Ancient clam gardens magnify bivalve production by moderating ambient temperature and enhancing sediment carbonate

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Approval

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Abstract

Humans have been developing management systems to support resilient food production through social-ecological feedbacks for millennia. On the Northwest Coast of North America, Indigenous peoples have sustained a diversity of fisheries through management innovations including designated access rights, harvest restrictions, and enhancement strategies. To elucidate how clam gardens, intertidal rock-walled terraces constructed by people in the Late Holocene, increased bivalve production, we quantified environmental variables and transplanted clams (*Leukoma staminea*) in present-day clam gardens and non-walled control beaches on the coast of western Canada. We found that higher bivalve biomass and densities in clam gardens could be attributed to the effect of terracing on ambient temperature and elevated sediment carbonate associated with crushed shell. These same variables drove detectable differences in transplanted clam growth rates. This study illuminates ecological mechanisms underlying this ancient innovation that could be used to enhance food security and confer resilience to impending oceanic changes.

Keywords: clam gardens; bivalves; mariculture; Indigenous peoples; Indigenous ecological knowledge; calcium carbonate

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Photo: Mareike Babuder

Introduction

“Ancestral knowledge systems resonate with science” Sm’hayetsk Teresa Ryan

Feeding the planet given its biophysical constraints is one of the central global challenges of the 21st century (Foley et al. 2011). Yet, humans have been modifying environments to support food production since at least the Late Pleistocene (Boivin et al. 2015). While some societies have suffered from severe resource depletion, resulting in collapse (Diamond 1997, Redman 1999), others have successfully maintained productive and resilient food systems (*sensu* Folke 2006; Johannes 1978, Trosper 2002, Corbett et al. 2008, Smith 2009, Campbell and Butler 2010, McKechnie et al. 2013, Rick et al. 2016, Watling et al. 2017, Braje et al. 2017, Blatrix et al. 2018). This success has likely been achieved in part through feedbacks between social and ecological systems (Fitzhugh 2018), whereby the incremental acquisition and development of ecological knowledge and conservation practices evolved by experimentation and learning (Turner and Berkes 2006). Here, we document the human-altered ecological mechanisms driving the productivity of a millennia-old engineered mariculture innovation (clam gardens), thereby providing insights into strategies for maintaining or enhancing the productivity, availability, and reliability of resilient marine-based food systems today.

Ecosystem engineering was an important component of many ancient Indigenous fisheries. Indigenous peoples worldwide created new ecological niches by building structures that intentionally concentrated fish, expanded habitats and/or altered environmental conditions (Smith et al 2011): In Amazonia, a fishery that combined earthen fish weirs and ponds built across floodplains to funnel and trap fish during seasonal out-migrations was in use as recently as 300 years ago (Blatrix et al. 2018). Along the Northwest Coast of North America, Indigenous peoples placed stone and wooden fish weirs and traps across rivers or in intertidal zones to harvest salmon and herring en masse during spawning migrations (Greene et al 2015, White 2003). Beginning at least 6600 yrs BP, the Gunditjmara peoples of present-day Australia built complex networks of canals and weirs in wetlands around lakes that expanded short-finned eel habitat and helped capture fish for harvest and farming (McNiven et al. 2012). Indigenous Hawaiians built and stocked fishponds across a range of salinities, maintaining and harvesting a diversity of freshwater and marine species (Costa-Pierce

1987). In each case, knowledge of water cycles, and the environmental conditions that influenced fish survival and growth were key to the functioning of these engineered systems. Further, these monumental construction efforts required both a colossal initial investment in human capital to build and multigenerational effort to maintain.

On the northwest coast of North America, coastal Indigenous peoples have actively managed a diversity of nearshore fisheries and resources through designated access rights (Turner and Jones 2000, Trosper 2009, Powell 2012), harvest restrictions (Cannon and Burchell 2009, Lepofsky and Caldwell 2013, Lepofsky et al. 2015), and enhancement strategies including the engineering of novel ecosystems (Lepofsky and Caldwell 2013, Turner et al. 2013, Lepofsky et al. 2015). In many places, managed estuarine root gardens, berry patches, eelgrass beds, and intertidal fish traps formed a continuous coastline of human-enhanced ecosystems (Deur and Turner 2005, Jackley et al. 2016). Among these diverse technologies are clam gardens, intertidal rock-walled, terraced, soft-sediment beaches built at the lowest low tide mark to magnify bivalve biomass (Fig. 1) (Groesbeck et al. 2014, Deur et al. 2015, Lepofsky et al. 2015, Jackley et al. 2016). Although only recently documented by Western science, many coastal First Nations words, such as l*úXwxiwey* and *wúxwuthin*, describe the process of building clam gardens (Deur et al. 2015, Lepofsky et al. 2015).

Hundreds of clam gardens have been documented from Alaska to Washington State (Harper 2007, Lepofsky et al. 2015, Moss and Wellman 2017) (Fig. 1a-g). Experiments and surveys of clam gardens along the west coast of Canada today have found that clam gardens are at least 2-4 times more productive than non-walled clam beaches, supporting greater densities, biomass, and higher growth rates of culturally and ecologically important clam species (Groesbeck et al. 2014, Jackley et al. 2016). By constructing extensive intertidal features, Indigenous peoples altered the seascape, and, given the ubiquity of clam gardens up and down the coast, likely radically transformed their food systems and expanded settlements.

The construction of clam garden rock walls, beginning at least 3,100 BP (Smith et al. *in prep.*), altered geomorphic and ecological processes that shaped these soft-sediment beaches (Neudorf et al. 2016). The presence of the wall increased the sedimentation rate up to four times (Neudorf et al. 2016). As sediment became trapped behind the wall, erosion of the shoreline decreased, resulting in a levelling out of the

beach over time. Heightened productivity within clam gardens has been partly attributed to this reduction in beach slope and expansion of the area at the optimal tidal height favouring clam growth and survival (Fig. 1h) (Groesbeck et al. 2014). Yet, clam gardens are also more productive than non-walled, control beaches at equivalent intertidal heights (Groesbeck et al. 2014), which indicates that other human-altered conditions must be contributing to enhanced clam production.

Tending practices were actively used to care for clam gardens as well as clam beaches more generally (Groesbeck et al. 2014, Deur et al. 2015, Lepofsky et al. 2015, H-GINPR Committee 2016), all of which were apparently to boost bivalve production. These practices involved the reduction of inter- and intra-specific competition, the removal of clam predators, and the enhancement of sediment quality. Specifically, the removal of seaweeds from the surface of the beach and the very act of digging the sediments was understood as a means of keeping sediments aerated and preventing clams from becoming smothered (Deur et al. 2015, Lepofsky et al. 2015, H-GINPR Committee 2016). Indigenous knowledge experts have also described how larger size classes of clams were selectively harvested and beaches were thinned to allow smaller clams to reach maturity and reduce density-dependence (Deur et al. 2015, Lepofsky et al. 2015). Moreover, while obtaining additional foods, people hunting, gathering or removing predators like river otters, minks, raccoons, sea ducks, geese, crabs and sea stars at beaches would have further decreased clam mortality (Deur et al. 2015). Finally, crushed shell and gravel were added to clam garden sediment to improve growing conditions for clams (Lepofsky et al. 2015, H-GINPR Committee 2016).

Here, we present experimental evidence revealing the ecological processes governing the increased production of ancient clam gardens. We conducted surveys of bivalves and abiotic conditions in clam gardens and non-walled, control beaches to examine the factors responsible for boosting clam production in clam gardens. We also transplanted littleneck clams (*Leukoma staminea*) into plots with and without crushed shell-enriched sediment to investigate the contribution of the Indigenous tending practice of returning crushed shell to beaches. Our analysis highlights how Indigenous peoples on the northwest coast of North America modified ecological processes through the construction and maintenance of clam gardens to increase clam production and thereby enhance food security.

Methods

To understand the relative effects of multiple abiotic conditions modified by these managed systems, we conducted bivalve surveys and a clam transplant experiment at replicate clam gardens (n=3) and non-walled clam beaches (n=3) and quantified a suite of environmental variables determined to be important drivers of clam production *a prior* based on previous research.

Study Area

Study sites were located on the northwest coast of Canada, on Quadra Island, which lies within the unceded territories of the Northern Coast Salish & the Southern Kwakwaka'wakw (Laich-kwil-tach) First Nations (Fig.1). Clam gardens densely line the shore of both Waiatt (n = 49 clam gardens) and Kanish Bay (n = 45 clam gardens) and are found adjacent to terrestrial archeological features including large, permanent human settlements dating to as early as 5000 years ago (Harper 2007, Toniello 2017). These clam gardens have likely not been tended in accordance with Indigenous practices since the early-to-mid 1900s (Deur et al. 2015). We selected clam garden and non-walled, control clam beaches based on previously surveyed sites reported in Harper (2007) and Groesbeck et al. (2014). While clam gardens were consistently characterized by shallower slopes than clam beaches that lacked human-built rock walls (Fig. S1), both soft-sediment communities encompassed the same species of bivalves including: the native littleneck clam (*Leukoma staminea*), butter clam (*Saxidomus gigantea*), macoma clam (*Macoma spp*.), heart cockle (*Clinocardium nuttallii*), horse clams (*Tresus nuttallii* and *Tresus capax*), and the non-native japanese littleneck (*Venerupis philippinarum*), eastern softshell clam (*Mya arenaria*) and varnish clam (*Nuttalia obscurata*).

Clam Surveys

At each clam beach, we surveyed clams in fifteen equally spaced plots (25 x 25 x 30 cm *depth*; volume = 0.01875 m^3) along a transect from the top of clam habitat (tidal station 1) to the top of clam garden wall or approximately 0.5 m above chart datum in non-walled beaches (tidal station 15) (Fig. 1h). Plot volume was adjusted for the presence of boulders, bedrock or other obstructions that prevented the full plot volume

from being dug. All visible bivalves were screened (mesh size = 8 mm) from the sediment matrix, identified to species, and measured along the maximum length and growth axis (Fig. S2). Biomass was calculated using Von Bertalanffy length – wet weight growth curves established for bivalves from Quadra Island (Table S1) (Groesbeck *in prep.*).

Clam Transplant Experiment

We transplanted juvenile native littleneck clams (*L. staminea*) (10-37 mm; collected from a nearby clam beach) along two parallel transects from the top of the beach (tidal station 1) to the top of clam garden wall or approximately 0.5 m above chart datum in non-walled beaches (tidal station 6) in our replicate clam garden (n=3) and non-walled beaches (n=3) (Fig. 1h). Control and treatment plots (50 x 50 x 10 cm *depth*) were placed 1 m apart at each tidal station. Controls contained *in situ* sediment while treatments contained the same parent sediment (clam garden sediment) combined with weathered shell composed mainly of littleneck clam, butter clam, and *semibalanus* barnacle from a local beach that was further crushed (grain size < 4mm) in cement mixers. Given that the clam gardens included in this study have not been actively maintained for many generations, our goal was to create a sediment mixture with more crushed shell than the current levels, mimicking the Indigenous tending practice and increasing the effect size. In each plot, twenty littleneck clams, marked with numbered vinyl tags and measured to the nearest hundredth mm, were enclosed in Vexar mesh bags and buried at a depth of 5 cm. Three times throughout the summer, we maintained treatment plots by adding a 1 cm-thick layer of the crushed shell mixture. During this process, control and treatment plots were similarly disturbed, and bags were repositioned at a depth of 5 cm. After six months, clams were collected, re-measured and weighed (dry weight of meat).

Environmental Variables

We measured six environmental variables at each clam beach along a transect from the top of the beach (tidal station 1) to the top of clam garden wall or approximately 0.5 m intertidal height in non-walled beaches (tidal station 6). If tidal station 6 was inaccessible below the low tide mark, then sample collection ended at tidal station 5.

Temperature. We installed temperature loggers on the sediment surface (Tidbit v2 and/or Hobo Pendant, Onset, Bourne, MA) at each tidal station at each site. Measurements were recorded every 5 minutes from May to October 2016 when loggers were both exposed to air and submerged in seawater. Temperature was summarized as monthly mean, minimum, maximum and standard error.

Water residency. At each tidal station at each site, the dissolution rate (g dissolved $hour^{-1}$) of ice-cube sized gypsum blocks of similar weights ($\pm$ 1 g) over 72 hours was assessed as an integrative index of relative water residency capturing variations in current velocity, water retention, and submersion time (Thompson and Glenn 1994, Boizard and DeWreede 2006).

Chlorophyll a. We took water samples for Chorophyll *a* at three tidal stations at each site (low, mid, and upper intertidal) during ebb and flood tides when 20-30 cm of water covered each station. Samples were analyzed by fluorometer (Trilogy, Turner Designs, San Jose, CA) using standard methods (Arar and Collins 1997). Given our low sample size for this abiotic variable, we excluded it from our models.

Carbonate. Sediment carbonate content (g/cm3) for each control and treatment plot was determined using sequential weight loss-on-ignition following methods adapted from Wang et al. (2011).

Sediment grain size. Grain size (% by weight) was determined by dry sieving with a set of seven grain sizes: 4.75 mm, 2 mm, 1 mm, 500 µm, 250 µm, 125 µm, and 63 µm. (Folk 1980)

Aragonite saturation state. Pore water was extracted using a PushPoint Sampler (MHE Products, East Tawas, MI) attached to a syringe to draw water samples from sediments at a depth of 5 cm. We collected samples during ebb tides in August 2016 as plots became exposed. If the tide did not drop low enough, samples were still drawn from submerged plots. Two samples were taken per plot and stored in 40 ml borosilicate glass vials with screw caps (Huang et al. 2012) for total alkalinity (TA) and dissolved inorganic carbon (DIC). We also collected six ambient surface seawater samples at each study site during low tide. Temperature of the sediment at a depth of 5 cm or of the sample directly were recorded with a handheld thermometer (Digi-Sense Traceable, Cole-Parmer, Vernon Hills, IL). Within one month of sampling, TA was

determined through open cell titration after Dickson et al. (2007), while DIC was measured using Apollo SciTech's DIC analyzer (AS-C3, Newark, DE). Salinity was also assessed during TA analysis using a handheld salinity meter (SympHony H10c, VWR, Radnor, PA). No nutrients (phosphate and silicate) data were collected. We used the CO2SYS program (Lewis and Wallace 1998) with the seawater scale; the first and second dissociation constants of carbonic acid from Mehrbach et al. (1973), refit by Dickson and Millero (1987); the dissociation constant for the bisulphate ion from Dickson (1990); the concentration of total boron from Uppstrom (1974) and the saturation solubility product for aragonite from Mucci (1983) to derive the aragonite saturation state (Ω_{Ar}) of each plot from DIC, TA, salinity, temperature and pressure. Aragonite saturation state describes the stability of the aragonite calcium carbonate ($CaCO_3$) mineral phase in seawater:

$$\Omega_{Ar} = \frac{[\mathrm{Ca}^{2+}][\mathrm{CO_3}^{2-}]}{[K_{sp}']}$$

$[Ca^{2+}]$ and $[\mathrm{CO_3}^{2-}]$ are the concentrations of calcium and carbonate ions and Ksp' is the solubility product, which is dependent on salinity. Thermodynamically, an aragonite saturation state greater than one favours precipitation of calcium carbonate while a state less than one favours dissolution.

Statistical Analyses

We took a model selection approach to assess the relative strength of evidence for the effect of beach type (non-walled beach or clam garden), treatment (control or crushed shell mixture) and tidal station on bivalve biomass, density, and growth (Burnham and Anderson 2002). To assess the causal mechanisms underlying these effects on bivalves, we then quantified the relative strength of evidence for alternative environmental variables using the same model selection approach. This complementary analysis captured the variability in abiotic conditions experienced at a given beach type, treatment, and tidal station potentially responsible for differences detected in bivalve biomass, density and growth.

Bivalve Surveys. We used general and generalized linear mixed effects models to assess the fixed effects of beach type, tidal station, and beach type*tidal station on

bivalve biomass and density. Because bivalve biomass and density vary nonlinearly with tidal station, peaking in the mid intertidal (Groesbeck at al. 2014), we modeled the effect of tidal station as a second order polynomial. We also used mixed effects models to evaluate the relative effect of environmental variables on bivalve biomass and density. All models considered site as a random factor. For models of bivalve biomass (kg/m^3), we used a Gaussian likelihood on log transformed data. For models of bivalve density (count/plot), we used a Negative Binomial likelihood, log link function, and an offset to account for plot volume. In two survey plots where no bivalves were found, we replaced zeros with half of the next lowest value for biomass and density to enable model convergence.

Clam Transplant Experiment. We used general and generalized linear mixed effects models to assess the relative effect of 1) beach type, tidal station, treatment, beach type*tidal station, and beach type*treatment; and 2) environmental variables on *L. staminea* growth, proportional growth, final biomass and survivorship. Similarly, tidal station was included as a second order polynomial. In these models, plot nested in site was treated as a random factor. *L. staminea* growth (mm) and log-transformed final biomass (dry weight of meat, g) were fit using linear models with Gaussian likelihoods. Proportional growth ((l_f-l_i/l_i)/160days) and survival (survivorship/160 days) were fit with a Gamma likelihood and log link function, and a Binomial likelihood and logit link function, respectively. During the experimental set up, to reduce size-based differences in *L. staminea* productivity metrics, care was taken to ensure that bags contained comparable size (maximum length) frequency distributions of clams. Further, post-experiment, surviving clams greater than 32.5 mm were excluded from analyses to eliminate significant differences between plot-level frequency distributions.

Model Selection and Model Averaging. For all response variables, we fit all subsets of the global models. Each fixed effect in the global models was selected *a priori* based on the experimental design, and knowledge of the ecology of *L. staminea* and soft-sediment systems (Burnham and Anderson 2002). We selected error distributions and link functions, and/or transformed response variables to ensure that residuals of each global model met the assumption of homogeneity of variances, and checked for overdispersion. We assessed collinearity between predictors using Variance Inflation Factors (VIFs), only permitting VIFs < 10 (Quinn and Keough 2002). Predictors were standardized (centered and scaled by two standard deviations) following Gelman (2008)

for models with multiple continuous fixed effects to enable comparisons between coefficients. Models were assessed with Aikaike's Information Criterion corrected for small sample size (AICc) and ΔAICc. We used model averaging of the subset of models with ΔAICc less than 4 to obtain coefficients and assess the Relative Variable Importance (RVI) of each variable (Burnham and Anderson 2002). RVIs were calculated by summing the Akaike weights across all models in which that variable occurred.

Top models with Gaussian error distributions were refit with Restricted Maximum Likelihood (REML). Where applicable, confidence intervals for mixed effects models were computed by bootstrapping (nsim =1000), drawing from the joint probability distribution of the parameter estimates of the model, or by the Wald method. All linear and generalized linear mixed effects models were fit in R using the lme4 package (Bates et al. 2015), except for models with beta likelihoods which were run with the glmmADMB package (Fournier et al. 2012). Model selection and model averaging was performed using the MuMin (Barton 2016) package in R.

Assumptions and Limitations

Sites designated as either clam gardens or non-walled beaches differ in characteristics other than the presence of a rock wall, which presents a challenge when selecting replicates and controls. While clam gardens and non-walled beaches share common features, each lies along a continuum of the dimensions of intertidal soft-sediment habitats with some non-walled, control beaches more similar to clam gardens in one or more dimensions and vice versa. Moreover, the oceanographic context will play a role in the productivity of any site. Beaches dominated by tidal currents are known to offer better growing conditions than low-energy sites at the head of a bay (Smith 1928 in Chew 1987). People may have selectively built clam gardens on existing highly productive soft-sediment beaches in favourable oceanographic contexts, instead of enhancing less productive areas. The fact that we find clam gardens built on bedrock or boulder outcrops, resulting in a hundred percent increase in clam habitat (Lepofsy et al. 2015, Toniello 2017), suggests that this was not always the case. Yet, the high density of clam garden sites in Waiatt and Kanish bay indicates that nearly every suitable site may have been transformed into a clam garden. Inevitably, we had to make assumptions in selecting replicate and control beaches.

Results

Clam Surveys

Clam density and biomass were on average 1.5 and 2.5 times greater in clam gardens than non-walled clam beaches (Fig. 2). Moreover, we found strong evidence that both clam biomass and densities varied nonlinearly from the top to the bottom of the beach (i.e. with tidal station) and that this effect was mediated by beach type (i.e. clam garden vs. non-walled clam beach) (Fig. 2; Table S2; Table S3). Differences in clam densities between beach types were primarily driven by bent-nosed and pointed macoma clams (*Macoma spp*.) whereas differences in clam biomass were driven by butter (*S. gigantea*) and littleneck clams (*L. staminea*), which were more common and reached greater sizes in clam gardens than non-walled beaches, especially towards the top of the beach (i.e. tidal Station 1-9) (Fig. S3).

Clam density and biomass were most strongly influenced by mean intertidal temperature at the sediment surface with lower temperatures favouring greater densities and biomass (RVI =1, 1, respectively; Fig. 3; Table S4). In comparison with non-walled clam beaches, clam garden terraces experienced less variability in seawater and air temperatures at the sediment surface over the growing season (Fig. 4a, S4a). On average, clam gardens remained cooler in the height of summer (July/month 7; Fig. 4a) and warmer in the fall (October/month 10; Fig. 4b) than non-walled beaches (Table S5; Table S6). Overall, mean intertidal surface temperature across tidal stations mirrored beach slope, with shallow-sloping clam gardens experiencing a narrower range of temperatures from the top to the bottom of the beach than the steeper-sloping non-walled beaches (Fig. S1, S5). Notably, non-walled beaches reached higher mean temperatures at tidal stations towards the top of the beach where clam biomass and densities are markedly lower compared with clam gardens (Fig S5; Table S5; Table S6).

Water residency had a positive and moderately important effect on clam density (RVI = 0.5; Fig. 3a, Table S4), and was consistently higher, although more variable, in clam gardens compared to non-walled clam beaches across all tidal stations (Fig. 4c; Tables S5; Table S7). Within clam garden terraces, water residency tended to be greatest near the bottom of the beach, closer to sea level. Water residency had a less

important effect on clam biomass relative to other variables we measured (RVI = 0.28; Fig. 3b; Table S4).

Mean chlorophyll tended to be higher, albeit highly variable, at high and mid tidal levels in clam garden terraces relative to non-walled beaches; however, we did not detect strong evidence for an overall effect of beach type on this variable (Fig S6; TableS5; Table S7). Limited data and its ecological correlation with water residency precluded its inclusion in further analyses.

Carbonate content of sediment had an equally important and strong effect on clam biomass (RVI = 1; Fig. 3b; Table S4) as surface temperature, yet a relatively less important and imprecise effect on clam density (RVI = 0.42; Fig 3a; Table S4). In clam gardens, sediment carbonate was between 2.8 - 12.9 times greater than sediment in non-walled beaches (Fig. 4d) and beach type was a relatively important determinant of sediment carbonate (RVI = 1; Table S5, Table S7).

We did not detect a precise or relatively strong effect of beach type or tidal station on the aragonite saturation state of pore water (Fig. 4e; Table S5; Table S7) and both clam biomass and density were relatively uninfluenced by this variable (Fig. 3; Table S4).

On average, clam garden sediments contained a smaller percentage of silt than non-walled beaches. This trend was consistent across tidal stations with silt tending to decrease closer to the bottom of the beach in clam gardens and to increase in non-walled beaches (Fig. 4f; Table S5; Table S7). While the percentage of silt within the sediment had a negative effect on both clam density and biomass, its effect was relatively weak and imprecise compared to the other variables we tested (RVI = 0.39, 0.34, respectively; Fig. 3; Table S4).

Clam Transplant Experiment

We detected a positive effect of our experimental addition of crushed shell (treatment) on transplanted littleneck clam growth and final tissue biomass (Fig. 5a; Fig. S10a and b; Table S8; Table S9). In fact, this addition of carbonate via crushed shell increased littleneck growth and final clam tissue biomass in both clam gardens and non-walled beaches (RV1 = 0.86 and 1, respectively; Fig. 5b; Fig S11a; Table S10). In

contrast, although we detected a relatively important positive effect of our treatment on littleneck proportional growth and survival (RVI = 1, 0.62, respectively; Fig. S12 a and b; Table S8), the influence of carbonate on these metrics was small and imprecise (RVI = 0.38 and RVI = 0.14, respectively; Fig. S11 b and c; Table S10). Mean intertidal surface temperature also drove detectable differences in transplanted littleneck growth with a decline in growth as mean temperature increased (RVI = 0.85, respectively; Fig. 5b; Table S8). Notably, silt content had as equally important and strong of an effect as sediment carbonate on final littleneck clam tissue biomass with greater silt being associated with higher final tissue biomass (RVI = 1, Fig S11a; Table S10).

Indeed, the addition of crushed shell successfully modified key sediment characteristics. We detected a relatively strong and important effect of treatment on sediment carbonate (RVI = 1; Table S5; Table S7) and aragonite saturation state of pore water (RVI = 0.94, Table S5; Table S7). Both sediment characteristics were elevated with the addition of crushed shell relative to the un-manipulated control plots in clam gardens and non-walled beaches (Fig. 6a and b; Fig S8). Compared to control plots, on average, sediment carbonate content was 1.9 and 7.2 times greater, and aragonite saturation state was 1.3 and 1.6 times greater in both clam garden and non-walled beach treatment plots, respectively. Further, on average, the aragonite saturation state of treatment plots was higher than ambient surface seawater at study sites (Fig. 6b; Fig S7a; Table S5, Table S7). The addition of crushed shell to treatment plots also reduced silt and gravel (RVI = 1, 1, respectively; Fig. 6c and d; Fig. S9; Table S5; Table S7). Specifically, in non-walled beaches silt was on average 1.5 lower in crushed shell addition plots than controls. On average, gravel was 2.2 and 1.3 times lower in clam garden and non-walled beach treatment plots than controls, respectively.

As predicted, littleneck growth also varied nonlinearly with tidal station and this effect as well as the treatment effect, were mediated by beach type (Fig. 5a; Fig. S10a; Table S8; Table S9). However, counter to our hypothesis, we also detected an overall negative, albeit imprecise, effect of beach type on littleneck growth driven by higher growth in the non-walled beach controls than clam garden controls across tidal stations. Strong evidence supports the same conclusions with respect to the final tissue biomass of littlenecks (Fig. S10b; Table S8; Table S9).

Discussion

Mounting evidence suggests that productive and resilient food systems around the world likely co-evolved through a series of social-ecological feedbacks (Fitzhugh 2018). Here, we provide strong empirical and experimental evidence that ancient clam gardens stabilize ambient temperature and enrich sediment carbonate thereby magnifying clam biomass. Specifically, greater clam biomass, which was on average 2.5 times greater in clam gardens than non-walled clam beaches, is driven by lower sediment surface summer temperatures and higher sediment carbonate. Similarly, these same environmental variables drove detectable differences in experimentally transplanted clam growth, with higher growth associated with the addition of crushed shell in both clam gardens and non-walled beaches, thereby substantiating our observational results. Ultimately, we provide evidence for the role of ambient temperature and sediment carbonate, conditions altered by clam garden construction and maintenance, in both short-term (i.e. growth) and long term (i.e. the accumulation of biomass over time) productivity.

Environmental Variables Affecting Clam Density, Biomass, and Growth

Temperature is often cited as the most important environmental variable affecting metabolic performance, and subsequent growth and survival, in poikilotherms like clams (Jorgensen 1966, Houghton and Moore 1977, Bernard 1983). Specifically, stable temperatures enhance growth while temperature extremes induce physiological stress (Bernard 1983, Rodnick and Li 1983). In butter clams, somatic growth is favoured by temperatures between 10-17°C with an optimum at 14°C and in littleneck clams by temperatures between 12-18 °C with an optimum at 15°C (Bernard 1983). At our study clam gardens and non-walled beaches, mean temperatures at the sediment surface throughout the growing season were well within these ranges. However, non-walled beaches experienced daily and seasonal temperature extremes that greatly exceeded these ranges compared with clam gardens (Fig. 4a and b). This can be attributed to greater seawater residency in shallow sloped clam gardens relative to non-walled beaches (Fig. 4c) and the greater heat capacity of water compared to air. For clams, extreme high temperatures are known to be more lethal than low temperatures (Kinné

1963, Bernard 1983), with die-offs sometimes occurring the next winter (Cronin 1968). Indeed, clam densities and biomass were lower in non-walled beaches compared to clam gardens, particularly at the top of beaches (Fig. 2) where these temperature differences were magnified. This supports our finding that relatively lower mean temperatures during the summer growing season provide better conditions for clam growth and survival, resulting in greater densities and biomass over time.

While temperature is a major driver of bivalve productivity, other parameters like current velocity (Ekman et al. 1989, Fraser and Smith 1928 in Chew and Ma 1987), dissolved oxygen concentrations (Bayné 1971) and food supply (Jorgensen 1966) are also known to play interrelated roles in growth and survival. We found evidence that higher water residency, a measure that integrates current velocity, water retention and submersion time, drove higher clam densities at clam gardens compared to non-walled beaches (Fig. 3a). In addition to moderating ambient temperature, we hypothesize that greater water residency could increase densities by increasing the delivery of clam larva to beaches. Previous evidence from clam gardens elsewhere revealed higher recruitment of clams (0.5-2mm) at clam gardens than non-walled beaches (Jackley et al. 2016). Moreover, water residency could increase post-settlement survival of clam recruits through alternative, although not mutually exclusive mechanisms.

Water residency could improve clam growth and survival by enhancing food supply (Goodwin 1973) and dissolved oxygen regeneration (Charbonnier et al. 2016). For example, both higher water residency and stable temperatures at clam gardens compared to non-walled beaches may simultaneously support a more continuous delivery and production of phytoplankton, thereby decreasing competition among clams for their primary food resource. Greater water residency may also promote mixing and oxygenation of water. While bivalves tend to be more resistant to hypoxia than other taxa (Vaquer-Sunyer and Duarte 2008), low oxygen conditions can decrease survival especially at early life stages (Gobler et al. 2014), and could be responsible for lower standing stock densities at non-walled beaches that experience lower water residencies. Repeated sampling of chlorophyll *a* and dissolved oxygen at sites could help tease apart these mechanisms.

Coarse sediments generally provide suitable habitat for filter feeding clam species like littleneck and butter clams (Fraser and Smith 1928 in Chew and Ma 1987,

Fitch 1953, Quayle and Bourne 1972, Goodwin 1973, Rodnick and Li 1983). Indeed, our data revealed that clam garden sediments are made up of more gravel and crushed shell compared to non-walled beach sediments (Fig. 4d and f), supporting previous qualitative observations (Haggan et al. 2006, Groesbeck et al. 2014, Lepofsky et al. 2015, Jackley et al. 2016). Many clam gardens are nestled between rocky outcrops, which in addition to the tending practice of returning crushed shell to clam beaches, likely contributes to the supply of shell, in this case from barnacle plates and other calcium carbonate shelled macroinvertebrates. Indeed, littleneck and butter clams are commonly found in beaches with a mix of shell, coarse sand, and fine gravel (Fraser and Smith 1928 in Chew and MA 1987, Fitch 1953, Quayle and Bourne 1972, Goodwin 1973, Rodnick and Li 1983). Beaches along rocky shorelines are known to have more shell and provide better habitat for butter clams (Quayle and Bourne 1972). While sediment preferences for infaunal species are well documented, the relative contribution of different causal mechanisms remains poorly understood (Snelgrove 1998). Here, we found evidence that carbonate conditions within beach sediments contribute to observed species-sediment preferences.

Sediment carbonate may enhance larval bivalve settlement (Gray et al. *in prep.)* and post-recruitment growth and survival through a variety of non-mutually exclusive ecological and biogeochemical mechanisms (Kidwell and Jablonski 1983, Gutierrez et al. 2003, Gazeau et al. 2007, Green et al.2009, Green et al. 2013, Waldbusser et al. 2013, Gray et al. *in prep.).* Here, we found strong evidence that greater sediment carbonate content, supplied by a dense accumulation of crushed shell, drove higher clam density and biomass in our surveys and higher growth rates among our experimentally transplanted clams (Fig. 3 and 5). The taphonomic feedback hypothesis (Kidwell and Jablonski 1983) conceptualizes a relationship between the shell content of sediments (i.e. sediment carbonate) and population dynamics of calcifying organisms: shell provides a hard substrate where larvae settle and when bivalves die, their shells, made of mostly mineral calcium carbonate ($CaCO_3$) (Weiner and Hood 1975), add more carbonate to the sediment, which in turn promotes larval settlement in a positive feedback loop. If shell material is continually removed through shellfish harvest, then sediment carbonate, and in turn bivalve populations, will decline through a negative feedback process. This hypothesis parallels Indigenous ecological knowledge of the benefits of returning crushed shell to beaches (Lepofsky et al. 2015, H-GINPR

Committee 2016). While shell provides habitat for settling larvae (Quayle and Bourne 1972, Gutierrez et al. 2003), interactions between coastal carbonate cycling and species physiology underpin this relationship.

Carbonate chemistry in coastal waters and sediments is highly variable as it is regulated by interactions across multiple scales, including watershed inputs, local biological and physical processes, and interactions with the open ocean (Duarte et al. 2013). Moreover, the availability of carbonate ions (CO_3^{-2}) in coastal sediment pore water is often lower than in the overlying water because of diagenetic processes like microbial mineralization of organic matter that produces carbon dioxide (CO_2) and other acids (Widdicombe et al. 2011, Clements and Hunt 2017); thus, increases in carbonate to benthic micro habitats can be pivotal to the suitability for bivalve settlement, growth and survival. Bivalves form shells by precipitating calcium carbonate from seawater in a process that produces carbon dioxide and decreases alkalinity as carbonate ions are incorporated into the mineral phase. The opposite reactions occur during shell dissolution or bioerosion, which regenerates carbonate alkalinity, potentially buffering against corrosive conditions. Thus, calcifying organisms may play an ecosystem-scale role in coastal carbonate cycling (Walbusser et al. 2013), while at a local scale shell content of sediment may contribute to buffering these metabolic acids and increase net calcification (sum of dissolution and calcification) (Green et al. 2009, 2013). Given the potential biogeochemical function of shell material in coastal sediments, our findings match our hypothesis that higher percentages of sediment carbonate, as in the shell-rich sediments of clam gardens, can support greater standing stock densities and biomass, and faster growth rates of clams.

The availability of carbonate ions, which drives dissolution and to a lesser degree calcification, may not correlate with the shell contents of sediments, especially within the spatially and temporally variable coastal carbonate system. While calcium is generally conservative in seawater, the concentration of carbonate ions decreases as seawater becomes more acidic (lower pH). As such, aragonite saturation state (Ω_{ar}), the measure of the capacity of seawater to precipitate calcium carbonate in the aragonite crystal form, is more strongly dependent on the concentration of carbonate ions than calcium. Studies show correlations between higher aragonite saturation states of sediment pore water and increases in infaunal bivalve settlement and recruitment (Green et al. 2009, 2013), burrowing behaviour (Green et al. 2013, Clements and Hunt 2014), and calcification and

survival (Green et al. 2004, 2009) (summarized in Clements and Hunt (2017)). Like Green et al. (2009, 2013), we were able to boost the aragonite saturation state of pore water through the addition of crushed shell to sediments. We found, on average, that pore water was super-saturated ($\Omega_{ar} > 1$) with respect to aragonite and, further, values were higher than surface seawater samples (Fig. 6); however, we did not find evidence for an effect of aragonite saturation state on clam density, biomass, or growth.

The frequency and timing of pore water sampling may explain why we did not observe an effect of aragonite saturation state on clam density, biomass or growth. Carbonate chemistry of coastal sediments displays high spatio-temporal variability (Green et al. 2013), and we collected pore water samples over only one low tide series during August. To fully characterize the carbonate system we would need to take repeated samples. This is especially true in our study area (Strait of Geµorgia) where there is high seasonal and inter-annual variability (Moore-Maley et al. 2016). Model simulations reveal that the Strait is under-saturated ($\Omega_{ar} < 1$) with respect to aragonite for long periods in the winter and likely during summer when freshwater discharge is high (Moore-Maley et al. 2016). During these periods, sediment carbonate thermodynamics may be important in preventing shell dissolution, especially in winter under the additional stress of low food availability.

Given this snapshot sampling of aragonite saturation state, we primarily expected to find a relationship with the growth rate of transplanted clams, rather than standing stock density and biomass of clams. We hypothesized that growth rates would be higher since, in theory, calcification may be less energy intensive under higher aragonite saturation state conditions, even when values remain above one (Gazeau et al. 2007, Green et al. 2013,). However, bivalves often use bicarbonate (HCO_3^-) or metabolic carbon dioxide (CO_2) as substrates for calcification rather than carbonate (Cryonak et al. 2015b). The ability of an organism to use bicarbonate for calcification, known as the substrate-to-inhibitor ratio (SIR = $[HCO_3^-]/[H+]$) is not always positively correlated with aragonite saturation state (Fassbender et al. 2016). Thus, although thermodynamically an aragonite saturation state less than one causes shell dissolution, at values greater than one, aragonite saturation state may not be the best indicator of calcification conditions (Fassbender et al. 2016).

Finally, as carbonate is consumed during shell formation, the signature of the positive impact of higher aragonite saturation states may be lost, especially on beaches with a higher standing stock of clams like clam gardens. Over the long-term, sediment carbonate may serve as a better integrative measure of the year-round buffering capacity of sediments and, in turn, predictor of bivalve growth and survival in coastal waters.

Policy makers and the scientific community recognize the importance of returning shell to sediments and oyster reefs for the health of bivalve populations (Abbe 1988, Green et al. 2009, Kelly et al. 2011, WSBRP 2012, Green et al. 2013, Walbusser et al. 2013). After overharvesting of oysters in Chesapeake Bay, Maryland a shell planting program was implemented between 1960 and 2006 to stimulate recovery (Walbusser et al. 2013). Today, the impact of ocean acidification on shellfish aquaculture in the Pacific Northwest (Haigh et al. 2015; Cooley et al. 2012, Ekstrom et al. 2015) has brought new attention to the notion of shell recycling for alkalinity regeneration (Kelly et al. 2011, WSBRP 2012). While the impacts of overharvesting and coastal ocean acidification have generated a flurry of recent research on the topic, this positive feedback between bivalve populations and shell resources may have been widely recognized and applied by coastal Indigenous peoples involved in tending clam gardens (H-GINPR Committee 2016).

As an alternative, non-mutually exclusive hypothesis, crushed shell, like coarse gravel, in sediments may act as a predator refuge for small clams (Glude 1978), for example, by making it more difficult for crabs to dig into the sediment (Sponaugle and Lawton 1990). Moreover, corrosive conditions created by low sediment carbonate and increased ocean acidification can result in smaller individuals or thinner shells that are more susceptible to predation (Sanford et al. 2014). This mechanism may play a role in the observed standing stock of clams but would not be a factor in the transplant experiment where juveniles were protected by mesh bags. In addition, such benefits from increased carbonate in the treatments would not likely be observed in the timescale of our experiment with the size classes (10mm - 32.5mm) of clams we used in the experiment.

While results from our bivalve surveys corroborate the findings of other modern ecological experiments on clam garden productivity, those from our transplant

experiment do not (Groesbeck et al. 2014 and Jackley et al. 2016, Gray et al. *in prep*). Groesbeck et al. (2014) found higher growth rates of littleneck clams in clam gardens compared to non-walled beaches at the top and bottom of the beach. In contrast, we found weak evidence for higher growth in our non-walled beach controls than clam garden controls. However, our experiment was not a replication of Groesbeck et al. (2014) because we maintained the experimental crushed shell mixture throughout the summer, disturbing both control and treatment plots. We hypothesize that this disturbance could have aerated silt-laden sediments at non-walled beaches, and in turn, allied properties like transport of dissolved oxygen from the overlying water to the sediment pore water (Charbonnier et al. 2015), resulting in improved growing conditions. Additionally, the increased diffusion of carbonate from the treatment plots to areas of lower concentration in the carbonate-poor non-walled beaches could have disproportionately enhanced growth in control plots due to the lower standing stock of clams at non-walled beaches.

An alternative, yet non-mutually exclusive hypothesis may explain these seemingly paradoxical results. We used small clams (95% < 25 mm), which are known to experience high mortality rates relative to larger clams. Higher mortality rates likely increased variability in growth and decreased our power to detect changes.

Moreover, the discrepancy between findings may be caused by annual variability in environmental variables that affect growth such as temperature and food availability. The temperature moderating effects of beach terracing and the conditions set up by enhanced sediment carbonate may play a compensatory role in years with unfavourable growing conditions. Nonetheless, we can infer from the accumulation of larger bivalves surveyed at clam gardens compared to non-walled beaches that growth and/or survival must be improved over the long-term.

Clam Garden Ecology in an Ever-Changing Human-Enhanced Seascape

On Quadra Island where clam gardens have likely not been actively managed since the early-to-mid 1900s (Deur et al. 2015), the heightened clam density and biomass in gardens compared to non-walled beaches reflects a legacy of tending and maintenance practices. Ethnographic accounts by Kwaxsistalla, Clan Chief of

Qawadiliqalla (Wolf Clan) within the Tsawataineuk (D^{Z}awada7enux^{W}) tribe of the Kwakwaka'wakw (BKwakiutl^) Nation, describe learning to build, maintain and harvest clam gardens, known in Kwak'wala as *loxiwey* meaning "to roll", from his grandparents during the 1930's (Deur et al. 2015). Throughout the 20th century, the loss of intergenerational knowledge sharing and access to resources caused by colonial genocide, including the forced displacement of Indigenous peoples from their lands, the removal of 150,000 Indigenous children from their families to attend Canadian Indian Residential Schools, and participation in the wage economy resulted in less intensive use and maintenance of human-enhanced ecosystems like clam gardens by Indigenous peoples (Turner and Turner 2007). Thus, we hypothesize that actively tended clam gardens would be even more productive than the levels observed today.

In the transplant experiment, we created a crushed shell-enhanced mixture to increase the percentage of shell beyond that observed today at non-walled beaches, but also beyond background levels at these untended or "legacy" clam gardens. We intended to simulate levels of crushed biogenic carbonates, such as bivalve shell and barnacle plates, that might be expected with active maintenance of the rock wall and the practice of returning crushed shell to beaches. Though we only replicated one dimension of the multiple ways beaches were cared for, the higher growth rates observed in plots with the crushed shell mixture reflect yet another way that coastal Indigenous peoples were successfully managing these spaces and the many species they relied on for food.

The paleoecological record provides another source of evidence as to how clam ecology shifted throughout the Holocene and the positive impact of Indigenous shellfish management. Toniello (2017) reconstructed butter clam (*Saxidomus gigantea*) growth rates in Waiatt and Kanish Bays on Quadra Island for the last 11,500 years: from the early-to-mid Holocene growing conditions for clams improved as surface temperatures warmed, sea level stabilized, and gravel and sand became deposited on beaches. As harvesting pressure by humans settling in the area gradually intensified beginning 5000 yrs BP, stable growth rates and consistent size at harvest suggest that tending practices and clam garden construction (~2000 BP) supported sustainable clam populations. The growth rates of clams in gardens today, however, are lower than those from the clam garden context dating to before European contact ~ 250 BP. While it is difficult to exclude alternative hypotheses like changes in ocean primary productivity, the correlated

decrease in clam growth rates with the diminished presence of coastal Indigenous peoples on the seascape further suggests that tending practices may have had a significant impact on the health of bivalve populations and lends support to the findings of our transplant experiment.

Along the coast today, Indigenous peoples continue to harvest and care for clam gardens and clam beaches to different extents (Augustine and Dearden 2014). Knowledge holders recall the process of clam garden construction and the tending practices used to care for beaches (Deur et al. 2015, H-GINPR Committee 2016). For example, Hul'qumi'num and W̱SÁNEĆ peoples alongside Parks Canada staff are restoring clam gardens in the Gulf Island National Park Reserve and managing clam beaches guided by knowledge holders from Coast Salish communities (H-GINPR Committee 2016).

In sum, the initial investment in building clam gardens creates an ecological inheritance (Odling - Smee 1988) whose benefits are still measurable today at untended clam gardens. The multigenerational effort to maintain and tend gardens was likely integral to sustaining healthy, even more productive, bivalve populations. Finally, although the intensive use and maintenance of clam gardens was disrupted to varying degrees by colonization, this period is relatively short compared to the history of shellfish management by Indigenous peoples along the coast of North America, which continues today.

Buffering Capacity of Clam Gardens Fosters Resilience and Enhances Food Security

Northwest coast Indigenous resource management fostered productive and resilient shellfish populations, providing a reliable resource near human settlements (Cannon and Burchell 2009, Toniello 2017). Shellfish are often characterized as an easily and safely gathered food, compensating for a lack of other resources in times of scarcity; however, this accessibility also theoretically makes shellfish more susceptible to unsustainable levels of harvest (Erlandson et al 2008). We show that by reducing beach slope and enhancing sediment carbonate, clam gardens buffer against environmental fluctuations in temperature and carbonate conditions. This buffering capacity likely not only generates a greater, but also a more reliable supply of shellfish. Indeed, clam

gardens and associated tending practices added redundancy to the system with clam populations showing no sign of resource depression despite the expansion of settlements and harvesting pressure (Toniello 2017). Moreover, in some cases, conservation practices like the intensive harvesting of clam beaches at temporary camps instead of near permanent settlements would have provided an additional form of insurance (Cannon and Burchell 2009). Broadly, clam gardens are one of a portfolio of human-enhanced nearshore resources (Lepofsky et al. 2015, Jackley et al. 2016). This diversity likely helped confer resilience and sustainability to the overall food system, enhancing food security.

Productive and resilient food systems among northwest coast Indigenous peoples emerged and persisted through a series of social-ecological feedbacks developed over millennia (Trosper 2009). For instance, the mechanisms underlying the enhanced productivity of clam gardens reflect the ecological knowledge gained over generations of experimentation and learning. Equally important, these food systems were nested within complex governance systems and protocols, including stewardship principles like contingent proprietorship, that were integral to the resilience of these social ecological systems of the Pacific Northwest (Trosper 2009, Jackley et al. 2016). Likewise, worldviews of reciprocity and respect, reinforced the continued existence of the overall social ecological system (Troper 2009, Campbell and Butler 2010) that contributed to the sustainable use of many nearshore resources (Trosper 2002, McKechnie et al. 2013, Toniello 2017).

Conclusion

Creating resilient food systems in the face of increased climate variability, ocean acidification, and centralized food distribution will be important for the growing human population. Looking to innovations and technologies that were developed by Indigenous peoples over the past 11,000 years, may help implement resiliency across multiple scales for people today. Here, we show that the construction and maintenance of clam gardens ensures a greater supply of clams by buffering against environmental fluctuations in temperature and sediment carbonate conditions. These ancient practices are particularly applicable in the contemporary context of environmental change. Climate-related changes are expected to trigger a decline in the catch potential of culturally and economically important species to coastal Indigenous communities in British Columbia including butter and littleneck clams (Weatherdon et al. 2016). Restoring “legacy” clam gardens and degraded beaches could increase the abundance of clams, boosting food security for local First Nations communities. Moreover, the act of restoring clam gardens and caring for beaches creates opportunities for cultural revitalization and access to cultural foods (Augustine and Dearden 2014). More broadly, similar practices could be applied to more intensive forms of aquaculture, especially to address the mounting concern regarding the impacts of ocean acidification on the shellfish industry (Cooley et al. 2012, Ekstrom et al. 2015, Haigh et al. 2015). For instance, programs that return shell to sediments could help to regenerate alkalinity, and buffer against corrosive conditions in coastal waters (Green et al. 2009, Kelly et al. 2011, Green et al. 2013 Waldbusser 2013). In sum, incorporating multiple forms of knowledge can inform innovative solutions while resulting in more inclusive and equitable pathways towards resilient and productive food systems (Tëngo et al 2017, Salomon et al. 2018).

Figures

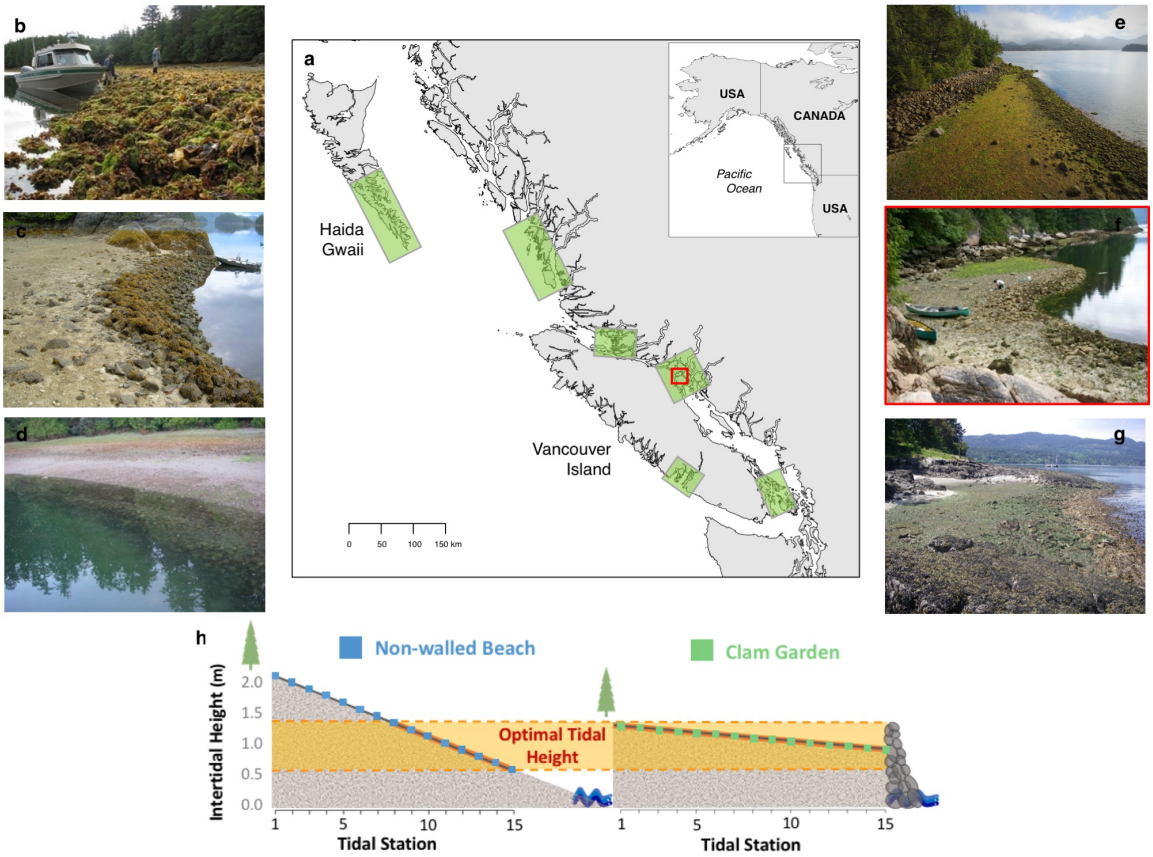

Figure 1. **Known distribution of clam gardens, and survey and experimental design.** (a) Clam gardens in regions along the west coast of Canada (green rectangles) where sites have been documented: (b) Haida Gwaii (photo: Quentin Mackie),(c) Broughton Archipelago (photo: John Harper), (d) West Coast Vancouver Island (photo: Ian McKechnie), (e) Central Coast (photo: Keith Holmes), (f) Discovery Islands (photo: Amy Groesbeck), and (g) Gulf Islands (photo: Nicole Smith). In Waiatt Bay on Quadra Island (red square), (h) we surveyed clams in fifteen equally spaced plots (blue and green squares) along a transect from the top of the beach (tidal station 1) to the top of clam garden wall or approximately 0.5 m intertidal height in non-walled beaches (tidal station 15) in replicate clam garden (n=3) and non-walled beaches (n=3). We also transplanted littleneck clams (*Leukoma staminea*) in six equally spaced plots with and without the addition of the crushed shell-enriched mixture along a transect from the top of the beach (tidal station 1) to the top of clam garden wall or approximately 0.5 m intertidal height in non-walled beaches (tidal station 6) at the same study sites. The thick orange line indicates the available space within the optimal tidal height for clam growth and survival in each beach context. Redrawn from Groesbeck et al. 2014.

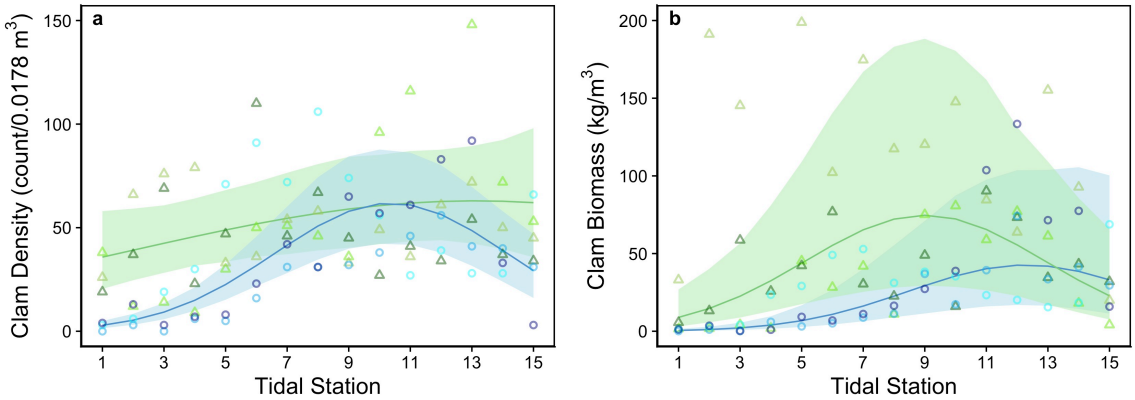

Figure 2. **Mixed effects model predictions for clam surveys**. The relationship between tidal station (1= top of the beach, 15 = top of clam garden wall or approximately 0.5 m intertidal height in non-walled beaches) and (a) clam density (count/0.0178 m3) and (b) clam biomass (kg/m3). Lines and shaded areas represent model predictions with bootstrapped 95% confidence intervals for clam gardens (green) and non-walled beaches (blue). Darker shades indicate overlapping confidence intervals. Actual biomass and densities shown for clam gardens (triangles in shades of green, n =3) and non-walled beaches (circles in shades of blue, n =3). One actual value lies outside the plotting area in both (a) and (b).

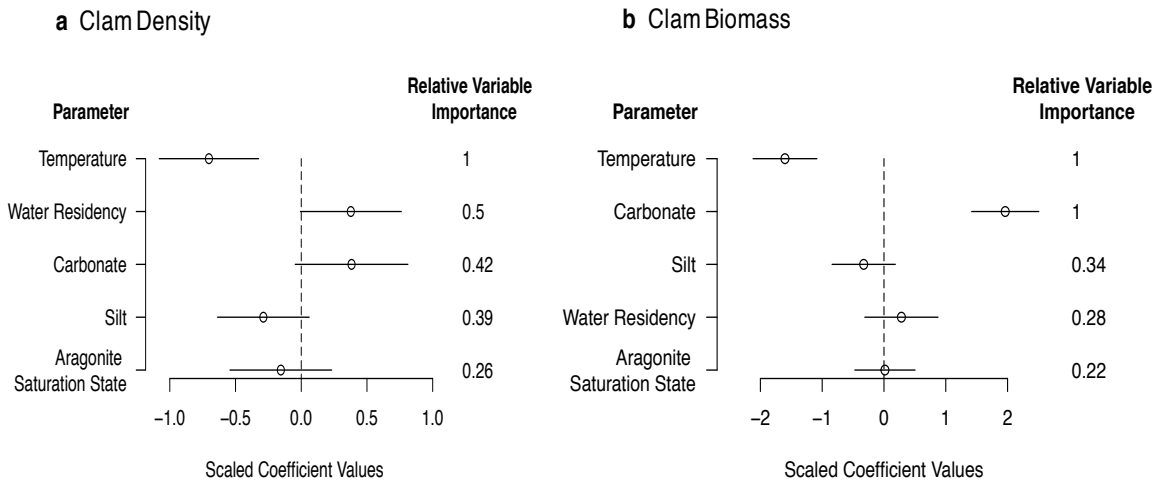

Figure 3 **Model averaging for clam surveys.** Parameter estimates with unconditional 95% confidence intervals and corresponding relative variable importance from averaged mixed effects models (AICc <4) for (a) clam density (count/plot) and (b) clam biomass (kg/m3) across clam garden and non-walled beach study sites (n = 6). Predictor variables included mean temperature (℃), water residency (g dissolved/hr), and sediment characteristics: sediment carbonate content (g/cm3), silt content (% by weight), and aragonite saturation state of pore water. Coefficients standardized on two SD (Gelman, 2008)

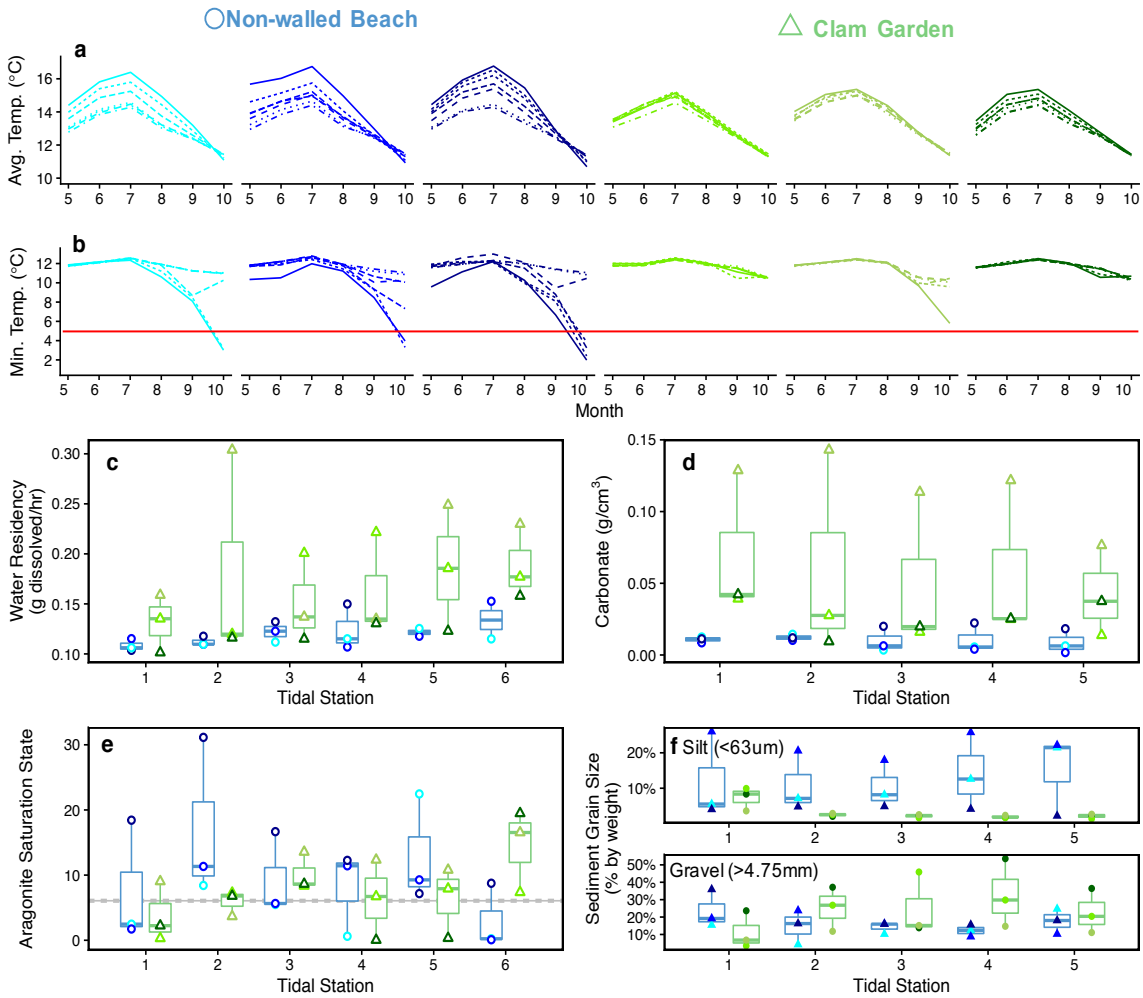

Figure 4 **Effect of beach type and tidal station on** (a) average monthly temperature (°C), (b) minimum monthly temperature (°C), (c) water residency (g dissolved/hr), (d) sediment carbonate content (g/cm^3), (e) sediment grain size (% by weight), and (f) aragonite saturation state of sediment pore water in clam gardens (shades of green, n = 3) and non-walled beaches (shades of blue, n = 3). Linetypes in (a) and (b) indicate tidal station and red line indicates lower thermal tolerance of butter and littlenecks clams (Bernard 1983). Grey lines in (f) indicate the mean aragonite saturation state ± SE of ambient seawater collected at study sites.

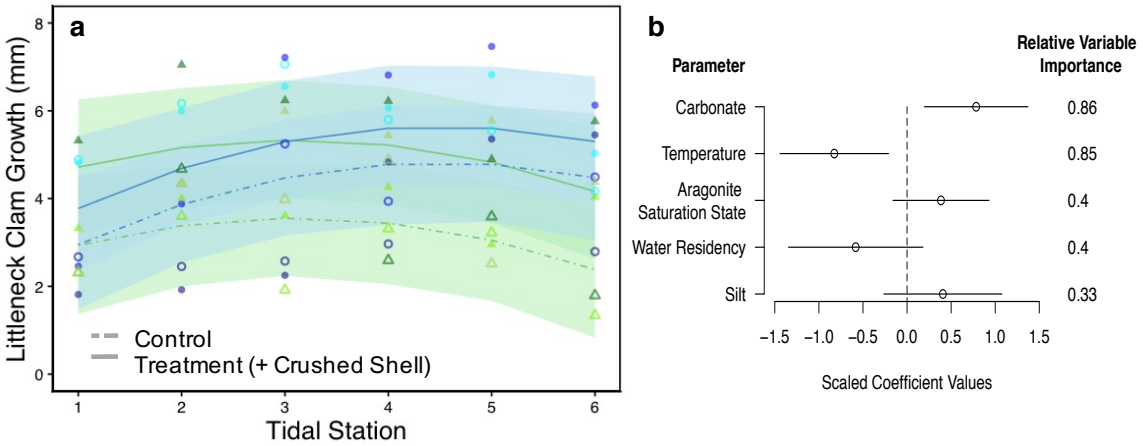

Figure 5 **Littleneck clam (*L. staminea*) growth (mm) in transplant experiment.** (a) Predicted and actual clam growth (mm) as a function of tidal station (1= top of beach, 6 = top of clam garden wall or approximately 0.5 m intertidal height in non-walled beaches). Lines and shaded areas represent mixed effects model predictions with bootstrapped 95% confidence intervals for controls (dashed lines) and crushed shell treatments (solid lines) in clam gardens (green) and non-walled beaches (blue). Darker shades indicate overlapping confidence intervals. Actual growth shown for control (open symbols) and crushed shell treatments (filled symbols) in clam gardens (triangles in shades of green, n =3) and non-walled beaches (circles in shades of blue, n =3). (b) Model averaged parameter estimates with unconditional 95% confidence intervals and corresponding relative variable importance from mixed effects models (AICc <4) for clam growth (mm) across clam garden and non-walled beach study sites (n = 6). Predictor variables included mean temperature (℃), water residency (g dissolved/hr), and sediment characteristics: sediment carbonate content (g/cm^3), silt content (% by weight), and aragonite saturation state of pore water. Clams and sediment characteristics of both control and crushed shell treatment plots included. Coefficients standardized by two SD (Gelman, 2008)

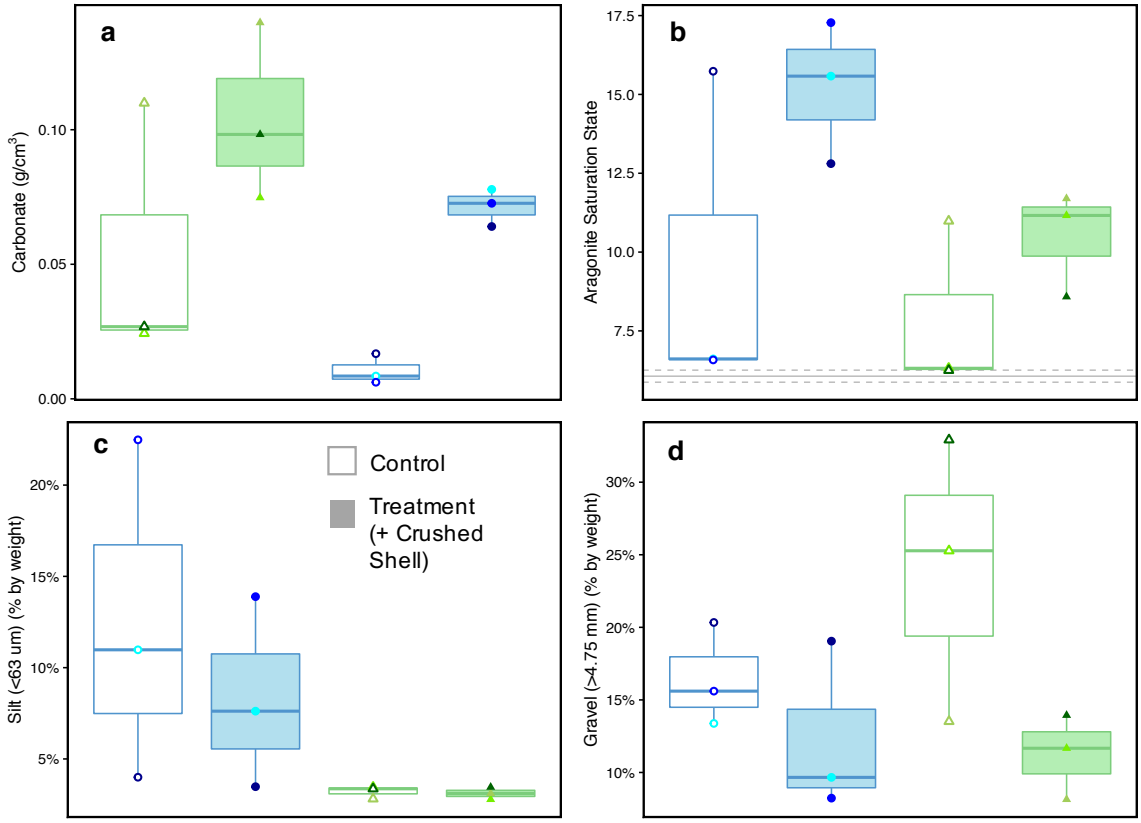

Figure 6 **Effect of beach type and experimental addition of crushed shell on** (a) sediment carbonate content (g/cm^3), (b) aragonite saturation state of sediment pore water, and (c and d) sediment grain size (% by weight) from control (open symbols) and crushed shell treatment plots (filled symbols) in clam gardens (green triangles, n = 3) and non-walled beaches (blue circles n = 3). Grey lines in (b) indicate mean aragonite saturation state ± SE of seawater collected at study sites.

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Appendix. Supplemental Tables and Figures

Table S1. Constants by species for clam length - wet weight regressions (Groesbeck *in prep.*). W = a × L^b where W = weight (kg), L = maximum length (mm), and alpha (a) and beta (b) are constants.

Species	alpha	beta
Littleneck (*L. staminea*)	9.57E-08	3.34
Butter (*S. gigantea*)	9.43E-08	3.28
Macoma spp.	1.07E-08	3.77
Cockle (*C. nuttalii*)	7.64E-08	3.45
Manila (*V. philippinarum*)	9.24E-08	3.29
Varnish clam (*N. obscurata*)	5.38E-09	4.00

Table S2. Strength of evidence for alternative models of clam density and biomass surveyed in clam gardens (n=3) and non-walled clam beaches (n=3).

Response Variable – Likelihood (link) Model	***K***	**AIC_c**	**ΔAIC_c**	**AIC_c weight**	**R^2_{LR}**
Clam Density – Negative Binomial (log)					
Beach Type + poly(Station,2) + Beach Type*poly(Station,2)	8	816.4	0.00	1.00	0.64
Beach Type + poly(Station,2)	6	843.1	26.69	0.00	0.49
poly(Station,2)	5	846.5	30.03	0.00	0.46
Beach Type	4	882.4	66.00	0.00	0.18
Intercept	3	884.0	67.59	0.00	0.14
***Log*(Clam Biomass) – Gaussian**					
Beach Type + poly(Station,2) + Beach Type*poly(Station,2)	8	260.0	0.00	1.00	0.67
Beach Type + poly(Station,2)	6	280.3	20.34	0.00	0.56
poly(Station,2)	5	282.0	22.03	0.00	0.54
Beach Type	4	333.2	73.18	0.00	0.17
Intercept	3	335.0	74.98	0.00	0.14

Models with varying numbers of parameters (*K*) were compared using small-sample bias corrected Akaike's Information Criterion (AIC_c), AIC_c differences (ΔAIC_c), normalized Akaike weights (W_i) log – likelihood (LL); R^2_{LR}, likelihood-ratio based pseudo-R-squared. Site is treated as a random factor in all models.

Table S3. Parameter estimates for the most parsimonious model (ΔAIC=0) predicting clam biomass and density from surveys at clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Parameter	**Estimate**	**SE**	**Confidence Interval**
Clam Density – Negative Binomial (log)			
(Intercept)	-6.51	0.17	(-6.85, -6.19)
Beach Type - Clam Garden	0.70	0.23	(0.23, 1.16)
poly(Station,2)1	6.80	0.93	(5.05, 8.76)
poly(Station,2)2	-5.50	0.88	(-7.45, -4.00)
Beach Type - Clam Garden**poly*(Station,2)1	-5.19	1.25	(-7.63, -2.72)
Beach Type - Clam Garden**poly*(Station,2)2	4.89	1.22	(2.51, 7.34)
Log(Clam Biomass) – Gaussian			
(Intercept)	9.38	0.43	(8.52, 10.27)
Beach Type - Clam Garden	1.19	0.61	(-0.049, 2.33)
poly(Station,2)1	12.15	1.26	(9.61, 14.75)
poly(Station,2)2	-5.44	1.26	(-7.96, -3.05)
Beach Type - Clam Garden*poly(Station,2)1	-9.40	1.78	(-13.10, -5.81)
Beach Type - Clam Garden* poly(Station,2)2	0.23	1.78	(-3.36, 3.59)

Site is treated as a random factor in all models. Non-walled beach was the reference category. SE, standard error. 95% bootstrapped confidence intervals.

Table S4. Strength of evidence for alternative models (ΔAIC_c <4) of clam density and biomass surveyed in clam gardens (n=3) and non-walled clam beaches (n=3).

Response Variable – Likelihood (link) Model	*K*	AIC_c	ΔAIC_c	AIC_c weight	R^2_{LR}
Clam Density – Negative Binomial (log)					
Temperature + Water Residency	5	771.5	0.00	0.16	0.26
Temperature	4	772.1	0.71	0.11	0.23
Temperature + Silt + Carbonate	6	772.3	0.83	0.10	0.27
Temperature + Silt + Water Residency	6	772.8	1.31	0.08	0.27
Temperature + Carbonate	5	772.8	1.31	0.08	0.25
Temperature + Water Residency Carbonate	6	772.9	1.47	0.08	0.27
Temperature + Water Residency + Saturation State	6	773.3	1.82	0.06	0.27
Temperature + Silt	5	773.3	1.88	0.06	0.24
Temperature + Silt + Water Residency + Carbonate	7	773.4	1.97	0.06	0.29
Temperature + Saturation State	5	773.7	2.26	0.05	0.24
Temperature + Carbonate + Saturation State	6	774.6	3.11	0.03	0.25
Temperature + Silt + Carbonate + Saturation State	7	774.6	3.12	0.03	0.28
Temperature + Water Residency + Carbonate + Saturation State	7	774.8	3.31	0.03	0.27
Temperature + Silt + Water Residency + Saturation State	7	774.9	3.42	0.03	0.27
Temperature + Silt + Saturation State	6	775.4	3.89	0.02	0.25
***Log*(Clam Biomass) – Gaussian**					
Temperature + Carbonate	5	279.9	0.00	0.35	0.43
Temperature + Carbonate + Silt	6	281.0	1.11	0.20	0.43
Temperature + Carbonate + Water Residency	6	281.5	1.58	0.16	0.43
Temperature + Carbonate + Saturation State	6	282.2	2.33	0.11	0.43
Temperature + Carbonate + Silt + Water Residency	7	283.1	3.15	0.07	0.44
Temperature + Carbonate + Silt + Saturation State	7	283.4	3.45	0.06	0.43
Temperature + Carbonate + Water Residency + Saturation State	7	283.9	3.97	0.05	0.43

Models with varying numbers of parameters (K) were compared using small-sample bias corrected Akaike's Information Criterion (AICc), AICc differences (ΔAICc), normalized Akaike weights (Wi) log – likelihood (LL); R^2LR, likelihood-ratio based pseudo-R-squared. Site is treated as a random factor in all models.

Table S5. Strength of evidence for alternative models of environmental variables measured in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Model	*K*	AIC_c	ΔAIC_c	AIC_c weight	R^2_{LR}
Water Residency – Gamma (log)					
Station	4	-138.2	0.00	0.52	0.53
Beach Type + Station	5	-137.3	0.86	0.34	0.55
Beach Type + Station + Beach Type*Station	6	-134.5	3.69	0.08	0.55
Intercept	3	-132.9	5.24	0.04	0.40
Beach Type	4	-132.6	5.60	0.03	0.44
Mean Temperature – Gamma (identity)					
Beach Type + Station + Beach Type* Station	6	-19.3	0.00	1.00	0.87
Station	4	12.6	31.89	0.00	0.61
Beach Type + Station	5	14.8	34.14	0.00	0.62
Intercept	3	44.8	64.15	0.00	-0.054
Beach Type	4	46.5	65.83	0.00	-0.028
Min Temperature – Gamma (identity)					
Beach Type + Station + Beach Type*Station	6	149.9	0.00	1.00	0.79
Beach Type + Station	5	166.4	16.44	0.00	0.63
Station	4	169.7	19.73	0.00	0.56
Beach Type	4	195.8	45.89	0.00	0.064
Intercept	3	197.2	47.23	0.00	-0.046
Max Temperature – Gamma (identity)					
Beach Type + Station + Beach Type* Station	6	212.6	0.00	0.66	0.24
Intercept	3	215.1	2.46	0.19	-0.028
Station	4	216.9	4.31	0.08	-0.0074
Beach Type	4	217.6	4.98	0.05	-0.027
Beach Type + Station	5	219.6	6.96	0.02	-0.0052
SE Temperature – Gamma (identity)					
Beach Type + Station + Beach Type* Station	6	-304.5	0.00	0.96	0.55
Station	4	-297.1	7.41	0.02	0.35
Beach Type + Station	5	-296.6	7.91	0.02	0.39
Intercept	3	-282.8	21.71	0.00	-0.057
Beach Type	4	-282.3	22.26	0.00	0.0021
Chlorophyll a – Gamma (inverse)					
Station	4	160.0	0.00	0.37	0.28
Intercept	3	161.8	1.80	0.15	0.18
Beach Type + Station + Beach Type* Station	6	162.1	2.09	0.13	0.35
Beach Type + Station	5	162.5	2.52	0.10	0.28
Station + Tide	5	162.7	2.71	0.10	0.28
Beach Type	4	164.0	4.03	0.05	0.19
Tide	4	164.3	4.36	0.04	0.18
Beach Type + Station + Tide + Beach Type*Station	7	165.2	5.23	0.03	0.35
Beach Type + Station + Tide	6	165.4	5.42	0.02	0.28

Beach Type + Tide	5	166.8	6.77	0.01	0.19
Silt – Beta (logit)					
Beach Type + Treatment + Station + Beach Type*Station	7	-251.2	0.00	0.48	-
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	-251.2	0.03	0.47	-
Beach Type + Station + Beach Type*Station	6	-246.7	4.51	0.05	
Beach Type + Treatment + Station	6	-215.8	35.41	0.00	-
Beach Type + Station	5	-215.8	35.46	0.00	-
Beach Type	4	-215.7	35.56	0.00	-
Beach Type + Treatment	5	-215.6	35.65	0.00	-
Beach Type + Treatment + Station + Beach Type*Treatment	7	-215.1	36.16	0.00	-
Beach Type + Treatment + Beach Type*Treatment	6	-214.7	36.58	0.00	
Intercept	3	-214.3	36.93	0.00	-
Treatment	4	-214.2	37.04	0.00	-
Treatment + Station	5	-214.1	37.14	0.00	-
Station	4	-214.1	37.16	0.00	-
Gravel – Beta (logit)					
Treatment + Station	5	-119.6	0.00	0.31	-
Treatment	4	-119.1	0.56	0.24	-
Beach Type + Treatment + Station	6	-118.1	1.52	0.15	-
Beach Type + Treatment	5	-117.8	1.86	0.12	-
Beach Type + Treatment + Station + Beach Type*Station	7	-116.2	3.42	0.06	-
Beach Type+ Treatment + Station + Beach Type*Treatment	7	-116.1	3.55	0.05	-
Beach Type + Treatment + Beach Type*Treatment	6	-115.6	4.03	0.04	-
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	-114.1	5.58	0.02	-
Intercept	3	-109.7	9.92	0.00	-
Station	4	-109.7	9.98	0.00	-
Beach Type	4	-108.3	11.30	0.00	-
Beach Type + Station	5	-108.1	11.57	0.00	-
Beach Type + Station + Beach Type* Station	6	-105.8	13.89	0.00	-
Aragonite Saturation State – Gaussian					
Beach Type + Treatment	5	497.2	0.00	0.31	0.12
Treatment	4	498.5	1.38	0.16	0.074
Beach Type + Treatment + Beach Type*Treatment	6	498.8	1.60	0.14	0.13
Beach Type + Treatment + Station	6	499.2	2.04	0.11	0.12
Treatment + Station	5	500.5	3.36	0.058	0.079
Beach Type	4	500.7	3.49	0.055	0.047
Beach Type + Treatment + Station + Beach Type*Treatment	7	500.9	3.71	0.049	0.13

Beach Type + Treatment + Station + Beach Type*Station	7	501.6	4.45	0.034	0.13
Intercept	3	501.9	4.69	0.030	0.000041
Beach Type + Station	5	502.7	5.49	0.020	0.051
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	503.4	6.20	0.014	0.13
Station	4	503.8	6.63	0.011	0.0042
Beach Type + Station + Beach Type*Station	6	505.0	7.82	0.006	0.052
Alkalinity – Gamma (log)					
Beach Type + Treatment + Station + Beach Type*Treatment	7	1128.8	0.00	0.31	0.41
Beach Type + Treatment + Station	6	1129.2	0.36	0.26	0.38
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	1129.9	1.07	0.18	0.42
Beach Type+ Treatment + Station + Beach Type*Station	7	1130.1	1.32	0.16	0.40
Treatment + Station	5	1132.1	3.24	0.06	0.34
Beach Type + Station	5	1136.3	7.52	0.01	0.30
Beach Type + Station + Beach Type*Station	6	1137.6	8.78	0.00	0.31
Station	4	1139.6	10.77	0.00	0.24
Beach Type + Treatment	5	1143.2	14.40	0.00	0.22
Beach Type + Treatment + Beach Type*Treatment	6	1143.8	14.93	0.00	0.25
Treatment	4	1146.2	17.42	0.00	0.17
Beach Type	4	1149.0	20.19	0.00	0.13
Intercept	3	1152.4	23.58	0.00	0.061
Dissolved Inorganic Carbon – Gamma (identity)					
Station	4	1092.2	0.00	0.47	0.17
Beach Type + Station	5	1093.9	1.67	0.20	0.18
Treatment + Station	5	1094.5	2.32	0.15	0.17
Beach Type + Station + Beach Type*Station	6	1096.2	4.01	0.06	0.18
Beach Type + Treatment + Station	6	1096.3	4.06	0.06	0.18
Beach Type + Treatment + Station + Beach Type*Treatment	7	1098.5	6.30	0.02	0.18
Beach Type + Treatment + Station + Beach Type*Station	7	1098.7	6.48	0.02	0.18
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	1101.0	8.79	0.01	0.18
Intercept	3	1101.0	8.81	0.01	0.031
Beach Type	4	1102.7	10.45	0.00	0.040
Treatment	4	1103.2	11.01	0.00	0.032
Beach Type + Treatment	5	1104.9	12.73	0.00	0.040
Beach Type + Treatment + Beach Type*Treatment	6	1107.2	14.94	0.00	0.042
Carbonate – Gamma (log)					
Beach Type + Treatment + Beach Type*Treatment	6	-294.2	0.00	0.56	0.75

Beach Type + Treatment + Station + Beach Type*Treatment	7	-293.3	0.97	0.35	0.76
Beach Type + Treatment + Station + Beach Type*Treatment + Beach Type*Station	8	-290.6	3.61	0.09	0.76
Beach Type + Treatment	5	-275.4	18.79	0.00	0.65
Treatment	4	-274.1	20.11	0.00	0.62
Beach Type + Treatment + Station	6	-274.0	20.20	0.00	0.65
Treatment + Station	5	-272.8	21.38	0.00	0.63
Beach Type + Treatment + Station + Beach Type*Station	7	-271.6	22.62	0.00	0.65
Beach Type	4	-222.1	72.14	0.00	0.13
Intercept	3	-220.9	73.31	0.00	0.082
Beach Type + Station	5	-219.7	74.50	0.00	0.13
Station	4	-218.6	75.59	0.00	0.082
Beach Type + Station + Beach Type*Station	6	-217.3	76.94	0.00	0.13

Models with varying numbers of parameters (K) were compared using small-sample bias corrected Akaike's Information Criterion (AICc), AICc differences (ΔAICc), normalized Akaike weights (Wi) log – likelihood (LL); R^2LR, likelihood-ratio based pseudo-R-squared. Site is treated as a random factor in all models.

Table S6. Parameter estimates for the most parsimonious model (ΔAIC=0) predicting environmental variables measured in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Parameter	Estimate	SE	Confidence Interval
Mean Temperature – Gamma (identity)			
(Intercept)	14.77	0.12	(14.53,15.01)
Beach Type - Clam Garden	-0.86	0.17	(-1.20, -0.53)
Station	-0.29	0.02	(-0.32, -0.25)
Beach Type - Clam Garden* Station	0.96	0.48	(0.16, 0.26)
Minimum Temperature – - Gamma (identity)			
(Intercept)	0.84	0.63	(-0.40, 2.08)
Beach Type - Clam Garden	8.38	1.31	(5.81,10.96)
Station	1.87	0.16	(1.56, 2.18)
Beach Type- Clam Garden* Station	-1.65	0.32	(-2.28, -1.02)
Maximum Temperature – Gamma (identity)			
(Intercept)	42.23	2.61	(37.12, 47.34)
Beach Type - Clam Garden	-8.66	3.62	(-15.76, -1.55)
Station	-1.63	0.52	(-2.65, -0.61)
Beach Type - Clam Garden* Station	2.58	0.75	(1.12, 4.05)
Standard Error of Temperature – Gamma (identity)			
(Intercept)	33.27	7.27	(19.02, 47.52)
Beach Type - Clam Garden	49.24	12.62	(24.50, 73.98)
Station	15.07	2.36	(10.44, 19.70)
Beach Type - Clam Garden* Station	-12.69	3.54	(-19.63, -5.74)

Site is treated as a random factor in all models. Non-walled beach was the reference category. SE, standard error. 95% Wald Confidence intervals.

Table S7. Model averaged (ΔAICc <4) parameter estimates for environmental variables measured in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Parameter	Estimate	Unconditional SE	Confidence Interval	RVI
Water Residency – Gamma (log)				
(Intercept)	-2.21	0.15	(-2.51, -1.91)	
Beach Type - Clam Garden	0.27	0.18	(-0.10, 0.64)	0.45
Station	0.051	0.019	(0.013, 0.089)	1.00
Beach Type - Clam Garden* Station	0.013	0.035	(-0.059, 0.086)	0.09
Chlorophyll a – Gamma (inverse)				
(Intercept)	0.20	0.057	(0.083, 0.31)	
Beach Type - Clam Garden	-0.079	0.012	(-0.26, 0.098)	0.28
Station	0.013	0.088	(-0.011, 0.036)	0.82
Beach Type - Clam Garden* Station	0.030	0.016	(-0.0029, 0.062)	0.15
Tide - Flood	0.0041	0.023	(-0.044, 0.052)	0.11
Silt – Beta (logit)				
(Intercept)	-3.22	0.32	(-3.85, -2.58)	
Beach Type - Clam Garden	1.05	0.45	(0.14, 1.96)	1.0
Treatment - Treatment	-0.35	0.13	(-0.61, -0.083)	1.0
Station	0.33	0.049	(0.24, 0.43)	1.0
Beach Type - Clam Garden* Station	-0.58	0.078	(-0.74, -0.41)	1.0
Beach Type - Clam Garden* Treatment - Treatment	0.34	0.21	(0.0078, 0.76)	0.5
Gravel – Beta (link = logit)				
(Intercept)	-1.62	0.28	(-2.18, -1.06)	
Beach Type - Clam Garden	0.21	0.30	(-0.39, 0.82)	0.41
Treatment - Treatment	-0.63	0.18	(-0.99, -0.26)	1.00
Station	0.092	0.063	(-0.035, 0.22)	0.61
Beach Type - Clam Garden* Station	0.093	0.12	(-0.14, 0.32)	0.06
Beach Type - Clam Garden* Treatment - Treatment	-0.25	0.34	(-0.93. 0.44)	0.06
Aragonite Saturation State – Gaussian				
(Intercept)	10.20	1.93	(6.36, 14.04)	
Beach Type - Clam Garden	-2.85	2.00	(-6.84, 1.14)	0.76
Treatment - Treatment	4.44	1.95	(0.55, 8.33)	0.94
Station	-0.29	0.49	(-1.26, 0.69)	0.25
Beach Type - Clam Garden* Treatment - Treatment	-2.95	3.32	(-9.58, 3.68)	0.21
Alkalinity – Gamma (log)				
(Intercept)	8.25	0.073	(8.11, 8.40)	
Beach Type - Clam Garden	-0.17	0.095	(-0.36, 0.018)	0.94
Treatment - Treatment	0.17	0.060	(0.048, 0.29)	1.00
Station	-0.056	0.015	(-0.086, -0.026)	1.00
Beach Type - Clam Garden* Station	0.028	0.023	(-0.018, 0.074)	0.35

Beach Type - Clam Garden* Treatment - Treatment	-0.14	0.081	(-0.30, 0.025)	0.51
Dissolved Inorganic Carbon – Gamma (identity)				
(Intercept)	2686.99	119.28	(2449.34,	
Beach Type - Clam Garden	-184.03	99.88	(-383.44, 15.34)	0.25
Treatment - Treatment	-3.58	89.64	(-182.55,	0.18
Station	-109.19	26.24	(-161.56,	1.00
Carbonate – Gamma (log)				
(Intercept)	-4.56	0.29	(-5.14, -3.98)	
Beach Type - Clam Garden	1.48	0.39	(0.70, 2.26)	1.00
Treatment - Treatment	2.01	0.17	(1.68, 2.35)	1.00
Station	-0.048	0.043	(-0.13, 0.037)	0.44
Beach Type - Clam Garden* Station	0.047	0.023	(-0.15, 0.16)	0.09
Beach Type - Clam Garden* Treatment - Treatment	-1.17	0.23	(-1.64, 2.35)	1.00

Site is treated as a random factor in all models. Non-walled beach, control and ebb tide were the reference categories. 95% Wald Confidence intervals. SE, standard error; RVI, relative variable importance.

Table S8. Strength of evidence for alternative models of littleneck clam (*L. staminea*) growth, proportional growth, survival and final biomass from the transplant experiment in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Model	*K*	AIC_c	ΔAIC_c	AIC_c weight	R^2_{LR}
Growth – Gaussian					
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment + Beach Type **poly*(Station,2)	11	2031.7	0.00	0.00	0.36
Beach Type+ Treatment + *poly*(Station,2) + Beach Type**poly*(Station,2)	10	2034.0	2.23	2.23	0.36
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment	9	2036.2	4.45	4.45	0.35
Treatment + *poly*(Station,2)	7	2037.0	5.29	5.29	0.34
Beach Type + Treatment + *poly*(Station,2)	8	2038.4	6.68	6.68	0.35
Treatment	5	2042.9	11.14	11.14	0.33
Beach Type + Treatment + Beach Type*Treatment	7	2042.9	11.19	11.19	0.34
Beach Type + Treatment	6	2044.4	12.64	12.64	0.33
Beach Type + *poly*(Station,2) + Beach Type**poly*(Station,2)	9	2055.9	24.18	24.18	0.33
poly(Station,2)	6	2056.0	24.26	24.26	0.32
Beach Type + *poly*(Station,2)	7	2057.4	25.65	25.65	0.32
Intercept	4	2058.8	27.12	27.12	0.31
Beach Type	5	2060.3	28.60	28.60	0.31
Proportional Growth – Gamma (log)					
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment + Beach Type**poly*(Station,2)	11	-618.4	0.00	0.27	0.20
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment	9	-618.2	0.23	0.24	0.19
Treatment + *poly*(Station,2)	7	-618.1	0.32	0.23	0.19
Beach Type+ Treatment + *poly*(Station,2) + Beach Type**poly*(Station,2)	10	-616.6	1.86	0.11	0.20
Beach Type + Treatment + *poly*(Station,2)	8	-616.3	2.09	0.10	0.19
Treatment	5	-613.7	4.68	0.03	0.17
Beach Type + Treatment + Beach Type *Treatment	7	-612.9	5.49	0.02	0.18
Beach Type + Treatment	6	-611.9	6.51	0.01	0.17
poly(Station,2)	6	-606.2	12.25	0.00	0.16
Beach Type + *poly*(Station,2)	7	-605.5	13.96	0.00	0.17
Intercept	4	-603.9	14.49	0.00	0.15
Beach Type + *poly*(Station,2) + Beach Type**poly*(Station,2)	9	-603.4	15.07	0.00	0.17
Beach Type	5	-602.2	16.26	0.00	0.15
Survival – Binomial (logit)					

Treatment	4	414.3	0.00	0.35	-
Intercept	3	415.3	1.00	0.21	-
Beach Type + Treatment	5	416.4	2.09	0.12	-
Treatment + *poly*(Station,2)	6	417.1	2.89	0.08	-
Beach Type	4	417.3	3.01	0.08	-
poly(Station,2)	5	418.1	3.84	0.05	-
Beach Type+ Treatment + Beach Type*Treatment	6	418.6	4.37	0.04	-
Beach Type+ Treatment + *poly*(Station,2)	7	419.4	5.12	0.03	-
Beach Type+ *poly*(Station,2)	6	420.3	5.99	0.02	-
Beach Type+ Treatment + *poly*(Station,2) + Beach Type*Treatment	8	421.8	7.55	0.01	-
Beach Type+ Treatment + *poly*(Station,2) + Beach Type**poly*(Station,2)	9	422.7	8.46	0.01	-
Beach Type+ *poly*(Station,2) + Beach Type **poly*(Station,2)	8	423.5	9.26	0.00	-
Beach Type+ Treatment + *poly*(Station,2) + Beach Type *Treatment + Beach Type * *poly*(Station,2)	10	425.3	11.03	0.00	-
***Log*(Biomass) – Gaussian**					
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment + Beach Type* *poly*(Station,2)	11	1012.7	0.00	0.84	0.26
Beach Type + Treatment + *poly*(Station,2) + Beach Type**poly*(Station,2)	10	1016.2	3.49	0.15	0.25
Beach Type + *poly*(Station,2) + Beach Type* *poly*(Station,2)	9	1022.4	9.65	0.01	0.24
Beach Type + Treatment + Beach Type*Treatment	7	1027.7	14.97	0.00	0.23
Treatment	5	1028.6	15.85	0.00	0.22
Beach Type + Treatment + *poly*(Station,2) + Beach Type*Treatment	9	1029.8	17.08	0.00	0.23
Beach Type + Treatment	6	1030.1	17.32	0.00	0.22
Treatment + *poly*(Station,2)	7	1031.0	18.27	0.00	0.22
Intercept	4	1032.2	19.44	0.00	0.21
Beach Type + Treatment + *poly*(Station,2)	8	1032.4	19.68	0.00	0.22
Beach Type	5	1033.6	20.92	0.00	0.21
poly(Station,2)	6	1034.8	22.11	0.00	0.21
Beach Type + *poly*(Station,2)	7	1036.3	23.54	0.00	0.21

Models with varying numbers of parameters (K) were compared using small-sample bias corrected Akaike's Information Criterion (AICc), AICc differences (ΔAICc), normalized Akaike weights (Wi) log – likelihood (LL); R^2LR, likelihood-ratio based pseudo-R-squared. Plot nested in site is treated as a random factor in all models.

Table S9. Parameter estimates for the most parsimonious model (ΔAIC=0) predicting littleneck clam (*L. staminea*) growth, and final biomass from the clam transplant experiment in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Parameter	**Estimate**	**SE**	**Confidence Interval**
Growth – Gaussian			
(Intercept)	4.28	0.66	(2.84, 5.74)
Beach Type - Clam Garden	-1.14	0.94	(-3.07,0.80)
Treatment - Treatment	0.82	0.33	(0.13, 1.49)
poly(Station,2)1	10.26	3.60	(3.30, 17. 98)
poly(Station,2)2	-8.36	3.49	(-15.35, -1.79)
Beach Type - Clam Garden* Treatment - Treatment	0.96	0.48	(-0.015, 1.95)
Beach Type - Clam Garden**poly*(Station,2)1	-15.30	5.33	(-25.86, -4.74)
Beach Type - Clam Garden**poly*(Station,2)2	0.69	5.38	(-10.08, 10.97)
***Log*(Biomass) – Gaussian**			
(Intercept)	5.34	0.20	(4.92, 5.71)
Beach Type - Clam Garden	-0.40	0.29	(-0.98, 0.18)
Treatment - Treatment	0.06	0.12	(-0.15, 0.30)
poly(Station,2)1	4.33	1.26	(1.79, 6.85)
poly(Station,2)2	-1.52	1.22	(-4.05, 0.63)
Beach Type - Clam Garden*Treatment - Treatment	0.38	0.17	(0.064, 0.71)
Beach Type - Clam Garden* *poly*(Station,2)1	-8.84	1.87	(-12.31, -5.09)
Beach Type - Clam Garden* *poly*(Station,2)2	0.64	1.89	(-2.89, 4.48)

Non-walled beach and control were the reference categories. Plot nested in site is treated as a random factor in all models. SE, standard error. 95% bootstrapped confidence intervals.

Table S10. Strength of evidence for alternative models (ΔAIC_c <4) of littleneck clam (*L. staminea*) growth, proportional growth, survival and final biomass from the transplant experiment in clam gardens (n = 3) and non-walled beaches (n = 3).

Response Variable – Likelihood (link) Model	*K*	AIC_c	ΔAIC_c	AIC_c weight	R^2_{LR}
Growth – Gaussian					
Temperature + Carbonate + Water Residency	7	1662.4	0.00	0.14	0.36
Temperature + Carbonate	6	1662.4	0.02	0.14	0.35
Temperature + Carbonate + Saturation State	7	1662.9	0.54	0.11	0.36
Temperature + Carbonate + Water Residency + Saturation State	8	1663.3	0.96	0.09	0.36
Temperature + Carbonate + Silt	7	1663.5	1.12	0.08	0.36
Temperature + Carbonate + Water Residency + Silt	8	1664.0	1.65	0.06	0.36
Temperature + Carbonate + Saturation State + Silt	8	1664.2	1.87	0.06	0.36
Carbonate + Silt	6	1664.4	2.03	0.05	0.35
Temperature	5	1664.7	2.33	0.04	0.35
Temperature + Saturation State	6	1664.8	2.40	0.04	0.35
Temperature + Carbonate + Water Residency + Saturation State + Silt	9	1665.1	2.72	0.04	0.36
Carbonate	5	1665.3	2.91	0.03	0.35
Carbonate + Saturation State + Silt	7	1665.5	3.13	0.03	0.35
Temperature + Water Residency	6	1665.6	3.19	0.03	0.35
Temperature + Water Residency + Saturation State	7	1666.0	3.59	0.02	0.35
Carbonate + Saturation State	6	1666.1	3.77	0.02	0.35
Carbonate + Water Residency + Saturation State	7	1666.4	3.99	0.02	0.35
Proportional Growth – Gamma (log)					
Temperature	5	-518.0	0.00	0.10	0.25
Intercept	4	-517.9	0.13	0.10	0.24
Temperature + Carbonate	6	-517.6	0.35	0.09	0.25
Carbonate	5	-517.2	0.82	0.07	0.25
Temperature + Saturation State	6	-516.8	1.16	0.06	0.25
Saturation State	5	-516.6	1.41	0.05	0.24
Silt	5	-516.3	1.72	0.04	0.24
Temperature + Carbonate + Saturation State	7	-516.2	1.75	0.04	0.25
Carbonate + Silt	6	-516.2	1.82	0.04	0.25
Temperature + Water Residency	6	-516.0	1.94	0.04	0.25
Temperature + Silt	6	-515.9	2.05	0.04	0.25
Temperature + Carbonate + Water Residency	7	-515.9	2.08	0.04	0.25
Water Residency	5	-515.8	2.15	0.04	0.24
Temperature + Carbonate + Silt	7	-515.7	2.23	0.03	0.25
Carbonate + Saturation State	6	-515.7	2.31	0.03	0.25
Carbonate + Water Residency	6	-515.1	2.88	0.02	0.25
Saturation State + Silt	6	-514.9	3.13	0.02	0.24
Temperature + Saturation State + Water Residency	7	-514.8	3.18	0.02	0.25

Temperature + Saturation State + Silt	7	-514.8	3.23	0.02	0.25
Water Residency + Saturation State	6	-514.6	3.38	0.02	0.24
Carbonate + Saturation State + Silt	7	-514.5	3.50	0.02	0.25
Temperature + Carbonate + Saturation State + Water	8	-514.4	3.61	0.02	0.25
Silt + Water Residency	6	-514.3	3.72	0.02	0.24
Temperature + Carbonate + Saturation State + Silt	8	-514.3	3.73	0.02	0.25
Carbonate + Silt + Water Residency	7	-514.1	3.88	0.01	0.25
Survival – Binomial (logit)					
Water Residency	4	344.3	0.00	0.17	-
Intercept	3	344.3	0.03	0.16	-
Temperature	4	345.2	0.95	0.10	-
Water Residency + Temperature	5	346.1	1.81	0.07	-
Water Residency + Saturation State	5	346.3	2.05	0.06	-
Silt	4	346.4	2.08	0.06	-
Saturation State	4	346.5	2.18	0.06	-
Temperature + Silt	5	346.5	2.25	0.05	-
Carbonate	4	346.6	2.28	0.05	-
Water Residency + Silt	5	346.7	2.36	0.05	-
Water Residency + Carbonate	5	346.7	2.37	0.05	-
Temperature + Saturation Sate	5	347.4	3.14	0.03	-
Temperature + Carbonate	5	347.5	3.24	0.03	-
Water Residency + Temperature + Silt	6	348.2	3.90	0.02	-
Water Residency + Temperature + Saturation State	6	348.2	3.96	0.02	-
***Log*(Biomass) – Gaussian**					
Carbonate + Temperature + Water Residency + Silt	8	833.9	0.00	0.24	0.27
Carbonate + Silt	6	834.3	0.38	0.20	0.26
Carbonate + Water Residency + Silt	7	834.4	0.49	0.18	0.26
Carbonate + Temperature + Silt	7	835.6	1.73	0.10	0.26
Carbonate + Temperature + Water Residency + Silt + Saturation State	9	835.7	1.81	0.10	0.27
Carbonate + Water Residency + Silt + Saturation State	8	836.1	2.20	0.08	0.26
Carbonate + Silt + Saturation State	7	836.3	2.32	0.07	0.26
Carbonate + Temperature + Silt + Saturation State	8	837.7	3.73	0.04	0.26

Models with varying numbers of parameters (K) were compared using small-sample bias corrected Akaike's Information Criterion (AICc), AICc differences (ΔAICc), normalized Akaike weights (Wi) log – likelihood (LL); R^2LR, likelihood-ratio based pseudo-R-squared. Plot nested in site is treated as a random factor in all models.

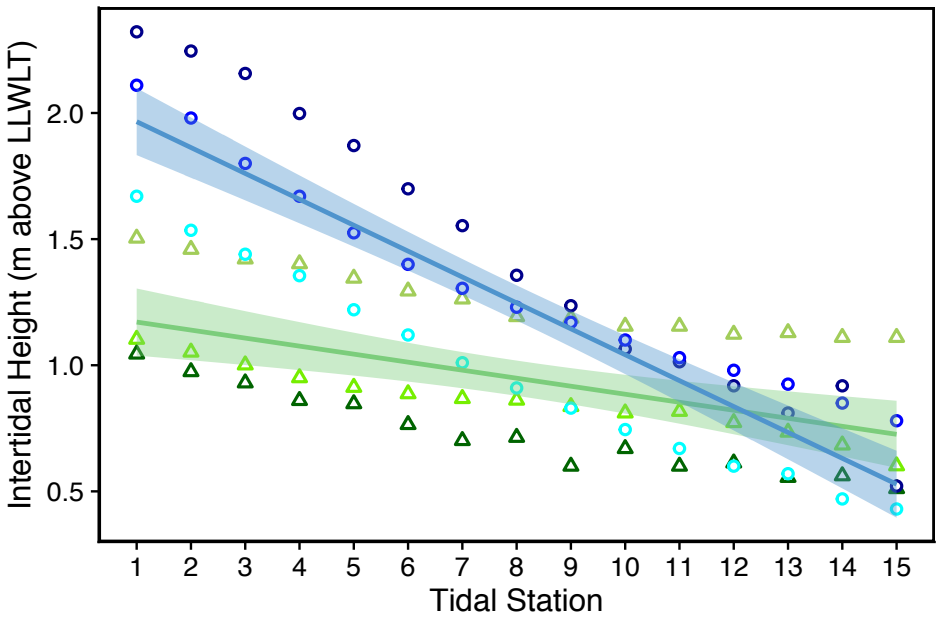

Figure S1 **Effect of beach type on slope measured as the change in intertidal height over fifteen equally spaced tidal stations.** Llinear model fits with 95% confidence intervals (shaded area) for clam gardens (green) and non-walled beaches (blue). Darker shades indicate overlapping confidence intervals. Actual intertidal heights shown for clam gardens (triangles in shades of green, n =3) and non-walled beaches (circles in shades of blue, n =3)

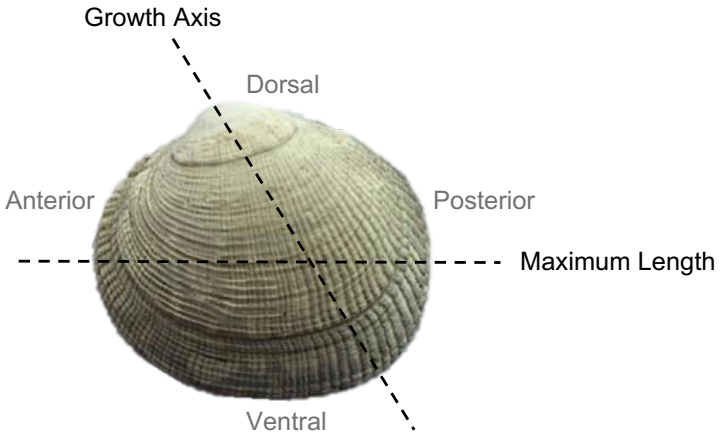

Figure S2 **Clam morphometrics**. We measured survey and transplant experiment clams along the maximum length and growth axis. The maximum length is the greatest distance between the anterior and posterior margin of the shell. The growth axis is the greatest distance between the umbo and the ventral margin of the shell. Species shown: littleneck clam (*L. staminea*).

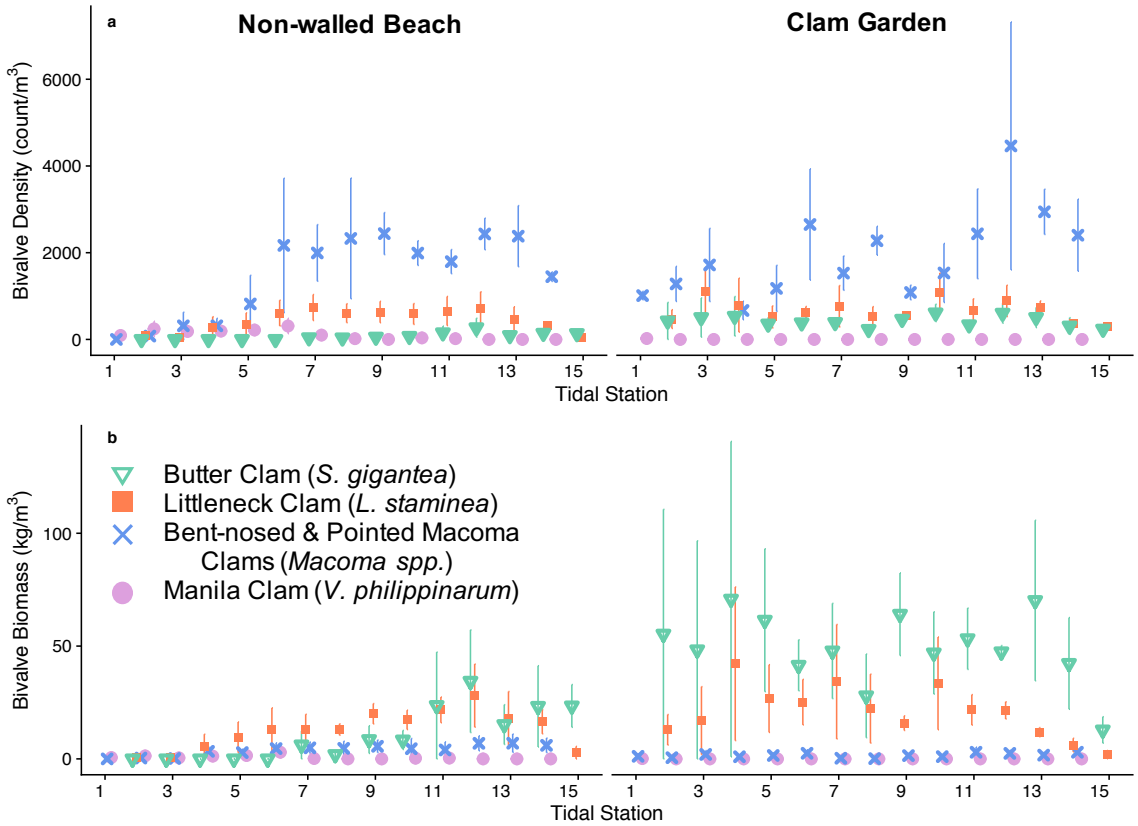

Figure S3 **Effect of beach type and tidal station on clam species** (a) density (count/0.0178 m3) and (b) biomass (kg/m3). Standard errors shown.

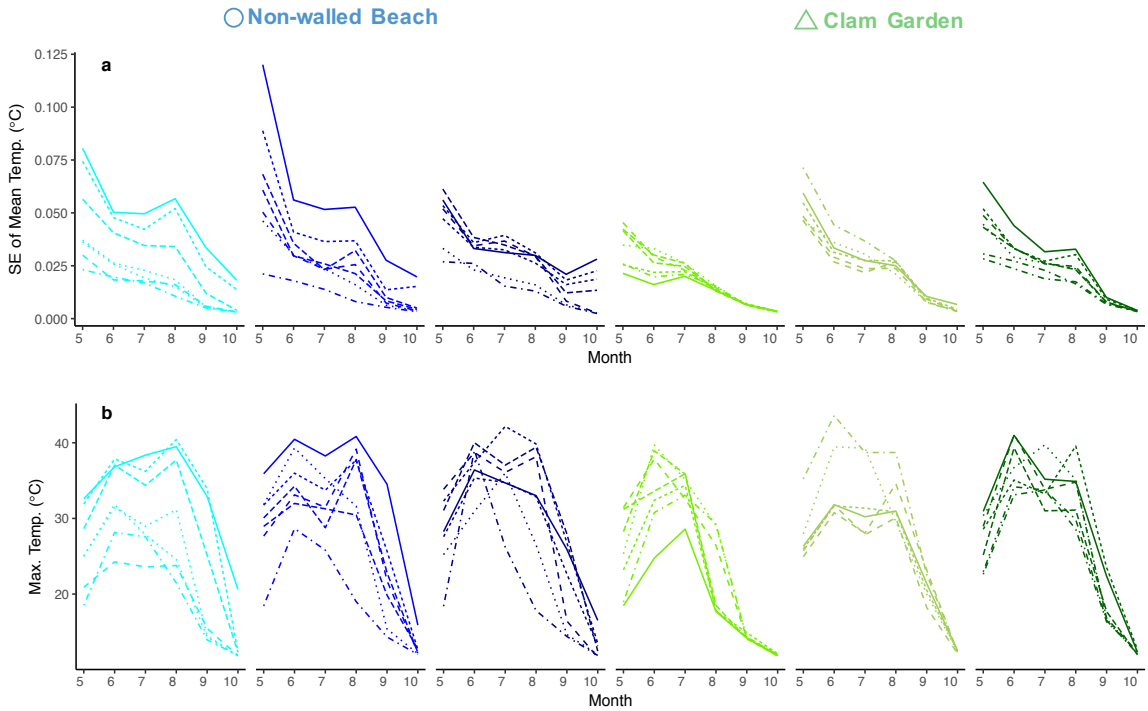

Figure S4 **Effect of beach type and tidal station on** (a) standard error of the mean monthly temperature (℃), and (b) maximum monthly temperature (℃) from May to October. Linetypes indicate tidal station.

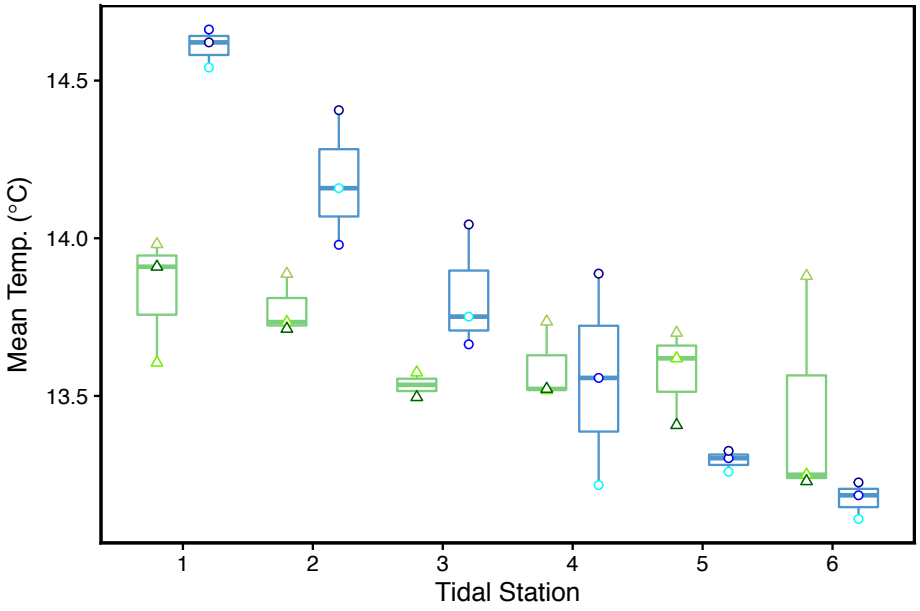

Figure S5 **Effect of beach type and tidal station on mean temperature** (℃) from May to October for clam gardens (triangles in shades of green, n =3) and non-walled beaches (circles in shades of blue, n =3).

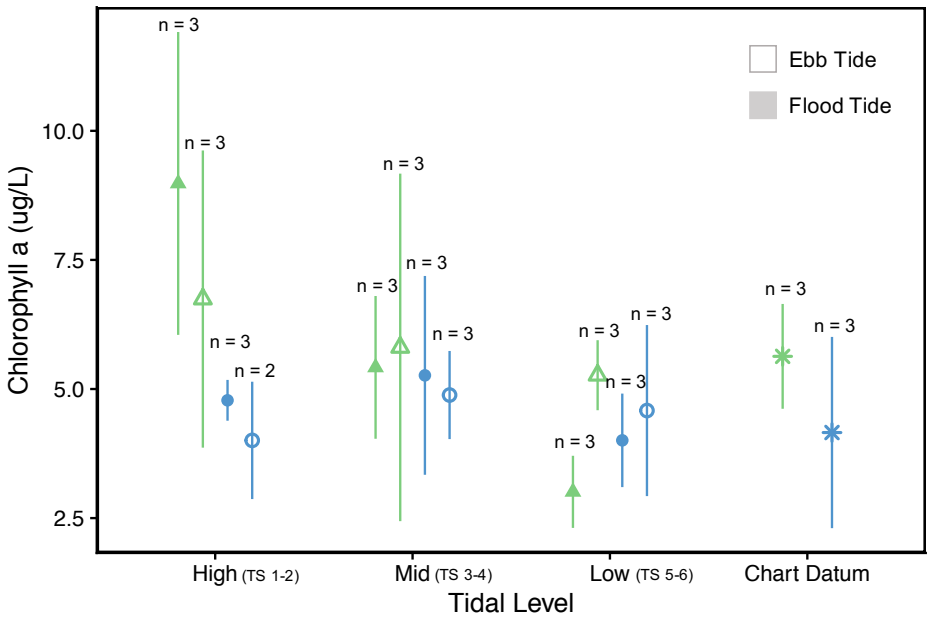

Figure S6 **Effect of beach type, tidal level and tide cylce on chlorophyll a** (ug/L). Samples were takend during at chart datum and during the ebb (open symbols) and flood (filled symbols) tide at clam gardens (green triangles, n = 3) and non-walled beaches (blue circles, n = 3).TS, tidal station.

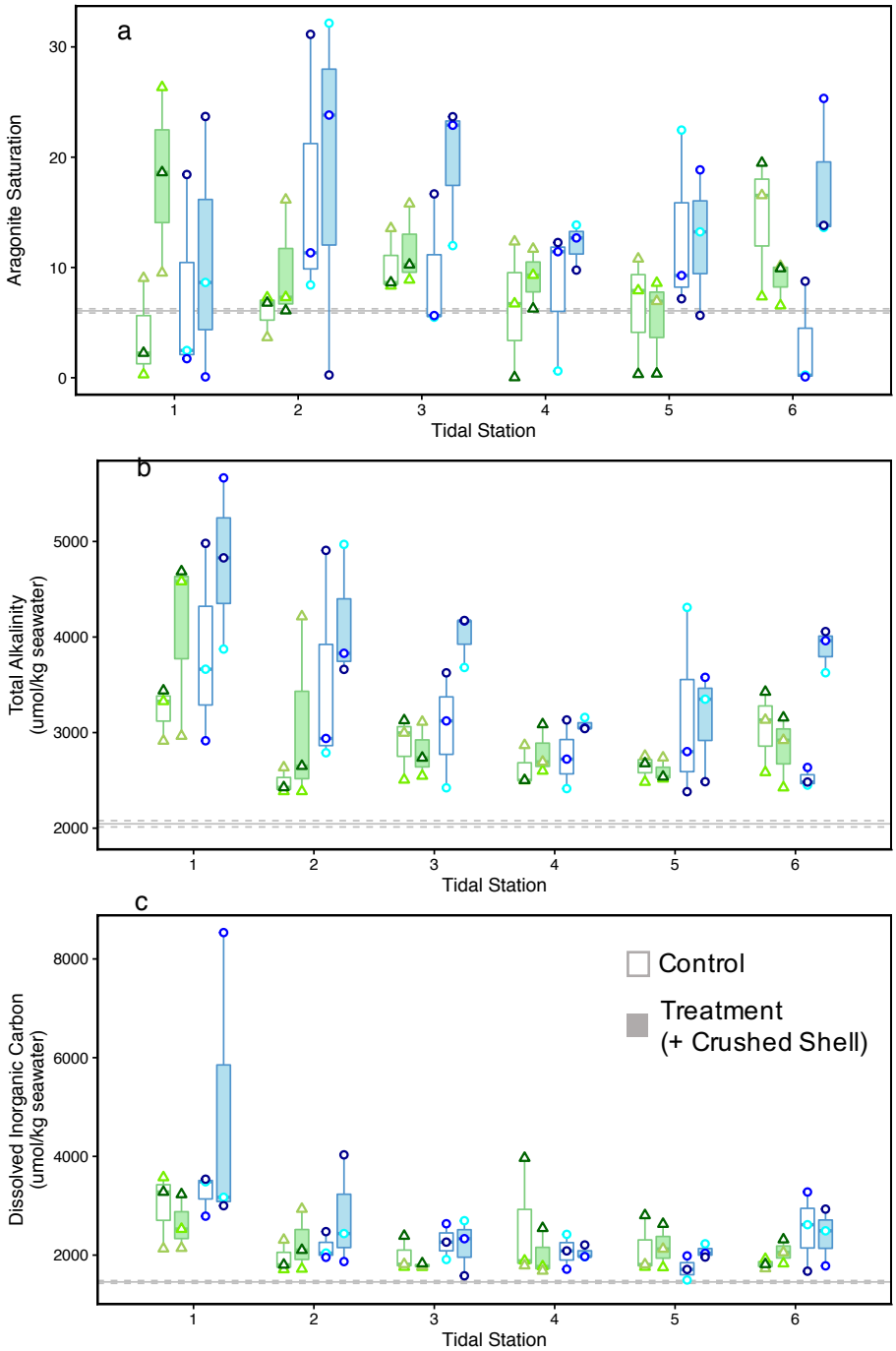

Figure S7 **Effect of beach type, tidal station and experimental addition of crushed shell on** (a) aragonite saturation state, (b) total akalinity (umol/kg seawater) and (c) dissolved inorganic carbon (umol/kg seawater). Control (open boxplot) and crushed shell treatment plots (filled boxplot) in clam gardens (triangles in shades of green, n = 3) and non-walled beaches (circles in shades of blue, n = 3). Grey lines indicate the mean ± SE of ambient seawater collected at study sites.

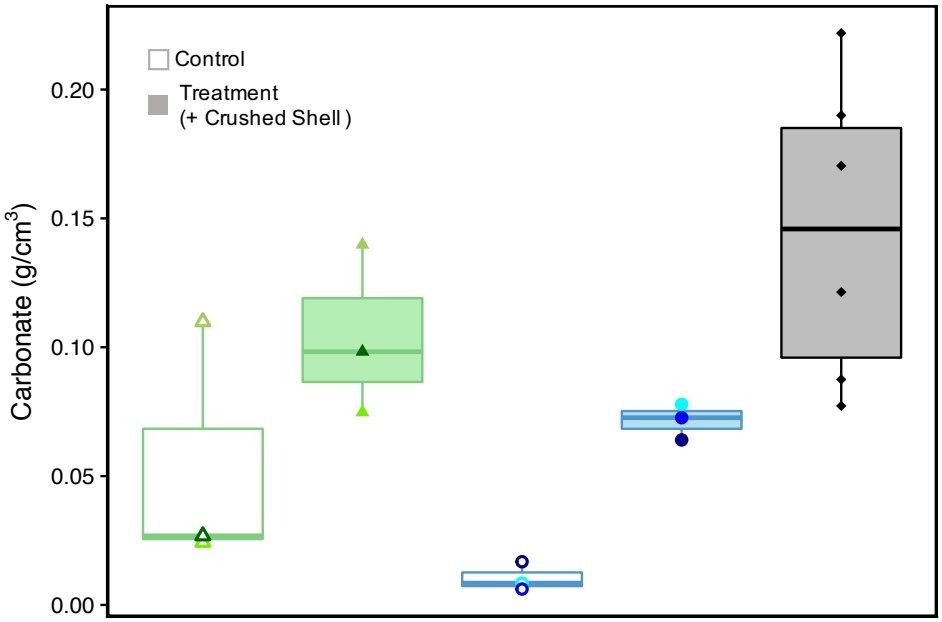

Figure S8 **The effect of beach type and experimental addition of crushed shell on sediment carbonate** (g/cm^3)**.** Control (open symbols) and crushed shell treatment plots (filled symbols) in clam gardens (triangles in shades of green, n = 3) and non-walled beaches (circles in shades of blue, n = 3) compared to samples of the initial crushed shell mixture (black diamonds).

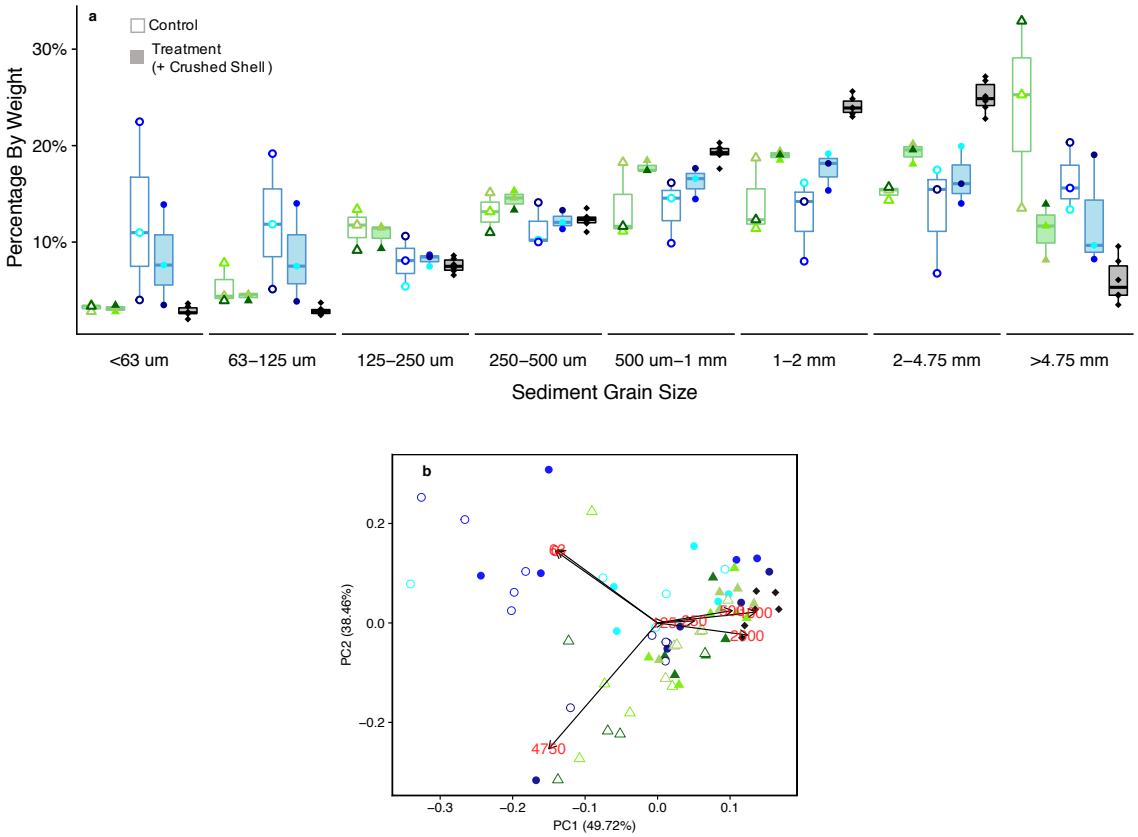

Figure S9 **Effect of beach type and experimental addition of crushed shell on sediment grain size** as (a) percentage by weight and (b) visualized in multidimensional space with principal component 1 and 2 explaining 88% of the variance. Control (open symbols) and crushed shell treatment plots (filled symbols) in clam gardens (triangles in shades of green, n = 3) and non-walled beaches (circles in shades of blue, n = 3) compared to samples of the initial crushed shell mixture (black diamonds).

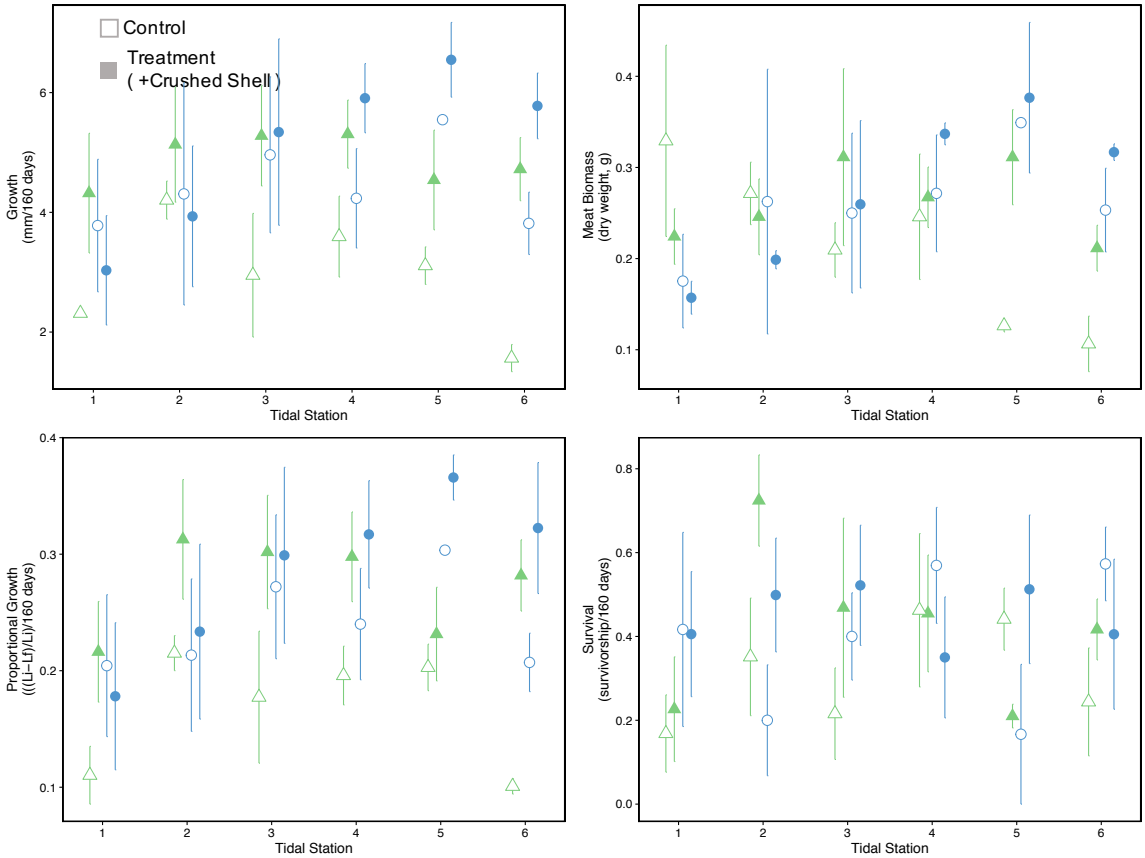

Figure S10 **Effect of beach type, tidal station, and experimental addition of crushed shell on littleneck clam (*L. staminea*)** (a) growth (mm/160days), (b) meat biomass (dry weight, g), (c) proportional growth ($(L_i-L_f)/L_i)/160$ days) and (d) survival (survivorship/160 days). Control (open symbols) and crushed shell treatment (filled symbols) in clam gardens (green triangles, n =3) and non-walled beaches (blue circles, n =3).Standard errors shown.

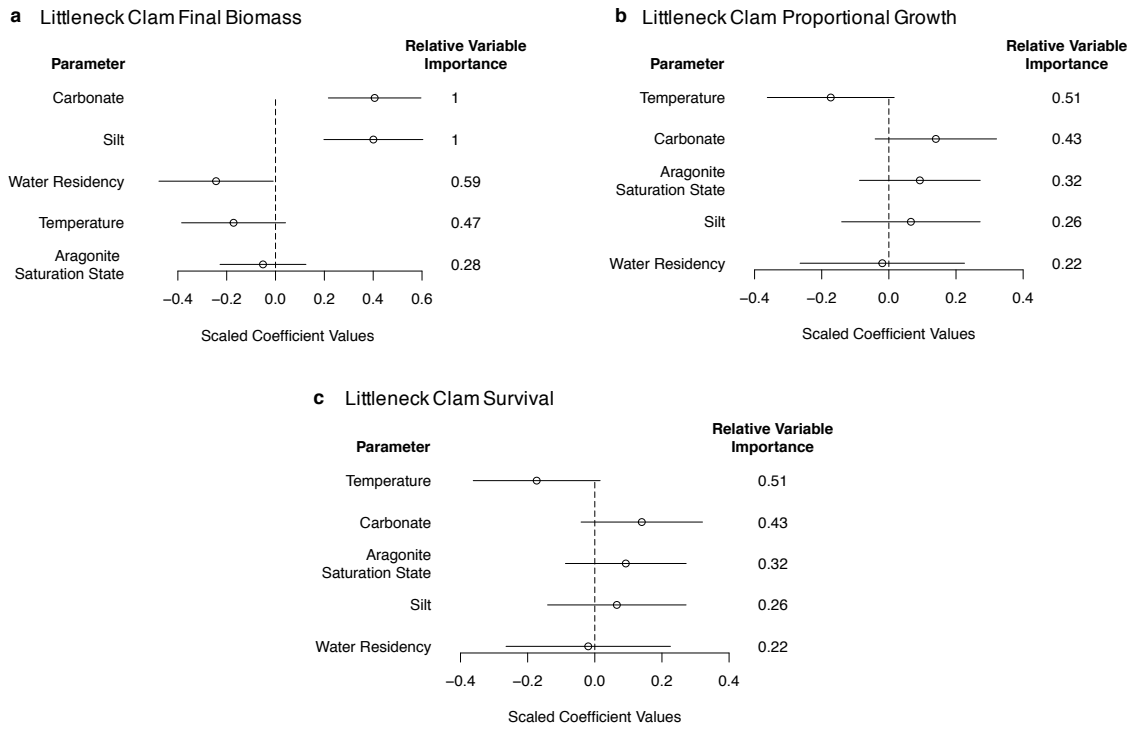

Figure S11 **Model averaged parameter estimates and corresponding relative variable importance from mixed effects models of littleneck clam (*L. staminea*)** (a) meat biomass (dry weight, g), (b) proportional growth ((L_i-L_f)/L_i)/160 days) and (c) survival (survivorship/160 days) across clam garden and non-walled beach control and treatment plots. Unconditional 95% confidence intervals shown. Only models with AICc <4 included in estimates. Predictor variables used are mean temperature (℃), water residency (g dissolved/hr), and sediment characteristics: sediment carbonate content (g/cm^3), silt content (% by weight), and aragonite saturation state of pore water. Clams and sediment characteristics of both control and crushed shell treatment plots included. Coefficients standardized by two SD (Gelman, 2008).

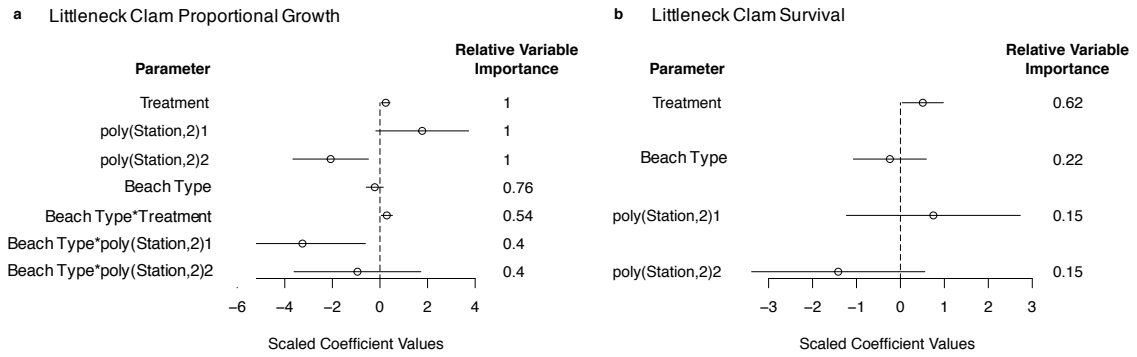

Figure S12 **Model averaged parameter estimates and corresponding relative variable importance from mixed effects models of littleneck clam (*L. staminea*)** (a) proportional growth ((L_i-L_f)/L_i)/160 days) and (b) survival (survivorship/160 days) across clam garden and non-walled beach control and treatment plots. Unconditional 95% confidence intervals shown. Only models with AICc <4 included in estimates. Predictor variables used are beach type, treatment, beach type*treatment, poly(Station,2)1, poly(Station,2),2, beach type* poly(Station,2)1, and beach type* poly(Station,2),2.