Intertidal Resource Cultivation Over Millennia Structures Coastal Biodiversity

by

Kieran D. Cox

B.Sc., University of Victoria, 2014

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We acknowledge with respect the Lekwungen peoples on whose traditional territory the university stands and the Songhees, Esquimalt and W̱SÁNEĆ peoples whose historical relationships with the land continue to this day.

Supervisory Committee

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Abstract

Cultivation of marine ecosystems began in the early Holocene and has contributed vital resources to humans over millennia. Several more recent cultivation practices, however, erode biodiversity. Emerging lines of evidence indicate that certain resource management practices may promote favourable ecological conditions. Here, I use the co-occurrence of 24 First Nations clam gardens, shellfish aquaculture farms, and unmodified clam beaches to test several hypotheses concerning the ecological implications of managing intertidal bivalve populations. To so do, in 2015 and 2016, I surveyed epifaunal (surface) and bivalve communities and quantified each intertidal sites' abiotic conditions, including sediment characteristics and substrate composition. In 2017, I generated three-dimensional models of each site using structure-from-motion photogrammetry and measured several aspects of habitat complexity. Statistical analyses use a combination of non-parametric multivariate statistics, multivariate regression trees, and random forests to quantify the extent to which the intertidal resource cultivation structures nearshore biodiversity

Chapter 1 outlines a brief history of humanity's use of marine resources, the transition from extracting to cultivating aquatic taxa, and the emergences of the northeast Pacific's most prevalent shellfish cultivation practices: clam gardens and shellfish farms.

Chapter 2 evaluates the ability of epifaunal community assessment methods to capture species diversity by conducting a paired field experiment using four assessment methods: photo-quadrat, point-intercept, random subsampling, and full-quadrat assessments. Conducting each method concurrently within multiple intertidal sites allowed me to quantify the implications of varying sampling areas, subsampling, and photo surveys on detecting species diversity, abundance, and sample- and coverage-based biodiversity metrics. Species richness, density, and sample-based rarefaction varied between methods, despite assessments occurring at the same locations, with photo-quadrats detecting the lowest estimates and full-quadrat assessments the highest. Abundance estimates were consistent among methods, supporting the use of extrapolation. Coverage-based rarefaction and extrapolation curves confirmed that these dissimilarities were due to differences between the methods, not the sample completeness. The top-performing method, random subsampling, was used to conduct Chapter 4’s surveys.

Chapter 3 examines the connection between shellfish biomass and the ecological conditions clam garden and shellfish farms foster. First, I established the methodological implications of varying sediment volume on the detection of bivalve diversity, abundance, shell length, and sample- and coverage-based biodiversity metrics. Similar to Chapter 2, this examination identified the most suitable method, which I used during the 2015 and 2016 bivalve surveys. The analyses quantified several interactions between each sites’ abiotic conditions and biological communities including, the influence of substrate composition, sediment characteristics, and physical complexity on bivalve communities, and if bivalve richness and habitat complexity facilitates increases in bivalve biomass.

Chapter 4 quantifies the extent to which managing intertidal bivalves enhance habitat complexity, fostering increased diversity in the epifaunal communities. This chapter combines 2015, 2016, and 2017 surveys of the sites' epifaunal communities and habitat complexity metrics, including fractal dimension at four-resolutions and linear rugosity. Clam gardens enhance fine- and broad-scale complexity, while shellfish farms primarily increase fine-scale complexity, allowing for insights into parallel and divergent community responses.

Chapter 5 presents an overview of shellfish as a marine subsidy to coastal terrestrial ecosystems along the Pacific coast of North America. I identified the vectors that transport shellfish-derived nutrients into coastal terrestrial environments, including birds, mammals, and

over 13,000 years of marine resource use by local people. I also examined the abundance of shellfish-derived nutrients transported, the prolonged persistence of shellfish subsidies once deposited within terrestrial ecosystems, and the ecological implications for recipient ecosystems.

Chapter 6 contextualizes the preceding chapters relative to the broader literature. The objective is to provide insight into how multiple shellfish cultivation systems influence biological communities, how ecological mechanisms facilitate biotic responses, and summarize the implications for conservation planning, Indigenous resource sovereignty, and biodiversity preservation. It also explores future work, specifically the need to support efforts that pair Indigenous knowledge, and ways of knowing with Western scientific insights to address conservation challenges.

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Acknowledgements

The research within this dissertation was conducted with an incredible group of collaborators and mentors to whom I am very grateful. First, I would like to express my sincere gratitude to my advisors Dr. Sarah Dudas and Dr. Francis Juanes, for helping me grow academically and personally over the past six years. The research environment, guidance, and unwavering support you provided have been vital to my development as an emerging scholar. I am excited to carry the knowledge and passion you imparted on me into future projects. This research was conducted in collaboration with the Hakai Institute. I was fortunate to work closely with several exceptional individuals during this collaboration, including Dr. Margot Hessing-Lewis and Ben Millard-Martin, with guidance and encouragement from Eric Peterson and Christina Munck. I am grateful to my committee, Drs Francis Juanes, Sarah Dudas, Verena Tunnicliffe, and Natalie Ban, for guiding my dissertation research, encouraging me to reach my scientific potential, and ensuring I continue to develop my scientific writing abilities. Funding for my dissertation research was generously provided by the Hakai Institute, the Natural Sciences and Engineering Research Council of Canada, the Montalbano Scholars Fellowship, the PADI Foundation, and the University of Victoria.

The field research component of this project was conducted on British Columbia's central and south coasts within the territories of the Heiltsuk, Wuikinuxv, Xwémalhkwu (Homalco), Wei Wai Kai, Wei Wai Kum, and K'omoks Nations. My time in Victoria and at the University of Victoria was spent within the territories of the Lekwungen-speaking peoples and the Songhees, Esquimalt and WSÁNEĆ peoples. I am grateful to these Nations for their continued stewardship of these lands.

I was fortunate to work with a broad collaborative network on a range of endeavours throughout my Ph.D. Many of these colleagues became friends over the years; this made any

hardship easier. Morgan Black, Hailey Davies, Natalia Filip, Matthew Miller, Kayla Long, Kayla Suhan, Raquel Greiter Loerzer, Thaise Freitas, and Dr. Travis Gerwing's support was vital to my dissertation research. The Clam Garden Network, specifically Skye Augustine (Hwsyun'yun), Amy Groesbeck, Dr. John Harper, Dr. Dana Lepofsky, Dr. Nicole Smith, and Dr. Anne Salomon, were integral to my understanding of this research topic. Dr. Thomas Reimchen's mentorship and friendship throughout my Ph.D. encouraged me to explore interesting ecological questions and think broadly. External to my thesis research, I collaborated on several examinations of aquatic soundscapes. These examinations were made possible by support from Audrey Looby, Amalis Riera, Sarah Vela, Santiago Bravo, Rodney Rountree, Francis Juanes, Laura Reynolds, Charles Martin and Xavier Mouy. Dr. Garth Covernton and I worked closely while he was a graduate student at the University of Victoria, providing personal and academic support, and an avenue for investigating novel pollutants.

I would also like to thank my incredible support system. My parents David Cox and Susan Lopatecki, provided me with needless opportunities to learn and grow, and were always there when I faced adversity. My partner, Jenna Bright, provided unwavering encouragement throughout my Ph.D. She was a pillar of support, trusted confidante, a copy-editor, and a scientific collaborator throughout this process. I could not have done this without the support of Jenna, Susan and David.

Dedication

To my parents,

David Cox and Susan Lopatecki,

who provided me with the environment I needed to find my way.

Positionality Statement

Research carries the biases, personal history, and motivations of the researcher. I wish to be transparent about my relationship to this research project, as well as the lens through which I view the world. The importance of this acknowledgement is amplified as the research questions examined here are at the nexus of Indigenous and settler societies. The purpose of this positionality statement is to help readers identify my strengths and weaknesses, as well as any nuances in interpretation related to my social, experiential, or cultural biases.

I am a white Canadian male who grew up in the Okanagan with my twin brother, older sister and parents. My mother’s parents moved to the Okanagan centuries earlier after meeting in a prison of war camp during the Second World War. My father grew up in Vancouver and met my mother near what is now our family home. My brother and I spent most of our childhoods exploring Okanagan lake. Despite an avid fondness for nature, I failed to excel academically throughout elementary and high school. One of the factors contributing to this was identified early in my childhood when educators became aware my brother and I had learning disabilities that primarily impacted reading and writing. Over the following decade, learning assistance centres (then known as centres for students with disabilities) were a vital component of my elementary and high school experience. University was of minimal interest to me following graduation, and poor grades meant I was of little interest to universities. I was fortunate to begin SCUBA diving in my early 20s, which spurred an interest in aquatic ecosystems that motivated me to attend Okanagan College, upgrade my high school courses and start an undergraduate degree. I then transferred to the University of Victoria to complete my undergraduate degree. As a result, my involvement in academic institutes has and always will be motivated by the time I spend in natural environments.

My interest in this research stems from my eagerness to understand better the management practices that have shaped coastal ecosystems for millennia. I am also motivated by my awareness of the need to conserve coastal species. To me, clam gardens and shellfish farms exemplify a framework for elevating adverse environmental impacts while enhancing food production and increasing the awareness of longstanding management strategies. I recognize that several aspects of these stories, especially those within the study of clam gardens, are not mine to tell. I have always strived for my contribution to this field to be grounded in my expertise as a marine community ecologist. While doing so, I recognize that I still have much learning and unlearning to do and am grateful to those who have contributed to my understanding of the space I occupy.

Chapter 1: Introduction

1.1 Human-Marine Ecosystem Interactions

Human reliance on marine ecosystems began over 300,000 years ago, with evidence that increased intensity of marine resource use is unique to *Homo sapiens*, relative to earlier hominins (Lewis and Maslin 2015, Erlandson 2021). The incorporation of marine resources into human diets provided access to dependable, highly nutritious foods that were harvestable with relatively modest technologies (Fitzpatrick 2020). Marine-derived nutrients may have provided human populations with the resources required to expand their ranges, develop more prosocial behaviours, and engineer early technologies (Marean et al. 2007, Fitzpatrick 2020). Consequently, the connection between humans and marine resources can be tracked from inception, to the present day by following human movement across the planet (Lewis and Maslin 2015, Erlandson 2021). Extracting marine species along vast temporal and spatial scales is not without consequences. Variation in species sizes, distributions, and behaviours have evolved in response to this ecological driver (Sullivan et al. 2017). Species responses to human predators are generally the most severe when selective pressures are applied unidirectionally, to a specific feature (*e.g.* size), or extraction rates outpace those applied by natural predators rates (Darimont et al. 2015). Unfortunately, human predators commonly apply these conditions, causing declines in size-related traits and shifts in life-history traits (Sullivan et al. 2017). However, several occurrences of marine resource extraction have exhibited sustainability for millennia, with metrics of overharvesting (*e.g.* size reductions, population declines) unresponsive to human predation (Rick et al. 2016, Toniello et al. 2019, Thompson et al. 2020b). An emergent theme in these predator-prey systems is that the predator's actions either directly increase the prey populations' ability to persist, or do so indirectly, through modifications to the environment.

1.2 The Origins of Aquaculture

The transition from extraction to cultivation produced a reliable and abundant source of targeted taxa (Nakajima et al. 2019, Fitzpatrick 2020). The common carp, *Cyprinus carpio*, was domesticated 8,000 years ago in Early Neolithic China using a rice paddy and fish co-culture system, signifying the beginning of aquaculture (Nakajima et al. 2019). Parallel cultivation systems evolved globally to domesticate a range of taxa (Fitzpatrick 2020). Nearshore structures built from stones or shells that use tidal influxes to capture fish in holding pods were constructed throughout the Pacific, in accordance with societal preferences, targeted taxa and environmental conditions. Fijian moka, and Hawaiian Loko Wai, and watercourts in the southern United States, exemplify the diversity of enhancement strategies and tenure systems used to cultivate aquatic taxa (Fitzpatrick 2020, Thompson et al. 2020b). The onset of shellfish aquaculture is more challenging to resolve. Archaeological evidence for shellfish management spans the Holocene; however, distinguishing between harvesting, management, and cultivation poses challenges given the range of transplant, selection, and enhancement practices used to manage shellfish populations (Lepofsky et al. 2015, Fitzpatrick 2020). This issue is compounded by the debate surrounding archaeological interpretation of various shell deposits and a misconception that Indigenous societies were predominately "hunter-gatherers" (Turner 2020, Erlandson 2021). Technologies engineered by Indigenous peoples throughout the northeast Pacific clarify these issues and provide insight into First Peoples’ 14,000-year continuous coastal occupation (Lepofsky et al. 2015, McLaren et al. 2018, Toniello et al. 2019).

1.3 Clam Gardens

Indigenous Peoples created and enhanced clam habitats throughout the northeast Pacific by building "clam gardens"—mid to low intertidal rock walls with soft-sediment terraces (Fig. 1) (Deur et al. 2015, Lepofsky et al. 2015, Neudorf et al. 2017, Smith et al. 2019). Built continuously over the past 3,500 years clam gardens are heterogeneously distributed from Alaska to British Columbia (Harper et al. 1995, H-GINPR 2016, Jackley et al. 2016, Moss and Wellman 2017, Smith et al. 2019). Garden walls increase sedimentation rates in the intertidal, up to fourfold, altering the beach slope at tidal heights optimal for clam production (Neudorf et al. 2017, Smith et al. 2019). The soft-sediment terrace between the wall and the shoreline is maintained using a suite of tending practices, including predator exclusion, soil aeration, size-selective harvesting, and depositing bivalve shells to encourage larval settlement (Deur et al. 2015, Lepofsky et al. 2015, H-GINPR 2016). Collectively, these management practices increase clam abundances, providing stable shellfish production adjacent to coastal human populations. European-introduced diseases in the late 1700s, and residential schools in the 1870s, led to drastic losses of Indigenous populations and subsequent decline in mariculture practices, causing many gardens to not be managed with the same intensity as they were during prior millennia (Toniello et al. 2019, Turner 2020). However, recent scientific investigations of ecological responses to clam gardens illustrate the extent to which clam gardens influence nearshore ecosystems, and Indigenous-led restoration efforts have begun restoring clam gardens (Groesbeck et al. 2014, Augustine and Dearden 2014, H-GINPR 2016, Jackley et al. 2016, Cox et al. 2019).

1.4 Shellfish Farming

Contemporary shellfish aquaculture along the northwest coast of North American began in the mid-1800s with the commercial extraction of Olympia Oysters (*Ostrea lurida*), the region's only indigenous oyster (Kirby 2004, White et al. 2009). Unfortunately, the combination of overexploitation, habitat destruction, and disrupted settlement cues due to shell removal resulted in an unsustainable fishery that showed signs of imminent collapse by 1930 and had collapsed by 1960 (White et al. 2009). With the demise of *O. lurida* looming, the Atlantic Oyster (*Crassostrea virginica*) from the east coast of North America and the Pacific Oyster (*Magallana gigas*) from Japan's Sendai Bay were introduced (Ruesink et al. 2005, White et al. 2009). The *C. virginica* fishery was short-lived due to failed reproduction, but *M. gigas* was successfully cultivated and harvested by the early 1920s (Kirby 2004, White et al. 2009). Concurrently, the Manila clam (*Ruditapes philippinarum*) was introduced accidentally with *M. gigas* (Silver 2014). This introduced clam is functionally analogous the Pacific littleneck clam (*Leukoma staminea*) and was integrated into the aquaculture market in the 1980s (British Columbia et al. 2002). By 2010, British Columbia had issued 480 permits to modify intertidal ecosystems and cultivate non-indigenous shellfish, of which *M. gigas* and *R. philippinarum* comprised 89% by weight and 78% by volume (Fig. 1). British Columbia now produces ten thousand tons of shellfish annually; to a wholesale value of approximately $32.5 million (British Columbia et al. 2002).

1.5 Ecological Considerations

Social-ecological responses to shellfish cultivation through the northeast Pacific have highlighted the complexities of maximizing production and ecological benefits while mitigating environmental impacts (Deur et al. 2015, Lepofsky et al. 2015, Froehlich et al. 2017b, 2017a). Emerging research indicates that cultivation practices, abundant shellfish populations, and shellfish-derived nutrients crossing the marine-terrestrial interface may be transformative to nearshore ecosystems (Trant et al. 2016, Fisher et al. 2019). While concerns surrounding the ecological stability, environmental impact and future of shellfish aquaculture have been raised by the public, several coastal Indigenous communities, and those within the industry (Howlett 2004, Froehlich et al. 2017b, 2018, Holden et al. 2019). These concerns generally characterized contemporary aquaculture as a foe to conservation efforts (Froehlich et al. 2017b). Society's additional requirements to address the global biodiversity crisis, changing climatic conditions, and declining food security amplify these concerns (Froehlich et al. 2017a, Hilborn et al. 2018, Stentiford et al. 2020, Gephart et al. 2021). However, there is a collective recognition that improved understanding of the ecological implications of shellfish farming is vital to developing adaptive management strategies, conservation planning, and governance (Stentiford et al. 2020, Gephart et al. 2021). Establishing this understanding within intertidal resource cultivation systems, that have been engineered and implemented over millennia, will establish a framework for evaluating broad-level environmental challenges, while fostering food systems of cultural and economic importance.

1.6 Thesis Objectives and Structure

This research aims to quantify how nearshore intertidal resource cultivation structures coastal biodiversity. The co-occurrence of 24 clam gardens, shellfish farms, and unmodified beaches along British Columbia's coast provides a natural experiment capable of examining this inquiry (Fig. 1). Chapter 2 evaluates the ability of multiple substrata community assessment methods to capture ecological communities and implications of each method regarding species richness, abundance, and Hill numbers. Chapter 2 has been published in *Ecology and Evolution* (Cox et al. 2017). Chapter 3 quantifies diversity and density of the bivalve communities within each intertidal site and evaluates the communities' association with the habitat's substrate composition, sediment characteristics, and physical complexities using structure-from-motion photogrammetry to generate 3D habitat models. A specific focus of this analysis is to ask whether species richness and habitat complexity may facilitate increases in bivalve biomass. This chapter also establishes the methodological implications of varying sediment volume on the detection of bivalve diversity, abundance, shell length, and sample- and coverage-based biodiversity metrics. Chapter 4 examines if managing intertidal bivalves enhances habitat complexity, fostering more diversity in the epifaunal communities that are not the primary cultivation target. Chapter 5 reviews vectors that transport shellfish-derived nutrients into coastal terrestrial environments, including birds, mammals, and over 13,000 years of marine resource use by people. Evidence from recipient ecosystems is then summarized to determine the ecological implications of this previously undescribed spatial subsidy. Chapter 5 is published in *Ecography* (Cox et al. 2020). Chapters 2,3,4 and 5 have been written as manuscripts for specific journals. Therefore, minor differences in formatting may persist across the chapters. Several aspects of Chapters 3 and 4's methods overlap considerably—specifically, the rendering of three-dimensional models and assessments of substrate composition. I errored on the side of caution and included overlapping sections as the descriptions vary and this was in keeping with the agreed upon format.

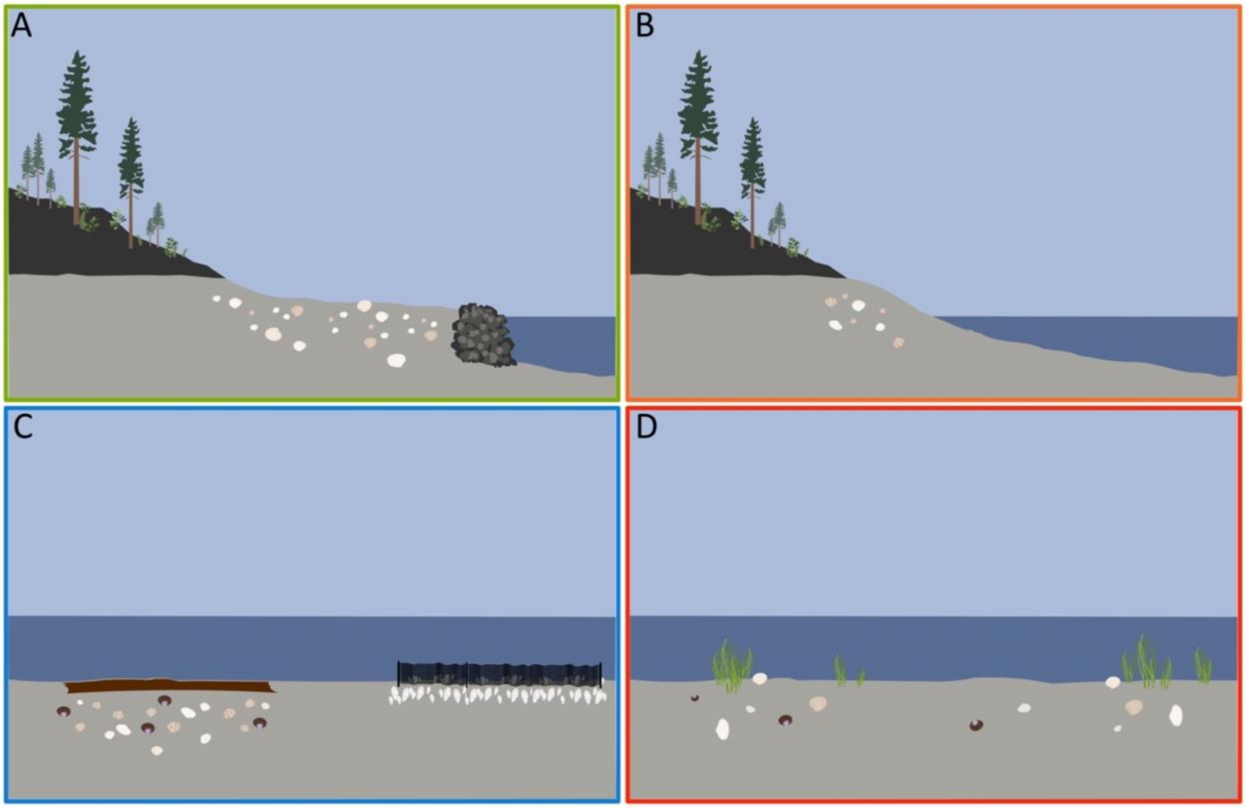

Figure 1: Illustrations of example site types that this thesis examines. Image border colours are retained throughout Chapters 3 and 4. A) clam garden B) unmodified clam garden reference beach C) shellfish farm D) unmodified shellfish farm reference beach.

Chapter 2: Community Assessment Techniques and the Implications for Rarefaction and Extrapolation with Hill Numbers

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2.0 Abstract

Diversity estimates play a key role in ecological assessments. Species richness and abundance are commonly used to generate complex diversity indices that are dependent on the quality of these estimates. As such, there is a longstanding interest in the development of monitoring techniques, their ability to adequately assess species diversity, and the implications for generated indices. To determine the ability of substratum community assessment methods to capture species diversity, we evaluated four methods: photo quadrat, point intercept, random subsampling, and full quadrat assessments. Species density, abundance, richness, Shannon diversity, and Simpson diversity were then calculated for each method. We then conducted a method validation at a subset of locations to serve as an indication for how well each method captured the totality of the diversity present. Density, richness, Shannon diversity, and Simpson diversity estimates varied between methods, despite assessments occurring at the same locations, with photo quadrats detecting the lowest estimates and full quadrat assessments the highest. Abundance estimates were consistent among methods. Sample-based rarefaction and extrapolation curves indicated that differences between Hill numbers (richness, Shannon, and Simpson) were significant in the majority of cases, and coverage-based rarefaction and extrapolation curves confirmed that these dissimilarities were due to differences between the methods, not the sample completeness. Method validation highlighted the inability of the tested methods to capture the totality of the diversity present, while further supporting the notion of extrapolating abundances. Our results highlight the need for consistency across research methods, the advantages of utilizing multiple diversity indices, and potential concerns and considerations when comparing data from multiple sources.

2.1 Introduction

Effectively quantifying species diversity is a fundamental pillar in ecology. Regardless of the ecosystem, diversity estimates play a vital role in environmental monitoring (Underwood 1994), ecosystem comparisons, anthropogenic stressor evaluation (Lovejoy 1994), and informing conservation efforts. Richness and abundance estimates are two of the simplest ways to depict biodiversity and are important to consider when assessing any ecosystem (Stirling and Wilsey 2001) They are also used to generate more complex ecological indices (Magurran 1988), including Hill numbers, the most commonly used of which includes the diversity of all species, richness, the exponential of Shannon entropy or otherwise known as Shannon diversity, and Simpson diversity. Initially used by ecologist Macarthur (1965), and further developed and described by Hill (1973), Hill numbers have recently gone through a resurgence (see Jost 2006). Hill numbers have now been extended to create an integrated approach to quantifying species diversity and abundance via sample- and coverage-based rarefaction (Colwell et al. 2012, Chao and Jost 2012, Chao et al. 2014a). This modified approach allows for Hill numbers to be expressed in terms of the completeness or the proportion of individuals within an assemblage that belong to species represented in a sample (coverage) and species diversity as a function of sampling effort (Chao and Jost 2012, Chao et al. 2014a). Both of which can be extrapolated to allow ecologists to more accurately estimate species richness and further understand the differences in the diversity that exists between communities.

There is a long-standing interest in the development of assessment techniques and improving their ability to adequately assess species diversity (Underwood 1994, Stewart-Oaten' and Bence 2001). Data collection is an expensive and labor-intensive process; resource limitations place constraints on selecting the most effective approach to rigorous quantitative assessment (Oliver and Beattie 1996). As a result, most community assessments still lack standardized sampling protocols and alterations to experimental design is a common occurrence (Ferrer-Paris et al. 2013). To mitigate shortcomings, rapid, readily available, and cost-effective techniques play an essential role in the assessment of most ecosystems and often involve a range of sampling methods being utilized during a single assessment (Sparrow et al. 1994).

One of the original techniques used in ecological studies is quadrats, which were initially developed as a sampling unit used to detect patterns in plant communities (Greig-Smith 1952) and have since been used in a range of ecological studies investigating numerous habitats. Photo quadrats are also frequently used to assess various substrata by superimposing points onto photographs (Preskitt et al. 2004). The flora or fauna directly underneath the points can then be identified and quantified as either abundance or percent cover. Point intercept sampling, which is very similar to photo quadrats except that it is quantified in the field, is another commonly utilized assessment method where the taxon directly underneath randomly selected points created by the intersecting grid formed by a strung quadrat are visually identified (Benedetti-Cecchi et al. 1996). Alternatively, strung quadrats can be subdivided into smaller portions that decrease assessment time relative to evaluating the entire area. Selecting a random subsample can optimize effort without compromising the validity of the results, especially if certain taxa are too abundant to be counted within a reasonable time frame (Barbour and Gerritsen 1996).

To determine how commonly utilized substratum assessment methods capture species diversity (Hill numbers), we conducted a comparison of four methods: photo quadrats, point intercept, random subsampling, and full quadrat assessments of a smaller area (1/4 the size of the other methods). We evaluated the species density, abundance, richness, Shannon diversity, and Simpson diversity detected by each method, as well as the time each method required in situ. Furthermore, to determine the validity of each method, we conducted a method validation at a subset of the locations assessed by the previously mentioned methods. All methods were carried out in the marine intertidal, as these ecosystems have a long history of serving as model system for identifying processes that generate community patterns and structure (*e.g.,* Paine 1966). Furthermore, soft-sediment benthic communities have been widely used to assess and monitor natural and anthropogenic stressors (*e.g.,* Gerwing et al. 2016).

We hypothesize that species density will vary according to assessment method and will be the highest when using methods that require the most effort (time). We also postulate that species abundance, once extrapolated to account for assessment area, will not vary between methods, regardless of the effort needed to conduct each assessment. The differences in species diversity and consistencies within species abundance estimates will result in similar differences within derived Shannon and Simpson diversity.

2.2 Methods

2.2.1 Study area

This study was conducted within Baynes Sound, which is a 20 km long body of water located on the east coast of Vancouver Island, British Columbia, Canada, that consists of open shoreline, estuaries, inshore marshes, protected bays, and forests (Murray and D'Anna 2015; Fig. 2). Water circulation is primarily north to south due to flood and ebb tides and the wind-influenced currents. Baynes Sound supports an extensive shellfish farming industry, which primarily grows Pacific oysters (*Crassostrea gigas*) and Manila clams (*Venerupis philippinarum*) (Silver 2014). The study site (49.468417°, −124.767383°) was representative of the area and consisted of a low sloping (~3%) intertidal zone comprised of soft sediments, cobble, and a relatively high abundance of bivalves.

The survey area consisted of an 80 m baseline running parallel to the shore along the 2.2 m tideline, and a 67 m baseline running perpendicular to the shoreline from the 2.2 m tideline to the 1.5 m tideline, creating a 5,360 m^2 total assessment area (Fig. 3). Perpendicular lines were extended at predetermined distances along the perpendicular and parallel baselines. Assessments occurred at the intersection of these extended lines. Distances at which lines were extended along the vertical distances were chosen a priori using a random number generator, while horizontal distances increased in increments of five meters (5, 10, 15, etc.) to ensure the entire horizontal distance was covered. To decrease the risk that areas within the assessment zone were missed, an additional nine quadrats were placed at horizontal distances where selected vertical distances resulted in large gaps between adjacent quadrats. Even with these additional quadrats, none of the 26 quadrats were within five meters of each other.

Four methods were conducted at each of the 26 assessment locations, in order of least to most invasive, to decrease the risk that initial methods influenced and/or biased subsequent methods. This resulted in methods being conducted in the following order: photo quadrats, point intercept, random subsampling, and full quadrat assessments. During each assessment, all surface species (epifaunal organisms), including algae >1 mm, were identified down to the lowest reliable taxonomic unit (Appendix 1).

A method validation was conducted at a subset of the assessment locations (n = 6) during which all species within the 0.5 × 0.5 m quadrat were counted. Assessments of this nature are not logistically feasible to conduct at dozens of locations due to the time required to assess potentially thousands of individuals, as such this validation served as a baseline comparison for how well each method captured the richness and abundance present at each location.

The evaluation of the initial four methods and the method validation were considered as separate assessments. This resulted in two examinations: the results of the photo quadrats, point intercept, subsampling, and full quadrat comparison were analyzed using the data from all 26 assessment locations, and the method validation using the data collected from six of the assessment locations.

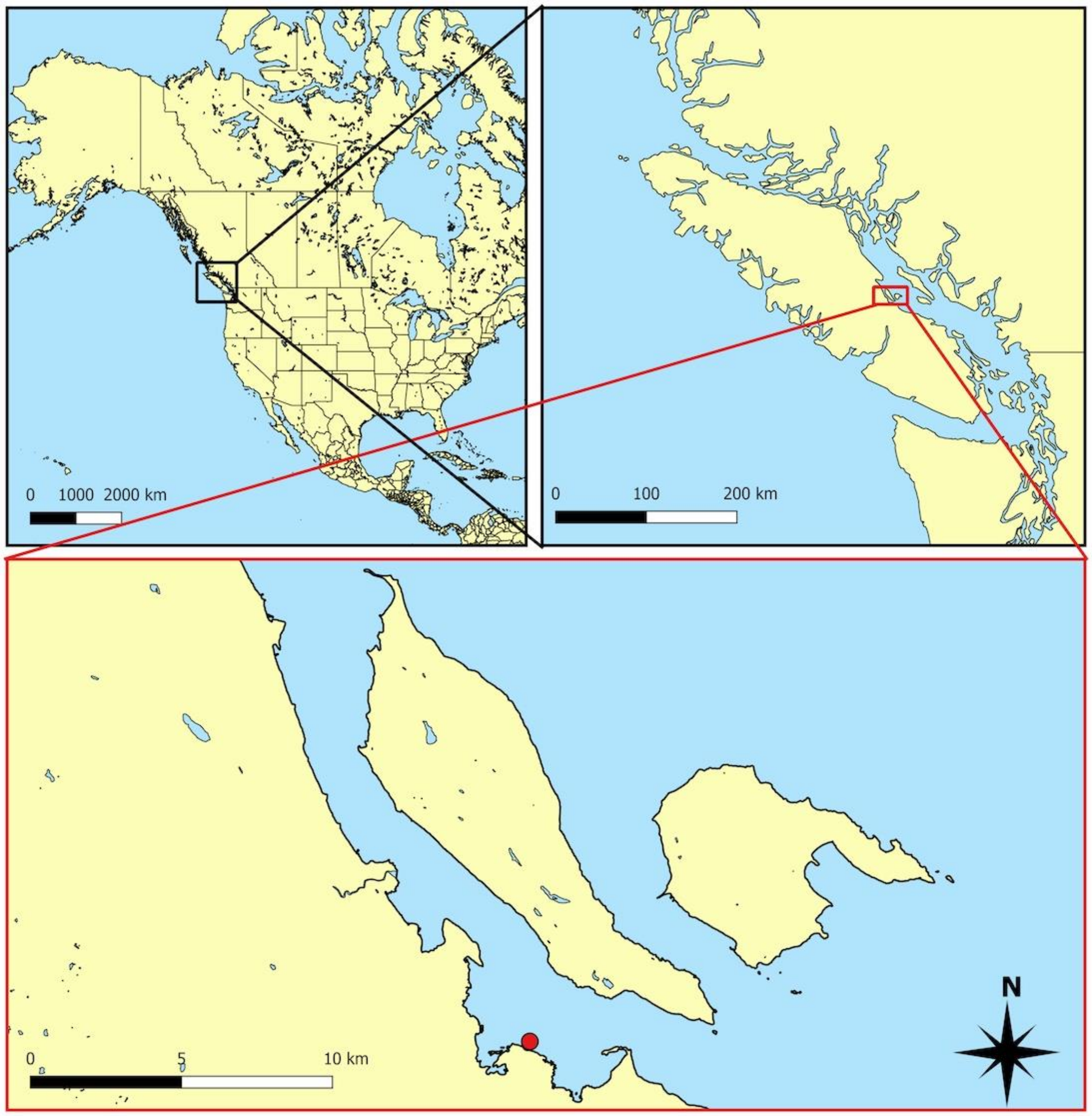

Figure 2: Study location in Baynes Sound, Canada (49.468417°, -124.767383°**)**. Assessments were conducted in the intertidal ecosystems adjacent to Vancouver Island, British Columbia.

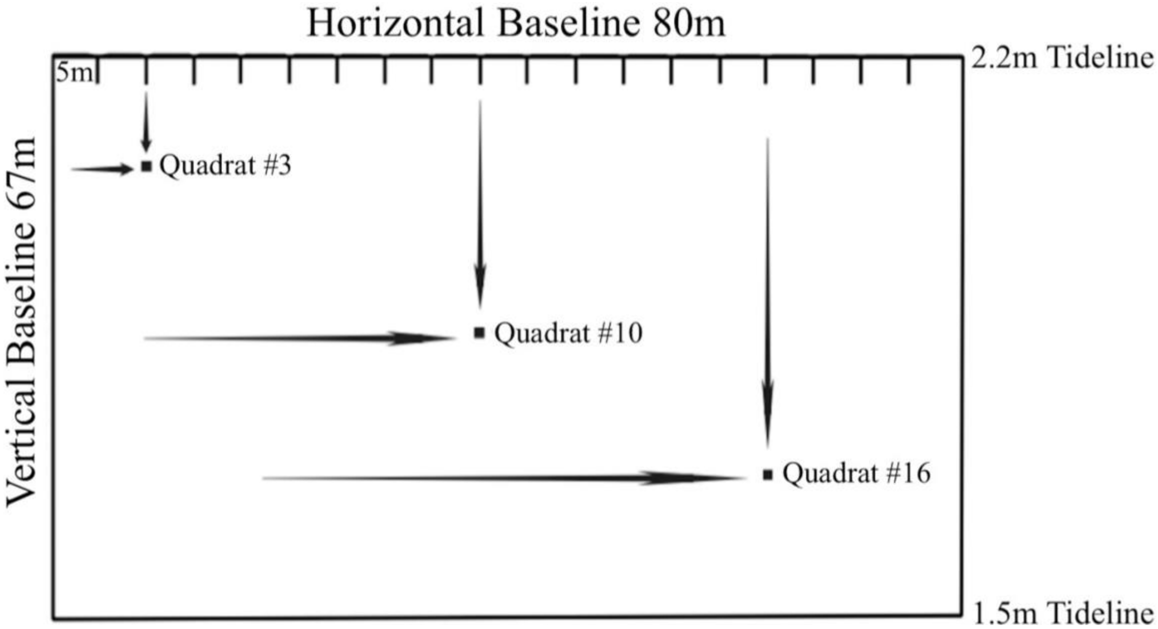

Figure 3: Assessment area and quadrat placements used during the methodological comparison. The 5,360m^2 assessment area consisted of horizontal and vertical baselines running parallel and perpendicular to the shoreline, respectively. Quadrat placement was at the intersection of perpendicular lines extended from the horizontal and vertical baselines. Examples of quadrat placement are illustrated by the placement of the 3rd, 10th, and 16th quadrats.

2.2.2 Assessment Methods

Method 1: Photo Quadrats

Quadrats were photographed in the field using a Nikon AW120 camera held 1 m above the 0.5 × 0.5 m quadrats. Images were later cropped to the 0.5 × 0.5 m area inside the quadrat (final resolution: 2,832 × 2,832 pixels). Fifty points were randomly generated onto each image using the software Image J (Schneider et al. 2012). Organisms directly under each point were identified to the lowest possible taxonomic unit (Appendix 1).

Method 2: Point Intercept

A 0.5 × 0.5 m quadrat with string running vertically and horizontally every 5 cm to create 100 equal squares and 81 intersecting points was used. Fifty intersections were randomly selected and organisms directly under each point were identified.

Method 3: Random Subsample

Ten randomly selected 0.5 × 0.5 cm squares were chosen from the 100 squares formed by the strung quadrat described above. All organisms within each square were counted and identified. Abundances were multiplied by 10 to estimate total abundance.

Method 4: Full Quadrat

A 0.25 × 0.25 m quadrat was placed in the bottom left corner of the 0.5 × 0.5 m quadrat, and all species within this area were identified. Abundance values were multiplied by four to estimate the total abundance.

Method Validation

A 0.5 × 0.5 m quadrat assessment occurred at six of the 26 assessment locations. During this assessment, all organisms within the quadrat were counted and identified.

2.2.3 Statistical Analysis

The analysis was conducted in R-studio (R Core Team 2019). The “dunn.test” package was used to conduct multiple nonparametric pairwise comparisons after Kruskal–Wallis rank sum tests were performed (Dinno 2016). Richness, Shannon diversity, Simpson diversity, and rarefaction and extrapolated curves were generated using the “iNEXT” package (Hsieh et al. 2016).

Species Density, Abundance, Maximum Richness and Assessment Effort

Species density and abundance were calculated for the initial four assessment methods (N = 26) and the method validation (N = 6). As the validation method was too labor intensive to be conducted consistently, assessment effort was only calculated for the initial four methods. Species abundance consisted of the number of individuals observed during each sampling unit. The amount of time each sample took to conduct in the field was considered to be a proxy for effort. Density was calculated as the number of taxa detected in each sampling unit, while maximum richness was calculated as the total number of taxa detected by each method. Both density and richness were considered to be taxonomic density and richness, which accounts for not all organisms being identified to the species level (Gerwing et al. 2016).

Histograms and Shapiro–Wilk tests determined that density, abundance, and sampling effort were non-normal, despite the use of standard transformations (data not shown); as such, nonparametric tests were used. Density and assessment effort estimates were compared using Kruskal–Wallis rank sum tests and Dunn's tests to investigate differences between the methods. Total abundance was compared in the same manner as density and effort, but as the data were not comparable across all methods, photo quadrats and point intercepts, that determined abundance as individuals per assessment, were compared, and random subsampling and full quadrat assessments, that determined abundance as individuals per unit area, were compared. Additionally, random subsampling, full quadrat, and validation estimates were compared during the method validation analysis.

Hill Numbers

Species richness, Shannon diversity, and Simpson diversity were calculated for the initial four assessment methods (N = 26) and the method validation (N = 6). Hill numbers were chosen due to their numerous advantages over other diversity indices (see Chao et al., 2014) and calculated according to Hsieh et al. (2016), and Chiu and Chao (2014). See Jost (2006) for a more thorough review of the benefits of Hill numbers in relation to other indices or Ellison et al. (2010) for an indication of the current consensus within the ecological community.

Richness was calculated using the following (Equation 1), where S denotes the number of species, Pi indicates the proportion of species relative to all other species detected and species are indexed by i = 1, 2, 3, 4. q denotes the sensitivity of the measure to the relative abundances and as such when q = 0, the equation considers species equally regardless of their relative abundances, which is richness (Hill 1973, Chiu and Chao 2014, Hsieh et al. 2016).

$$^{q}D = \left(\sum_{i=1}^{s} p_i^q\right)^{1/(1-q)}$$

Eq. 1

Shannon diversity, which can be considered as the number of common species in the assemblage, is frequently used in biological studies as a measure of diversity (Hill 1973, Chiu and Chao 2014, Hsieh et al. 2016). Shannon diversity was determined for each method as denoted by Equation 2 (Hsieh et al. 2016). Shannon diversity is roughly equated to q = 1, although the equation is undefined when q = 1, as q approaches 1, it is the exponential of Shannon entropy (which is referred to as Shannon diversity). As q = 1 results in all individuals being considered equally, Shannon diversity counts species proportionately to their abundances (Chao et al. 2014b, 2014a).

$$^{1}D = \lim_{q \to 1} {}^{q}D = exp\left(-\sum_{i=1}^{s} p_i \ \log pi\right)$$

Eq. 2

Simpson diversity considers the dominant species within an assemblage while disregarding the rare species (Chiu and Chao 2014, Hsieh et al. 2016). This occurs when q = 2, which is also the inverse of the Simpson concentration (Chao et al., 2014). Simpson diversity was determined for each method as denoted by Equation 3 (Chao et al. 2014a)).

$$^{2}D = 1/\sum_{i=1}^{s} p_i^2$$

Eq. 3

Rarefaction Interpolation and Extrapolation

Sample- and coverage-based rarefaction and extrapolation curves were generated to determine how diversity increases with increasing sampling effort and completeness. Rarefaction and extrapolation of richness, Shannon diversity, and Simpson diversity were conducted for each method according to Hsieh et al. (2016) and further discussed in Colwell et al. (2012), Chao and Jost (2012), and Chao et al. (2014a). Sample-based curves evaluated the number of individuals in a sample by plotting diversity estimates in relation to the number of sampling units. Coverage-based curves were plotted against rarefied sample completeness to illustrate diversity estimates in relation to sample coverage. All extrapolation curves were plotted using a doubling in sample size, and 500 bootstrap replicates were used to estimate 95% confidence intervals. Ninety-five percent confidence intervals, a known alternative to standard statistical testing (Colwell et al. 2004), were used to determine if differences between methods were statistically significant. Nonoverlapping 95% confidence intervals, whether rarefied or extrapolated curves are considered, indicate definite significant differences at a level <5% (Chao and Jost 2012, Chao et al. 2014a).

2.3 Results

2.3.1 Method Comparison

Maximum Richness

Sessile invertebrates and mobile invertebrates were the lowest in photo quadrats, increased during point intercept assessments and random subsampling, and were the highest during full quadrat assessments. Algal richness was consistent across methods (Table 1).

Table 1: Maximum taxonomic richness observed by the four assessment methods. Note that list of the species comprising each group is available in Appendix 1.

	Photo Quads	Point Intersect	Subsampling	Full Quads
Algae	3	3	3	3
Sessile Invertebrates	2	2	4	4
Mobile Invertebrates	3	7	13	15
Maximum Observed Diversity	8	13	20	22

Assessment Effort

The amount of field time required to complete each assessment was the lowest in photo quadrats and increased during point intercept, random subsampling, and full quadrat assessments (Fig. 4; Kruskal– Wallis $\chi_4{}^2 = 63.97$, $p < .01$). Photo quadrats took significantly less field time than any other method. The time needed to conduct point intercept assessments did not differ significantly from that of random subsampling or full quadrat assessments. Random subsampling took significantly less time than full quadrat assessments (Fig. 4; Table 2)

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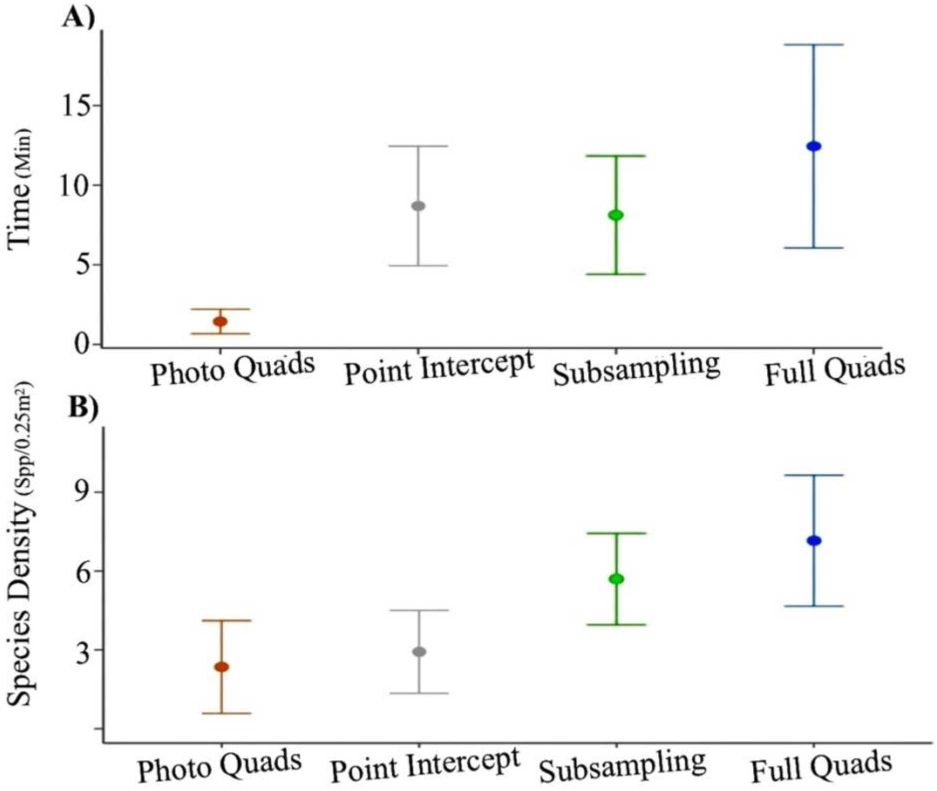

Figure 4: Kruskal-Wallis rank sum tests determining whether the time needed to conduct the assessment (effort) varied between the assessment methods. Assessment effort (N=26). Kruskal-Wallis rank sum test chi-squared = 63.97, df = 4, $p < 0.001$. B) Density (N=26). Kruskal-Wallis chi-squared = 68.09, df = 4, $p < 0.001$.

Table 2: Results of separate Dunn Test analyses conducting non-parametric multiple pairwise comparisons to determine if the time (effort) needed to conduct the assessment or the number of taxa (richness) detected during each assessment varied between methods. The Dunn's tests were conducted post hoc following a Kruskal-Wallis rank sum test. Significant p values <0.05 are indicated via *, p values >0.01 are indicated via **

		Photo Quads	**Point Intersect**	**Subsampling**
Effort	**Point Intersect**	0.000**		
	Subsampling	0.000**	0.379	
	Full Quads	0.000**	0.071	0.033*
		Photo Quads	**Point Intersect**	**Subsampling**
Richness	**Point Intersect**	0.253		
	Subsampling	0.000**	0.000**	
	Full Quads	0.000**	0.000**	0.085

Species Density

The species density detected by each method increased in the order in which the assessments were carried out. Density estimates were the lowest in photo quadrats, increased during point intercept assessments, further increased in random subsampling, and were the highest in full quadrat assessments (Fig. 4; Kruskal-Wallis $X^2_4 = 68.09$, $p < 0.01$). The density detected by subsampling and full quadrat assessments was significantly higher than the richness detected by photo quadrats or point intercepts. However, increases in density were not significant between photo quadrats and point intercept assessments, and random subsampling and full quadrat assessments (Fig. 4; Table 2).

Species Abundances

Abundance estimates varied marginally during either photo quadrat and point intercept comparisons or random subsampling and full quadrat comparisons. There was no statistical difference between species abundance observed by photo quadrats or point intercepts (Fig. 5; X^2_1= 4.15 p> 0.1). Additionally, there was no significant difference between abundances detected by random subsampling and full quadrat assessments, once the initial values were extrapolated to determine the number of individuals likely present within the 0.5x0.5 m area (X^2_1= 0.01, p> 0.1).

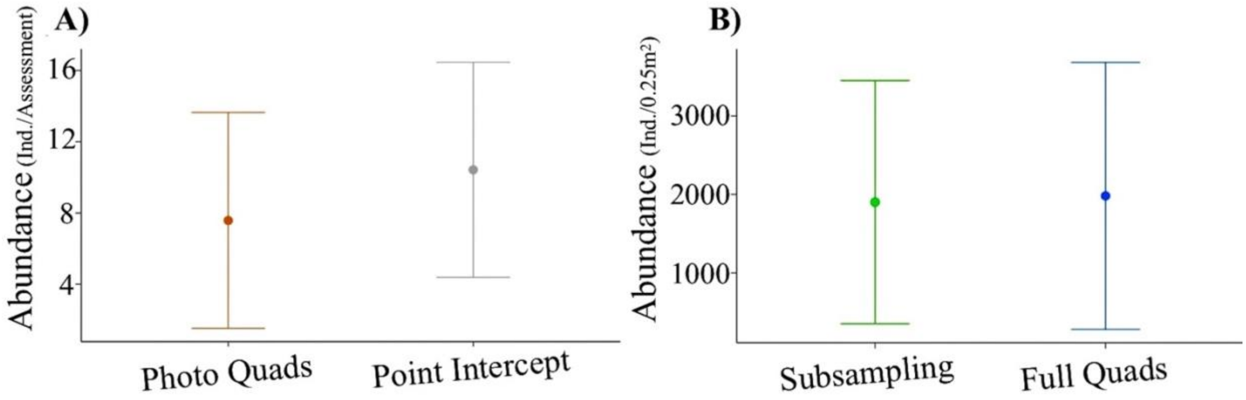

Figure 5: Kruskal-Wallis rank sum tests determining whether species abundances varied between methods. A) Photo quadrats and point intercepts comparison (N=26). Kruskal-Wallis rank sum test chi-squared = 2.21, df = 1, p> 0.1. B) Random subsampling, and full quadrat assessments comparison (N=26). Kruskal-Wallis chi-squared = 0.012, df = 1, p>0.1.

Hill Numbers

The sample- and coverage-based rarefaction and extrapolation curves of the validation method had the highest number of observed species as well as the most predominant detection rate compared to the other methods (Fig. 6). However, increases in richness detected by sample-based rarefaction and extrapolation were only significant relative to photo quadrat and point intercept assessments as confidence intervals for random subsampling, full quadrat assessments, and the validation method converged during rarefaction and more so during extrapolation. Coverage-based curves indicated that sampling method coverages were above 80% in all cases, with the validation method being the only method with 100% coverage. Given the consistency of coverage values across methods and the notion that even if all methods were scaled to the base coverage value, the order of species detected would not change, the methods' diversity estimates were not corrected based on their coverage.

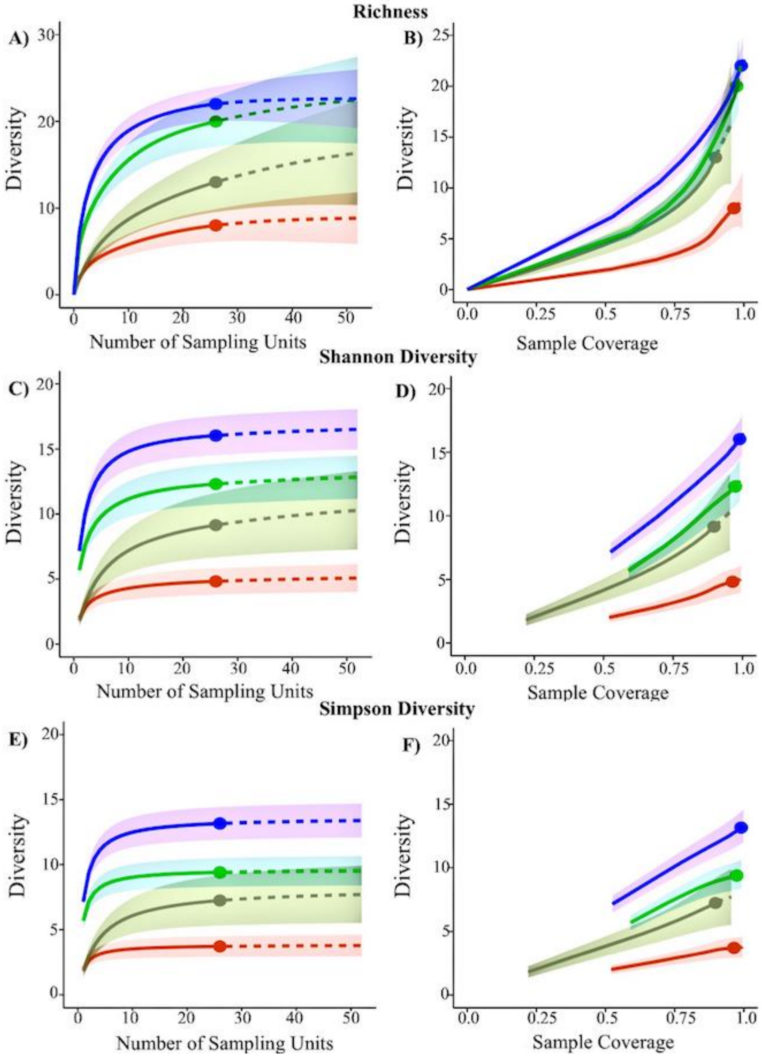

Figure 6: Four method comparison using sample- and coverage-based rarefaction and extrapolation of Hills numbers. Orange = photo quadrats, Grey = point intercept, Green = subsampling, Blue = full quadrat. A) Richness (q=0) sample-based rarefaction and extrapolation B) Richness (q=1) coverage-based rarefaction and extrapolation C) Shannon diversity (q=1)

sample-based rarefaction and extrapolation D) Shannon diversity (q=2) Coverage-based rarefaction and extrapolation E) Simpson diversity (q=2) sample-based rarefaction and extrapolation F) Simpson diversity (q=2) coverage-based rarefaction and extrapolation. All extrapolation curves were plotted to a doubling in sample size, and 500 bootstrap replicates were used to estimate 95% confidence intervals.

Much like richness, Shannon and Simpson diversities detected by the sample- and coverage-based rarefaction and extrapolation curves increased according to the order in which the assessment methods were carried out. Again, both curves indicated that Shannon diversity and Simpson diversity were the lowest in photo quadrats, increased during point intercept assessments, further increased in random subsampling, and were the highest in full quadrat assessments (Fig. 6). However, unlike richness, Shannon diversity and Simpson diversity estimates detected by sample-based rarefaction and extrapolation curves were statistically higher during full quadrat assessments than any of the other methods, and photo quadrats were statistically lower than the three other methods. Much like richness estimates, coverage-based rarefaction and extrapolation indicated that sample completeness was relatively consistent across methods as coverage values were all over 95%, and in most cases, confidence intervals did not overlap.

The vast majority of the sample-based rarefaction and extrapolation curves assessing richness, and all of the curves addressing Shannon and Simpson diversity, plateaued during the 26 quadrat assessments (Fig. 6). Plateauing richness curves suggests that each method reached its detection limits and the majority of species that could be detected using each method were indeed identified, despite undetected species still being present within the ecosystem. Plateauing Shannon and Simpson diversity indicated that each assessment method reached the maximum value for these metrics given the diversity and abundance present within the ecosystem and each method's detection capabilities.

2.3.2 Method Validation

Richness and Abundances Estimates

Abundances observed during the method validation did not differ from those determined by random subsampling or full quadrat assessments (Fig. 7; Table 3). The species richness detected by the method validation was significantly higher than the richness detected by photo quadrats, point intercept, or random subsampling. Although validation assessments detected higher richness than the full quadrat assessments, the increase was not significant (Table 3).

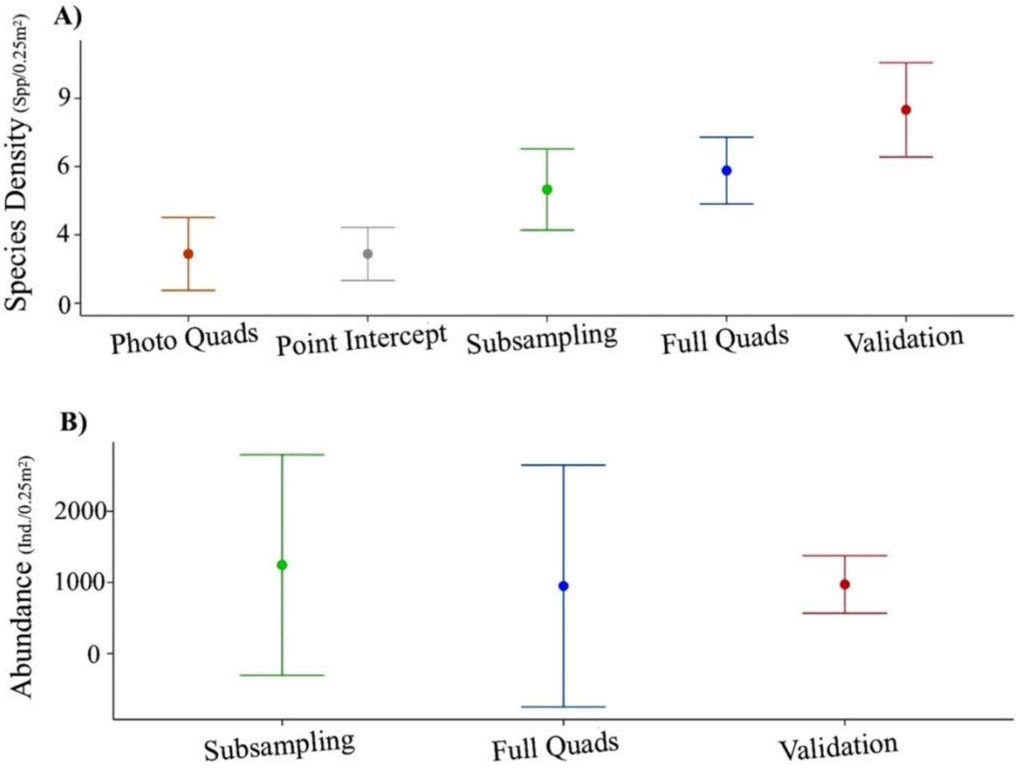

Figure 7: Results of Kruskal-Wallis rank sum tests determining whether species abundances and richness determined during the method validation varied between assessment methods. A) Species abundance. Kruskal-Wallis chi-squared = 1.06, df = 2, $p > 0.05$. B) Species richness Kruskal-Wallis chi-squared = 21.09, df = 4, $p < 0.001$.

Table 3: Results of separate Dunn Test analyses conducting non-parametric multiple pairwise comparisons to determine if abundances and richness varied between methods during the method validation (N=6). The Dunn's tests were conducted post hoc following a Kruskal-Wallis rank sum test. Significant p values <0.05 are indicated via *, p values >0.01 are indicated via **

		Photo Quads	**Point Intersect**	**Subsampling**	**Full Quads**
Abundance	**Full Quads**			0.1790	
	Validation			0.4784	0.1935
		Photo Quads	**Point Intersect**	**Subsampling**	**Full Quads**
Richness	**Point Intersect**	0.5000			
	Subsampling	0.0268*	0.0268*		
	Full Quads	0.0058**	0.0058**	0.2762	
	Validation	0.0001**	0.0001**	0.0374*	0.1174

Hill Numbers

The sample- and coverage-based rarefaction and extrapolation curves of the validation method had the highest number of observed species as well as the most predominant detection rate compared to the other methods (Fig. 8). However, increases in richness detected by sample-based rarefaction and extrapolation were only significant relative to photo quadrat and point intercept assessments as confidence intervals for random subsampling, full quadrat assessments, and the validation method converged during rarefaction and more so during extrapolation. Coverage-based curves indicated that sampling method coverages were above 80% in all cases, with the validation method being the only method with 100% coverage. Given the consistency of coverage values across methods and the notion that even if all methods were scaled to the base coverage value, the order of species detected would not change, the methods' diversity estimates were not corrected based on their coverage.

Shannon and Simpson diversity estimates determined by the sample- and coverage-based rarefaction and extrapolation curves were higher in the validation than any other method (Fig. 8). However, these increases in Shannon diversity were only significant when comparing the validation method to photo quadrats and point intercept assessments, and increases in Simpson diversity were only significant when comparing the validation method to photo quadrats, point intercept, and subsampling assessments. Much like richness, coverage-based curves detected coverage values that ranged from 80% to 100%, with the validation method being the only method to reach 100% coverage. Again, as coverage values did not differ drastically and reducing all Shannon and Simpson diversity estimates to the base coverage would not alter the hierarchy of the assessment’s methods, comparing methods at their current coverage values was deemed appropriate.

Of the sample-based rarefaction and extrapolation curves evaluating increases in richness with additional sampling effort, only photo quadrats and the validation method plateaued within the extrapolation curve. However, all methods plateaued if extrapolation was increased from a doubling to a quadrupling (*i.e.*, 24 sampling units), while the relative order of the methods remained unchanged (data not shown) indicating that the detection capabilities of each method was reached or was within reach given the sampling effort. Similarly, to the method comparison, the majority of the sample-based rarefaction and extrapolation curves evaluating Shannon and Simpson diversities plateaued within the extrapolation curve, and those that did not plateau, did, if the extrapolation curve was extended. Again, this implies that the maximum Shannon and

Simpson diversity values possible were reached given the detection capabilities of each method, and the diversity and abundance within the ecosystem were reached.

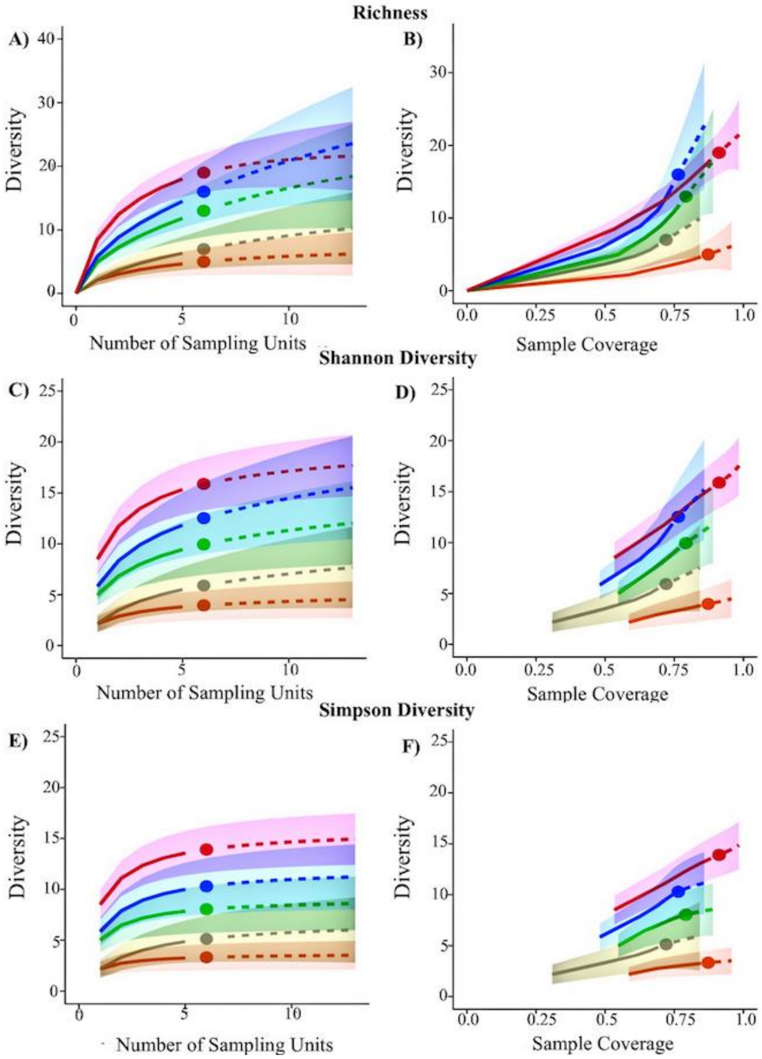

Figure 8: Method Validation using sample- and coverage-based rarefaction and extrapolation of Hills numbers. Orange = photo quadrats, Grey = point intercept, Green = subsampling, Blue = full quadrat, Red = validation. A) Richness (q=0) sample-based rarefaction and extrapolation B) Richness (q=1) coverage-based rarefaction and extrapolation C) Shannon diversity (q=1) sample-based rarefaction and extrapolation D) Shannon diversity (q=2) Coverage-based rarefaction and extrapolation E) Simpson diversity (q=2) sample-based rarefaction and extrapolation F) Simpson diversity (q=2) coverage-based rarefaction and extrapolation. All extrapolation curves were plotted to a doubling in sample size, and 500 bootstrap replicates were used to estimate 95% confidence intervals.

2.4 Discussion

To determine the relative effectiveness of commonly used substratum assessment methodologies, as well as their implications for diversity indices, we conducted a comparison of four assessment methods and derived Hill numbers. A method validation was also conducted to determine how well each method captured the diversity present at each location.

Method Comparison

Species density, maximum richness, and assessment effort were the highest in the full quadrat assessments, which was the most invasive, labor-intensive method, and the lowest during photo quadrats, which was the least invasive of the methods. However, the increase in the density of species detected by full quadrat assessments relative to random subsampling was not significant, but the additional time needed to conduct full quadrat assessments was significant. These findings suggest that the average number of species detected and the effort needed to conduct the assessments increased in a similar fashion until detection rates plateaued despite further increases in effort. Stabilizing detection rates are likely a function of the detection capabilities of each method. Therefore, if field assessments are required, random subsampling would be preferential to full quadrat use as it detects similar densities in less time. Additionally, density estimates detected by photo quadrats and point intercepts did not differ significantly, but the effort needed to conduct point intercept was significantly higher; thus, if time in the field is a limiting factor, photographing substrata for later analysis is likely an appropriate course of action. However, it is worth noting that the time required to process images was not included in the comparison and any costs that may be incurred during image processing must be considered before deeming photo quadrats a suitable alternative to point intercept assessments. Variation between methods highlights an observation made decades ago by May (1988) and later elaborated by Gotelli and Colwell (2001) that although diversity is a natural measurement, it can be quite difficult to quantify properly. Subsequently, if the assessment methods result in errors in species detection it is possible to underestimate the occurrence of common species (Gu and Swihart 2004). Unfortunately, given the low species detection rates within photo quadrats or point intercept assessments, this may be the case in studies utilizing these methodologies to sample anything but flora. These results are especially concerning for studies comparing multiple data sets, data collected under varying conditions or assessments that use multiple methods. Any differences in communities assessed under these circumstances may be attributed to differences in diversity but could also be the result of variations in the methods or effort.

Due to the differences between the methodologies, abundance estimates were separated into a comparison of photo quadrats and point intercepts, and random subsampling and full quadrat assessments. Both comparisons indicated that extrapolated abundances result in comparable estimates. Additionally, point intercepts took significantly longer than photo quadrats, and full quadrat assessments took significantly longer than random subsampling without significant increases in abundances being detected in either case, further supporting the notion that increases in effort are not necessarily associated with increases in detection rates. Based on this observation, photo quadrats are preferential to point intercept assessments, if photo-processing time is not a concern, and random subsampling is preferential to full quadrat assessments. Moreover, extrapolating abundances may decrease assessment effort without altering the quality of the estimate. These results support past studies in which abundance estimates were extrapolated based on subsample estimates (Kunin 1998). As species abundance is commonly used to generate more complex indices and inform conservation efforts, these findings help to validate index generation by showing consistency within abundance estimates across different methods. This supports the use of abundance estimates and derived indices when making ecologically relevant decisions.

Although not a formal cost-benefit analysis, the finding that species detection rates plateaued despite increases in effort and that extrapolating abundances is an appropriate course of action suggests that concerns surrounding the validity of subsampling techniques although understandable are likely not justified (Barbour and Gerritsen 1996). Furthermore, this comparison provides the framework for conducting a statistically credible and cost-effective ecological assessment.

Sample-based rarefaction and extrapolation curves of richness, Shannon, and Simpson diversities indicated that each method had a significantly higher detection rate than the previous methods, the majority of these increases being statistically significant. The curves of each method matched the previously determined maximum species richness, indicating that these curves can provide reliable estimates of total species richness, a fact that despite growing evidence (Thompson and Withers 2003) is still under debate (He and Hubbell 2011). As the majority of the curves plateaued, especially when extrapolation was considered, it can be assumed the differences between curves are a function of the differences between the sampling processes and their detection rates, not a lack of sampling effort (Chao and Jost 2012). It is worth noting that this finding is not well addressed when discussing rarefaction, extrapolation, or any comparable species accumulation curves. The traditional viewpoint is that if curves plateau then the majority of the species within the system have been detected (see Olszewski 2004, Schloss and Handelsman 2004, Tringe 2005). However, as these results highlight, the majority of curves plateaued, despite species still being present within the ecosystem. Thus, under most circumstances, plateauing, regardless of extrapolation, does not indicate that the majority of species have been detected, but instead indicates the detection capabilities of the method have been reached.

Coverage-based rarefaction and extrapolation curves of richness, Shannon, and Simpson diversities indicated that the majority of assessment methods have similar relative abundances of observed species (Chao et al. 2014a), with all four methods reporting over 90% coverage (completeness). Under these circumstances, accounting for the difference in coverages by reducing all methods to the base coverage was not warranted. However, this analysis does highlight the need for coverage-based rarefaction and extrapolation, as initially highlighted by Jost (2010), and further developed by Chao and Jost (2012). Comparing coverage-based curves allows for the degree to which diverse communities differ to be attributed to differences between those communities and not sampling effort. Although in this instance a standard coverage was not necessary, coverage-based curves further solidified the notion that observed differences between communities are due to differences between the assessment methods, not the assessment effort. Future studies addressing the differences between assessment methodologies, especially cost-benefit analyses, could benefit from including a coverage- based stopping principle to allow for sampling to be conducted until a predetermined level of coverage. Methodologies compared at a level of equal completeness, not sample size, would allow for further insight into the differences between communities rather than samples (Chao and Jost 2012).

Method Validation

During the method validation, no significant differences in abundances estimates were detected between random subsampling, full quadrats, and validation assessments. The lack of variation between extrapolated abundances supports the notion that using a method that decreasing assessment effort by extrapolating abundances is likely an acceptable practice (Kunin 1998). However, species density estimates were much higher in validation assessments, and with the exception of full quadrat assessments, the increased density was significant in all cases. The lack of difference between the full quadrat and validation assessments may be a function of the small sample sizes or may indicate that full 1/4th quadrat assessments adequately captured the species present despite their reduced size. The differences between the four methods and the validation assessment highlight that in all cases, species density estimates were lower than what is possible if assessment effort is not a concern. This result is concerning, as numerous studies have used these or similar methodologies and may have failed to capture the totality of the richness present.

Sample- and coverage-based rarefaction and extrapolation curves showed a similar trend to the previous four method comparison, as richness, Shannon diversity, and Simpson diversity were all higher in the validation method than any of the other assessment methods. Although the statistical significance of these increases varied somewhat according to the method, they still indicated that diversity estimates, detection rates, and sample completeness were lower than what is possible if assessment effort is not a concern. Again, the majority of the sample- based curves plateaued, which may indicate that the majority of species within the ecosystem have been detected (see Olszewski 2004, Schloss and Handelsman 2004, Tringe 2005); however, as the initial method comparison illustrated, this is not the case and each method has simply reached its detection capabilities.

Conclusion

To determine how well commonly used substratum assessment methodologies capture species diversity, we conducted a methodological comparison using four assessment methods and derived Hill numbers. A method validation was also conducted to determine how well each method captured the total diversity present at each location. Results indicated that species density, richness, Shannon diversity, and Simpson diversity vary significantly between methods, while abundance estimates do not. Under these conditions, random subsampling was preferential to photo quadrats, point intercepts, or full quadrat assessments, in terms of species detected and effort required. Coverage-based curves confirmed that differences between assessment methods were not due to varying levels of completeness between methods, but instead fundamental differences between the detection capabilities of each method.

Ecosystem assessments should consider methodologies that seek to minimize sampling effort through subsampling or extrapolating and whenever possible indices should be used in conjunction with each other. These findings provide the framework necessary to effectively quantify species across a range of ecosystems, further the development of readily available, cost-effective techniques, and the efficient use of ecological indices to portray ecological trends, all of which are fundamental to the application and preservation of ecology.

2.5 Author Contributions

Kieran Cox: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization; Writing - original draft. **Francis Juanes:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing. **Sarah Dudas:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing - review & editing. **All other authors:** Investigation, Writing - review & editing.

Chapter 3: Shellfish Cultivation Over Millennia Bolsters Bivalve Communities and Diversity-Biomass Relationships

Kieran D. Cox[1,2*], Hailey L. Davies[2], Ben Millard-Martin[1], Margot Hessing-Lewis[1], Francis Juanes[2], Sarah E. Dudas[1,2,3]

3.0 Abstract

Marine ecosystems provide humans with access to nutritious food. The discussion surrounding the cultivation and management of intertidal resources focuses on recent decades, disregarding millennia of complex social-ecological interactions, climate mitigation, and environmental stewardship. Here, we test the hypothesis that intertidal resource management practices engineered and implemented over millennia increase contemporary bivalve communities' diversity, productivity, and stability. The co-occurrence of clam gardens, shellfish farms, and unmodified beaches along British Columbia's coast provides a natural experiment capable of testing this hypothesis. We quantified the diversity and density and estimate the biomass of the bivalve communities within each intertidal site and evaluated the communities' association with the habitat's substrate composition, sediment characteristics, and physical complexity using 3D habitat models. We show that clam gardens enhance fine- and broad-scale complexity, while shellfish farms primarily increase fine-scale complexity. Both cultivation methods create distinct biological communities, with unique taxonomic increases. Cumulative biomass was comparable across cultivation methods but varied considerably among taxa. Bivalve biomass correlates positively with species richness; an ecological link highly influenced by habitat complexity. Our work contributes to the mounting evidence that the cultivation of

shellfish provides a framework for averting potential adverse environmental impacts while enhancing food production.

3.1 Introduction

Access to nutritious food is one of the most fundamental requirements for human existence. The transition from hunting and gathering to cultivating resources represents a pivotal stage in the history of human-ecosystem interactions (Lewis and Maslin 2015, Nakajima et al. 2019, Fitzpatrick 2020). The ability to cultivate, harvest, and store food contributed substantially to the establishment of complex socioeconomic systems and thriving societies (Lewis and Maslin 2015, Fitzpatrick 2020). To maintain this trajectory, humanity must identify food production methods that can meet increasing global demands while limiting environmental degradation; a necessity to sustain a population that will reach 10 billion people by 2050 (Lewis and Maslin 2015, Gentry et al. 2017, Fróna et al. 2019, Short et al. 2021). Marine ecosystems are vital to achieving this objective. Sustainable supply curves indicate that edible seafood production could experience a 44 million ton increase by 2050, a 74% upswing compared to current yields and 25% of the estimated animal protein required to sustain 10 billion people (Costello et al. 2020). Compared to land-based systems these ‘blue foods’ reduce environmental impacts by creating less greenhouse gases, nitrogenous waste, and ecological stressors (Hilborn et al. 2018, Gephart et al. 2021).

Aquaculture will contribute the majority of aquatic protein consumed by the global population in 2050 (Stentiford et al. 2020). The transition away from wild fisheries, motivated in part by declining wild stocks, has already begun as more seafood was cultivated in 2020 than was extracted from wild populations (FAO 2020). This novel stage in the history of marine ecosystem-human interactions provides the foundation for meeting increasing global demands (Gentry et al. 2017, Costello et al. 2020, Gephart et al. 2021). For aquaculture to deliver sustainable aquatic protein, accurate measurements of its impacts on environmental integrity, cultivated organism health, and sociality are vital (Stentiford et al. 2020). While recent decades have emphasized developing adaptive technologies, expanding cultivation into underdeveloped habitats, and lowering fish-in–fish-out ratios, evidence suggests that shellfish aquaculture may provide a model for averting potential negative impacts while enhancing production (Gentry et al. 2019, Stentiford et al. 2020, van der Meer 2020, Naylor et al. 2021). Shellfish harvesting is one of the earliest known interactions between humans and marine resources, originating over 164,000 years ago (Marean et al. 2007). The progression from harvesting to cultivation occurred on several spatial and temporal scales as early humans expanded globally (Lepofsky and Caldwell 2013, Fitzpatrick 2020, Turner 2020). Contemporary aquaculture recognizes shellfish cultivation as a blue food that generates less environmental stressors, with low energy requirements, and a global potential that has yet to be achieved (Gentry et al. 2017, Hilborn et al. 2018, Gephart et al. 2021).

The dialogue surrounding the cultivation and management of shellfish, unfortunately, centers on recent decades, disregarding millennia of complex social-ecological interactions, climate mitigation, and environmental stewardship that shapes humanity's connection with marine resources (Bostock et al. 2010, Gentry et al. 2019, Naylor et al. 2021). This narrow focus neglects over 3,500 years of intertidal resource management and deprioritizes the need to examine the origin of higher trophic level cultivation, including an 8000-year history of multitrophic systems (Nakajima et al. 2019, Fitzpatrick 2020). This limitation also negates the role of human harvesting and management as an ecological driver of species evolution (Sullivan et al. 2017). The implications of this interpretation are exacerbated within shellfish cultivation relative to higher trophic level systems due to the disproportionate risk that shifts in temperature and ocean acidification pose to shellfish populations (Froehlich et al. 2018). However, this narrow view of shellfish cultivation is changing as the global movement to decolonize environmental policy pairs Indigenous knowledge and ways of knowing with Western science (Reid et al. 2021).

Here, we test the hypothesis that intertidal resource management systems, engineered and implemented over millennia, increase the diversity, productivity, and stability of contemporary biological communities. We then examine if community responses are proportional to cultivation modifications to the physical complexity of intertidal habitats. We test this hypothesis along the coastline of British Columbia, which supports a unique combination of First Nations clam gardens, shellfish aquaculture farms, and unmodified clam beaches. We quantified the diversity, density, and biomass of the bivalve communities within each intertidal site and evaluated the communities' association with the habitat's substrate composition, sediment characteristics, and physical complexity using structure-from-motion photogrammetry to generate three-dimensional mosaic models. Our analyses used a combination of non-parametric multivariate statistics, fractal dimension and rugosity, multivariate regression trees, and random forests to determine: (1) the methodological implications of varying survey volume on the detection of bivalve diversity, abundance, shell length, and sample- and coverage-based biodiversity metrics, (2) the physical complexity of each intertidal survey location using three-dimensional habitat models, (3) the extent to which diversity profile curves, community composition, and biomass differ among site types, (4) how sediment grain size, organics, carbonates, and water content influence clam garden and shellfish farm communities, and (5) if cumulative bivalve biomass correlates positively with species richness and whether habitat complexity and substrate composition influence this relationship.

3.2 Methods

3.2.1 Study Locations

Coastal British Columbia

Coastal British Columbia is a variant of the Coastal Western Hemlock biogeoclimatic zone (Meidinger and Pojar 1991). The area's foreshore experiences fluctuating seasonal precipitation that creates cool summers and wet winters (Meidinger and Pojar 1991). The province's 28,530 km coastline includes 40,000 coastal islands, shallow bays, and many rivers, creating an array of estuarine conditions, productive marine waters, and heterogeneous micro and macro habitats (Meidinger and Pojar 1991). This dynamic environment facilitates taxonomically diverse communities (Zacharias and Roff 2001). The dominant substrate classification along Canada's Pacific shelf is soft sediment. Comprised of mud and sand composite, soft sediments cover over 60% of the coastal shelf, a percentage that rises with increasing distance from the high intertidal (Gregr et al. In Press).

British Columbia's nearshore ecosystems provide coastal populations with abundant marine resources, supporting the development of governance systems that steward these ecosystems (Lepofsky and Lertzman 2008, Lepofsky and Caldwell 2013, Deur et al. 2015, Turner 2020). The enhancement, management and harvesting of shellfish, specifically bivalves, is central to this connection. Throughout Coastal Indigenous Peoples' 13,000-year continuous occupation of the central coast, established expansive traditional habitation sites, large winter villages, and clam gardens—mid to low intertidal rock walls and soft-sediment terraces that enhance clam production (Deur et al. 2015, Jackley et al. 2016, Trant et al. 2016, McLaren et al. 2018, Cox et al. 2019). These intertidal structures reside within the Heiltsuk and the Wuikinuxv Nations' territories, shape coastal ecosystems and form an integral component of the surrounding 6.4-million-hectare Great Bear Rainforest. Extensive shellfish cultivation systems have also been implemented further south to enhance bivalve populations (Groesbeck et al. 2014, Holden et al. 2019, Holmes et al. 2020). Northern Coast Salish Peoples established an abundance of permanent and short-term settlement sites throughout northern Quadra Island, Laich-kwil-tach and northern Coast Salish territory. Clam garden construction in the region began at least 3,500 years ago, with gardens built continuously, maintained, and harvested into the 20th century (Smith et al. 2019). Currently, 35% of Kanish and Waiatt Bays have clam garden walls, creating 113,000 m^2 of terraced beaches (Holmes et al. 2020, Lepofsky et al. 2021). The region's shellfish farms are spread over hundreds of square kilometres predominantly on the Island's south end (Holden et al. 2019). Intertidal shellfish cultivation primarily focuses on *Crassostrea gigas* and *Ruditapes philippinarum*. On eastern Vancouver Island, Baynes Sound supports abundant mariculture, with over 129 shellfish aquaculture licenses covering 11.57 km^2 (D'Anna and Murray 2015), producing over half of all shellfish cultured in the province (British Columbia et al. 2002, Silver 2014, Holden et al. 2019).

3.2.2 Survey Locations

This study examined three regions within British Columbia's central and south coast; the Hakai Lúxvbálís Conservancy "Calvert Island", Quadra Island and Baynes Sound (Fig. 9). Surveys of twenty-four intertidal sites occurred in 2015, 2016, and 2017. The site types examined were clam gardens, unmodified clam garden reference beaches (hereafter, 'garden references’), shellfish farms, and unmodified shellfish farm reference beaches (‘farm references’). Reference sites were beaches that would support the establishment of either a clam garden or a shellfish farm. The sites were dispersed between the regions with three clam gardens and three garden reference sites within the Hakai Lúxvbálís Conservancy; three clam gardens, three garden reference, three shellfish farms, and three farm reference sites surrounding Quadra Island; and three shellfish farms and three farm reference sites within Baynes Sound (Fig. 9). Primary comparisons of interest were between clam gardens and garden reference sites, and shellfish farms and farm reference sites. Surveys of the bivalve communities, surface substrate composition, and sediment characteristics occurred in 2015 and 2016. Habitat complexity surveys occurred in 2017. Long-term monitoring of several of the sites indicated habitat complexity is conserved year to year. All surveys occurred between May and July, with a single region and comparison surveyed over a tidal window to minimize season effects (e.g. Baynes Sound shellfish farms and reference sites). Two shellfish farms and two farm reference sites within Baynes Sound were used to investigate survey methods (see Method Comparison below) and the implications for detecting bivalve diversity, abundance, and shell length (Fig. 9). This methodological comparison occurred in July and August of 2015.

3.2.3 Field Surveys

Field surveys were similar to Cox et al. (2017) and Cox et al. (2019). In 2015, site surveys involved laying 40-m baselines along the 3.0, 2.2, 1.5 and 0.8 m tidal heights lines, and a perpendicular baseline from the 3.0 to the 0.8 m tideline through the start of each parallel baseline (Fig. B1). These baselines established the tidal zones: high (3.0–2.2 m), mid (2.2–1.5 m), and low (1.5–0.8 m). If specific tidal heights could not be accessed, the baselines were laid as close as possible to these tidal heights. Lines were extended at predetermined distances along the perpendicular and parallel baselines within each tidal zone (Fig. B1). Distances along the perpendicular baselines were chosen *a priori* using a random number generator, while parallel distances increased in ten-meter increments to cover the entire horizontal distance. Assessments occurred at the intersection of these extended lines, quantifying the bivalve communities, substrate composition, and sediment characteristics (Fig. B1). Five assessments within each zone were attempted; however, limited access to each intertidal zone caused only three assessments to occur in some cases. In 2016, an identical methodology was followed; however, only the mid-zone was surveyed based on insight from the previous year's surveys. Specifically, coastal zonation's influence on comparisons warrants focusing on a single zone.

3.2.4 Method Comparison Surveys

A multi-method comparison examined several bivalve survey methods to determine the implications of varying sampling volume on observed species diversity, abundances, and length. Three commonly used bivalve assessment methods were employed concurrently. A 'large quadrat' surveys method involved a 50 × 50 cm, dug to 20 cm depth. A 'small quadrat' method involved a 25 × 25 cm quadrat dug to 20 cm. This quadrat was placed in the center of the 50 × 50 cm quadrat to ensure an overlapping sample and was surveyed before the rest of the large quadrat area using the same 5 mm mesh protocol. Using a 'core' method we collected a 7 × 20 cm core adjacent to the large quadrat, which was removed from the beach and later sieved through a 5 mm screen in the laboratory. All survey methods identified, counted, and anteroposteriorly measured all bivalves. All surveys occurred within the mid-intertidal zone.

Twenty-three core surveys and twenty-one small quadrat surveys were conducted at the four sites, with 1,691 bivalves observed across the three sampling methods.

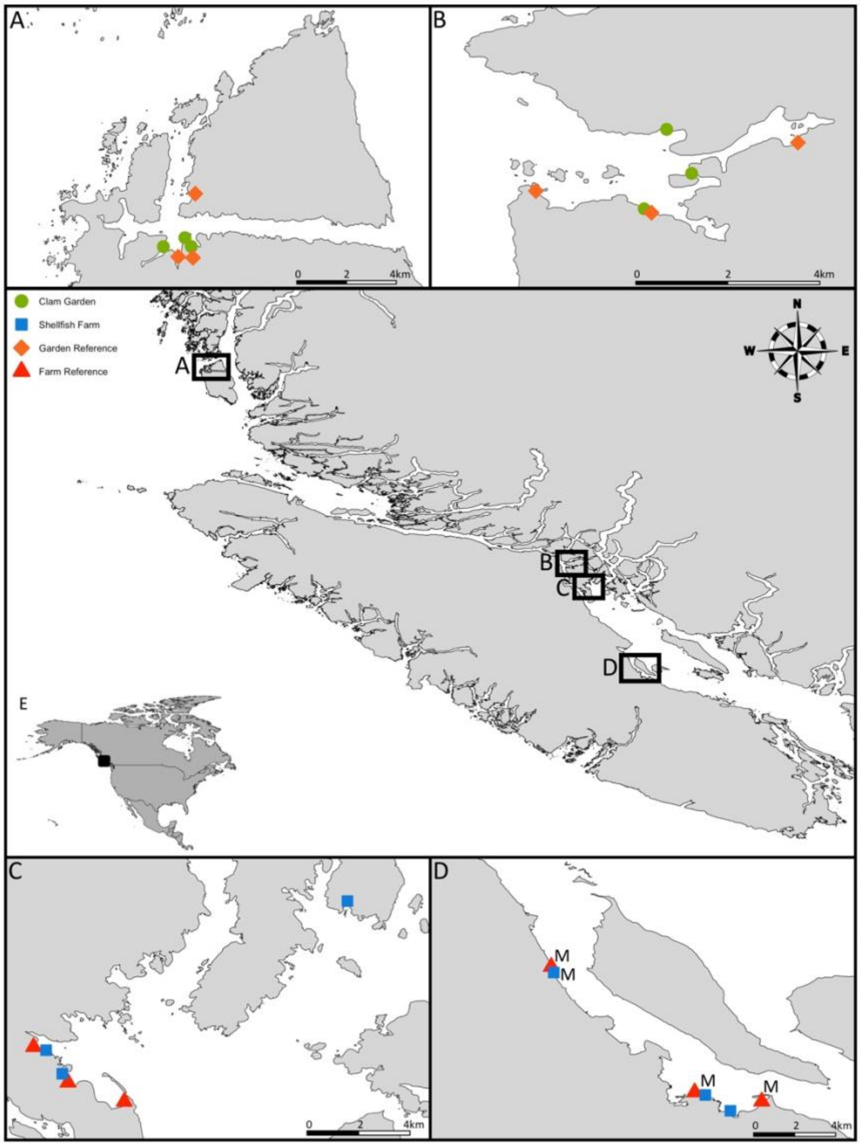

Figure 9*:* The distribution of study sites along British Columbia's central and south coast, Canada. Clam gardens (green circles), shellfish farms (blue squares), unmodified clam garden reference beaches (orange triangles), and unmodified shellfish farm reference beaches (red triangles). A) Calvert and Hecate Islands within the Hakai Lúxvbálís Conservancy, B) northern Quadra Island, C) southern Quadra Island, D) Baynes Sound between Denman Island and Vancouver Island ('M's denote locations of method comparison study), and. E) British Columbia coastline within the Northeast Pacific. Specific site locations are not provided as not to publish culturally modified areas.

3.2.5 Bivalve Community Surveys

Surveys quantified the infaunal (animals living in the sediment) bivalve communities present at each assessment location. Each survey used a 50 × 50 cm quadrat to establish the assessment area. Quadrats were dug to a depth of 20 cm, with the excavated sediment sieved and washed through 5 mm mesh while being examined for bivalves. All observed bivalves were identified, counted, and measured anteroposteriorly (shell length) to the nearest whole millimetre. Fourteen taxa (*e.g.* species, genera) were observed across the study sites. The resulting community data were expressed as bivalve species richness and abundance within 0.05 m^3 (the volume of the surveyed area).

3.2.6 Substrate Composition

Examinations of substrate types were conducted in a similar manner to Cox et al. (2019). Briefly, the percent cover of the substrate types observed within the 0.5 × 0.5 m quadrats was quantified to evaluate the importance of each intertidal substrate type. Each quadrat was photographed before the bivalve surveys (resolution: 2,832 × 2,832 pixels). Substrate photos were analyzed in an unordered fashion using ImageJ to derive surface cover metrics (Schneider et al. 2012). Percent cover was determined by dividing each substrate's area by the total quadrat area. Algal taxa were primarily *Sargassum muticum*, *Mastocarpus* spp., *Ulva* spp., *Gracilaria* spp., *Fucus* spp., Phaeophyceae (Brown Algae), and *Zostera* spp. (eelgrasses). Habitat-forming calcareous shells and tests (skeletons) were denoted as oyster shells, clam shells, and dead *Dendraster excentricus* (sand dollars). The Wentworth scale was used to classify each quadrat's sediments as boulders, cobble, gravel, sand, and mud/silt. Sediment classification, algal identification, and corresponding percent covers were also recorded in the field, allowing for *a priori* resolution of any discrepancies in the substrate composition analysis.

3.2.7 Sediment Characteristics

Grain size, water content, organics and carbonates were determined by collecting two cores adjacent to survey quadrats during the 2015 field season. A 5 cm diameter core taken to a depth of 15 cm was used to assess the sediment profile. A 3 cm diameter core taken to a depth of 5 cm was used to determine the water content, organic and carbonate content. One hundred and eighty-five sediment cores and eighty-seven organics, carbonates, and water content cores were collected and processed during the 2015 surveys (Table B1 and B2). The disparity in sample sizes is due to the challenges of processing organics, carbonates, and water content cores while conducting work in remote regions (*i.e.* Calvert Island). Sediment particle-size was determined by drying each 5 cm diameter sediment core at 60°C for 24 hours to remove interstitial water content, then sieving the sample into eight size classes (< 63 µm, 63-125 µm, 125-250 µm, 250-500 µm, 500-1000 µm, 1-2 mm, 2-4.75 mm, > 4.75 mm). The amount of sediment within each fraction was expressed as a percent relative to the total dried sample weight.

The water, organic matter, and carbonate contents within the 3 cm diameter cores were quantified using a three-step process. The water content of each sample was determined by drying the 3 cm diameter core sample at 100°C for 24-hour intervals to remove all the interstitial water. At least two drying intervals were used for each sample, but a third drying period occurred if weights changed drastically between dryings. Total organic matter content was measured through loss-on-ignition and involved further drying of the water content samples in a muffle furnace at 435°C for 8 hours. The amount of carbonate within each sample was determined through further drying at 950°C for 2 hours (Heiri et al. 2001). The water, organic matter, and carbonate contents were calculated as the weight lost during drying relative to the sample's net weight, expressed as a percentage.

3.2.8 Habitat Complexity

Survey Area

Structure-from-motion (SfM) photogrammetry was used to quantify the structural characteristics of the 24 clam gardens, shellfish farms, and unmodified beaches in 2017. These habitat surveys use 2D images to generate high-resolution 3D reconstructions of the physical environments (Westoby et al. 2012). At each site, a 10 × 10 m assessment area was established with the top corners at the 2.2 m tideline (Fig. B2). This assessment location was within the mid-intertidal zone, where most of the biodiversity surveys occurred. The GPS coordinates of ground control points (GCPs) placed at the corners and midpoints of the area were recorded, allowing the resulting models to be georeferenced (Fig. B2).

Image acquisition

The 100 m^2 survey areas were photographed until the entire area had been adequately covered (Westoby et al. 2012). Image acquisition used a Canon SL1 digital SLR camera with a 10–18 mm lens. Camera settings were: a shutter speed above 1/100, an aperture of f/8-11, a focal length of 18 mm, and ISO as low as conditions would allow. Image acquisition occurred in a boustrophedonic pattern while holding the camera ~2 meters above the substrate (Fig. B2). Subsequent photos were taken from around the survey area, aiming the camera at acute angles relative to substrate features. Depending on the complexity of the assessment area, image acquisition captured between 440 and 2,030 photos.

3D habitat model generation

Agisoft Metashape Standard Edition (v1.7.4) was used to generate three-dimensional reconstructions of the 24 sites. Model generation followed the Agisoft Metashape manual, and was further clarified by Young et al. (2017). Model generation and succeeding examinations used a Dell Alienware Aurora R8 Desktop with 64GB RAM, an NVIDIA GeForce GTX 1070 Ti graphics card, and an Intel Core i7 8700 processor. The four key model generation stages were: aligning photos, dense point cloud construction, mesh construction, and building texture (Fig. 14A). Stage specifics are outlined in Westoby et al. (2012, Young et al. (2017). The three-dimensional habitat models were exported as wavefront files for further analysis.

Quantification of spatial properties

Habitat models were analyzed using Rhinoceros 3D (v7). The structural metrics quantified were linear rugosity (R) and fractal dimension (D). Habitat models were scaled using the ‘scale’ function and each model’s four 0.42 m scale bars. Linear R was quantified using an extendible chain method to measure the topographic distance covered by a straight-line distance. Consequently, linear R measurements are between 1 and 0 with lower values denoting more complex surfaces. To avoid confusion, linear R is considered on an inverted scale (*i.e.* 0-1), to allow increased in linear R to reflect increases in complexity. Three nine-meter linear R measurements were taken in both directions using a virtual chain with a 2 cm link length (Fig. 14B). A custom Python script adapted from (Young et al. 2017) allowed chains measurements to be consistent across models. The six chain measurements were averaged to determine each site's mean linear R.

Fractal dimension measures how surface area changes with resolution. This is accomplished by quantifying the slope of a model's resolution relative to its surface area on a logarithmic scale, effectively indicating how complexity changes with scale (Young et al. 2017). Customizable resolutions allow for the consideration of different sizes. Commonly, resolutions are selected based on species dimensions, habitat characteristics, or designated multiple size categories. Fractal dimension measurements are between 2 and 3, with higher values representing amplified surface heterogeneity. Fractal dimension was measured at four spatial resolutions, 2.5-5, 5-25, 25-50, and 50-100 cm. Effectively, these resolutions measure complexity within these size ranges. These resolutions encapsulate complexity relevant to invertebrate body sizes (2.5-5 cm), physical structures added during shellfish farm and clam garden construction (5-25 and 25-50 cm), and prominent naturally occurring or augmented physical features (50-100cm). Five D measurements at the four spatial resolutions were taken for each model, one in the middle and one at each corner to maximize the distance between measurement locations (Fig. 14B).

3.2.9 Statistical Analyses

Data analyses were conducted in RStudio version 3.6.1(R Core Team 2019). Data visualizations used the 'ggplot2' package and base R (Wickham 2016). Analyses were conducted using the 'vegan', 'mvpart' and 'randomForestSRC' packages (De'ath 2014, Oksanen et al. 2019, Ishwaran et al. 2021). All frequentist inference base statistical analyses used an α value of 0.05 to detect significance.

Method Comparison

The ecological and statistical implications of the bivalve survey method were examined by conducting three alternative methods concurrently and evaluating the ability of each method to describe several characteristics of the bivalve community. The richness (species/sample) and density (individuals/m^3) of bivalves detected by each method were compared using two nonparametric Kruskal-Wallis rank sum tests and post hoc Dunn's tests to conduct multiple pairwise comparisons. Bivalve richness and density were the number of unique taxa and their abundances detected per sampling unit, respectively. Abundance estimates were extrapolated to a consistent volume of one cubic meter to facilitate comparisons. The frequency and abundance of shell lengths observed by each sampling method were plotted to examine differences in the size spectra detected.

The bivalve communities detected by the survey methods were characterized using three indices are also known as Hill numbers. The first index was richness, which indicates the number of unique taxa. The second index, Shannon diversity, elucidates the relationship between richness and evenness. Inverse Simpson, the third index, considers richness and evenness while weighting dominant taxa more than Shannon diversity. They can be represented by q-value, denoting the sensitivity of each index to the relative abundances of taxa, with richness, Shannon diversity, and inverse Simpson being $q = 0$, 1, and 2, respectively (Hsieh et al. 2016, Cox et al. 2017). Sample-and coverage-based rarefaction and extrapolation curves examined how Hill numbers varied with increasing sampling effort and completeness (Hsieh et al. 2016, Cox et al. 2017). Sample-based curves plot diversity relative to the number of sampling units, illustrating species detection per sampling unit. Coverage-based curves plot rarefied sample completeness, depicting diversity relative to sample coverage. Extrapolation curves were limited to a doubling in sample size (Hsieh et al. 2016). The ninety-five percent confidence intervals of rarefaction and extrapolation allowed interval overlap to be used in lieu of statistical testing (Chao and Jost 2012, Chao et al. 2014b).

Habitat Complexity

The complexity metrics of the twenty-four sites were averaged according to the four site types, illustrating the structural differences between the habitats. Each site's five D measurements and linear R were averaged prior to quantifying the site type's mean D and mean linear R. The D measurements determined complexity at fine and broad scales via decreasing resolutions (2.5-5, 5-25, 25-50, 50-100 cm). For example, an increase in D within the 50-100 cm resolution would indicate elevated broad-scale complexity. Conversely, linear R considers topographic distance divided by chain length, causing more complex surfaces to have lower R values. This relationship is attributed to increases in surface complexity decreasing topographic distances. A flat surface, for example, would have equal topographic and chain distances.

Community Composition

Bivalve communities were characterized using Hill numbers to examine the variability between the taxonomic diversity and abundances present at clam gardens, shellfish farms, and reference sites. A value for the three indices as a function of order q, in addition to all other q orders up to five, was generated for each site type and regional comparison (*e.g.* Quadra Island clam gardens and reference sites) (Chao et al. 2014b). The values were plotted as diversity profile curves to illustrate diversity as a function of increasing order q. The slope of the curve reflects community evenness, with shallower curves signifying even abundances (Chao et al. 2014b). These analyses only considered the 2015 and 2016 surveys conducted within the mid-intertidal zone, providing a balanced sampling effort (N = 235 quadrats).

The composition of the bivalve communities at each site type was characterized using non-parametric multivariate analyses (Mcardle and Anderson 2001, Anderson et al. 2008, Oksanen et al. 2019). These analyses considered biodiversity surveys conducted within the mid-intertidal zone to ensure a balanced sampling effort. The site's quadrats were averaged for each year; then, the site-year values were averaged according to site type (*e.g.* shellfish farm, clam garden). A resemblance matrix of bivalve densities was calculated using Bray-Curtis coefficients and a dummy variable of 1 to correct cells where no biota was observed. Multidimensional scaling (nMDS) plots illustrated the composition of each site type and regional comparison. Permutational Multivariate Analysis of Variance (PERMANOVA) conducted on the resemblance matrix evaluated if communities differed statistically among the site types and regions. PERMANOVAs examined the site type's community dissimilarities within and among each of the three regions. Consequently, five PERMANOVAs were run: Clam Garden, Shellfish Farms, and Reference Sites; Calvert Island Gardens and Reference Sites; Quadra Island Gardens and Reference Sites; Quadra Island Shellfish Farms; Baynes Sound shellfish Farms. Year, site type, and the interaction between year and site type were integrated into each PERMANOVA as fixed factors. A Similarity Percentages (SIMPER) analysis then determined percent dissimilarity between the site types and regions. SIMPER was run using 999 permutations to elucidate the differences in each taxon between site types. The average dissimilarity between each taxon (Diss) was divided by the standard deviation (SD) to determine the taxon's contribution to community dissimilarity (Diss/SD) (Anderson et al. 2008). Dissimilarities between the site types and regions were plotted to visualize differences between communities.

Bivalve Biomass

The distributions of bivalve shell lengths and estimated bivalve biomass per sampling unit were examined to evaluate productivity within each site type. The frequency and abundance of shell lengths observed within each site type were plotted for *Saxidomus gigantea*, *Leukoma staminea*, *Ruditapes philippinarum*, *Nuttallia obscurata*, *Mya arenaria*, *Macoma inquinata*, and *Macoma nasuta*, excluding *Limecola* balthica, *Macoma* spp. and *Nutricola tantilla* due to insufficient length data. The primary focus of this analysis was the four species primarily targeted by shellfish cultivation: *S. gigantea* and *L. staminea* are culturally and economically significant to Indigenous First Peoples, and *R. philippinarum*, and *N. obscurata* comprise a substantial portion of British Columbia's shellfish aquaculture market (British Columbia et al. 2002, Silver 2014, Groesbeck et al. 2014, Jackley et al. 2016).

The biomass of the focal species was determined using studies that measured between 880 and 47,357 individuals of the target species (Table B3). Although literature values provide a suboptimal proxy for biomass as the length-weight relationships can vary by site, this approach allowed the relationship to be derived from over 71,000 individuals collected from various coastal regions (Table B3). Plotting the total length of each focal species within a sample unit confirmed that length trends paralleled biomass relationship but detected more variance across taxa, and length differences are less relevant for examining productivity (Fig. B3). These surveys derive the α and β parameters from the length-weight relationship using the equation $W = \alpha L\beta$, where W is the total weight of a clam in grams and L is the shell length in millimetres.

The weights of *S. gigantea, L. staminea, R. philippinarum, and N. obscurata* (the 'focal species') for a given length were determined by plotting $W = \alpha L\beta$, using the literature-derived α and β parameters, and a length value continuously increasing from 1 mm to the maximum observed length of each taxon. Biomasses per quadrat of focal species were derived using the abundance of shell lengths observed in the field surveys and each species' length-weight relationship. Quadrat biomasses were averaged for each year; then, the site-year values were averaged. Bivalve biomasses within clam gardens, unmodified clam garden reference beaches, shellfish farms, and unmodified shellfish farm reference beaches were analyzed using an ANOVA. The model considered site, year, area, and the interaction between site type and species. A histogram of residuals illustrated a normal distribution (Fig. B4).

Bivalve Community-Substrate Associations

Multivariate regression trees (MRTs) analyzed the association between bivalve communities, substrate composition, organics, carbonates, and water content. MRTs are a machine learning technique that extends univariate regression trees to consider multiple response variables, allowing explorations of complex ecological data to describe and predict relationships between taxa and environmental characteristics (De'ath 2002). Two MRTs were fitted using the 'mvpart' package (De'ath 2014). The first MRT examined the interaction between bivalve community composition and sediment grain sizes using the 185 co-occurring bivalve surveys and sediment cores. The second MRT examined the interaction between bivalve community composition and organic, water content and inorganic content using the 87 co-occurring bivalve surveys and organics, carbonates, and water content cores—the construction of both MRTs following a similar process. Bivalve densities were log-transformed following the addition of a dummy variable of 1. The MRTs evaluated bivalve density as the response variable, and either the percent abundance of sediment grain sizes (< 63um, 63-125 um, 125-250 um, 250-500 um, 500-1000 um, 1-2 mm, 2-4.75 mm, > 4.75 mm) or organics, water content, and carbonates. The optimal tree size for each MRT was determined following one-thousand-fold cross-validation. The MRT evaluating bivalve association with grain size was pruned to the minimum cross-validation error rate, creating a five-leaf tree. The MRT evaluating bivalve association with organics, carbonates, and water content was pruned to seven leaves, which was one standard error above the recommended five-leaf model. This pruning approach increased the descriptive capabilities of the MRT. The default bar plots of each tree were replaced with boxplots to provide more detailed information. The taxa that contributed the most to each split in the MTRs were determined using a discrimination analysis. This analysis identified taxa that contribute the most variance at each node, the directionality of their contribution, and the probability that the contribution was non-random.

Mechanisms Facilitating Bivalve Biomass

The ecological covariates sustaining bivalve biomass were quantified. The first examination evaluated the relationship between the cumulative biomass of the four primary cultivation species (*i.e. S. gigantea, L. staminea, R. philippinarum,* and *N. obscurata)* and bivalve species richness within each sampling unit. This investigation only considered the 2015 and 2016 surveys conducted within the mid-intertidal zone an unbalanced sampling design. The twenty-four site’s quadrats were averaged according to year, creating 48 diversity-biomass values. The relationship between biomass and bivalve species richness within and among site types was explored graphically.

A random forest (RF) analysis quantified the importance of each ecological covariate for bivalve biomass. This analysis increases predictive accuracy by creating a collection of decorrelated trees using bootstrapping and split-variable randomization (Breiman 2001, Segal and Xiao 2011). The predictive accuracy of the forest can be examined using a portion of the data (*i.e.* training) to construct the forest and the remaining portion to evaluate the model's performance (*i.e.* testing). The RF was constructed using survey data from all intertidal zones (N = 412 bivalve surveys). Therefore, the RF quantified the importance of substrate composition, habitat complexity, site, site type, area, intertidal zone, and bivalve species richness to log bivalve biomass. Habitat complexity metrics included mean linear R and mean D at 2.5-5, 5-25, 25-50, and 50-100 cm resolutions, denoted as D2.5, D5, D25, and D50. Substrate composition included percent cobble, gravel, sand, mud/silt, clam shells, oyster shell, *Fucus spp.*, *Mastocarpus* spp., Phaeophyceae (brown algae), *Sargassum muticum*, *Ulva* spp., and *Zostera* spp. The RF consisted of 6,000 trees grown to a maximum node depth of six to avoid overfitting (Fig. B5). The number of candidate variables randomly selected for splitting a node was 9, following the p/3 recommendation for regression, where p is the number of variables. The minimum terminal node size was 5, following the regression default. Variable importance was calculated by randomly permuting the variables' values, running them through the model, and calculating changes in mean squared error. As a result, the importance of a variable is proportional to its relative effect on MSE, with higher values having more influence on accuracy (Breiman 2001). The variable importance analysis identified several ecological covariates with a negligible influence on biomass. Therefore, year, percent *S. muticum,* Phaeophyceae, (dead) *Dendraster*, oyster shell, *Zostera* spp., *Gracilaria* spp., *Fucus* spp., *Mastocarpus* spp., and cobble, were removed and the RF was reconstructed using the remaining variables and same construction parameters (Fig. B5). A complementary analysis constructed separate RFs using clam garden and shellfish farm data to examine the ecological covariates supporting biomass within each site type. These RFs were constructed using identical parameters as the initial RFs and all ecological covariates.

A subsequent analysis examined the RF's ability to predict bivalve biomass. The predictive accuracy of the RF was determined using 70% of the data to train the model and 30% of the data to evaluate the model's predictions. The training and predictive models used parameters that were identical to the variable importance analysis.

3.3 Results

3.3.1 Methods Comparison

The multi-method comparison determined the ecological and statistical implications of the survey method relative to alternative approaches. Species diversity increased significantly with increasing sample volume, ranging from one to four species detected per sample unit on average (Kruskal–Wallis $\chi2 = 39.21$, df= 2, $p < 0.001$; Fig. 10A; Table B4). Detection of bivalve densities exhibited a similar trend; however, the small and large quadrat methods were equivalent (Kruskal–Wallis $\chi2 = 12.28$, df= 2, $p < 0.001$; Fig. 10B; Table B4). Although the abundance of shell lengths observed by each sampling method differing drastically, the frequency of shell lengths was mirrored among methods (Fig. 10C). The only minor deviation was that increased sample volumes better capture 30-50 cm bivalves. Rarefaction and extrapolation of each method’s Hill numbers illuminated the implications of difference in species richness detected per sampling unit, and to a lesser extent, dissimilarities in species densities. Furthermore, plateauing richness, Shannon, and inverse Simpson rarefaction curves indicated that the surveys reached each method’s detection capabilities and that observed community differences would persist regardless of additional sampling effort (Fig. 10). Rarefaction and extrapolation of richness reflected previously observed diversity and density trends. By 25 samples, however, the 95% confidence intervals began to converge despite (Fig. 10E). Shannon and inverse Simpson did not mirror this trend as detection and coverage differed among sampling methods irrespective of sample units (Fig. 10G-J). These trends persisted despite all rarefaction curves plateauing and adequate sample coverage.

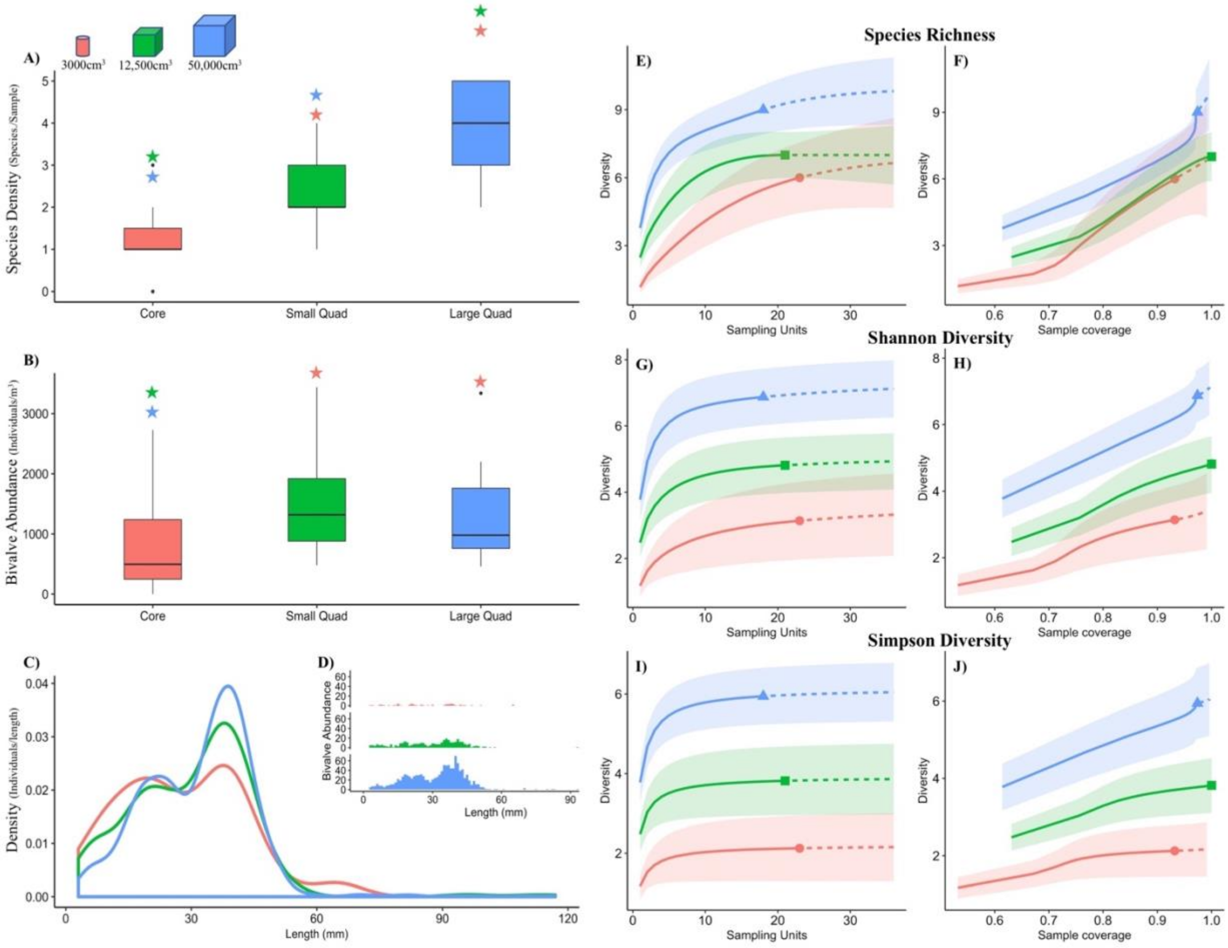

Figure 10: Methodological implications of varying survey volume. Bivalve diversity, abundance, shell length, and sample- and coverage-based biodiversity metrics when using a 3,000 cm^3 core, 12,500 cm^3 cube, and 50,000 cm^3 cube to survey four intertidal sites. A) Bivalve species richness detected per sample. B) Abundance of bivalves detected per cubic meter. A-B)

Stars denote statistical significance between sampling methods, with star color indicating the comparison. C) The frequency of shell lengths observed by each sampling method. D) The abundance of shell lengths observed by each sampling method. E-J) Comparisons of rarefaction and extrapolation of Hill numbers with 95% confidence intervals. E, G, I) sample-based rarefaction and extrapolation. F, H, J) coverage-based rarefaction and extrapolation. E & F) Richness (q = 0). G &H) Shannon diversity (q = 1). I & J) Simpson diversity.

3.3.2 Community Composition

Diversity Profile Curves

The biological communities of clam garden and shellfish farm differed from their respective reference beaches, with Hill numbers varying according to cultivation method and region. Across all regions, clam gardens and garden reference sites exhibited increases in Shannon and inverse Simpson diversity relative to shellfish farms and farm reference sites (Fig. 11A). Communities within clam gardens and garden reference sites were also more even, as evidenced by the slope of the order-q line. However, richness was higher within shellfish farms and farm reference sites due to *R. philippinarum* or *Macoma* spp. being observed only in these site types. Comparisons of clam gardens, shellfish farms, and respective reference sites demonstrated regional species responses. Clam gardens within the Hakai Lúxvbálís Conservancy and shellfish farms surrounding Quadra Island exhibited elevated Shannon and inverse Simpson diversity (Fig. 11B). Alternatively, clam gardens surrounding Quadra Island and the shellfish farms within Baynes Sound displayed diversity metrics similar to reference sites (Fig. 11C-E).

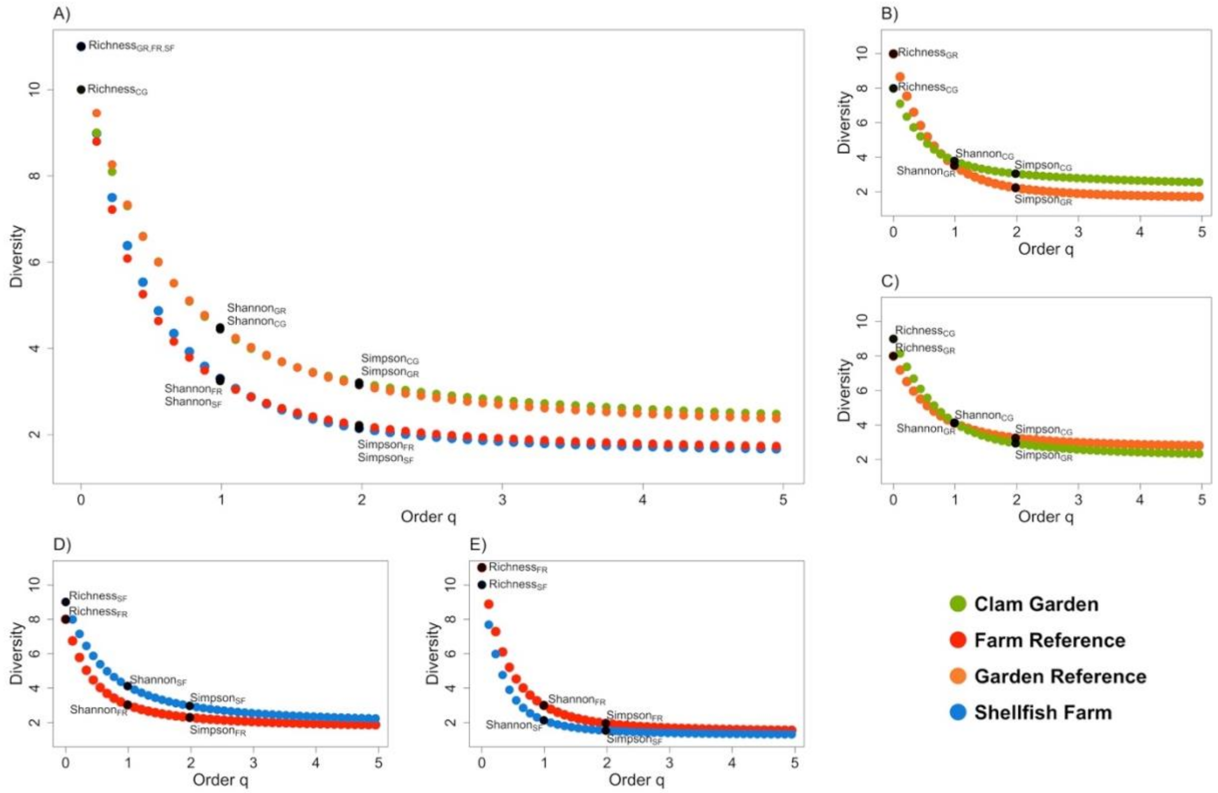

Figure 11: Diversity profile curves illustrating diversity as a function of order q values for clam gardens (green), unmodified clam garden reference beaches (orange), shellfish farms (blue), and unmodified shellfish farm reference beaches (red). Black dots denote Hill numbers: species richness (q = 0), Shannon diversity (q = 1), and Simpson inverse diversity (q = 2). The slope of the curve reflects community evenness. A) Bivalve diversity across all regions. B-E) Diversity within B) the Hakai Lúxvbálís Conservancy, C) northern Quadra Island, D) southern Quadra Island, and E) Baynes Sound.

nMDS and SIMPER

The composition of bivalve communities differed significantly among site types, years, and sites (Fig. 12A, Table B5). Community differences generally persisted within each regional comparison, except for clam gardens and garden reference sites surrounding Quadra Island, which displayed considerable community overlap (Fig. 12B-E, Table B5, PERMANOVA, F =0.81, p = 0.54, Fig. 12A). The stress levels of non-Metric Multi-Dimensional Scaling (nMDS) plots ranged from 0.09 to 0.13, signifying an appropriate model fit amongst comparisons (Fig. 12). The SIMPER analyses quantified taxa-specific contributions to the community differences depicted by the nMDS plots. Comparable levels of dissimilarity were observed between clam gardens (52.91% dissimilar), shellfish farms (50.50% dissimilar) and respective reference sites (Fig. 12F-G, Table B6). The majority of taxa increased within cultivated sites; however, taxa-specific responses varied considerably according to the cultivation method. The abundances of *M. inquinata*, *L. staminea*, *S. gigantea*, *R. philippinarum*, and *M. nasuta* increased within clam gardens, contributing 88.33% of the cumulative dissimilarity (Table B6). Community differences within shellfish farms were primarily attributed to increases in two introduced bivalves, *R. philippinarum* and *N. obscurata*, which accounted for 67.62% of the cumulative dissimilarity. Differences between site types and references sites varied regionally (Fig. B6, Table B6). Notably, *S. gigantea* within clam gardens surrounding Calvert Island increased, while *M. inquinata* abundances decreased (Fig. B6, Table B6). Further south on Quadra Island, *S. gigantea* and *L. staminea* populations were less abundant than their northern clam garden counterparts on Calvert Island, paralleling the community overlap depicted by nMDS plots. Community responses to shellfish farming were consistent across the regions, with only *M. inquinata* abundance increasing within the Quadra Island and Baynes Sound farms (Fig. B6, Table B6).

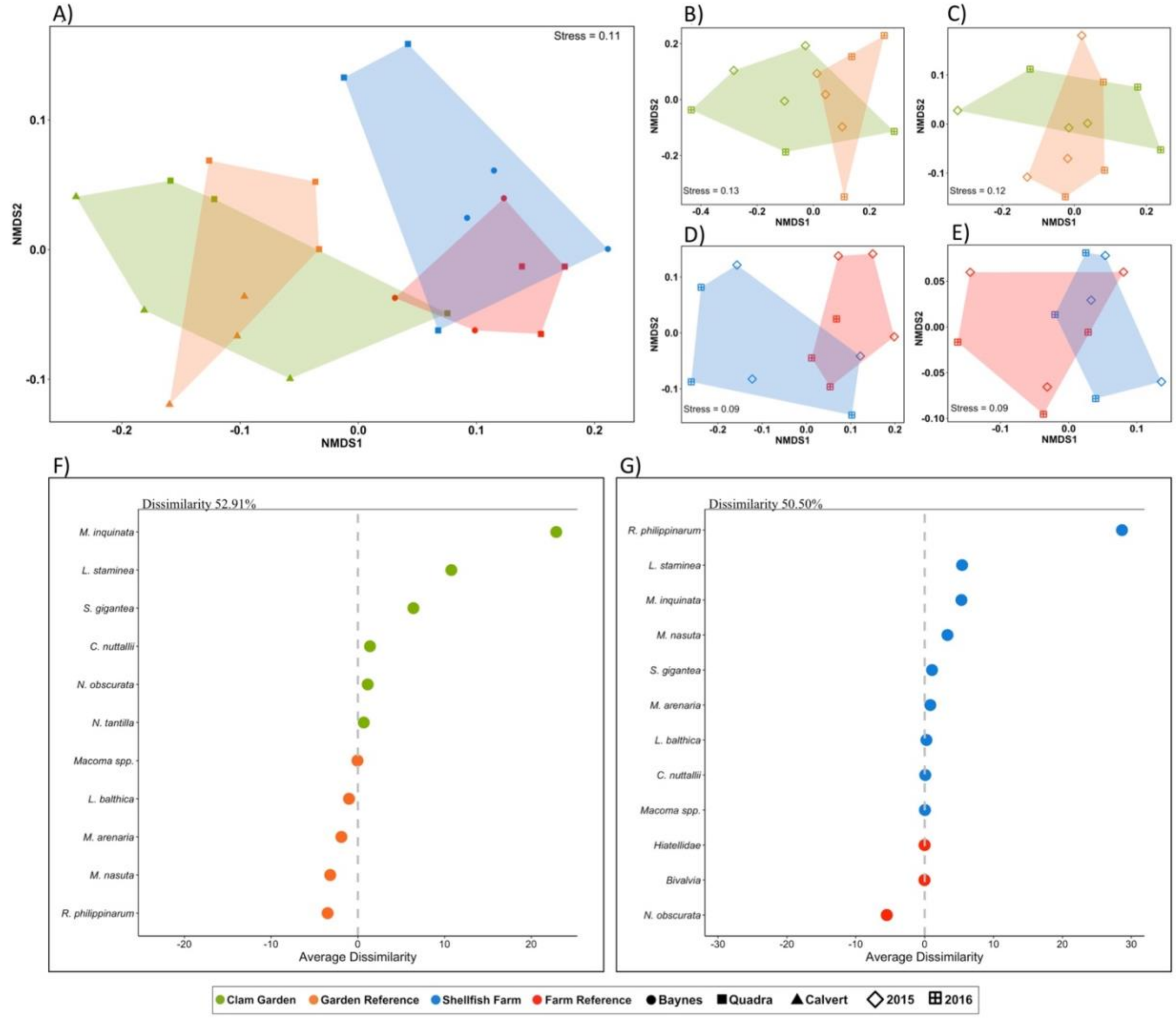

Figure 12: Non-metric multidimensional (nMDS) scaling plots and taxa-specific dissimilarity. Colors designate clam gardens (green), unmodified clam garden reference beaches (orange), shellfish farms (blue), and unmodified shellfish farm reference beaches (red). A) Community composition pooled across regions: Baynes Sound (circles), north and south Quadra island (squares), Calvert Island (triangle). Community composition within B) Calvert Island, C) northern Quadra Island, D) Southern Quadra Island, and E) Baynes Sound, with symbol shape denoting years. F-G) Average taxa-specific dissimilarity between cultivated habitats and unmodified sites. F) Clam gardens and unmodified clam garden reference sites.

3.3.3 Bivalve Length and Estimated Biomass

Bivalve abundance and length frequencies varied within and among the site types and according to taxa. *S. gigantea* abundances within clam gardens exhibited an elevated bimodal distribution relative to garden reference sites. Substantial increases in *S. gigantea* below 18 mm retained this bimodality within the density distribution and elevated the density of juveniles above mature *S. gigantea*, a state not exhibited within any other site type (Fig. 13A). Across the length spectrum, *L. staminea* was more abundant within clam gardens and shellfish farms than in respective reference sites (Fig. 13B). Again, populations within clam gardens exhibited high juvenile densities (*i.e.* <20 mm); however, garden reference sites demonstrated a similar but less pronounced pattern Fig. 13B). In contrast, *L. staminea* populations within shellfish farms and farm reference sites had proportionally more 30-50 mm individuals, creating unimodal distributions (Fig. 13B). *Ruditapes philippinarum* populations within shellfish farms and farm references sites had unimodal distributions centered around 38 mm, with shellfish farms displaying a two-fold increase in the abundance of 30-55 mm individuals (Fig. 13C). Within clam garden and garden reference sites, *R. philippinarum* abundances were lower across all sizes, but the length distribution in garden reference sites followed a similar pattern to shellfish farms (Fig. 13C). *Nuttallia obscurata* populations within shellfish farms and farm reference sites paralleled *R. philippinarum* abundances and densities, with shellfish farms and farm reference presenting a more pronounced unimodal distribution (Fig. 13D). This distribution was emulated by the sparse *N. obscurata* population detected within clam gardens. Garden reference sites were devoid of *N. obscurata* (Fig. 13D). The abundance and frequency of *M. arenaria, M. inquinata* and *M. nasuta* populations were relatively consistent across site types (Fig. B7). Cumulative biomass within clam garden was 4.67 kg per m^3, garden reference sites was 2.98 kg per m^3, shellfish farms was 3.55 kg per m^3, and shellfish farms reference sites 1.90 kg per m^3.

Length-weight relationships varied slightly across the four focal taxa, translating to evident differences in biomass at maximum length or when per quadrat when considered in combination with surveyed lengths (Fig. 13E-F). *Saxidomus gigantea* had the highest possible weight at 370 g. *Leukoma staminea* exhibited the steepest growth curve but reflected *R. philippinarum* maximum weight of approximately 180 g for an 80 mm individual (Fig. 13E). Growth rate and maximum weight were the lowest for *Nuttallia obscurata,* with a limit of 64 mm and 40 g. Distinct length-weight relationships and differential abundances in length were reflected in species biomasses within the four site types (ANOVA, F =3.26, p = 0.001, Table B7). *Saxidomus gigantea* contributed most of the biomass observed within clam gardens, with considerable reductions in grams of *S. gigantea* per quadrat detected within shellfish farms and farm reference sites (Fig. 13F). Conversely, *R. philippinarum,* and to a lesser extent *N. obscurata,* accounted for most of the biomass observed within shellfish farms and farm reference sites. Clam gardens exhibited a minor increase in *L. staminea* biomass, but generally this taxon’s mass was relatively consistent across site types (Fig. 13F).

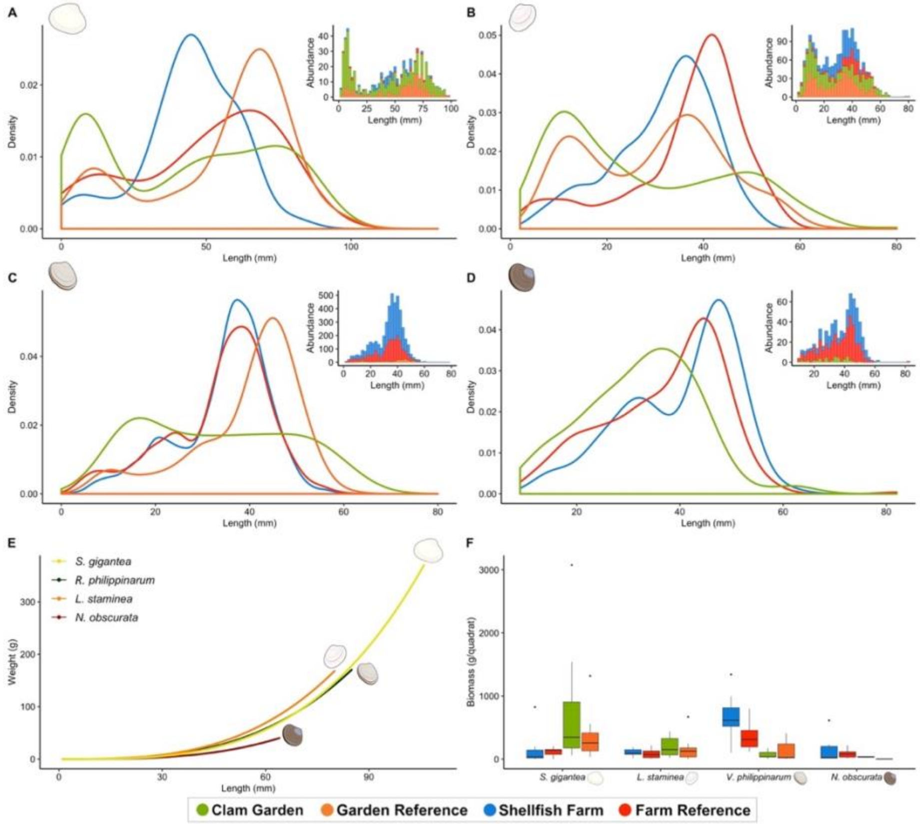

Figure 13: Bivalve length distributions within cultivated and unmodified habitats, and bivalve biomass per sampling unit. A-D) Main and subplots display length frequencies and length abundances, respectively. A) Butter clam (*Saxidomus gigantea*). B) Pacific littleneck clam (*Leukoma staminea*). C) Manila clam (*Ruditapes philippinarum*). D) Varnish clam (*Nuttallia obscurata*). E) *S. gigantea* (yellow), *L. staminea* (orange), *R. philippinarum* (black) *and N. obscurata* (burgundy) length-weight relationships obtained by plotting literature derived length-weight equations relative to a continuous increase in length. F) Focal species estimated biomasses per quadrat, derived using observed lengths (A-D) and length-weight relationships (E). Quadrats were 50 cm in length and width, dug to 20 cm depth.

3.3.4 Habitat complexity

Examining three-dimensional reconstructions of the twenty-four sites quantified multiple aspects of each location's structural complexity (Fig. 14). The habitat reconstructions were more similar within than among site types, although considerable variability was evident within each site type (Fig. 14B, Fig. B8). Clam gardens and shellfish farms displayed elevated linear R relative to the corresponding reference sites, with clam gardens exhibiting more topographic complexity (Fig. 14G). Fractal dimension showed a similar trend as linear rugosity, with complexity elevated within clam gardens and shellfish farms (Fig. 14F). Increases in complexity were more prominent within clam gardens than shellfish farms. Both unmodified reference site types had similar levels of complexity (Fig. 14F). Fractal dimension was highest at fine-scale resolutions within each site type and declined with decreasing resolution (Fig. 14H). Clam gardens deviated the most from this trend as 5-25 and 25-50 cm resolutions displayed the highest complexity of the four spatial scales considered.

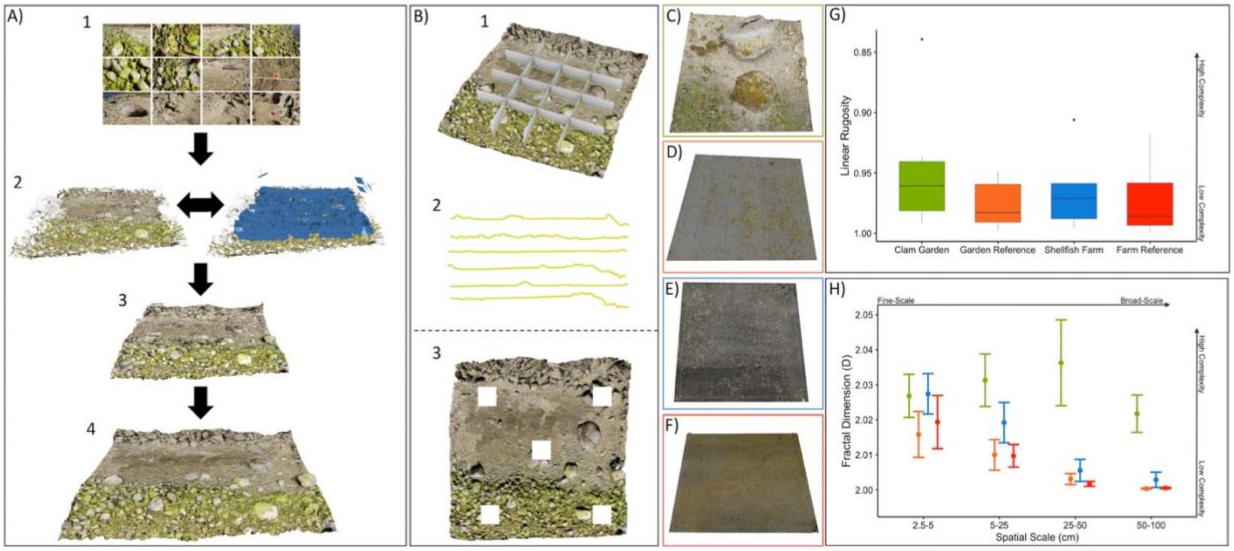

Figure 14: Physical complexity of intertidal survey locations. A) A flow diagram illustrating the 1) image acquisition, 2) image alignment and spare cloud generation, 3) dense point cloud generation, and 4) tiled mesh construction. B) Complexity analyses diagrams: illustrating the 1) six 9-meter rugosity chains laid out at equidistantly across the model, 2) curvatures resulting from model and chain interactions, and 3) five 1 × 1 m fractal dimension assessment locations. C-F) Example three-dimensional reconstructions of the site types: C) clam garden, D) unmodified clam garden reference, E) shellfish farm, and F) unmodified shellfish farm reference. G) Each site type's mean linear rugosity. Y-axis inverted as lower rugosity values denotes higher complexity. H) Each site type's fractal dimension value at four spatial resolutions. Plots show mean and standard error values. Colours in G-H) correspond to site types in C-F).

3.3.5 Habitat-Community Associations

Multivariate regression trees quantified the extent to which bivalve communities correlate with sediment grain sizes and other characteristics. The root node of the MRT examining sediment grain sizes identified differences in community composition between farm and farm reference sites, and clam garden and garden reference sites, as the principal covariate. *Ruditapes philippinarum, N. obscurata,* and *M. inquinata* were the discrimination taxa informing this split, with *R. philippinarum* and *N. obscurata* supporting the left split and *M. inquinata* the right (Fig. 15A, Table B8). Within shellfish farms and farm reference sites, the proportion of coarse sediments further structured biological communities. Less than 15.29% of 4.75 mm sediments, the largest grain size category, were associated with this branch's most diverse community, with *M. nasuta, M. inquinata* and to a lesser extent, *S. gigantea* increasing in abundance (Fig. 15A, Table B8). Alternatively, fine sediments structured the clam garden and garden reference site branch, with 5.65% of 63-125 µm spilling the branch into two terminal leaves (Fig. 15A). Although a relatively small amount of fine grain sediments split the branch, the communities differed considerably, with *R. philippinarum* and *L. staminea* densities exhibiting a 2-fold increase if less than 5.65% of 63-125 µm sediment was observed (Table B8). Both terminal leaves were more diverse than any other leaves on the shellfish farm branches.

The MRT investigating associations between sediment organic, carbonate, and water concentrations and bivalve communities also identified cultivation method and associated reference sites as the root node (Fig. 15B). Water content structured the first node of each branch with approximately 10% water modulating each split. However, each node's discrimination species differed considerably (Table B9). The left branch split was dictated by *N. obscurata* exhibiting a 6-fold increase if water content levels within the shellfish farm and farm reference site were above 10.25%. *Saxidomus gigantea, L. staminea,* and *M. inquinata* association with water content levels above 10.93% were the primary driver of the right branch's split, with *S. gigantea* abundances increasing several-fold (Table B9). The remaining terminal leaf were structured by interactions between water content and organics or carbonates (Fig. 15B). For example, within farms and farm reference sites, between 10.25 and 13.63% water content and below 2.15% organics are correlated with of *L. staminea* and *R. philippinarum* populations.

The RF variable importance analysis determined the extent to which habitat complexity, substrate composition and spatial factor (*e.g.* area, intertidal zone) structure bivalve communities. Variable importance ranged from 1.5 to 31.1%, with bivalve richness, gravel, mud and silt, D 25-50 cm, D 2.5-5 cm, D 50-100 cm and D 5-25 cm among the most important variables (Fig. 15D). Area, site type, intertidal zone, and site were the highest-ranked spatial variables. The RF model explained 46.5% of the variability in bivalve biomass (Table B10), with additional insight gained into several ecological relationships. Notably, the weak relationship between the diversity of bivalves and the cumulative biomass within a quadrat became more predominant when incorporated into the RF model and examined concurrently with additional ecological covariates (Fig. 15C). The order of variable importance differed when clam garden and shellfish farms were analyzed separately, except for bivalve richness which remained the most influential variable within both site types (Fig. 15E-F). Habitat complexity, specifically D 25-50 cm, D 5-25 cm, D 2.5-5 cm, and linear R were the most important variables within clam gardens. In contrast, bivalve biomass within shellfish farms was primarily associated with structural variables including site, intertidal zone, and area (Fig. 15E-F, Fig. B9).

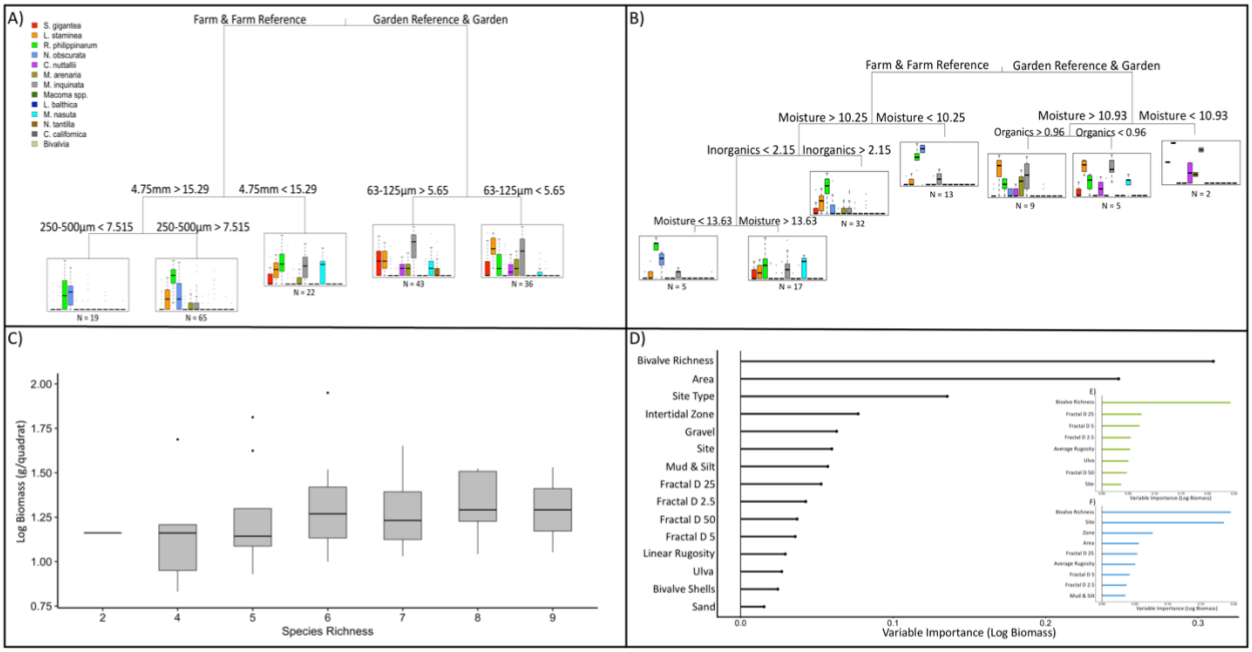

Figure 15: The mechanisms facilitating bivalve community responses and sustaining elevated bivalve estimated biomass. A) Multivariate regression tree (MRT) analysis of sediment grain sizes and associated bivalve communities (N = 185 sediment cores and bivalve surveys). Sediment grain sizes considered include >4.75 mm, 2-4.75 mm, 1-2 mm, 500 µm-1 mm, 250-500 µm, 125-250µm, 125-63 µm, and < 63 µm. B) An MRT analysis of the interaction between bivalve communities and substrate organics, carbonates, and water content (denoted as 'moisture') (N = 87 cores and bivalve surveys). C) The relationship between the cumulative biomass of the four primary cultivation species (S. gigantea, L. staminea, *R. philippinarum*, and *N. obscurata*) and bivalve species richness within each quadrat. D) Random forest variable importance analysis examining the influence of substrate composition, habitat complexity, site type, area, intertidal zone, and bivalve species richness on log bivalve biomass (N =412 bivalve surveys). Predictor variables are scaled by decreases in the mean squared error, with higher bars equating to greater importance. E-F) Random forest variable importance analyses conducted on E) clam garden data and F) shellfish farm data.

3.4 Discussion

Here, we quantify the extent to which shellfish cultivation practices, implemented over millennia, structure intertidal bivalve communities, which in turn facilitates and sustains increases in shellfish biomass. We demonstrate that these community responses stem from the structural complexity that shellfish cultivation contributes to nearshore ecosystems. Complexity alters flow regimes, intertidal sediments and nutrients (Commito and Rusignuolo 2000, Cardinale et al. 2002, Cheng et al. 2021), which we demonstrate promote the proliferation of bivalve communities within cultivated habitats. However, the heterogeneous taxa-specific responses that we observed across populations and cultivation methods generated stark contrasts in bivalve biomass within each intertidal site type. Collectively, these findings identify the mechanisms (*e.g.* complexity, sediment) by which bivalve populations of the Northeast Pacific have been continually enhanced and managed over the past 3,500 years, providing abundant and stable sustenance for coastal peoples. The detection of ecological responses within bivalve communities across several metrics demonstrates that these mechanisms elicit broad ecosystem alterations. Most notably, the connection between biological diversity and productivity, as demonstrated by inferred biomass, results from elevated diversity through increased ecological reliance and functional redundancies. (Worm et al. 2006, Duffy et al. 2016). We propose that this previously unidentified relationship between diversity-biomass is fundamental to the maintenance of nearshore bivalve communities and that an ecosystem wide approach to the conservation and management of these ecosystems is required, informed by insights from Indigenous knowledge and Western science.

We first establish the validity of several bivalve survey methodologies, providing insight into the ecological implications of comparing diversity, extrapolating taxonomic abundances, and conflating acceptable sample coverage and rarefaction while adequately capturing biological communities. Our comparison underscored the advantage of considering method-specific detection capabilities, a concept that has implications well beyond the study of intertidal ecosystems. Extrapolating abundances to estimate densities within a standard volume was acceptable across two of the sample methods. However, non-linear species-area relationships limit the legitimacy of this practice, a concern that is exacerbated when comparing species diversity across sampling methods (Neigel 2003). Consequently, sample volume, habitat heterogeneity, and survey area emerge as critical factors to consider when designing a sampling protocol or comparing different surveys. However, the implications of method-specific species detections for the rarefaction and extrapolation of Hill numbers suggest that evaluation of a sampling method should include the intended statistical analysis.

An unintentional consequence of our comparison is the observation that the rarefaction curves of the three methods plateaued, illustrating that the samples exhibited sufficient coverage. This finding highlights the critical distinction between adequately capturing an ecological community and reaching the detection capabilities of a technique. Mathematically, the primary focus of rarefaction curves is the advantages that they provide for comparing species richness based on samples of equal completeness instead of equal size, facilitating meaningful standardization and comparisons of datasets (Gotelli and Colwell 2001, Chao and Jost 2012, Chao et al. 2014b). In application, however, ecologists commonly use rarefaction and coverage to infer the extent to which a community has been detected (Hsieh et al. 2016, Cox et al. 2017, Kays et al. 2020). Although understandable, this approach is a fallacy as adequate coverage or a plateauing rarefaction curve indicates the detection capabilities of the method have been reached. If the sampling protocol is modified, even when sampling the same community, species detection will be altered as well. In the present study, the employed sampling methods had the highest detection capabilities. Subsequent analyses also identified a lack of statistical difference between quadrats within the sites, indicating consistent communities, relatively homogenous local conditions, or accurately detected variability. Collectively, this suggests that the employed method reached its detection limit and was suitable for the study system.

Most bivalve species, even those that are not the primary focus of cultivation, showed increased in abundance within shellfish farms and clam gardens, with focal species increasing by several orders of magnitude. The emphasis on multi-trophic taxa imbedded within the construction, stewardship, and governance of clam gardens initiates and sustains these responses (Lepofsky and Caldwell 2013, Deur et al. 2015, Turner 2020). This broader community focus likely contributes to the observed evenness of clam garden communities. Decreasing beach slope, adjusting flow conditions, and increasing sedimentation rates along a spectrum of beach types transforms nearshore ecosystems, prompting a desired and predictable community response (Groesbeck et al. 2014, Neudorf et al. 2017, Smith et al. 2019). Ecological responses to shellfish farming are well documented (Crawford et al. 2003, Dumbauld et al. 2006, Callier et al. 2018). However, the majority of these examinations' hypotheses assess ecosystem degradation, a potential byproduct of the contentious and ecologically destructive practices of distantly related finfish aquaculture (Froehlich et al. 2017b, Barrett et al. 2018). Previous examinations frequently observed limited evidence for environmental degradation (Dumbauld et al. 2006, Munroe and McKinley 2007, Maslo et al. 2020), or interpreted changing community dynamics, especially benthic predators capitalizing on increased clam densities, as a negative impact (Whiteley and Bendell-Young 2007, Bendell 2014).

Shellfish farming is not without ecological consequences, especially the intended and accidental introduction of exotic taxa (Turbelin et al. 2017, Barrett et al. 2018), which may contribute to the differential perceptions of ecological responses between shellfish farms and clam gardens. Alternatively, Indigenous First Peoples view themselves, their actions, and stewardship as an integral component of the ecosystem, contrasting the Western science opinion that humanity exists external to the natural environment and that management practices should be based on avoidance and discourage interactions (Turner et al. 2000, Lertzman 2009, Artelle et al. 2019, Turner 2020, Reid et al. 2021). The former view is becoming increasingly important given the consequences of mismanaging interactions between people, predators, and shared prey (Darimont et al. 2009a, 2015). For example, recovering sea otters (*Enhydra lutris*) in the Northeast Pacific may increase ecosystem biomass yields by 37%, amounting to 54.6-million-dollars' worth of ecosystem services, while concurrently inducing a 7.3-million-dollar loss to invertebrate fisheries (Gregr et al. 2020). Coastal First Peoples have previously addressed this concern when managing clam populations to ensure stable clam harvests by increasing clam productivity and limiting otter access through elevating and excluding sea otters from harvesting areas(Foster 2021).

The ecological mechanisms facilitating biomass increases within clam gardens and shellfish farms are well established. Shellfish farms are situated on optimal clam habitat or habitat that is enhanced (*e.g.* through shell or gravel addition), artificially increases clam densities and excludes predators to inflate biomass (Munroe et al. 2015, van der Schatte Olivier et al. 2018, Naylor et al. 2021). Reciprocal transplant experiments between clam gardens and non-walled beaches determined that juvenile *L. staminea* in clam gardens grow 1.7 times faster with increased survivorship and *S. gigantea* densities increased by 2.5-fold, yielding a 2-fold increase in biomass (Groesbeck et al. 2014, Jackley et al. 2016). These investigations examine how a reduction in beach slope and thus an increase in the optimal tidal area within clam gardens influence clam growth and survival. They do so by using tidal stations *in lieu* of tidal height to account for changes in beach slopes across walled and non-walled beaches. Contributing to this knowledge, we examined clam size and abundance while controlling for tidal height, thus isolating the ecological responses to wall construction and other intertidal zone-specific factors, from processes associated with coastal zonation. We observed heterogeneous responses across populations, with *L. staminea* and *S. gigantea* within clam gardens displaying prominent bimodal distributions. Such bimodality implies distinct cohorts, a plausibly attributed to the addition of optimal juvenile habitat, and perhaps retention of spawning events more locally due to altered flow conditions (Commito and Rusignuolo 2000, Cardinale et al. 2002, Cheng et al. 2021). In contrast, shellfish farms contained more mid- to large-size *L. staminea* and *R. philippinarum*, likely due to predator exclusion mechanisms safeguarding taxa until harvested and farms seeding specific cohorts (Munroe et al. 2015).

Elevated bivalve biomass within cultivated shorelines is one of the most vital ecosystem services that clam gardens and shellfish farms provide (Groesbeck et al. 2014, van der Schatte Olivier et al. 2018). Here, we observed a 406.8- and 41.2-gram per 0.25m^2 increase of *S. gigantea* and *L. staminea* within clam gardens relative to reference sites, respectively. Considering that clam garden construction within Kanish Bay, Northern Quadra Island, created 112,979 m^2 of beach terraces (Lepofsky et al. 2021), we can infer that clam gardens have potentially increased *S. gigantea* and *L. staminea* biomass within the region by 183,785 and 18,595 kg, respectively. Similarly, *R. philippinarum* biomass increased 278.5 g per 0.25m^2 in shellfish farms relative to reference sites. Baynes Sound currently has 129 shellfish farms covering 1,157 ha or 11,570,000 km^2 (D’Anna and Murray 2015), with R. *philippinarum* being the primary infaunal bivalve. Therefore, shellfish cultivation in the region has potentially increased R. *philippinarum* biomass by 12,887,833 kg. These substantial increases in biomass provide access to stable and abundant intertidal resources, supporting coastal ecosystems and communities (Lepofsky and Caldwell 2013, Groesbeck et al. 2014, Toniello et al. 2019, Fitzpatrick 2020). Cumulative biomass within clam garden and shellfish farms were estimated to be 4.67 kg per m^3 and 3.55 kg per m^3, respectively. These estimates refute Munroe et al. (2015) conclusions that clam gardens are unable to meet shellfish farming production levels.

Bivalve community responses and increased biomass are linked ecologically to the structural complexity that shellfish cultivation contributes to nearshore ecosystems. Clam gardens enhance fine- and broad-scale complexity, while shellfish farms primarily increase fine-scale complexity. Different levels of complexity result from dissimilarities in the construction processes. Clam gardens are built on a more dynamic range of habitats, including soft sediment beaches with established clam populations, flat bedrock outcrops, or steep bedrock (Smith et al. 2019). The rock wall increases sedimentation rates fourfold, altering the beach slope at tidal heights optimal for clam production, thus creating or expanding available clam habitat regardless of the coastal features (Neudorf et al. 2017, Smith et al. 2019). In contrast, the construction of shellfish farms occurs on productive clam beaches, involving the input of predator exclusion nets, bivalve seed, cages, and altering sediments (British Columbia et al. 2002, Silver 2014). In both instances, added complexity likely alters flow regimes, intertidal sediments, and nutrients (Commito and Rusignuolo 2000, Cardinale et al. 2002, Cheng et al. 2021), promoting bivalve community proliferation within cultivation habitats. The MRT analyses support the notion that differences in complexity may alter the influence of flow regime on intertidal sediments. Our analysis indicates fine-grain sediments act as a mechanism structuring bivalve communities within clam gardens, while large-grain sediments occupy a similar ecological role within shellfish farms. Additionally, the lack of an MTR node differentiating between shellfish farms and farm reference sites sediments, supports previous findings that the influence of the sediment, organic carbon content, or other nutrients on shellfish cultivation does not outweigh the influence of tidal exchanges (Crawford et al. 2003, Dumbauld et al. 2006, Munroe and McKinley 2007).

The relationship between community diversity and biomass is a crucial ecological topic, with empirical studies only recently observing positive diversity-biomass associations within aquatic ecosystems (Fowler et al. 2012, Service et al. 2019). Understanding the ecological controls on shellfish biomass is central to maintaining sustainable extraction and promoting nutrients ecosystem management. We report the first observation of a positive relationship between bivalve diversity and biomass that persists within multiple cultivation methods and unmodified intertidal sites. Our RF model explained half of the variability in bivalve biomass, with bivalve richness identified as the most important variable. The contribution of habitat complexity to this relationship were more predominant within clam gardens, while shellfish farms were governed more by site-specific characteristics and intertidal zonation. Identification of this relationship provides several mechanisms for conserving shellfish populations and humanity's access to this vital protein source. The management of shellfish communities, including taxa that are not harvested, will promote higher productivity of bivalve biomass. An emerging theme within fisheries management, this approach yields higher ecosystem resilience and functional redundancy, improving the stability of populations and the services they provide in the face of changing climate conditions or local stressors (Worm et al. 2006, Duffy et al. 2016). This approach is currently embedded within Indigenous Peoples' stewardship of marine ecosystems; shellfish farming practices, however, would benefit from integrating considerations of the broader community into enhancement methodologies.

Shellfish populations throughout the Northeast Pacific have sustained Indigenous First Peoples for over 13,000 years, facilitating the population of North America, the evolution of complex economies and governance systems, and contributing to humanity's deep connection with marine ecosystems (Lepofsky and Caldwell 2013, Toniello et al. 2019, Becerra-Valdivia and Higham 2020, Turner 2020). Currently, shellfish farming is one of the world's fastest-growing food systems (Holden et al. 2019, FAO 2020). Many coastal Nations hold commercial clam licenses, manage shellfish operations, and all shellfish farming in British Columbia occurs on Coastal First Peoples' unceded territories (Silver 2014, Holden et al. 2019). Shellfish cultivation throughout the Northeast Pacific provides an opportunity to pair Indigenous knowledge and ways of knowing with Western science to foster a framework for sustaining human-ecosystem interactions that allow multiple perspectives and sources of coastal knowledge to unite against ecological challenges (Reid et al. 2021). The global distribution of bivalves, humanity's reliance on intertidal resources, and the Indigenous-led movement to decolonize resource management indicate that a framework for sustainable human-ecosystem interactions would affect a wide variety of socio-ecological landscapes.

3.5 Author Contributions

Kieran Cox: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization; Writing - original draft. **Hailey Davies:** Data curation, Investigation, Methodology, Visualization, Writing - review & editing. **Ben Millard-Martin:** Data curation, Investigation, Methodology, Project administration, Resources, Writing - review & editing. **Margot Hessing-Lewis:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing - review & editing. **Francis Juanes:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing. **Sarah Dudas:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing - review & editing.

Chapter 4: Intertidal Resource Cultivation Over Millennia Structures Contemporary Marine Biodiversity

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4.0 Abstract

Marine ecosystems have been cultivated for millennia, contributing vital resources to humans. Unfortunately, in many instances, cultivation erodes biodiversity. However, emerging research indicates that certain resource management practices may promote favourable ecological conditions. Here, we use the co-occurrence of 24 First Nations clam gardens, shellfish aquaculture farms, and unmodified clam beaches to test the hypothesis that managing intertidal bivalves' bolsters complexity, which fosters more diversity in the communities that are not the primary target of cultivation. To so do, we surveyed each site's epifaunal (surface) communities and abiotic conditions, including generating 3D habitat models, and used a combination of non-parametric multivariate statistics, multivariate regression trees, and random forests. We show that clam gardens and shellfish farms restructure epifaunal communities at several ecological and spatial scales, with increasing biological diversity correlated with each cultivation practice's

habitat alterations. We observed distinct biological communities within clam gardens and shellfish farms that are a function of habitat complexity, at 25-50 and 50-100 cm resolutions, and changes in the amount of gravel, oyster shells, and seaweeds (*i.e. Mastocarpus, Ulva, Gracilaria)*. The unique characteristics of each cultivation method suggest that observed ecological responses can be maintained with continuous harvesting and management, augmented through further intervention, and will persist even if reductions in management intensity occur. Given global declines in marine biodiversity and the consequences of diminishing marine resources, our findings highlight management and conservation strategies that contribute to achieving a sustainable balance within human-ecosystem interactions.

4.1 Introduction

Humans have used aquatic and terrestrial ecosystems for millennia (Lepofsky and Lertzman 2008, Lepofsky and Caldwell 2013, 2013, Becerra-Valdivia and Higham 2020). Today, anthropogenic activity influences the vast majority of marine and terrestrial ecosystems on earth (Vitousek et al. 1997, Halpern et al. 2008). Elevated biological resource (*e.g.* protein, timber) availability across coastal regions relative to offshore ecosystems has concentrated human influences along coastlines (Small and Nicholls 2003). Recently, the cultivation of marine ecosystems has become a considerable component of coastal anthropogenic activities (Diana 2009, Gentry et al. 2017). For example, more seafood was cultivated in 2020 than was extracted from wild populations (FAO 2020), signaling the emergence of a novel state in the history of human-marine ecosystem interactions. This expansion in cultivation efforts has resulted in remarkable accomplishments for humanity, including advancements in infrastructure, economics, and technology, but has also compromised many natural ecosystems (Krkosek et al.

2007, Diana 2009, Barrett et al. 2018, van der Schatte Olivier et al. 2018). Balancing food production with coastal resource management represents an emerging challenge facing 21st-century global conservation efforts.

Despite numerous human-ecosystem interactions leading to species loss, disrupted community dynamics, and environmental degradation, emerging research indicates that several anthropogenic activities create ecological states that foster robust biological communities (Boivin et al. 2016, Trant et al. 2016, Sullivan et al. 2017). For example, the technologies and management strategies Indigenous Peoples of the northeastern Pacific established to increase food production and ensure long-term sustenance have influenced ecosystems for millennia (Lepofsky and Lertzman 2008, Lepofsky and Caldwell 2013, Turner 2020). Along the central coast of British Columbia, Indigenous Peoples use a combination of intentional successive landscape burnings and the accumulation of marine-derived nutrients within terrestrial ecosystems to enhance forest productivity, increase plant species density, and facilitate forest succession (Trant et al. 2016, Hoffman et al. 2017, Cox et al. 2020). Similarly, shellfish cultivation methods implemented over millennia improved intertidal ecosystems' productivity, a condition that persists despite colonizers' efforts to halt bivalve management by Indigenous Peoples (Groesbeck et al. 2014, Jackley et al. 2016). This spatial-temporal model of how humans alter their environment suggests that these activities' influence on ecological communities can persist for thousands of years, even if the activity's frequency or intensity varies (Groesbeck et al. 2014, Jackley et al. 2016, Trant et al. 2016, Cox et al. 2019).

The northeast Pacific nearshore ecosystems provide coastal populations with an abundance of marine resources, supporting the development of complex governance systems that steward these ecosystems (Lepofsky and Lertzman 2008, Lepofsky and Caldwell 2013, Deur et al. 2015, Turner 2020). The harvesting, management and enhancement of bivalve populations are central components of these systems (Lepofsky and Caldwell 2013, Deur et al. 2015, Lepofsky et al. 2015, Holden et al. 2019, Toniello et al. 2019). Beginning over 3,500 years ago, Indigenous Peoples created and enhanced clam habitat by building "clam gardens"—mid to low intertidal rock walls and associated soft-sediment terraces (Deur et al. 2015, Lepofsky et al. 2015, Toniello et al. 2019). Clam gardens have been observed from Alaska to British Columbia (Harper et al. 1995, Moss and Wellman 2017). Garden walls increase sedimentation rates in the intertidal up to fourfold (Neudorf et al. 2017). The soft-sediment terrace between the clam garden wall and the shoreline is maintained using a suite of tending practices, including adding gravel, shell hash and whole shells to encourage bivalve larval settlement (Groesbeck et al. 2014, Deur et al. 2015, H-GINPR 2016, Smith et al. 2019). This process increases clam abundance and productivity, providing predictable and stable shellfish populations adjacent to coastal communities (Groesbeck et al. 2014, Jackley et al. 2016). Despite the extensive history of clam garden use, their existence and distributions are relatively new concepts to western science. Conversely, contemporary commercial shellfish farming in the northeast Pacific began in the mid-1800s with a harvesting of Olympia oysters (*Ostrea lurida*). Overexploitation and habitat destruction collapsed the fishery by 1960 (White et al. 2009). The Pacific oyster (*Crassostrea gigas*) was introduced and cultivated by 1925 (Ruesink et al. 2005, White et al. 2009). Introduced accidentally with *C. gigas*, the Manila clam (*Ruditapes philippinarum*), was integrated into the growing shellfish market in the 1980s (Silver 2014). Clam gardens and shellfish farms' heterogeneous distribution along the coast provide an opportunity to examine the spatial and temporal importance of bivalve management and quantify the ecological implications of human-ecosystem interactions that have persisted for millennia.

Here, we test the hypothesis that managing intertidal bivalves’ bolsters habitat complexity and alters substrate composition, fostering increased diversity in non-target communities (*i.e.* taxa that are not the primary cultivation target). We quantified the diversity and density of the epifaunal (surface) communities within 24 intertidal sites (6 clam gardens, 6 shellfish farms, and 12 unmodified beaches) and evaluated the communities' association with the habitat's physical complexity and substrate composition (Fig. 16). Our analysis examines non-target communities as clam gardens and shellfish farms' influence on cultivated bivalves is well established (Tenore et al. 1973, Silver 2014, Groesbeck et al. 2014, Jackley et al. 2016). To test our hypothesis, we determine (1) the physical complexity of each intertidal site using three-dimensional habitat models, (2) if and how diversity and community composition differ among site types, (3) the extent to which alterations in habitat complexity and substrate composition influence biological communities within clam gardens and shellfish farms.

This novel study analyzes how multiple intertidal resource management practices, engineered and implemented over millennia, shape contemporary ecosystems. We hope to contribute to the global recognition that Indigenous knowledge and ways of knowing must be paired with, not incorporated into, Western science (Reid et al. 2021). Furthermore, the global distribution of bivalves and humanity's extensive history of relying on intertidal resources suggest that the shellfish-ecosystem interactions examined here will affect a wide variety of coastal landscapes.

4.2 Methods

4.2.1 Survey Locations

This study was conducted within three regions along British Columbia's south and central coast; the Hakai Lúxvbálís Conservancy "Calvert Island" (51.65606° N, -128.13427° W), Quadra Island (50.21033° N, -125.26871° W) and Baynes Sound (49.52371° N, -124.82457° W) (Fig.16). Twenty-four intertidal sites were surveyed in 2015, 2016, and 2017. The 24 intertidal sites were distributed among the three regions with three clam gardens and three garden reference sites within the Hakai Lúxvbálís Conservancy; three clam gardens, three garden reference, three shellfish farms, and three farm reference sites surrounding Quadra Island; and three shellfish farms and three farm reference sites within Baynes Sound (Fig. 16). The primary comparisons of interest were between shellfish farms and farm reference sites, clam gardens and garden reference sites; however, the ecological responses unique to shellfish farms or clam gardens were also considered. Surveys of the biological communities and substrate composition occurred in 2015 and 2016. Surveys of the site's habitat complexity occurred in 2017. Annual monitoring of several sites indicated habitat complexity is relatively consistent year to year. Surveys occurred between May and July, with the comparisons within each region surveyed over a tidal window to minimize seasonal effects (*e.g.* Baynes Sound shellfish farms and reference sites). Chapter 3 and 4 surveys occurred concurrently, and thus the habitat complexity and substrate composition data are consistent across chapters.

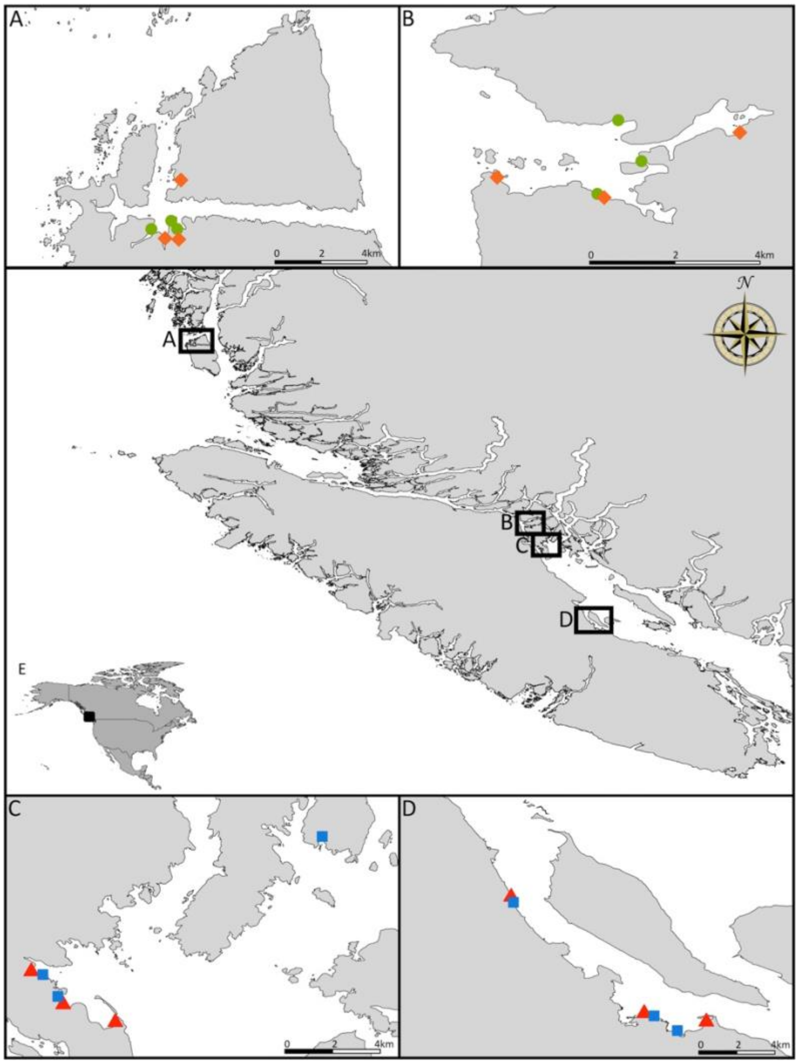

Figure 16: Study sites along British Columbia's central and south coasts, Canada. Clam gardens (green circles), clam garden reference beaches (orange triangles), shellfish farms (blue squares), and shellfish farm reference beaches (red triangles). (A) Calvert Island and Hecate Island (B) northern Quadra Island (C) Southern Quadra Island (D) Baynes Sound (E) British Columbia coastline within the northeast Pacific. Site-specific locations are not provided as not to disclose culturally modified locations.

4.2.2 Field Surveys

Surveys were conducted in a similar manner to (Cox et al. 2017). In 2015, site assessments involved running 40-m baselines along the 3.0, 2.2, 1.5 and 0.8 m tidelines, and a perpendicular baseline from the 3.0 to the 0.8 m tideline through the start of each parallel baseline (Fig. C1). These baselines established the relative high (3.0–2.2 m), mid (2.2–1.5 m), and low (1.5–0.8 m) tidal zones. In the event that the specific tidelines could not be accessed, baselines were laid as close to these tidal heights as possible. Within each tidal zone, lines were extended at predetermined distances along the perpendicular and parallel baselines. Distances along the perpendicular baselines were chosen *a priori* using a random number generator, while parallel distances increased in increments of ten meters to ensure the entire horizontal distance was covered. Assessments occurred at the intersection of these extended lines, with each quantifying the biological community and substrate composition (Fig. C1). Five assessments within each zone were attempted, but only three assessments occurred in some cases due to limited access to each intertidal zone. In 2016, the same methodology was followed; however, based on the results of the previous year's surveys, only the mid-zone was surveyed.

4.2.3 Biodiversity Surveys

Biodiversity surveys evaluated the epifaunal (surface) communities present at each of the assessment locations. Assessments used a 0.5 × 0.5 m quadrat strung vertically and horizontally every 5 cm to create 100 equal squares. Ten randomly selected 5 × 5 cm squares were chosen from the 100 squares formed by the strung quadrat (Fig. C2). All organisms within each square were counted and identified. If multiple layers (*i.e.* predator-exclusion nets, oysters) were present, the top and bottom layers were assessed separately and combined, representing the total epifaunal diversity present in the quadrat. The occurrence of multiple layers was low (11 of 435 surveys). Sixty taxa (*e.g.* species, genera) were observed across the study sites (Table C1). Abundances were multiplied by ten to estimate total abundance within the quadrat. Cox et al. (Cox et al. 2017) determined that despite extrapolation, this subsampling method accurately detects species diversity, reduces assessment effort and results in reliable species abundance estimates. Oysters were the only species not subsampled as their densities are easily assessed and respond poorly to extrapolation; thus, all oysters in each quadrat were counted. The resulting biodiversity data were denoted as species diversity and abundances within the 0.25m^2 area.

4.2.4 Substrate Composition

Percent cover of the substrate types observed within the 0.5 x 0.5 m quadrats was determined to evaluate ecological covariates of the associated intertidal substrate. Each quadrat was photographed before the biodiversity survey using a Nikon AW120 camera held 1 m above the quadrat (resolution: 2,832 × 2,832 pixels). Substrate photos were analyzed using ImageJ to derive surface cover metrics (Schneider et al. 2012). Percent cover was determined by dividing each substrate's area by the total quadrat area. Algal taxa were primarily genera, with *Gracilaria spp*., *Fucus spp*., *Mastocarpus spp*., Phaeophyceae (Brown Algae), *Sargassum muticum*, *Ulva spp*., and *Zostera spp*. (eelgrasses) being observed. Habitat-forming calcareous shells and skeletons (tests) were denoted as clam shells, oyster shells, and dead *Dendraster* (sand dollars). The several higher order algae classifications were required as several taxa could not be differentiated. Sediments were classified using the Wentworth scale to identify each quadrant's boulder, cobble, gravel sand, and mud/silt composition. As a precaution, algal identification, sediment classification and associated percent covers were recorded directly in the field, allowing any discrepancies during the substrate composition analysis to be resolved a priori.

4.2.5 Habitat Complexity

Survey Region

The structural characteristics of the 24 clam gardens, shellfish farms, and reference beaches were quantified using structure-from-motion (SfM) photogrammetry in 2017. This method generates high-resolution georeferenced 3D reconstructions of the physical environments using 2D images (Westoby et al. 2012). A 10 × 10 m assessment area was established at each site, with the top corners at the 2.2 m tideline (Fig S9). The spatial location of ground control points (GCPs) placed at the corners and midpoints of the area were recorded using GPS coordinates (Fig S9).

Image acquisition

Image acquisition used a Canon SL1 digital SLR camera with a 10–18 mm lens. The camera was set to a focal length of 18 mm, a shutter speed above 1/100, an aperture of f/8-11 and ISO as low as environmental conditions would allow. The 100 m^2 survey areas were photographed until the entire area had been adequately covered (Westoby et al. 2012; Fig. C3).

3D habitat model generation

Three-dimensional reconstructions of the 24 sites were generated using Agisoft Metashape Standard Edition (v1.7.4). Model generation followed the steps outlined in Agisoft Metashape, further clarified in Young et al. (2017) and Bayley and Mogg (2020). The four key stages were: aligning photos, dense point cloud construction, mesh construction, and building texture (Fig. C4A). Stage specifics are outlined within the supplemental material (Supplemental Text). Rendered 3D habitat models were exported as wavefront files for further analysis.

Quantification of spatial properties

The habitat models were analyzed using Rhinoceros 3D (v7), a commercial 3D computer graphics program developed for surface modelling. The structural metrics explored were rugosity (R) and fractal dimension (D). The habitat models were scaled using Rhinoceros ‘scale’ function and the four 0.42 m scale bars within each model.

Linear R is measured using an extendible chain method to measure the topographic distance covered by a theoretical straight-line distance. Consequently, lower linear R values denote more complex surfaces. To avoid confusion, linear R is considered on an inverted scale (*i.e.* 0-1), to allow increased in linear R to reflect increases in complexity. Measurements can be taken at multiple locations on the same model. Triplicate nine-meter linear R measurements were taken in both directions (6 total) using a virtual chain with a 2 cm link length (Fig. C4B). Measurements were taken using a custom Python script adapted from Young et al. (Young et al. 2017), allowing consistent application of the chains across models. Each site's mean linear R was determined by averaging the six measurements.

Fractal dimension (D) measure how surface area changes with resolution by quantifying the slope of a model’s resolution relative to the surface area on a logarithmic scale (*i.e.* how complexity changes with scale). Customizable dimensions allow for the consideration of different sizes. These can be selected based on particular species dimensions, unique habitat characteristics, or a measure of complexity given multiple size categories. Measurements of D are between 2 and 3, with higher values signifying increased surface heterogeneity. Fractal dimension was measured at four spatial resolutions, 2.5-5, 5-25, 25-50, and 50-100 cm; effectively, this measures the complexity within these size ranges. Five D measurements at the four spatial resolutions were taken for each model, one at each corner and in the middle (Fig.

C4C). These measurements were averaged to determine mean D within each of the four spatial resolutions.

4.2.6 Statistical Analyses

All data analyses were conducted in RStudio version 3.6.1 (R Core Team 2019). Data visualizations and analyses utilized the ‘ggplot2’, ‘vegan’, ‘mvpart’ and ‘randomForestSRC’ packages (De’ath 2014, Wickham 2016, Oksanen et al. 2019, R Core Team 2019, Ishwaran et al. 2021).

Community Composition

Epifaunal communities were characterized using three indices to examine the variability between the taxonomic diversity and abundances present at clam gardens, shellfish farms, and reference sites. The first index used was richness, which denotes the number of unique taxa present. The second index, Shannon diversity, is the metric most commonly used to explore the relationship between richness and evenness, placing less weight on dominant taxa. The third index, inverse Simpson, considers both richness and evenness while weighting for dominant taxa. Collectively, these indices are Hill number and can be represented by q-value, which denotes the sensitivity of the measurement to the taxa’s relative abundances where $q = 0$ is richness, $q = 1$ is Shannon diversity, and $q = 2$ is inverse Simpson (Chao et al. 2014a, Cox et al. 2017). In the present study, a value for each of the three indices as a function of order q, in addition to all other q orders until a maximum of five, was generated for each site type and regional comparison (*e.g.* Quadra Island clam gardens and reference sites). The values were plotted as diversity profile curves, illustrating diversity as a function of order q. The resulting curve slope reflects community evenness, with steeper curves denoting uneven abundances. Taxa unique to each site type, co-occurring between comparisons, and those present among all habitats, were examined using a Venn diagram (Table C2), effectively illustrating the allocation of landscape species richness (gamma diversity) into the various ecological compartments. These analyses considered only the 2015 and 2016 biodiversity surveys conducted within the mid-intertidal zone to ensure a balanced sampling effort (N = 235 quadrats).

Community composition was characterized using non-parametric multivariate analyses to examine the biological communities present at each site type (Mcardle and Anderson 2001, Anderson et al. 2008). Analyses were conducted using the 'vegan' package (Oksanen et al. 2019), and again considered only biodiversity surveys conducted within the mid intertidal zone to ensure a balanced sampling effort. Quadrat values for each year were averaged according to the site's mid-intertidal zone and then the site-year values were averaged according to the site types (*e.g.* clam garden, garden reference). A resemblance matrix of epifaunal densities was calculated using Bray-Curtis coefficients and a dummy variable of 1 to correct cells where no biota were observed. The community composition of each site type and regional comparison were visualized using non-metric multidimensional scaling (nMDS) plots. Permutational Multivariate Analysis of Variance (PERMANOVA) conducted on the resemblance matrix determined if community composition differed statistically among the site types and regions. Separate PERMANOVAs examined the site type's community dissimilarities observed within and among each of the three regions. Therefore, five PERMANOVAs were run: Clam Garden, Shellfish Farms, and Reference Sites; Calvert Island Gardens and Reference Sites; Quadra Island Gardens and Reference Sites; Quadra Island Shellfish Farms; Baynes Sound shellfish Farms. Site type, year, and the interaction between site type and year were included as fixed factors in each PERMANOVA, and an α of 0.05 was used to detect significance.

Percent dissimilarity between the site types and regions was calculated using a Similarity Percentages (SIMPER) analysis. SIMPER elucidates the differences in taxa between site types. The average dissimilarity (Diss) between each taxon over the standard deviation (SD) was measured as Diss/SD, determining a taxa's contribution to community dissimilarity. Values greater than 1 represent groups that consistently contributed to the observed differences between site types (Anderson et al. 2008). *Balanus glandula* and Barnacle Spp. were merged during this analysis, due to taxonomic resemblances; the majority of Barnacle Spp. were likely juvenile *B. glandula* that could not be differentiated from juvenile *Chthamalus dalli.*

Substrate-Epifaunal Community Associations

Multivariate regression trees (MRTs) were used to analyze the association between the abundances of epifaunal taxa and substrate composition. Developed by De'ath (2002), MRTs are a machine learning technique that extends univariate regression trees to consider multiple response variables. This extension enables analyses of complex ecological data to explore, describe, and predict relationships between taxa and environmental characteristics. Multivariate regression trees are robust when the relationship between the response and explanatory variables are non-linear, or high-order interactions among explanatory variables are present (De’ath 2002, Segal and Xiao 2011). The MRTs were fitted in R studio using the package ‘mvpart’ (De’ath 2014). The 60 taxa observed during the biodiversity surveys were amalgamated into 24 higher-level taxonomic classifications to improve pattern visualization (*e.g.* family, order; Table C3). Densities were log-transformed, following the addition of a dummy variable of 1.

Multivariate regression trees analyzed taxonomic densities within and among site types. Garden and shellfish reference sites were pooled for this analysis to improve the description of the substrate types that structure the ecological communities within these habitats. Therefore, four separate MRTs were constructed: sites combined, clam gardens, shellfish farms, and reference sites. This approach illuminated the environmental characteristics that predict taxonomic diversity within site types and among intertidal ecosystems. It also allowed the high, mid and low intertidal zone surveys (N = 435 quadrat) to be considered without influencing the validity of comparisons (*e.g.* creating an unbalanced sample comparison).

Each MRT evaluated invertebrate taxonomic density as the response variable, and intertidal zone, percent boulder, cobble, gravel, sand, mud/silt, clam shells, oyster shell, *dead Dendraster*, *Gracilaria spp*., *Fucus spp*., *Mastocarpus spp*., Phaeophyceae (Brown Algae), *Sargassum muticum*, *Ulva spp*., and *Zostera spp* as explanatory variables. The optimal tree size for each MRT was determined following one-hundred-fold cross-validation. The three MRTs considering each site type separately were pruned to the lowest cross-validation error rate. The sites combined MRT was pruned according to the one standard error rule, which states that the most parsimonious model is one with an error rate within one standard error of the best model (De’ath 2002, Segal and Xiao 2011). This multi-method approach to pruning provided a more informative description of the substrate features important within each site type and a more conservative estimate of the substrate features relevant across intertidal sites. The tree's splits were chosen using a sum of squares criteria that minimizes each node's sums of squared distances. The four MTR trees were pruned to 4-7 'leaves' to avoid over fitting. The default tree leaves’ bar plots were replaced with boxplots to provide more detailed information.

The taxa that contributed the most to each split in the sites combined MTR were determined using a discrimination analysis. This analysis identified the taxa that explain the most variance at each node, the directionality (i.e. left vs right split) of their contribution, and the probability that the contributed variance was non-random. Effectively, this identified the taxa most closely associated with the substrate conditions elucidated by the MTRs.

Substrate Variable Importance

Random forests construct a collection of decorrelated trees based on the same principles as classification and regression trees (CART) to improve upon CART's major limitations—predictability, stability, and performance (Breiman 2001, Segal and Xiao 2011). This increase in prediction accuracy is achieved through bootstrapping and split-variable randomization (Breiman 2001, Segal and Xiao 2011). Bootstrapping allows each tree to be grown from a resampled data set, increasing decorrelation between trees relative to other methods (*e.g.* bagging). Split-variable randomization limits each search for a split variable to a random subset. The predictive accuracy of the forest can be quantified using a portion of the data (*i.e.* training) for construction and the remaining data to evaluate the model's performance (*i.e.* testing).

A multivariate random forest (MRF) was constructed using survey data from all habitats, intertidal zones, and the 'randomForestSRC' package to determine which of the habitat variables substrate types identified by the previous MRTs were the most important to epifaunal taxa (Ishwaran et al. 2021). The MRF considered the importance of percent cobble, gravel, clam shells, *Mastocarpus spp*., *Ulva spp*., oyster shell, mud/silt, *Dendraster*, *Gracilaria*, *spp*., for the surveyed 24 taxa (Table C3). Site type, region, site, and intertidal zone were included in this investigation to identify the extent to which features not captured in the substrate survey may be contributing to diversity patterns. The MRF consisted of 6000 trees grown to a maximum node depth of six to avoid overfitting (Fig. C5). The number of candidate variables randomly selected for splitting a node was 4, following the default p/3 recommendation for regression, where p equals the number of variables. The minimum terminal node size was 5, again, following the regression default. The implications of different node sizes, number of trees, node depth, and candidate variables were explored. However, varying these conditions had minimal influence on the outcomes. Variable importance was calculated by randomly permuting the variables' values, running them through the model, and evaluating the change in mean squared error (MSE). As a result, the importance of a variable is proportional to its relative effect on MSE, with higher values having more influence on model accuracy (Breiman 2001). Variable importance was determined for each of the 24 taxa and averaged among taxa.

A subsequent analysis examined MRF’s ability to predict species occurrences. The predictive accuracy of the MRF was determined using 80% of the data to train a model, and the remaining 20% of the data to evaluate the model's predictions. Model construction used identical parameters to the variable importance analysis. This analysis determined the MRF’s capacity to explained each taxa's variance and the training data's error rate.

Habitat Complexity-Epifaunal Communities Association

The complexity metrics were averaged accordingly to each site type to illustrate the structural differences between the habitats. Each site's five D measurements (resolutions 2.5-5, 5-25, 25-50, 50-100 cm) and linear R were averaged before determining each site type's mean D and mean linear R. The D measurements illuminated complexity at fine and broad scales via decreasing resolutions. For example, an elevated D value within the 2.5-5 cm resolution would indicate a high level of fine-scale complexity. Linear R denotes complexity as the topographic distance divided by a 9 m chain, meaning the lower the value, the more complex the surface.

An MRF analysis determined which of the habitat complexity measurements were the most important to epifaunal communities. The analysis used the 2015 and 2016 mid intertidal zone epifaunal survey data to increase the spatial overlap between the rendered models' measurements and the surveys while ensuring a balanced sampling effort. Epifaunal survey values were averaged according to the site's mid-intertidal zone for each year, then the 2015 and 2016 values were averaged for each site. Epifaunal data were log10 transformed following the addition of a plus one dummy variable. The MRF considered site type, region, average R, and D2.5, D5, D25, D50 for the surveyed 24 taxa. The 'site' term was not included in the MRF as the biodiversity and complexity data were considered at the site level. The MRF consisted of 6000 trees grown to a maximum node depth of six to avoid overfitting. The minimum terminal node size was 3, which deviated from the default setting for regression base on the "tune node' functions recommendation. In keeping with previous MRFs, the importance of each variable was calculated by randomly permuting the variables' values, running them through the model, and evaluating the change in mean squared error. Variable importance was determined for each of the 24 taxa and averaged among the taxa.

A subsequent analysis examined the extent to which the MRF could predict species occurrences based on observed habitat complexity. The predictive accuracy of the MRF was determined using 80% of the data to train a model, and the remaining 20% of the data to evaluate the model's predictions. Model construction used identical parameters as the previous variable importance analysis.

4.3 Results

4.3.1 Community Composition

Distinct biological communities were found on clam gardens and shellfish farms relative to their respective reference beaches (Fig. 17). However, the extent to which observed communities differed varied among regions and according to cultivation method. Across all regions, clam gardens had elevated taxonomic richness. Of 60 total observed taxa, clam gardens contained 35 taxa, whereas shellfish farms contained 28 taxa, compared to the 27 and 26 taxa observed within garden and farm reference beaches, respectively (Fig. 17A, Table C1, Table C2). Reduced diversity within garden reference beaches persisted when comparing Shannon diversity and inverse Simpson; both indices were considerably lower within reference sites (Fig. 17A). Comparatively, shellfish farms, clam gardens, and shellfish farm reference beaches exhibited relatively similar Shannon diversity and inverse Simpson values. Cultivated sites' exhibited more even communities, as evident by the slope of the order-q line stabilizing the Shannon diversity and inverse Simpson values (Fig. 17). Elevated taxonomic richness was more pronounced at clam gardens within the Hakai Lúxvbálís Conservancy and Baynes Sound's shellfish farms (Fig. 17B, Fig. 17D). Across the site types, unique taxa were present within the majority of the ecological compartments considered (Fig. 17F, Table C2). Eight taxa were unique to clam gardens, four taxa were unique to shellfish farms, and fifteen taxa were common across all site types (Table C2).

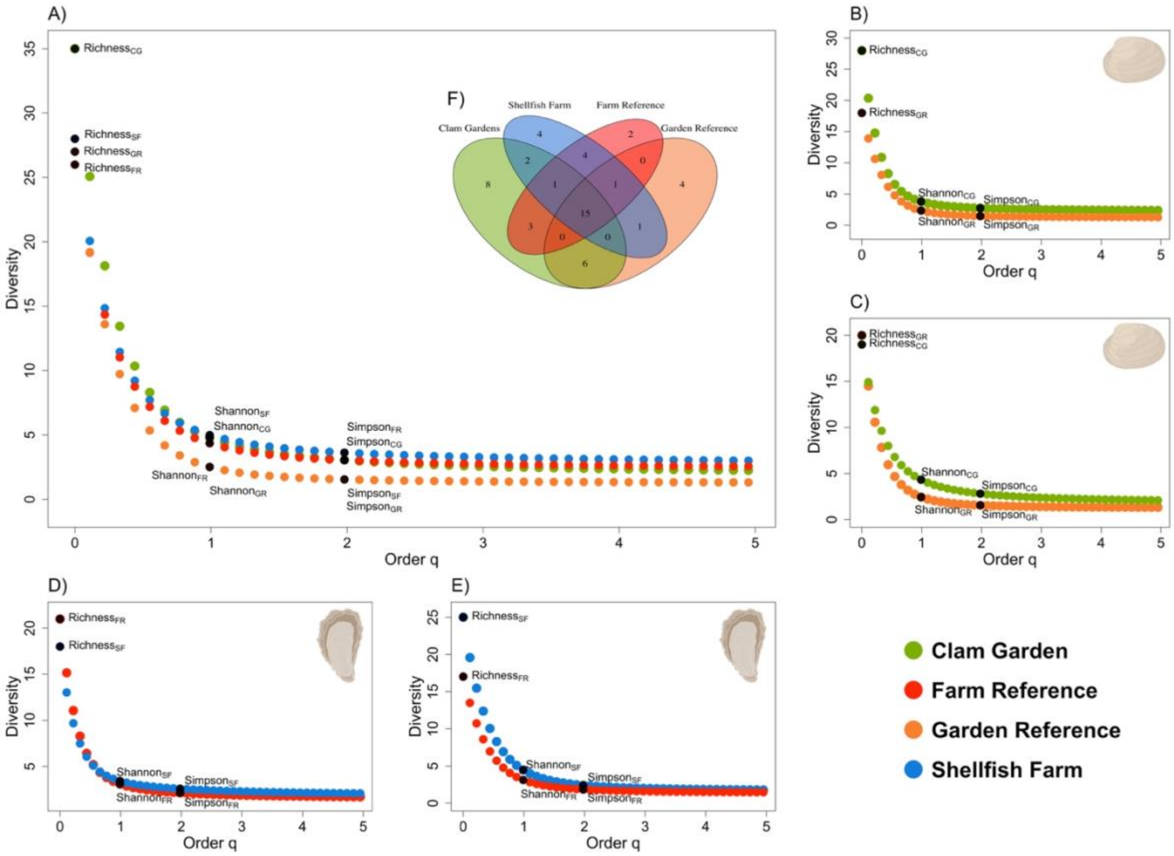

Figure 17: Diversity profile curves illustrating diversity as a function of order q values for clam gardens (green), clam garden reference beaches (orange), shellfish farms (blue), and shellfish farm reference beaches (red). Black dots denote Hill numbers: species richness (q = 0), Shannon diversity (q = 1), Simpson inverse diversity (q = 2). The curve's slope reflects community evenness. A) Diversity pooled across regions. B-E) Diversity within B) Hakai Lúxvbálís Conservancy C) northern Quadra Island D) Southern Quadra Island E) Baynes Sound. F) Venn diagram of taxa unique to each possible comparison. Illustrations depict the primary cultivation target: B-C) Butter clams (*Saxidomus gigantea*), D-E) Pacific Oysters (*Magallana gigas*).

There were significant differences in community composition between site types, years, and sites (Fig. 18, Table C4). These differences were present among and within regions. The non-Metric Multi-Dimensional Scaling (nMDS) plots stress ranged from 0.08 to 0.14, indicating an appropriate model fit between comparisons (Fig. 18). Among regions, the communities observed within clam garden, garden reference sites, shellfish farms and farm reference sites differed (PERMANOVA, F =4.98, p = 0.018, Fig. 18A), as did the communities observed annually and within each site (Table C4). Regionally, comparisons between the clam gardens within the Hakai Lúxvbálís Conservancy, Baynes Sound’s shellfish farms, and respective reference beaches exhibited a high degree of divergence between communities (Clam Garden PERMANOVA, F =3.42, p = 0.029, Shellfish Farm PERMANOVA, F =4.88, p = 0.005, Fig. 18, Table C4). Year and site were different within all regional comparisons, except for the clam gardens within the Hakai Lúxvbálís Conservancy and clam garden reference beaches (Fig. 18; Table C4). Non-metric multidimensional scaling plots of mid-intertidal substrate composition display similar differences in community composition (Fig. C6).

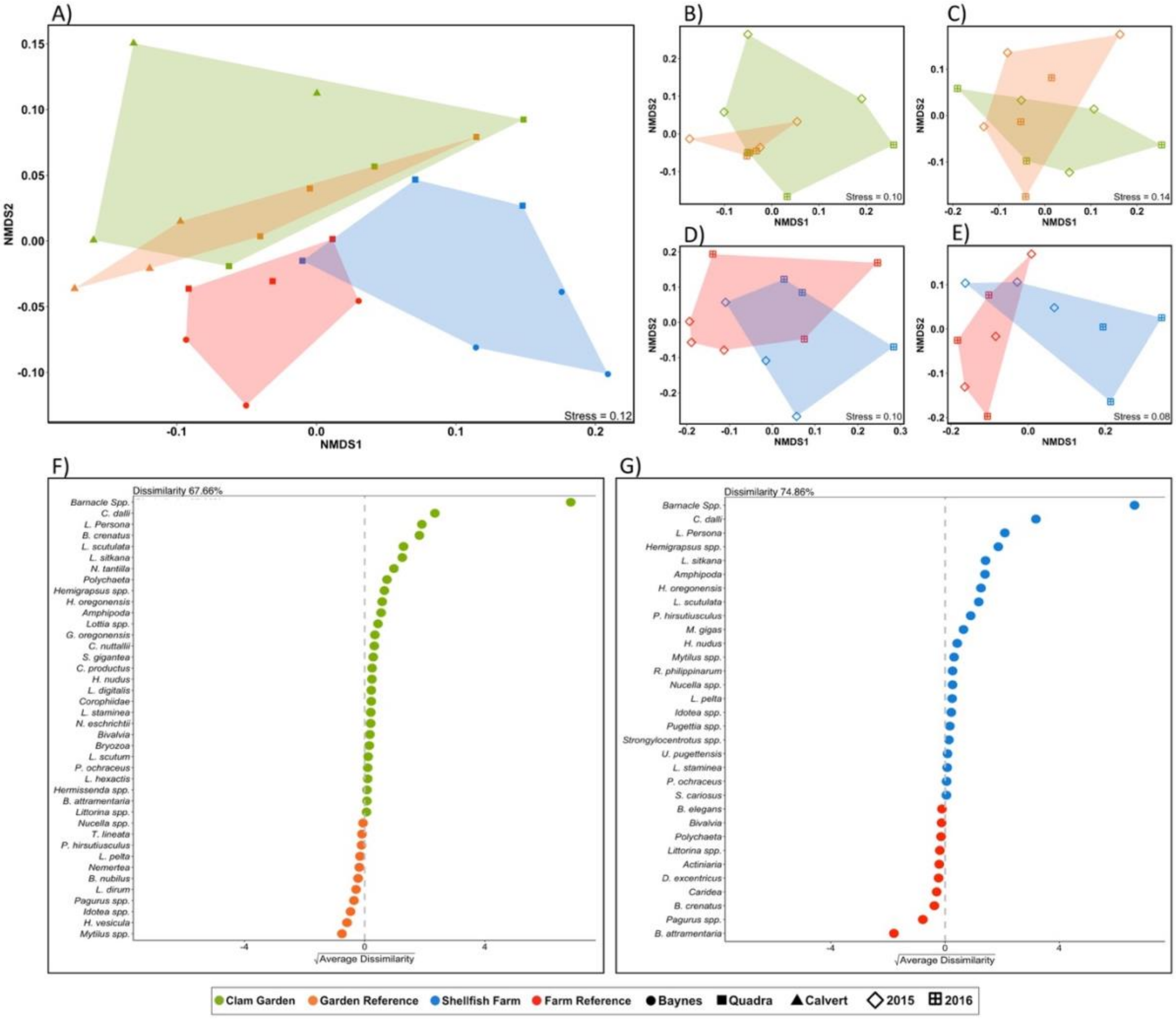

Figure 18: Non-metric multidimensional scaling plots and taxa-specific dissimilarity. Colors denote clam gardens (green), clam garden reference beaches (orange), shellfish farms (blue), and

shellfish farm reference beaches (red). (A) Community composition pooled across regions, with shapes denoting the study regions: Baynes Sound (circles), north and south Quadra island (squares), Hakai Lúxvbálís Conservancy "Calvert Island" (triangle). Community composition within (B) Hakai Lúxvbálís Conservancy (C) northern Quadra Island (D) Southern Quadra Island (E) Baynes Sound, with fill type denoting years. (F-G) Average taxon-specific dissimilarity between cultivated and reference sites. Square root of average dissimilarity plotted to improve visualization. (F) Clam gardens and clam garden reference beaches. (G) Shellfish farms and shellfish farm reference beaches. (F-G) Increases in taxanomic densities in clam gardens denoted in green, gardens reference sites in orange, shellfish farms in blue) or farms reference sites in red.

Taxon-specific dissimilarity varied substantially between site types, with the vast majority of taxa increasing in abundance within cultivated habitats (Fig. C7). The SIMPER analysis determined that clam garden and reference beach communities were 67.66% dissimilar (Fig. 18F). This dissimilarity was driven primarily by increased densities of *Balanus glandula, Chamalus dalli, Lottia persona, Balanus crenatus, Lottia scutulata, and Lottia sitkana* (Fig. 18F). Collectively, these taxa contributed over 90% of the cumulative dissimilarity, with numerous taxa (e.g. *Chamalus dalli, Balanus crenatus, Lottia scutulata*) exhibiting up to a 4-fold increase in abundance (Table C5). Although contributing considerably less to cumulative dissimilarity, clam gardens also displayed reduced abundances in several taxa, including *Mytilus spp.*, *Haminoea vesicula*, and *Idotea spp.* (Fig. 18F, Table C5).

The SIMPER analysis of shellfish farms and reference sites determined that communities were 74.86% dissimilar (Fig. 18G). Comparable to the analysis of clam gardens, this dissimilarity was driven primarily by increased abundances of *Balanus glandula, Chamalus dalli, Lottia persona, and Lottia sitkana* (Fig. 18G). Additionally, *Hemigrapsus spp. and Amphipoda abundances* within shellfish farms increased by 1.5 and 2.4-fold, respectively, accounting for 4.63% and 2.61% of the observed dissimilarity (Table C5). A notable 2-fold increase in *Batillaria attramentaria* abundances was observed within reference sites (Fig. 18G).

This increase accounted for 4.29% of the observed dissimilarity and was the only instance in which an increase in a taxon's density within reference sites contributed more than 1% (Table C5). The comparison of Quadra Island shellfish farms and reference beaches resulted in 77.30% dissimilarity, whereas the Baynes Sound comparison resulted in 72.14% dissimilarity.

4.3.2 Substrate-Epifaunal Community Associations

The MRT analysis considering all sites combined illustrated that diversity and density of the 24 higher-level taxonomic classifications were primarily associated with gravel, oyster shell, cobble, and *Mastocarpus spp.* (Fig. 19A, Table C3). The root node of this tree identified gravel as the substrate type most closely associated with the epifaunal communities. Littorinidae, Lottiidae, and Sessilia were the discrimination taxa informing this split, all of which had higher right split mean values due to their association with gravel percentages above 7.31% (Table C6). In habitats that met this gravel condition, the subsequent decision node was dictated by the amount of cobble present. The co-occurrence of relatively high gravel and cobble form a terminal or 'leaf' node with a community comprised of the discrimination taxa, Decapoda, Mytilidae, and Batillariidae (Fig. 19A). In habitats with relatively low amounts of cobble, the abundance of oyster shells and gravel dictated community composition. Specifically, an abundance of oyster shells promotes a terminal node community comprised of discrimination taxa, Decapoda, Sessilia, Ostreidae, Lottiidae, and Asteriidae. The other terminal nodes were structured by combinations of gravel oyster shellfish, and *Mastocarpus spp.* (Fig. 19A).

Within shellfish farms, *Mastocarpus spp.* structured the root node with gravel, mud and silt forming subsequent branches (Fig. 19C). Higher *Mastocarpus spp.* abundances produced a diverse terminal node with increases in Amphipoda, Batillariidae, Decapoda, Littorinidae, Lottiidae, Mytilidae, and Sessilia. Low amounts of *Mastocarpus spp.* produced a decision node based on mud and silt, which, at lower mud and silt percentages, interacted with gravel to form two terminal nodes—the more taxonomically diverse and dense of these nodes corresponded to increases in the amounts of gravel present.

The root node identified gravel within clam gardens at a relatively high percentage of 60.67 % as the substrate type most influential for community composition (Fig. 19D). Habitats with amounts of gravel above this were structured by intertidal zone and *Ulva*. Under the root node condition of lower gravel, bivalve shell structures communities. If bivalve shells were abundant, gravel and bivalve shells act in combination to structure communities with gravel constrained by the initial root condition. This interaction generates four-terminal nodes exhibiting considerable taxonomic diversity and densities. Of these nodes, the co-occurrence of gravel between 45.29 to 60.67%, and less than 31.19% bivalve shell, produced the most diverse and abundant community, comprised of Amphipoda, Cerithiidae, Decapoda, Lottiidae, Polychaeta, and Venerida.

The MRT analysis of reference beaches illustrated that gravel, *Dendraster*, *Gracilaria*, and intertidal zone, structure these biological communities (Fig. 19E). The root node identified gravel as the most influential substrate type. Low gravel percentages interacted with a *Dendraster* based decision node, with increases in *Dendraster* generating the more diverse terminal node. Substrates within high percentages of gravel were further structured by *Gracilaria*, which, if abundant, interacted with intertidal zone to produce two terminal nodes.

4.3.3 Substrate Variable Importance

The MRF variable importance analysis determined the extent to which each substrate type and spatial factor (*e.g.* region, site) contributed to the resulting epifaunal communities. Average variable importance, a measure of change in the mean squared error, ranged from 0.08 to 17.15% (Fig. 19B), with region, gravel, *Mastocarpus spp.*, site type, *Ulva*, and oyster shell the most important factors averaged across taxa. However, variable importance differed considerably when considering taxa independently (Fig. C8), with several robust taxa-variable associations evident. For example, the importance of the associations between *Mastocarpus spp.*, region, and gravel for Amphilepidida, varied between 77.15%, 68.52%, and 42.46%, respectively (Fig. C8, Table C7).

The variance explained by the MRF model differed considerably among taxa, and as such, so did the model's ability to predict taxonomic variability (Table C7). Explained model variance was the highest in taxa that were consistently observed across the study sites or exhibited a high degree of site type fidelity. For example, the random forest model explained 48.64%, 46.43%, and 43.35% of the variability observed in Batillariidae, Decapoda, and Sessilia abundances. The trained model's predictive capabilities mirror this trend, with the testing dataset's explained variance proportional to the full model's performance (Table C7).

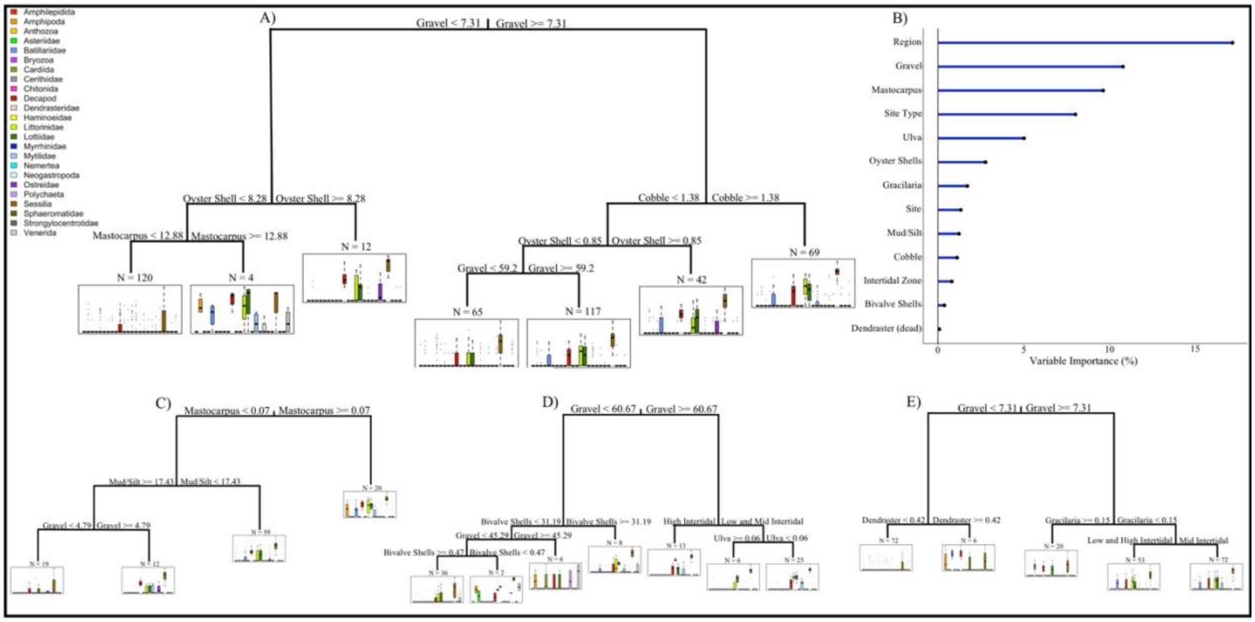

Figure 19: Multivariate regression trees (MRT) and multivariate random forest (MRF) variable importance analyses of the interaction between epifaunal communities and substrate composition. Each MRTs decisions nodes denotes the split value for each respective substrate type. The MRT terminal node box plots illustrate log taxonomic densities. (A) An MRT constructed using all regions and site types data. (B) MRF relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. (C) MRT constructed using shellfish farms (D) MRT constructed using clam gardens (E) MRT constructed using clam garden reference sites and shellfish farm reference sites.

4.3.4 Habitat Complexity-Epifaunal Community Associations

Analyzing three-dimensional reconstructions of the 24 sites quantified multiple aspects of each site's structural complexity, and determined the importance of habitat structure for the resident epifaunal communities (Fig. 20). The reconstructions were more similar within than among site types, although considerable variability was evident within each site type (Fig. C9). Linear rugosity was elevated within clam gardens and shellfish farms relative to the corresponding reference sites, with clam gardens exhibiting the most rugged substrate (Fig. 20E, Fig. C10). Fractal dimension (D) among the site types exhibited a similar trend as linear rugosity; complexity was elevated within clam gardens and shellfish farms (Fig. 20C&F, Fig. C10). These increases in complexity were more prominent within clam gardens than shellfish farms. Unmodified garden and farm reference sites had similar levels of complexity (Fig. 20F). Within each site type, the majority of the site's D complexity was highest at fine-scale resolutions and declined with decreasing resolution (Fig. 20F). Clam gardens deviated from this trend the most as 5-25 and 25-50 cm resolutions exhibited the highest complexity of the four spatial scales considered.

The MRF variable importance analyses determined that of the complexity metrics considered, D 25-50 cm, D 50-100, and D 5-25, had the most notable impact on epifaunal community structure (Fig. 20G). However, variable order differed considerably for each taxon (Fig. C11), illuminating the unique combination of structural metrics that support each group. Similarly, the variability explained by the MRF model and the model's predictive accuracy also varied among taxa (Table C8). Model quality was strongly linked with population abundance, whereby the MRF model explained more variability for taxa consistently observed across the majority of sites, or exhibited a high degree site type fidelity. Generally, high quality models also generated the most accurate predictions. The MRF model was able to explain up to 39% of the variability in taxonomic abundance and was relatively robust in predicting Decapoda, Batillariidae, Venerida and Cerithiidae.

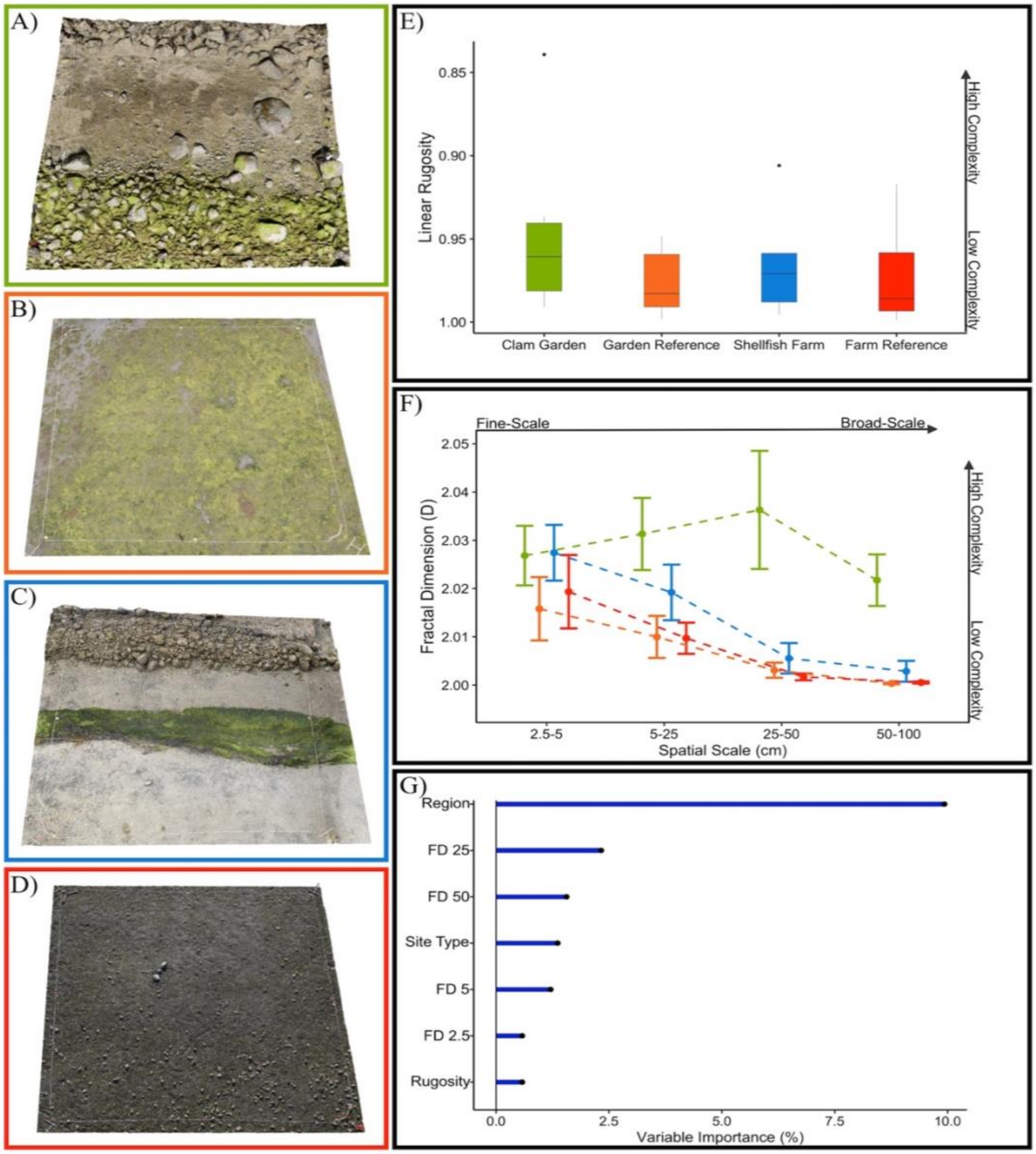

Figure 20: Habitat complexity and multivariate random forest (MRF) variable importance analyses of the association between epifaunal communities and three-dimensional complexity. (A-D) Example three-dimensional reconstructions of the site types. Border colors correspond to E and F plot colors. (A) clam garden, (B) clam garden reference, (C) shellfish farm, (D) shellfish farm reference. (E) Each site type's mean linear rugosity; y-axis is inverted as lower rugosity values denote higher complexity due the ratio used to determine rugosity (*i.e.* topographic distance divided by a straight-line distance). (F) Each site type's fractal dimension value at four spatial resolutions; b. Bar plots are of mean and standard error values. (G) MRF relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted; higher bars equate to greater variable importance. Fractal dimension value and spatial resolutions denoted as FD and respective cell size (*e.g.* FD 25 is the spatial scale 25-50 cm).

4.4 Discussion

Evidence that contemporary ecological communities are a function of human-ecosystem interactions is becoming increasingly vital to global conservation efforts (Sullivan et al. 2017, Artelle et al. 2019, Reid et al. 2021). We add support to the notion that the northeast Pacific's coastal ecosystems are shaped by intertidal resource cultivation practices, engineered and implemented over millennia. Our examination shows that clam gardens and shellfish farms restructure epifaunal communities at several ecological and spatial scales, with community responses linked to each cultivation practice's habitat alterations. This finding supports the supposition that the cultivation of intertidal resources using both traditional and modern-day practices creates distinct nearshore communities, with biodiversity maximized at clam gardens (Groesbeck et al. 2014, Jackley et al. 2016, Trant et al. 2016, Cox et al. 2019).

Shellfish cultivation alters the diversity and composition of intertidal epifaunal communities, with clam gardens and shellfish farms producing distinct communities relative to reference beaches. Several taxa, namely, *Balanus glandula, Chamalus dalli, Lottia persona,* and *Lottia sitkana,* exhibited similar increases in abundance in response to both cultivation methods. Conversely, numerous taxonomic responses were divergent. Convergent as well as divergent responses were ecologically linked to the unique conditions promoted by each cultivation practice. Notably, clam gardens' alteration of tidal heights, which is known to increases bivalve productivity (Groesbeck et al. 2014, Jackley et al. 2016), also conceivably promotes the previously mentioned species' proliferation, while excluding taxa that reside above or below optimal clam habitat (e.g. *Mytilus spp.*) or that co-occur with a habitat that would otherwise occupy the area (*e.g. Haminoea vesicular)*.

Clam gardens further promote unique intertidal communities through the emergence of two substrate compositions: elevated amounts of gravel and either abundant bivalve shells or *Ulva*, which provide substrate, prompt larval settlement, and enhance fine-scale complexity (Groesbeck et al. 2014, Deur et al. 2015, H-GINPR 2016, Neudorf et al. 2017, Smith et al. 2019). Although both conditions support communities, coastal Indigenous Peoples' oral history, communicated by Kwakwaka'wakw Clan Chief Kwaxistalla Wathl'thla Adam Dick in Deur et al. (2015), state that garden tending removes seaweeds from the beach surface and aerates the sediments by altering the density of shell fragments (Marinov et al. 2007, Lepofsky et al. 2015, H-GINPR 2016). The MRT and MRF analyses reinforced this conclusion by illustrating that the combination of 45-60% gravel and less than 31% bivalve shells promotes the most biologically diverse communities observed within clam gardens.

Within shellfish farms, *Mastocarpus spp.*, the seaweed genus that grows on predator-exclusion nets, fostered diverse communities that varied depending on the amount of gravel, mud, and silt present. The role of sediment in this relationship is well- established. Broadly, species diversity and density correlate positively with mud and silt percentages until increases in fine-grain sediments facilitate oxygen depletion, resulting in toxic by-product accumulation, and organic loading cause diversity to decline (Thrush et al. 2003, Hyland et al. 2005). Therefore, under optimal conditions, increased niche space provided by *Mastocarpus spp.* elevates biological diversity beyond the capacity of reference beaches.

Ecological communities generally responded proportionally to cultivation intensity. However, the prevalence of regional stressors may alter the magnitude of diversity responses. For example, taxonomic richness was elevated at clam gardens in the Hakai Lúxvbálís Conservancy, and shellfish farms within Baynes Sound were elevated relative to the reference and cultivated beaches surrounding Quadra Island. Calvert Island's nearshore ecosystems are less influenced by anthropogenic activities, with minimal shoreline modifications, overwater structures, and industrial logging relative to more southern regions (Iacarella et al. 2018, Shackelford et al. 2018). This difference suggests that the comparatively weaker ecological responses within the Quadra Island sites may be due to anthropogenic stressors, specifically industrial logging (Toniello et al. 2019). Conversely, the scale and magnitude of shellfish farming within Baynes Sound surpasses northern counterparts (Bendell 2014, Holden et al. 2019), creating a novel ecosystem that maximizes ecological responses to cultivation.

Elevated taxonomic richness within clam gardens relative to shellfish farms is conceivable due to the increased structural complexity observed at several spatial scales. Clam garden construction can involve considerable foreshore modifications, including the input of large cobble and boulders to establish rock walls that alter beach slope, increase sedimentation rates, and stabilize shorelines (Neudorf et al. 2017, Smith et al. 2019). These cobble and boulders inputs are within the 25-50 and 50-100 cm spatial scales that coincide with the observed increased complexity. The intertidal rock wall and associated soft-sediment terrace are then managed for generations, and adapted to meet changing conditions and community requirements (Lepofsky and Caldwell 2013, Deur et al. 2015, Lepofsky et al. 2015). This process can transform a range of intertidal habitats into clam gardens, including bedrock, otherwise lacking an established clam population (Smith et al. 2019). Alternatively, shellfish farming usually occurs on beaches with existing bivalve populations, involve limited interactions with society, and cultivation began more recently (Diana 2009, Silver 2014, Bendell 2014, Holden et al. 2019).

The application of SfM photogrammetry and machine learning techniques to nearshore systems demonstrates the utility of applying these new tools for examining these dynamic ecosystems. An evident advantage to this approach is the capacity to re-analyze habitat reconstructions as innovative complexity metrics emerge. However, several aspects of the employed techniques require further consideration—notably, MRF's descriptive and predictive capabilities reliance on population abundance and data availability. Multivariate analyses inherently consider taxa individually instead of examining a univariate metric, such as taxonomic richness (De'ath 2002, Segal and Xiao 2011). Therefore, model quality increases if taxa were consistently observed across sites or exhibited a high degree of regional or site type fidelity. Amalgamating the 60 surveyed taxa into 24 higher-level classifications increased taxa distribution among sites, but still, the rarity of several taxonomic classifications limited insights. Moreover, SfM photogrammetry is a time-intensive process that yields site-level complexity for the 24 sites, contrasting the examination of substrate composition that used 435 samples across the sites. Each examination generated novel insights; however, as machine learning techniques become increasingly prevalent in ecology, it is important to consider the number of samples required to maximize the potential of these approaches. Limitations also exist within the examination of habitat reconstructions. For example, the MRF classified linear rugosity as an ineffective predictor of biodiversity, but rugosity within clam gardens paralleled other structural metrics. This disparity is due to contrasting scenarios in which a single prominent feature or multiple minor features could yield similar linear rugosity measurements. This constraint does not impact fractal dimension measurements. However, abandoning linear rugosity is not warranted as its historical importance suggests considering it concurrently with other metrics (*e.g.* fractal dimension, vector dispersion).

Directly comparing ecological communities' responses to clam gardening and shellfish farming should be interpreted with caution because currently, coastal Nations continue to harvest from clam garden beds, but most gardens are not managed with the same intensity as they were during prior millennia (Groesbeck et al. 2014, Augustine and Dearden 2014, Deur et al. 2015, Toniello et al. 2019). This reduction in the frequency and intensity of garden management suggests that the observed ecological responses are an underestimate (Groesbeck et al. 2014, Jackley et al. 2016, Cox et al. 2019), a notion sustained by ongoing garden restoration (Augustine and Dearden 2014, H-GINPR 2016). Conversely, shellfish farming is currently one of the world's fastest-growing food systems, with farms carrying capacities elevated by hatcheries genetically altering taxa, increasing survivorship, and manipulating carbonate chemistry (Holden et al. 2019, FAO 2020). Furthermore, simply comparing management practices is ineffective, potentially divisive, and would fail to appreciate the complexity surrounding shellfish cultivation within the northeast Pacific (Reid et al. 2021). This is especially true given the large number of commercial clam licenses held by coastal Nations, the robust shellfish operations they manage, and that all shellfish farming in British Columbia occurs on coastal First Peoples' unceded territories (Silver 2014, Holden et al. 2019).

A notable portion of the examinations of aquaculture focus on environmental degradation, mismanaged introduced species, limited stakeholder consultation, and declining ecosystem health (Krkosek et al. 2007, Bendell 2014, Murray and D'Anna 2015, Barrett et al. 2018). Shellfish cultivation, however, is unique relative to finfish aquaculture in that shellfish require fewer nutrient inputs, pose less of an escapement risk, and occupy a lower trophic position (Cassandra 2020). These characteristics may explain, in part, why ecological responses to shellfish cultivation persist despite variability in frequency and intensity of management.

Ecological responses may lessen over time, but limited feed inputs or broodstock maintenance allows niche alterations attributed to construction to be maintained indefinitely. This is a particularly evident situation within clam gardens as the primary cultivation species, *S.gigantea* and *L, staminea*, occupy surrounding habitats, allowing broadcast spawn to continue seed beaches (Groesbeck et al. 2014, Jackley et al. 2016, Cox et al. 2019). Ecological responses to shellfish cultivation may cause less degradation than other aquaculture systems, but environmental impacts still occur. *B. attramentaria*, introduced into the northeast Pacific as early as 1928 alongside *M. gigas* (Gillespie 2007), exhibits a 2-fold increase within reference sites. Proliferation adjacent to the introduction site implies an invasion model in which the vector distributes the invader into a suboptimal habitat. The introduced taxon then flourish once it reaches a more suitable habitat, in this instance, nearby mudflats. Functionally, this implies invasive species management requires surveying beyond introduction sites, and that numerous introduced taxa may be on route to habitats that will support proliferation.

A series of local and global stressors threaten the cultivation of intertidal resources, many of which have become increasingly predominant in recent decades. Warming ocean temperatures, rising sea levels, increasing acidity, and lack of societal engagement in food security threaten shellfish aquaculture (Murray and D’Anna 2015, Holden et al. 2019, Stewart-Sinclair et al. 2020). Humanity's ability to mitigate these ecological challenges will improve significantly if Indigenous knowledge is at the forefront of management plans (Holden et al. 2019, Artelle et al. 2019, Turner 2020, Reid et al. 2021). As clam gardens exemplify sustainability on a timescale of millennia, including adapting to changing climatic conditions and human community requirements, the knowledge necessary to endure pending disasters has been well-established by coastal peoples (Groesbeck et al. 2014, Toniello et al. 2019, Lepofsky et al.

2021). Pairing the cultural, economic, and environmental knowledge developed during 3,500 years of clam garden construction and management with the lessons gained over the last 200 years of shellfish farming poses an opportunity to promote the coexistence of these cultivation practices, enhance local food security, and mitigate pending environmental disasters (Groesbeck et al. 2014, Toniello et al. 2019, Lepofsky et al. 2021). This process is ongoing throughout the northeast Pacific, as evidenced by Nation-led clam digging, Indigenous shellfish farm ownership, and Nation-directed clam garden restoration projects (Silver 2014, H-GINPR 2016, Holden et al. 2019). For example, the Clam Garden Restoration project led by the Hul’q’umi’num and W̱SÁNEĆ Nations, in partnership with Parks Canada, has restored gardens within the Gulf Islands National Park Reserve using traditional practices guided by Elders and knowledge holders (Augustine and Dearden 2014, H-GINPR 2016).

Conclusions

Scientific evidence that the robust and dynamic history of human-ecosystem interactions structures ecological communities is mounting (Trant et al. 2016, Hoffman et al. 2017, Toniello et al. 2019, Cox et al. 2019, 2020). A fact well-known by coastal First Peoples, these interactions are not limited to the ecological communities and cultivation methods described here, as fish weirs, root gardens, landscape terracing, and shellfish cultivation, are spatially and temporally abundant throughout the northeast Pacific (Lepofsky and Lertzman 2008, Lepofsky et al. 2015, Trant et al. 2016, Hoffman et al. 2017, Turner 2020) Here, we contribute to this scientific evidence and reaffirm Indigenous knowledge and ways of knowing. We show that intertidal resource management practices engineered and implemented over millennia structure contemporary biological communities that are not the primary target of cultivation, with biotic responses a function of each cultivation practices' unique method and the subsequent habitat alterations. We propose that the addition of habitat structural complexity and alterations to substrate composition that occur as part of clam garden or shellfish farm construction and maintenance provide the increases in available niche space required to foster distinct and biological diversity communities. Uniquely, ecological responses can be maintained with continual harvesting and management, elevated through further intervention (e.g. introducing broodstock, excluding predators), and may persist even if reductions in management intensity occur. Understanding the robust history of enduring intertidal resource cultivation practices is vital to illuminating the resource management and conservation strategies that contribute to achieving balanced human-ecosystem interactions. Shellfish cultivation exemplifies a framework for addressing diminishing marine resources and declining marine biodiversity, while achieving local and global food security.

4.5 Author contributions

Kieran Cox: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Visualization; Writing - original draft. **Hailey Davies:** Data curation, Investigation, Methodology, Visualization, Writing - review & editing. **Ben Millard-Martin:** Data curation, Investigation, Methodology, Project administration, Resources, Writing - review & editing. **Margot Hessing-Lewis:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing - review & editing. **Francis Juanes:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing - review & editing. **Sarah Dudas:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Visualization, Writing - review & editing.

Chapter 5: Shellfish Subsidies Along the Pacific Coast of North America

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5.0 Abstract

Spatial subsidies are associated with pronounced ecosystem responses, as nutrients cross ecological boundaries and cascade through food webs. While the importance of subsidies is known, the role of shellfish, specifically molluscs, as a marine subsidy has not been formally described. Focusing primarily on the Pacific coast of North America, we identify vectors that transport shellfish-derived nutrients into coastal terrestrial environments, including birds, mammals, and over 13 000 yr of marine resource use by people. Evidence from recipient ecosystems suggests shellfish drastically influence soil chemistry, forest productivity and the diversity of primary producers at the regional and landscape level. Responses in higher trophic levels have not yet been investigated, but given documented responses in lower trophic levels,

this may be due to a lack of examination. To determine if the processes we describe within the northeast Pacific are pertinent to coastal environments worldwide, we also explore shellfish subsidies globally, with a specific focus on temperate and tropical islands. As shellfish are not as spatially or temporally constrained as other subsidies, our examination suggests our findings are applicable to many other geographical regions along the marine–terrestrial interface.

5.1 Marine Subsidies

Marine subsidies occur when nutrients are transferred from marine to terrestrial ecosystems, anywhere along the 594 000 km of global coastline (Hammond 1990). These subsidies can take the form of seabird guano (Sanchez-Pintero and Polis 2021), marine mammal carcasses (Polis and Hurd 1996), spawning fishes (Fox et al. 2015, Reimchen 2018)) or macroalgae deposition (Spiller et al. 2010). While all of these subsidies play important roles in shaping terrestrial productivity, their effect sizes vary over space and time. For example, relatively brief, intense pulses of marine nutrients are deposited in riparian forests during annual Pacific salmon *Oncorhynchus* spp. autumn spawning (Gende et al. 2002, Reimchen et al. 2002, Reimchen 2018), while beaches generally receive marine nutrients year-round through macroalgal deposition (Barreiro et al. 2011). Spatial variation in marine subsidy strength also mediates the extent that terrestrial ecosystems respond (Darimont et al. 2009b). At some point, all marine subsidies decrease in availability with increasing distance from the source (e.g. increasing distance inland, (Polis and Hurd 1996)), but their effect is context specific. For example, the effects of macroalgae-derived nutrients on abundances and diets of terrestrial consumers (e.g. spiders and mice) decline within 200 m from shore (Polis and Hurd 1996), while salmon-derived nutrients within grizzly bear *Ursus arctos* diets extends for hundreds of kilometers inland (Adams et al. 2017). These marine-derived nutrients are often limited in the temperate forests along the Pacific coast of North America and critical to recipient ecosystems (Box 1).

The effects of marine subsidies are seen at multiple trophic levels, from the fertilization of plants, to the numerical increase of prey (e.g. terrestrial arthropods) for terrestrial consumers (Spiller et al. 2010, Collins and Baxter 2014). Additionally, marine subsidies can have more nuanced and complex implications for the recipient communities. (Hocking et al. 2013) found that Pacific salmon subsidies can increase the body size-biomass relationships in terrestrial fly larvae (Cyclorrhaphan), creating a temporary ‘escape’ from body size restrictions during autumn salmon spawning. Rich marine resources can also facilitate intra-population niche variation in large terrestrial carnivores, and influence trophic interaction strength (Darimont et al. 2009b, Adams et al. 2017).

The wide-reaching effects of marine subsidies, particularly Pacific salmon and marine bird guano, have been thoroughly documented compared to other less visible and therefore less considered avenues of marine subsidy. Spatial subsidies not associated with large pulses of nutrients and energy transfer are rarely considered despite their potential to be more temporally and spatially available than conventionally considered subsidies. Despite global distribution and easy accessibility, the role of shellfish as a marine subsidy has never been formally considered or evaluated in modern science. Fortunately, a growing literature on the prevalence and importance of shellfish-derived nutrients transferred into adjacent terrestrial ecosystems has laid the foundation for evaluating the role of shellfish as a spatial subsidy (Erlandson and Moss 2001, Carlton and Hodder 2003, Cook-Patton et al. 2014, Trant et al. 2016; Fig. 21a–c). As a subsidy, shellfish occupy the entire Pacific Coast of North America, in relatively stable abundances that exhibit limited seasonal fluctuations. Therefore, despite being relatively less concentrated than pulse-driven subsidies such as salmon, shellfish have a higher spatial and temporal availability, with comparatively more stable intra-annual abundances (Gosling 2003), which allows shellfish-derived nutrients to contribute to a significant portion of coastal ecosystems for a more extended period.

Here we present an overview of shellfish as a marine subsidy to coastal terrestrial ecosystems along the Pacific coast of North America. We primarily focus on molluscs, specifically bivalves including clams, oysters and mussels, but acknowledge other shellfish as well (e.g. abalone, crabs). We consider the vectors (birds, mammals and humans) that transport shellfish into coastal terrestrial ecosystems, the abundance of shellfish-derived nutrients transported, and the prolonged persistence of shellfish subsidies once deposited within terrestrial ecosystems. We also summarize known and potential implications for recipient ecosystems. Our evaluation focuses primarily on coastal regions and processes occurring along the Pacific coast of North America due to the area's known importance as an intact model ecosystem highly influenced by various marine subsidies (Reimchen et al. 2002, Fox et al. 2015, Reimchen 2018). The global distribution of shellfish suggests these findings are pertinent to many other geographical areas with a marine–terrestrial interface. To evaluate the broader relevance of our findings, we consider shellfish subsidies globally, with a focus on islands as specific regions of interest, and the worldwide human consumption of shellfish. This evaluation illustrates that the processes we describe in the northeast Pacific likely apply to marine– terrestrial interfaces worldwide.

Box 1

Marine-derived nutrients are commonly rich in nitrogen (N), phosphorus (P), and lipids, which are limited in temperate terrestrial ecosystems (Vitousek and Howarth 1991, Elser et al. 2007). This limitation is primarily due to a lack of symbiotic N fixers (Vitousek and Howarth 1991), insufficient lipid sources, and young soils, which impact the potential for P sequestration via mineralogical transformations (Walker and Syers 1976). Nitrogen is an essential element present in amino acids, which form the building blocks of proteins, promote growth, and facilitate development (Elser et al. 2007). Phosphorus is a component of nucleic acids, which promotes protein synthesis, cell division and the development of new tissues (Walker and Syers 1976, Newman 1995). Within plants, for example, N and P availability influences key processes like photosynthesis, seed formation and biomass accumulation (Walker and Syers 1976, Sinclair and Horie 1989, Newman 1995). Marine-derived lipids are essential fatty acids such as eicosapentaenoic acid (EPA) and docosahexaenoic acid (DPA), which support numerous species' physiological processes related to the central nervous system, the cardiovascular system, and the immune system (Twining et al. 2016).

These critical nutrients help support relatively high productivity within terrestrial environments that otherwise might exhibit much lower productivity. Consequently, throughout the Pacific coast of North America, the flow of marine-derived nutrients into terrestrial ecosystems supports healthy, thriving, ecosystems (Gende et al. 2002). The enrichment of terrestrial ecosystems with marine-derived N and P among other nutrients produces positive synergistic responses (Elser et al. 2007). These nutrient subsidies can be measured using stable isotope analysis. As terrestrial N and carbon (C) sources undergo less trophic accumulation, isotope ratio mass spectrometry allows for enriched marine N and C to be detected within terrestrial ecosystems. Elevated enriched N and C signatures in terrestrial consumers indicates a marine-based diet (e.g., Darimont et al. 2009b), while enriched N but not C is indicative of the indirect consumption of marine nutrients (e.g., Hocking and Reimchen 2002). Furthermore, the coupling between marine-derived nutrients and primary productivity allows for marine nutrients, especially N, to be detected within the annual growth rings of trees. This allows old growth forests to serve as an archive of marine subsidy abundance (Reimchen et al. 2002, Reimchen 2018, Reimchen and Arbellay 2018).

Figure 21: (a) Shell fragments litter the high intertidal of beaches along British Columbia's central coast. (b) Shellfish remains can be seen woven within the root structures of fallen trees, commonly associated with a diversity of flora. (c) Mollusc remains, possibly *Mytilus trossulus,* deposited as scat, atop Calvert Island, West beach lookout, at an elevation of over 60 m a.s.l.

5.2 Vectors of shellfish transfer into terrestrial systems

5.2.1 Coastal Birds

Numerous species of coastal bird's forage in the intertidal zone, and carry shellfish back to their nests to consume or feed to their offspring (Fig. 22a–c). Well-known for their consumption of salmon and scavenged mammals, bald eagles *Haliaeetus leucocephalus* along the Pacific coast of North America also consume a substantial amount of abalone, mussels and other molluscs (Grubb and Hensel 1978, Erlandson and Moss 2001). In a similar fashion, multiple gull and crow species, including common gulls *Larus canus*, kelp gulls *Larus dominicanus* and northwestern crows *Corvus caurinus* consume an assortment of marine organisms including mussels and clams (Siegfried 1977, Erlandson and Moss 2001). Gulls and crows also engage in shell dropping behaviour to crack open shellfish and gain access to the flesh, which occurs on hard substrates, occasionally up to 240 m away from the collection location (Siegfried 1977, Whiteley et al. 1990, Erlandson and Moss 2001). Additionally, surf *Melanitta perspicillata* and white-winged *Melanitta fusca* scoter ducks prey predominantly on clams and other molluscs; bivalves account for over 70% of the total fecal dry mass (Lewis et al. 2007). These species prey on Manila clams *Venerupis philippinarum* and varnish clams *Nuttallia obscurata*, with a case study indicating that over three million clams were removed from sites within the Strait of Georgia, British Columbia by scoter ducks in a single season (Lewis et al. 2007).

Birds as vectors for shellfish subsidies deposit substantial amounts of shellfish remains in terrestrial ecosystems. These remains form middens under nests, often at the base of trees, that have been mistaken for long-term archeological deposits due to their size and age (Erlandson and Moss 2001). The presence of avian-derived shellfish middens hundreds of meters inland have been observed adjacent to gull, eagle and crow nesting sites and colonies (Erlandson and Moss 2001). Along the Oregon coast, seagull middens of 100 m^2 contain thousands of fragments of mussel *Mytilus californianus*, crabs *Cancer* spp., chitons (Polyplacophora) and other shells (Erlandson and Moss 2001). Furthermore, these birds, which may be nesting at coastal margins to take advantage of the shellfish food source, excrete substantial amounts of nitrogen and phosphorus, derived in part from their consumption of shellfish. As such, coastal birds create large middens of accumulated shellfish-derived nutrients, and as a consequence, deposit nitrogen- and phosphorus-rich guano across vast portions of coastal terrestrial ecosystems (Fig. 22a–c, Fig. 23). These nutrients subsequently accumulate within terrestrial ecosystems and positively affect primary and secondary productivity (Cocks et al. 1998).

5.2.2 Coastal mammals

Coastal mammals often rely heavily upon marine-derived food, especially shellfish (Fig. 22d–h). Through inter- and sub-tidal foraging, coastal mammals act as vectors for marine nutrients in a similar manner as avian vectors, scattering shellfish remains throughout the terrestrial environment during feeding activities and excretion (Erlandson and Moss 2001, Carlton and Hodder 2003). While the opportunity to forage intertidal shellfish or scavenge shellfish remains is utilized by almost every mammalian trophic level, from insectivorous shrews to apex carnivores such as bears, many species rely upon shellfish as a major constituent in their diets (Carlton and Hodder 2003).

Figure 22: Vectors that transport shellfish-derived nutrients into northwest Pacific terrestrial ecosystems. (a–c) Bald eagles *Haliaeetus leucocephalus*, gulls *Larus* spp. and crows *Corvus caurinus* consume shellfish, create middens below nests and engage in shell-dropping. (d–f) River otters *Lontra canadensis*, mink *Neovison vison* and raccoons *Procyon lotor* forage subtidally, returning to terrestrial areas to consume and excrete prey. (g) Sea otters *Enhydra lutris* frequent haul-out sites and contribute feces. (h) Grizzly bears *Ursus arctos* transport shellfish fragments several kilometers inland. (i) Clam gardens, clam digging and associated large shellfish middens from coastal First Nations have contributed to substantial transfer of shellfish-derived nutrients. (j) Over 13 000 yr of coastal habitation has involved extensive cultivation, harvesting and consumption of shellfish by coastal people. In many instances, these shellfish-derived nutrients are transported great distances inland.

Several mustelid mesopredators are responsible for transporting and depositing shellfish along coastlines. River otter *Lontra canadensis* forage subtidally for fish and shellfish, but return habitually to terrestrial platforms up to 20 m inland to consume and deposit prey (Larsen 1983, Ben-David et al. 1998). At these locations, middens of considerable size accumulate the hard remains and unconsumed flesh of prey such as abalone and mussel shells, urchin tests, crab carapaces and chiton skeletons (Haggarty et al. 1991, Bowyer et al. 1994). In extreme cases, middens of 96 m^2 containing hundreds of shellfish fragments have been documented (Erlandson and Moss 2001).

Likewise, river otter latrine sites are laden with marine-derived nutrients and fragments of shellfish prey (Stenson et al. 1984, Erlandson and Moss 2001). While most studies focused on the Pacific highlight the importance of finfish (as opposed to shellfish) in river otter diets (Stenson et al. 1984, Ben-David et al. 1998), bivalves, gastropods, crustaceans, chitons and other shellfish, can account for over half of their food consumption (Bowyer et al. 1994). However, (Bowyer et al. 1994) observed consumption of only soft viscera of mussels *Mytilus edulis* and scallops *Chlamys* spp., material that would not be detected when analyzing faecal samples or gut contents. The combination of shell-laden midden sites and this observation suggests shellfish are an important, but possibly underestimated prey source.

Similar to river otter, mink *Neovison vison* also create middens and latrine sites littered with shell fragments. Along the Pacific coast from Washington to Alaska, mink have been recorded consuming bivalves, gastropods, crustaceans and echinoderms (see records in Carlton and Hodder (2003)). Hatler (1976) reported predation on shellfish to be rare, but noted that mink will scavenge soft parts of shellfish (e.g. horse clam siphons), or dissect out soft internal viscera from clams (Svihla and Svihla 1931). In addition, mink will cache or hide food underground for later consumption, which may supply another route of subsidies to the terrestrial environment (Hatler 1976, Erlandson and Moss 2001). Furthermore, we have observed many mink latrine sites littered with abalone shells, urchin tests and chiton exoskeletons, which suggests mink (and possibly other consumers) may eat only the soft components of shellfish prey (Davidson unpubl.).

Raccoons *Procyon lotor*, are also opportunistic mesopredators that will capitalize on intertidal prey. While most of this predation is focused on crabs and fish, consumption of bivalves and gastropods occurs from Oregon to British Columbia (see records in Carlton and Hodder 2003), as evident by remains of mussels in terrestrial latrine sites (Simmons et al. 2014). Raccoons can consume 7.5 ± 3.2 clams per 5 min, often choosing species that maximize energy intake (Simmons et al. 2014). The result being a substantial amount of shellfish-derived nutrients, including nitrogen and phosphorus, entering terrestrial ecosystems via excretion and urination by raccoons. As opportunistic mesopredators, raccoons may contribute a more dynamic range of shellfish-derived nutrients into terrestrial ecosystems than many other coastal mammals.

Perhaps less documented, and rarely considered a key marine subsidy vector, is the terrestrial activity of sea otters *Enhydra lutris*. While they are often described as the keystone predator that specializes in red sea urchins *Mesocentrotus franciscanus*, observational studies indicate that they will switch to clams, other bivalves and crustaceans once urchin populations are depleted, especially when large sea otter colonies occupy soft-sediment habitats (Kvitek et al. 1988, Rechsteiner et al. 2019). In certain instances, the clam species *Tresus nuttallii* and *Saxidomus nuttalli* can comprise over half of the prey harvested from nearshore habitats (Kvitek et al. 1988). Sea otters will frequently haul-out to rest on rocky points, sand beaches and even grassy areas (up to 75 m inland) adjacent to their offshore feeding grounds, where large quantities of fecal matter are deposited (Kenyon 1969). In the Aleutian Islands, haul-out sites are used habitually and frequently, with accumulated fecal deposits containing up to 94% mollusc and crustacean remains (Kenyon 1969).

Bears, due to their relatively high density along the coast, substantial metabolic requirements, and large home ranges, may be one of the more predominant vectors of shellfish nutrients into terrestrial ecosystems via scat and urination. Grizzly bears (*Ursus arctos*) spend up to 5% of their time digging for clams, where they can catch and consume 1-2 clams a minute (Smith and Partridge 2004). As bears are highly mobile there is elevated potential for the marine shell fragments to be transported several kilometers inland from the coast (Erlandson and Moss 2001). Haggarty et al. (1991) observed such transport along the Alaskan Peninsula, where low-density surface scat has accumulated from thousands of years of bear activity, and can be seen adjacent to fresh meter-wide clusters of scat containing high concentrations of bivalve shell fragments.

It is important to note that most dietary studies focus upon morphological examination of fecal content. These studies may underestimate the importance of shellfish, as many consumers are able to remove and consume only soft parts of shellfish which are not detectable using most conventional visual scat analysis methods. For example, mink and raccoon are more dexterous than many other shellfish consumers, and can crush and pry open clams to consume the soft viscera (Svihla and Svihla 1931, Simmons et al. 2014). Similarly, sea and river otters may break open shells or tests using force (or tools in the case of sea otters), allowing for the consumption of only soft viscera. These abilities, combined with the common occurrence of shells and exoskeletons in mammal latrines and middens (Davidson unpubl.) suggest that shellfish are an important, but possibly under-appreciated marine subsidy. Furthermore, urination by coastal mammals contributes a substantial amount of marine-derived nutrients into terrestrial ecosystems, especially nitrogen, but is less evident than scat or shell remnants. For example, up to 97% of the nitrogen deposited by brown bears onto the riparian area is added via urination (Hilderbrand et al. 1999). It is reasonable to assume this process is similar whether the nitrogen is derived from fish or shellfish, and supports the notion that current inputs of shellfish-derived nutrients are vast underestimates. Furthermore, given the number of coastal mammals that forage in nearshore habitats (Carlton and Hodder 2003), it is likely that numerous other mammals not discussed here also consume shellfish and act as vectors for nutrient transfer inland via direct deposition, excretion or urination (e.g. *Canis lupus*).

5.2.3 Coastal humans

Marine-derived foods have been critical for sustaining coastal human populations since time immemorial. Coastal First Peoples have migrated along the Pacific coast of North America for over 13 000 yr, inhabiting coastal refugia during glaciation, and sustaining populations by accessing marine foods via watercraft and cultivation (Lepofsky et al. 2015, McLaren et al. 2018). Among other seafoods, marine shellfish were, and continue to be, key food sources for coastal communities (Deur et al. 2015, Lepofsky et al. 2015, Jackley et al. 2016), with the occupation of Coast Salish winter villages and shellfish-harvesting camps, including those within the Strait of Juan de Fuca, Washington, being largely driven by the availability of marine resources (Hutchinson et al. 2019).

To ensure a consistent, easily-accessible supply of shellfish, some coastal communities engineered extensive clam gardens near habitation sites (Fig. 22i; Lepofsky et al. 2015, Jackley et al. 2016). Constructed by building rock walls in the mid to low intertidal, clam gardens increase sedimentation rates by at least four-fold, which alters the beach slope at tidal heights optimal for clam production (Groesbeck et al. 2014, Deur et al. 2015, Neudorf et al. 2017). These intertidal rock walls and associated terraces represent one of several coastal habitat alterations created over millennia by Coast Salish people to steward marine resources, increase clam productivity and ensure stable shellfish abundances adjacent to coastal communities to support economies, cultural practices and governance (Lepofsky et al. 2015, H-GINPR 2016). Recent radiocarbon dates and scientific investigations into taphonomic processes, indicate clam garden construction throughout Northern Quadra Island, British Columbia, began at least 3500 yr before present (Smith et al. 2019). In addition to supplying a reliable food source for communities, clam gardening is integral to governance systems that dictated land use and stewardship, which continues to the present day (Deur et al. 2015, Lepofsky et al. 2015, H-GINPR 2016). The thousands of clam gardens heterogeneously distributed along the coast provide not only an opportunity to appreciate the complexities of traditional resource management, but also an indication that shellfish play an important role in sustaining coastal populations (Harper et al. 1995, Deur et al. 2015, Lepofsky et al. 2015), and that certain communities transfer shellfish-derived nutrients into terrestrial ecosystems at substantial rates.

Once harvested and consumed, large quantities of shell and fragments were scattered throughout coastal forests for various functions. Shellfish remains were terraced into soil to modify sloping landscapes into flat, leveled areas, potentially forming the foundation for housing structures or other buildings (Sawbridge and Bell 1972). Concurrently, shell middens improved habitat and soil drainage for culturally important terrestrial plants (Trant et al. 2016, Fisher et al. 2019). Alternatively, shellfish remains were deposited as refuse into middens adjacent to settlement areas. Long-term consumption of shellfish has resulted in middens that have been active for well over 5000 yr of continuous use (Cannon and Yang 2006), with vocation largely driven by consistent availability of marine resources, including shellfish (Cannon and Yang 2006, Hutchinson et al. 2019).

These shellfish deposits, which are common along the Pacific coast of North America, can reach over 5 m in depth, span hundreds of square-meters, and extend up to 110 m inland (Erlandson and Moss 2001, Cannon and Yang 2006, Cook-Patton et al. 2014). The number of shellfish deposits along the Pacific coast of North America remains largely unresolved, however, substantial efforts by First Nations heritage managers and by archaeologists has elucidated at minimum 5300 recorded coastal shell deposits that exist along the coast of British Columbia (McKechnie, 2013). The Broken Group archipelago, for example, contains at least 73 shell deposits (McKechnie, 2013). The result of long-term human occupation throughout the region, many of the deposits are associated with houses, terraces, and connected to Indigenous oral history of the villages. Collectively, the deposits amass more than 114 000 m^2 of shellfish remains spread throughout the archipelago (McKechnie, 2013). If representative, this observation suggests that tens of thousands of shell deposits, amassing millions of cubic meters of shellfish-derived nutrients, may exist along the Pacific coast of North America.

Although the amount of shellfish transported by humans into terrestrial ecosystems remains unquantifiable, cultural practices such as clam gardening, and the longstanding practices surrounding shellfish resource management, suggest that shellfish-derived nutrients have been, and will continue to be, deposited in large quantities into terrestrial ecosystems by coastal human populations.

5.3 Shellfish out of water

5.3.1 Shellfish-derived nutrients

Shellfish are commonly deposited as hard shells and shell fragments in the terrestrial environment, impacting both physical and chemical properties of terrestrial forests. Additional nutrients are also supplied to forests through excretion and discarded soft viscera. Used for terracing by coastal First Nations, or discarded as refuse by coastal people, mammals or birds, hard shells and shell fragments act as a coarse, bulk material, improving soil drainage while maintaining stability (Trant et al. 2016). Moderately drained, nutrient-rich soils promote growing conditions for primary producers (Sawbridge and Bell 1972, Trant et al. 2016). Shellfish middens commonly co-occur with other components of coastal First Nations' long-term management of terrestrial ecosystems, including charcoal from fires or controlled burns (Hoffman et al. 2016, 2017, Trant et al. 2016). With mixed-severity controlled burns recurring at minimum for six centuries as part of coastal First Nations stewardship (Hoffman et al. 2016, 2017), shellfish nutrients deposited by coastal birds and mammals, would be exposed to similar conditions. The addition of calcium carbonate and charcoal causes the surrounding soil pH to increase, which facilities the availability of phosphorus and other macronutrients, increases the soils cation exchange capacity and biotic activity, and promotes porosity (Johnson 1992, Demeyer et al. 2001).

The composition and quantity of shellfish-derived nutrients deposited in the terrestrial environment will vary based on the species considered, and the form it takes in the terrestrial environment (i.e. components of scat vs. hard body parts in middens). Generally, molluscs are low in fat (Nettleton and Exler 1992) and high in calcium carbonate and protein (Box 1; Gosling 2003). For example, a medium-sized (20 g) clam contains: 2.56 g of protein, 0.19 g of fat, 220 mg of nitrogen and 34 mg of phosphorus, while their shells are more than 90% calcium carbonate (Reitsma et al. 2017; Table 8). However, other shellfish contain more protein and essential fatty acids (Table 8). For example, 225 g of Pacific oysters, 175 g of blue mussels or 122 g of Dungeness crab would transfer comparable amounts of protein into the terrestrial environment as 100 g of sockeye salmon (Table 8). Furthermore, shellfish generally contain proportionally more unsaturated than saturated fats, which promotes development, growth and cellular functions in animals (Simopoulos 1991). For example, fatty acid composition in Dungeness crabs is 57% polyunsaturated fats, 23% mono-saturated and 20% saturated, with the Manila clam and Pacific oyster having similar ratios. Comparatively, salmon are composed of 37% polyunsaturated, 40% mono-saturated and 23% saturated (King et al. 1990). Shellfish-derived nutrients also represent considerable sources of minerals, including iron, zinc and copper, which are found in high quantities within shellfish compared to finfish (Table 8).

Whole shellfish (soft body plus shell) transported into terrestrial ecosystems are a rare occurrence; nutrients will either be transferred indirectly through feces or urination, or directly through shell and flesh deposits into middens and other high nutrient transfer areas (Fig. 23a). Driven primarily by shellfish deposits and centuries of forest stewardship, soil nutrients surrounding long-term habitation sites on the central coast exhibit higher levels of boron, calcium, manganese, sodium, potassium, inorganic carbon, zinc, exchangeable calcium, and increased effective cation exchange capacity (Fisher et al. 2019). On the east coast of North America, middens comprised primarily of eastern oyster *Crassostrea virginica*, razor clam *Tagelus plebeius* and hard clam *Mercenaria mercenaria* shells in the Chesapeake Bay area exhibit soils with 45-times more calcium, 6.7-times more nitrates, a more neutral pH, and increased concentrations of other elements such as boron and manganese, relative to soils adjacent to middens (Cook-Patton et al. 2014). Compared to commonly considered spatial subsidies such as salmon that deposit primarily nitrogen and lipids, which become depleted relatively quickly (Johnson 1992), these nutrients can be more persistent (Cook-Patton et al. 2014) and have potential long-term cascading effects on terrestrial food webs.

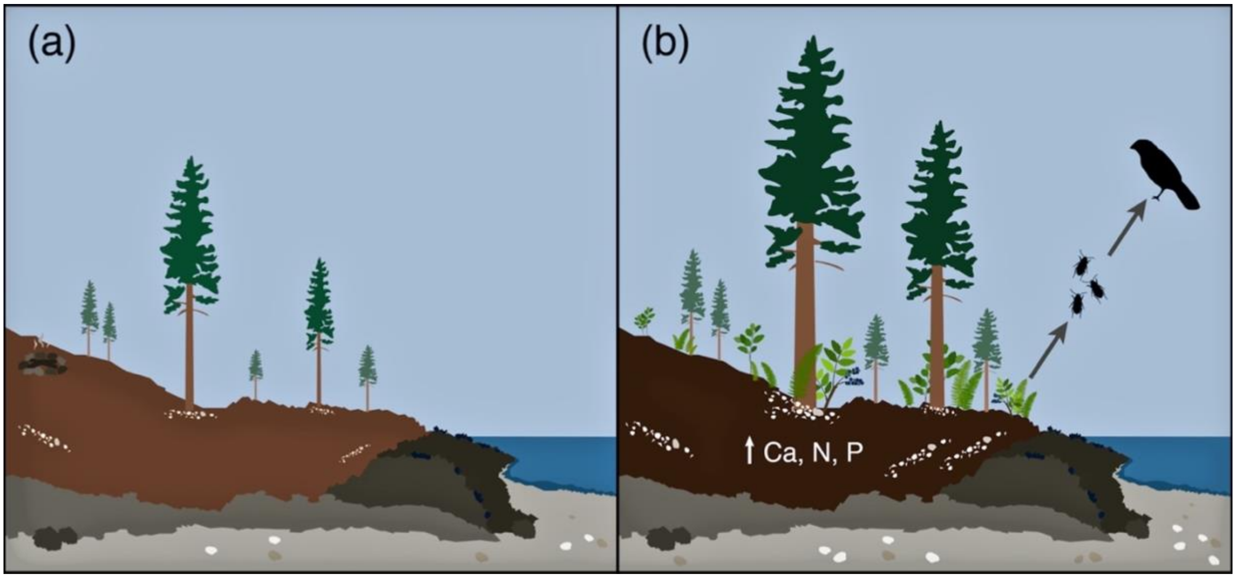

Figure 23: (a) Coastal ecosystem with shellfish nutrient influx from animals and human habitation (including terracing). (b) Coastal ecosystem response to added shellfish nutrients including an increase in soil nutrients (especially calcium, nitrogen and phosphorus), greater radial growth and increased height of trees, and a greater abundance and diversity of vegetation that may support a more diverse community of insects and potentially birds.

Shell fragments and shellfish-derived nutrients persist in the terrestrial environment much longer than other marine-derived nutrients (*e.g.* δ15N from salmon carcasses; Johnson 1992, Cook-Patton et al. 2014, Trant et al. 2016). Globally, excavation of middens deposited 70 000 yr before the present suggests that shellfish-derived nutrients, especially calcium, deposited into terrestrial ecosystems may persist until utilized (O’Connor et al. 2002). Evidence from the northeast Pacific suggests that once transported inland shellfish-derived nutrients will decrease with time but have the potential to persist for millennia, and may influence forest ecosystems on boundless timescales (Sawbridge and Bell 1972, Trant et al. 2016, Fisher et al. 2019). These nutrients accumulate within coastal ecosystems by forming large mounds in the high intertidal, being incorporated into the root systems of the surrounding flora, or being deposited on hill tops by various vectors (Fig. 21a–c). Especially, calcium that is released slowly from degrading shells and is commonly deficient in forested ecosystems. Again, these processes persist well beyond the majority of the nutrients delivered during spatial and temporal limited subsidies, such as spawning Pacific salmon or herring.

Table 4: Nutritional value of common shellfish and sockeye salmon, per 100 grams of raw edible portion, including protein, fat, eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA), iron, phosphorus, zinc, and copper. Sources: King et al. 1990, Nettleton and Exler 1992, Dong 2001, Exler and Pehrsson 2007, Wright et al. 2018

	Protein (g)	Total Fat (g)	EPA and DHA (g)	Vitamin B12 (ug)	Iron (mg)	Phosphorus (mg)	Zinc (mg)	Copper (mg)
Pacific oyster, (*Magallana gigas*)	9.45	2.3	0.69	16	5.11	162	16.62	1.58
Clam, mixed species	12.77	0.96	0.14	49	14	169	1.37	0.34
Blue mussel, (*Mytilus edulis*)	11.9	2.24	0.44	12	3.95	197	1.6	0.09
Scallop, mixed species	16.78	0.76	0.103	1.41	0.38	334	0.9	0.05
Dungeness crab, (*Metacarcinus magister*)	17.41	0.97	0.31	9	0.37	182	4.27	0.67
Sockeye salmon, (*Oncorhynchus nerka*)	21.3	8.56	1.17	5	0.47	266	0.54	0.05

5.3.2 Primary productivity responses

Shellfish remains contribute high levels of several nutrients, including calcium and phosphorus, to the soil surrounding deposit sites (Cook-Patton et al. 2014, Trant et al. 2016, Fisher et al. 2019), while excretion and discarded soft viscera contribute substantial amounts of nitrogen, phosphorus, lipids and trace minerals to the riparian zone (King et al. 1990, Dong 2001, Reitsma et al. 2017). Furthermore, shell fragments facilitate favorable physical conditions within forest landscapes, which if co-occurring with additional features of long-term habitation (e.g. charcoal, terraced landscapes), are extremely advantageous for primary production (Hoffman et al. 2016, 2017, Trant et al. 2016).

The slow release of calcium from degrading shells is a persistent source of nutrients for primary producers, while excretion and discarded soft viscera contribute nitrogen that is more readily available (Sawbridge and Bell 1972). If the surrounding conditions have facilitated decreased soil acidity (i.e. the presence of charcoal), decomposition of organic matter increases due to favorable conditions for microbial activity (Kuzyakov et al. 2000). This increased carbon elicits fine root production in mycorrhizal fungi and supports root exudation (Treseder 2004). As mycorrhizal fungi stimulate nitrogen cycling by increasing the decomposition of organic matter in soils, capturing organic and inorganic nitrogen, and transferring nitrogen to host plants, soil conditions surrounding shellfish deposits increase primary producers’ access to soil nitrogen (Kuzyakov et al. 2000, Treseder 2004). As nitrogen often limits temperate forest productivity, increased uptake of nitrogen supports photosynthesis, plant reproduction and increases overall plant growth (Sinclair and Horie 1989, Newman 1995, Elser et al. 2007). As such, landscapes surrounding shellfish deposits, especially those subjected to centuries of forest stewardship, will have reduced carbon to nitrogen ratios, due to increased nitrogen, which allows plant species that would be otherwise nitrogen-limited to succeed (Sawbridge and Bell 1972, Fisher et al. 2019).

Increased nutrients, drainage and pH elicit increased productivity within plant communities above shellfish deposits. Trees growing adjacent to deposits exhibit greater radial growth and increased height, which decreases with increasing distance from shell deposits (Trant et al. 2016). Inputs of calcium increase the wood calcium levels of trees and reduce the rate of top die-back, a condition thought to be partially induced by calcium deficiency (Trant et al. 2016). Furthermore, altered soil chemistry leads to increased forest diversity by shifting plant community structure on shellfish deposit sites from woody to herbaceous vegetation, resulting in more vegetative cover and higher species richness (Cook-Patton et al. 2014). Fisher et al. (2019) observed that plants species with higher nutrient requirements and cultural significance persist indefinitely within culturally modified landscapes, even after intense habitation has ceased. As such, responses within primary producers occur at the landscape-level and are evident within herb, grass and tree species (Meigs 1938, Cook-Patton et al. 2014).

Unlike other marine subsidies, the capacity of shellfish-derived nutrients to elicit responses within terrestrial primary producers is less spatially constrained in some aspects, and possibly supplies important marine nutrients to terrestrial habitats lacking other subsidy pathways. For example, throughout the northeast Pacific, shellfish are deposited on many small, isolated islands with high perimeter to area ratios (e.g. peninsulas, rugged coastlines) that do not support salmon or herring spawning (Fig. 24a). Increased perimeter-to-area ratios allow for greater influx of marine nutrients by increasing vector access to marine resources, and decreasing the relative distance required for subsidies to permeate into and influence more of the terrestrial environment (Polis and Hurd 1996). As such, responses within terrestrial primary productivity will be the most pronounced in areas with abundant shellfish populations and low-productivity terrestrial ecosystems where species are dependent on marine resources; both of which will be highly influenced by the structural characteristics of the coastal environment.

5.3.3 Higher trophic level responses

Primary, secondary, tertiary and quaternary consumer responses to shellfish-derived nutrients have not been observed, potentially due to the lack of emphasis on shellfish as a spatial subsidy. As many species that consume shellfish directly or benefit from an increased abundance of species that do, also capitalize on other, better-documented marine subsidies (e.g. salmon and herring; Erlandson and Moss 2001, Gende et al. 2002, Fox et al. 2015), it is possible that these higher-level consumers respond to shellfish subsidies in similar ways. These responses would potentially include effects on population dynamics and carrying capacity, trophic interactions and physiology (Jefferies 2000). If so, responses within primary consumer populations would be influenced by shellfish-derived nutrients transferred to soil and vegetation. Responses would occur in a similar fashion to those associated with salmon subsidies, with shellfish nutrients influencing terrestrial invertebrate forest litter communities, including detritivores and certain omnivores (Hocking and Reimchen 2002), which would be detectable through increases in enriched nitrogen, but not enriched carbon (Box 1; Reimchen et al. 2002).

While we have discussed the differences between salmon and shellfish subsidies, the similarities between them support the potential cascading effects of shellfish subsidies, in addition to effects on direct consumers. If terrestrial ecosystems respond to these subsidies in similar ways, then shellfish-derived nutrients facilitate direct and indirect responses within primary, secondary, tertiary and quaternary consumer populations. For example, a plethora of secondary consumers are known to respond to influxes of marine nutrients, including dipterans and other insects (Hocking and Reimchen 2006). If these consumers respond to shellfish-derived nutrients, then shellfish remains will be colonized, supporting an increased abundance of dipteran larvae, which in turn will further disperse nutrients into terrestrial ecosystems. (Christie and Reimchen 2008) demonstrated a pathway by which shellfish-derived nutrients may influence primary, secondary and tertiary consumers when investigating the role of salmon in supporting higher plant productivity and invertebrate abundances, which in turn facilitates increases in songbird abundance (Fig. 23b).

Given the positive relationships between the habitat heterogeneity provided by primary producers and animal species diversity (Tews et al. 2004), impacts of shellfish-nutrients on terrestrial ecosystems would not be limited to the flow of nutrients. The previously mentioned responses in terrestrial vegetation community structure, diversity and growth would impact invertebrate, avian and even mammal ecology, based on alterations to the physical environment, potentially providing increased habitat heterogeneity and associated niche spaces (Tews et al. 2004, Collins and Baxter 2014).

Further inquiry is needed to quantify the extent to which shellfish act as a marine subsidy, and how terrestrial responses set in motion by the input of marine derived nutrients may cascade through ecosystems. However, there is sufficient evidence to suggest that shellfish-derived marine nutrients are an integral part of coastal terrestrial ecosystems. Further investigation into the ecological role of shellfish subsidies should seek to discover the specific nutrient inputs from shellfish in comparison to other marine-derived nutrients (*e.g.* macroalgae or salmon), and pinpoint the mechanisms by which shellfish-derived nutrients permeate terrestrial ecosystems (directly or indirectly). Experimental designs focused on fertilization comparisons and eDNA traces may shed light on these specific interactions, with the primary objective being to contribute a piece of the puzzle that is the holistic understanding of the diverse pathways in which marine resources influence the terrestrial environment.

5.4 Shellfish subsidies globally

The global distribution of shellfish suggests that these findings are pertinent to many other geographical regions along the marine–terrestrial interface. Ecologically, the majority of the vectors transporting shellfish into coastal ecosystems throughout the northeast Pacific have analogous counterparts globally that potentially perform similar functional roles within their respective ecosystems. Globally, arctic foxes *Vulpes lagopus*, coyotes *Canis latrans,* domestic dogs *Canis familiaris* and domestic pigs *Sus scrofa domesticus* cumulatively prey on numerous species of bivalves and crustaceans throughout North America, Greenland, South America and Eurasia, respectively (Murie 1959, Carlton and Hodder 2003). Furthermore, many of the coastal mammals evaluated within the northeast Pacific, including river otter, mink, brown bears and raccoons, occupy substantial ranges worldwide, and would perform similar functional roles if in close proximity to a marine–terrestrial interface. At minimum, over 30 bivalve species are prey for over a dozen mammals worldwide (Carlton and Hodder 2003). A similar phenomenon is true, potentially more so given their diversity, distribution and reliance on marine resources, for coastal birds globally. Throughout the Asia-Pacific, Pacific gulls and other seabirds create 2 m wide middens containing shell fragments that are commonly mistaken for ancient deposits by coastal human populations (Jones and Allen 1978, Szabó and Amesbury 2011). These middens represent the transport of shellfish-derived nutrients into terrestrial ecosystems globally that spans millennia.

5.4.1 Islands

To illustrate the influence of shellfish subsidies globally, it is essential to contemplate additional environments that span ecological landscapes. Islands exhibit considerable variability in geographical structure, and with an innumerable abundance globally, they represent an extensive portion of the marine–terrestrial interface. The perimeter to area ratio of islands determines the extent that nutrients can be deposited by physical agents (Polis and Hurd 1996), with small islands most affected by ocean-borne disturbances (Neufeld et al. 2017). This suggests that as size decreases, islands become more oligotrophic and reliance on marine inputs is more extensive and instrumental compared with large islands. Marine inputs subsidizing islands, including seabird guano and seaweeds, are known to increase nitrogen and phosphorus availability, enhance plant productivity and restructure food–web interactions (Polis and Hurd 1996, Piovia-Scott et al. 2011, Sanchez-Pintero and Polis 2021). Recently, seabird guano assimilating back into fringing marine communities and promoting the growth of ecologically essential species was illuminated (Savage 2019), highlighting the continuum that exists between marine and terrestrial nutrients in tropical marine ecosystems. Akin to the northeast Pacific, the role of shellfish, specifically molluscs, as a marine subsidy on tropical islands has not been formally described, despite extensive interactions between island species adjacent to shellfish communities, and the potential for nutrient transfer into island ecosystems (Spear et al. 2007, Szabó and Amesbury 2011, Salem et al. 2014, Thomas 2014; Fig. 24b). An evaluation of the 30 most common seabirds in the eastern tropical Pacific Ocean determined that on average consumption of non-cephalopod invertebrates, including mollusks and crustaceans, accounted for 16% by abundance and 0.3% by mass of the average seabird diet. Although a relatively nominal percentage by mass, the population of seabirds considered consisted of between 28.5 and 35 million individuals (Spear et al. 2007), as such, even small percentages of individual diets represents a substantial amount of potential for shellfish-derived nutrients to be deposited into seabird colonies as guano. Furthermore, Spear et al. (2007) observed species of solitary feeders, particularly petrels and terns, that consumed above average amounts of epipelagic non-cephalopod invertebrates, specifically, pelagic gooseneck barnacles (*Lepas* sp.), portunid crab, crab megalops and pelagic sea snails (*Janthina* sp.). For example, members of *Stercorariidae* and *Laridae*, including the sooty tern *Onychoprion fuscata*, gray-backed tern *Onychoprion lunatus*, white tern *Gygis alba* and parasitic jaeger *Stercorarius parasiticus* consume 39.2% invertebrates by abundance and 8.4% by mass. Seasonal shorebird predation on bivalve communities is also predominant throughout tropical intertidal systems. (Salem et al. 2014) evaluated predation pressure of Banc d'Arguin, Mauritania's, most dominate molluscivore, the red knot *Calidris canutus* and the less abundant oystercatcher *Haematopus ostralegus* on benthic invertebrates. Three-quarters of biomass consumed by the 300 000 seasonal shorebird population was attributed to west-African bloody cockle *Senilia senilis*. Depending on the shorebird species considered, these shellfish-derived nutrients may enter tropical terrestrial ecosystems through a variety of mechanisms, most notably through guano and discarded shell fragments (Fig. 24b).

More recently, with the global spread of invasive rats, evidence is mounting that the Norway rat *Rattus norvegicus* is influencing marine–terrestrial interactions on islands in a similar way to other invasive species (Harper and Bunbury 2015). Culminating in the global decline of a number of bird species, Norway rats are effective predators of marine molluscs, crustaceans, birds and plants (Towns and Daugherty 1994). Similar to coastal mesopredators within the northeast Pacific, the Norway rat represents a considerable vector for shellfish-derived nutrients entering terrestrial ecosystems (Fig. 24b).

Parallel to coastal human populations throughout the northeast Pacific, the importance of molluscs as a dependable source of food across the tropical islands throughout the Pacific cannot be overemphasized (Szabó and Amesbury 2011, Thomas 2014). An extensive history attests to the role of molluscs as a food resource for non-sapiens hominids and early modern humans throughout the Asia-Pacific (Choi and Driwantoro 2007, Stringer et al. 2008). Evident throughout the Pleistocene and Holocene, modern humans' relationship with shellfish for sustenance and tool use is clearly visible in shell middens deposited throughout the Asia-Pacific region. Many of which coincide with the first appearance of modern humans in the region, and draw a strong link between pressure on shellfish populations and human population growth (Szabó and Amesbury 2011). Early utilization of shellfish largely targeted freshwater species (O'Connor et al. 2002), with mid to late Holocene middens throughout the region reflecting an increased focus on marine mollusc species, including *Meretrix meretrix*, *Anadara antiquata* and *Strombus gibberulus gibbosus*, depending on the ecological conditions of the site (Szabó and Amesbury 2011). The importance of shellfish within tropical ecosystems has persisted since the first appearance of modern humans into contemporary island cultures, especially on atolls and low coral islands that lack fertile soils and perennial surface freshwater (Thomas 2014). With over 300 atolls and low coral islands in the Pacific Islands region, including the Tuamotu, Marshall Islands, Tuvalu and Kiribati, these regions exemplify the marine–terrestrial interface, and importance of subsisting on and managing marine subsides (Thomas 2014, Watson et al. 2016). Currently on Kiribati, combined shellfish catches can exceed 40% by weight of landed marine resources, with as high as 10% of households depending on shellfish, largely *Anadara uropigimelana*, *Tridacna gigas* and *Tridacna maxima*, as their main protein source (Thomas 2014). Much like consumption of shellfish nutrients throughout the Pacific northeast, this consumption results in the deposition of large middens, potentially spanning meters and persisting indefinitely (Fig. 24b).

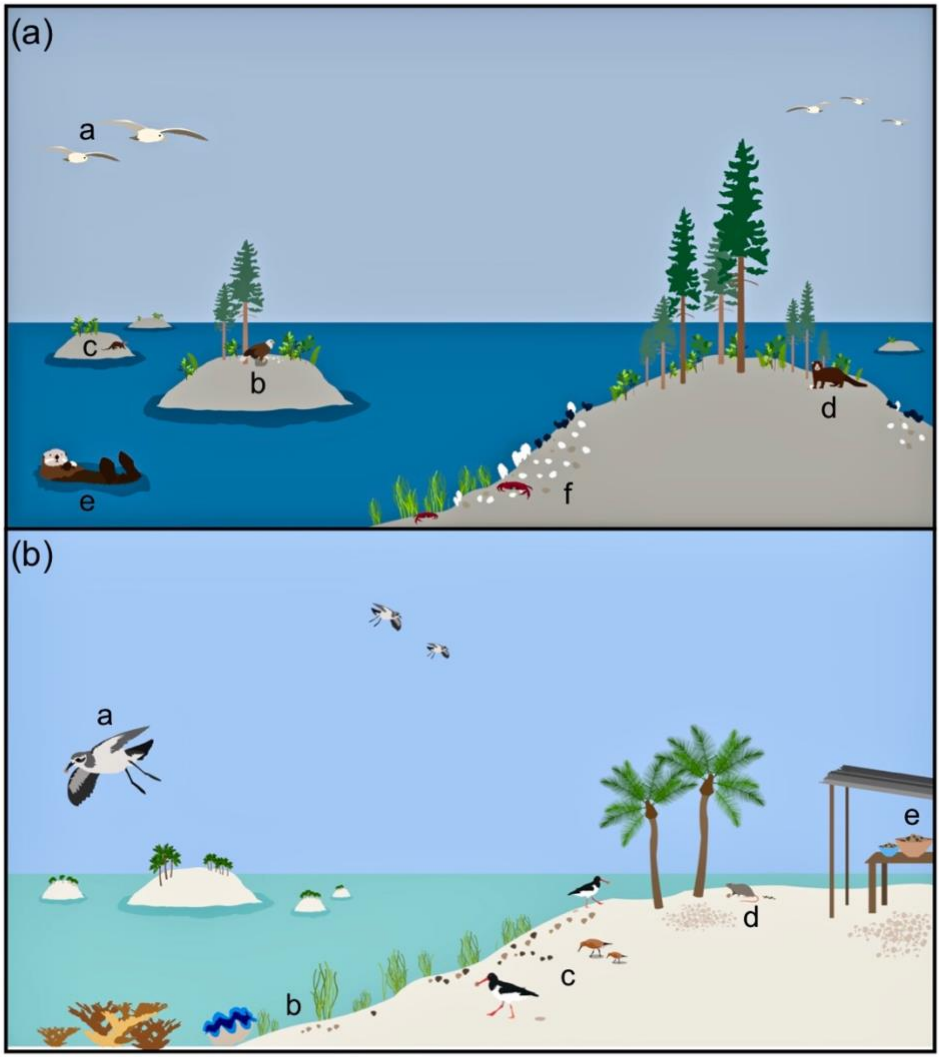

Figure 24: Vectors that transport shellfish-derived nutrients into temperate and tropical island ecosystems. (a) Temperate islands: (a–b) gulls *Larus* spp. and bald eagles *Haliaeetus leucocephalus* forage around temperate islands, consuming shellfish and discarding nutrients onto adjacent islands. (c–d) River otters *Lontra canadensis* and mink *Neovison vison* forage inter- and sub-tidally around temperate islands, returning to terrestrial areas to consume and excrete prey. (e) Sea otters *Enhydra lutris*, discard nutrients adjacent to temperate islands, frequent haul-out sites and contribute feces to temperate islands. (f) Red rock crabs *Cancer productus*, oysters (Ostreidae), mussels *Mytilus* spp., Venus clams (Veneridae) and other shellfish derived nutrients occur in high abundance surrounding temperate islands, especially relative to other potential subsidies (e.g. Pacific salmon) with pathways into terrestrial island ecosystems (e.g. lack of salmon-bearing streams). (b) Tropical islands: (a) white-faced storm petrels *Pelagodroma marina* and other seabirds commonly consume shellfish and transport nutrients via guano. (b) Giant clams *Tridacna* spp. are a major protein source in tropical locations. (c) Oystercatchers *Haematopus ostralegus*, red knots *Calidris canutus* and other intertidal shorebirds consume vast numbers of bivalves, especially west-African bloody cockle *Senilia senilis*. (d) The Norwegian rat Rattus norvegicus is becoming an increasingly prevalent shellfish vector as it is invasive in many ecosystems globally. (e) Evidence of shellfish collection

and consumption by humans, including midden formation in areas of frequent shellfish deposition, such as beneath trees or around gathering locations.

5.4.2 Global human populations

The relationship between coastal human populations and shellfish-derived nutrients is not limited to the northeast Pacific. This relationship may be especially evident within the northeast Pacific due to the rich cultural history of the region, a wealth of Traditional Ecological Knowledge, and substantial research efforts (Deur et al. 2015, Lepofsky et al. 2015, Trant et al. 2016, Fisher et al. 2019); however, systematic utilization of shellfish by coastal populations is a global occurrence. For example, two shell middens, Sea Harvest and Hoedjies Punt in Saldanha Bay, South Africa, suggest coastal populations have been depositing shellfish-derived nutrients into terrestrial ecosystems for a minimum of 60,000 to 70,000 years before present (Volman 1978). In both instances, the biological material within these middens is composed predominantly of molluscs. Furthermore, 100 km north along the western Cape coast of South Africa, shellfish gathering from mid to low-intertidal zones was consistent throughout the late Holocene, with collections spanning further into the upper subtidal within the last 600 years (Jerardino 1997). The excavation of the Pancho’s Kitchen Midden, in Elands Bay, South Africa, illustrates shellfish harvesting in the region beginning at minimum 3,500 years before present and resulted in a stratified shellfish midden comprised of between 75 and 99% percent black mussels (*Choromytilus meridionalis*) across several defined layers (Jerardino 1997). Similarly, evidence of the relationship between coastal human populations and shellfish-derived nutrients has been observed throughout the Pacific Line Islands (Thomas 2014), the Asia-Pacific (Szabó and Amesbury 2011), Australia (Bird et al. 2002)) and throughout North-West Europe (Schulting et al. 2004).

Despite being less evident within contemporary culture, the removal of molluscs and other shellfish from marine ecosystems by coastal human populations is a global phenomenon, elevated due to expansion of aquaculture (FAO 2016). Currently, 18.8 million metric tons of non-cephalopod molluscs are landed annually by wild and aquaculture fisheries (FAO 2016), which comprise 11% of all global seafood production. Although the role this transfer of nutrients plays within terrestrial ecosystems remains unknown, if even a fraction of these nutrients enters terrestrial ecosystems, the potential for ecological responses is evident. As annual seafood consumption is set to increase by 1.5 kg per person in the coming decade (Delgado et al. 2003, FAO 2016), and especially as shellfish farming is incorporated in marine planning initiatives and developed with local ecological context (Holden et al. 2019), any effect on terrestrial ecosystems related to shellfish removal by industrial fisheries will only increase.

5.5 Conclusions

The current focus of spatial subsidies has been aimed at large nutrient-rich pulses, such as spawning Pacific salmon, that result in dramatic ecosystem responses. However, studies are increasingly showing that there are multiple avenues of marine subsidy acting to influence coastal terrestrial ecosystems (Ben-David et al. 1998, Spiller et al. 2010, Fox et al. 2015). Shellfish as a marine subsidy has received relatively less attention than many other sources of marine nutrients. Here we have summarized the known information regarding vectors of shellfish transfer to land, as well as documented and hypothesized effects to the adjacent terrestrial ecosystems. Given that shellfish are released from many temporal and spatial constraints imposed upon other marine subsidies, we suggest that they are an important, but under-represented source of marine nutrients. While recent archaeological work is beginning to shed light on the importance of shellfish on land

(Trant et al. 2016), there is still much to be done to understand the role of shellfish subsidies across larger spatial and temporal scales, and the impacts on multiple trophic levels.

Wild shellfish populations, much like salmon and seabird colonies, have suffered drastic reductions due to harvesting, habitat degradation and climate change. As an integral part of coastal ecosystems globally, further declines in shellfish populations will undoubtedly have far-reaching consequences. As such, there is a need to understand the extent that shellfish-derived nutrients contribute to terrestrial ecosystems, if the diverse coastal ecosystems shellfish have supported for millennia are to be maintained.

5.6 Author Contributions

Kieran Cox: Conceptualization, Investigation, Methodology, Project administration, Software, Visualization; Writing - original draft. **Hailey Davies:** Visualization, Writing - review & editing. **Katie Davidson:** Writing - review & editing. **Travis Gerwing:** Writing - review & editing. **Francis Juanes:** Project administration, Resources, Supervision, Writing - review & editing. **Sarah Dudas:** Project administration, Resources, Supervision, Writing - review & editing.

Chapter 6: Discussion

Mediating environmental degradation while ensuring sufficient resource extraction is one of the longest-standing challenges of human-ecosystem interactions. The ecological and societal benefits of achieving an appropriate balance between the two have transitioned humans' interactions with shellfish, from harvesting intertidal mollusks 164,000 years ago, to producing 20 million metric tons of mollusks in 2020 (Marean et al. 2007, FAO 2020, Naylor et al. 2021). This connection is so spatially and temporally robust that the use of mollusks, specifically, the creation of shellfish middens, has been proposed as a proxy for ancient human activities and a marker for determining when the Anthropocene Epoch began (Erlandson 2013, Thompson et al. 2020a). Nevertheless, concurrent examinations between ecological implications of clam gardens and shellfish farms are lacking. Separate examinations, however, have led to insight into how intertidal resource extraction, directly and indirectly, influences ecological communities. Here I contribute to current literature on each topic and present the first scientific examination of both practices concurrently.

Cultivation's influences on bivalve productivity is a primary interest in both clam gardens and shellfish farms research (British Columbia et al. 2002, Bostock et al. 2010, Jackley et al. 2016, FAO 2020, Naylor et al. 2021). Chapter 3 supports Groesbeck et al.’s (2014) observation that biomass within clam gardens increases due to the ecological conditions created by wall construction, beach composition, and sediment alterations, and expands this understanding to include a comparison of clam productivity when controlling for tidal height. Examining clam gardens and shellfish farms concurrently also refutes a sparse comparison made by Munroe et al. (2015), which concluded that Groesbeck et al. (2014) observed 2 kg of biomass per m^3 and Munroe (2006) observed 4 kg per m^3 meaning clam gardens could not achieve shellfish farming production levels. Munroe's comparison and conclusions are invalid for several reasons. Munroe

(2006) surveyed *Venerupis philippinarum* using a 15 cm diameter core dug to depths of 15 cm, whereas Groesbeck et al. (2014) surveyed *Leukoma staminea* and *Saxidomus gigantea* using a 25 x 25 cm quadrat dug to depths of 30 cm. Contrasting population parameters collected using a 2-fold difference in depths when sampling populations primarily distributed in the top 15 cm of sediment is inaccurate, especially true densities are compared (e.g. kg per m^3). The biomass estimates in Chapter 3 offer a more reasonable comparison as all surveys used 25 x 25 cm quadrats dug to 20 cm depths. Clam gardens contribute an additional 1.79 kg of *L. staminea* and *S. gigantea* beyond reference site productivity. The cumulative biomass of *S. gigantea*, *L. staminea*, *R. philippinarum* and *N. obscurata*, within clam gardens was 4.7 kgs per m^3. Shellfish farms dug to the same depths yielded 3.6 kg per m^3, a 1.1kg reduction in standing biomass. Finally, Munroe et al. (2015) asserts that clam garden harvesting practices remove nearly all available biomass, causing annual depletions. Several lines of evidence indicate that clam garden management includes size selection, broodstock enrichment, and seeding (Groesbeck et al. 2014, Deur et al. 2015, Lepofsky et al. 2015, H-GINPR 2016, Turner 2020).

Ecological responses to cultivation are the principal focus of this thesis, with a specific interest in how taxa that are not the primary targets of cultivation respond. Examining this question within clam gardens poses several challenges. Although termed clam gardens, numerous taxa were harvested from these intertidal terraces, with the well-known adage "when the tide is out, the table is set". Still, broad comparisons such as those presented in Chapter 3 provide insight into epifaunal community responses. Furthermore, it is worth considering the habitat that is excluded when a clam garden is constructed. Limited scientific data exist on the topic, but presumably, communities that require sloping intertidal beaches are excluded (e.g. eelgrass) and communities that benefit from subtidal hard substrates (*e.g.* kelps) benefit. Species responses to shellfish farming are well-documented, the primary concern being introduced taxa (Whiteley and Bendell-Young 2007, Callier et al. 2018, Whalen et al. 2020). Chapter 4 observed similar species responses as Bendell (2014), but interprets responses quite differently. For example, Bendell (2014)'s conclusion that increases in *Hemigrapsus oregonensis* warrant concern did not seem accurate when considering epifaunal and bivalve species abundances concurrently. Bendell (2014) also observed *Batillaria attramentaria*, the Japanese mud snail, increases within reference sites, but provided limited insight into how a 'hitch-hiker' that arrived with shellfish seed becomes more abundant at unmodified sites. Chapter 4 postulates that such an observation is worth considering as it suggests an invasive species model, where the introduction vector (*i.e.* oyster seed) allocates the species to suboptimal habitat, and proliferation occurs once the species reaches an optimal habitat. It is also worth noting that most of the taxa introduced intentionally or accidentally to shellfish farms are now present on clam gardens. The ecological ramifications of these introductions are unresolved but are important to consider with clam garden restoration efforts continuing.

My research also integrates several novel techniques and validates established survey methods. Chapter 2 established that epifaunal surveys using subsample techniques and extrapolating abundances are viable across a range of soft-sediment habitats. Chapter 3 demonstrated that although sediment cores are a more common sampling method, dug quadrats offer substantially improved detection of diversity and abundances (Munroe 2006, Cox et al. 2019, Gerwing et al. 2020). The use of Structure from Motion SfM photogrammetry is becoming increasingly common. However, most of the scientific fields using SfM have used increasingly innovative habitat complexity metrics over the past few decades, making them more capable of adopting novel technologies (Burns et al. 2015, Young et al. 2017, Bayley and Mogg 2020).

Here I employed SfM within habitats, broadly considered to lack complexity, gaining valuable insight into how increasing habitat complexity can foster distinct biological communities. The novel application of SfM, in this instance, suggests that the quality of the rendered models will support comparison in a majority of habitat types. It also indicates that examining habitat complexity is relative, and it is possible to glean information from areas with seemingly low complexity. Furthermore, models created with SfM generate a permanent record of habitats' conditions. This attribute is becoming increasingly valuable in habitats experiencing anthropogenically mediated simplification (*e.g.* coral reefs), an unfortunate warning for research in adjacent systems (Magel et al. 2019, Pascoe et al. 2021).

Emerging evidence indicates that shellfish cultivation has ecological implications that span well-beyond the intertidal. Most notably throughout the northeast Pacific is when shellfish-derived nutrients are transported across the marine-terrestrial interface and deposited within forest ecosystems (Trant et al. 2016, Fisher et al. 2019). Chapter 5 illustrates several vectors facilitating shellfish subsidies, providing a detailed account of why these subsidies should be considered concurrently to salmon or herring (Hocking and Reimchen 2006, Darimont et al. 2009c, Hocking and Reynolds 2011, Fox et al. 2015). Furthermore, several Indigenous stewardship practices purposely deposit shellfish within terrestrial ecosystems (*e.g.* landscape terracing, promoting drainage). Over time these deposits interact with other longer-term management systems, particularly, controlled burns that modify soil chemistry and increase forest productivity. Ecosystem management at this spatial and temporal scale provides a representative example of Indigenous stewardship (Hoffman et al. 2016, Trant et al. 2016). Unfortunately, they also provide a jarring record of the influence of European diseases' and other impacts of colonization on Indigenous stewardship (Deur et al. 2015, Hoffman et al. 2016, Smith et al. 2019).

The ecological processes identified throughout my thesis research are conceivably attributed to changing habitat complexity or ecological disturbances. Similarly, Theuerkauf et al. (2021) documents how the provisioning of structured habitat by shellfish farms influences species richness and abundance, concluding that oyster culture yields the most taxonomic responses. The provisioning of food resources along with enhanced reproduction and recruitment potential also contribute to the magnitude of species responses. These ecological processes are likely not limited to shellfish farms, nor are they taxonomically constrained. Shellfish farm infrastructure serves as fish aggregating devices and artificial reefs with several observed attraction and repulsion mechanisms (Callier et al. 2018). For example, bivalves, echinoderms, and polychaetes are attracted to shellfish farms, whereas eelgrass is competitively excluded (Kelly et al. 2008, Callier et al. 2018).

One of the primary mechanisms by which habitat complexity fosters ideal conditions for bivalves and increases in biodiversity is mediating water flow rates. Recent research has shown that shells deposited within soft-sediment habitats expedite the onset of sediment transport while simultaneously reducing ripple dimensions and slowing ripple migration (Cheng et al. 2021). Furthermore, there is a positive correlation between shell content and near-bed flow velocity due to reduced surface friction, partly attributed to decreases in average ripple size and occurrence (Cheng et al. 2021). Functionally, high naturally occurring or augmented shell concentrations in soft-sediment ecosystems will considerably influence the habitat's morphodynamics (Cheng et al. 2021). The addition of epifaunal bivalves will further regulate this process as these taxa are fractal at a spatial scale relevant to hydrodynamics, with greater regulatory control as the height of the oyster reef or rock wall increases (Commito and Rusignuolo 2000, Hogan and Reidenbach 2021). Collectively, this means the addition of shells and live bivalves promotes flow conditions ideal for these taxa.

Disturbance-mediated opportunities are another possible mechanism facilitating ecological responses within clam gardens and shellfish farms. Although disturbance as a unifying ecological force has been the topic of warranted debate (Gerwing et al. 2017, 2018), its role in limiting community homogenization, increasing genetic diversity, and ecological resilience is evident (Foster 2021). If applicable to clam gardens and shellfish farms, this suggests the process of digging clams, aerating sediments, and altering complexity, increases diversity at several ecological scales (e.g. genetic, taxonomic community). Therefore, the proposed link between taxonomic diversity and biomass illustrated in Chapter 3 may indirectly be a function of management-related disturbances.

A predominant model in conservation separates humanity from nature. Two distinct views facilitate this: numerous anthropogenic forces directly oppose natural processes, but also, there is an opinion that to conserve a species or ecosystem, avoid it (Robb et al. 2015, Ban et al. 2019, Tran et al. 2020). Indeed, an avoidance model has irrefutable positive outcomes for conservation; however, it is not always feasible (Venter et al. 2006). Alternative approaches, including community-based conservation, propose including humans as an integral component within a complex adaptive system (Berkes 2004). This strategy reaffirms several aspects of Traditional Ecological Knowledge and Indigenous stewardship (Turner et al. 2000, Artelle et al. 2019, Berkes et al. 2021). Clam gardens have exemplified this approach to human-ecosystem interactions for millennia. Shellfish farms appear to have similar potential. Examining these management practices in parallel has the potential to promote plural coexistences of both systems and contributes to a more equitable and sustainable future (Reid et al. 2021). This examination would provide foundation for a broader dialogue on historical and current coastal resource use, multiple species management, and biodiverse conservation (Berkes 2004, Brown et al. 2009, Froehlich et al. 2017a, Berkes et al. 2021). My doctoral research contributes an essential step towards this objective by illustrating that ongoing processes have shaped coastal ecosystems over the past millennia. The cultivation and stewardship of coastal species will continue to be an interconnected component of conserving the northeast Pacific's dynamic ecosystems.

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Appendices

Appendix A: Chapter Two Supplementary Material

Supporting Information For

Chapter 2: Community Assessment Techniques and the Implications for Rarefaction and Extrapolation with Hill Numbers

A1: Species Diversity (Mean +/- standard error) detected by the five assessment methodologies utilized during this study.

		Photo Quads	Point Intersect	Subsampling	Full Quads	Validation
Sessile Invertebrates	*B. glandula*	0	6.12 +/-0.9	142.46 +/-23.8	344.92 +/-66.2	706.50 +/-112.2
	C. dalli	0	0	0.19 +/-0.1	0.88 +/-0.6	1.83 +/-1.2
	Mytilus Spp.	0	0	0.35 +/-0	1.15 +/-0	0.83 +/-0.7
	Balanus Spp.	4.42 +/-0.7	0	0	0	0.33 +/-0.3
	C. gigas	1.35 +/-0.3	1.50 +/-0.4	0.19 +/-0.1	0.69 +/-0.3	1.50 +/-1.0
	A. Artemisia	0	0	0	0.04 +/-0	0
Mobile Invertebrates	*M .columbiana*	0	0	0.60 +/-0.2	2.77 +/-0.9	4.50 +/- 2.0
	T. persona	0	0.50 +/-0.2	7.85 +/-2	27.12 +/ 6	47.33 +/-19.0
	P. torva	0	0	0	0	0.17 +/-0.2
	L. sitkana	0	0.04 +/-0	2.04 +/-0.6	3.46 +/-1.0	13.33 +/-7.2
	H. oregonensis	0	0.19 +/-0.1	2.31 +/-0.5	6.54 +/-2.0	7.50 +/-2.2
	P. spp	0	0	0	1.00 +/-0.5	0.33 +/-0.3
	Hemigrapsus Spp	0	0.46 +/-0.2	12.50 +/-4.2	29.69 +/-5.1	57.83 +/-36.4
	B. attramentaria	0	0.58 +/-0.3	0.88 +/-0.4	12.73 +/-11.4	3.17 +/-1.7
	Nucella Spp.	0.08 +/-0.1	0	0.12 +/-0.1	0.54 +/-0.2	0.83 +/-0.7
	L. scutulata	0	0	0.69 +/-0.4	2.54 +/-1.4	7.50 +/-6.6
	Littorina Spp	0.04 +/-0	0.04 +/-0	0.12 +/-0.1	0	0.50 +/-0.5
	H. nudus	0	0.04 +/-0	0.04 +/-0	0.65 +/-0.3	0
	P. caurinus	0	0	0	0.04 +/-0	0
	I. wosnesenskii	0	0	0.35 +/-0.3	0.58 +/-0.5	0
	V. philippinarum	0	0	0	0.08 +/-0.1	0
	P. peregrina	0	0	0.04 +/-0	0.08 +/-0.1	0
	U. pugettensis	0	0	0.04 +/-0	0	0

	T. scutum	0.12 +/-0.1	0	0	0	0
Algae	*Hildenbrandia Spp.*	0	0	0	40.38 +/-19.2	64.67 +/64.7
	Gracilaria Spp	0.04 +/-0	0.58 +/-0.2	6.54 +/-4.9	18.38 +/-10.7	52.00 +/-33.3
	Ulva Spp.	0.23 +/-0.2	0.08 +/-0.1	0	0	0.50 +/-0.5
	M.jardinii	0	0.12 +/-0.1	9.92 +/-5.7	0	0
	Ceramium Spp	0.65 +/-0.2	0.19 +/-0.2	3.00 +/-2.1	1.27 +/-1.1	0
	E. muricata	0.65 +/-0.2	0.00 +/-0	0.00 +/-0	0	0

Appendix B: Chapter Three Supplementary Material

Supporting Information For

Chapter Three: Shellfish Cultivation Over Millennia Bolsters Bivalve Communities and Diversity-Biomass Relationships

Supplemental Figures:

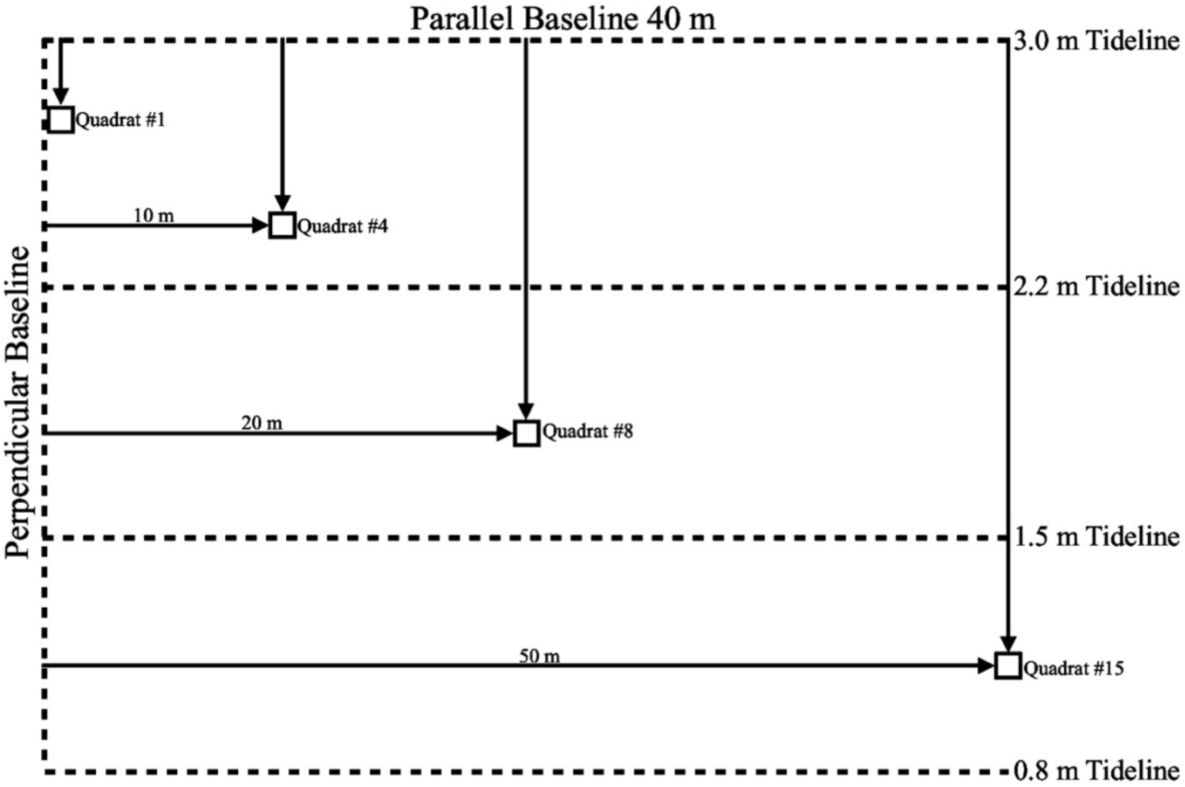

Fig. B1. Assessment area and quadrat placements during the field assessments. The assessment area was established using horizontal and vertical baselines that ran parallel and perpendicular to the shoreline, respectively. Quadrat placement was at the intersection of lines extended from the horizontal and vertical baselines. Five quadrats were placed within each zone. Examples of quadrat placement are illustrated by the 1st, 4th, 8th and 15th quadrats.

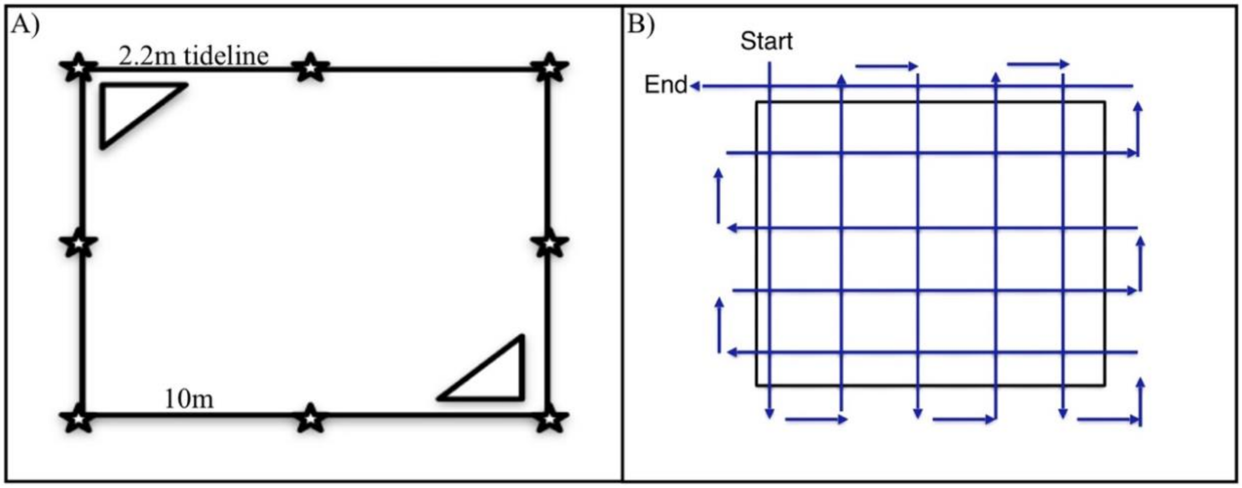

Fig. B2. Structure from Motion (SfM) Photogrammetry site assessment diagrams. A) 10 × 10 m SfM assessment area. Ground control point locations are denoted by stars. Length bars used for calibration are indicated as triangles. Top area was placed along the 2.2 m tideline. B) Example site assessment patterns used to ensure the entire assessment area was covered. Deviations from this pattern occurred if the assessment area responded poorly to trampling (e.g. intertidal mudflats).

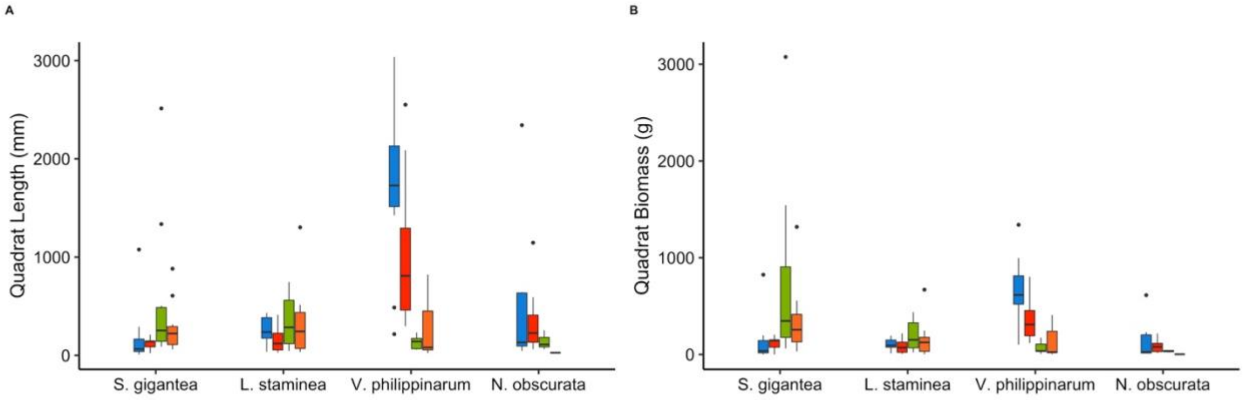

Fig. B3. A) Cumulative length per focal species averaged across sites. Reported as mm per quadrat (50 x 50 cm and 25 cm depth. B) Focal species estimated biomasses per quadrat, derived using observed lengths and length-weight equations.

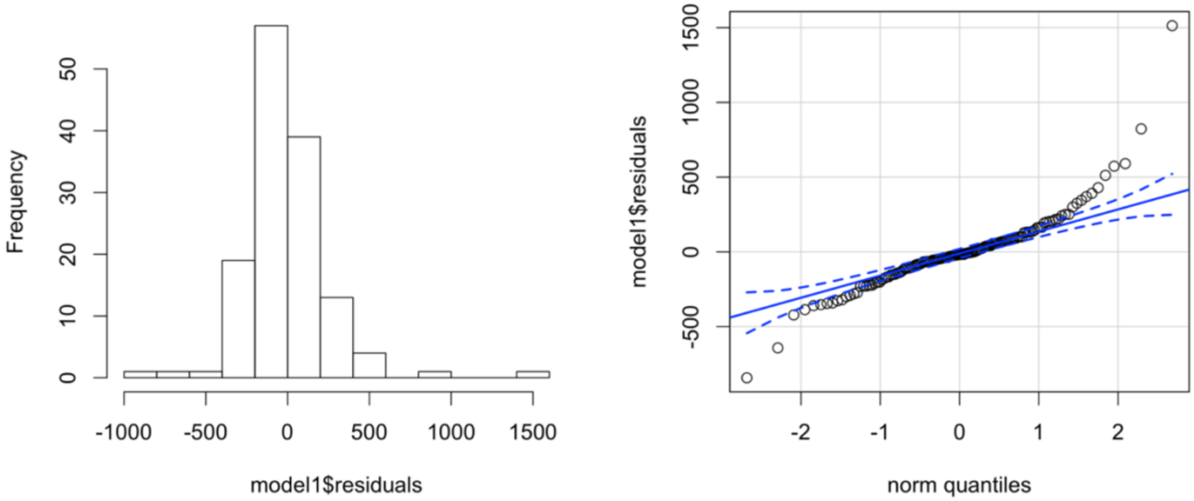

Fig. B4. Histogram of residuals and a Q-Q plot resulting from an ANOVA of bivalve biomasses within clam gardens, unmodified clam garden reference beaches, shellfish farms, and unmodified shellfish farm reference beaches. Four focal species biomasses were considered.

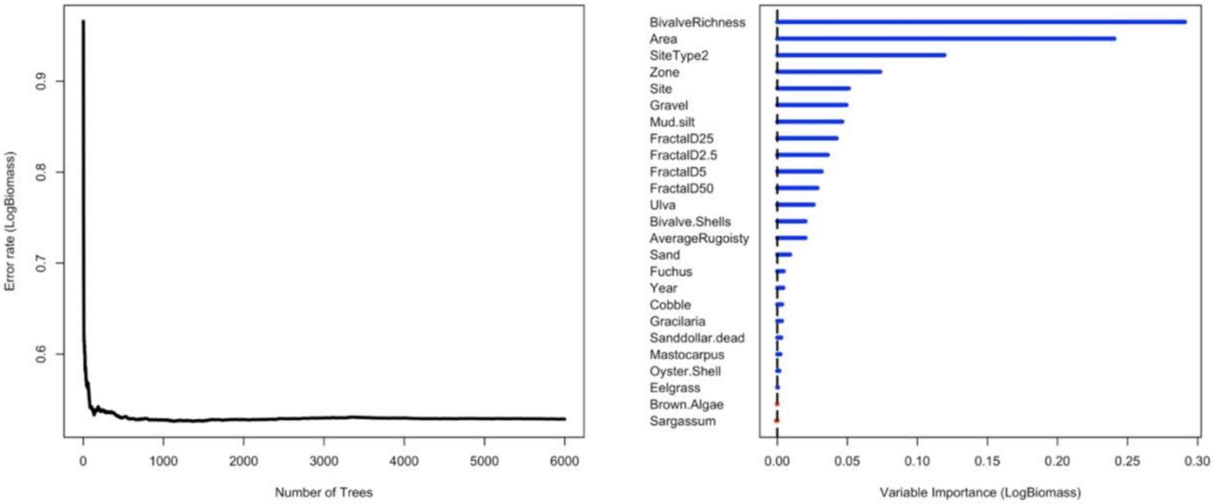

Fig. B5. Random forest trees selection process and variable importance analysis.
A low and stable error rate indicated the number of trees required. The resulting random forest was constructed using 6,000 trees. Variable importance analysis examining the influence of substrate composition, habitat complexity, site type, area, intertidal zone, and bivalve species richness on log bivalve biomass. Decreases in the mean squared error scale showed the relative importance of the predictor variables. Higher bars equate to greater variable importance. Variables of low importance (e.g. Sargassum, Brown.Algae, Oyster.Shell, Eelgrass, Sanddollar.dead, Mastocarpus, Fuchus, Gracilaria, Cobble, Year) were subsequently removed to improve the descriptive and predictive capabilities of the model.

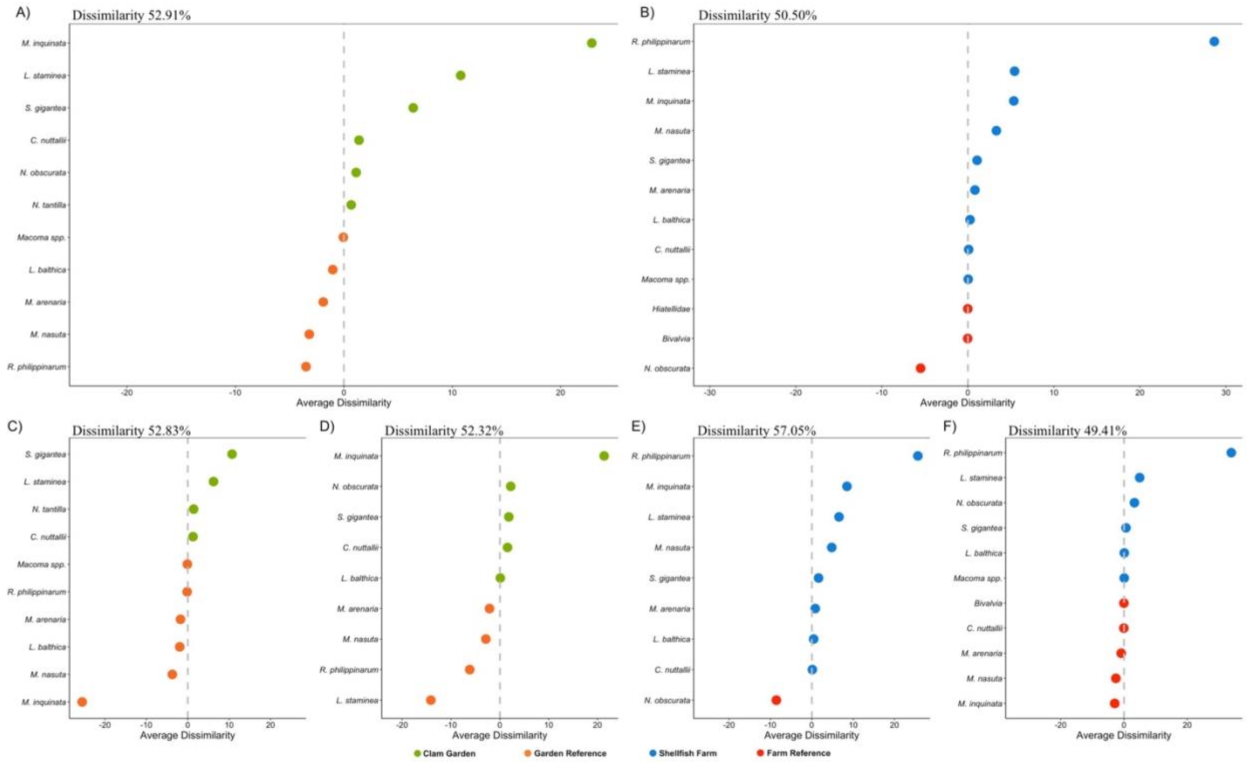

Fig. B6 Taxa-specific average dissimilarity between cultivated habitats and unmodified beaches derived from similarity percentage analyses. Average densities increase in clam gardens (green) or unmodified beaches (orange). Average densities increase in shellfish farms (blue) or unmodified beaches (red). A) Clam gardens and unmodified clam garden reference beach comparison. B) Shellfish farms and unmodified shellfish farm reference beach comparison. Clam gardens and unmodified clam garden reference beach comparison within C) Hakai Lúxvbálís Conservancy and D) Northern Quadra Island. Shellfish farms and unmodified shellfish farm reference beach comparison within E) Southern Quadra Island and F) Baynes Sound.

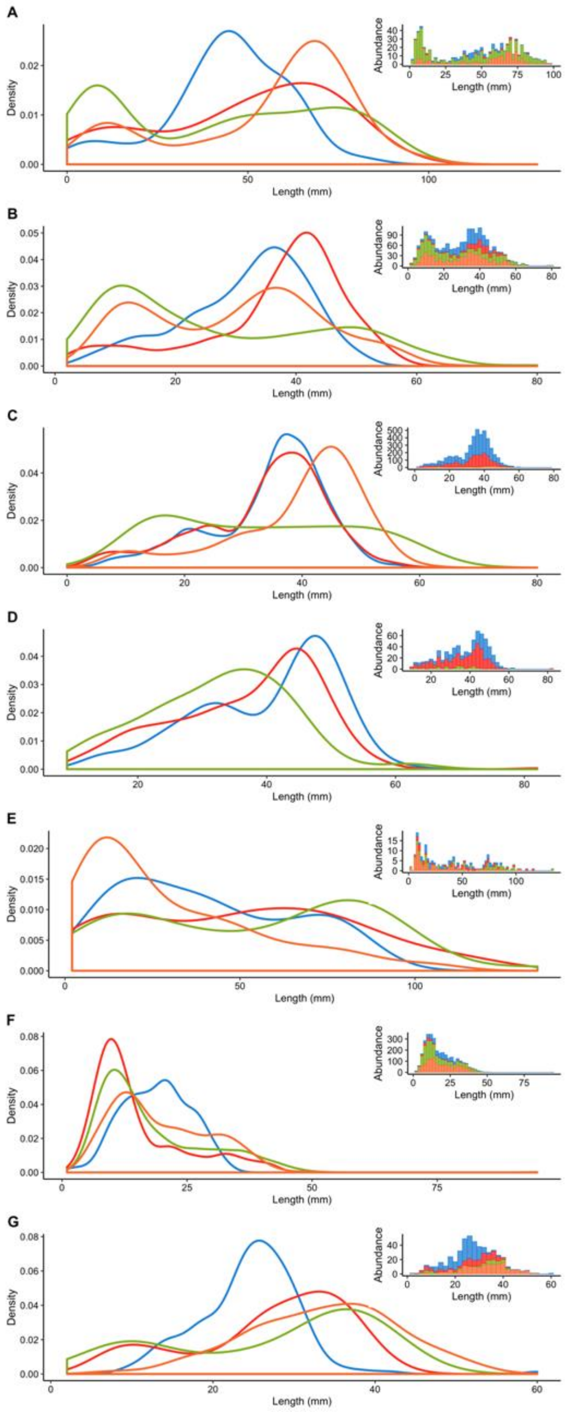

Fig. B7. Bivalve length distributions within cultivated and unmodified habitats, and bivalve biomass per sampling unit. Main and subplots display length frequencies and length abundances, respectively. A) *S. gigantea*, B) *L. staminea*, C) *V. philippinarum*, D) *N. obscurata* E) *M. arenaria*, F) *M. inquinata*, G) *M. nasuta*.

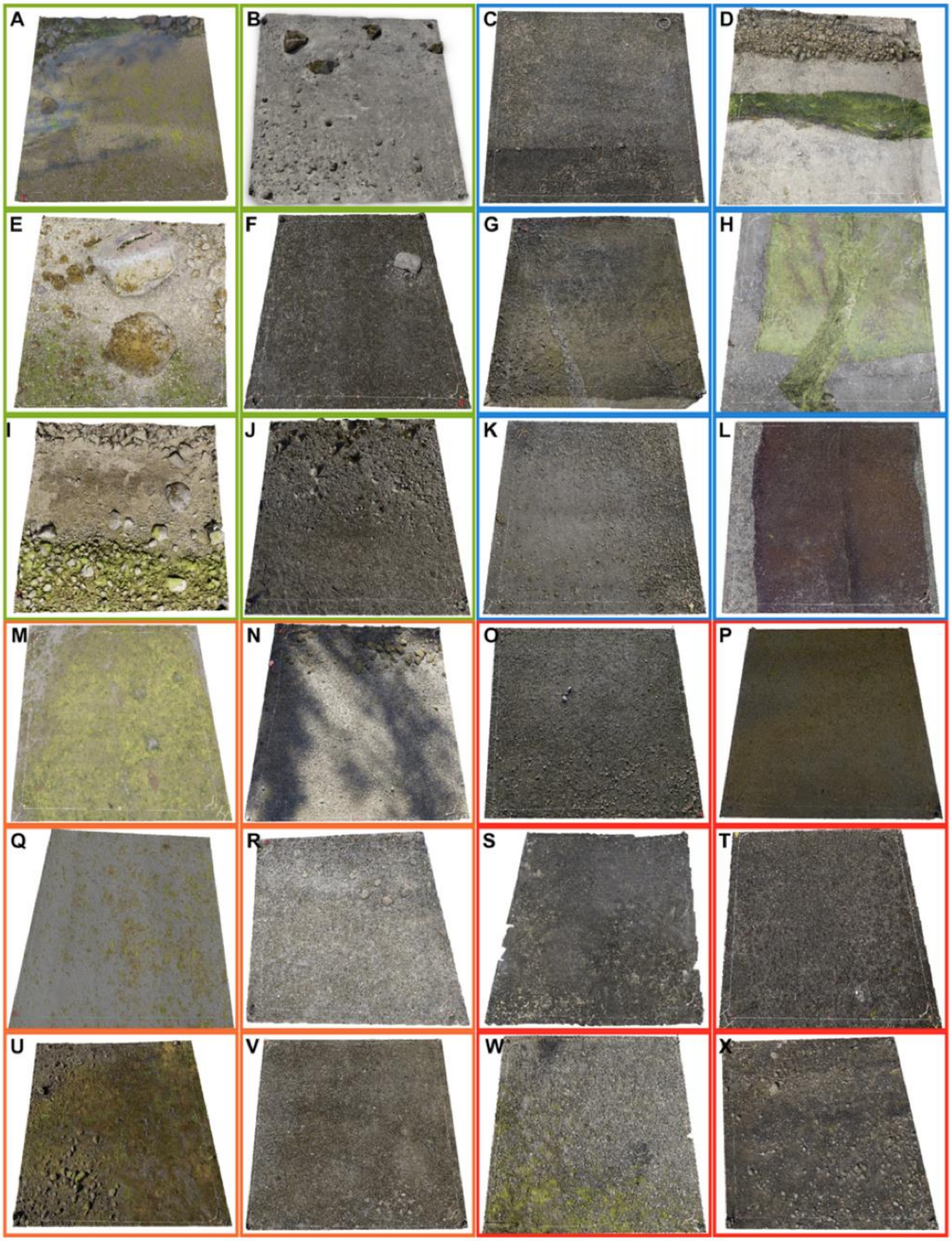

Fig. B8. Three-dimensional reconstructions of the 24 sites. **A, E, I)** Calvert Gardens. **B, F, J)** Quadra Gardens. **C, G, K)** Quadra Shellfish Farms. **D, H, L)** Baynes Shellfish Farms. **M, Q, U)** Calvert Garden References. **N, R, V)** Quadra Garden References. **O, S, W)** Quadra Farm Reference. **P, T, X)** Baynes Farm Reference.

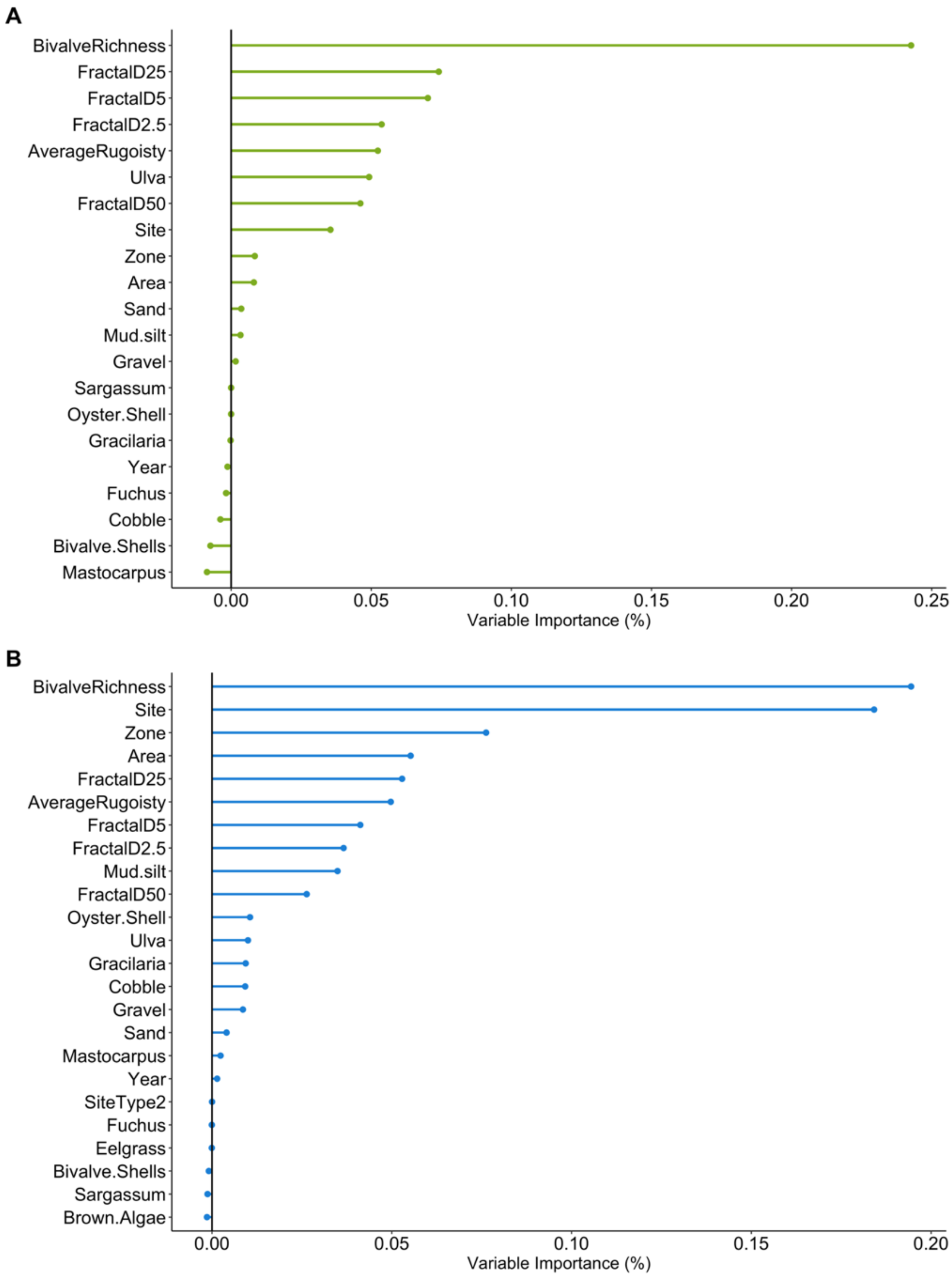

Fig. B9. The mechanisms facilitating elevated bivalve estimated biomass. Random forest variable importance analysis examining the influence of substrate composition, habitat complexity, site type, area, intertidal zone, and bivalve species richness on log bivalve biomass. Random forest variable importance analyses conducted on E) clam garden data and F) shellfish farm data.

Supplemental Tables

Table B1. Samples used for a multivariate regression tree analysis of sediment grain sizes and associated bivalve communities. Samples are co-occurring sediment cores and bivalve surveys. One hundred eighty-five samples were collected across the three survey regions.

Area	Site Type	Site	Zone	Sample Size
Baynes	Farm	REID	High	3
			Mid	3
			Low	3
		Taylor	High	3
			Mid	5
			Low	3
		TRAN	High	3
			Mid	3
			Low	3
	Farm Reference	DBR	High	3
			Mid	3
			Low	3
		NOT	High	3
			Mid	3
			Low	3
		RES	High	3
			Mid	3
			Low	3
Calvert	Garden	CGN	Mid	1
			Low	3
		NUXI	Mid	3
			Low	3
		TWG	Mid	4
			Low	2
	Garden Reference	HCG	Mid	3
			Low	3
		MBR	High	3
			Mid	3
			Low	3
		Piles	High	3
			Mid	3
Quadra	Farm	FAB	High	2
			Mid	3
			Low	3
		LHB	High	2
			Mid	3
			Low	3
		SMB	High	3
			Mid	3
			Low	3
	Farm Reference	HBI	High	1
			Mid	3
			Low	4
		LEN	High	4
			Mid	1

			Low	3
			High	3
		WWK	Mid	3
			Low	3
			High	1
		KB11	Mid	3
			Low	3
			High	2
	Garden	KB25	Mid	5
			Low	3
			High	3
		KB7	Mid	5
			Low	3
		KB12	Mid	4
	Garden Reference	KB8	Mid	5
		SWC	Mid	5

Table B2. Samples used for a multivariate regression tree analysis of the interaction between bivalve communities and substrate organics, carbonates, and water content. Samples are co-occurring organics, carbonates, and water content cores and bivalve surveys. Eighty-seven samples were collected across the three survey regions.

Area	Site Type	Site	Zone	Sample Size
Baynes	Farm	REID	High	3
			Mid	3
			Low	3
		Taylor	High	3
			Mid	5
			Low	3
		TRAN	High	3
			Mid	3
			Low	3
	Farm Reference	DBR	High	3
			Mid	3
			Low	3
		NOT	High	3
			Mid	3
			Low	3
		RES	High	3
			Mid	3
			Low	3

Quadra	Farm	FAB	Mid	3
		LHB	Mid	3
			Low	3
		SMB	Mid	3
	Farm Reference	WWK	High	1
	Garden	KB11	Mid	3
		KB25	Mid	5
		KB7	Mid	2
	Garden Reference	KB12	Mid	4
		SWC	Mid	4

Table B3. Length-weight relationships for the four primary targets of shellfish cultivation. The weight (W) of a clam, given its shell length (L), is determined using α and β parameters to solve $W = \alpha L^{\beta}$. α and β parameters are derived from field surveys examining Length-weight relationships.

Taxa	Sample Size	α	β	Survey Location	Source
Butter clam (*Saxidomus gigantea)*	5,052	0.00007324	3.31	Puget Sound. Bivalve regions 8 and 14	(Bradbury et al. 2005)
Pacific littleneck clam (*Leukoma staminea)*	18,700	0.0002185	3.093	Puget Sound. Bivalve regions 5 and 14	(Bradbury et al. 2005)
Manila clam (*Ruditapes philippinarum*)	47,357	0.0001821	3.095	Puget Sound. Bivalve regions 8 and 21	(Bradbury et al. 2005)
Varnish clam (*Nuttallia obscurata)*	880	0.00006	3.2255	Áyhus Island	(Gillespie et al. 1999)

Table B4. Analyses of bivalve diversity and densities detected by the three survey methods. Core = 5,000 cm^3, small quad = 12,500 cm^3, large quad = 50,000 cm^3. A) Separate Kruskal-Wallis rank sum tests of the detected bivalve diversity and densities. B) Separate Dunn's test analyses conducting nonparametric multiple pairwise comparisons to determine if the bivalve diversity or density detected during each assessment varied between methods. The Dunn's tests were conducted post hoc following a Kruskal–Wallis rank sum test. Significant p values (< 0.05) are indicated via *, p values < 0.01 are indicated via **.

A)	**Chi-squared**	**Degrees of Freedom**	**p-value**
Species Diversity~ Survey Method	39.21	2	3.057e-9**
Species Density~ Survey Method	12.28	2	0.002151**

B)			
		Core	**Large Quad**
Species Diversity~ Survey Method	**Large Quad**	0.0000**	
	Small Quad	0.001**	0.0061**
		Core	**Large Quad**
Species Density~ Survey Method	**Large Quad**	0.0057**	
	Small Quad	0.0018**	0.33

Table B5. PERMANOVA (permutational multivariate analysis of variance) assessing if bivalve community composition varied between clam gardens, shellfish farms, and unmodified reference beaches. A) Comparison of all habitat types. Comparisons of clam gardens and unmodified clam garden reference beaches within B) Hakai Lúxvbálís Conservancy "Calvert Island" and C) northern Quadra Island. Comparisons of shellfish farms and unmodified shellfish farm reference beaches within D) southern Quadra Island and F) Baynes Sound. Mean of Squares 'MS', Degree of Freedoms 'DF', Sum of Squares 'SS'.

A)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Clam Garden	Site Type	3	9.88	3.29	32.52	0.001
	Shellfish Farms	Year	1	0.28	0.28	2.80	0.028
	Garden Reference	Site Type: Site	20	9.36	0.47	4.62	0.001
	Farm Reference	Residuals	210	20.46	0.10		

B)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Calvert Island Gardens and Reference Sites	Site Type	1	0.53	0.53	4.44	0.007
		Year	1	0.29	0.29	2.45	0.076
		Site Type: Site	4	1.91	0.48	4.01	0.003
		Site Type: Site: Quad	31	3.33	0.11	0.90	0.693
		Residuals	17	2.02	0.12		

C)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***

	Quadra Island Gardens and Reference Sites	Site Type	1	0.16	0.16	0.81	0.540
		Year	1	0. 36	0.36	1.76	0.144
		Site Type: Site	4	1.85	0.46	2.26	0.027
		Site Type: Site: Quad	43	4.70	0.11	0.54	0.999
		Residuals	7	1.43	0.20		

D)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Quadra Island Shellfish Farms and Reference Sites	Site Type	1	0.69	0.69	4.61	0.004
		Year	1	0.34	0.34	2.29	0.053
		Site Type: Site	4	1.52	0.38	2.56	0.013
		Site Type: Site: Quad	41	5.32	0.13	0.87	0.719
		Residuals	9	1.34	0.15		

E)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Baynes Sound Shellfish Farms and Reference Sites	Site Type	1	1.10	1.10	11.59.88	0.002
		Year	1	0.21	0.21	2.21	0.106
		Site Type: Site	4	1.62	0.41	4.26	0.003
		Site Type: Site: Quad	42	3.12	0.07	0.78	0.815
		Residuals	9	0.86	0.10		

Table B6. SIMPER (Similarity Percentages) analyses of each taxonomic group's contribution to differences observed between intertidal study site types. A) Clam gardens and unmodified clam garden reference beach comparison. B) Shellfish farms and unmodified shellfish farm reference beach comparison. Clam gardens and unmodified clam garden reference beach comparison within C) Hakai Lúxvbálís Conservancy "Calvert Island" and D) northern Quadra Island. Shellfish farms and unmodified shellfish farm reference beach comparison within E) Southern Quadra Island and F) Baynes Sound.

Taxa	**Average Density**	**Average Density**	**Average Dissimilarity (%)**	**Contribution Standard Deviation**	**Average S.D. ratio.**	**Contribution (%)**	**Cumulative (%)**
A)	**Clam Gardens**	**Reference Sites**			**Average dissimilarity = 52.91%**		
M. inquinata	26.72	23.05	22.87	16.48	1.39	43.24	43.24
L. staminea	12.83	10.64	10.77	9.73	1.11	20.37	63.6
S. gigantea	8.6	4.03	6.4	9.25	0.69	12.1	75.71
R. philippinarum	2.47	3.81	3.49	6.42	0.54	6.6	82.3
M. nasuta	2.09	3.78	3.19	5.49	0.58	6.03	88.33
M. arenaria	1.85	2.46	1.9	3.92	0.49	3.59	91.92
C. nuttallii	2.45	1.85	1.4	1.68	0.83	2.64	94.56
N. obscurata	1.94	1.03	1.13	4.18	0.27	2.14	96.7
L. balthica	1.45	1.59	1.02	3.31	0.31	1.93	98.63
N. tantilla	1.83	1.1	0.68	1.59	0.43	1.28	99.91

Macoma spp.	1	1.03	0.05	0.41	0.12	0.09	100

B)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 50.50%**		
R. philippinarum	49.64	29.6	28.65	18.74	1.53	56.73	56.73
N. obscurata	5.05	6.96	5.5	8.4	0.65	10.89	67.62
L. staminea	8.07	5.04	5.43	5.24	1.03	10.74	78.36
M. inquinata	8.51	3.4	5.33	7.89	0.68	10.56	88.92
M. nasuta	4.42	2.89	3.31	5.68	0.58	6.55	95.47
S. gigantea	2.14	1.39	1.07	2.64	0.4	2.11	97.58
M. arenaria	1.68	1.46	0.81	1.31	0.62	1.61	99.19
L. balthica	1.42	1.07	0.25	1.21	0.21	0.5	99.69
C. nuttallii	1.07	1.04	0.08	0.37	0.23	0.17	99.85
Macoma spp.	1.05	1	0.03	0.25	0.13	0.06	99.92
Bivalvia	1.02	1.02	0.03	0.17	0.17	0.06	99.97
Hiatellidae	1	1.02	0.01	0.11	0.13	0.03	100

C)	**Clam Gardens**	**Reference Sites**			**Average dissimilarity = 52.83%**		
M. inquinata	27.6	27.7	25.53	17.83	1.43	48.33	48.33
S. gigantea	15.56	5.83	10.71	11.46	0.93	20.27	68.6
L. staminea	10.08	3.1	6.22	5.52	1.13	11.78	80.38
M. nasuta	1.4	4.53	3.74	6.37	0.59	7.07	87.45
L. balthica	1.8	2.17	1.95	4.53	0.43	3.68	91.14
M. arenaria	1.56	2.4	1.76	4.8	0.37	3.32	94.46
N. tantilla	2.76	1.2	1.41	2.13	0.66	2.67	97.13
C. nuttallii	2.04	1.9	1.26	1.35	0.93	2.39	99.52
R. philippinarum	1	1.13	0.15	0.53	0.29	0.29	99.81
Macoma spp.	1	1.07	0.1	0.61	0.16	0.19	100

D)	**Clam Gardens**	**Reference Sites**			**Average dissimilarity = 52.32%**		
M. inquinata	25.93	18.24	21.34	15.81	1.35	40.79	40.79
L. staminea	15.29	18.45	14.13	11.29	1.25	27	67.79
R. philippinarum	3.79	6.59	6.17	8.06	0.77	11.8	79.59
M. nasuta	2.71	3	2.88	5.08	0.57	5.5	85.09
N. obscurata	2.79	1.07	2.21	5.82	0.38	4.22	89.3
M. arenaria	2.11	2.52	2.13	3.08	0.69	4.07	93.37
S. gigantea	2.39	2.17	1.83	2.85	0.64	3.49	96.86
C. nuttallii	2.82	1.79	1.56	2.04	0.76	2.98	99.84
L. balthica	1.14	1	0.08	0.44	0.19	0.16	100

E)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 57.05%**		
R. philippinarum	38.21	29.86	25.64	17.9	1.43	44.94	44.94
N. obscurata	2.34	11.75	8.59	9.86	0.87	15.05	59.99
M. inquinata	15.31	2.79	8.48	9.91	0.86	14.87	74.86
L. staminea	8.72	5.11	6.56	6.47	1.01	11.5	86.35
M. nasuta	7.79	1.96	4.8	6.93	0.69	8.42	94.77
S. gigantea	2.83	1.43	1.62	3.7	0.44	2.84	97.61
M. arenaria	1.86	1.18	0.81	1.33	0.61	1.43	99.03
L. balthica	1.79	1.11	0.43	1.69	0.25	0.75	99.79
C. nuttallii	1.1	1.04	0.12	0.49	0.25	0.21	100

F)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 49.41%**		
R. philippinarum	60.7	29.34	33.91	19.38	1.75	68.63	68.63
L. staminea	7.43	4.97	4.95	4.51	1.1	10.01	78.64
N. obscurata	7.67	2.34	3.29	7.35	0.45	6.67	85.31
M. inquinata	1.93	4	2.94	4.58	0.64	5.95	91.26
M. nasuta	1.17	3.79	2.57	4.6	0.56	5.2	96.46
M. arenaria	1.5	1.72	0.89	1.4	0.63	1.8	98.26
S. gigantea	1.47	1.34	0.62	1.05	0.59	1.25	99.51
L. balthica	1.07	1.03	0.09	0.37	0.24	0.18	99.69
Macoma spp.	1.1	1	0.07	0.36	0.18	0.13	99.82
C. nuttallii	1.03	1.03	0.05	0.23	0.24	0.11	99.93
Bivalvia	1	1.03	0.03	0.2	0.17	0.07	100

Table B7. Examination of bivalve biomass within clam gardens, unmodified clam garden reference beaches, shellfish farms, and unmodified shellfish farm reference beaches. ANOVA summarized the analysis of model variance. Mean of Squares ‘MS’, Degree of Freedoms ‘DF’, Sum of Squares ‘SS’. A histogram of residuals illustrated a normal distribution.

	DF	**SS**	**MS**	**F-value**	**Pr (>F)**
Site	23	5779129	251266	2.88	0.00015
Year	1	11961	11961	0.14	0.71203
Species	3	2477987	825996	9.46	1.50E-05
Site Type*Species	9	2557616	284180	3.26	0.00165
Residuals	100	8728536	87285		

Table B8. Analysis of the decision nodes formed during the multivariate regression tree (MRT) analyzing the interaction between bivalve communities and sediment grain size. The respective MRT analyzed the interaction between bivalve communities and substrate composition. A) Discriminant taxa, left and right split means, and the deviance explained at each node. Only discriminant species contributing at least 10% of the explained variance at a particular node are listed. B) Indicator species, directional clusters and the probability of the taxonomic cluster occurred randomly.

(A) Node	Discriminant Species	Explained Deviance (%)	Left Split Mean	Right Split Mean
Root Node	*R. philippinarum*	42.62	1.16	0.28
Site Type = Farm, Farm Reference & Garden, Garden Reference	*N. obscurata*	12.10	0.54	0.08
Complexity = 20.18	*M. inquinata*	26.00	0.37	1.05
Left Node 1	*N. obscurata*	25.80	0.65	0.14
>475mm =15.29	*M. inquinata*	39.04	0.24	0.86
Complexity = 4.31	*M. nasuta*	26.30	0.12	0.63
Left Node 2:	*L. staminea*	20.56	0.12	0.54
250-500µm = 7.515	*R. philippinarum*	73.78	0.60	1.38
Complexity = 3.00				
Right Node 1	*L. staminea*	44.99	0.63	1.18
63-125µm = 5.65	*R. philippinarum*	21.05	0.11	0.49
Complexity = 3.31	*M. inquinata*	11.77	1.18	0.90

(B) Node	Indicator Species	Cluster	Indicator Value	Probability
	R. philippinarum	Left	0.69	0.001
Root Node	*N. obscurata*	Left	0.48	0.001
Site Type = Farm, Farm Reference & Garden, Garden Reference	*L. staminea*	Right	0.57	0.001
Complexity = 20.18	*M. inquinata*	Right	0.56	0.001
	C. nuttallii	Right	0.44	0.001
	S. gigantea	Right	0.40	0.001
	M. arenaria	Right	0.36	0.001
	N. tantilla	Right	0.23	0.001
	N. obscurata	Left	0.53	0.001
Left Node 1	*M. inquinata*	Right	0.61	0.001
>4.75mm =15.29	*M. nasuta*	Right	0.50	0.001
Complexity = 4.31	*L. staminea*	Right	0.48	0.013
	S. gigantea	Right	0.30	0.021
Left Node 2	*R. philippinarum*	Right	0.63	0.001

250-500µm = 7.515	*L. staminea*	Right	0.51	0.007
Complexity = 3.00	*M. arenaria*	Right	0.29	0.045
	M. nasuta	Left	0.41	0.007
Right Node 1	*N. tantilla*	Left	0.27	0.011
63-125µm = 5.65	*L. staminea*	Right	0.65	0.001
Complexity = 3.31	*R. philippinarum*	Right	0.48	0.001
	N. obscurata	Right	0.17	0.037

Table B9. Analysis of the decision nodes formed during the multivariate regression tree (MRT) analyzing the interaction between bivalve communities and sediment organics, carbonates, and water content. The respective MRT analyzed the interaction between bivalve communities and substrate composition. A) Discriminant taxa, left and right split means, and the deviance explained at each node. Only discriminant species contributing at least 10% of the explained variance at a particular node are listed. B) Indicator species, directional clusters and the probability that the taxonomic cluster occurred randomly.

(A) **Node**	**Discriminant Species**	**Explained Deviance (%)**	**Left Split Mean**	**Right Split Mean**
Root Node	*L. staminea*	22.30	0.48	1.25
Site Type = Farm, Farm Reference & Garden, Garden Reference	*R. philippinarum*	27.94	1.20	0.44
Complexity = 28.22	*M. inquinata*	23.82	0.34	1.03
Left Node 1	*N. obscurata*	85.36	0.26	1.68
Water Content =10.25				
Complexity = 8.05				
Left Node 2:	*L. staminea*	11.26	0.36	0.63
Carbonates = 2.15	*R. philippinarum*	50.94	0.81	1.40
Complexity = 5.67	*M. nasuta*	26.65	0.51	0.08
Left Node 3	*R. philippinarum*	24.25	1.27	0.68
Water Content = 13.63	*N. obscurata*	30.78	0.76	0.10
Complexity = 3.50	*M. nasuta*	30.09	0.00	0.66
Right Node 1	*S. gigantea*	39.40	0.12	0.93
Water Content = 10.93	*L. staminea*	22.21	1.17	1.78
Complexity = 1.84	*R. philippinarum*	15.56	0.51	0.00
	M. inquinata	15.44	0.97	1.47
Right Node 2	*M. arenaria*	18.72	0.51	0.16
Organics = 0.96	*M. inquinata*	29.07	0.81	1.25

Complexity = 1.34	*M. nasuta*	35.08	0.09	0.57

(B) **Node**	**Indicator Species**	**Cluster**	**Indicator Value**	**Probability**
Root Node Site Type = Farm, Farm Reference & Garden, Garden Reference Complexity = 28.22	*R. philippinarum*	Left	0.6318	0.002
	L. staminea	Right	0.6749	0.001
	M. inquinata	Right	0.6566	0.002
	C. nuttallii	Right	0.4364	0.001
	M. arenaria	Right	0.4217	0.007
Left Node 1 Water Content =10.25 Complexity = 8.05	*N. obscurata*	Right	0.72	0.003
Left Node 2 Carbonate = 2.15 Complexity = 5.67	*M. nasuta*	Left	0.47	0.001
	M. inquinata	Left	0.42	0.026
	R. philippinarum	Right	0.59	0.005
Left Node 3 Water Content = 13.63 Complexity = 3.50	*N. obscurata*	Left	0.71	0.006
	M. nasuta	Right	0.71	0.023
Right Node 1 Water Content = 10.93 Complexity = 1.84	*R. philippinarum*	Left	0.86	0.043
	S. gigantea	Right	0.89	0.009
Right Node 2 Organics = 0.96 Complexity = 1.34	*M. nasuta*	Right	0.69	0.011

Table B10. Variability explained by a 6000-tree Random Forest (RF) analysis examining the influence of substrate composition, habitat complexity, site type, area, intertidal zone, and bivalve species richness on log estimated bivalve biomass (N =412 bivalve surveys). The predictive accuracy of the RF was determined by using 80% of the data to train a model and the remaining 20% of the data to evaluate the model's predictions.

	Random Forest Model			**Prediction**	
Variable	**Explained Variance (Percent)**	**Error Rate**	**Standardize Error Rate**	**Variance Explained**	**Test Set Error Rate**
Log Quadrat Biomass	46.49	0.51	0.54	41.94	0.46

Appendix C: Chapter Four Supplementary Material

Supporting Information For

Chapter Four: Intertidal Resource Cultivation Over Millennia Structures Contemporary Marine Biodiversity.

Supplemental Text

3D model generation

Rendering three-dimensional reconstructions of the 24 sites followed the workflow developed by Agisoft Metashape, and modified for ecological applications by (Burns et al. 2015), (Young et al. 2017) and (Bayley and Mogg 2020). The four key stages were: aligning photos, dense point cloud construction, mesh construction, and building texture. Prior to photo alignment, images were reviewed in Metashape following a two-stage process to ensure a minimum standard was met prior to the reconstruction process. First, survey images were manually screened to remove poor quality images (e.g. blurry, obstructions, dark). Metashape's "Image Quality" was then used to exclude images with a quality value of less than 0.65. Although exclusion of quality values of less than 0.5 is generally recommended, it became evident that a higher quality standard is beneficial when modelling habitats with minute details of interest.

Photo alignment produces a sparse 3D point cloud using the projections from the different image orientations. The model's photo alignment deviated from the default settings, using the highest accuracy, a key point limit of 0, and a tie point limit of 10,000. These settings allowed Metashape to identify as many key points as possible within each image and for every image to have an upper limit of 10,000 matching points. The tie points generated between images allow them to be aligned and camera position estimated. This is done by algorithmic detection of invariant features in multiple images, creating a geometrical projective matrix to determine the camera's position and orientation (Westoby et al. 2012). Ground control points (GCPs) were used to create a local coordinate system for effective scaling and alignment of the point cloud, allowing photos that failed to align correctly to be rest or those that did not align to be aligned manually (maybe cite Verhoeven, 2012). Sparse clouds were trimmed considerably using Metashape's 'gradual selection' feature. Generally, reconstruction uncertainty and projection accuracy were set to 10, and reproduction error was reduced by ~40% of the initial value, which varied considerably across models. This feature had a substantial influence on the resulting model quality. Cumulatively, photo alignment took several hours, primarily due to the time required to realign photos.

Dense point cloud construction, mesh construction and texturing occurred in consecutive order with setting defined to improve resulting model quality. Dense point cloud construction is based on the triangulation of the tie points to identify pixels found in overlapping photos. The cloud construction settings were high quality and mild depth filtering. Constructing each model's dense cloud took between 5-10 minutes to generate the depth map and 20-40 minutes to create the density cloud. Mesh construction interpolates surface areas surrounding points in the dense point cloud. Mesh construction used a maximum number of polygons in the final mesh (face count) as 10,000,000, with interpolation enabled and an arbitrary surface to account for variable habitat types. Mesh construction took between 10-20 minutes. Texturing overlays the texture and color of the original photos onto the mesh, with a 16,384-texture size and blending mosaic mode, a process that, generally, took 10 minutes to complete. The rendered 3D models of each of the 24 sites were exported as wavefront files for further analysis.

Supplemental Figures

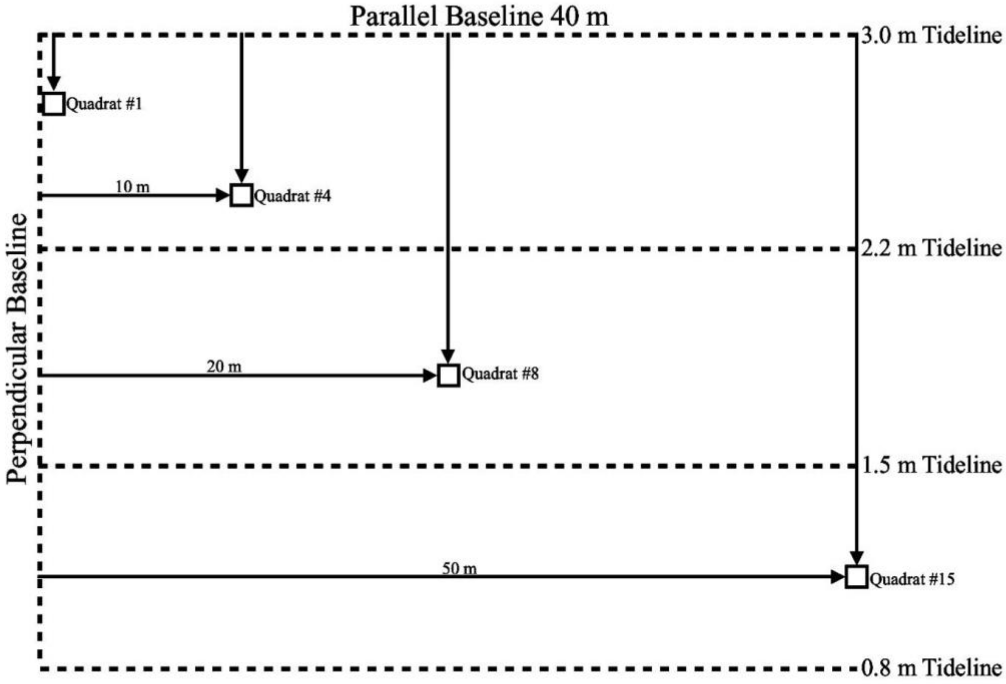

Fig C1 | Site assessment area and quadrat placements used during the field surveys. Dashed lines denote horizontal and vertical baselines running parallel and perpendicular to the shoreline, respectively. Quadrat placement was at the intersection of perpendicular lines extended from the horizontal and vertical baselines. Examples of quadrat placement are illustrated by the placement of the 1st, 4th, 8th and 15th quadrats. Five quadrats were placed within each zone.

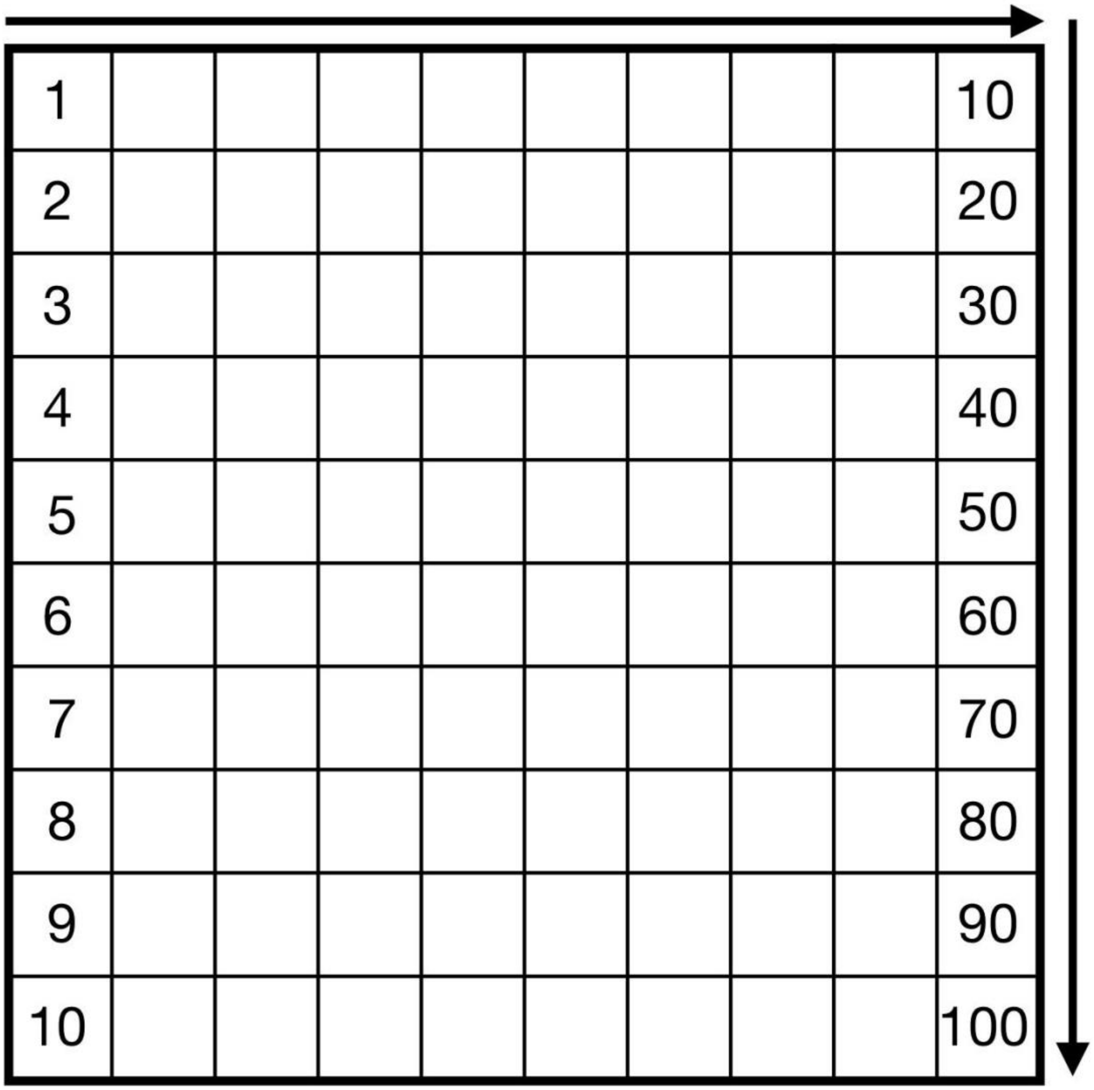

Fig C2 | Epifaunal taxonomic surveys 0.5 × 0.5 m strung quadrat diagram. Vertical and horizontal strings every 5 cm created 100 equal squares, of which ten squares were randomly selected and subsampled.

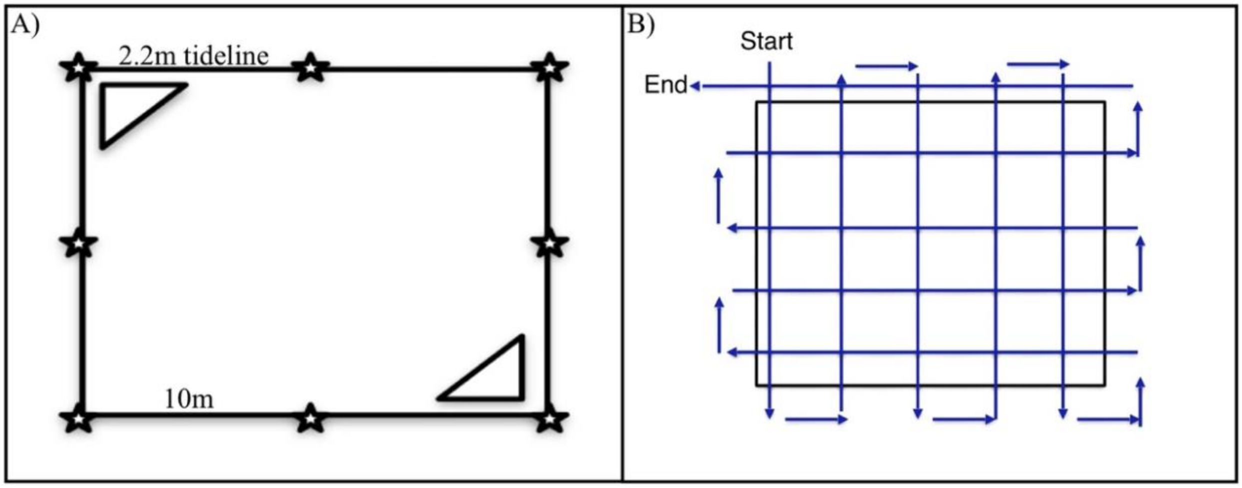

Fig C3 | Structure from Motion (SfM) Photogrammetry site assessment diagrams A) 10 x 10m SfM assessment area. Stars denote ground control point locations. Triangles indicate known length bars used for calibration. Bottom of area placed along the 1.0 m tideline C) Ideal site assessment patterns used to ensure the entire assessment area was covered. Deviations from this pattern occurred if the assessment area responded poorly to trampling (e.g. intertidal mudflats).

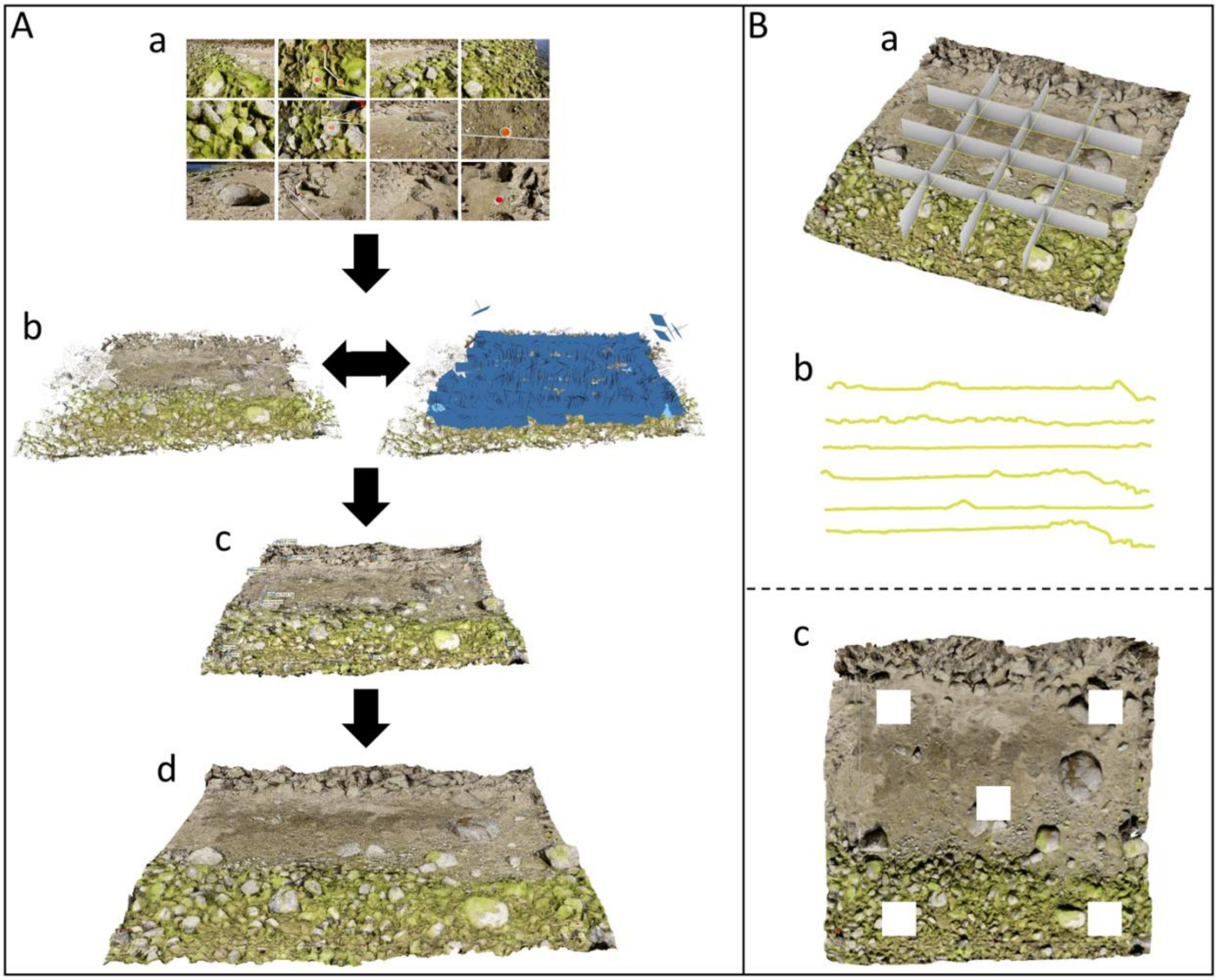

Fig C4 | A) A flow diagram illustrating the a) image acquisition, b) image alignment and spare cloud generation c) dense point cloud generation, and c) tiled mesh construction. **B)** Complexity analyses diagrams a) six 9-meter rugosity chains laid at equidistantly across the model, b) curvatures resulting from interacting the model and chains. C) five 1x1m fractal dimension assessment locations.

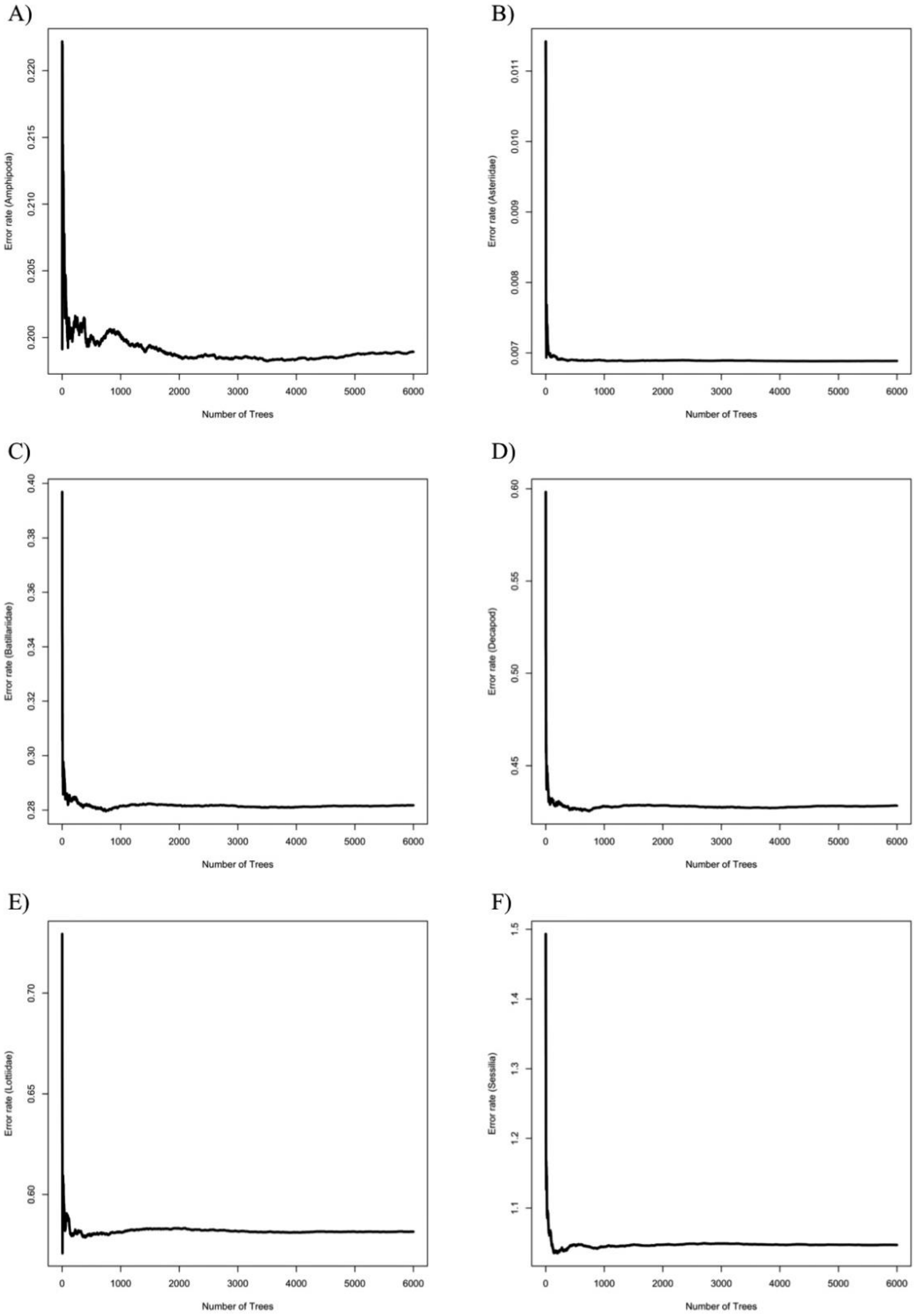

Fig C5 | Multivariate Random Forest number of trees selection process. The number of trees required was determined via a low and stable error rate. Six examples of the 24 taxa considered are depicted.

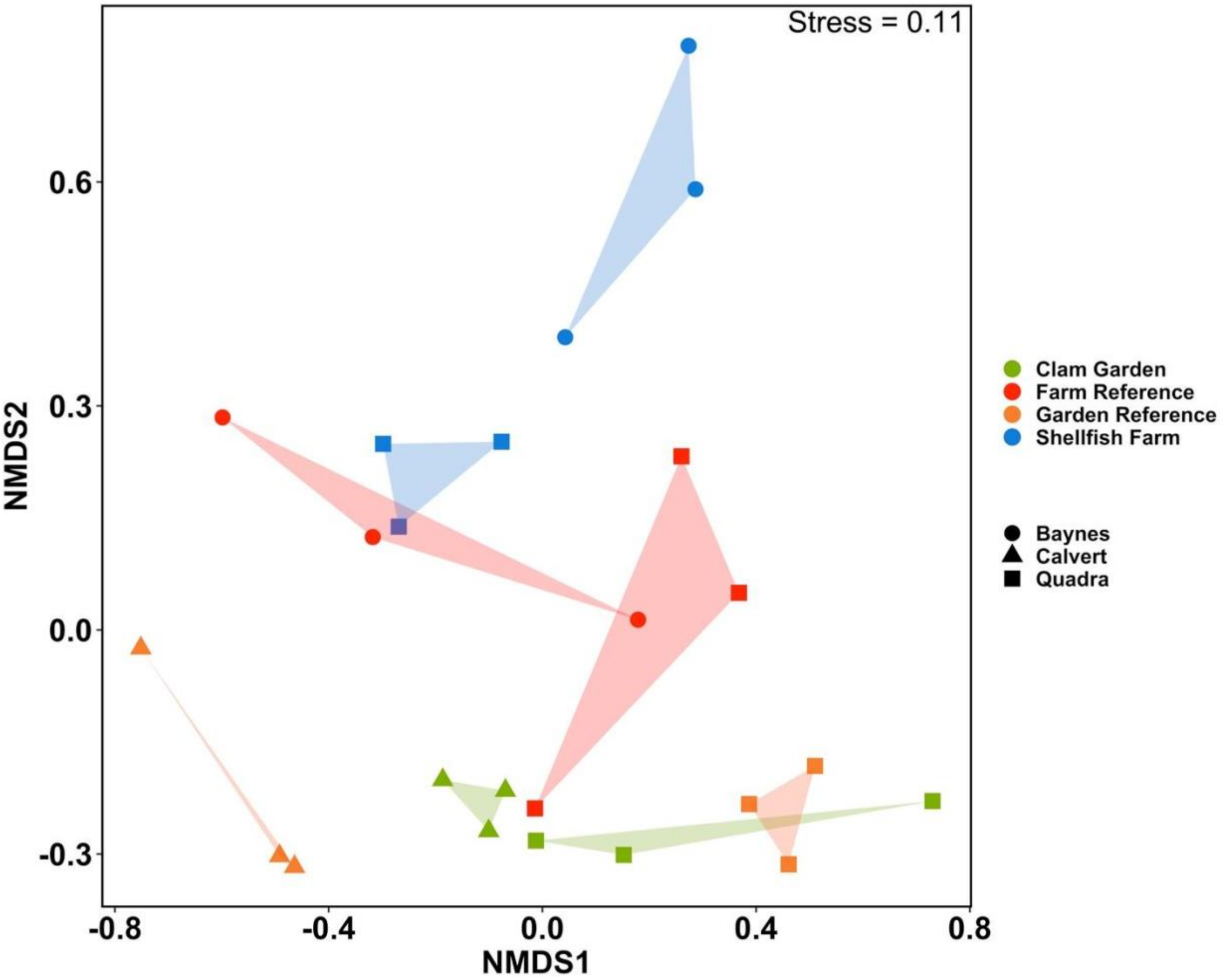

Fig C6 | Non-metric multidimensional scaling plots of mid-intertidal substrate composition averaged by site and illustrated accordingly to region and site type. Colors denote clam gardens (green), clam garden reference beaches (orange), shellfish farms (blue), and shellfish farm reference beaches (red). Shapes denote the study regions: Baynes Sound (circles), north and south Quadra island (squares), Hakai Lúxvbálís Conservancy "Calvert Island" (triangle).

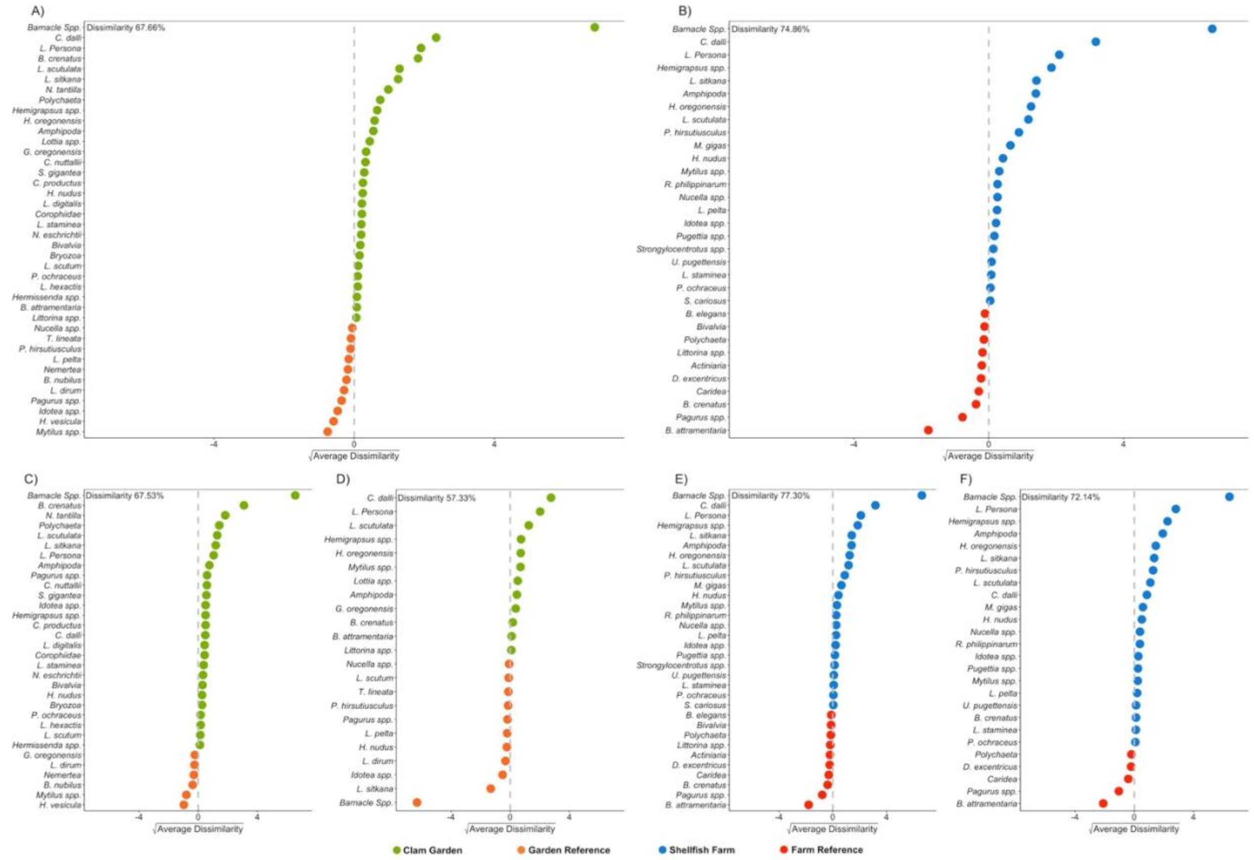

Fig C7 | Taxa-specific average dissimilarity between cultivated habitats and reference beaches derived from similarity percentage analyses. Square root of average dissimilarity plotted to improve visualization. Average densities increase in clam gardens (green) or reference beaches (orange). Average densities increase in shellfish farms (blue) or reference beaches (red). A) Clam gardens and clam garden reference beach comparison. B) Shellfish farms and shellfish farm reference beach comparison. Clam gardens and clam garden reference beach comparison within C) Hakai Lúxvbálís Conservancy "Calvert Island" and D) northern Quadra Island. Shellfish farms and shellfish farm reference beach comparison within E) Southern Quadra Island and F) Baynes Sound.

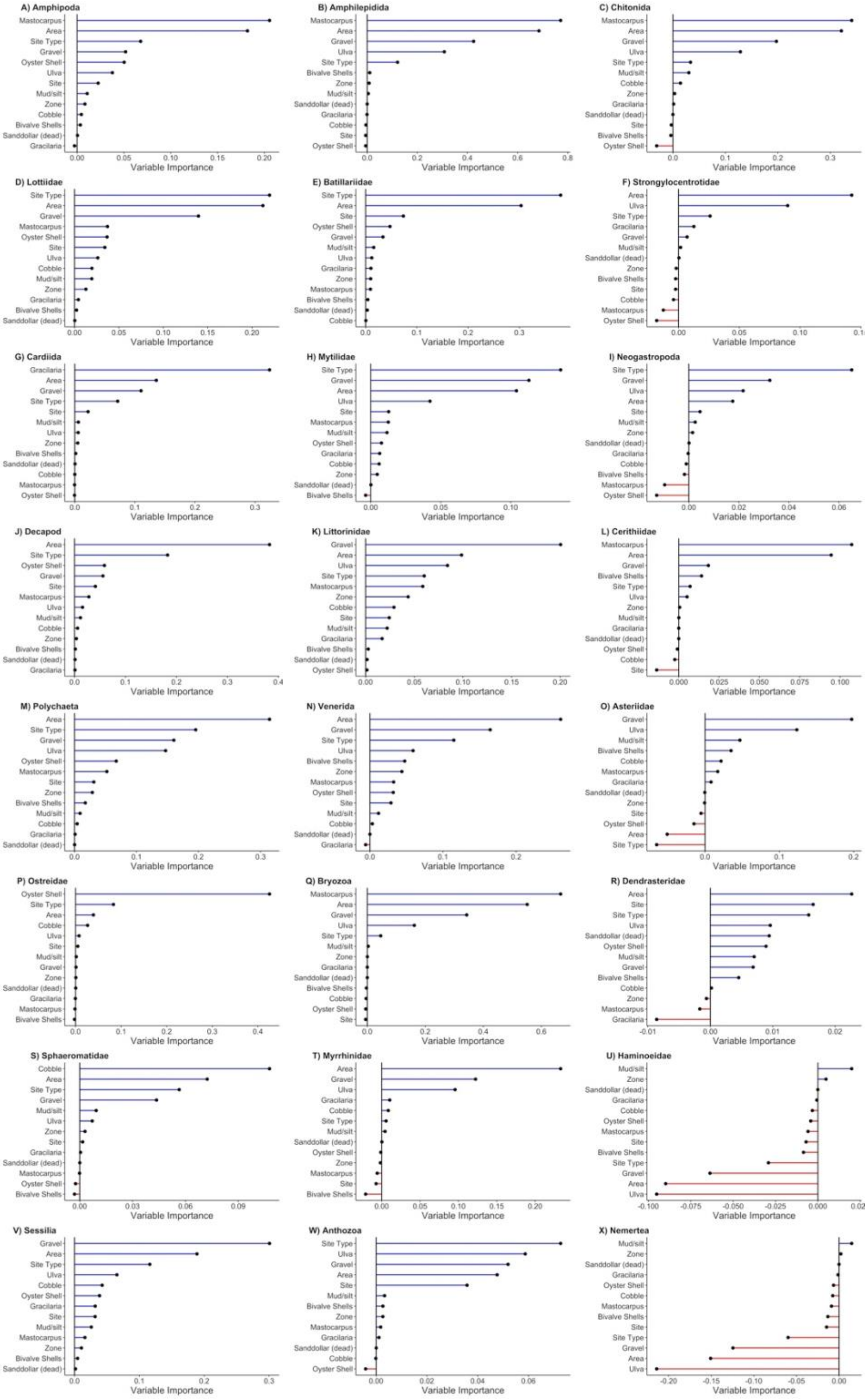

Fig C8 | Variable importance analyses of the interaction between epifaunal taxa and substrate composition. Derived from a multivariate random forest consisting of 6000 trees. Variable importance depicted for the 24 taxa examined. Relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. Higher bars equate to great variable importance.

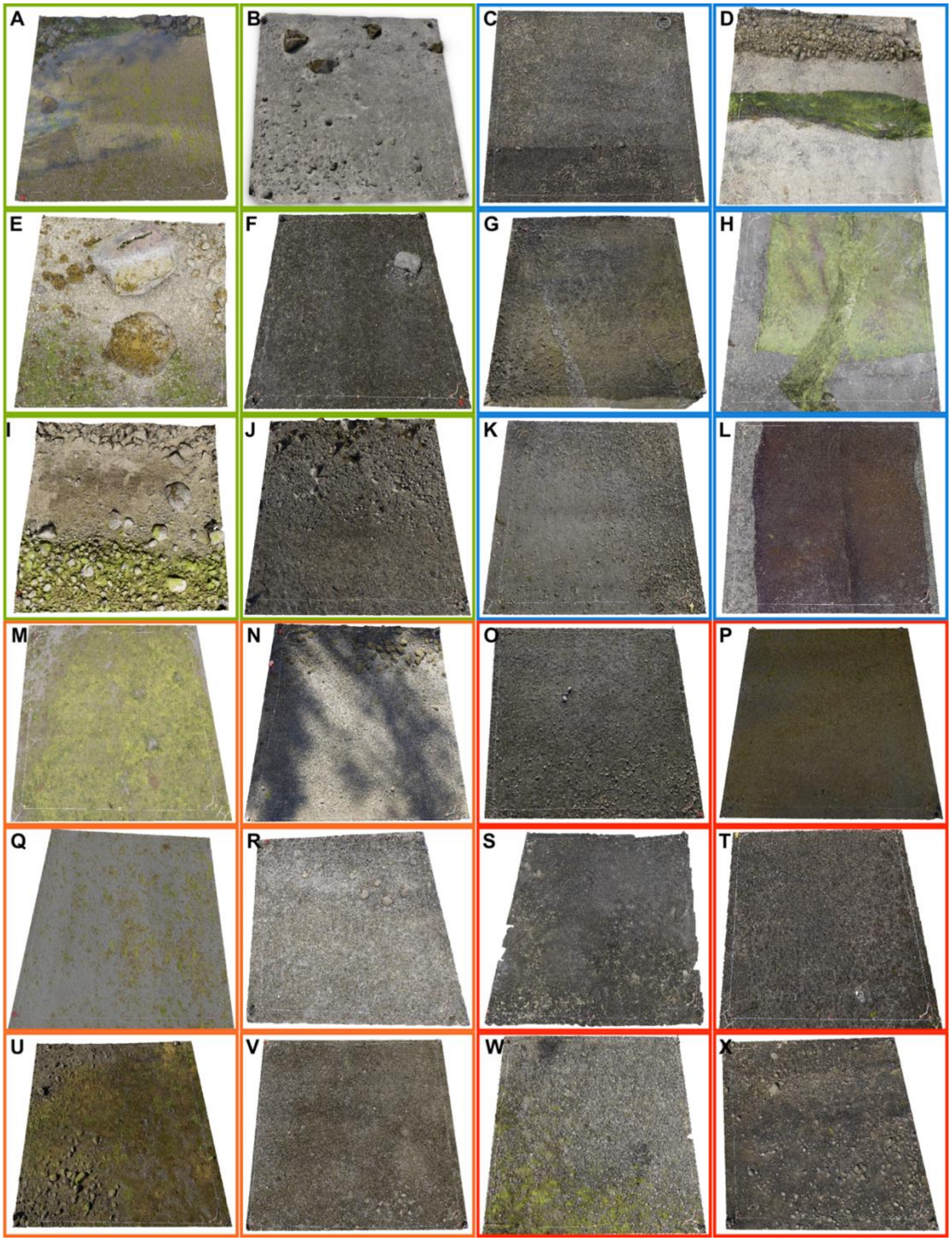

Fig S9 | Three-dimensional reconstructions of the 24 survey sites. **A, E, I)** Calvert Gardens. **B, F, J)** Quadra Gardens. **C, G, K)** Quadra Shellfish Farms. **D, H, L)** Baynes Shellfish Farms. **M, Q, U)** Calvert Garden References. **N, R, V)** Quadra Garden References. **O, S, W)** Quadra Farm Reference. **P, T, X)** Baynes Farm Reference.

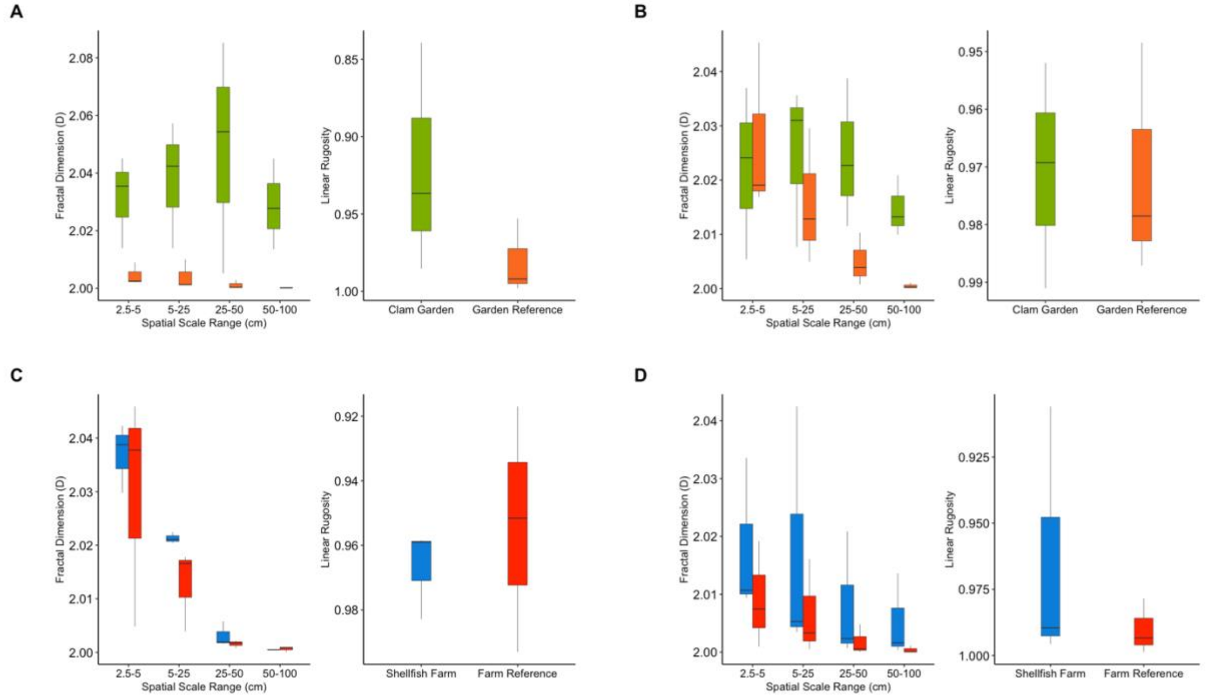

Fig C10 | Average fractal dimension and linear rugosity within each of the regions. clam gardens (green), garden reference (orange), shellfish farms (blue), farm reference (red) A) Calvert Island B) Quadra Island C) Quadra Island D) Baynes Sound.

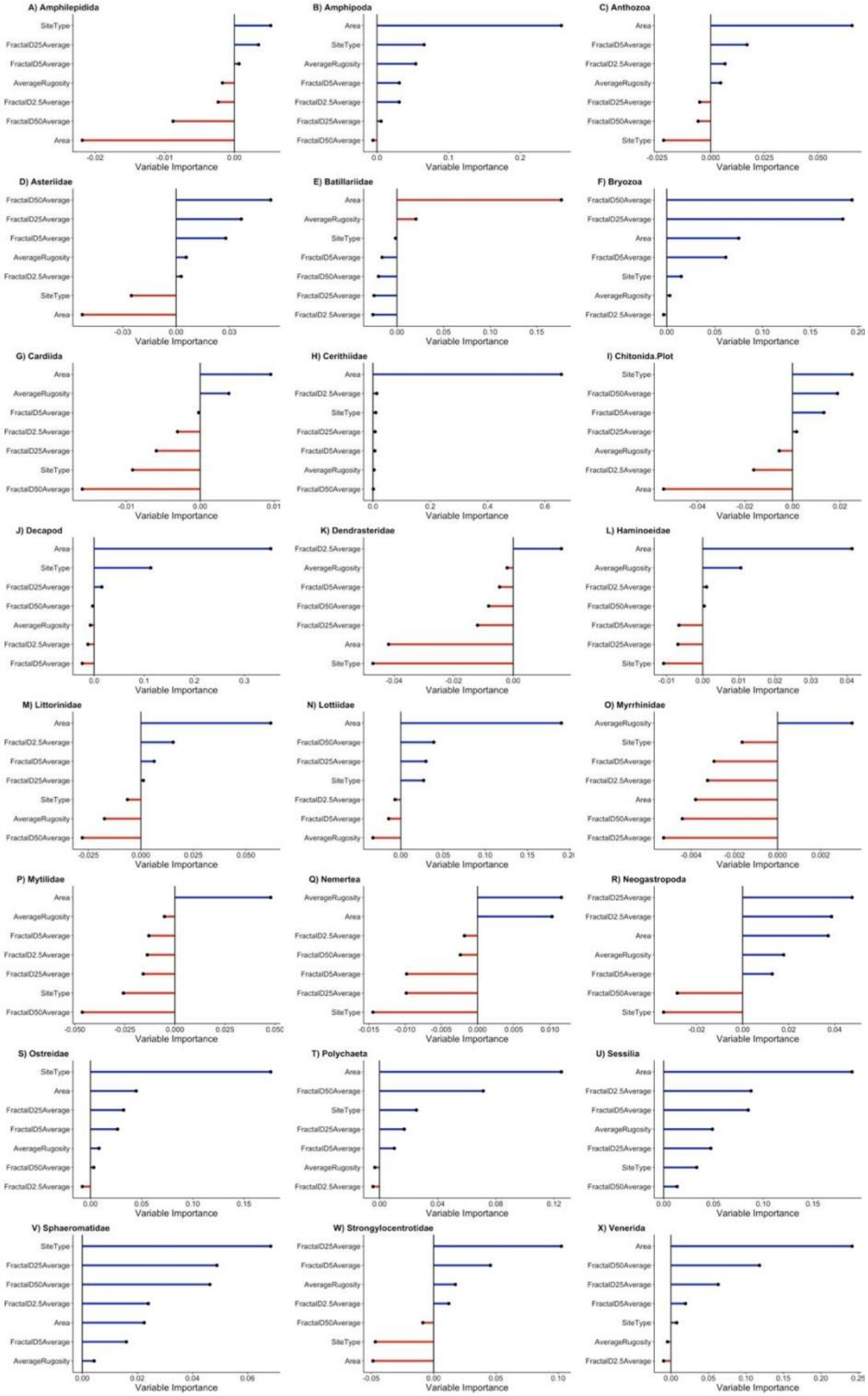

Fig C11 | Variable importance analyses of the interaction between epifaunal taxa and habitat structural complexity. Derived from a multivariate random forest consisting of 6000 trees. Variable importance depicted for the 24 taxa examined. Relative importance of the predictor variables scaled by decreases in the mean squared error of the model when the variable is permuted. Higher bars equate to great variable importance.

Supplemental Tables

Table C1 | Taxa observed within each habitat type.

Clam Garden	**Shellfish Farm**	**Clam Garden Reference**	**Shellfish Farm Reference**
Amphipoda	Amphipoda	Amphipoda	Amphipoda
Balanus crenatus	*Balanus crenatus*	*Balanus crenatus*	Anenome
Balanus glandula	*Balanus glandula*	*Balanus glandula*	*Balanophyllia elegans*
Barnacle spp.	*Barnacle spp.*	*Balanus nubilus*	*Balanus crenatus*
Batillaria attramentaria	*Batillaria attramentaria*	*Barnacle spp.*	*Balanus glandula*
Bivalvia	Caridean Shrimps	*Chthamalus dalli*	*Barnacle spp.*
Bryozoa	*Chthamalus dalli*	*Clinocardium nuttallii*	*Batillaria attramentaria*
Cancer productus	*Dendraster excentricus*	*Gnorimosphaeroma oregonensis*	Bivalvia
Chthamalus dalli	*Hemigrapsus nudus*	*Haminoea vesicula*	*Caridean Shrimps*
Clinocardium nuttallii	*Hemigrapsus oregonensis*	*Hemigrapsus nudus*	*Chthamalus dalli*
Corophiidae	*Hemigrapsus spp.*	*Hemigrapsus oregonensis*	*Dendraster excentricus*
Gnorimosphaeroma oregonensis	*Idotea spp.*	*Hemigrapsus spp.*	*Hemigrapsus nudus*
Hemigrapsus nudus	*Leukoma staminea*	*Idotea spp.*	*Hemigrapsus oregonensis*
Hemigrapsus oregonensis	*Littorina scutulata*	*Lirabuccinum dirum*	*Hemigrapsus spp.*
Hemigrapsus spp.	*Littorina sitkana*	*Littorina scutulata*	*Idotea spp.*
Hermissenda.spp.	*Lottia pelta*	*Littorina sitkana*	*Littorina scutulata*
Idotea spp.	*Lottia persona*	*Lottia pelta*	*Littorina sitkana*
Leptasterias hexactis	*Magallana gigas*	*Lottia persona*	*Littorina.spp.*
Leukoma staminea	*Mytilus spp.*	*Lottia scutum*	*Lottia pelta*
Lirabuccinum dirum	*Nucella spp.*	*Mytilus spp.*	*Lottia persona*
Littorina scutulata	*Pagurus hirsutiusculus*	Nemertea	*Magallana gigas*
Littorina sitkana	*Pagurus spp.*	*Neostylidium eschrichtii*	*Mytilus spp.*
Littorina spp.	*Pisaster ochraceus*	*Nucella spp.*	*Pagurus hirsutiusculus*
Lottia digitalis	*Pugettia spp.*	*Nutricola tantilla*	*Pagurus spp.*
Lottia pelta	*Ruditapes philippinarum*	*Pagurus hirsutiusculus*	Polychaeta
Lottia persona	*Semibalanus cariosus*	*Pagurus spp.*	*Ruditapes philippinarum*
Lottia scutum	*Strongylocentrotus spp.*	*Tonicella lineata*	

Lottia spp.	*Upogebia pugettensis*
Mytilus spp.	
Neostylidium eschrichtii	
Nutricola tantilla	
Pagurus spp.	
Pisaster ochraceus	
Polychaeta	
Saxidomus gigantea	

Table C2 | Taxa observed across all habitat types, unique to each comparison, and unique to each habitat type. Complements the Venn Diagram (Fig 2F). Shellfish Farms = SF, SFRB= Shellfish Farm Reference Beaches, CG=Clam Garden, CGRB= Clam Garden Reference Beaches

Common Taxa	**Unique SF and SFRB Taxa**	**Unique CG and CGRB Taxa**	**Unique SF Taxa**	**Unique SFRB Taxa**	**Unique CG Taxa**	**Unique CGRB Taxa**
Amphipoda	*Batillaria attramentaria*	*Clinocardium nuttallii*	*Pugettia spp.*	Anenome	Bryozoa	*Balanus nubilus*
Balanus crenatus	Caridean Shrimps	*Gnorimosphaeroma oregonensis*	*Semibalanus cariosus*	*Balanophyllia elegans*	*Cancer productus*	*Haminoea vesicula*
Balanus glandula	*Dendraster excentricus*	*Lirabuccinum dirum*	*Strongylocentrotus spp.*		Corophiidae	Nemertea
Barnacle spp.	*Magallana gigas*	*Lottia scutum*	*Upogebia pugettensis*		*Hermissenda spp.*	*Tonicella lineata*
Chthamalus dalli	*Pagurus hirsutiusculus*	*Neostylidium eschrichtii*			*Leptasterias hexactis*	
Hemigrapsus nudus	*Ruditapes philippinarum*	*Nutricola tantilla*			*Lottia digitalis*	
Hemigrapsus oregonensis					*Lottia spp.*	
Hemigrapsus spp.					*Saxidomus gigantea*	
Idotea spp.						
Littorina scutulata						
Littorina sitkana						
Lottia pelta						

Lottia persona

Mytilus spp.

Pagurus spp.

Table C3| Higher-level taxonomic classifications to improve pattern visualization during multivariate regression tree (MRT) and multivariate random forest (MRF) analyses. The 60 epifaunal taxa observed during the biodiversity surveys were amalgamated into 24 higher-level taxonomic classifications as detailed below.

MRT and MFT Taxa	**Classification**	**Included Taxa**
Amphilepidida	Order	Amphilepidida
Amphipoda	Order	Gammaridae, Gammaridae, Amphipoda, Caprellidae
Anthozoa	Class	Anenome, *Balanophyllia elegans*
Asteriidae	Family	*Leptasterias hexactis*, *Pisaster ochraceus*
Batillariidae	Family	*Batillaria attramentaria*
Bryozoa	Phylum	Bryozoa
Cardiida	Order	*Macoma inquinata*, *Clinocardium nuttallii*, *Macoma* spp.
Cerithiidae	Family	*Neostylidium eschrichtii*
Chitonida	Order	Mopalia muscosa, Mopalia ciliata, Tonicella lineata
Decapoda	Order	*Cancer productus*, *Pugettia* spp., *Pagurus hirsutiusculus*, *Pagurus* spp., *Pandalus platyceros*, *Pinnotheres pisum*, *Upogebia pugettensis*, *Hemigrapsus nudus*, *Hemigrapsus oregonensis*, *Hemigrapsus* spp.
Dendrasteridae	Family	*Dendraster excentricus*
Haminoeidae	Family	*Haminoea vesicula*
Littorinidae	Family	*Littorina sitkana*, *Littorina scutulata*, *Littorina* spp.

Lottiidae	Family	*Lottia scutum*, *Lottia* spp., *Lottia pelta*, *Lottia digitalis*, *Lottia persona*, *Idotea* spp.
Myrrhinidae	Family	*Hermissenda* spp.
Mytilidae	Family	*Mytilus* spp.
Nemertea	Phylum	Nemertea
Neogastropoda	Order	*Nucella* spp., *Lirabuccinum dirum*
Ostreidae	Family	*Magallana gigas*
Polychaeta	Class	Polychaeta
Sessilia	Order	*Balanus glandula*, *Chthamalus dalli*, *Balanus nubilus*, *Semibalanus cariosus*, *Balanus crenatus*, barnacle spp.
Sphaeromatidae	Family	*Gnorimosphaeroma oregonensis*
Strongylocentrotidae	Family	*Strongylocentrotus* spp.
Venerida	Order	*Saxidomus gigantea*, *Ruditapes philippinarum*, *Nutricola tantilla*, *Leukoma staminea*, unidentified bivalve

Table C4 | PERMANOVA (permutational multivariate analysis of variance) assessing if epifaunal community composition varied between clam gardens, shellfish farms, and reference beaches. A) Comparison of all habitat types. Comparison of clam gardens and clam garden reference beach within B) Hakai Lúxvbálís Conservancy "Calvert Island" C) northern Quadra Island. Comparison of shellfish farms and shellfish farm reference beaches within D) Southern Quadra Island and F) Baynes Sound.

A)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Clam Garden, Shellfish Farms, and Reference Sites	Habitat Type	3	3.3	1.098	4.98	0.018
		Year	1	1.5	1.495	6.78	0.001
		Habitat Type: Site	20	18.1	0.904	4.1	0.001
		Residuals	210	46.3	0.221		

B)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Calvert Island Gardens and Reference Sites	Habitat Type	1	0.7	0.704	3.42	0.029
		Year	1	0.49	0.491	2.39	0.056
		Habitat Type: Site	4	1.31	0.328	1.59	0.085
		Habitat Type: Site: Quad	32	8.7	0.272	1.32	0.086
		Residuals	18	3.71	0.206		

C)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Quadra Island Gardens and Reference Sites	Habitat Type	1	0.73	0.729	4.5	0.012
		Year	1	0.52	0.518	3.2	0.029
		Habitat Type: Site	4	1.67	0.417	2.58	0.011
		Habitat Type: Site: Quad	44	7.75	0.176	1.09	0.382
		Residuals	8	1.29	0.162		

D)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Quadra Island Shellfish Farms and Reference Sites	Habitat Type	1	0.9	0.9	3.25	0.007
		Year	1	3.69	3.69	13.36	0.001
		Habitat Type: Site	4	0.88	0.22	0.8	0.73
		Habitat Type: Site: Quad	42	11.62	0.28	1	0.488
		Residuals	10	2.76	0.28		

E)	**Comparison**	**Source**	**DF**	**SS**	**MS**	***Pseudo-F***	***p***
	Baynes Sound Shellfish Farms and Reference Sites	Habitat Type	1	1.08	1.081	4.88	0.005
		Year	1	0.53	0.534	2.41	0.046
		Habitat Type: Site	4	3.52	0.881	3.98	0.001
		Habitat Type: Site: Quad	42	8.49	0.202	0.91	0.687
		Residuals	11	2.44	0.221		

Table C5 | SIMPER (Similarity Percentages) tables showing the contribution of each taxonomic grouping to the observed differences between intertidal study site types (clam garden, shellfish farms, and reference beaches) along the Central Coast of British Columbia, Canada. A) Clam gardens and clam garden reference beach comparison. B) Shellfish farms and shellfish farm reference beach comparison. Clam gardens and clam garden reference beach comparison within C) Hakai Lúxvbálís Conservancy "Calvert Island" and D) northern Quadra Island. Shellfish farms and shellfish farm reference beach comparison within E) Southern Quadra Island and F) Baynes Sound.

Taxa	**Average Density**	**Average Density**	**Average Dissimilarity (%)**	**Contribution S.D**	**Average to S.D ratio**	**Contribution (%)**	**Cumulative (%)**
(A)	**Clam Gardens**	**Reference Sites**		**Average dissimilarity = 67.66%**			
barnacle *Spp.*	941.18	905.58	47.07	29.22	1.61	69.57	69.57
C. dalli	144.86	44.90	5.47	9.67	0.57	8.08	77.65
L. persona	75.91	50.32	3.62	4.66	0.78	5.36	83.01
B. crenatus	35.39	8.63	3.31	11.00	0.30	4.90	87.91
L. scutulata	45.39	15.92	1.67	2.35	0.71	2.47	90.38
L. sitkana	25.56	21.17	1.57	2.74	0.57	2.32	92.70
N. tantilla	5.39	1.85	0.95	3.81	0.25	1.40	94.10
Mytilus spp.	7.49	7.61	-0.57	1.28	0.45	0.85	94.94
Polychaeta	3.63	1.00	0.55	4.84	0.11	0.82	95.76
Hemigrapsus spp.	8.37	4.73	0.43	1.00	0.43	0.64	96.40
H. vesicula	1.00	2.69	-0.35	2.91	0.12	0.51	96.91
H. oregonensis	7.32	5.75	0.34	0.70	0.48	0.50	97.41
Amphipoda	2.75	2.02	0.30	1.47	0.20	0.44	97.85
Idotea spp.	3.28	3.88	-0.22	0.79	0.28	0.33	98.18
Lottia spp.	4.51	1.00	0.20	1.59	0.12	0.29	98.47
Pagurus spp.	1.53	1.68	-0.13	0.74	0.17	0.19	98.66
G. oregonensis	3.46	1.85	0.12	0.66	0.18	0.17	98.83
C. nuttallii	1.18	1.17	0.10	0.80	0.13	0.15	98.98
L. dirum	1.35	2.86	-0.08	0.33	0.25	0.12	99.10
S. gigantea	1.53	1.00	0.08	0.66	0.12	0.12	99.22
C. productus	1.18	1.00	0.06	0.64	0.10	0.09	99.31
H. nudus	2.05	1.51	0.06	0.18	0.32	0.09	99.40
Corophiidae	1.18	1.00	0.05	0.49	0.10	0.07	99.47
L. digitalis	1.18	1.00	0.05	0.49	0.10	0.07	99.54
B. nubilus	1.00	1.17	-0.05	0.52	0.09	0.07	99.61

L. staminea	1.35	1.00	0.04	0.30	0.13	0.06	99.68
N. eschrichtii	1.18	1.17	0.04	0.32	0.12	0.06	99.73
Nemertea	1.00	1.17	-0.03	0.32	0.10	0.05	99.78
Bivalvia	1.53	1.00	0.03	0.25	0.12	0.04	99.82
L. pelta	1.18	1.85	-0.02	0.14	0.17	0.04	99.86
Bryozoa	1.35	1.00	0.02	0.19	0.12	0.03	99.90
L. scutum	1.18	1.17	0.01	0.08	0.18	0.02	99.91
P. hirsutiusculus	1.00	1.17	-0.01	0.09	0.12	0.02	99.93
L. hexactis	1.18	1.00	0.01	0.08	0.12	0.01	99.95
P. ochraceus	1.18	1.00	0.01	0.08	0.12	0.01	99.96
T. lineata	1.00	1.17	-0.01	0.07	0.12	0.01	99.97
Hermissenda spp.	1.35	1.00	0.01	0.05	0.13	0.01	99.98
B. attramentaria	1.35	1.00	0.01	0.03	0.19	0.01	99.99
Littorina spp.	1.18	1.00	0.00	0.03	0.13	0.01	100.00
Nucella spp.	1.00	1.17	0.00	0.02	0.13	0.00	100.00

(B)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 74.86%**		
Barnacle Spp.	1765.56	939.44	43.98	28.81	1.53	58.75	58.75
C. dalli	437.20	95.58	10.10	19.77	0.51	13.49	72.24
L. persona	108.29	18.12	4.37	7.54	0.58	5.84	78.08
Hemigrapsus spp.	50.66	34.83	3.46	6.42	0.54	4.63	82.71
B. attramentaria	14.90	36.10	-3.21	8.21	0.39	4.29	87.00
L. sitkana	33.03	16.08	2.00	4.98	0.40	2.68	89.67
Amphipoda	24.22	10.17	1.96	5.42	0.36	2.61	92.29
H. oregonensis	29.83	6.64	1.58	2.57	0.61	2.10	94.39
L. scutulata	42.22	8.39	1.39	2.74	0.51	1.85	96.24
P. hirsutiusculus	17.95	6.76	0.80	3.16	0.25	1.07	97.32
Pagurus spp.	6.42	6.93	-0.61	2.02	0.30	0.81	98.13
M. gigas	10.80	1.29	0.41	1.28	0.32	0.55	98.68

H. nudus	4.22	1.41	0.18	0.55	0.32	0.24	98.92
B. crenatus	1.17	6.93	-0.14	1.05	0.14	0.19	99.11
Mytilus spp.	4.39	1.29	0.10	0.24	0.40	0.13	99.24
Caridea	1.17	1.68	-0.09	0.87	0.10	0.12	99.36
R. philippinarum	2.36	1.17	0.07	0.30	0.22	0.09	99.45
Nucella spp.	2.02	1.00	0.07	0.34	0.20	0.09	99.54
L. pelta	2.03	1.12	0.06	0.27	0.22	0.08	99.62
D. excentricus	1.08	1.17	-0.05	0.41	0.13	0.07	99.69
Idotea spp.	1.68	1.51	0.05	0.22	0.21	0.06	99.75
Actiniaria	1.00	1.73	-0.04	0.26	0.16	0.06	99.81
Littorina spp.	1.00	2.53	-0.03	0.28	0.12	0.05	99.85
Pugettia spp.	1.17	1.00	0.03	0.25	0.11	0.04	99.89
Polychaeta	1.00	1.17	-0.02	0.22	0.09	0.03	99.92
Strongylocentrotus spp.	1.17	1.00	0.02	0.16	0.11	0.02	99.94
Bivalvia	1.00	1.17	-0.02	0.15	0.10	0.02	99.96
B. elegans	1.00	1.37	-0.01	0.10	0.12	0.02	99.98
U. pugettensis	1.17	1.00	0.01	0.06	0.12	0.01	99.99
L. staminea	1.17	1.00	0.01	0.04	0.13	0.01	99.99
P. ochraceus	1.17	1.00	0.00	0.02	0.13	0.00	100.00
S. cariosus	1.51	1.00	0.00	0.02	0.13	0.00	100.00

(C)	**Clam Gardens**	**Reference Sites**			**Average dissimilarity = 67.53%**		
Barnacle Spp.	978.41	285.33	43.03	35.52	1.21	63.72	63.72
B. crenatus	71.74	16.00	9.57	19.01	0.50	14.17	77.89
N. tantilla	10.26	2.67	3.36	7.77	0.43	4.98	82.87
Polychaeta	6.56	1.00	2.02	10.10	0.20	3.00	85.87
L. scutulata	42.85	3.00	1.65	2.80	0.59	2.45	88.32
L. sitkana	18.41	3.33	1.40	4.02	0.35	2.08	90.39
L. persona	15.07	7.67	1.09	2.11	0.52	1.62	92.01
H. vesicula	1.00	4.33	-0.95	5.10	0.19	1.40	93.41
Mytilus spp.	3.59	6.67	-0.64	1.76	0.36	0.94	94.35
Amphipoda	2.11	1.67	0.57	2.88	0.20	0.84	95.19
Pagurus spp.	2.11	1.33	0.36	1.44	0.25	0.53	95.73

C. nuttallii	1.37	1.33	0.34	1.58	0.22	0.51	96.24
S. gigantea	2.11	1.00	0.30	1.46	0.21	0.45	96.69
Idotea spp.	1.37	1.33	0.25	1.32	0.19	0.37	97.06
C. productus	1.37	1.00	0.25	1.44	0.17	0.37	97.43
Hemigrapsus spp.	1.37	1.00	0.25	1.44	0.17	0.37	97.79
C. dalli	6.56	1.00	0.23	0.98	0.24	0.35	98.14
Corophiidae	1.37	1.00	0.19	1.06	0.18	0.27	98.41
L. digitalis	1.37	1.00	0.19	1.06	0.18	0.27	98.69
B. nubilus	1.00	1.33	-0.14	0.95	0.15	0.21	98.89
L. staminea	1.74	1.00	0.14	0.61	0.22	0.20	99.10
N. eschrichtii	1.37	1.33	0.10	0.56	0.19	0.15	99.25
Nemertea	1.00	1.33	-0.09	0.55	0.15	0.13	99.38
Bivalvia	2.11	1.00	0.08	0.44	0.19	0.12	99.50
H. nudus	2.11	1.00	0.07	0.24	0.28	0.10	99.60
Bryozoa	1.74	1.00	0.07	0.36	0.19	0.10	99.70
L. dirum	1.00	2.00	-0.06	0.35	0.17	0.09	99.79
G. oregonensis	1.00	2.33	-0.05	0.29	0.18	0.08	99.87
L. hexactis	1.37	1.00	0.03	0.15	0.19	0.04	99.91
P. ochraceus	1.37	1.00	0.03	0.15	0.19	0.04	99.95
L. scutum	1.37	1.00	0.02	0.11	0.19	0.03	99.98
Hermissenda spp.	1.74	1.00	0.01	0.07	0.20	0.02	100.00

(D)	**Clam Gardens**	**Reference Sites**			**Average dissimilarity = 57.33%**		
Barnacle Spp.	907.67	1547.21	-39.66	26.32	1.51	69.17	69.17
C. dalli	269.33	90.31	7.58	8.59	0.88	13.23	82.40
L. persona	130.67	94.45	4.08	3.83	1.07	7.11	89.51
L. sitkana	32.00	39.62	-1.73	2.36	0.73	3.02	92.53
L. scutulata	47.67	29.28	1.57	1.98	0.79	2.74	95.27
Hemigrapsus spp.	14.67	8.59	0.53	0.81	0.66	0.93	96.20
H. oregonensis	13.00	10.66	0.51	0.73	0.70	0.88	97.08
Mytilus spp.	11.00	8.59	0.48	0.78	0.62	0.84	97.92
Idotea spp.	5.00	6.52	-0.26	0.64	0.41	0.46	98.38
Lottia spp.	7.67	1.00	0.26	1.52	0.17	0.45	98.84
Amphipoda	3.33	2.38	0.20	0.73	0.28	0.35	99.19

G. oregonensis	5.67	1.34	0.14	0.65	0.21	0.24	99.43
L. dirum	1.67	3.76	-0.10	0.32	0.32	0.18	99.60
H. nudus	2.00	2.03	-0.05	0.13	0.40	0.09	99.70
L. pelta	1.33	2.72	-0.04	0.19	0.23	0.08	99.77
Pagurus spp.	1.00	2.03	-0.03	0.19	0.18	0.06	99.83
B. crenatus	2.67	1.00	0.03	0.16	0.18	0.05	99.88
P. hirsutiusculus	1.00	1.34	-0.02	0.12	0.17	0.03	99.92
T. lineata	1.00	1.34	-0.02	0.09	0.17	0.03	99.94
L. scutum	1.00	1.34	-0.01	0.06	0.18	0.02	99.96
B. attramentaria	1.67	1.00	0.01	0.04	0.26	0.02	99.98
Nucella spp.	1.00	1.34	-0.01	0.03	0.19	0.01	99.99
Littorina spp.	1.33	1.00	0.01	0.03	0.18	0.01	100.00

(E)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 77.30%**		
Barnacle *spp.*	2562.30	1343.69	48.13	31.12	1.55	62.27	62.27
C. dalli	836.87	193.41	18.21	24.44	0.75	23.56	85.83
L. sitkana	25.00	21.34	2.53	7.08	0.36	3.27	89.10
B. attramentaria	17.67	15.52	1.95	5.45	0.36	2.52	91.62
L. scutulata	52.07	11.55	1.76	2.90	0.61	2.27	93.89
Hemigrapsus spp.	34.00	11.55	1.20	3.26	0.37	1.55	95.44
H. oregonensis	25.70	5.59	1.12	1.96	0.57	1.45	96.89
L. persona	31.33	12.03	0.89	1.67	0.53	1.15	98.04
M. gigas	7.53	1.59	0.46	1.56	0.29	0.60	98.64
B. crenatus	1.00	13.07	-0.26	1.48	0.18	0.34	98.98
Mytilus spp.	6.00	1.59	0.14	0.30	0.46	0.18	99.16
Pagurus spp.	2.00	2.72	-0.12	0.57	0.20	0.15	99.31
H. nudus	2.67	1.14	0.11	0.55	0.20	0.14	99.45
Actiniaria	1.00	2.48	-0.09	0.40	0.23	0.12	99.57
L. pelta	2.03	1.24	0.08	0.34	0.24	0.11	99.67
Littorina spp.	1.00	4.10	-0.07	0.39	0.17	0.09	99.76

D. excentricus	1.17	1.00	0.05	0.48	0.11	0.07	99.83
Bivalvia	1.00	1.34	-0.04	0.26	0.14	0.05	99.87
Strongylocentrotus spp.	1.33	1.00	0.03	0.21	0.16	0.04	99.92
B. elegans	1.00	1.76	-0.02	0.15	0.16	0.03	99.95
Idotea spp.	1.33	1.34	-0.02	0.08	0.23	0.02	99.97
Amphipoda	1.00	1.38	-0.02	0.11	0.16	0.02	100.00
S. cariosus	2.00	1.00	0.00	0.02	0.19	0.00	100.00

(F)	**Shellfish Farms**	**Reference Sites**			**Average dissimilarity = 72.14%**		
Barnacle *Spp.*	941.34	548.67	41.51	25.52	1.63	57.54	57.54
L. persona	187.90	24.00	8.02	9.48	0.85	11.11	68.65
Hemigrapsus spp.	67.90	57.33	4.87	6.49	0.75	6.76	75.41
B. attramentaria	12.03	56.00	-4.06	8.23	0.49	5.63	81.04
Amphipoda	48.24	18.67	3.66	6.51	0.56	5.08	86.12
H. oregonensis	34.10	7.67	2.13	3.25	0.65	2.95	89.07
L. sitkana	41.34	11.00	1.82	3.88	0.47	2.53	91.60
P. hirsutiusculus	35.48	12.33	1.61	4.17	0.39	2.23	93.83
L. scutulata	32.03	5.33	1.21	3.04	0.40	1.68	95.51
Pagurus spp.	11.00	11.00		2.51	0.42	1.48	96.98
C. dalli	23.76	1.00	0.75	3.12	0.24	1.04	98.03
M. gigas	14.17	1.00	0.35	0.96	0.36	0.48	98.51
H. nudus	5.83	1.67	0.27	0.60	0.45	0.37	98.88
Nucella spp.	3.07	1.00	0.15	0.53	0.29	0.21	99.09
Caridea	1.34	2.33	-0.15	0.93	0.16	0.21	99.30
R. philippinarum	3.76	1.33	0.15	0.44	0.33	0.20	99.50
Idotea spp.	2.03	1.67	0.07	0.28	0.27	0.10	99.61
Pugettia spp.	1.34	1.00	0.06	0.40	0.16	0.09	99.70
Mytilus spp.	2.72	1.00	0.06	0.16	0.35	0.08	99.77
D. excentricus	1.00	1.33	-0.04	0.29	0.14	0.06	99.83
L. pelta	2.03	1.00	0.04	0.15	0.26	0.05	99.89
Polychaeta	1.00	1.33	-0.03	0.23	0.15	0.05	99.93

U. pugettensis	1.34	1.00	0.02	0.09	0.18	0.02	99.95
B. crenatus	1.34	1.00	0.02	0.08	0.18	0.02	99.98
L. staminea	1.34	1.00	0.01	0.06	0.18	0.02	99.99
P. ochraceus	1.34	1.00	0.01	0.03	0.19	0.01	100.00

Table C6 | Analysis of the decision nodes formed during construction of the multivariate regression tree (MRT). The respective MRT analyzed the interaction between epifaunal communities and substrate composition. A) Discriminant taxa, left and right split means, and the deviance explained at each node B) Indicator species, directional clusters and the probability the taxonomic cluster occurred randomly.

(A) **Node**	**Discriminant Species**	**Explained Deviance (%)**	**Left Split Mean**	**Right Split Mean**
Root Node Gravel = 7.305 Complexity = 12.45	Littorinidae	18.18	0.32	1.08
	Lottiidae	11.28	0.40	1.00
	Sessilia	61.17	1.05	2.45
Left Node 1 Oyster Shell = 8.275 Complexity = 2.64	Decapoda	24.73	0.42	1.61
	Sessilia	54.35	0.89	2.66
Left Node 2: *Mastocarpus* = 12.88 Complexity = 2.23	Amphipoda	19.95	0.11	1.76
	Decapoda	24.27	0.36	2.19
	Littorinidae	14.39	0.22	1.63
	Lottiidae	21.86	0.28	2.01
Right Node 1 Cobble = 1.384 Complexity = 3.01	Littorinidae	40.76	0.90	1.64
	Lottiidae	11.34	0.90	1.30
	Sessilia	43.92	2.26	3.04
Right Node 2 Oyster Shell = 0.8453 Complexity = 1.96	Decapoda	41.14	0.77	1.52
	Lottiidae	13.21	0.82	1.25
	Ostreidae	17.55	0.00	0.50
	Sessilia	23.01	2.16	2.72
Right Node 3 Gravel = 59.2 Complexity = 2.33	Littorinidae	36.65	0.49	1.18
	Lottiidae	14.54	0.54	0.98

	Sessilia	36.64	1.71	2.41

(B) Node	Indicator Species	Cluster	Indicator Value	Probability
Root Node Gravel = 7.305 Complexity = 12.45	Cerithiidae	Left	0.04	0.004
	Dendrasteridae	Left	0.02	0.028
	Sessilia	Right	0.63	0.001
	Littorinidae	Right	0.47	0.001
	Lottiidae	Right	0.44	0.001
	Decapoda	Right	0.40	0.001
	Batillariidae	Right	0.24	0.002
	Mytilidae	Right	0.16	0.005
Left Node 1 Oyster Shell = 8.275 Complexity = 2.64	Decapoda	Right	0.73	0.001
	Sessilia	Right	0.69	0.001
	Lottiidae	Right	0.50	0.002
	Ostreidae	Right	0.48	0.001
	Littorinidae	Right	0.31	0.014
Left Node 2 Mastocarpus = 12.88 Complexity = 2.23	Amphipoda	Right	0.94	0.001
	Decapoda	Right	0.86	0.001
	Littorinidae	Right	0.66	0.003
	Lottiidae	Right	0.66	0.004
	Batillariidae	Right	0.64	0.005
	Mytilidae	Right	0.45	0.014
	Venerida	Right	0.42	0.018
Right Node 1 Cobble = 1.384 Complexity = 3.01	Littorinidae	Right	0.57	0.001
	Sessilia	Right	0.56	0.001
	Lottiidae	Right	0.45	0.003
	Sphaeromatidae	Right	0.05	0.041
Right Node 2 Oyster Shell = 0.8453 Complexity = 1.96	Decapoda	Right	0.58	0.001
	Sessilia	Right	0.56	0.002
	Ostreidae	Right	0.45	0.001
	Lottiidae	Right	0.43	0.012
	Asteriidae	Right	0.05	0.032
Right Node 3 Gravel = 59.2 Complexity = 2.33	Venerida	Left	0.16	0.001
	Polychaeta	Left	0.11	0.002
	Cardiida	Left	0.05	0.042
	Sessilia	Right	0.52	0.002
	Littorinidae	Right	0.47	0.001
	Lottiidae	Right	0.39	0.008

Table C7 | Substrate composition-epifaunal community associations determined by taxa-specific variability explained by the multivariate random forest (MRF) model, and the predictive accuracy of the MRF determined. 80% of the data were used to train a model and the remaining 20% of the data to evaluate the model's predictions. Model construction used identical parameters to the variable importance analysis.

	Random Forest Model			Prediction	
Species	Explained Variance (Percent)	Error Rate	Standardize Error Rate	Variance Explained	Test Set Error Rate
Batillariidae	48.64	0.24	0.51	48.17	0.3
Decapoda	46.43	0.39	0.54	45.51	0.41
Sessilia	43.35	0.94	0.57	36.14	1.13
Ostreidae	33.92	0.08	0.66	35.22	0.02
Littorinidae	33.77	0.61	0.66	30.68	0.66
Lottiidae	33.31	0.54	0.67	30.61	0.54
Cardiida	32.72	0.01	0.68	Inf	0
Amphipoda	27.67	0.18	0.72	23.26	0.21
Venerida	21	0.11	0.78	32.52	0.15
Mytilidae	12.27	0.19	0.88	14.41	0.13
Polychaeta	8.69	0.05	0.91	12.48	0.1
Anthozoa	4.7	0.01	0.95	6.26	0.02
Dendrasteridae	0.88	0.02	0.99	-2.47	0.01
Cerithiidae	0.71	0.02	0.99	-12.85	0.01
Haminoeidae	0.71	0.01	0.99	Inf	0
Sphaeromatidae	0.46	0.03	1	Inf	0
Neogastropoda	-1.4	0.05	1.02	-20.03	0.03
Strongylocentrotidae	-3	0.01	1.03	-1.22	0.01
Asteriidae	-3.42	0.01	1.03	-0.22	0.02
Myrrhinidae	-3.93	0.01	1.04	-2.57	0
Chitonida	-5.83	0.01	1.06	-0.29	0.01
Amphilepidida	-7.89	0.01	1.08	0.52	0.03
Bryozoa	-8.79	0.01	1.08	1.04	0.04
Nemertea	-10.55	0	1.11	Inf	0

Table C8 | Habitat complexity-epifaunal community associations determined by taxa-specific variability explained by the multivariate random forest (MRF) model, and the predictive accuracy of the MRF. 80% of the data were used to train a model and the remaining 20% of the data to evaluate the model's predictions. Model construction used identical parameters to the variable importance analysis.

	Random Forest Model			Prediction	
Species	Explained Variance (Percent)	Error Rate	Standardize Error Rate	Variance Explained	Test Set Error Rate
Amphilepidida	-23.81	0.2	1.24	Inf	0.01
Amphipoda	24.68	236.15	0.75	-409.1	86.55
Anthozoa	-6.16	1.79	1.06	Inf	0.12
Asteriidae	-19.45	0.14	1.19	-0.34	0.4
Batillariidae	6.67	530.33	0.93	46	138.83
Bryozoa	31.37	0.19	0.69	Inf	0.06
Cardiida	-23.78	1.01	1.24	Inf	0.32
Cerithiidae	38.68	0.08	0.61	23.77	0.21
Chitonida	-19.11	0.06	1.19	Inf	0.01
Decapoda	20.89	2778.45	0.79	69.85	846.8
Dendrasteridae	-12.94	4.14	1.13	0.51	0.2
Haminoeidae	-18.98	1	1.19	-2499.49	0.58
Littorinidae	-14.08	3972.49	1.14	-45.49	1087.28
Lottiidae	3.28	5450.76	0.97	-717.79	2363.69
Myrrhinidae	-23.53	0.21	1.24	-299.14	0.01
Mytilidae	-26.71	17.29	1.27	1.5	15.41
Nemertea	-22.66	0.01	1.23	Inf	0.01
Neogastropoda	-14.83	3.38	1.15	Inf	1.03
Ostreidae	5.05	105.48	0.95	-6859.78	15.35
Polychaeta	-7.85	20.95	1.08	12.25	55.96
Sessilia	27.97	851360.09	0.72	64.67	284879.4
Sphaeromatidae	-2.94	1.34	1.03	7.98	0.74
Strongylocentrotidae	-11.08	0.03	1.11	63.77	0
Venerida	14.08	17.87	0.86	25.25	37.8