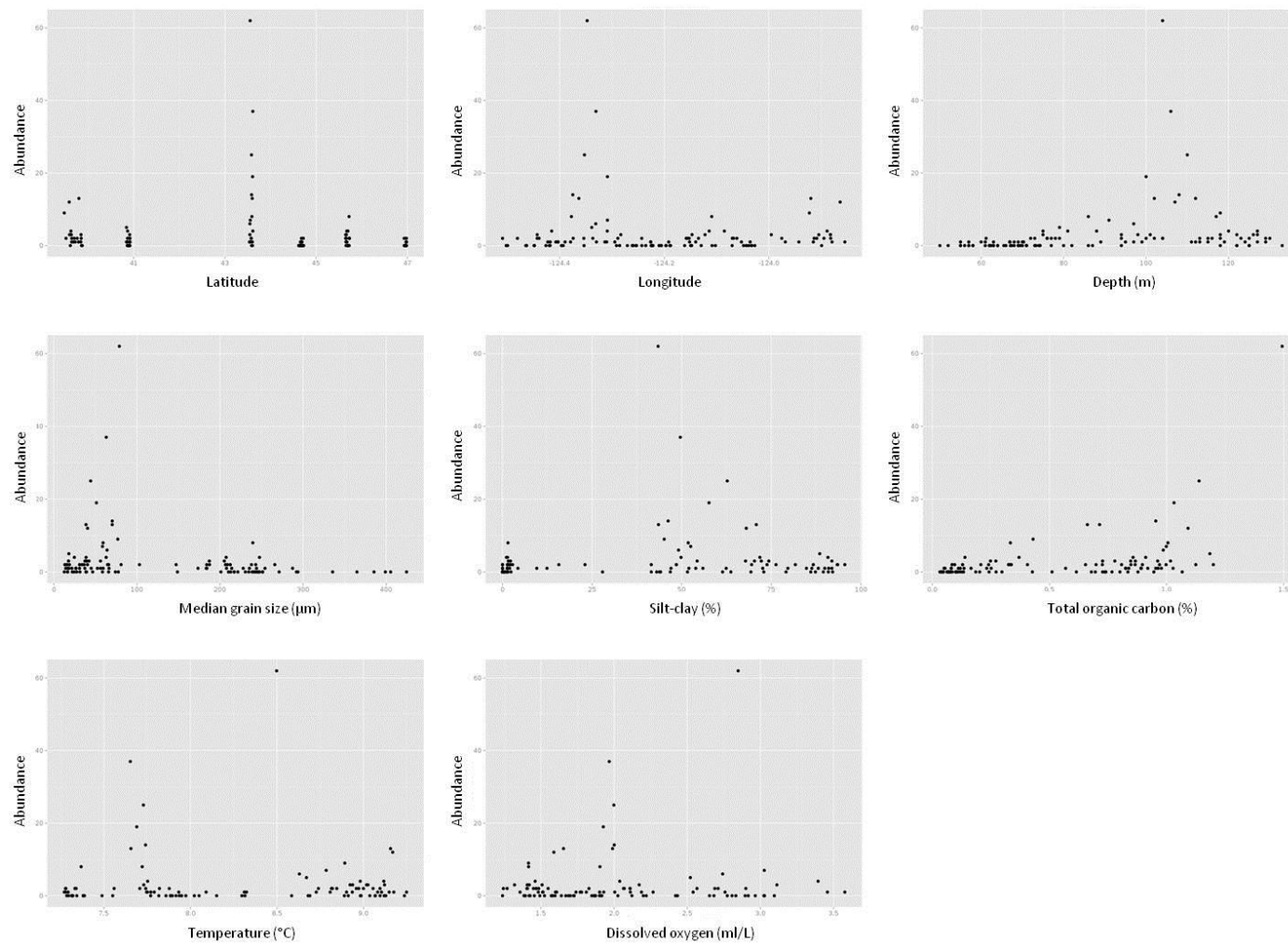


Figure 20. Scatterplots of *Acila castrensis* abundance in relation to environmental variables.

Table 9. Negative binomial models for the most abundant bivalve species. Significance is denoted by stars:
 $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***)).

Species	Theta	BIC		(Intercept)	Longitude	Depth	Depth ²	Temp	Temp ²	DO	DO ²	Silt-clay	Silt-clay ²
<i>Axinopsida serricata</i>	1.333	933.6	Est.	4.2737***	-2.1990*	-0.0313***		0.1524	-0.9038**			0.0099	-0.0006***
			Std. Err.	0.2820	0.8802	0.0071		0.3502	0.3401			0.0081	0.0001
<i>Ennucula tenuis</i>	0.976	470.8	Est.	1.0986*	2.8966	-0.0039	-0.0018***	-2.1382***	2.1105**	1.5734**	1.5767***	0.0376**	-0.0007***
			Std. Err.	0.4794	1.5090	0.0127	0.0003	0.6122	0.6592	0.5103	0.4443	0.0137	0.0002
<i>Macoma carlottensis</i>	1.599	426.4	Est.	2.5575***				-0.7259**		0.1524	-1.5077**	0.0164**	-0.0013***
			Std. Err.	0.2274				0.2568		0.2519	0.5102	0.0050	0.0002
<i>Acila castrensis</i>	1.497	401.2	Est.	2.4837***		0.0286***	-0.0021***					0.0159***	-0.0008***
			Std. Err.	0.2679		0.0076	0.0003					0.0045	0.0002

4. DISCUSSION

4.1. Sediment type and bivalve assemblages

Although sediment was expected to be a major influence on bivalve presence and abundance, it did not hold true that all sites with similar sediment characteristics contained the same bivalve assemblages. The southern sites (NSAF, Eureka, and Siltcoos) tended to have sediment which was, on average, at least 50% silt-clay; these sites did look similar in their average bivalve assemblages. However, stations in these sites generally fell into one of three bivalve assemblage groups: shallow, very silty stations (Eureka); mid-depth, sand/silt mix stations (Siltcoos); and deep stations with sand/silt mix to mostly silty sediment (Siltcoos and NSAF). It appears that, at least for characteristic bivalve assemblages within relatively silty areas, differences in distribution were more representative of differences in depth than differences in actual percent silt-clay.

Within the very sandy sites (Newport, Nehalem), there were also large differences in bivalve assemblages between sites. Although Newport and Nehalem displayed similar sediment characteristics (<4% silt-clay top core, <1.5% silt-clay mid-core), and were also extremely similar in regards to all other examined environmental variables, they displayed very different bivalve assemblages. The additional sandy site sampled in 2012 corroborates the importance of even small amounts of silt-clay in sandy sediment: both the sediment (<1% silt-clay) and bivalve assemblage (dominated by *Nutricula lordi*) at Cape Perpetua were more similar to Newport than to Nehalem. Ultimately, within sandy areas, differences in observed bivalve assemblages were reflective of differences in actual percent silt-clay of sediment. The difference in sediment did not need to be large – here, a change from 0% to less than 4% silt-clay was associated with a complete change in bivalve assemblage.

4.2. Latitude and bivalve richness

Although the latitudinal range covered in the BOEM surveys wasn't exceptionally large, it did cover a substantial portion of the US west coast continental shelf. As such, it was expected that if any trend was observed, it would be that bivalve richness (number of bivalve species) would be highest at the southernmost site and decrease northward. However, for the 2010 data, bivalve richness actually showed a general increase from south to north, with the exception of Newport, which had very low richness. In fact, the northernmost site (Grays Harbor) contained the greatest number of bivalve species.

Interestingly, Roy et al. (2000) found that for bivalves in general, and infaunal bivalves in particular, although the general trend is decreasing richness towards the pole, there is actually a slight increase in richness between 45 and 50 degrees north. Grays Harbor falls within this range, so it is possible that the richness of this site is not due solely to the diversity of habitats sampled (including the only gravel stations), but rather in line with larger scale patterns of infaunal bivalve richness. High richness in this latitudinal area could be due an overlap of arctic and temperate marine ecoregions (e.g. Spalding et al. 2007): bivalve species usually found in the Alaskan/Arctic ecoregions could have traveled south into the Oregon/Washington ecoregion. Although, if overlapping ecoregions was the cause for increased richness, the ecoregion-adjacent sites of NSAF and Eureka would be expected to have relatively high richness, which was not the case.

When the two 2012 sites are considered with the six 2010 sites, the original pattern becomes less clear, although Grays Harbor still contained the highest bivalve richness. Richness at Cape Perpetua was relatively low, like Newport, not surprising since both sites contained similar sediment and bivalve assemblages. Coquille displayed much lower richness than Siltcoos, which was the closest site in terms of latitude. This could be due to the presence of gravel stations at Coquille, which generally contained fewer bivalves than sand/silt stations and fewer bivalves compared to the Grays Harbor gravel stations in particular.

4.4. Dominant bivalve species

Abiotic models did not fit well for the most abundant bivalve species. *Axinopsida serricata* was found in high abundance throughout the survey range, and seems to be a habitat generalist, so an environmental model of habitat variables was not able to effectively describe patterns in abundance. Models for *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis* displayed poor fit due to pre-existing clustering in the abundance data which could not be adequately explained by the examined environmental variables. For these three species, broad habitat limitations/preferences appear to exist, but biotic interactions or unexamined abiotic interactions are likely influential in structuring abundance patterns within generally favorable habitat. In the following discussion, I focus on the associations of species' abundance with environmental variables to the extent that such associations appear to exist and are useful in describing distribution patterns. This thesis is limited to the analysis of abiotic factors, but fully acknowledges that for the majority of the most abundant bivalve species, biotic or unexamined abiotic interactions are necessary components in adequately describing spatial patterns of species abundance.

4.4.1. Axinopsida serricata

Axinopsida serricata was the most abundant bivalve observed across all 118 BOEM stations sampled in 2010. It was the dominant bivalve species at every site except Newport, with the highest average abundance observed at Siltcoos. The species was found at nearly every station and displayed no apparent habitat restrictions in regards to any of the individual environmental variables considered.

As would be expected of a widespread, abundant species, *Axinopsida serricata* was a characteristic species for every unique bivalve assemblage, except the assemblage found at a single NSAF station. In fact, although characteristic abundance varied from assemblage to assemblage, *Axinopsida serricata* was the most abundant characteristic

bivalve for every assemblage except the Newport assemblage (for which *Nutricula lordi* was the most abundant characteristic bivalve).

Axinopsida serricata appears to be a habitat generalist, with few or no restrictions in regards to examined environmental variables. Although the abundance data for this species wasn't as clustered as it was for the other species, the residual plot of the negative binomial model suggested that the mean of the residuals was slightly below zero (a well-fitting model should produce a residual plot with points randomly scattered but centered around zero). Therefore, the model was not the best fit for the *Axinopsida serricata* abundance data. As would be expected of a generalist species, environmental variables were inadequate to properly model abundance patterns of the species. Since abiotic, environmental factors do not appear to limit abundance within the survey range, it is likely that other factors, such as food availability or abundance of predators, would more accurately model and describe abundance patterns for *Axinopsida serricata*.

Axinopsida serricata is a suspension feeder (Dufour 2005, Macdonald et al. 2010) and therefore might be expected to be found primarily in sand. However, since many species can switch feeding guilds (Snelgrove and Butman 1994) and multiple feeding guilds can utilize the same food source (Kamermans 1994), a strict suspension feeder/sand versus deposit feeder/silt split is unlikely and overlap between feeding guilds in a habitat is certainly possible (Snelgrove and Butman 1994). Therefore, being a suspension feeder does not necessarily mean that *Axinopsida serricata* should be restricted to sandy areas.

Although *Axinopsida serricata* is determined here to be a habitat generalist, this conclusion applies only to the spatial extent covered in these surveys. Essentially the entire range of soft-sediment habitat was sampled (100% sand to 100% silt), so referring to *Axinopsida serricata* as a soft-sediment habitat generalist is appropriate. (Although the focus of this thesis is on soft-sediment habitats, it should be noted that *Axinopsida serricata* was rarely observed in areas with gravel, possibly because its small size and delicate shell make it too fragile for non-soft-sediment habitats.) Stations shallower than

50 meters or deeper than 133 meters were not sampled, so this survey cannot speak to possible depth limitation outside this depth range.

Fortunately, previous research about the spatial distribution of this species corroborates the characterization of *Axinopsida serricata* as a (soft-sediment) habitat generalist. Lie (1968) noted that the distribution of *Axinopsida serricata* couldn't be explained by either depth or sediment type in the Puget Sound – the species was found in all areas sampled. Likewise, Lie and Kisker (1970) found that *Axinopsida serricata* was present in all three described benthic infaunal communities (deep water mud-bottom, intermediate depth sand-bottom, and shallow water sand-bottom) on the continental shelf off Washington. These described communities covered a greater depth range than did the BOEM sites, suggesting depth limitation for *Axinopsida serricata* is unlikely.

Latitudinal restrictions, however, remain a possibility. Although a relatively large range of coastline was covered in the BOEM surveys, sites generally fell within the Oregon/Washington/Vancouver Coast ecoregion. A 2003 survey by the Environmental Protection Agency (EPA) of the continental shelf for the entire US West Coast (Nelson et al. 2008) suggested a latitudinal pattern of increasing abundance poleward for *Axinopsida serricata*, which is most apparent outside the latitudinal range covered by the BOEM surveys. In the EPA survey, *Axinopsida serricata* displayed lower abundances in the Southern California Bight/Northern California ecoregions and higher abundances in the Oregon/Washington/Vancouver Coast ecoregion, with the highest abundances observed north of the Grays Harbor site sampled during the BOEM survey. In the BOEM surveys, although *Axinopsida serricata* abundance did not display a strong association with latitude, the species did exhibit relatively low abundances at the southernmost site of NSAF, which could be a reflection of the transition from the Oregon/Washington/Vancouver Coast ecoregion to the Northern California ecoregion.

4.4.2. *Nutricula lordi*

Nutricula lordi was observed primarily at Newport, with both the highest relative abundance and highest absolute abundance observed at that site. This species was especially unique because despite its limited range, it was the second most abundant bivalve across all six 2010 sites. Compared to the other abundant species considered, *Nutricula lordi* appeared to be the most specialized in terms of habitat.

Although *Nutricula lordi* was observed primarily at a mid-latitude site (Newport), the SIMPER results support the conclusion that *Nutricula lordi* is restricted by sediment type (<1-2% silt-clay), rather than latitude in particular: the Newport SIMPER group (i.e. the bivalve assemblage dominated by *Nutricula lordi*) also included two Nehalem stations and three Grays Harbor stations which were different in latitude but very similar in sediment type. The SIMPER assemblage results also support the conclusion that it is sediment, rather than depth, which was most influential: Grays Harbor stations of a similar depth to Newport, but with different sediment, were not included in the Newport-dominated *Nutricula lordi* assemblage group.

The very different bivalve assemblages at Newport and Nehalem provide support for the theory that *Nutricula lordi* is restricted by sediment to very sandy (<1-2% silt-clay) areas. *Nutricula lordi* was very abundant at Newport but essentially absent at Nehalem even though the sites were very similar in terms of environmental variables, with only a small difference in sediment type: Newport had an average of 0.05% silt-clay (top core and mid-core) and Nehalem sediment averages ranged from 1.48% (mid-core) to 3.91% (top core) silt-clay. Based on the differences in overall bivalve assemblages and *Nutricula lordi* abundance between the two sites, *Nutricula lordi* seems limited to sandy sediment with essentially no silt-clay (generally less than 1-2% silt-clay).

This theory is further corroborated by data from the regional survey conducted by the EPA in 2003 (Nelson et al. 2008). In that survey, *Nutricula lordi* was found at only a few stations, which were spread across a range of latitudes and other environmental variables. Percent silt was the only meaningful common factor among stations: as in the

BOEM survey, *Nutricola lordi* was observed only in stations with very low silt (nearly 100% sand).

Because nearly all high abundances of *Nutricola lordi* were observed in <1% silt-clay, differences in MGS better reflect actual differences in abundance within these very sandy areas. For instance, within the Newport stations with 0% silt-clay, there was a difference of over 150 μm between the smallest and largest MGS. The differences in MGS within Newport and Cape Perpetua, and between these two sites, suggest a potential optimal sand grain size for *Nutricola lordi*: the highest abundances were observed in stations with 250-300 μm MGS, and there was a general trend of decreased abundance above 400 μm . Thus, the larger MGS at Cape Perpetua can explain the lower average abundance of *Nutricola lordi* at that site compared to Newport. It seems that while silt-clay is an indicator of presence/absence of *Nutricola lordi*, MGS is the best environmental predictor of *Nutricola lordi* abundance within very sandy (<1% silt-clay) areas.

The habitat limitation of *Nutricola lordi* may be related to its feeding guild. Suspension feeders are generally assumed to be generalists in regards to food (likely because many are sessile) whereas deposit feeders are more specialized (likely because they are often more mobile) (Levinton 1972, Olafsson 1986). Consequently, as Olafsson (1986) put it: “while deposit-feeder population densities should be closely related to variables concerned with food availability, i.e. density-dependent regulation, suspension-feeder populations should be more related to physical characteristics of the sediment-water interface, i.e. non-density dependence.” Since *Nutricola lordi* functions as a suspension feeder (Macdonald et al. 2010), it is not unexpected that its abundance would be strongly associated with abiotic, environmental parameters. (Although clearly, the association is not universal – both *Axinopsida serricata* and *Nutricola lordi* are suspension feeders, but appear to be habitat generalist and specialist species, respectively.)

Although sediment type seems to be influential on the distribution of *Nutricola lordi*, the reproductive strategy of this species could also contribute to the limited spatial range of this species observed in the BOEM survey. Although there is little direct information about the life history of *Nutricola lordi*, closely related species have been studied in more detail and can provide information about likely characteristics of *Nutricola lordi*. For example, a well-studied bivalve in the same family, *Gemma gemma*, has no pelagic stage, but rather broods its young, skipping an independent larval stage and being released as fully-shelled infaunal juveniles (Sellmer 1967). Consequently, dispersal is a result of juvenile and adult movement via passive bedload and suspended load transport, which is reflected in local abundances (Commito et al. 1995). Likewise, two species in the same genus as *Nutricola lordi* – *Nutricola tantilla* and *Nutricola confusa* – are also brooding bivalves (Geraghty et al. 2008), so dispersal is entirely due to juvenile and adult travel. Therefore, it is likely that *Nutricola lordi* also lacks a pelagic larval stage, in which case, limited range would be expected.

Since these conclusions are based on observational data, sediment preference experiments would be required to demonstrate a causal link between variable *Nutricola lordi* abundance in sand, and *Nutricola lordi* absence in silt. In such an experiment, *Nutricola lordi* larvae would be given a choice of sediment upon which to settle and preferences would be recorded. Such experiments could also test whether it is some other property of sediment, besides lack of silt and grain size (i.e. biological or chemical cues) which make this type of sediment attractive for the species (see Gray 1974 for a review of the general methods of such experiments). Experiments such as these would be able to separate preferable sediment from limited dispersal range in terms of which property is more important in determining *Nutricola lordi* abundance.

In summary, based on the above discussion, I conclude that *Nutricola lordi* is likely restricted by sediment type to very sandy (<1-2% silt-clay) environments; within these areas, abundance is governed primarily by median grain size.

4.4.3. *Ennucula tenuis*

Ennucula tenuis was the third most abundant bivalve in the 2010 BOEM survey. The highest abundances were found at relatively shallow (60-80 m), very silty stations, which was somewhat unusual since, aside from Eureka, shallow stations were typically sandier. *Ennucula tenuis* distribution appeared to follow a hierarchy of habitat preferences. Based on the patterns observed in exploratory plots, depth was the first criteria, followed by sediment type: *Ennucula tenuis* was generally found in areas shallower than 110 meters and within that depth range, it was observed in sediment with >1% silt-clay.

It is unclear whether *Ennucula tenuis* has a planktonic larval stage during which depth and sediment would be important for settlement preference. Thorson (1936) noted that the species is either non-pelagic or has only a very short pelagic stage. Information from the genus and family level does little to resolve the issue. Some sublittoral species from the same family as *Ennucula tenuis* have a planktonic larval stage (*Nucula proxima* and *Nucula annulata*) while others undergo direct development without a pelagic stage (*Nucula delphinodonta*) and a deep-sea species from the same genus (*Ennucula similis*) undergoes direct development with no pelagic stage (Schetlema and Williams 2009). Without further information or experiments about the possible pelagic stage of *Ennucula tenuis* larvae, it is difficult to say whether the absence of this species in sand is due to a larval settlement preference or some other factor.

For instance, the apparent sediment restriction could be due to competition with other bivalve species. At an assemblage level, the Siltcoos- and Nehalem-dominated groups (E and G) were characterized by the same four species (*Axinopsida serricata*, *Macoma carlottensis*, *Acila castrensis*, and *Ennucula tenuis*), but *Ennucula tenuis* was respectively the least abundant and most abundant characteristic bivalve, even though there were similar abundances of it in both groups. The abundance patterns could be a result of *Ennucula tenuis* outcompeting other common bivalve species in sandier environments (such as Nehalem) as long as there was >1% silt-clay, since as a deposit

feeder (Koulouri et al. 2006, Macdonald et al. 2010), it would likely be at a disadvantage in pure sand environments due to decreased TOC.

Although depth and sediment restrictions are most easily identified, distribution patterns could also be associated with water column variables. Both temperature and DO terms were included in the *Ennucula tenuis* model and, since the variables were correlated with one another, it is not possible to conclude which is of primary importance. However, given that DO alone explained almost 30% of variability in abundance of *Ennucula tenuis* – more than twice the variability that temperature explained alone – DO may be more influential in determining spatial variability for this species. Patterns in DO can also explain the apparent depth limitation, since deeper stations tended to have lower DO than shallower stations. However, since this is only an observational study, laboratory experiments would be required to determine threshold concentrations of DO for this species as well as possible subsequent behavioral effects, such as reduction of burial depth.

4.4.4. Macoma carlottensis

Macoma carlottensis was the fourth most abundant bivalve observed across the six 2010 BOEM sites. The highest absolute abundances for this species were observed at Siltcoos, but certain stations at Grays Harbor also contained high abundances of *Macoma carlottensis*. Due to its relatively wide range in regards to environmental variables, characteristic average abundances were observed in four unique bivalve assemblages, with the highest characteristic abundance in the Siltcoos-dominated SIMPER group, as would be expected.

The instances of abundant *Macoma carlottensis* at the two very different sites of Siltcoos (deep, sand/silt mix) and Grays Harbor (shallow, sandy) can be explained by the feeding method of *Macoma carlottensis*, which can function as both a suspension feeder and a deposit feeder (Bright and Ellis 1989, Todd 2001, Macdonald et al. 2010). Olafsson (1986) found that the closely related species *Macoma balthica* functioned as a deposit

feeder in muddy sediment and a suspension feeder in sandy sediment. The abundant *Macoma carlottensis* at the shallow, sandy Grays Harbor stations likely function as suspension feeders and can be considered a separate type of population than that observed at Siltcoos.

Outside the Grays Harbor population, it appeared as though the spatial pattern of *Macoma carlottensis* could be partially explained by percent silt-clay of sediment: *Macoma carlottensis* was found primarily in areas where sediment was comprised of a relatively equal mix of sand and silt (i.e. Siltcoos), and generally not found in areas which were very silty. The inclusion and significance of silt-clay terms into the *Macoma carlottensis* model lend support to the importance of sediment in regards to abundance distribution. Although depth was not included in the models, it was highly correlated with percent silt-clay. Since silt-clay was associated with abundance, depth was also expected to be associated with abundance distribution. However, considering these results in light of the variable feeding guild of *Macoma carlottensis*, sediment characteristics are likely more influential than depth and latitude: difference in feeding guild can explain *Macoma carlottensis* populations in different types of sediment, but differences in depth, while correlated with differences in sediment, are unlikely to be influential per se on abundance.

Given the Grays Harbor (sandy) and Siltcoos (sand/silt mix) populations, the absence of a *Macoma carlottensis* population in silty areas suggests some other factor may be working in conjunction with silt-clay to drive spatial distribution. This concept has been noted previously: Lie (1968) found that although *Macoma carlottensis* did seem to show a preference for fine sediment over coarse sediment, sediment type could not entirely explain its distribution. Additionally, Dunnill and Ellis (1969) found that of 13 *Macoma* species, *Macoma carlottensis* was the “most tolerant” of changes in sediment type.

Differences in TOC could explain the observed variations in *Macoma carlottensis* abundance in sand/silt and silty areas. Although TOC was dropped from model analysis

due to high correlation with other variables, it was significantly positively correlated with silt-clay and could potentially be the sediment variable of primary importance for this species. For instance, *Macoma carlottensis* was observed primarily at Siltcoos, the site which had the highest average TOC as well as the most equal mix of silt-clay and sand. In the 2010 BOEM survey, there was not much change in average TOC observed in sediments with 40-100% silt-clay. Therefore, there was no advantage from a deposit feeding perspective to prefer a higher percentage of silt-clay over 40-50%. A TOC-rich sand/silt mix could provide an advantage to a species which could switch feeding methods: rather than being restricted to a certain feeding guild by its sediment environment, a mix of sand and silt would allow *Macoma carlottensis* to base its feeding mode on food availability instead. Depending on whether water column particles or sediment-based particles were more plentiful at any given time, *Macoma carlottensis* could function as either a suspension feeder or deposit feeder. In a mixed sediment environment, the ability to switch feeding guilds could confer a competitive advantage against other bivalves, which may be more restricted in their feeding methods, or simply be a way to take advantage of open niche space.

4.4.5. Acila castrensis

Acila castrensis was the fifth most abundant bivalve observed across the six 2010 BOEM sites. Although *Acila castrensis* was relatively most abundant at NSAF, the highest absolute abundances were observed at Siltcoos. This species was most rare at Newport. As a result, *Acila castrensis* was observed primarily between 100-120 meters and 40-70% silt-clay.

The model for *Acila castrensis* was comprised entirely of depth and silt-clay terms. *Acila castrensis* has a pelagic development stage (Zardus and Morse 1998), so depth and sediment type would play a role in where larvae settle. Since *Acila castrensis* is a deposit feeding bivalve (Stasek 1961, Todd 2001, Macdonald et al. 2010), TOC would also play an important role in post-settlement growth and survival. Although excluded

from the modeling process, TOC was significantly positively correlated with silt-clay and a quadratic equation of TOC alone explained about 43% of the variability in abundance of *Acila castrensis*.

In an observational study such as this, it isn't possible to definitively conclude which of the three correlated variables – depth, silt-clay, TOC – is the primary influence on abundance distribution for this species. However, I hypothesize that the apparent depth and sediment limitation could be due to a preference for higher TOC. In the BOEM survey, the depth range where *Acila castrensis* was observed was the depth range of the non-sandy (40-100% silt-clay) stations – a sediment preference could explain the apparent depth restriction. Likewise, observing *Acila castrensis* primarily in 40-70% silt-clay could be due to the TOC in the sediment: generally, higher abundances of *Acila castrensis* were associated with higher TOC, but there was not much change in average TOC in sediment with over 40% silt-clay.

More generally, it could be that while depth and sediment are predictors of *Acila castrensis* presence/absence, abundance of adult populations is associated with amount of TOC in the sediment. The association between deposit feeding species and TOC is well-established. As noted previously, deposit feeders are likely regulated by density dependence and/or food availability (Levinton 1972, Olafsson 1986), and TOC is certainly a food source for deposit feeders (Lopez and Levinton 1987). TOC is often correlated with the distribution of benthic species and benthic communities (e.g. Longbottom 1970, Santhanam 2009) and has been hypothesized to be the actual causal factor responsible for the correlation of grain size with species distribution (Sanders 1958, Snelgrove and Butman 1994).

4.3 Variables for individual species versus bivalve assemblages

The spatial distribution of the most abundant bivalve species appeared to be influenced to some extent by sediment type, except for *Axinopsida serricata*, which appeared to be a true generalist within soft-sediment habitat. *Nutricula lordi* displayed

strict sediment limitations (<1-2% silt-clay) while *Macoma carlottensis* appeared to have two types of populations: those in sandy areas and those in sand/silt mix areas. The species *Ennucula tenuis* and *Acila castrensis* were associated with specific depth ranges as well as sediment type, with differences in DO and TOC, respectively, potentially further explaining variations in observed abundance.

Based on the BIO-ENV analysis, MGS, depth, and longitude had the highest correlation with all observed bivalve species, across sites. Given the importance of sediment to infaunal bivalve distribution in general, and the examined species in particular, it was expected that some measure of sediment type would be included in the best correlation. Both MGS and silt-clay are measures of sediment composition, but they are not exactly the same. MGS is representative of the average particle size, rather than percent sediment type, which can sometimes mask small changes in silt-clay: for instance, a change from 0.5% to 2% silt-clay is a four-fold difference, easily observed in a percentage scale and perhaps of great practical significance to a bivalve species, but the change in silt-clay would have only a small, even negligible, impact on the MGS. Although MGS is sometimes poor at reflecting changes in small particles, it does incorporate variability which can be masked by categorizing sediment as “sand,” which encompasses a range of grain sizes, from fine sand to very coarse sand (Wentworth 1922). While it is true that MGS sometimes fails to reflect practical differences in sediment type, the measure of particle size does incorporate percent silt-clay as well as differences in sand grains. Therefore, it’s not entirely unexpected that MGS, rather than silt-clay, would be the primary sediment characteristic best correlated to distribution of all bivalves.

The inclusion of longitude presents an interesting case. The variable was apparently important for all bivalve species throughout the BOEM survey (i.e. included in the best BIO-ENV correlation), as well as specifically associated with some of the individual species assessed (i.e. included in the species models). Longitude is likely associated with distribution because it is reflective of distance offshore along the

coastline. Since depth is a function of distance from shore, depth can be considered to vary with longitude. Furthermore, because the coastline curves and the shelf width is not constant, this depth/longitude relationship varies with latitude. However, latitude was never included as an important variable in the BIO-ENV output. Additionally, if longitude was reflecting how depth varies with distance from shore (which varies with latitude) depth wouldn't necessarily also be included as a single variable. Either depth is important enough to be present in two forms, perhaps masking the latitudinal variability, or longitude must incorporate a variety of factors not otherwise included. These factors could include shelf width itself, which is linked to riverine input (Chase et al. 2007) and primary production (Chase et al. 2005).

4.5 Limits to models and analysis

There are multiple possible drivers of spatial differences in species abundance. Generally, factors influential on community composition and species abundance can be considered bottom-up forces, such as resource availability or environmental factors, or top-down forces, such as predation (Hairston et al. 1960). These two types of forces are not mutually exclusive and communities are often impacted by a combination of both types of drivers (Hunter and Price 1992).

In the case of this research, which focuses on bottom-up/abiotic factors, top-down/biotic forces constitute important missing variables, especially since competition and predation can have a large effect on the spatial distribution of soft-sediment infauna (Wilson 1991). For bivalves specifically, distribution could be patchy or clumped due to biotic factors such as limited dispersal distance, due to lack of a pelagic stage or certain pelagic life history characteristics (Shanks 2009), or presence of conspecifics as a positive settlement cue (Tamburri et al. 1996). For juvenile and adult bivalves, intraspecific competition can strongly affect species' populations (e.g. Vincent et al. 1994).

Given the absence of intra- and inter-species interaction information for all sites, and hence biotic predictor data for all bivalve species examined, the relative variability explained by the environmental variables for each species gives an indication of not only which variables matter, but to what extent environmental variables in general are important for a particular species. That is, if physical variables can't explain most of the variation (i.e. an abiotic model isn't a good fit for the data), then biotic factors are likely influential in determining species' spatial distribution. However, since the five bivalves assessed here are for the most part unstudied, the necessary life history data to construct a better model would require extensive experimentation beyond the scope of these observational BOEM surveys and this thesis.

While biotic factors likely play a role, there is also the possibility that other abiotic factors, not investigated during the BOEM surveys and hence not included as explanatory variables in the models, would be strongly associated with species distribution and better able to describe patterns in species abundance. As noted previously, flow conditions can affect larval choice of habitat and settlement (Snelgrove et al. 1993, Abelson and Denny 1997, Snelgrove et al. 1998) possibly by resuspending larvae which subsequently act like passive particles (Butman et al. 1988). In fact, it has been argued that bottom flow, rather than grain size or sediment type, is the main determinant of spatial distribution for infaunal species. In a review paper, Snelgrove and Butman (1994) contend that since grain size is a "super parameter" (Jansson 1976) – with covariates including amount of organic matter, pore-water chemistry, and microbial presence – it is the covariate factors, rather than grain size, that are most likely the actual casual factors influencing distribution. Furthermore, because these covariate factors are all impacted by the hydrological regime – particularly boundary-layer and near-bed flow – it is flow conditions that ultimately drive spatial distribution (Snelgrove and Butman 1994).

Even if bottom flow isn't responsible for spatial distribution via impacts on grain size covariates, it might account for the strong relationship between species distribution and sediment in another way. Snelgrove and Butman (1994) note:

“...larvae may be deposited onto the seabed as passive particles...if characteristics of passive larvae and transported sediment grains (e.g. size, specific gravity, and gravitational fall velocity) are similar, then larvae and sediment could be hydrodynamically sorted in a similar manner...resulting in distinct animal-sediment associations. This mechanism...explicitly accounts for correlations between infauna and grain-size distributions, but grain size per se is irrelevant in producing the pattern.”

Therefore, variability in larval forms and larval transport may also constitute missing variables important for explaining spatial distribution of benthic infauna.

Near-bottom flow and bedload transport also affect post-settlement dispersal of juveniles (e.g. Sigurdsson et al. 1976, Lundquist et al. 2004) which has large impacts on patterns of adult distribution (Jennings and Hunt 2009). For settled bivalves, current speed of the boundary layer affects growth via food availability (Wildish and Kristmanson 1984): reduced flow means reduced food availability which in turn is associated with reduced growth. Furthermore, along with current speed, vertical mixing also plays a role (Frechette et al. 1993).

Ultimately, although the environmental variables assessed here are useful, there are inevitably other variables – whether measures of biotic interactions or abiotic factors, especially those at the small scale of the water/sediment interface – that have a large impact on the distribution and abundance patterns of benthic infauna, such as the bivalves discussed here. The missing variables do not necessarily detract from the conclusions drawn here, but rather emphasize the need for further research in order to better understand and describe the causal factors driving differences in spatial distribution for these species.

With the right explanatory variables (identified through extensive laboratory experiments), it would be possible to extend the species' models here to become predictive models, intended for more widespread practical use. Along with negative

binomial models, there are other, more complex, statistical methods available for modeling species distribution (e.g. Legendre et al. 1997, Thrush et al. 2003, Anderson 2008). For example, generalized additive models could prove useful for the species discussed here (see Meynard and Quinn 2007) .

5. RESEARCH SIGNIFICANCE

The oceanic environment is not static. Ocean conditions are changing globally, regionally, and locally – not only in response to changes in seasonal, inter-annual, or decadal environmental conditions but also in response to anthropogenic impacts (Boyd and Hutchins 2012). As climate change becomes a global issue (e.g. IPCC 2007), new and emerging “green” technologies are becoming highly sought after to meet energy demands.

The Oregon Renewable Portfolio Standard (RPS), enacted in 2007, requires Oregon large utilities to provide 25% of their electricity from renewable energy sources by 2025. To be on track for this goal, the RPS has a target of 15% renewable energy by 2015 (ODOE 2013). Large utilities in Oregon are primarily using wind energy to meet renewable demands but will need to increase renewable projects in order to meet the 2015 target (PacifiCorp 2012, Sickinger 2012). Wave energy is one renewable source that has the potential to meet these energy needs: the Pacific Northwest has substantial wave energy potential (Tillotson and Komar 1997, Lenée-Bluhm et al. 2011), with Oregon alone estimated to have 179 TWh/yr of available wave energy along the outer continental shelf and 143 TWh/yr along the inner shelf (EPRI 2011). Technical limitations restrict the amount of energy practically available, with about 42% of available wave energy along the US west coast estimated to be recoverable (EPRI 2011). Given that 1 TWh/yr can supply 93,850 homes with electricity for a year (BOEM 2013), a large amount of wave energy is available along Oregon’s coast, even with only a portion of potential energy recoverable.

Ocean wave energy conversion (WEC) devices are expected to have a significant ecological impact on the benthic environment. Direct effects include the alteration of the local hydrological regime, which may in turn alter local sediment transport dynamics and increase turbidity (Gill 2005, Cada et al. 2007). This disturbance, analogous to dredging/fishing disturbance, will likely cause a loss of sedentary infauna at local scales (Gill 2005). Additionally, sediment transport which alters neighboring habitats has the

potential to change the spatial distribution of local species as well as to attract new species to the area. These impacts are not limited to benthic infauna: decreases in abundance or changes in the spatial distribution of lower trophic levels will impact higher level predatory species (Gill 2005), which could in turn further affect their infaunal prey. These impacts are generally applicable to benthic environments; however, exact ecological responses will necessarily be site-specific. For some areas, impacts due to WEC projects are expected to be small compared to naturally occurring spatial and temporal variations (Langhamer 2010).

Although impacts due to WEC devices may be small compared to natural variations, these impacts are not occurring in a vacuum, but in conjunction with a host of other anthropogenic impacts. Benthic communities are expected to be under considerable pressure with predicted changes in seawater pH and temperature. Hale et al. (2011) concluded that “ocean acidification induced changes in marine biodiversity will be driven by differential vulnerability within and between different taxonomical groups,” with molluscs displaying the greatest vulnerability, in terms of abundance and diversity, to decreased pH and increased temperature. Furthermore, benthic responses are predicted to vary according to sediment type, with impacts occurring faster and to a greater extent on organisms in sandy sediment than organisms in muddy sediment (Widdicombe et al. 2008). Changes in abundance and diversity at multiple taxonomic levels will have far-reaching impacts, as a decrease in abundance of keystone species and/or ecosystem engineers will greatly change broad-scale community dynamics (Hale et al. 2011). In addition to the impacts of climate change, coastal zones (the locations of WEC sites) are often already highly impacted by human activities such as fisheries development, oil and gas production, nutrient pollution and eutrophication, and hypoxic events; wave energy development will add to the already substantial pressures faced by coastal ecosystems (Gill 2005). Given the large number of pressures already affecting potential WEC sites, cumulative impacts are an important aspect of WEC devices which will need to be considered (Cada et al. 2007).

In light of the complex interplay of potential impacts, prospective WEC sites need a significant amount of baseline research in order to assess site suitability as well as identify impacts following installation so that mitigation plans can be executed. Regional surveys about spatial variation in factors of interest can provide baseline data as well as inform possible outcomes of WEC impacts. Characterizing benthic habitats and communities is useful not only for providing a snapshot of current benthic composition, as discussed here, but also for providing baseline data which will be useful for future environmental assessments and environmental impact statements. For example, alterations in local benthic substrate may change available habitat at a small scale. If species-specific relationships with sediment are known, potential changes in local bivalve assemblages can be predicted. For instance, species such as *Nutricula lordi* which are sensitive to even small amounts of silt-clay in sediment may be expected to be more vulnerable to, or impacted by, changes in local substrate. Conversely, species with broad tolerances to soft-sediment types, such as *Axinopsida serricata*, may be expected to be robust to localized sediment alterations.

Furthermore, site selection, baseline data collection, and continual monitoring are expensive and labor-intensive tasks, so the “transferability” of sample data – whether the collected data would be applicable to, or representative of, another site with similar environmental variables – is of great interest. It is in this context that understanding the environmental characteristics associated with bivalve assemblages and/or individual species becomes important. In the BOEM surveys, the Newport/Nehalem difference serves as a cautionary tale about using a broad sediment type (e.g. sand, <4% silt-clay) as a defining characteristic for a bivalve assemblage: although both sites fit this sediment criteria, the benthic bivalve assemblages were very different, which can be attributed primarily to the presence of a single species, *Nutricula lordi*. When selecting control sites or using pre-existing samples within sand-dominated areas (<10% silt-clay), exact percent silt-clay of the sediment is the main factor (rather than depth or latitude) to consider when bivalve assemblages are of interest. Conversely, within silt-dominated

environments (>50% silt-clay), depth is a more useful predictor of bivalve assemblages than exact percent silt-clay. Consequently, control/proxy sites of a similar depth to an experimental site of interest likely contain a more similar bivalve assemblage than control/proxy sites selected to match exact latitude or sediment characteristics. Designing experiments with these factors in mind may increase the number of useful control/proxy sites available to researchers.

6. CONCLUSION

Along the continental shelf of the Pacific Northwest, sediment type seems to be more influential in determining distribution of bivalve assemblages than latitude or depth. For sandy areas, small differences in percent silt-clay were associated with a complete change in the observed bivalve assemblage. Conversely, within silty areas, similarity in depth was more useful for distinguishing bivalve assemblages than similarity in exact sediment composition.

Sediment type was also useful for discussions at the species level, since assemblage composition varied at least partially due to the environmental restrictions of certain species. For example, whereas the suspension feeding bivalve *Axinopsida serricata* was a generalist and found in every bivalve assemblage observed, the suspension feeder *Nutricula lordi* was a specialist, restricted to very sandy (<1-2% silt-clay) sediment and the assemblages observed therein. Other common bivalve species displayed more complex habitat restrictions: high abundances of the deposit feeder *Ennucula tenuis* were associated with specific combinations of depth, sediment type, and DO, while distribution of the deposit feeder *Acila castrensis* was most associated with depth, sediment type, and TOC. *Macoma carlottensis*, which can function as either a suspension or deposit feeder, displayed the highest abundances in sediment with an equal mix of silt/sand and high TOC.

However, for *Axinopsida serricata*, *Ennucula tenuis*, *Macoma carlottensis*, and *Acila castrensis*, biotic interactions or “missing” environmental variables are likely at least as influential, if not more influential, in structuring abundance patterns as the environmental, abiotic variables discussed here. Further consideration of potential biotic or abiotic factors responsible for patchy distribution – e.g. conspecific settlement cues, limited dispersal ability, boundary layer flow influence on resuspension of larvae – would be necessary to better describe abundance patterns for each species.

The general assemblage and species-level associations discussed here are of practical use. Predicting and understanding changes in bivalve assemblages due to human

impacts such as wave energy devices relies upon a solid, working knowledge of current bivalve assemblages and the distribution of the abundant, characteristic species of those assemblages. Information about assemblages' and species' associations with physical, environmental variables can inform which sites are most useful to sample, for study sites or for control sites, as well as which previously sampled sites could serve as legitimate proxy data.

BIBLIOGRAPHY

- Abelson, A. and M. Denny. 1997. Settlement of marine organisms in flow. Annual Review of Ecology and Systematics **28**:317-339.
- Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control **19**:716-723.
- Alfaro, A. C., T. Young, and A. M. Ganesan. 2011. Regulatory effects of mussel (*Aulacomya maoriana* Iredale 1915) larval settlement by neuroactive compounds, amino acids and bacterial biofilms. Aquaculture **322-323**:158-168.
- Anderson, M. J. 2008. Animal-sediment relationships re-visited: Characterising species' distributions along an environmental gradient using canonical analysis and quantile regression splines. Journal of Experimental Marine Biology and Ecology **366**:16-27.
- Anestis, A., A. Lazou, H. O. Pörtner, and B. Michaelidis. 2007. Behavioral, metabolic, and molecular stress responses of marine bivalve *Mytilus galloprovincialis* during long-term acclimation at increasing ambient temperature. American Journal of Regulatory, Integrative and Comparative Physiology **293**:R911-R921.
- Bergen, M., S. B. Weisberg, R. W. Smith, D. B. Cadien, A. Dalkey, D. E. Montagne, J. K. Stull, R. G. Velarde, and J. A. Ranasinghe. 2001. Relationship between depth, sediment, latitude, and the structure of benthic infaunal assemblages on the mainland shelf of southern California. Marine Biology **138**:637-647.
- BOEM. Ocean Wave Energy. Bureau of Ocean Energy Management
- Boyd, P. W. and D. A. Hutchins. 2012. Understanding the responses of ocean biota to a complex matrix of cumulative anthropogenic change. Marine Ecology Progress Series **470**:125-135.
- Bright, D. A. and D. V. Ellis. 1989. Aspects of histology in *Macoma carlottensis* (Bivalvia: Tellinidae) and *in situ* histopathology related to mine-tailings discharge. Journal of Marine Biological Association of the United Kingdom **69**:447-464.
- Butler, P. A. 1953. Oyster growth as affected by latitudinal temperature gradients. Commercial Fisheries Review **15**:7-12.
- Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the emerging role of hydrodynamical processes. Oceanography and Marine Biology: an Annual Review **25**:113-165.
- Butman, C. A., J. P. Grassle, and C. M. Webb. 1988. Substrate choices made by marine larvae settling in still water and in a flume flow. Nature **333**:771-773.
- Cada, G., J. Ahlgrimm, M. Bahleda, T. Bigford, S. D. Stavrakas, D. Hall, R. Moursund, and M. Sale. 2007. Potential impacts of hydrokinetic and wave energy conversion technologies on aquatic environments. Fisheries **32**:174-181.
- Carroll, M. L. and W. G. Ambrose, Jr. 2012. Benthic infaunal community variability on the northern Svalbard shelf. Polar Biology **35**:1259-1272.

- Cerame-Vivas, M. J. and I. E. Gray. 1966. The distributional pattern of benthic invertebrates of the continental shelf off North Carolina. *Ecology* **47**:260-270.
- Chase, Z., K. S. Johnson, V. A. Elrod, J. N. Plant, S. E. Fitzwater, L. Pickell, and C. M. Sakamoto. 2005. Manganese and iron distributions off central California influenced by upwelling and shelf width. *Marine Chemistry* **95**:235-254.
- Chase, Z., P. G. Strutton, and B. Hales. 2007. Iron links river runoff and shelf width to phytoplankton biomass along the U.S. West Coast. *Geophysical Research Letters* **34**:L04607.
- Cimberg, R. L., R. W. Smith, and D. B. Cadien. 1993. Distribution of benthic infaunal communities in the vicinity of Point Conception, California. Pages 221-232 in F. G. Hochberg, editor. *Third California Islands Symposium - Recent Advances in Research on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara, CA.
- Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**:117-143.
- Clarke, K. R. and M. Ainsworth. 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**:205-219.
- Clarke, K. R. and R. N. Gorley. 2006. *PRIMER v6: User Manual/Tutorial*. PRIMER-E, Plymouth.
- Clarke, K. R. and R. M. Warwick. 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. 2nd edition. PRIMER-E Ltd., Plymouth, United Kingdom.
- Commito, J. A., C. A. Currier, L. R. Kane, K. A. Reinsel, and I. M. Ulm. 1995. Dispersal dynamics of the bivalve *Gemma gemma* in a patchy environment. *Ecological Monographs* **65**:1-20.
- Crisp, D. J. and D. A. Ritz. 1967. Temperature acclimation in barnacles. *Journal of Experimental Marine Biology and Ecology* **1**:236-256.
- Dame, R. F. 2011. *Marine Science, Volume 34: Ecology of Marine Bivalves: An Ecosystem Approach*. 2nd edition. CRC Press, London, GBR.
- de Goeij, P. and P. Luttikhuisen. 1998. Deep-burying reduces growth in intertidal bivalves: field and mesocosm experiments with *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* **228**:327-337.
- Drent, J. 2002. Temperature responses in larvae of *Macoma balthica* from a northerly and southerly population of the European distribution range. *Journal of Experimental Marine Biology and Ecology* **275**:117-129.
- Dufour, S. C. 2005. Gill anatomy and the evolution of symbiosis in the bivalve family Thyasiridae. *Biological Bulletin* **208**:200-212.
- Dunnill, R. M. and D. V. Ellis. 1969. The distribution and ecology of sub-littoral species of *Macoma* (Bivalvia) off Moresby Island and in Satellite Channel, near Victoria, British Columbia. *Veliger* **12**:207-219.

- Dye, A. H. 1979. The effect of acute and long term temperature changes on the respiration of two sand-dwelling bivalves. *Comparative Biochemistry and Physiology* **63(A)**:405-409.
- EPRI. 2011. Mapping and assessment of the United States Ocean Wave Energy Resource. Electric Power Research Institute.
- Fischer, A. G. 1960. Latitudinal variations in organic diversity. *Evolution* **14**:64-81.
- Frechette, M., D. Lefaivre, and C. A. Butman. 1993. Bivalve feeding and the benthic boundary layer. Pages 325-369 in R. F. Dame, editor. *Bivalve filter feeders in estuarine and coastal ecosystem processes*. Springer-Verlag.
- Gaston, K. J. 1996. Biodiversity - latitudinal gradients. *Progress in Physical Geography* **20**:466-476.
- Geraghty, J., M. P. Russell, and D. Normal. 2008. A quantitative assessment of spermatozoan morphology in *Nutricula confusa* and *Nutricula tantilla* (Bivalvia: Veneridae). *The Veliger* **50**:263-268.
- Gill, A. B. 2005. Offshore renewable energy: ecological implications of generating electricity in the coastal zone. *Journal of Applied Ecology* **42**:605-615.
- Gray, J. S. 1974. Animal-sediment relationships. *Oceanography Marine Biology Annual Review* **12**:223-261.
- Green, M. A., G. G. Waldbusser, L. Hubazc, E. Cathcart, and J. Hall. 2013. Carbonate mineral saturation state as the recruitment cue for settling bivalves in marine muds. *Estuaries and Coasts* **36**:18-27.
- Hadfield, M. G. 2011. Biofilms and marine invertebrate larvae: what bacteria produce that larvae use to choose settlement sites. *Annual Review of Marine Science* **3**:453-470.
- Hairton, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *The American Naturalist* **94**:421-425.
- Hale, R., P. Calosi, L. McNeill, N. Mieszkowska, and S. Widdicombe. 2011. Predicted levels of future ocean acidification and temperature rise could alter community structure and biodiversity in marine benthic communities. *Oikos* **120**:661-674.
- Harrell, F. E. J. 2013. Harrell Miscellaneous.
- Heiberger, R. M. 2013. *HH: Statistical analysis and data display*: Heiberger and Holland.
- Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. *The American Naturalist* **163**:192-211.
- Hoegh-Guldberg, O. and J. S. Pearse. 1995. Temperature, food availability, and the development of marine invertebrate larvae. *American Zoologist* **35**:415-425.
- Hoey, G. V., S. Degraer, and M. Vincx. 2004. Macrobenthic community structure of soft-bottom sediments at the Belgian Continental Shelf. *Estuarine, Coastal and Shelf Science* **59**:599-613.
- Hunter, M. D. and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**:724-732.

- Huz, R. d. l., M. Lastra, and J. Lopez. 2002. The influence of sediment grain size on burrowing, growth, and metabolism of *Donax trunculus* L. (Bivalvia: Donacidae). *Journal of Sea Research* **47**:85-95.
- Hyland, J., E. Baptiste, J. Campbell, J. Kennedy, R. Kropp, and S. Williams. 1991. Macroinfaunal communities of the Santa Maria Basin on the California outer continental shelf and slope. *Marine Ecology Progress Series* **78**:147-161.
- Imabayashi, H. 1986. Effect of oxygen-deficient water on the settled abundance and size composition of the bivalve *Theora lubrica*. *Bulletin of the Japanese Society for the Science of Fish* **52**:391-397.
- IPCC. 2007. Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.
- Jansson, B. O. 1976. The significance of grain size and pore water content for the interstitial fauna of sandy beaches. *Oikos* **18**:311-322.
- Jayaraj, K. A., J. Josia, and P. K. Dinesh Kumar. 2008. Infaunal macrobenthic community of soft bottom sediment in a tropical shelf. *Journal of Coastal Research* **24**:708-718.
- Jennings, L. B. and H. L. Hunt. 2009. Distances of dispersal of juvenile bivalves (*Mya arenaria* (Linnaeus), *Mercenaria mercenaria* (Linnaeus), *Gemma gemma* (Totten)). *Journal of Experimental Marine Biology and Ecology* **376**:76-84.
- Jørgensen, C. B. and K. Ockelmann. 1991. Beat frequency of lateral cilia in intact filter feeding bivalves - effect of temperature. *Ophelia* **33**:67-70.
- Kamermans, P. 1994. Similarity in food source and timing of feeding in deposit- and suspension-feeding bivalves. *Marine Ecology Progress Series* **104**:63-75.
- Kennedy, V. S. and J. A. Mihursky. 1972. Effects of temperature on the respiratory metabolism of three Chesapeake Bay bivalves. *Chesapeake Science* **13**:1-22.
- Koulouri, P., C. Dounas, C. Arvanitidis, D. Koutsoubas, and A. Eleftheriou. 2006. Molluscan diversity along a Mediterranean soft bottom sublittoral ecotone. *Scientia Marina* **70**:573-583.
- Labrune, C., A. Grémare, J.-M. Amuoroux, R. Sardá, J. Gil, and S. Taboada. 2008. Structure and diversity of shallow soft-bottom benthic macrofauna in the Gulf of Lions (NW Mediterranean). *Helgoland Marine Research* **62**:201-214.
- Langhamer, O. 2010. Effects of wave energy converters on the surrounding soft-bottom macrofauna (west coast of Sweden). *Mar Environ Res* **69**:374-381.
- Lee, A.-C., Y.-C. Lee, and T.-S. Chin. 2012. Effects of low dissolved oxygen on the digging behavior and metabolism of the hard clam (*Meretrix lusoria*). *Aquaculture Research* **43**:1-13.
- Legendre, P., S. F. Thrush, V. J. Cummings, P. K. Dayton, J. Grant, J. E. Hewitt, A. H. Hines, B. H. McArdle, R. D. Pridmore, D. C. Schneider, S. J. Turner, R. B. Whitlatch, and M. R. Wilkinson. 1997. Spatial structure of bivalves in a sandflat: scale and generating processes. *Journal of Experimental Marine Biology and Ecology* **216**:99-128.

- Lenée-Bluhm, P., R. Paasch, and T. Ozkan-Haller. 2011. Characterizing the wave energy resource of the US Pacific Northwest. *Renewable Energy* **36**:2106-2119.
- Levinton, J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist* **106**:472-486.
- Lie, U. 1968. A quantitative study of benthic infauna in Puget Sound, Washington, USA, in 1963-1964. *FiskDir. Skr. Ser. HavUnders.* **14**:229-556.
- Lie, U. and D. S. Kisker. 1970. Species composition and structure of benthic infauna communities off the coast of Washington. *Journal of the Fisheries Research Board of Canada* **27**:2273-2285.
- Long, W. C., B. J. Brylawski, and R. D. Seitz. 2008. Behavioral effects of low dissolved oxygen on the bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* **359**:34-39.
- Longbottom, M. R. 1970. The distribution of *Arenicola marina* (L.) with particular reference to the effects of particle size and organic matter of the sediments. *Journal of Experimental Marine Biology and Ecology* **5**:138-157.
- Lopez, G. R. and J. S. Levinton. 1987. Ecology of deposit-feeding animals in marine sediments. *The Quarterly Review of Biology* **62**:235-260.
- Lundquist, C. J., C. A. Pilditch, and V. J. Cummings. 2004. Behaviour controls post-settlement dispersal by the juvenile bivalves *Austrovenus stutchburyi* and *Macomona liliana*. *Journal of Experimental Marine Biology and Ecology* **306**:51-74.
- Macdonald, T., B. Burd, V. Macdonald, and A. Van Roodselaar. 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. Pages 1-63. Canadian technical report of fisheries and aquatic sciences.
- Marquardt, D. W. 1970. Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. *Technometrics* **12**:591-612.
- Meynard, C. N. and J. F. Quinn. 2007. Predicting species distributions: a critical comparison of the most common statistical models using artificial species. *Journal of Biogeography* **34**:1455-1469.
- Nel, R., A. McLachlan, and D. P. E. Winter. 2001. The effect of grain size on the burrowing of two *Donax* species. *Journal of Experimental Marine Biology and Ecology* **265**:219-238.
- Nelson, W. G., J. L. Hyland, H. Lee II, C. L. Cooksey, J. O. Lamberson, F. A. Cole, and P. J. Clinton. 2008. Ecological conditions of coastal ocean waters along the U.S. western continental shelf: 2003. Page 137, EPA 620/R-08/001, U.S. EPA, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Newport OR, 97365; and NOAA Technical Memorandum NOS NCCOS 79, NOAA National Ocean Service, Charleston, SC 29412-9110.
- Nilsson, H. C. and R. Rosenberg. 1994. Hypoxic response of two marine benthic communities. *Marine Ecology Progress Series* **115**:209-217.

- ODOE. 2013. A Renewable Portfolio Standard (RPS) for Oregon. Oregon Department of Energy.
- Odum, E. P., J. T. Finn, and E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *BioScience* **29**:349-352.
- Olafsson, E. B. 1986. Density dependence in suspension-feeding and deposit-feeding populations of the bivalve *Macoma balthica*: a field experiment. *Journal of Animal Ecology* **55**:517-526.
- Oug, E. 1998. Relating species patterns and environmental variables by canonical ordination: an analysis of soft-bottom macrofauna in the region of Tromsø, northern Norway. *Marine Environmental Research* **45**:29-45.
- PacifiCorp. 2012. PacifiCorp Renewable Portfolio Standard, Oregon Implementation Plan 2013-2017.
- Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanography Marine Biology Annual Review* **30**:273-335.
- Philippart, C. J. M., H. M. van Aken, J. J. Buekema, O. G. Bos, G. C. Cadée, and R. Dekker. 2003. Climate-related change in recruitment of the bivalve *Macoma balthica*. *Limnology and Oceanography* **48**:2171-2185.
- Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**:131-144.
- Porri, F., T. Jordaan, and C. D. McQuaid. 2008. Does cannibalism of larvae by adults affect settlement and connectivity of mussel populations? *Estuarine, Coastal and Shelf Science* **79**:687-693.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rabalais, N. N., R. J. Diaz, L. A. Levin, R. E. Turner, D. Gilbert, and J. Zhang. 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* **7**:585-619.
- Ramsey, F. L. and D. W. Schafer. 2013. *The Statistical Sleuth: A Course in Methods of Data Analysis*. Third edition. Brooks/Cole Cengage Learning.
- Rhoades, D. C. and D. K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**:150-178.
- Rosenberg, R., B. Hellman, and B. Johansson. 1991. Hypoxic tolerance of marine benthic fauna. *Marine Ecology Progress Series* **79**:127-131.
- Roy, K., D. Jablonski, and J. W. Valentine. 2000. Dissecting latitudinal diversity gradients: functional groups and clades of marine bivalves. *Proc. R. Soc. Lond. B* **267**:293-299.
- Sanders, H. L. 1958. Benthic studies in Buzzards Bay. I. Animal-sediment relationships. *Limnology and Oceanography* **3**:245-258.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* **102**:243-282.

- Santhanam, H. 2009. Influence of the sediment composition and total organic carbon on distribution of benthic organisms at Pulicat Lagoon, South East coast of India. *Journal of Ecotoxicology and Environmental Monitoring* **19**:541-548.
- Savage, N. B. 1976. Burrowing activity in *Mercenaria mercenaria* (L.) and *Spisula solidissima* (Dillwyn) as a function of temperature and dissolved oxygen. *Marine Behavior and Physiology* **3**:221-234.
- Schetlema, R. S. and I. P. Williams. 2009. Reproduction among protobranch bivalves of the family Nuculidae from sublittoral, bathyal, and abyssal depths off the New England coast of North America. *Deep-Sea Research II* **56**:1835-1846.
- Schwarz, G. 1978. Estimating the Dimension of a Model. *Annals of Statistics* **6**:461-464.
- Sellmer, G. P. 1967. Functional morphology and ecological life history of the gem clam, *Gemma gemma* (Eulamellibranchia: Veneridae). *Malacologia* **5**:137-223.
- Shanks, A. L. 2009. Pelagic larval duration and dispersal distance revisited. *Biological Bulletin* **216**:373-385.
- Shannon, C. 1948. A mathematical theory of communication. *Bell Systems Technological Journal* **27**:379-423, 623-656.
- Shepard, F. P. 1954. Nomenclature based on sand-silt-clay ratios. *Journal of Sedimentary Petrology* **24**:151-158.
- Sickinger, T. 2012. Portland General Electric searching for more renewable energy to meet mandate. *The Oregonian*.
- Sigurdsson, J. B., C. W. Titman, and P. A. Davies. 1976. The dispersal of young post-larval bivalve molluscs by byssus threads. *Nature* **262**:386-387.
- Snelgrove, P. V. R. and C. A. Butman. 1994. Animal-sediment relationships revisited: cause versus effect. *Oceanography and Marine Biology: an Annual Review* **32**:111-177.
- Snelgrove, P. V. R., C. A. Butman, and J. P. Grassle. 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. 1 in microdepositional environment. *Journal of Experimental Marine Biology and Ecology* **168**:71-109.
- Snelgrove, P. V. R., J. P. Grassle, and C. A. Butman. 1998. Sediment choice by settling larvae of the bivalve, *Spisula solidissima* (Dillwyn), in flow and still water. *Journal of Experimental Marine Biology and Ecology* **231**:171-190.
- Sokołowski, A., K. Pawlikowski, M. Wołowicz, P. Garcia, and J. Namieśnik. 2008. Shell deformations in the Baltic Clam *Macoma balthica* from Southern Baltic Sea (the Gulf of Gdansk): hypothese on environmental affects. *AMBIO: A Journal of the Human Environment* **37**:93-100.
- Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, and J. Robertson. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* **57**:573-583.

- Stasek, C. R. 1961. The ciliation and function of the labial palps of *Acila castrensis* (Protobranchia, Nuculidae) with an evaluation of the role of the protobranch organs of feeding in the evolution of the Bivalvia. *Proceedings of the Zoological Society of London* **137**:511-538.
- Tamburri, M. N., C. M. Finelli, D. S. Wethey, and R. K. Zimmer-Faust. 1996. Chemical induction of larval settlement behavior in flow. *Ecological Bulletin* **191**:367-373.
- Thorson, G. 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. *Medd. Grønland* **100**:1-155.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biological Reviews* **25**:1-45.
- Thorson, G. 1957. Bottom communities (sublittoral or shallow shelf). *Treatise on marine ecology and peleoecology* **67**:461-534.
- Thrush, S. F., J. E. Hewitt, A. Norkko, P. E. Nicholls, G. A. Funnell, and J. I. Ellis. 2003. Habitat change in estuaries: predicting broad-scale response of intertidal macrofauna to sediment mud content. *Marine Ecology Progress Series* **263**:101-112.
- Tillotson, K. and P. D. Komar. 1997. The wave climate of the Pacific Northwest (Oregon and Washington): a comparison of data sources. *Journal of Coastal Research* **13**:440-452.
- Todd, J. A. 2001. Introduction to molluscan life habits databases. *Neogene Marine Biota of Tropical America*.
- Troost, K., R. Veldhuizen, E. J. Stamhuis, and W. J. Wolff. 2008. Can bivalve veligers escape feeding currents of adult bivalves. *Journal of Experimental Marine Biology and Ecology* **358**:185-196.
- Venables, W. N. and B. D. Ripley. 2002. *Modern Applied Statistics with S*. Fourth edition. Springer, New York.
- Verardo, D. J., P. N. Froelich, and A. McIntyre. 1990. Determination of organic carbon and nitrogen in marine sediments using the Carlo Erba NA-1500 analyzer. *Deep Sea Research Part 1: Oceanographic Research Papers* **37**:157-165.
- Vernberg, W. B. and J. F. Vernberg. 1972. *Environmental physiology of marine animals*. Springer-Verlag, New York.
- Vincent, B., D. Joly, and M. Harvey. 1994. Spatial variation in growth of the bivalve *Macoma balthica* (L) on a tidal flat - effects of environmental factors and intraspecific competition. *Journal of Experimental Marine Biology and Ecology* **181**:223-238.
- Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *The Journal of Geology* **30**:377-392.
- Weston, D. P. 1988. Macrobenthos-sediment relationships on the continental shelf off Cape Hatteras, North Carolina. *Continental Shelf Research* **8**:267-286.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, New York.

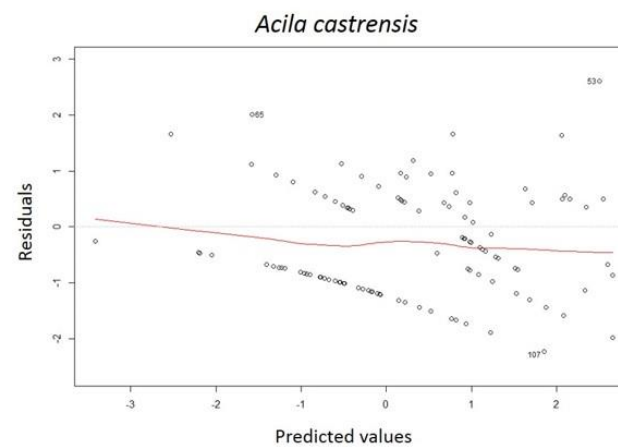
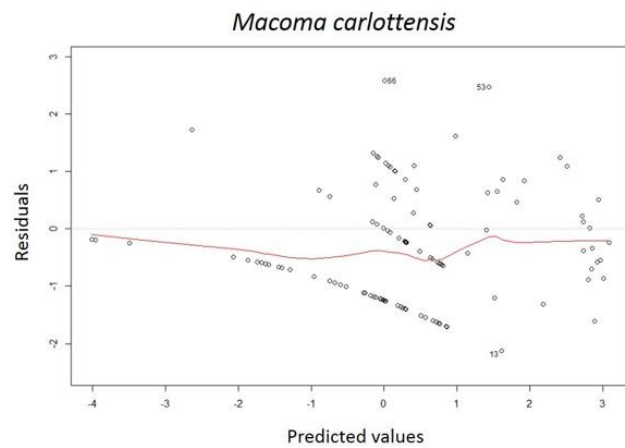
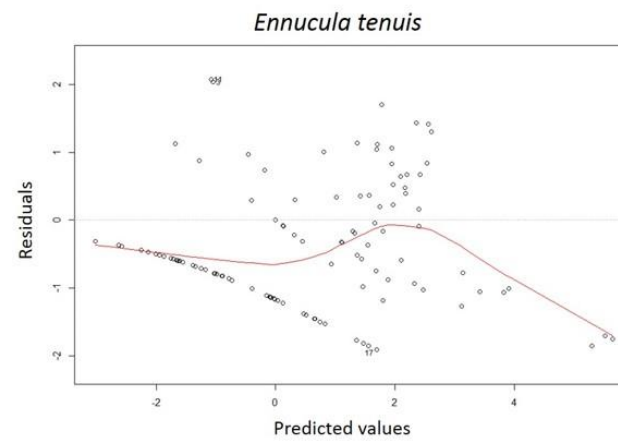
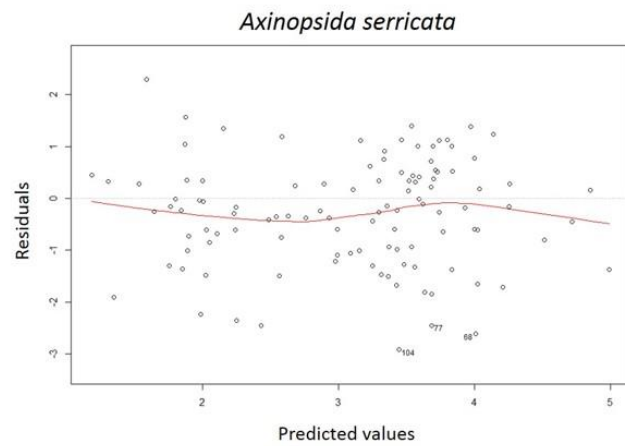
- Widdicombe, S., S. L. Dashfield, C. L. McNeill, H. R. Needham, A. Beesley, A. McEvoy, S. Oxnevad, K. R. Clarke, and J. A. Berge. 2008. Effects of CO₂ induced seawater acidification on infaunal diversity and sediment nutrient fluxes. *Marine Ecology Progress Series* **379**:59-75.
- Wildish, D. J. and D. D. Kristmanson. 1984. Importance to mussels of the benthic boundary layer. *Canadian Journal Fisheries and Aquatic Sciences* **14**:1618-1625.
- Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* **34**:273-309.
- Wilson, W. H. 1991. Competition and predation in marine soft-sediment communities. *Annual Review of Ecology and Systematics* **21**:221-241.
- Woodin, S. A. 1986. Settlement of infauna: larval choice? *Bulletin of Marine Science* **39**:401-407.
- Woodin, S. A. 1991. Recruitment of infauna: positive or negative cues? *American Zoologist* **31**:797-807.
- Zardus, J. D. and P. M. Morse. 1998. Embryogenesis, morphology and ultrastructure of the pericalymma larva of *Acila castrensis*. *Invertebrate Biology* **117**:221-244.

APPENDIX

Results

Negative binomial model for *Nutricola lordi*

A negative binomial model was unable to be constructed for *Nutricola lordi* because of the large number of zero values. A zero-inflated negative binomial model was attempted to address this issue. However, because nearly all *Nutricola lordi* non-zero values were for Newport, the environmental variables at the site were almost perfectly correlated with both each other and with *Nutricola lordi* abundance, which impeded the proper functioning of the model construction program. Since *Nutricola lordi* was the most restricted species, in terms of range, and fairly strong conclusions could be drawn based on exploratory analysis alone, a model was not created or discussed for this species.



Appendix Figure 1. Residual plots of final negative binomial models for each species.

