


Original Article

Infaunal community responses to ancient clam gardens

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Aquatic ecosystems have been managed for millennia. Indigenous communities in North America pioneered numerous marine resource management strategies to ensure food security and support thriving economies, which have been active throughout the Northwest Coast of North America for over 14 000 years. Developed to increase shellfish productivity, clam gardens have been active for millennia. The diverse infaunal communities within these ecosystems can act as indicators of habitat alterations and provide an opportunity to study ecological community responses to seascapes shaped by millennia-old resource management structures. To determine how community structure differs between clam gardens and unmodified areas, we assessed infaunal diversity and density between intertidal mudflats, sandflats, and clam gardens. Differences in community composition were found among site types, with certain taxa, including culturally important species increasing within clam gardens. Per cent similarity analyses indicated that infaunal communities were more dissimilar among, than within site types. Furthermore, regression trees indicated that increases in diversity and density were closely correlated with the amount of shell and gravel within each habitat, which are associated with clam garden function and management practices. Species-specific and environmental responses to clam gardens indicate that human modifications in nearshore habitats created novel and distinct types of soft sediment communities.

Keywords: ancient shellfish mariculture, clam gardens, community compositions, infauna diversity, marine invertebrates, marine resource management

Introduction

Aquatic and terrestrial ecosystems have been utilized, managed, and stewarded by humans for millennia (Erlandson *et al.*, 2008; Lepofsky and Lertzman, 2008). Today, between a third to a half of terrestrial ecosystems and the entire marine environment are influenced by anthropogenic activity (Vitousek *et al.*, 1997; Halpern *et al.*, 2008). As coastal regions are three times more populated than the global average, anthropogenic activity is focused around coastlines, primarily due to resource availability (Cohen *et al.*, 1997; Small and Nichols, 2003). Historically, and to

the present day, North American Indigenous communities pioneered numerous technologies and management strategies to increase food production, ensure food security, support economies, cultural practices, and ceremonies (Cohen *et al.*, 1997; Berkes *et al.*, 2000; Berkes and Turner, 2006; Deur *et al.*, 2015; HGINPR, 2016). Throughout the Northwest Coast of North America, these innovations play a critical role in coastal First Nations' 14 000 years or more continuous stewardship of British Columbia's Coastline (McLaren *et al.*, 2015, 2018). As coastal and marine ecosystems have been critical to human use, management,

and settlement for thousands of years and continue to be central today, coastal communities live within close proximity to vital marine resources (Deur *et al.*, 2015; Lepofsky *et al.*, 2015).

One of the marine resource management systems involves intertidal terraces running parallel to the coastline, known as clam gardens (Harper *et al.*, 1995; Augustine and Dearden, 2014; Smith *et al.*, 2019). Constructed by building extensive rock walls in the mid to low intertidal (0.5–1.8 m above chart datum), these structures increase sedimentation rates by at least fourfold, altering the beach slope at tidal heights optimal for clam production, thus creating or expanding available idyllic clam habitat (Neudorf *et al.*, 2017). Current estimates suggest the majority of construction begun throughout the latter half of the Holocene, with construction details varying in accordance with the physical properties of the intertidal zone (Caldwell *et al.*, 2012; Lepofsky and Caldwell, 2013; Lepofsky *et al.*, 2015; Smith *et al.*, 2019). Recent radiocarbon dates and investigations into sea level history and taphonomic processes, place clam garden construction throughout Northern Quadra Island, British Columbia, 3500 years before present, with shellfish management present over 3000 years prior to garden construction (Toniello, 2017; Smith *et al.*, 2019).

Generally, clam gardens were maintained incrementally over time, likely over multiple generations, spanning thousands of years (Neudorf *et al.*, 2017). The soft sediment area between the clam garden wall and the shoreline is maintained using a suite of tending or “gardening” practices, including predator exclusion (Erlandson *et al.*, 2008), and the provision of larval settlement cues such as gravel, shell hash, and whole shells (Butman *et al.*, 1988; Groesbeck *et al.*, 2014; Deur *et al.*, 2015; H-GINPR, 2016). The intertidal terraces created by clam gardens increases clam abundance and productivity, providing predictable and stable shellfish populations adjacent to coastal communities (Augustine and Dearden, 2014; Groesbeck *et al.*, 2014). In certain instances, shell middens adjacent to clam beds indicate that strategies for managing marine resources, including shellfish harvesting, were continuous active for at least 5000 years (Cannon *et al.*, 2008). Clam gardens have now been observed from Alaska to British Columbia (Harper *et al.*, 1995; Harper, 2007; Moss and Wellman, 2017). Despite this long history, their existence and distributions are relatively new to western science.

Many human–ecosystem interactions have led to species loss, disruption of community dynamics, and ecosystem degradation, as such, it is now well-established that the planet has entered the Anthropocene (Jackson *et al.*, 2001; Crutzen, 2002; Crain *et al.*, 2008). However, emerging research indicates that certain anthropogenic activities, even those associated with species extraction or habitat alterations, may elicit positive ecological responses, even after the activity has ceased (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016; Fisher *et al.*, 2019). For example, long-term intertidal resource use along British Columbia’s Central Coast can enhance forest productivity (Trant *et al.*, 2016). Specifically, shell middens associated with habitation can increase vegetation cover, density, diversity, and overall forest productivity, by elevating the abundances of limited nutrients in the soil and altering soil chemistry (Meigs, 1938; Cook-Patton *et al.*, 2014; Trant *et al.*, 2016). Furthermore, the vegetation at long-term habitation sites reflects cultural plant use centuries after intense habitation has ceased (Fisher *et al.*, 2019). Similarly, within intertidal systems clam gardens structure ecosystem processes by altering the physical landscape, and in turn, increase clam abundance and productivity,

even if currently fallow (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016). These examples highlight how coastal First Nations’ practices alter community dynamics, resulting in more productive and diverse ecosystems. Given that bivalve and univalve middens are found worldwide (Bailey *et al.*, 2013), ecological interactions with shellfish cultivation likely affect a wide variety of coastal landscapes. Although clam garden studies have found that bivalve productivity increases with intertidal terracing (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016), there has been minimal scientific inquiry about the effects of intertidal cultivation practices and human engineering on other benthic communities.

Ecological responses to clam gardens are likely present among various components of the surrounding ecosystems, however, infaunal species (animals living in the sediment) offer a unique opportunity to study how individual species and communities respond. Infaunal communities exhibit pronounced responses to ecological disturbances due to high diversity and abundance (Nilsson and Rosenberg, 2000; De Juan and Hewitt, 2014; Gerwing *et al.*, 2016, 2017a). Furthermore, these communities are known to experience intense resource competition (Ferguson *et al.*, 2013), exhibit rapid community turnover (De Juan and Hewitt, 2014; Gerwing *et al.*, 2016), and are influenced by a suite of abiotic and biotic forces (Gerwing *et al.*, 2016, 2018). As such, infaunal communities are an appropriate avenue for evaluating the ecological responses to clam gardens and associated habitat alterations, including increased abundances in shell hash and sedimentation.

To determine how infaunal communities in clam gardens compared to unmodified sheltered mudflats and exposed sand beaches, we assessed differences in taxonomic diversity and density of infaunal communities between these habitats, and determined their association with benthic habitat variables. We hypothesized that infaunal communities would differ between the site types, and communities would be more dissimilar across site types than within sites types. We predicted that these responses would likely be closely associated with the environmental variables modified by clam garden construction, including increased shell fragments and fine sediments, amongst others. This study represents the first scientific empirical quantification of clam garden influence on marine biodiversity.

Material and methods

Study location

This study was conducted in the territories of the Heiltsuk Nation, and the Wuikinuxv Nation, on Calvert and Hecate Islands (51.656059°, –128.134267°) on British Columbia’s Central Coast, Canada. The territories lands and waters have been carefully managed by Heiltsuk and Wuikinuxv people since time immemorial (Brown and Brown, 2009; Heiltsuk Nation, 2019; HLUP, undated living document; Wuikinuxv Nation, 2019), and the region has evidence of this longstanding relationship in the form of numerous traditional habitation sites, including large winter villages, and marine resource harvesting sites (McLaren and Christensen, 2014; Jackley *et al.*, 2016; Trant *et al.*, 2016). Human habitation and stewardship of this area spans at least 14 000 years before present (McLaren and Christensen, 2014; McLaren *et al.*, 2018).

Nine intertidal sites within close proximity to the Hakai Institute Calvert Island Ecological Observatory were sampled during August 2016. These sites were: First Nations clam gardens,

unmodified sheltered mudflats and unmodified exposed sandflats. We assessed three of each site type (Figure 1). The First Nations clam gardens considered in this study have not been managed to the extent as they once were; however, the terraced beaches and associated transformed seascape are unmistakable. The clam gardens and unmodified sheltered mudflats were within Kwakshua Channel, a 12 km channel that runs between Calvert and Hecate Islands characterized by rocky coastlines, protected bays, and eelgrass habitats. The exposed sandflats were on the northwest side of Calvert Island within Choked Passage, which consisted of sandy beaches exposed to open seas, and adjacent to kelp forests and rocky outcroppings. The foreshore of both Calvert and Hecate Islands is a temperate rainforest; specifically, a hypermaritime variant of the Coastal Western Hemlock biogeoclimatic zone classification (Pojar et al., 1991).

Field collections

Site surveys were conducted in a similar manner to Cox et al.'s (2017) sampling method. Briefly, a 40 m baseline was run parallel to the shore along the 2.2 m tideline, bisected with a perpendicular baseline running from 2.2- to 1.5-m tideline. Cores (7 × 20 cm) were collected at the intersection of lines run from the parallel and perpendicular baseline, which formed a grid across the study area (Supplementary Figure S1). Line spacing along the parallel baseline was determined *a priori* and increased in 5- or 10-m intervals, while line spacing along the perpendicular baseline was randomly selected *in situ*. This spacing ensured that species assessments were conducted at comparable intertidal heights across sites, and that the entire assessment area was covered. Three to five cores were collected at each site.

Core processing

Infaunal core samples were passed through a 250 µm sieve (Crewe et al., 2001; Gerwing et al., 2016), stored in 95% ethanol, and identified to the lowest practicable taxonomic unit at a later date (Gerwing et al., 2017a, b). The 250 µm sieve was chosen to ensure that the majority of species within the sample was detected. Briefly, Cumaceans were identified to species, Nemertean to species and genus, Chironomidae indet. (Chromatid larvae) to family, Nematoda (all nematodes) to phylum, Oligochaeta (all oligochaetes) to subclass, Ostracoda (all ostracods) to class. Polychaetes were identified to species when possible, and when not, to species complexes, genus, or family (e.g. *Notomastus tenuis*, *Capitella capitata* complex, *Naineris* sp., Maldanidae). In addition, *Leptochelia dubia* complex, *Pinnixa* sp., Acoela indet., *Archaeomysis grebnitzkii* (order Mysida) were observed (Supplementary Table S1).

Benthic habitat analysis

To evaluate ecological covariates of the associated benthic habitat, 0.5 × 0.5 m quadrats placed at the site of each core collection were photographed using a Nikon AW120 camera held 1 m above the quadrat (resolution: 2832 × 2832 pixels). Benthic photos were analysed using ImageJ photo processing and analysis software (Abramoff et al., 2004) to derive surface cover metrics. All quadrat photos were processed by the same individual in an unordered fashion to avoid observer bias. Per cent cover of all epifauna and sediment types was determined by dividing the area covered by each type by the total quadrat area. Algal abundance was measured as per cent cover and identified to genera, with

Ulva spp., *Fucus* spp., and *Mazzaella* spp. being observed. Sediment size classes were classified using the Wentworth scale to identify the boulder, cobble, gravel sand, and mud (silt/clay) in each quadrat (Wentworth, 1922). Sediment size classes were determined using the ratio of the width of the sediment to the known width of the quadrat. The amount of each sediment grain size class present was determined by summing each identified size class relative to the known area of the quadrat. In addition, epifauna algal identification, sediment classification, and associated per cent covers were recorded directly in the field, which allowed any discrepancies that occurred during the benthic habitat analysis to be resolved *post hoc*.

Data analysis

Community-level analyses were conducted using the statistical program PRIMER with the PERMANOVA (Permutational Multivariate Analysis of Variance) add-on (McArdle and Anderson, 2001; Clarke and Gorley, 2015). Fifty-six taxa (e.g. species, species complexes, genera) were observed across the study sites (Supplementary Table S1). A resemblance matrix of infaunal densities was calculated using Bray–Curtis coefficients, and a dummy variable of 1 to correct for cores where no biota was observed (Clarke and Gorley, 2015). Densities were fourth-root transformed to improve assessment of rare and common taxa on community structure (Clarke and Gorley, 2015). Community composition of mudflats, clam gardens, and sandflats were visualized using a non-metric multidimensional scaling (nMDS) plot.

To determine if the community composition varied among the three site types, a PERMANOVA (9999 permutations) was conducted on the resemblance matrix described above. A single fixed factor, site type, was included in the PERMANOVA, and an α of 0.05 was used to detect significance.

Per cent dissimilarity between each site type was calculated using PRIMER's Similarity Percentages or SIMPER routine (Clarke, 1993; Clarke and Ainsworth, 1993). SIMPER elucidates the differences in taxa between site types. The ratio of each group's average dissimilarity to the standard deviation of the dissimilarities (Diss/SD) represents how consistently each group contributed to the observed differences among site types. Values >1 represent groups that consistently contribute to the observed differences between site types, whereas values <1 do not (Clarke, 1993; Clarke and Ainsworth, 1993; Clarke and Gorley, 2015).

Regression trees were used to evaluate patterns in taxonomic diversity and density in relation to the multiple benthic habitat variables (e.g. Cobble, Gravel, Sand, *Fucus*) and generated in R studio using the package "rpart" (R Core Team, 2017; Therneau et al., 2017). Regression trees were chosen because they are robust to nonlinear relationships and effective when evaluating how multiple explanatory variables predict observed patterns (De'ath and Fabricius, 2000; Therneau and Atkinson, 2018).

As the environmental variables driving taxonomic diversity and density within and across the site types were of interest, independent regression trees were generated for taxonomic diversity and density within each of the three site types, as well as the pooled data (eight regression trees total). Generally, each of the regression trees evaluated either taxonomic diversity or density as the response variable, and Site, % Cobble, % Gravel, % Mud, % Shell, % *Ulva*, % *Fucus*, and % *Mazzaella* as the independent variables (Supplementary Table S2). Models considering the pooled data from all three habitats did not include site type or site, to

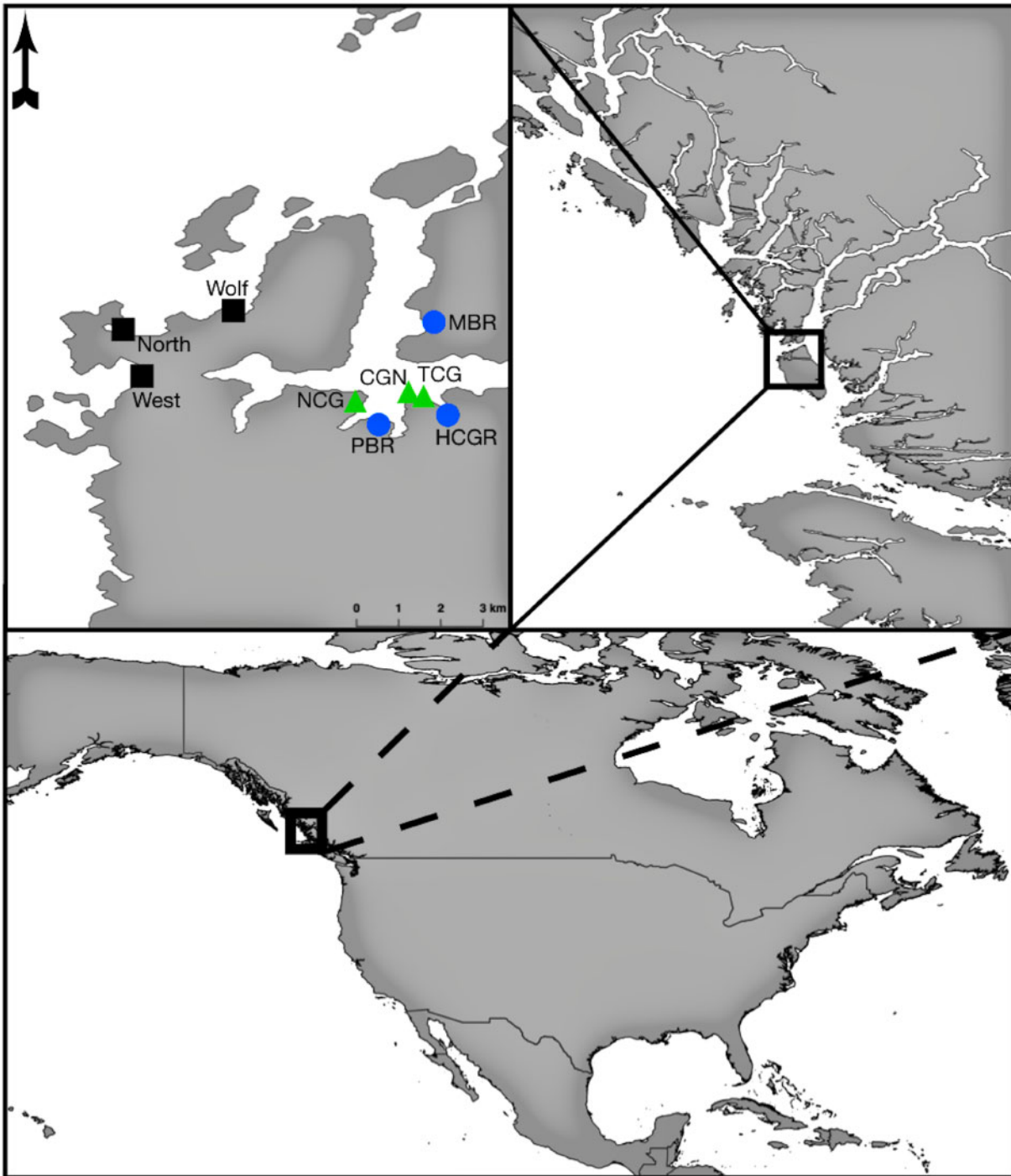


Figure 1. The study area within the Central Coast of British Columbia, Canada, included nine intertidal sites on either Calvert or Hecate Islands (51.656059°N, -128.134267°W). Triangle—the three clam garden sites within Kwakwaka'wakw Channel. Circle—the three unmodified sheltered mudflat sites within Kwakwaka'wakw Channel. Square—the three exposed sandflats within Choked passage.

better evaluate which environmental variables drove species diversity and density across all habitats. In all models, the tree-based analogue ANOVA function was used. The splitting method was used given the contiguous data structure (i.e. data were the total number of taxa observed in each core, at each site). A minimum terminal node size of 3–10 was used, which represented the

minimum number of observations necessary for a terminal node to be generated.

The size of each tree was determined by cross-validation following the one standard error rule to prune trees to the most parsimonious structure. This rule states that the most parsimonious model is one in which its estimated error rate is within one standard error of the best model (Breiman *et al.*, 1984; Hastie *et al.*,

2009; Venables and Ripley, 2013). The estimates of predicted error and standard errors were obtained by 100-fold cross-validation. This process was done graphically and involved plotting the relationship between the number of splits in the tree and the relative error rate to ensure that the selected number of splits obeyed this rule. In addition, residuals of each model were evaluated to further ensure that the finalized models were appropriate (Therneau and Atkinson, 2018). When considering taxonomic diversity and density pooled across site types, the pruning function was used to generate an additional tree for both diversity and density. Given the conservative nature of this function the aim was to identify the major predictor of species diversity and density across these habitats.

Results

Significant differences in infaunal community composition were observed among sites and site types, with nMDS plots having a stress <0.2, and thus considered a good two-dimensional representation of higher dimensional trends (Clarke, 1993; Figure 2 and Table 1). The average per cent dissimilarities among site types were: Mudflats and Clam Gardens, 43.93%; Clam Gardens and Sandflats, 80.99%; Mudflats and Sandflats, 81.74% (Table 2). Within site types, mudflats were 32–43% dissimilar from each other, sandflats were 72–77% dissimilar, and clam gardens were ~41% (Supplementary Table S3). Infaunal communities were more dissimilar among than within site types.

Taxon-specific dissimilarity between sites differed extensively. When comparing clam garden and mudflat habitats, Nematoda, Oligochaeta, *Scoletoma tetraura* complex (Polychaeta), Harpacticoida, *Mytilus* sp. (Bivalvia), Chironomidae indet. (Diptera), *Syllis alternata* (Polychaeta), *Eteone californica* (Polychaeta), and Anopla (Nemertea), were more abundant within clam gardens, and contributed substantially to the dissimilarity between site types, while, *L. dubia* complex (Tanaidacea), *Cumella vulgaris* (Cumacea), *Exogone lourei* (Polychaeta), *Kurtiella tumida* (Bivalvia), *Mediomastus californiensis* (Polychaeta), *C. capitata* complex (Polychaeta), Ostracoda, and *Foxiphalus falciformis* were more abundant within mudflats (Table 2). In addition, culturally important food species including the bivalves *Leukoma staminea* (Pacific littleneck clam), *Saxidomus gigantea* (butter clam), and *Macoma balthica* (Baltic clam), were all observed at high densities within clam gardens relative to mudflats (Supplementary Table S4). When comparing clam garden and sandflats, and mudflats and sandflats, the SIMPER analysis determined communities to be over 80% dissimilar. This dissimilarity was driven primarily by increased abundances of Nematoda, Oligochaeta, Harpacticoida, Ostracoda, *Nutricola tantilla* (Bivalvia), *S. tetraura* complex (Polychaeta), *Mytilus* sp. (Bivalvia), observed within clam gardens and mudflats, and higher densities of Calanoida within sandflats; a planktonic copepod deposited by the receding tide (Table 2).

Across all habitats, regression trees showed that increases in taxonomic diversity were primarily driven by the amount of shell, gravel, and *Ulva* spp. The amount of shell was the only variable associated with a split that resulted in a terminal node (Figure 3a). Increases in taxonomic density were most strongly associated with the amount of shell and gravel present (Figure 4a). However, in this instance *Fucus* spp., not *Ulva* spp. played a critical role in taxonomic density. Moreover, when models were extensively pruned, the amount of shell present was the primary predictor of diversity and density (Figures 3a and 4a).

When considering the habitats independently, shell, gravel, and *Ulva* spp. were associated with increases in taxonomic diversity within clam gardens (Figure 3b), whereas density was associated with gravel, shell, and site level differences (Figure 4b). Regression trees of mudflats and sandflats both identified site-level differences as key factors for diversity (Figure 3c and d). Within mudflats, the variables that further predicted taxonomic diversity differed depending on the site, with the amount of *Ulva* spp. being a critical variable within PBR and HCGR sites, while gravel was the predominant variable at MBR. Density within mudflats was associated with the amount of gravel, *Ulva* spp. and mud, with the amount of gravel being the only variable associated with a split that resulted in a terminal node. Within the sandflat-type sites, the amount of sand determined the differences observed in taxonomic diversity and density, with site type differences also contributing to the former (Figures 3d and 4d).

Discussion

To elucidate how marine biodiversity responds to ancient bio-cultural management practices and intertidal beach terracing, we assessed infaunal communities within sheltered mudflats, exposed beaches, and ancient clam gardens. Community composition differed among sites and site types, indicating that species assemblages varied between unmodified mudflats and engineered clam gardens. The range of per cent dissimilarity values observed within our mudflat (32–43%) and clam gardens sites (~41%). That is, these site types were relatively similar. However, differences among the three sandflats studied (72–77%) were much higher, indicating high dissimilarity among these communities. The observed difference between clam gardens and mudflats (43.93%) was relatively low, while differences between sandflats and mudflats (81.74%), and clam gardens and sandflats (80.99%) were high, suggesting that these intertidal communities are very different.

Despite shared species composition between clam gardens and mudflats, the SIMPER analysis determined that various taxa were more abundant in clam gardens (e.g. Nematoda, Harpacticoida, Chironomidae indet., *E. californica*) including culturally and economically important bivalve species such as *Saxidomus giganteus* and *L. staminea*. The regression trees determined that increases in taxonomic diversity and density were closely associated with the amount of shell and gravel present. As these environmental variables are known to increase during clam garden construction and maintenance (Deur et al., 2015; H-GINPR, 2016; Neudorf et al., 2017), it is likely the environmental changes set in motion when clam gardens are constructed facilitated increased taxonomic diversity, density, and associated alterations in community composition over time. Furthermore, Smith et al. (2019) categorized one of the predominate clam garden construction varieties as gardens built on soft sediment beaches with standing clam habitat that expands existing beach habitats. When considered in combination with Fisher et al. (2019) observation that species with higher nutrient requirements and cultural significance persist indefinitely within culturally modified landscapes, suggests pre-construction species composition at the clam garden sites built on soft sediment beaches resembled the unmodified mudflat communities, but garden construction and millennia of resource management has forever shaped these ecological communities. These clam gardens now support increased diversity and abundance of taxa that require optimal and stable, abiotic conditions. Species-specific responses to clam gardens centred largely around

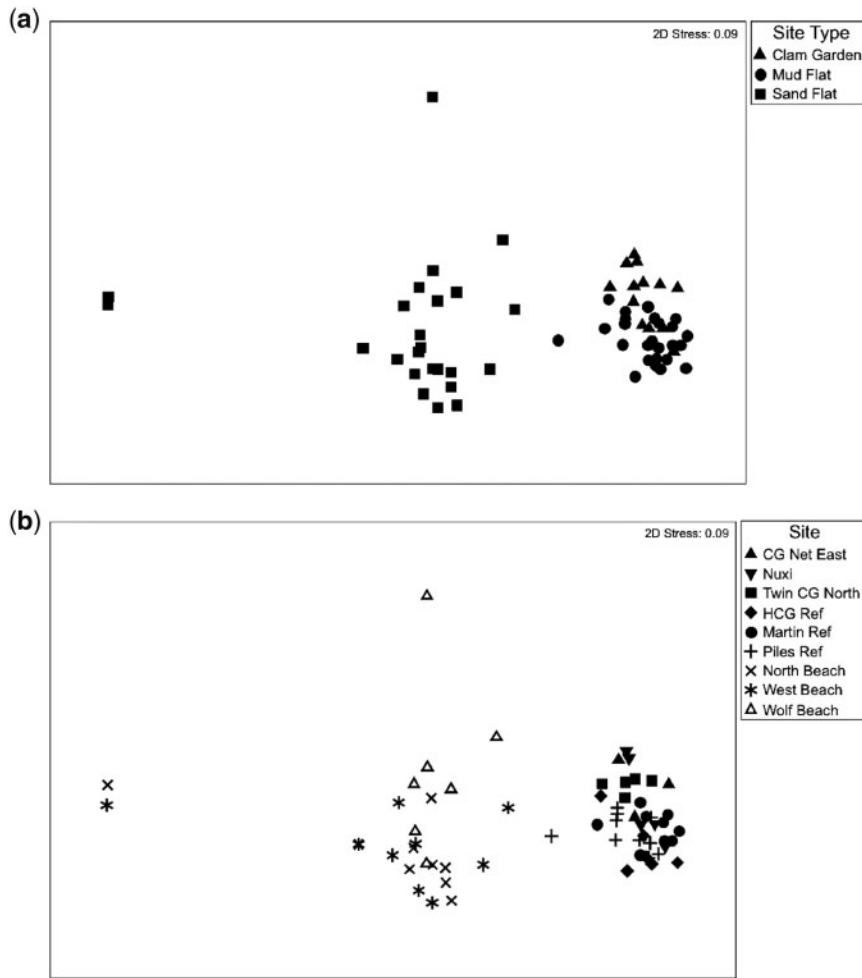


Figure 2. nMDS plots of community composition at (a) three sandflats, three mudflats, and three clam gardens along the Central Coast of British Columbia, Canada, and (b) considered at the site level.

Table 1. PERMANOVA (permutational multivariate analysis of variance) assessing if infaunal community composition varied between clam gardens, mudflats, and sandflats along the Central Coast of British Columbia, Canada.

Source	df	MS	Pseudo-F	Unique permutations	<i>p</i>
Site	8	4269.1	3.48	9962	0.0002
Clam garden vs. mudflat	1	3045	3.84	9975	0.003
Clam garden vs. sandflat	1	18 687	12.44	9937	0.0002
Mud flat vs. sandflat	1	17 302	10.73	9801	0.0002
Residual	54	1067.40			
Total	62				

Significant and interpretable *p*-values are in bold.

increased amounts of shell and gravel, and consistent environmental conditions across gardens. Specifically, Nematoda and Oligochaeta communities, among other taxa, are known to be highly influenced by sediment granulometry, with coarser sediments producing diverse communities (Steyaert *et al.*, 1999; Giere, 2006). Within the select clam gardens studied, the proliferation of these taxa was driven by an increase in medium-coarse sediment and shell hash that fills in the landward side of the clam garden wall, which is known to accumulate fourfold faster relative to unmodified sites. This increased sedimentation rate

corresponds to roughly 11 cm of sediment per thousand years (Neudorf *et al.*, 2017). Furthermore, Harpacticoida are restricted to upper sediment layers due to sensitivity to reductions in oxygen (Dahms and Qian, 2004), and *N. tantilla* favours epibenthic sediment habitats in protected bays (Pamatmat, 1968). In these instances, both taxa are responding to stable environmental conditions elicited through wall persistence. Stable environmental conditions, and increases in medium-coarse sediment and shell hash, also facilitated the propagation of bivalve communities, which has been well documented by Traditional Ecological

Table 2. SIMPER (Similarity Percentages) tables showing the contribution of each taxonomic grouping to the observed differences between intertidal study site types (clam garden, mudflats, and sandflats) along the Central Coast of British Columbia, Canada: (A) clam garden and mudflat, (B) clam garden and sandflat, (C) mudflat and sandflat.

Taxa	Average density	Average density	Average dissimilarity (%)	Diss/SD	Contribution (%)	Cumulative (%)
(A)	Clam garden	Mudflat			Average dissimilarity = 43.93%	
<i>L. dubia</i> complex	2.29	10.25	4.12	1.75	9.39	9.39
Nematoda	20.91	19.95	2.54	1.32	5.78	15.17
<i>C. vulgaris</i>	1.59	5.17	2.26	1.35	5.15	20.31
Oligochaeta	12.62	8.75	2.1	1.17	4.79	25.1
<i>S. tetraura</i> complex	3.54	2.92	2.04	1.09	4.64	29.74
Harpacticoida	12.52	9.46	2.04	1.38	4.64	34.38
<i>E. lourei</i>	1.62	4.23	2	1.22	4.56	38.95
<i>N. tantilla</i>	5.75	3.57	1.57	1.09	3.58	42.53
<i>K. tumida</i>	1.99	3.07	1.56	1.18	3.56	46.09
<i>M. californiensis</i>	2.38	4.02	1.56	1.31	3.55	49.64
<i>C. capitata</i> complex	1.86	2.94	1.48	1.22	3.37	53.01
Ostracoda	9.57	10.11	1.27	1.23	2.89	55.9
<i>F. falciformis</i>	0.48	2.27	1.15	0.67	2.62	58.52
<i>Mytilus</i> sp.	2.12	0.4	1.12	0.77	2.54	61.06
Calanoida	1.29	1.37	1.03	0.81	2.35	63.41
Chironomidae indet.	1.76	1.01	1.02	0.87	2.33	65.74
<i>S. alternata</i>	2.05	0	1.02	0.62	2.32	68.06
<i>E. californica</i>	1.7	0.63	0.98	0.83	2.24	70.3
<i>Anopla</i> sp.	1.66	0.8	0.92	0.87	2.11	72.41
(B)	Clam garden	Sandflat			Average dissimilarity = 80.99%	
Nematoda	20.91	7.05	12.15	1.75	15	15
Oligochaeta	12.62	0.45	10.3	3.22	12.72	27.72
Harpacticoida	12.52	1.17	9.84	2.59	12.15	39.88
Ostracoda	9.57	2.23	6.48	1.92	8	47.88
<i>N. tantilla</i>	5.75	0.45	4.66	2.01	5.75	53.63
<i>S. tetraura</i> complex	3.54	0	3.05	0.88	3.77	57.4
Calanoida	1.29	2.4	2.13	1.07	2.63	60.03
<i>Mytilus</i> sp.	2.12	0	1.88	0.71	2.32	62.35
<i>M. californiensis</i>	2.38	0	1.76	0.86	2.18	64.53
<i>S. alternata</i>	2.05	0	1.75	0.6	2.16	66.69
<i>L. dubia</i> complex	2.29	0	1.69	0.76	2.09	68.78
<i>P. platybranchia</i>	1.73	0.45	1.65	0.63	2.04	70.82
(C)	Mudflat	Sandflat			Average dissimilarity = 81.74%	
Nematoda	19.95	7.05	11.39	1.75	13.94	13.94
<i>L. dubia</i> complex	10.25	0	8.65	2.37	10.58	24.52
Harpacticoida	9.46	1.17	7.18	2.18	8.79	33.3
Oligochaeta	8.75	0.45	7.02	2.7	8.59	41.89
Ostracoda	10.11	2.23	7.02	1.84	8.59	50.48
<i>C. vulgaris</i>	5.17	0	4.36	1.4	5.34	55.82
<i>E. lourei</i>	4.23	0	3.34	1.16	4.09	59.9
<i>M. californiensis</i>	4.02	0	3.28	1.71	4.02	63.92
<i>N. tantilla</i>	3.57	0.45	3.01	1.12	3.68	67.6
<i>K. tumida</i>	3.07	0	2.62	1.09	3.21	70.81
<i>S. tetraura</i> complex	2.92	0	2.4	0.72	2.94	73.75
<i>C. capitata</i> complex	2.94	0	2.27	1.17	2.78	76.53
Calanoida	1.37	2.4	2.01	1.04	2.46	78.99
<i>F. falciformis</i>	2.27	0	1.77	0.6	2.16	81.15

Diss/SD represents the ratio of the dissimilarity to the standard deviation. Only contributions above 2% are listed. [Supplementary Table S4](#) lists all taxa and associated contributions. Den, density; Diss, dissimilarity; Cont, contribution.

Knowledge, including an extensive oral history (Deur *et al.*, 2015; Lepofsky *et al.*, 2015; H-GINPR, 2016), and previously quantified by Groesbeck *et al.* (2014) and Jackley *et al.* (2016). Our findings in combination with Neudorf *et al.* (2017) observations of how clam gardens alter sedimentation rates, and Smith *et al.* (2019) identification of three variations in clam garden construction conditions, including gardens built on soft sediment beaches with standing clam habitat, gardens built on flat bedrock outcrops,

and gardens constructed along steep, eroding, bedrock, support the notion that across an extensive range of environmental and geomorphological conditions, clam gardens generate a distinct biological community that incorporates a wide range of taxa to arise.

Multiple bivalve species were consistently more abundant in clam gardens than mudflats, similar to other findings (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016). However, in our study these

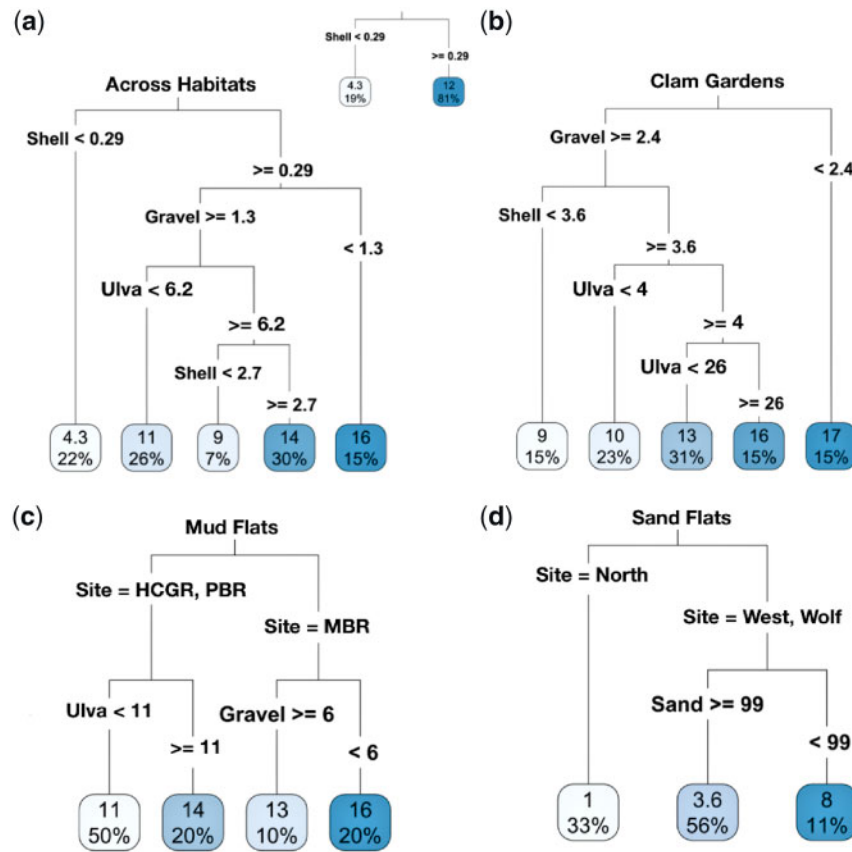


Figure 3. Regression tree analysis of environmental variables associated with taxonomic diversity within and across site types of interest. (a) All site types; sub-tree resulted from the same model pruned extensively, (b) ancient clam gardens, (c) sheltered mudflats, and (d) exposed sandflats.

contrasts were not as strong, in part because of differences in study goals and associated sampling methods. Our assessment of infaunal communities used methodologies designed to capture small (<5 mm) species and thus involved a trade-off between sample resolution and sampling volume. The resulting species composition depends largely on the number of replicates and the amount of sediment collected by each core (Shen *et al.*, 2012). Thus, larger infauna, especially species like Pacific littlenecks and butter clams, may be underestimated. As such, our findings are complementary to previous work, but highlight the full suite of diversity present at size classes not previously considered.

Long-term persistence of anthropogenic activity, especially when associated with human subsistence activities, results in habitat alterations that can have dramatic effects on natural ecosystems (Tovar *et al.*, 2014; Boivin *et al.*, 2016), with elevated abundances of culturally significant species persisting after occupation intensity has declined (Fisher *et al.*, 2019). As such, humans as ecosystem engineers can facilitate profound alterations to ecological communities (Sullivan *et al.*, 2017). Therefore, understanding the extent to which ecological community dynamics are altered by the cultivation and extraction of essential food species is critical to understanding human–ecosystem interactions, and how the legacy of long-term habitation shapes coastal ecosystems.

Our findings demonstrate that clam gardens support unique ecological communities. Mechanistically, the increases in

structural complexity due to the clam garden wall and associated changes in environmental conditions, specifically, the accumulation of shell hash and alterations to sediment composition, allow for the potential to support greater species richness, and communities unlike those in unmodified habitats. In combination with other observations of clam garden effects on sedimentation rates, clam habitats (Neudorf *et al.*, 2017), and clam production (Groesbeck *et al.*, 2014; Jackley *et al.*, 2016), we provide additional lines of ecological evidence supporting the notion that clam gardens promote unique ecological communities and should be considered functionally distinct intertidal habitats, from adjacent mud and sandflat ecosystems. These ecological responses, in turn, may enhance ecosystem function, and therefore, increase resistance to climatic events (Lefcheck *et al.*, 2015; Duffy *et al.*, 2016; Loke and Todd, 2016).

The clam gardens we studied were maintained by coastal communities for thousands of years, spanning hundreds of generations (Erlandson *et al.*, 2008; Deur *et al.*, 2015; Lepofsky *et al.*, 2015; Neudorf *et al.*, 2017). In recent decades these clam gardens have not been actively tended with the same regularity as they once were (Smith *et al.*, 2019). However, even without intense active harvesting, species responses within these and similar ecosystems have been observed. Traditional knowledge illustrates how consistent harvesting resulted in increased clam growth rates, maximum size, and abundance (Deur *et al.*, 2015; Lepofsky *et al.*, 2015). Consistent harvesting entailed actively digging sediments

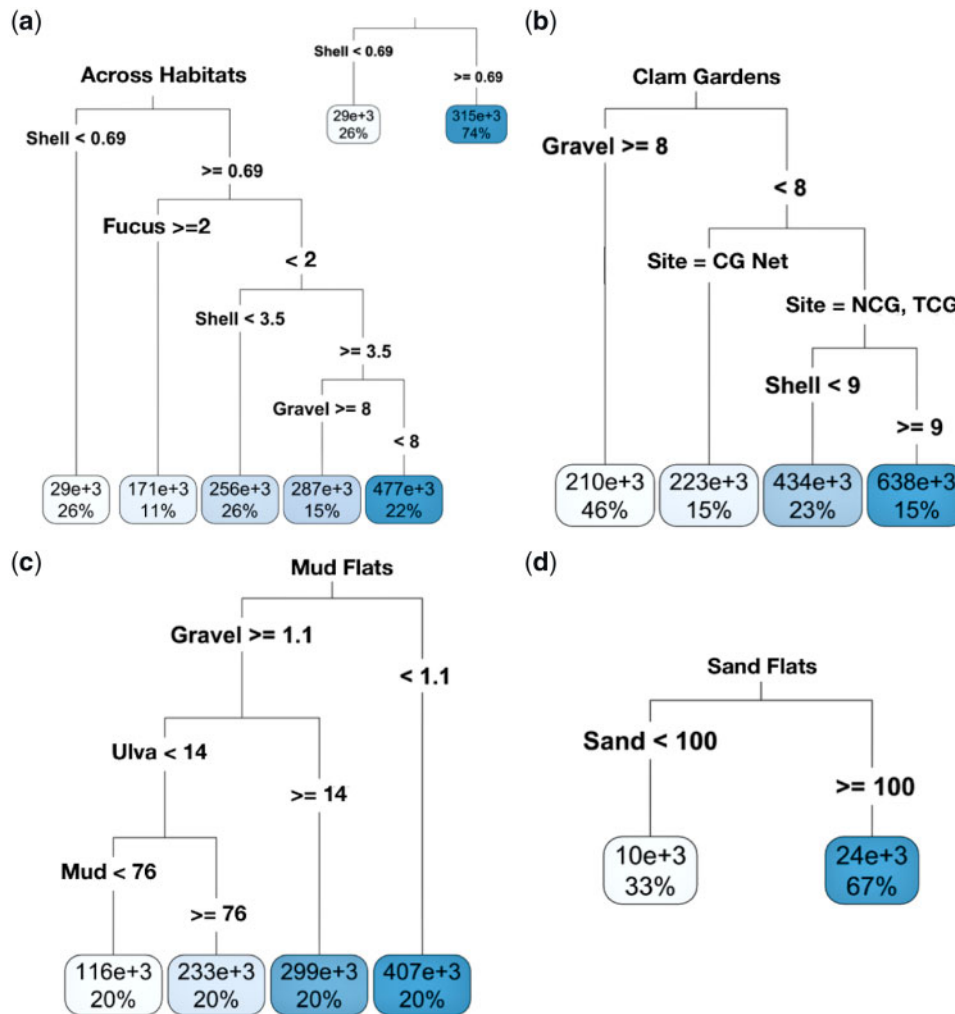


Figure 4. Regression tree analysis of environmental variables associated with taxonomic density within and across site types of interest. (a) All site types; sub-tree resulted from the same model pruned extensively, (b) ancient clam gardens, (c) sheltered mudflats, and (d) exposed sandflats.

causing increased aeration, and fine clays and silt to wash away in tides following harvesting events (Deur *et al.*, 2015). In the absence of harvesting, sediments can become anoxic, resulting in conditions less favourable for infaunal species. As responses have occurred without active harvesting or tending practices, observed results within this and similar studies are likely underestimates of species responses.

As culturally and biologically rich habitats, clam gardens play an important role in shaping coastal environments and sustaining coastal peoples. They demonstrate a unique balance between resource extraction and ecosystem function. However, the extent that clam gardens influence marine and terrestrial ecosystems have yet to be fully realized by the scientific community, and are likely not limited to the few ecological communities where responses have been scientifically observed. Although this work focused on infaunal communities, elucidating ecological responses at higher trophic levels would also be advantageous. Understanding how macroinvertebrates, fishes, coastal mammals, and other higher trophic levels respond to the structural complexity added during wall construction and long-term resource

management would provide a holistic view of the ecological responses to clam gardens. This is especially true for marine fishes, which have an extensive history of supporting coastal communities (Cannon and Yang, 2006; Campbell and Butler, 2010).

As a long-established marine resource management system, clam gardens represent a unique opportunity to investigate human–ecosystem interactions throughout the northeast Pacific. In addition, as shellfish are found within the majority of coastal ecosystems around the world (Bailey *et al.*, 2013), ecological phenomena surrounding the cultivation and extraction of bivalves have the potential to occur globally. Our findings, provide additional lines of scientific evidence suggesting that clam gardens facilitate habitat alterations that elicit species-specific responses, creating distinct intertidal habitats that only occur in the presence of human habitat modifications. In combination with the growing body of research surrounding historical anthropogenic activities causing profound ecological responses within natural ecosystems, our results suggest that a substantial portion of contemporary ecosystems are shaped by traditional anthropogenic activities.

Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.

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