



Summer 2021

Revaluating the use of mollusks for estimating paleodepth in the Pacific Northwest

E Worthington

Western Washington University, worthie2@wwu.edu

Follow this and additional works at: <https://cedar.wwu.edu/wwuet>



Part of the [Geology Commons](#)

Recommended Citation

Worthington, E, "Revaluating the use of mollusks for estimating paleodepth in the Pacific Northwest" (2021). *WWU Graduate School Collection*. 1051.

<https://cedar.wwu.edu/wwuet/1051>

This Masters Thesis is brought to you for free and open access by the WWU Graduate and Undergraduate Scholarship at Western CEDAR. It has been accepted for inclusion in WWU Graduate School Collection by an authorized administrator of Western CEDAR. For more information, please contact westerncedar@wwu.edu.

Revaluating the use of mollusks for estimating paleodepth in the Pacific Northwest

By

E. N. Worthington

Accepted in Partial Completion of the
Requirements for the Degree of
Master of Science

ADVISORY COMMITTEE:

Dr. Robyn Dahl, Chair

Dr. Doug Clark

Dr. Brady Foreman

GRADUATE SCHOOL

David Patrick, Dean

Master's Thesis

In presenting this thesis in partial fulfillment of the requirements for a master's degree at Western Washington University, I grant to Western Washington University the non-exclusive royalty-free right to archive, reproduce, distribute, and display the thesis in all forms, including electronic format, via any digital library mechanisms maintained by WWU.

I represent and warrant this is my original work and does not infringe or violate any rights of others. I warrant that I have obtained written permissions from the owner of any third party copyrighted material included in these files.

I acknowledge that I retain ownership rights to the copyright of this work, including but not limited to the right to use all or part of this work in future works, such as articles or books.

Library users are granted permission for individual, research, and non-commercial reproduction of this work for educational purposes only. Any further digital posting of this document requires specific permission from the author.

Any copying or publication of this thesis for commercial purposes, or for financial gain, is not allowed without my written permission.

E. N. Worthington

8/18/21

Reevaluating the use of mollusks for estimating paleodepth in the Pacific Northwest

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
E. N. Worthington
August 18, 2021

Abstract

Fossil records have the potential to extract important paleoenvironmental records, and by ground truthing our assumptions with modern mollusks we can improve our interpretations of the fossil record. Modern molluscan death assemblages from Rosario Strait were analyzed to: 1) determine to what extent the molluscan communities were controlled by grain size or depth; and 2) determine the extent to which age mixing was occurring in the death assemblage. Twenty-eight Van Veen grab samples were collected in Rosario Strait to represent range of depth and grain sizes. All samples were wet sieved to isolate mature mollusks (> 2.00 mm), and sediment samples were freed of biologic material and grain size determined using the Mastersizer. The proportions of mud, silt, and sand were recorded to determine grain size of the benthic habitat. Northern Arizona University Amino Acid Geochronology Laboratory determined the D/L ratios of several amino acids for the selection of bivalves sent to them using High-Performance Liquid Chromatographic Analysis.

D/L concentrations of aspartic acid (Asp) and alanine (Ala) were relatively consistent for *Cyclocardia* (*Cy*), *Chlamys* (*Ch*), and *Macoma* (*Ma*) both within a single genus at a single site (intra-site) and between a single genus at multiple sites (inter-site). Intra-site variability of Asp was on average 0.031 (*Cy*), 0.007 (*Ch*), and 0.006 (*Ma*); the intra-site variability of Ala was on average 0.008 (*Cy*), 0.004 (*Ch*), and 0.024 (*Ma*). Inter-site variability of Asp was on average 0.007 (*Cy*), 0.068 (*Ch*), and 0.085 (*Ma*); the inter-site variability of Ala was on average 0.013 (*Cy*), 0.036 (*Ch*), and 0.081 (*Ma*). This indicates that there is some amount of age mixing occurring at the sample sites. *Nuculana* displayed relatively higher intra-site variability with the average difference 0.062 for Asp and 0.064 for Ala but had inter-site variability similar to the other genera with the average difference being 0.063 for Asp and 0.042 for Ala. This indicates that the genus *Nuculana* has larger intraspecies D/L concentration variability and is therefore less suitable for AAR analysis; samples that have an exact age through ^{14}C or ^{210}Pb dating would be useful.

The molluscan death assemblages of Rosario Strait were dominated by *Macoma* (up to 77%), *Nutricola* (up to 41%), and *Calyptraea* (up to 12%). Grain size was not correlated with the presence/absence of genera nor their abundance. These results suggest that grain size played a smaller role than initially hypothesized in the molluscan community composition of Rosario Strait. Previous studies that assumed depth was the primary control on species composition used species composition to estimate Pleistocene paleodepth. The paleodepth was then used to calculate ice thickness, which was used to calculate changes in sea level. I found no basis in the death assemblage data for this proxy and that mollusks should not be used as the primary evidence for paleodepth interpretations.

Acknowledgements

I would like to begin by acknowledging that I lived and worked on the ancestral homelands of the Coast Salish Peoples, who have lived in the Salish Sea basin, throughout the San Juan Islands and the North Cascades watershed, from time immemorial. I want to express my deepest respect and gratitude for our Indigenous neighbors, the Lummi Nation, Nooksack Tribe, Samish Indian Nation, and the Swinomish Indian Tribal Community for their enduring care and protection of our shared lands and waterways.

This work was partially supported by NSF/GSA Graduate Student Geoscience Grant # 12765-20, which is funded by NSF Award # 1949901.

This work was partially supported by funds from the Western Washington University Research and Sponsored Programs (RSP) and the Geology Department's departmental advance.

Ben Paulson made all lab work possible and helped develop this project.

I also need to acknowledge Katie, Katie, Jess, Kiana, Erin, Ryan, and Carmi for their unrelenting support, encouragement, and edits.

Table of Contents

<i>Abstract</i>	<i>iv</i>
<i>Acknowledgements</i>	<i>v</i>
<i>List of Figures</i>	<i>vii</i>
<i>List of Tables</i>	<i>vii</i>
<i>Introduction</i>	<i>1</i>
<i>Geologic Setting</i>	<i>3</i>
<i>Salish Sea Mollusks</i>	<i>5</i>
<i>Methods</i>	<i>7</i>
<i>Shell identification</i>	<i>8</i>
<i>Grain size analysis</i>	<i>11</i>
<i>Results</i>	<i>12</i>
<i>Grain size</i>	<i>12</i>
<i>Species richness</i>	<i>12</i>
<i>Predation</i>	<i>14</i>
<i>Amino-acid racemization</i>	<i>14</i>
<i>Discussion</i>	<i>16</i>
<i>Conclusions</i>	<i>19</i>
<i>Future Work</i>	<i>19</i>
<i>References</i>	<i>38</i>

List of Figures

Figure 1. Map of sample locations and place names referenced in text.....	21
Figure 2. Summary of previous research.....	22
Figure 3. Labeled parts of a bivalve shell.....	22
Figure 4. Sample depth and latitude.....	23
Figure 5. Labeled Van Veen grab sampler.....	23
Figure 6. Non-taxonomically identifiable shell.....	24
Figure 7. Abundance of genera.....	25
Figure 8. Ternary plot of grain sizes.....	26
Figure 9. Ratio of D/L Aspartic Acid.....	27
Figure 10. Ratio of D/L Alanine.....	28

List of Tables

Table 1. Species used by Easterbrook (1962).....	33
Table 2. Samples chosen for AAR analysis.....	34
Table 3. T-test results for differences in actual and estimated latitude.....	35
Table 4. Predatory gastropods.....	36
Table 5. D/L values for Aspartic Acid and Alanine.....	37

Introduction

Late Pleistocene marine ecosystems have species, niches, and environmental conditions similar to modern ecosystems, providing an opportunity to study how modern species reacted to climate change in the past (Kidwell, 2013). Determining modern species composition is best accomplished using the death assemblage, which is the natural accumulation of sub-fossil material (shells < 10,000 years old) in the upper 10 to 20cm of sediment (Kidwell, 2001). Kidwell (2001) found that the fidelity of the death assemblage is high and can better reflect average composition than the snapshot provided by sampling live organisms. Organisms that are widespread, highly speciated, and preserve well are ideal for this type of study. Marine environments with high sedimentation rates provide a particularly advantageous environment for preservation in the sedimentary record. Mollusks such as bivalves and gastropods often live on or within the substrate and have hard parts that readily preserve, making them an excellent study system (Kidwell and Flessa, 1995). Over evolutionary time mollusks can respond to changes in physical conditions by modifying their shell or through limited migration which makes them useful for studying paleoclimate (Dickinson et al., 2012). For example, if water roughness increases then thicker shells are preferentially selected because they are more resistant to breaking (Stanley, 1970). Due to the high fidelity of death assemblages and ready preservation, mollusks can be used to answer questions of evolutionary response on timescales of thousands of years. The similarity between modern and Late Pleistocene marine ecosystems means there is a lot to learn from Late Pleistocene death assemblages.

Using the class Mollusca, the purpose of my study was two-fold: 1) evaluate what conditions allow modern molluscan communities to proliferate in Rosario Strait and 2) use that information to ground truth past interpretations of Late Pleistocene depositional environments in the PNW. Bivalves and gastropods are closely linked to their environment because they are frequently sessile or have limited mobility and experience local extinctions due to rapid environmental changes that occur faster than their evolutionary timescale (Kozloff, 1973). These biologic responses are potentially very useful in the PNW where icesheet retreat and advance likely impact environmental factors and sedimentation, thus impacting the habitat of the mollusks. If conditions change too quickly or too severely for the mollusks to react, they will die; this can be preserved in the death assemblage and the fossil record. This reaction to environmental shifts combined with their shells (hard parts), sessile lifestyle, and wide distribution allows the reaction that mollusks have to environmental shifts to be used as a paleoclimate indicator (Canuel et al., 2017; Pitts, 2020). I used a combination of grab sampling in and around Rosario Strait and data compiled by previous researchers (e.g., Keen, 1937; Easterbrook, 1962 and 1963) to accomplish this. My primary research goal was to characterize the modern community composition and habitat of molluscan species in Rosario Strait. I hypothesized that grain size, not depth, would be the most statistically significant predictor of community composition in Rosario Strait.

My hypothesis is in contrast to previous interpretations that assumed depth was the primary control on species composition, meaning that species composition could be used to estimate paleodepth (Easterbrook, 1962, 1963, 2003a, and 2003b; Weber, 2001; Table 1). These paleodepths were then used to estimate changes in sea level, ice thickness, and isostatic rebound for the Late Pleistocene, with implications for understanding eustasy, ice sheet dynamics, and tectonics. Yet Petersen

(1986) has provided evidence that mollusks are not accurate tools for estimating a definitive paleodepth and are better suited to identifying the general environment (i.e., littoral versus deep-water). This contradiction requires additional assessments that my study provides. In particular, my work has implications for past proposals of massive sea level change over short time intervals wherein a “yo-yo” tectonics model is invoked to justify the rapid rates of isostatic rebound, which argues that multiple emergences and submergences caused by isostatic rebound resulted in 1,250 ft to 1,650 ft of sea level change in under 2,000 years (Easterbrook, 2016; Figure 1). However, there is no significant geophysical evidence to support the “yo-yo effect” interpretation in Western Washington (Booth, 1987; Kovanen et al., 2020). The alternative explanation that I propose is that previous studies overestimated the rate of sea level change by an incorrect application of Mollusca proxies, resulting in inflated isostatic rebound rates.

Geologic Setting

My study location is Rosario Strait, located among the San Juan Islands in northwest Washington (Figure 1). The San Juan Islands and Rosario Strait are primarily composed of the Jurassic Fidalgo ophiolite sequence and the Eocene Chuckanut Formation (Lapen, 2000). The area has experienced extensive folding and tilting related to the subduction of the Juan de Fuca plate under the North American plate (Tucker, 2015). Erosion and deposition by repeated advances and retreats of the Cordilleran ice sheet formed the modern landscape, carving out the San Juan Islands and the surrounding channels (Kozloff, 1973). Although bedrock is at or near the surface in much of the area, there are locally extensive layers of glacial till and other glacially derived sediments exposed by river and sea cliffs throughout the area, providing insight to the

glacial history of the area (Easterbrook, 1962, 1963; Clague et al., 1977; Clark and Clague, 2020; Hernandez, 2021).

The last major glaciation in Washington was the Pleistocene Fraser Glaciation. It is divided into the: 1) Evans Creek Stade, 2) Vashon Stade, 3) Everson Interstade, and 4) Sumas Stade (Armstrong, 1984; Borden and Troost, 2001; Easterbrook et al., 2007). The exact timing of these phases is still debated because of differences in the interpretations of in ^{14}C ages and regional glacial stratigraphy (e.g., Clague et al., 1997, 1998; Kovanen and Easterbrook, 2002; Clark and Clague, 2020). Despite these differences, the broad timing of these phases is widely accepted as the framework for Late Pleistocene climate and ice sheet retreat in the Pacific Northwest (Figure 2). The Everson Interstade and Sumas Stade comprise the last local fluctuation of the Cordilleran ice sheet (Easterbrook, 2007). During the Everson Interstade there was substantial ice sheet retreat 14.5 to 15 thousand calibrated years before present shortly followed by sea level rise (Booth et al., 2003; Dethier et al., 1995). The type section for Everson age deposits along the Nooksack River consists of two stony diamictos containing marine fossils separated by a bedded sand (Easterbrook, 1962). Around 14 kyr BP during the Sumas event, the ice sheet readvanced across the International Boundary into the Fraser lowland into Bellingham Bay, then retreated northward again in a step-wise fashion forming the final recessional moraine approximately 13 to 12 kyr BP (Clague et al., 1997; Kovanen, 2002; Booth et al., 2003). This glacial activity carved the channels that comprise the floor of the Salish Sea.

The Rosario Strait study area was formed when eustatic sea level rise related to global deglaciation flooded the channel previously carved by the repeated advances of the Cordilleran ice sheet

(Kozloff, 1973). Sediment type is highly variable, even over small distances of a few meters, and is influenced by the distance from shore, the source material, and water current strength (Kozloff, 1973; Kozloff, 1996). As a result, sediment type across Rosario Strait ranges from fine mud to large cobbles regardless of water depth. Combined with the wide distribution of water depths this creates a variety of potential habitats for mollusks.

Rosario Strait and the surrounding bays are subject to twice daily tide cycles, with the larger cycle regularly having a magnitude of over 10 ft difference between high and low tide (NOAA, 2021). This high tidal energy in the modern channel causes the center of the channel to be regularly scoured, which minimizes the accumulation of sediment and the death assemblage at the center of the channel (Kozloff, 1996). Loose sediments are transported and deposited in lower energy environments closer to the islands and in bays. The islands and bays break up the waves and slow down the water which allows suspended sediments to settle, resulting in increased sedimentation rates and lower erosion rates. These semi-sheltered environments can preserve death assemblages.

Salish Sea Mollusks

In addition to the diverse range of habitats, biological factors contribute to the diversity of Salish Sea communities (Kozloff, 1973; Kozloff, 1996). Competition, predation, and physical factors can cause zonation, a process where different ecological zones have characteristic groups of organisms (Kozloff, 1973). Therefore, recording biologic factors like abundance (an indicator of competition) and predation is essential for untangling the influence of biologic and physical factors on species composition. Physical factors include temperature, salinity, oxygen concentration, and grain size (Petersen et al., 1986; Aguirre, 2003). Slower moving water results in less oxygen. Modern species

in the Pacific Northwest are adapted to high levels of oxygen, so abrupt changes in water movement and oxygen concentration can be a limiting factor in species composition (Kozloff, 1973).

Distinct molluscan communities can form in different habitats due to preferences in temperature, grain size, water energy, and other physical factors. (Kozloff, 1973). Quantifying these communities in modern death assemblages, where the environment can be directly constrained, allows for comparison to fossil assemblages in contested sediments (Kidwell, 2001; Kidwell, 2013). Past studies have relied on species depth for making these interpretations, but for most non-harvestable species depth is poorly constrained. Depth ranges are frequently based on the results of single research cruises, which collect limited samples over a small area and which do not take into account differences in substrate, temperature, or oxygen (Oldroyd, 1924; Abbott, 1974). Additionally, this type of analysis relies heavily on correct species level identification. This can be difficult due to postmortem degradation of delicate identifying features by abrasion or dissolution. For example, in the genus *Macoma* species are differentiated by the pallial sinus line, which can easily be obscured (Figure 3). Community based analysis is more forgiving of minor identification mistakes, which prevents outliers (misidentified shells) from dominating analysis. Gastropods tend to be more speciated than bivalves but are less abundant, so they are not discussed in detail here. Bivalves have fewer species and are more abundant, so understanding how genera are related to one another can be useful. The following list of bivalve groups is not comprehensive, it provides context for the relationships of the major bivalve groups referred to in this study (based on information in Stanley, 1970 and WoRMS, 2021; see “PNW_mollusks” in supplementary materials for images).

1. **Opponobranchia** Ponder and Lindberg, 2008: this group is comprised of primitive, infaunal taxa with abnormal gills
 - a. **Nuculoida** Dall, 1889: Includes *Acila*
 - b. **Solemyoida** Dall, 1889
2. **Nuculanoida** Campbell and Campbell, 2000: members of this group typically prefer muddy to silty bottoms, are deposit feeders, and are subtidal. Includes *Nuculana* and *Yoldia*
3. **Autobranchia** Grobben, 1894: gills (ctenidia) in this group are modified for filter feeding
 - a. **Pteriomorphia** Beurlen, 1944: composed of marine epifauna with asymmetric abductor mussels, can swim to varying degrees. Includes *Chlamys*, *Pododesmus*, and *Glycymeris*
 - b. **Heteroconchia** Cox, 1960:
 - i. **Paleoheterodonta** Newell, 1965: not found in this study
 1. **Trigonioida** Dall, 1889: members of this group are found in Australia
 2. **Unionoida** Stoliczka, 1871: this group is freshwater mussels
 - ii. **Heterodonta** Neumayr, 1883: this group includes most modern bivalves, and is primarily composed of filter feeders
 1. **Archiheterodonta** Ponder and Lindberg, 2008: pallial line lacks a sinus (“reflecting their non-siphonate condition”), very old group. Includes *Cyclocardia*, *Miodontiscus*, and *Astarte*
 2. **Euheterodonta** Giribet and Distel, 2003: most species, there’s a huge variety of habitats and forms. Includes *Ameritella*, *Macoma* (muddy to sandy, often small, thin shells), *Solen*, *Pandora*, *Lyonsia*, *Lucinoma*, *Humilaria*, etc.

Methods

In order to characterize the distribution, abundance, and habitat of modern bivalves and gastropods, I collected a series of grab samples using the Van Veen grab sampler on Western’s Shannon Point Marine Center R/V Zoea. I focused on sampling the lower energy environments that exist on the margins of the strait to account for this. Sample sites were selected to encompass as broad a range of depth and sediment types possible in order to accurately reflect the heterogenous nature of the strait (Figure 4). The grab used had a maximum effective sampling

depth of ~250 ft, preventing sampling in the deepest parts of the channel. When the grab hits the sea floor, the feet trigger the jaws to close, collecting the top ~5 cm to ~10 cm of substrate. The grab could not deploy and close fully in sediments composed primarily of cobbles or sticky mud, limiting sample locations. Rosario Strait has strong, tidally influenced currents that tend to remove sediments from the bottom (Kozloff, 1973). Samples were collected over two separate research excursions due to time and sample processing constraints. The first excursion in September 2020 focused on sampling 16 sites from deeper waters on the edges of the channel, while the second trip in October 2020 focused on sampling 12 muddy sediments from shallower surrounding areas, including Bellingham Bay (Figure 1).

The R/V Zoea was manned by our covid-limited crew of three. On the vessel, I recorded GPS coordinates and depth at each location. These data were verified by the captain, who checked the length of rope used for the grab (Figure 4). We prepped the grab sample and deployed from the back of the boat (Figure 5). The grab was retrieved and emptied into a plastic wash basin. The sample was hand agitated, and 3 plastic vials of sediment were collected from each grab to use for grain size analysis. Samples that contained primarily large rocks or living organisms were photographed and returned to the sea. Each sample that had collectable sediment was placed in either a 5-gallon bucket or plastic Ziploc bag for transportation back to Western Washington University's main campus.

Shell identification

Bulk samples were wet sieved using a 1 mm (no. 18) sieve. After drying at room temperature for 3 to 5 days, each sample was sieved through a 2 mm (no. 10) sieve. Limiting analysis to shells greater than 2 mm assures that the data more comparable to Late Pleistocene fossil assemblages

and sediment core data because those studies typically use a 2-4 mm sieve (Kidwell, 2001). Additionally, using a 2 mm sieve decreases the amount of larval and early juvenile shells, which are less likely to be preserved in the sedimentary record because they are more likely to dissolve or transported and have a strong seasonal bias (Kidwell, 2001). The 2-step sieving process allowed the 1-2 mm portion to be available for future analysis of larvae and early juveniles but was very time intensive. Animals that were alive at the time of collection were placed in ethanol to minimize smell and ease the removal of flesh. The “live” portion of each sample was kept separate from the “dead” portion so that the analysis would be of the death assemblage, which is less likely to have seasonal/ short term temporal bias. For example, several samples had living late juvenile members of the Tellinidae family (tellins), which would have completely dominated a relative abundance analysis). The grab samples from the second boat trip were wet sieved using just the 2 mm (no. 10) sieve to speed up the process. The “live” portion of these samples was placed in a fume hood to limit drying time and to minimize smell without the use of ethanol.

After sieving, samples were sorted to isolate taxonomically identifiable shells (Figure 6). A bivalve shell was considered identifiable if at least half of the hinge was moderately well-preserved, and a gastropod shell required a moderately well-preserved apex or aperture. Shells were identified to the lowest taxonomic level possible using Abbott (1974), Kozloff (1996), Walla Walla Invertebrates (<https://inverts.wallawalla.edu/>), E-fauna BC (<https://ibis.geog.ubc.ca/biodiversity/efauna/>), Pacific Northwest Shell Club (<http://www.bily.com/pnwsc/web-content/PNW-Marine-Life-Photos.html>) as guides. Shells were counted to determine relative abundance, and the presence of drill holes was recorded. We identified and counted predatory gastropod drill holes in shells from each site. Only gastropod drill holes were counted because the shape is easier to identify, and the predator is more

likely to be preserved than for cephalopods, worms, or sponges. Thus, estimates of predation should be considered minimal values. For bivalves, the final count was divided by 2 to ensure the number was not inflated by both valves of an organism being present. For the purposes of this study this method was more efficient than counting left and right valves separately. For gastropods, the number of apexes and apertures were counted, and the highest value was recorded as the abundance to avoid double counting a shell. These counts were also used to determine species richness, the number of species at a site.

After shells were identified, 30 valves were selected to be sent to the Northern Arizona University Amino Acid Geochronology Laboratory for amino acid racemization (AAR) analysis (Table 2). Shells that died within the last 100 years are too young for accurate radiocarbon dating, but AAR can be used to bridge that gap (Demarchi and Collins, 2014). L-chiral amino acids are naturally produced by living creatures and make up proteins. When the organism dies, the L-chiral amino acids start to decay to D-chiral, which are nonbiological amino acids. Over time the D-chiral amino acids spontaneously revert to L-chiral form; this process is called racemization. When the amount of L-chiral = D-chiral, the system has reached racemic equilibrium. By comparing the ratio of D/L, it is possible to assess the relative ages of shells. This is useful for assessing age mixing within the death assemblage at different locations in Rosario Strait. Five specimens were chosen from six sample sites to cover a range of latitudes, depths, and sediment types. Specimens were chosen for condition (the shell needed to be shipped to Arizona) from organisms with calcite shells. Calcitic shells are preferred over aragonitic shells because aragonite is susceptible to transforming to calcite; this recrystallization would interfere with AAR analysis. Species were limited to *Macoma inquinata*, *Chlamys hasata*, *Cyclocardia ventricosa*, and *Nuculana minuta* to allow for assessment

of intraspecies variability. A variety of species was used because there was no one species that had five reasonable specimens at all six sites. If comparing these AAR data to results from another lab, use the regressions provided in Wehmiller (2013). Differences in burial temperature, pH, and water availability can impact the rate of racemization, so Holocene and Pleistocene AAR values are not comparable without connecting the rates to absolute time by radioisotopes or other methods.

Grain size analysis

The three grain size samples from each sample site were wet sieved using a 1mm sieve to prepare them for analysis in the Mastersizer 2000. Each sample was air dried and weighed, and we used the splitter to separate ~1-2 g of sediment into the barcoded analysis tube. Organic matter was removed using concentrated (~30%) H₂O₂ and a sonicated warm water bath to speed the reaction (Appendix B). Once the organic matter was removed each sample was rinsed three times using DI water and a centrifuge. After the third rinse each tube was filled to the 50 mL mark with DI water.

To prevent grains from sticking together up to 5 g of Calgon (dispersant) was added to each sample and vigorously shaken to aid in dissolution. The Mastersizer 2000 Autosampler agitated each sample immediately prior to analysis to get all grain sizes in suspension. The autosampler was used with a full cleaning cycle between each sample to minimize risk of cross contamination. Grain size abundance was exported, formatted in Excel, and analyzed using R.

My primary research goal was to characterize the modern community composition and habitat of molluscan species in Rosario Strait. I hypothesized that grain size, not depth, would be the most statistically significant predictor of community composition in Rosario Strait.

Results

Grain size

Grain size ranged from mud to gravely-sand, representing a variety of benthic habitats (Figure 8). Sediments were poorly sorted, with the majority of sites having grains from 0.01 microns to cobbles several centimeters in diameter. There was variability between sites, with some sites being dominated by very fine sand, some dominated by silt, and some dominated by medium sand. Silt and sand sized sediments were preferentially sampled because they work best with the grab sampler; cobbles and gravel prevented the jaws from closing while sticky muds stopped the jaws from deploying. As a result, the 62.51 to 250 micron fraction (very fine to fine sand) was the most common grain size sampled (~36%) followed by the 250 to 500 micron fraction (medium sand) (~19%). Grain size was not correlated with depth or latitude; this was expected because Rosario Strait is a complex, high energy system.

Species richness

The full species abundance dataset is available in the “Abundance” spreadsheet provided in the supplementary materials. Sites 14 and 22 had the highest total species richness with 33 species while Site 5 had the lowest total species richness with only 3 species. The average number of bivalve species present was 11, and the average number of gastropod species was 7. *Macoma* and *Pododesmus* were the most common bivalve genera present (found at 92% and 81% of sites respectively). The limpet genus *Calyptraea* was the most frequently present gastropod (found at 77% of sites). *Nutricula*, *Calyptraea*, and *Macoma* were the most common genera overall, but the most abundant mollusks varied substantially among sites (Figure 7). Site 14 had the greatest abundance in the death assemblage with 456 individuals, and site 5 had the lowest abundance with only 3 individuals in the death assemblage.

I ran 2346 Pearson's product-moment correlation tests with a 95% confidence interval as determined by the number of sites, and then grain size and species abundance, in R to test my hypothesis that grain size, not depth, would be the most statistically significant predictor of community composition in Rosario Strait (Appendix A). Depth and species abundance were not correlated for any genera (see Appendix C in supplementary material, Figure 9). Grain size and species abundance were not correlated for all but one genus (see Appendix C in supplementary material, Figure 9). *Saxidomus* abundance was moderately positively correlated with grain size, $p < 0.001$. The presence of one genus was moderately positively correlated with another genus for 370 pairs of genera, $p < 0.05$. To better analyze these results, I focused on the 132 correlations where $p < 0.001$. *Mytilus* and *Nuculana* stand out as they present in are 9 out of the top 20 genera correlations.

Keen (1937) averaged the midpoints of the latitudinal range of all present species and found this median to be an accurate reflection of the latitude of sample collection, even without weighting the values to reflect species abundance. The average midpoint of all species ranged from 43.9°N at site 7 to 49.5°N at site 24, with the average being 46.615°N (Table 3). Based on a Welch Two Sample t-test the true difference of means is not equal to zero, indicating that there is a statistically significant ($p = 3.418 \times 10^{-7}$) difference between the estimated species midpoint for a site and the actual latitude, which is where the sample was collected (Table 3). Only 6 out of 25 sites (3, 4, and 5 were not counted) had a difference between midpoint and actual latitude of less than one degree. The average difference was 2.004 degrees.

Predation

There were 350 complete drill holes from 3,387 individual shell elements, constituting an ~10% predation rate. Twelve potential predatory species of gastropod were present in the study area (Table 4). Specimens from the bivalve genera *Nutricola* and *Cyclocardia* had the most total drill holes (86 and 59, respectively). While most sites had potential predators preserved in the death assemblage, sites 23, 24, and 26 had no gastropods at all while site 5 had no predatory gastropods despite the presence of multiple drill holes. Of the 26 sites, 85.7% had predated shell elements along with potential predatory gastropods, whereas 3.6% of sites had no signs of predation even though containing predatory gastropods, and 10.7% of sites contained shell elements predated with no predatory gastropods. There is a very small positive correlation between the abundance of potential predators and the number of drill holes ($R^2 = 0.0101$).

Amino-acid racemization

Four genera were used from five sites for AAR testing. D/L values can vary greatly depending on the genus so limited genera were used to study intraspecies variation (Table 2; Bakeman, 2006). Overlapping genera allowed for relative comparisons among sites (Figures 9 and 10). Analysis focused on Aspartic Acid (Asp, Figure 9) and Alanine (Ala, Figure 10) because they racemize the fastest, and many of the shells appeared relatively young (periostracum and fine ornamentation intact). D/L values are reported for both amino acid pairs used (Table 5). Shells from the genus *Nuculana* showed the largest Asp and Ala D/L ranges, 0.18 and 0.128 respectively. Asp D/L range in decreasing order was *Nuculana*, *Chlamys*, *Cyclocardia*, and *Macoma*. Ala D/L range in decreasing order was *Nuculana*, *Cyclocardia*, *Chlamys*, and *Macoma*. Site 18 had the highest *Cyclocardia* Ala and Asp values and slightly lower Ala and Asp *Macoma* values than site 20. The average Asp D/L for *Cyclocardia* was 0.1133 with standard deviation (SD) of 0.0116

(<https://www.mathsisfun.com/data/standard-deviation-calculator.html>). The average Asp D/L for *Nuculana* was 0.1223 with SD of 0.0534. The average Asp D/L for *Chlamys* was 0.1016 with SD of 0.0103. The average Asp D/L for *Macoma* was 0.0837 with SD of 0.0045. The average Ala D/L for *Cyclocardia* was 0.0818 with SD of 0.0119. The average Ala D/L for *Nuculana* was 0.0873 with SD of 0.0363. The average Ala D/L for *Chlamys* was 0.0604 with SD of 0.0077. The average Ala D/L for *Macoma* was 0.0787 with SD of 0.0111.

Discussion

My primary hypothesis was that the relative abundance of species distribution would vary significantly with grain size, but not with depth. Previous studies in the area (Easterbrook, 1962, Easterbrook, 2003a; Easterbrook, 2003b; Weber, 2001) have used presence of *Nuculana*, *Macoma*, *Chlamys*, and other mollusks to estimate water depth at time of deposition, which was then used to calculate ice thickness. The ice thickness was used to calculate rates of isostatic rebound to explain changes in sea level (Figure 2). What I found was that species distribution and abundance were not significantly correlated with grain size or water depth. Instead, the majority of significant correlations were between species, indicating that biological factors could be the dominant control on taxon distribution and richness in this area rather than physical factors. These factors could include competition for resources such as food and space or predation. Since shells from the genera *Nutricola* and *Cyclocardia* had the most drill holes and were also some of the most abundant genera, predation does not appear to be a limiting factor.

No correlation between species abundance and water depth (on the scale of tens of meters) is unsurprising based on work by Petersen (1986). It was unexpected that in my data there was no correlation between grain size and species, because substrate is one of the primary factors controlling bivalve life habits, which in turn exerts strong pressure on shell form (Stanley, 1970; Figure 9). It is noteworthy that grain size was not negatively correlated with *Solen sicarius* and *Nuculana minuta* abundance, since multiple past studies have found that those types of bivalves increase in abundance with decreasing grain size (Stanley, 1970; Thompson, 2017). At the genus level the shell form of mollusks in Rosario Strait are relatively consistent, i.e., species within genera have the same general shape and have similar life habits. The lack of correlation between

community composition and grain size is due to two potential factors: the presence of juveniles and the heavy tidal influence in Rosario Strait. Many of the shells were between 2 mm and 2.1 mm, and based on shell thickness, periostracum development, and decoration were likely juveniles. I used the 2 mm sieve to specifically avoid this problem as suggested by Kidwell (2001), but a larger sieve size would have lost much of the diversity. Typically, water movement is assumed to have a lesser effect on bivalve life habit compared to substrate and food availability (Stanley, 1970). However, I think the powerful tidal currents of Rosario Strait result in water movement having a greater impact on life habit than expected. Due to time and budget constraints data of water movement not collected at each site; this presents an avenue for future study in regions with various current dynamics.

The amino acid racemization D/L values do not vary significantly within genera between sites, indicating that the death assemblages are all a comparable age (Figures 9 and 10). L-Ser/L-Asp ratios were less than 0.8 for most samples, which indicates that the death assemblage has some older shells (J. Bright, personal communication, 2021). However, some very young shells are present in the samples (i.e., live at time of collection), indicating that time averaging is occurring. *Nuculana* had much larger Ala and Asp ranges than the other genera, which could indicate one or two things: 1) *Nuculana* have a higher natural amino acid variability than the other genera sampled and/or 2) that the *Nuculana* in the death assemblage accumulated over a longer time interval. Assessing the natural variability of *Nuculana* amino acids in the PNW would require measuring significant numbers of living *Nuculana*, which was beyond the time and monetary constraints of this study. It would make sense for *Nuculana* to accumulate over a larger time interval because they are infaunal, so they are burrowing into the substrate and therefore more

likely to be preserved than their epifaunal counterparts. The infaunal lifestyle increases the chance for redeposition as an articulated specimen, meaning articulated *Nuculana* in sediments could have been redeposited. The impossibility of reworked sediments containing articulated bivalves was used as conclusive evidence of in situ deposition, so in interpretations relying on this line of evidence should be reevaluated (Easterbrook, 1962; Weber, 2001).

The midpoint of the latitudinal range for all present species at each site were significantly different from measured latitude (p -value = $3.418e-07$). This result was unexpected given the massive dataset Keen (1937) worked with that support this assumption, which included ~2,000 ranges. Due to my much smaller sample size (77 ranges) and sampling area I am inclined to say the midpoint method is not invalid. It could potentially be used for environmental interpretations in larger, broader studies. Additionally, many of the species present in my samples have relatively broad ranges when compared to the narrow ranges some of the more specialized southern and northern species have. This could also be affecting my results from the midpoint method.

Conclusions

When using mollusks as paleodepth indicators, it is crucial to consider the full context of the animal in its ecosystem. Considering preferred sediment, morphology of the shell, and typical community associations is just as, if not more, important when interpreting sedimentary environments. Additionally, it is vital to recognize that most mollusks are capable of living over a broad depth range and should not be used to make depth estimates. My results do not support my hypothesis that grain size would be the most statistically significant predictor of community composition in Rosario Strait or the hypothesis that water depth is directly correlated with any of the species found in this study. Past studies using mollusks as paleodepth indicators for calculating sea level change or ice sheet thickness should be revisited. Finally, the presence of articulated bivalves in some sediments should not be used as conclusive evidence of in situ deposition, calling into question the glaciomarine origin of the Bellingham “GMD” proposed by Easterbrook (1963 and 2003).

Future Work

Going forward, I recommend sampling a wider variety of habitats, especially very muddy and very gravelly sediments. This would require using alternative sampling methods; potentially a box or vibracore. Doing so would provide more context for the preferred habitat of species that exist in these less favorable conditions. Furthermore, sampling the eastern sides of Vancouver Island and Admiralty Island would provide data from areas more directly impacted by ice. Based on satellite and sea level data both sites appear more like the type of environment interpreted for Bellingham during the Late Pleistocene. Lastly, while I previously hypothesized that *Nuculana* size could be

used as an indicator of climatic conditions, I no longer propose this hypothesis because infaunal suspension feeders tend to stay small to compensate for the environment (Stanley, 1970).

Figures

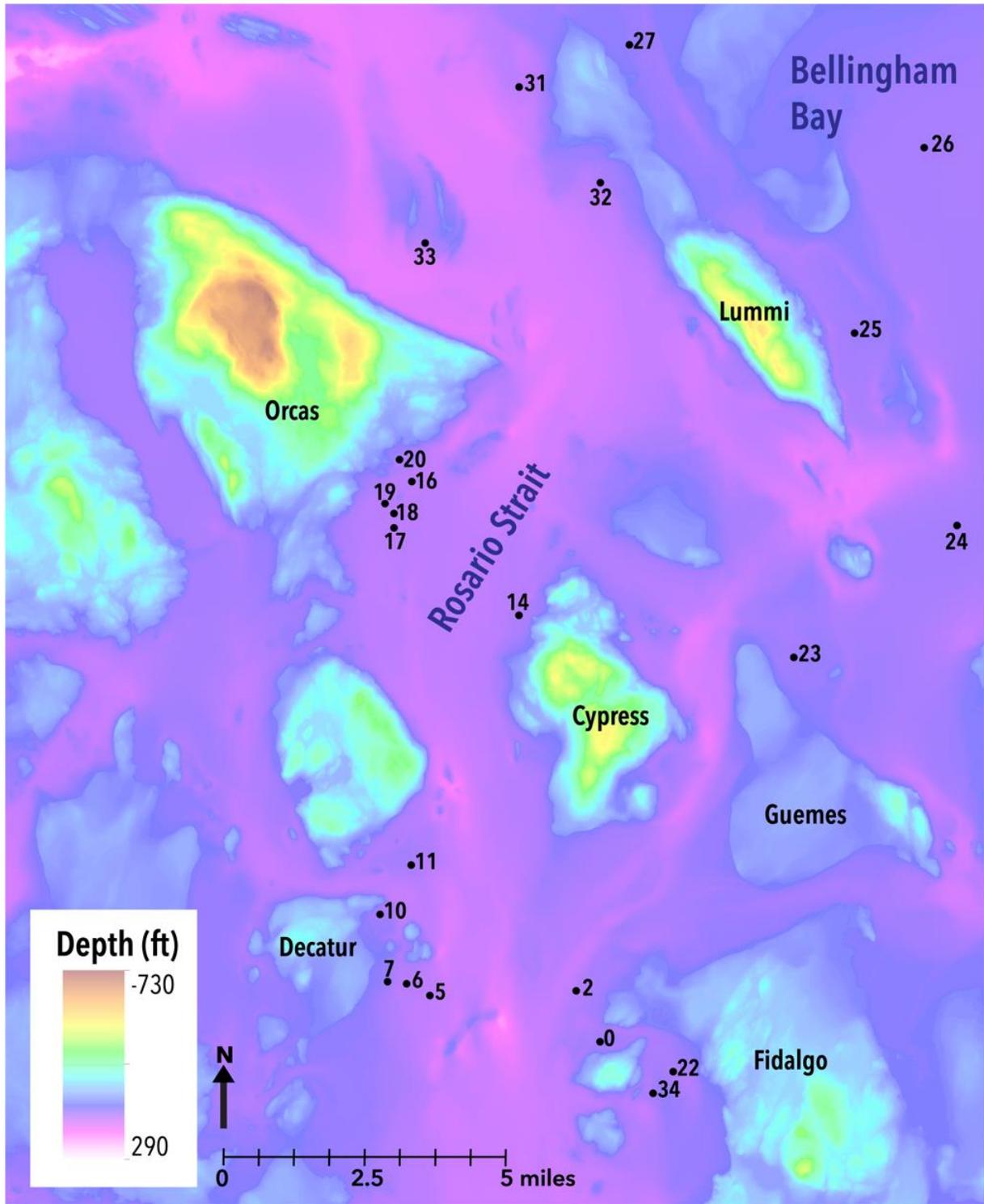


Figure 1. Map of sample locations and place names referenced in text.

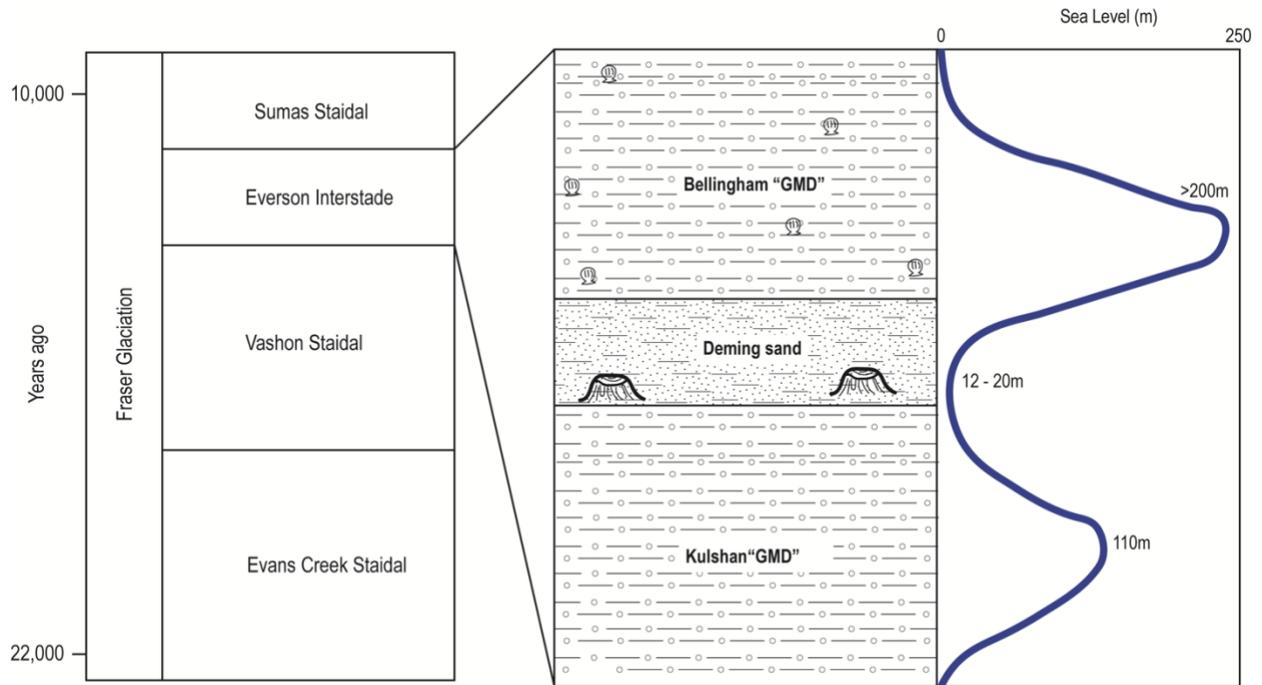


Figure 2. Summary of previous research by Easterbrook (1963, 1966, 2003, and 2007). “GMD” is used where prior work states the sediments are glaciomarine deposits and does not reflect my interpretations.

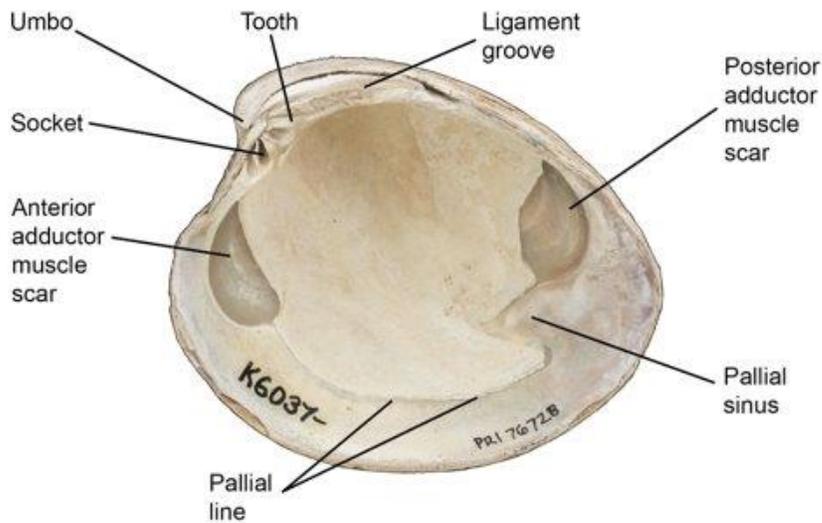


Figure 3. Image modified from The Digital Atlas of Ancient Life (Allmon and Mikkelsen, 2020): “Interior features of a valve of *Mercenaria mercenaria*. Specimen is from the collections of the [Paleontological Research Institution](#), Ithaca, New York. Width of specimen is approximately 10 cm.”

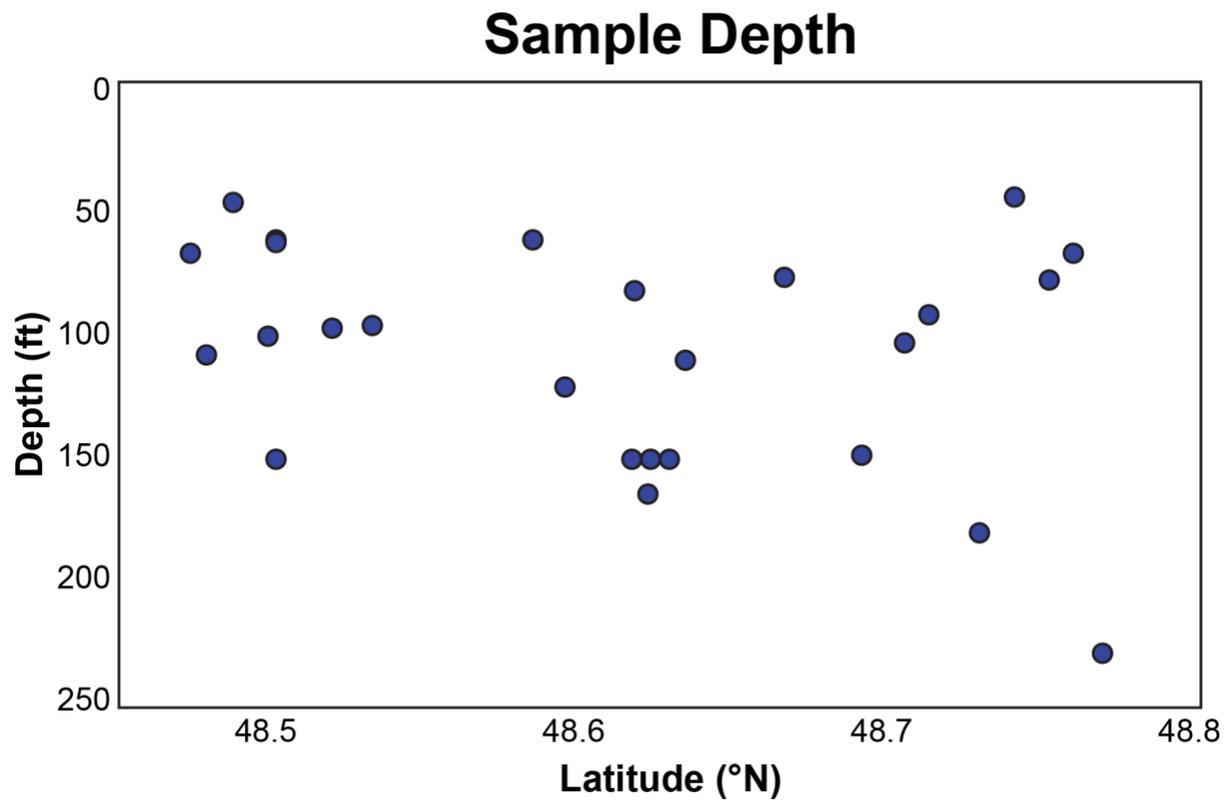


Figure 4. Sample depth in feet versus the latitude where the sample was collected.

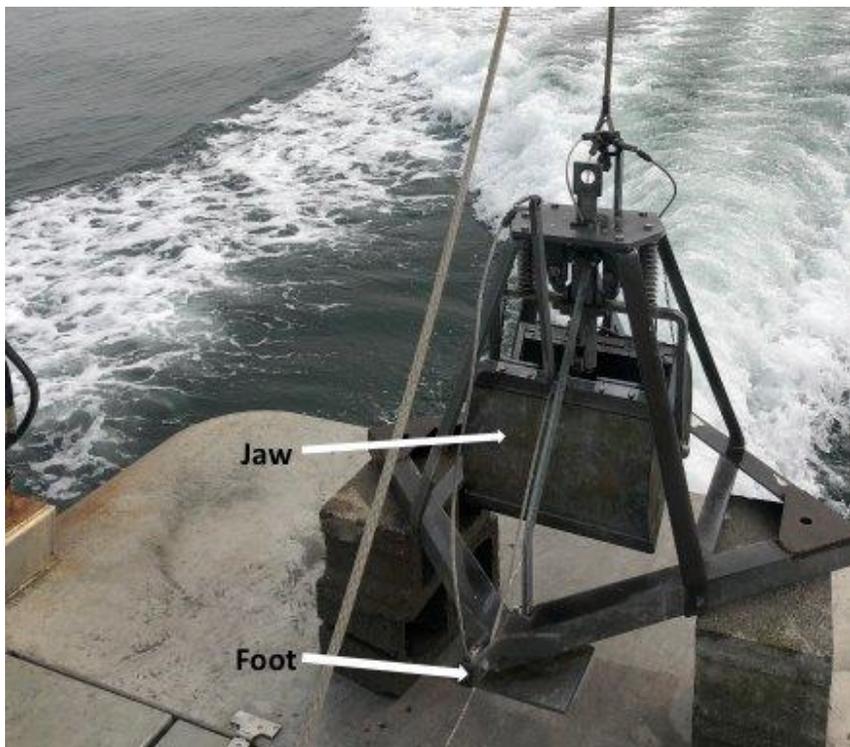


Figure 5. Van Veen grab sampler with the jaws and feet labeled.

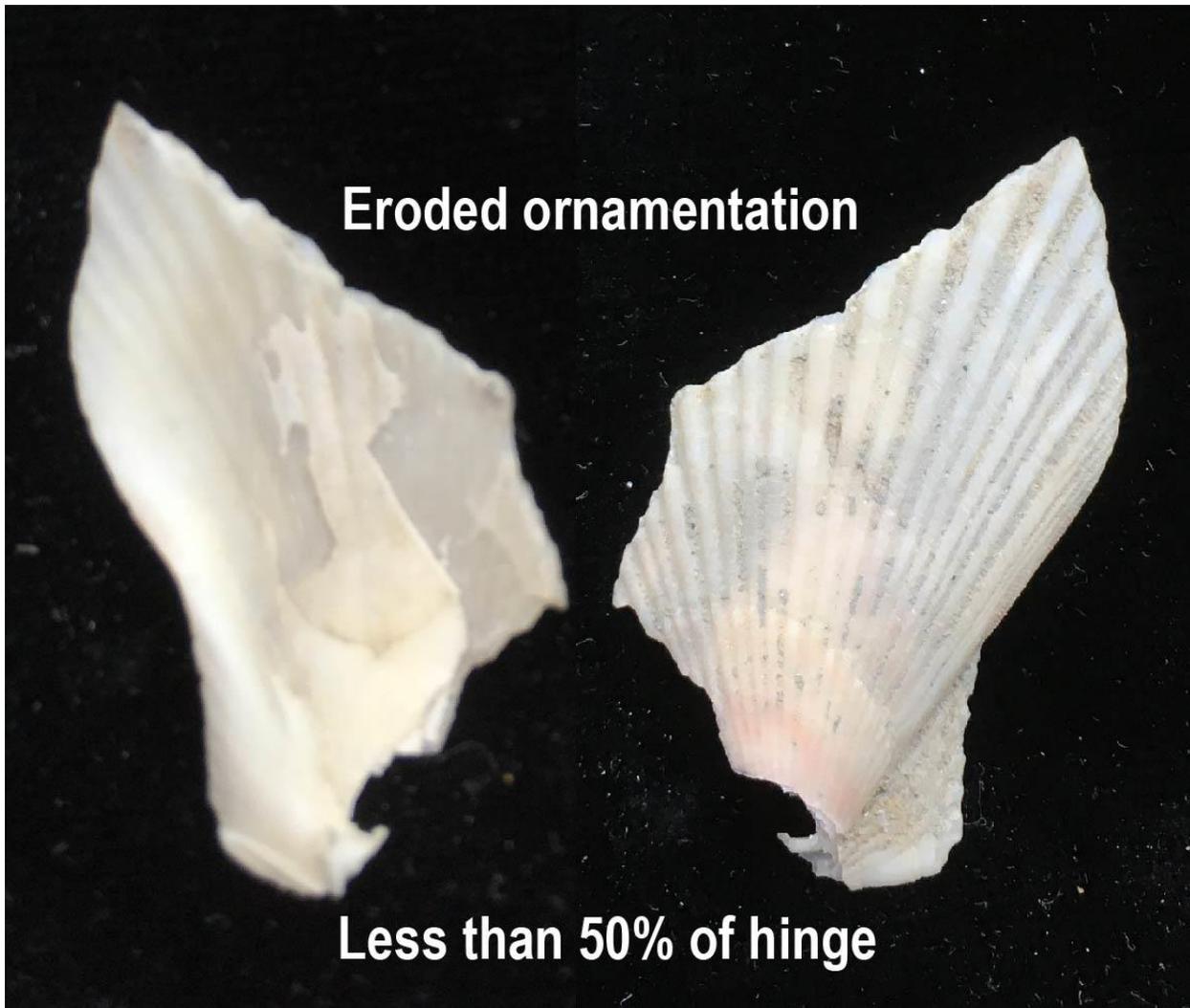


Figure 6. Non-taxonomically identifiable shell. The shell has less than 50% of the hinge present, so even though the shape of the shell and the eroded ornamentation identify it as *Chlamys* it was not counted as part of this study.

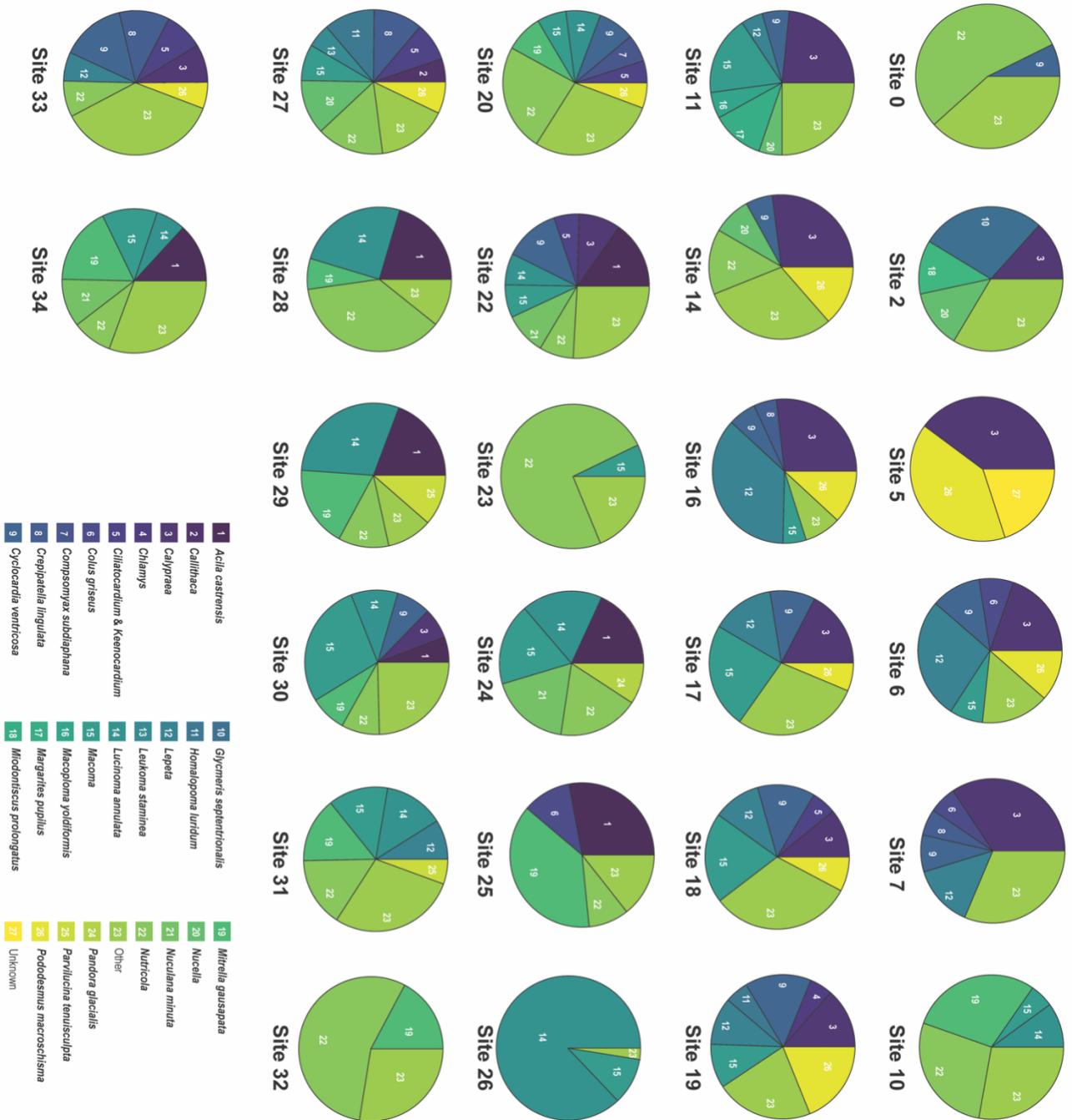
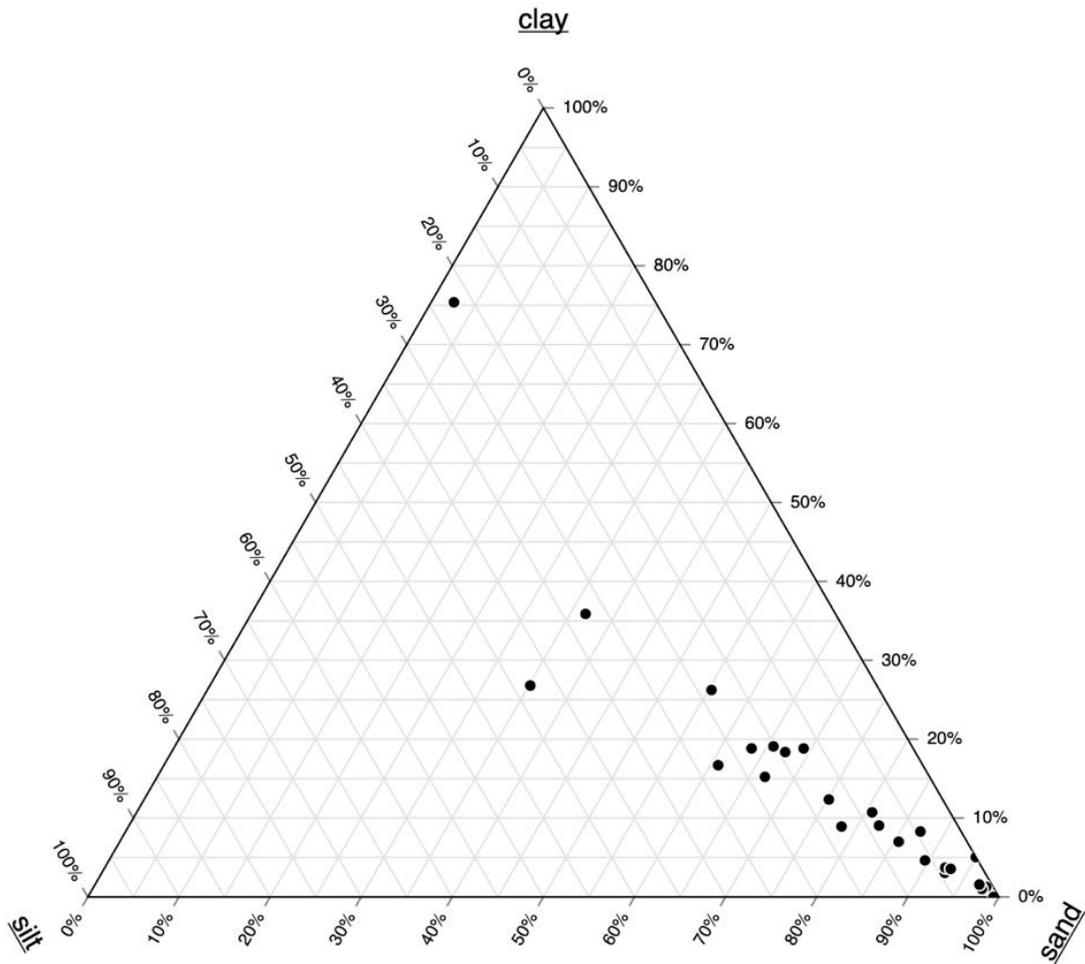


Figure 7. Abundance pie charts in site order. Each genus was assigned a number (white) and color (see explanation at bottom of figure).



Made with [TernaryPlot.com](https://www.ternaryplot.com)

Figure 8. Ternary plot of grain size use percent clay (less than 3.9 μm), silt (3.9 to 62.5 μm), and sand (greater than 62.5 μm). Made using <https://www.ternaryplot.com/>.

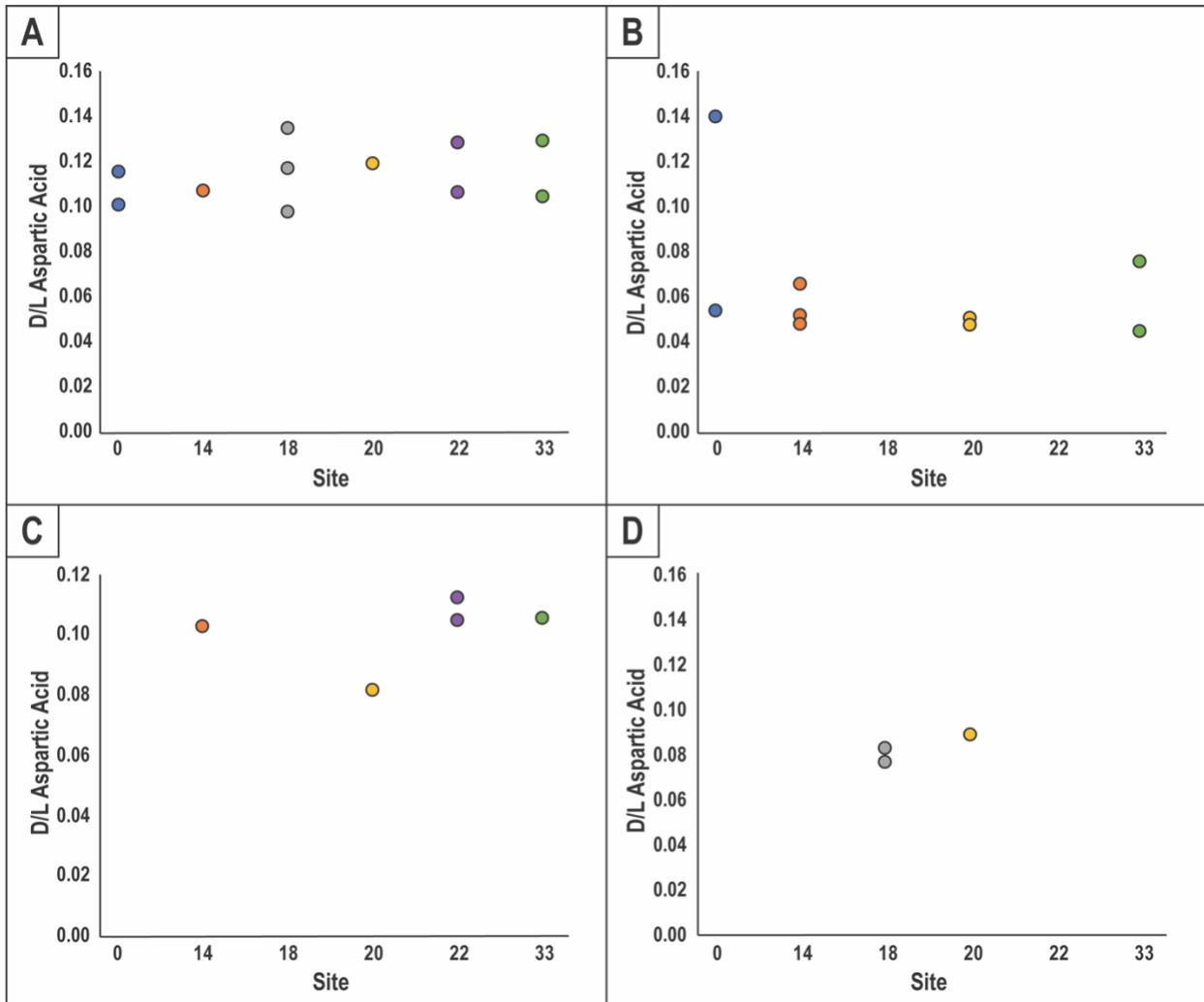


Figure 9. Ratio of D/L Aspartic Acid in the samples from the genera A) *Cyclocardia*, B) *Nuculana*, C) *Chlamys*, and D) *Macoma*. Samples from site 0 is blue, site 14 is orange, site 18 is grey, site 20 is yellow, site 22 is purple, and site 33 is green.

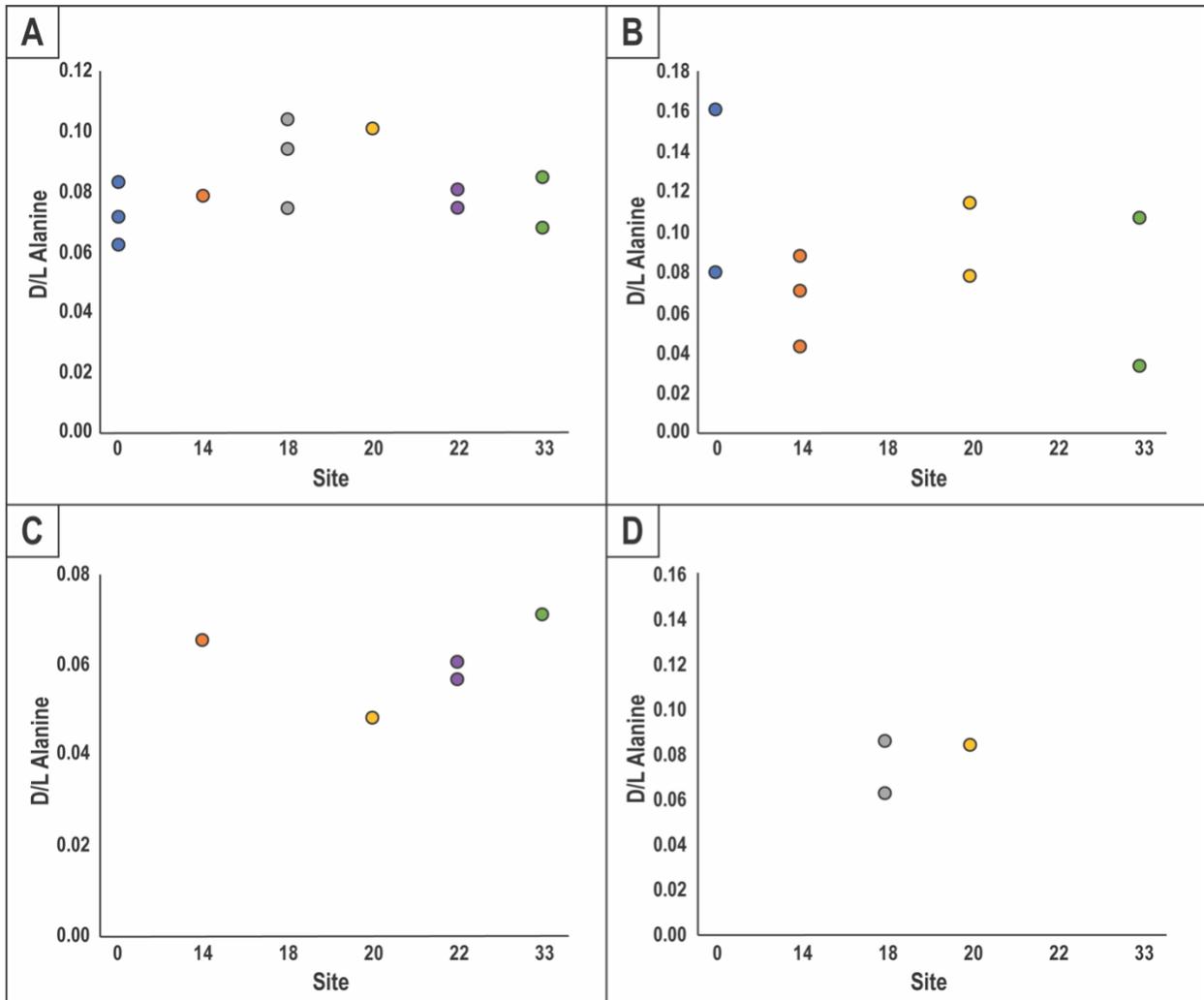


Figure 10. Ratio of D/L Alanine in the samples from the genera A) *Cyclocardia*, B) *Nuculana*, C) *Chlamys*, and D) *Macoma*. Samples from site 0 is blue, site 14 is orange, site 18 is grey, site 20 is yellow, site 22 is purple, and site 33 is green.

Appendix A: R Packages and code

Package ‘xlsx’

URL: <https://github.com/colearendt/xlsx>

Description: Provides R functions to read/write/format Excel 2007 and Excel 97/2000/XP/2003 file formats

*Note: Rtools, rJava, and [updated Java](#) (64bit) are required for this package to work

Package ‘tidyverse’

URL: <https://www.tidyverse.org/>

Description: Collection of R packages commonly used for data analysis/ science

Package ‘ggplot2’

URL: <https://github.com/tidyverse/ggplot2>

Description” An implementation of the Grammar of Graphics in R

Package ‘Hmisc’

URL: <https://cran.r-project.org/web/packages/Hmisc/index.html>

Description: Contains many functions useful for data analysis, high-level graphics, utility operations, functions for computing sample size and power, simulation, importing and annotating datasets, imputing missing values, advanced table making, variable clustering, character string manipulation, conversion of R objects to LaTeX and html code, and recoding variables.

```

#load data and clean
pres_ab <- read.csv("pres_ab.csv", header = TRUE)
pres_ab <- pres_ab[1:25, ]

scatter_plot <- ggplot(pres_ab, aes(clay_silt, Astarte))
scatter_plot +
  geom_point() +
  labs(x = "clay_silt%", y = "Astarte abundance") +
  geom_smooth(method="lm")

# Calculating Pearson's product-moment correlation for single
pair
cor.test(pres_ab$clay_silt,
         pres_ab$Astarte,
         method = "pearson",
         conf.level = 0.95)

# calculating Pearson's correlation for all pairs at once

# separate the data by grain size (this is for clay_silt only)

# remove other grain size columns and convert to matrix
pres_ab_clay_silt <- subset(pres_ab, select = -
c(vf_sand,coarse_sand))
pres_ab_clay_silt <- as.matrix(pres_ab_clay_silt)

# create correlation matrix

clay_silt <- rcorr(as.matrix(pres_ab_clay_silt, type =
"pearson"))

# extract p-values and correlation coefficients
clay_silt$P
clay_silt$r

# use a function to create a table
flattenCorrMatrix <- function(cormat, pmat) {
  ut <- upper.tri(cormat)
  data.frame(
    row = rownames(cormat)[row(cormat)[ut]],
    column = rownames(cormat)[col(cormat)[ut]],
    cor = (cormat)[ut],
    p = pmat[ut]
  )
}

```

Appendix B: Sample preparation for grain size analysis using the Coulter Laser Diffraction Unit (modified from Rodbell, 1998)

Items Needed:

- 1- and 2-mm sieves
- centrifuge and multiples of centrifuge tubes
- 15% 1M NaOH (40.0 g of NaOH dissolved in 1l of DI water)
- concentrated H₂O₂ (30%)
- Dispersant (25.0 g of sodium metaphosphate dissolved in 500 ml DI water)
- squirt bottle and plenty of DI water
- reciprocating shaker
- hotplate
- 5 ml pipette glass stir rods
- Disposable pipettes

Separation of Material > 1 mm

1. Wet sieve sample through a 1 mm sieve and collect all material < 1 mm; sieve material >1 mm through 2 mm sieve to collect all shells > 2 mm
2. Dry sample at room temperature for ~48 hours
3. Pick out any obvious pieces of organic matter and shell
4. Weigh labeled centrifuge tube to the nearest 10⁻² g (0.00 g)
5. Place between 0.40-0.60 g of material < 1 mm in a centrifuge tube; *use 0.40 g if sample is inorganic and fine grained; use 0.50 g if sample is organic and fine grained; use 0.60 g if sample lacks fines*
6. Let the sample dry at room temperature for ~48 hours
7. Reweigh tube
8. Record sample number, centrifuge tube number, and weight (to the nearest 0.01g)

Removal of Organic Matter

9. With sample in centrifuge tubes under hood and wearing gloves & respirator, add 5 ml of concentrated (30%) H₂O₂ from a calibrated pipette
10. Stir with a glass stirring rod and rinse rod off with DI water (rinse back into centrifuge tube so that no material is lost, and use as little DI water as possible)
11. After initial reaction wanes or if nothing happens, place centrifuge tube in beaker of water on hot plate set to 50° C
12. Watch reaction so that sample does not foam over or dry out; if latter occurs, immediately remove from heat and spray with DI water
13. Leave samples and hot plate under hood until reaction is complete
- 14. Do not let sample dry out**
15. Let sample react overnight, but do not leave hotplate on unless you are watching sample
16. Bring fluid level to even level by adding DI water to appropriate tubes (here we want a balanced load for the centrifuge)
17. Cap centrifuge tubes
18. Place in centrifuge at 5000-7000 RPM for 3 minutes
19. Carefully decant supernatant so that NO sediment escapes

20. If samples have a lot of organic matter, repeat steps 1-11; otherwise go to step 14
21. Fill tubes with DI water to $\frac{3}{4}$ level, cap and shake vigorously for at least 30 seconds
22. Repeat steps 10 and 11
23. Fill tubes with DI water to $\frac{3}{4}$ level, cap and shake vigorously for at least 30 seconds
24. Repeat steps 10 and 11

Dispersant

- Add 5 ml of dispersant to samples
- Stir vigorously with a glass stirring rod until all clods are broken up; rinse stirring rods between samples so there is no chance for sample contamination (rinse back into the centrifuge tube so that no material is lost).

Tables

Table 1. Species used by Easterbrook (1962).

<i>Nuculana fossa</i>
<i>Nuculana minuta</i>
<i>Hiatella arctica</i>
<i>Saxidomus nuttallii</i>
<i>Clinocardium nuttallii</i>
<i>Chlamys rubida</i>
<i>Chlamys hastata</i>
<i>Astarte alaskensis</i>
<i>Leukoma staminea</i>
<i>Macoma nasuta</i>
<i>Macoma incongrua</i>
<i>Macoma inquinata</i>
<i>Mya arenaria</i>
<i>Mya truncata</i>
<i>Lottia pelta</i>
<i>Lottia persona</i>
<i>Latisipho hallii</i>
<i>Latisipho jordani</i>
<i>Sinum scopulosum</i>
<i>Neverita lewisii</i>
<i>Trichotropis conica</i>
<i>Margarites pupillus</i>
<i>Admete</i> sp.
<i>Tresus nuttallii</i>

Table 2. Samples chosen for AAR analysis.

ID	Type	Site
00_01	<i>Cyclocardia</i>	0
00_02	<i>Cyclocardia</i>	0
00_03	<i>Cyclocardia</i>	0
00_04	<i>Nuculana</i>	0
00_05	<i>Nuculana</i>	0
14_01	<i>Chlamys</i>	14
14_02	<i>Cyclocardia</i>	14
14_03	<i>Nuculana</i>	14
14_04	<i>Nuculana</i>	14
14_05	<i>Nuculana</i>	14
18_01	<i>Cyclocardia</i>	18
18_02	<i>Cyclocardia</i>	18
18_03	<i>Cyclocardia</i>	18
18_04	<i>Macoma</i>	18
18_05	<i>Macoma</i>	18
20_01	<i>Cyclocardia</i>	20
20_02	<i>Macoma</i>	20
20_03	<i>Chlamys</i>	20
20_04	<i>Nuculana</i>	20
20_05	<i>Nuculana</i>	20
22_01	<i>Chlamys</i>	22
22_02	<i>Cyclocardia</i>	22
22_03	<i>Cyclocardia</i>	22
22_04	<i>Cyclocardia</i>	22
22_05	<i>Chlamys</i>	22
33_01	<i>Cyclocardia</i>	33
33_02	<i>Nuculana</i>	33
33_03	<i>Cyclocardia</i>	33
33_04	<i>Nuculana</i>	33
33_05	<i>Chlamys</i>	33

Table 3. “Species midpoint” is the average latitude of the species present at each site based on the values reported in Keen (1937). “Latitude” is the actual latitude where the sample was collected. “Difference” is the absolute value of “Species midpoint” minus “Latitude.”

Site	Species midpoint	Latitude	Difference
0	45.479	48.487	3.008
2	46.816	48.500	1.684
6	45.286	48.502	3.216
7	43.944	48.503	4.558
10	46.667	48.520	1.853
11	45.833	48.532	2.699
14	46.567	48.596	2.030
16	48.462	48.631	0.169
17	46.640	48.619	1.979
18	46.554	48.622	2.069
19	47.464	48.625	1.161
20	46.795	48.636	1.841
22	46.106	48.479	2.373
23	46.625	48.585	1.960
24	49.500	48.619	0.881
25	44.167	48.669	4.502
26	45.750	48.716	2.966
27	44.962	48.742	3.781
28	49.000	48.755	0.245
29	48.000	48.762	0.762
30	48.214	48.772	0.557
31	47.545	48.732	1.186
32	44.912	48.707	3.795
33	45.913	48.692	2.779
34	48.167	48.474	0.307

Table 4. Predatory gastropods found in samples from Rosario Strait.

<i>Colus griseus</i>
<i>Cryptonatica affinis</i>
<i>Melanella micans</i>
<i>Mitrella gausapata</i>
<i>Nassarius mendicus</i>
<i>Neverita lewisii</i>
<i>Nucella</i> sp.
<i>Odostomia columbiana</i>
<i>Paciocinebrina interfossa</i>
<i>Propebela fidicula</i>
<i>Trophonopsis orpheus</i>
<i>Turbonilla newcombei</i>

Table 5. D/L values for Aspartic Acid and Alanine sorted by genus.

Sample Number	Genus	DL Asp	DL Ala
14_01	<i>Chlamys</i>	0.103	0.065
20_03	<i>Chlamys</i>	0.082	0.048
22_01	<i>Chlamys</i>	0.105	0.057
22_05	<i>Chlamys</i>	0.112	0.061
33_05	<i>Chlamys</i>	0.106	0.071
00_01	<i>Cyclocardia</i>	0.102	0.063
00_02	<i>Cyclocardia</i>	0.101	0.083
00_03	<i>Cyclocardia</i>	0.116	0.072
14_02	<i>Cyclocardia</i>	0.107	0.079
18_01	<i>Cyclocardia</i>	0.118	0.104
18_02	<i>Cyclocardia</i>	0.135	0.095
18_03	<i>Cyclocardia</i>	0.098	0.075
20_01	<i>Cyclocardia</i>	0.12	0.102
22_02	<i>Cyclocardia</i>	0.129	0.075
22_03	<i>Cyclocardia</i>	0.107	0.081
22_04	<i>Cyclocardia</i>	0.106	0.081
33_01	<i>Cyclocardia</i>	0.105	0.068
33_03	<i>Cyclocardia</i>	0.129	0.085
18_04	<i>Macoma</i>	0.078	0.063
18_05	<i>Macoma</i>	0.084	0.087
20_02	<i>Macoma</i>	0.089	0.086
00_04	<i>Nuculana</i>	0.265	0.162
00_05	<i>Nuculana</i>	0.103	0.082
14_03	<i>Nuculana</i>	0.092	0.044
14_04	<i>Nuculana</i>	0.099	0.072
14_05	<i>Nuculana</i>	0.126	0.089
20_04	<i>Nuculana</i>	0.095	0.079
20_05	<i>Nuculana</i>	0.092	0.116
33_02	<i>Nuculana</i>	0.085	0.034
33_04	<i>Nuculana</i>	0.144	0.108

References

- Abbott, T., 1974, *American Seashells: The Marine Mollusca of the Atlantic and Pacific Coasts of North America* (second edition): New York, N.Y., Van Nostrand Reinhold Company, 663 p.
- Aguirre, M. L., 2003, Late Pleistocene and Holocene palaeoenvironments in Golfo San Jorge, Patagonia: molluscan evidence: *Marine Geology*, v. 194, p. 3-30.
- Allmon, W. D., and P. M. Mikkelsen, 2020, *Bivalvia*, in *The Digital Encyclopedia of Ancient Life*: <https://www.digitalatlasofancientlife.org/learn/mollusca/bivalvia> (accessed June 2021).
- Armstrong, J. E., 1984, Environmental and engineering applications of the surficial geology of the Fraser Lowland, British Columbia: Geological Survey of Canada; Hull, Québec, Canada, 54 p.
- Bakeman, V. R., 2006, Pacific and Atlantic coast mollusk shells: chromatographic amino acid racemization kinetics and interlaboratory comparisons [M.S. thesis]: University of Delaware, 272 p (<https://udspace.udel.edu/handle/19716/27395?show=full>).
- Balzarini, M. A., 1983, Paleoecology of Late Pleistocene glacial-marine sediments in Northwestern Washington and Southwestern British Columbia in Molnia, B. F. ed., *Glacial-Marine Sedimentation*: Boston, M.A., Springer, p. 571-592.
- Booth, D. B., 1987, Timing and processes of deglaciation along the southern margin of the Cordillera a ice sheet in Ruddiman, W. F., and Wright, H. E., Jr., eds., *North America and adjacent oceans during the last deglaciation*: Boulder, Colorado, Geological Society of America, *The Geology of North America*, v. K-3, 20p.
- Borden, R. K., and Troost, K. G., 2001, Late Pleistocene in the South-Central Puget Lowland, Pierce County, Washington. Washington State Department of Natural Resources. Open File Report no. 33, p. 1-34.
- Canuel, E. A., Brush, G., Cronin, T. M., Lockwood, R., and Zimmerman, A. R., 2017. Paleoecology studies in Chesapeake Bay: A model system for understanding interactions between climate, anthropogenic activities, and the environment in K. Weckström, K. M. Saunders, P. A. Gell, C. G. Skilbeck, eds., *Applications of Paleoenvironmental Techniques in Estuarine Studies: Developments in Paleoenvironmental Research* 20, p. 495-527.
- Clague, J. J., Mathewes, R. W., Guilbault, J. -P., Hutchinson, I., and Ricketts, B. D., 1997, Pre-Younger Dryas resurgence of the southwestern margin of the Cordilleran ice sheet, British Columbia, Canada: *Boreas*, v. 26, p. 261-278.
- Clague, J. J., Mathewes, R. W., Guilbault, J. -P., Hutchinson, I., and Ricketts, B. D., 1998, 'Pre-Younger Dryas resurgence of the southwestern margin of the Cordilleran ice sheet, British Columbia, Canada': Reply to comments: *Boreas*, v. 27, p. 229-230.

- Dethier, D. P., Pessl Jr., F., Keuler, R. F., Balzarini, M. A., and Pevear, D. R., Late Wisconsinan glaciomarine deposition and isostatic rebound, northern Puget Lowland, Washington: GSA Bulletin, v. 107, n. 11, p. 1288-1303.
- Dickinson, G. H., Ivanina, A. V., Matoo, O. B., Pörtner, H. O., Lannig, G., Bock, C., Beniash, E., and Sokolova, I. M., 2012, Interactive effects of salinity and elevated CO₂ levels on juvenile eastern oysters, *Crassostrea virginica*: Journal of Experimental Biology, v. 215, p. 29-43.
- Easterbrook, D. J., Pleistocene, 1962, Geology of the Northern Part of the Puget Lowland, Washington [PhD thesis]: University of Washington, 160 p.
- Easterbrook, D. J., 1963, Late Pleistocene glacial events and relative sea-level changes in the Northern Puget Lowland, Washington: GSA Bulletin, v. 74, n. 12, p. 1465-1483.
- Easterbrook, D. J., 2003a, Cordilleran ice sheet glaciation of the Puget Lowland and Columbia Plateau and alpine glaciation of the North Cascade Range, Washington, in Easterbrook, D. J., ed., Quaternary Geology of the United States, Field Guide: Desert Research Institute, v. 16, p. 265–286.
- Easterbrook, D. J., 2003b, Cordilleran ice sheet glaciation of the Puget Lowland and Columbia Plateau and alpine glaciation of the North Cascade Range, Washington, in Swanson, T. W., ed., Geological Society of America Field Guide 4, Western Cordillera and Adjacent Areas: Geological Society of America, p. 137–157.
- Easterbrook, D. J., 2016, Glaciation of the Puget Lowland, North Cascade Range, and Columbia Plateau, Washington, in Cheney, E. S., ed., The Geology of Washington and Beyond: From Laurentia to Cascadia. Seattle, Washington Department of Natural Resources, Division of Earth and Geology Resources, p. 257-286.
- Easterbrook, D. J., Kovanen, D. J., and Slaymaker, O., 2007, New developments in Late Pleistocene and Holocene glaciation and volcanism in the Fraser Lowland and North Cascades, Washington, in Stelling, P., and Tucker, D. S., eds., Floods, Faults, and Fire: Geological Field Trips in Washington State and Southwest British Columbia: Geological Society of America, Field Guide 9, p. 31-56.
- Giribet, G., 2008, Bivalvia in Ponder, W. F. and Lindberg, D. R., eds. Phylogeny and Evolution of the Mollusca: University of California Press, Berkeley and Los Angeles, California, p.105-141.
- Hutchings, J.A., and Haedrich, R.L., 1984, Growth and population structure in two species of bivalves (Nuculanidae) from the deep sea: Marine Ecology Progress Series, v. 17, p. 135-142.
- Keen, A. M., 1937, An Abridged Check List and Bibliography of West North American Marine Mollusca: Stanford University, California, 84 p.
- Kidwell, S. M., 2001, Preservation of species abundance in marine death assemblages: Science, v. 294, p. 1091-1094.

- Kidwell, S. M., 2013, Time-averaging and fidelity of modern death assemblages: Building a taphonomic foundation for conservation palaeobiology: *Palaeontology*, v. 56, p. 487-522.
- Kidwell, S. M., and Flessa, 1995, The quality of the fossil record: Populations, species, and communities: *Annual Review of Ecology Systematics*, v. 26, p. 269-299.
- Kovanen, D.J., 2002, Morphologic and stratigraphic evidence for Allerød and Younger Dryas age glacier fluctuations of the Cordilleran Ice Sheet, British Columbia, Canada and Northwest Washington, U.S.A.: *Boreas*, v. 31, p. 163-184.
- Kovanen, D. J., and Easterbrook, D. J., 2002, Timing and Extent of Allerød and Younger Dryas Age (ca. 12,500–10,000 14C yr B.P.) Oscillations of the Cordilleran Ice Sheet in the Fraser Lowland, Western North America: *Quaternary Research*, v. 57, p. 208-224.
- Kovanen, D. J., Haugerud, R. A., and Easterbrook, D. J., 2020, Geomorphic Map of Western Whatcom County, Washington: Pamphlet to accompany Scientific Investigations Map 3406, U.S. Geological Survey, 48 p.
- Kozloff, E. N., 1973, *Seashore life of the Northern Pacific Coast*: University of Washington Press.
- Kozloff, E. N., 1996, *Marine Invertebrates of the Pacific Northwest with additions and corrections*: University of Washington Press.
- Lapen, T. J., 2000, Geologic map of the Bellingham 1:100,000 quadrangle, Washington: Open File Report 2000-5, Scale 1:100,000.
- NOAA, 2021, NOAA Tide Predictions: https://tidesandcurrents.noaa.gov/tide_predictions.html (accessed 7/8/2021).
- Ockelmann, W. K., 1958, The zoology of East Greenland marine Lamellibranchiata: Bianco Lunos Bogtrykkeri A/S, Copenhagen, p. 15-20.
- Oldroyd, I. S., 1924, *Marine Shells of Puget Sound and Vicinity*, Seattle, University of Washington Press, v. 4, 272p.
- Petersen, K.S., 1986, Marine molluscs as indicators of former sea-level stands *in* van de Plassche, O. (ed.), *Sea-level Research: A Manual for the Collection and Evaluation of Data*: Dordrecht, Springer, p. 129-155.
- Pitts, B., 2020, Determining the Effects of the mid-Pliocene Warm Period on *Glycymeris subovata* Morphology [B.S. thesis]: College of William & Mary, 48p.
- Rodbell, 1998, Sample Preparation for Grain Size Analysis Using the Coulter Laser Diffraction Unit [Laboratory procedures]: Western Washington University, 3 p.

- Stanley, S. M., 1970, Relation of shell form to life habits of the Bivalvia (Mollusca): Boulder, Colorado, Geological Society of America Memoir, 296 p.
- Steffani, N., Sedick, S., Rogers, J., Gibbons, M.J., 2015, Infaunal Benthic Communities from the Inner Shelf off Southwestern Africa Are Characterised by Generalist Species: PLoS ONE, v. 10, 20 p.
- Thompson, C. M., 2017, Survey of molluscan fauna from the mid-Atlantic United States continental shelf [B.S. thesis]: College of William & Mary, 41 p.
- Tucker, D., 2015, Geology Underfoot in Western Washington: Missoula, Montana, Mountain Press Publishing Company, 374 p.
- Weber, S.J., 2001, Late Pleistocene littoral deposits in the Deming sand at Bellingham Bay, Washington, and their implications for relative sea level changes [M.S. thesis]: Western Washington University, p. 173.
- WoRMS Editorial Board, 2021, World Register of Marine Species: <http://www.marinespecies.org> at VLIZ, doi:10.14284/170 (accessed July 2021).