

**Ancient clam gardens increased production:
Adaptive strategies from the past can inform
food security today**

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Abstract

Maintaining food production while sustaining productive ecosystems is among the central challenges of our time, yet it has been for millennia. We quantified the productivity of ancient clam gardens, intertidal rock-walled terraces made by humans, by comparing the biomass and density of surveyed bivalves and growth rates of transplanted *Leukoma staminea* (littleneck clams) at replicate clam garden and non-walled beaches in British Columbia, Canada. We found that clam gardens had significantly shallower slopes, significantly greater densities of *L. staminea* and *Saxidomus giganteus*, and higher growth of transplanted *L. staminea*. As predicted, productivity varied as a function of tidal height, beach position and size class. Consequently, we provide strong empirical and experimental evidence that ancient clam gardens likely increased clam productivity by altering beach slope, expanding optimal intertidal habitat thereby enhancing growing conditions for clams. These results reveal how a traditional form of mariculture can inform resilient food security strategies today.

Keywords: clam garden; food security; mariculture; management; first nations; bivalves

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1. Introduction

Sustaining global food production presents one of the greatest environmental and humanitarian challenges of the 21st century. Given current global population and consumption trajectories, the world's food production must double by 2040 (Foley et al. 2011; FAO 2009) and its footprint must shrink substantially to reduce the degradation of land, water, biodiversity and climate. Consequently, society will need to develop clever ways to meet demands on terrestrial and marine resources efficiently, while maintaining ecosystem productivity and resilience. As is often the case, evidence from the past offers potential solutions to contemporary quandaries. Here, we provide empirical evidence describing an ancient form of mariculture that provides practical insights into sustainable harvest techniques which may help to inform local food security strategies of today.

Humans have been altering, exploiting and managing terrestrial and marine ecosystems for millennia (Turner 2005; Lepofsky and Lertzman 2008; Erlandson et al. 2008; Erlandson and Rick 2010; Lepofsky and Caldwell 2013). Throughout history, human hunting and fishing in coastal ecosystems has caused declines in key species (Jackson et al. 2001), reduced prey size (Braje et al. 2007; Erlandson et al. 2008; Erlandson and Rick 2010), triggered trophic cascades (Simenstad et al. 1978; Erlandson et al. 2005; Steneck 2012), and facilitated ecosystem regime shifts (Erlandson and Rick 2010). In other cases, the archaeological record indicates long term sustained yields, with no indication of resource depression (Butler and Campbell 2004). Furthermore, archaeological evidence and oral historical knowledge indicate that First Peoples actively managed nearshore ecosystems through enhancement to maintain and increase productivity (Turner and Deur 2005; Erlandson and Rick 2010; Caldwell et al. 2012; Lepofsky and Caldwell 2013). Marine resource management strategies range from the reduction of predatory sea otters to increase shellfish abundance (Erlandson et al. 2008) and size selective fishing practices to enhance salmon and halibut productivity (Brown and Brown 2009). Similarly, terrestrial examples of resource management include construction of root gardens to enhance camas harvest; transplanted and cultivation of berries to increase yields (Turner and

Turner 2007); and prescribed burns to clear land and magnify plant production (Lepofsky and Lertzman 2008).

Recently, archaeologists on the Northwest coast of North America have turned their attention to ancient mariculture in the form “clam gardens”. Clam gardens, human-made intertidal terraces have been recorded from Alaska, through British Columbia (BC), to Washington State and may have been constructed to maintain and enhance shellfish productivity (Harper et al. 1995; Harper and Morris 2004; Williams 2006; Harper 2007; Caldwell et al. 2012). First Peoples constructed these terraces by building rock walls in the low intertidal of soft-sediment clam beaches, thus creating a relatively flat intertidal zone above the wall. On Quadra Island, BC, clam gardens walls exist along coastlines and at the mouths of embayments, varying greatly in shape, length, width, and intertidal height in relation to chart datum (Canadian Lower Low Water Large Tide, LLWLT)(Fig 1A-D). Although the age of these ancient features is currently unresolved, the immense coastal shell middens associated with clam garden walls indicates the significance of clams as a staple food source for northwest coast First Nations for at least 5000 years (Moss 1993; Haggan et al. 2006; Cannon and Burchell 2009). The combination of the widespread occurrence of clam gardens on the northwest coast, their associated shell middens, and traditional knowledge passed down in song, story and practice (Turner and Deur 2005; Szimanski 2005) suggest that these intertidal features were constructed to increase clam yields. Knowing to what extent clam gardens boost clam productivity offers insights into making contemporary investments for local food security.

In this study, we investigate the productivity of ancient clam aquaculture in clam garden beaches on Quadra Island, BC through surveys and *in situ* transplant experiments. We ask a series of questions focusing on how bivalve composition and beach morphology differs between clam gardens and non-walled beaches, and what environmental factors contribute to differences in the productivity of these two beach contexts. Specifically, we ask, do clam gardens have higher clam densities, biomass and growth rates compared to non-walled beaches? And if so, what physical characteristics best explain these differences? Known mechanisms that drive bivalve productivity are temperature, food availability, salinity (Chew and Ma 1987), and position in the intertidal (i.e. tidal height) (Quayle and Bourne 1972). We hypothesized that clam gardens enhance the productivity of clam aquaculture by reducing the beach slope and thereby increasing the amount of optimal clam habitat driven by tidal height.

2. Methods

2.1. Study Area

We conducted our research on northern Quadra Island British Columbia (BC), Canada, where an exceptionally high density of replicate clam gardens have been documented (Harper 2007) in Kanish (n= 45 clam gardens) and Waiatt Bays (n= 49 clam gardens) (Fig 2). Quadra Island has an abundance of archaeological sites found throughout the landscape (Harper and Morris 2004), with shell middens representing both permanent settlements and short term camps (Lepofsky 2012). According to the archaeological record, northern Quadra Island has been occupied for over seven thousand years, falling within the traditional territories of the Northern Coast Salish and the Southern Kwakwaka'wakw (now Laich-kwil-tach) First Nations (Taylor and Duff 1956; Angelbeck 2009). Today, some of the descendants of these ancient settlements live in nearby Indian Reserves. Presently, Kanish and Waiatt Bays are only sparsely settled and bordered by second growth and active wood lots. They are popular recreation areas and anchorages encompassing two provincial parks, an active and a scallop farm, and an inactive fish farm operation. Clam digging, once a mainstay of the dense human population in the bays, is now only conducted sporadically.

The soft sediment, low wave energy, intertidal shores of Kanish and Waiatt Bays foster bivalve communities of *Leukoma staminea* (native littleneck) and *Saxidomus gigantean* (butter clams), both economically and culturally important clam species. Other common bivalves include the native *Macoma spp.* (macoma clams), *clinocardium nuttallii* (heart cockles), *Tresus nuttallii* and *Tresus capax* (horse clams), and the non-native *Venerupis philippinarum* (japanese littlenecks), and *Mya arenaria* (eastern softshell clams). Kanish Bay is a much larger deep bay, composed of multiple inlets. Although both bays open towards large, rapidly flowing channels, water flow within Kanish and Waiatt is markedly different. Most non-walled clam beaches along the edges of Quadra's northern inlets are characterized by steep slopes and mixed mud-sand-gravel sediments. Shallowly sloped clam garden terraces are abundant along the shoreline and

are comprised of unconsolidated mixes of sand, gravel and broken shell (“hash”) sediments and are often directly associated with terrestrial archaeological sites.

2.2. *Field Surveys*

We characterized beach slope at 11 clam gardens and 10 non-walled beaches to capture the difference in clam habitat available by constructing clam garden rock walls on non-walled clam bearing beaches. At each site, we established and surveyed a transect with 15 randomly stratified stations using a total station or laser level in meters above Canada chart datum, lowest low water large tide (LLWLT). Transects began at the highest intertidal height at which clams were found in test pits. In clam gardens, the bottom of each transect was anchored by the landward edge of the human-made rock wall. At non-walled clam beaches, each transect bottom was anchored at 0.75m above chart datum, which was established by the constraints in access for both past harvesting and current sampling imposed by summer tide elevations.

To test for differences in bivalve composition, density, size, and biomass between the 11 clam gardens and 10 non-walled clam beaches, we dug sample units (30x30x20cm = 0.018 m³) at the 15 tidal stations along the vertical transect (Fig 3A). Live clams were identified to species, and wet weight, maximum longitudinal valve length, and width were measured.

2.3. *Clam Transplant Experiment*

To test if clam gardens increase the growth rates of native *L. staminea*, we conducted a transplant experiment across six clam gardens and five non-walled clam beaches during the growing season from May to October 2011. Clams 11-34mm in length were collected from Waiatt and Kanish Bay, measured to the nearest 0.1 mm, weighed to the nearest 1.0 gram, and labelled with two uniquely numbered vinyl tags. Fifteen individuals, representing the range of sizes collected, were placed inside a 34cm x 24cm Vexar mesh bag. Five bags of *L. staminea* were evenly spaced at five tidal stations along a single vertical transect, perpendicular to shore, from the top of clam habitat to ~0m intertidal height at non-walled beaches and at the edge of rock wall in clam gardens (Fig 3A). Each bag was buried approximately 10cm below the surface and secured with a flagged and labelled rebar stake. Transplanted clams were left *in situ* for 160

days. Upon retrieving the transplanted clams, max lengths, widths, and weights were recorded. We noted all losses, mortalities, and evidence of predation.

2.4. *Predictions*

By constructing a rock-walled terrace in the intertidal, we predicted that clam gardens expand optimal clam habitat by altering the slope of the beach and increasing habitat at targeted intertidal heights (Fig 3a). We expect to find heightened clam density and biomass linked to increased habitat within optimal tidal height, and similarly enhanced clam growth rates in our transplant experiment. Differences in these parameters between clam gardens and non-walled beaches should be most obvious at the first and last tidal stations (Fig 3B) and extreme high and low of intertidal heights (Fig 3C) in clam gardens compared to non-walled beaches. Peak clam productivity (as measured by density, biomass, or growth) is expected at the same intertidal height in both clam gardens and non-walled beaches, but the magnitude of productivity is predicted to be greater (due to increased water retention) and smaller variance (due to the reduction in beach slope) in clam gardens relative to non-walled beaches (Fig 3C).

2.5. *Data Analysis*

All GLM and GLMM modelling was conducted in R (R Core Team 2012).

2.5.1. *Physical Site Characteristics*

To test for an effect of *beach type* (i.e., clam garden (n=11) vs. non-walled beach (n=10)) and an effect of *bay* (Kanish vs. Waiatt Bay) on beach slope, we used a general linear model (GLM). We used the same strategy to examine differences in heights of clam garden walls and mean heights of garden terraces between bays. Slope, Wall Top Height, and Terrace Height models were fit with a Restricted Maximum Likelihood (REML), a Gaussian error distribution, and identity link function using the `lme` function in the `nlme` package (Pinheiro et al. 2012).

2.5.2. Field surveys

To test for differences in clam density and biomass between clam gardens (n=11) and non-walled clam beaches (n=10), we constructed general linear mixed effects models (GLMMs) where *beach type* was treated as a fixed effect and *site* was treated as a random effect. These models were constructed for the three most dominant species (*L. staminea*, *S. giganteus*, and *Macoma* spp.) and total clams. To test for differences in *L. staminea* density among different size classes, we ran the same models described above on five different size classes of clam (1-13, 14-26, 27-39, 40-52, 53-65mm). Differences in clam density and biomass between clam gardens (n=11) and non-walled clam beaches (n=10) as a function of tidal station in both Kanish and Waiatt Bay were assessed using the same GLMMs as described above, with the additional fixed effects of *bay* and the interaction of *beach type*tidal station*. *Beach type*, *bay*, and *type*tidal station* were specifically chosen as treatments to be tested, *beach type* to detect a clam garden effect, *bay* to detect an effect of oceanographic context, and *type*tidal station* to detect our predicted across-beach effect of tidal station in clam gardens and non-walled beaches (Fig 3B). Clam biomass models were fit with a REML, a Gaussian error distribution, and identity link function using the `lme` function in the `nlme` package (Pinheiro et al. 2012). Clam density models were fit with Laplace Approximation, a Poisson error distribution, and log link function using the `lmer` function and `lme4` package (Bates et al 2012).

2.5.3. Optimal Clam Habitat Models

To assess if and how clam garden engineering altered intertidal height and optimal growing conditions for clams, we quantified the relationship between intertidal height and a) density and biomass of surveyed *L. staminea* and b) survivorship and growth of transplanted *L. staminea* in clam gardens and non-walled beaches in both bays, by fitting Gaussian models (Eq.1) to each metric of clam productivity (*y*) as a function of *intertidal height*. We then compared these parameters across clam gardens and non-walled beaches in both bays based on our predictions (Fig 3A,B,C).

$$y = \alpha * e^{-0.5\left(\frac{x-\mu}{\sigma}\right)^2}$$

Equation 1. Gaussian model of clam productivity where a describes the magnitude of clam productivity (biomass, density, or growth rate), μ is the intertidal height at which productivity is greatest, and σ describes the standard deviation in clam productivity (σ).

2.5.4. *Experimental Transplants*

We tested for differences in survival and growth rates of *L. staminea* transplanted in clam gardens (n=6) and non-walled clam beaches (n=5) in Waiatt Bay, using generalized GLMMs where *beach type* was a fixed effect and *site* was a random effect. To test for differences in *L. staminea* growth and survival across tidal stations within clam gardens and non-walled beaches, we constructed the same GLMMs as above, with *beach type*, *bay* and *beach type*tidal station* as fixed effects. Growth rates models were fit with REML, Gaussian error distribution, and identity link function using the `lme` function in the `nlme` package (Pinheiro et al. 2012). Survivorship models were fit with Laplace Approximation, a Binomial error distribution, and logit link function using the `lmer` function and `lme4` package (Bates, Maechler, and Bolker 2012). Survivorship and growth was compared among different clam size classes using the same models described above on three size classes of transplanted *L. staminea* (11-16, 17-22, 23-28mm).

3. Results

3.1. Physical Characteristics of Beach Types

On Quadra Island, BC, clam garden terrace heights varied between bays, but their slopes were consistently shallower than unaltered beaches (Fig 4, S2A, Table S1, $F_{(1,19)}=6.914$, $p=0.017$). On average, mean intertidal heights of clam garden terraces in Waiatt Bay were significantly lower than those in Kanish Bay (Fig 4, S1, S2A, Table S1, $F_{(1,9)}=15.848$, $p=0.003$). In Waiatt Bay, clam garden terraces were located on average at 0.97m (+/- 0.31SE) above chart datum, while rock wall features averaged 0.68 m (+/- 0.36m SE) in intertidal height (Fig 4,S1). In contrast, Kanish clam garden terraces were located on average at 1.57m (+/-0.21m SE) above chart datum and rock walls wall features averaged 1.3 (+/- .19m SE) in intertidal height (Table S2). Non-walled beach slopes and mean intertidal heights did not differ between bays (Fig S2A,B).

We observed greater variation in the intertidal height of clam gardens in Waiatt Bay. There, clam garden terraces were located between 0.53-1.45m above chart datum, with four of the six clam gardens (WB33, WB36, WB39, WB42) having mean terrace heights between 0.78-1.16m, while two (WB10 and WB31) having mean terrace heights of 0.53m and 1.45m respectively (Fig 4, S1).

3.2. Field Surveys

L. staminea and *S. giganteus* dominated the bivalve community in clam gardens and non-walled beaches, both in biomass and density, (Fig 5B,C). We detected significantly higher densities of *L. staminea*, in clam gardens (93 ± 26 SE count/ 0.270m^3) than in non-walled beaches (37 ± 6 SE count/ 0.270m^3) ($p=0.03$) (Fig 5A, Table 1,S2). Differences were more pronounced at smaller size classes (Fig 5A, Table 1,S2). Densities of *S. giganteus* were also significantly greater in clam gardens (32 ± 12 SE count/ 0.270m^3) compared to non-walled beaches (8 ± 4 SE count/ 0.270m^3) (Fig 5A, Table 1,S2), and these clams tended to be larger in

clam gardens, yielding on average higher biomass ($3.3 \pm 1.0\text{SE kg}/0.270\text{m}^3$) compared to non-walled beaches ($0.94 \pm 0.3\text{SE kg}/0.270\text{m}^3$) (Fig 5c, Table 1,S2). The density and biomass of other documented bivalve species did not differ as a function of beach type (Table 1). Even though the overall average bivalve biomass was nearly double, and density appears to be increased within clam gardens ($6.02 \pm 1.55\text{SE kg}/0.270\text{m}^3$, $281 \pm 63\text{SE count}/0.270\text{m}^3$) compared to non-walled beaches ($3.43 \pm 0.88\text{SE kg}/0.270\text{m}^3$, $191 \pm 39\text{SE count}/0.270\text{m}^3$) (Fig 5A,B), overall bivalve biomass did not differ with statistical significance between beach type alone (Fig 5B,C, Table 1,S2).

By examining clam density and biomass as a function of tidal station and beach type in both bays, we found that *L. staminea* and *S. giganteus* densities and biomass were significantly greater in clam gardens than non-walled beaches and as predicted (Fig 3B), this relationship varied as a function of tidal station (Fig 6,8, Table 2). Specifically, clam densities and biomass tended to be higher at the first 6-7 tidal stations. The beneficial effect of tidal station position was highly significant and observed for total clam densities, and densities of *L. staminea* (all sizes, 12-26mm, 27-39mm), *S. giganteus*, and *V. philippinarum* (Fig 6, Table 2). As a side note, the density and biomass of the invasive *V. philippinarum* varied significantly as a function of tidal station and was significantly higher in Kanish Bay (Fig 6, Table 2).

3.3. *The Effect of Beach Engineering on Optimal Clam Habitat*

As predicted (Fig 3c), the magnitude of *L. staminea* productivity (a) in terms of biomass, density and growth, was higher in clam gardens than non-walled beaches, and the standard deviation (σ) was lower (Fig 7A-D, Table 3). Contrary to expectations, the intertidal height at which little neck clams reach their maximum density, biomass and growth (μ) was consistently higher in clam gardens than non-walled beaches in Kanish Bay (Fig 7, Table 3), meaning that clam gardens in Kanish, peak productivity was shifted slightly higher on the beach. In Waiatt, maximum *L. staminea* productivity (μ) was not found to differ significantly between site types for density and growth, and biomass did not conform to a gaussian relationship within non-walled beaches.

3.4. *Experimental Transplants*

Transplanted *L. staminea* grew significantly faster in clam gardens than non-walled beaches and as predicted (Fig 3c), and this effect varied as a function of tidal station (Fig 8,S3, Table 4,S3). Specifically, clams grew proportionally faster at tidal station extremes (the first and last tidal station) in clam gardens compared to non-walled beaches. Furthermore, in line with our expectations, the overall magnitude of growth rates as a function of tidal height was higher and less variable in clam gardens than non-walled beaches (Fig7, Table 3). Size appears to be a major predictor of survivorship - small size classes of *L. staminea* (11-22mm) were significantly more likely to survive in clam gardens than non-walled beaches, although clam garden habitat did not appear to effect survivorship when all size classes were pooled. This size dependent effect, as predicted, tended to vary as a function of tidal station (Fig 8, Table 5).

4. Discussion

This investigation provides strong empirical and experimental evidence that ancient clam gardens likely increased clam productivity. By altering the slope of soft-sediment beaches (Fig 4), these human-made, intertidal, rock-walled terraces expanded the optimal intertidal habitat and enhanced growing conditions for clams. Specifically, we detected significantly greater densities of *S. giganteus* and *L. staminea* in clam gardens compared to non-walled beaches, particularly among smaller size classes of clams (Fig 5). As predicted, the magnitude of this relationship varied from the top to the bottom of the beach, whereby clam productivity (density, biomass, growth and survivorship) responses were enhanced in clam gardens than non-walled beaches nearer the top and bottom of the beach, the areas where clam gardens extend optimal clam habitat (Fig 6,8). The pattern of increased clam productivity by clam gardens appears to be driven by the modification of intertidal height (Fig7) and is confirmed by our experimental results indicating higher *L. staminea* growth rates within clam gardens (Fig 7E,8). Interestingly, elevated clam densities, biomass and growth rates at equivalent intertidal heights in both clam gardens and non-walled beaches suggest that additional mechanisms appear to be magnifying productivity. Candidate hypotheses of elevation mechanisms include factors known to influence shellfish growth such as water flow (Fraser and Smith 1928), primary productivity (Smith 1928), temperature and salinity (Phibbs 1971) to name a few.

4.1. *Mechanisms Enhancing Productivity in Clam Gardens*

Within clam gardens and non-walled beaches, we have confirmed that clam productivity is significantly linked to beach slope, intertidal height, and location across a beach from top to bottom. However, because we observed elevated clam productivity in clam gardens even within optimal clam habitat, we know that there are additional mechanisms driving elevated productivity within clam gardens. In addition to altering beach slope and extending intertidal habitat at optimal tidal heights for clam survival and growth, we hypothesize that clam gardens

terraces may have enhanced clam productivity in numerous ways. Over the diurnal tidal exchange, we observed increased water retention over clam gardens and increased pore water relative to natural sloping non-walled beaches. Water retention may increase the opportunity and success of larval clam recruitment in the clam garden. In fact, a Hul'qumi'num First Nation reported that clam gardens were a way to "trap the seeds and keep them here" (Parks Canada 2011). Larval settlement success is critical for future productivity (Quayle and Bourne 1972), and as planktonic clam larvae are at the mercy of currents, shallow and low velocity water are optimal conditions for mature larval settlement (Roegner 2000). The shallow slope and increased water retention of clam gardens may function to contribute to spring and summer warming thereby increasing phytoplankton growth rates (Eppley 1972) and fuelling secondary production and spawning in clams (Phibbs 1971; Quayle and Bourne 1972). Increased water temperatures in temperate intertidal systems are known to enhance bivalve growth rates (Shaw 1986; Menge et al. 2008).

Northwest Coast First Nations employed a variety of other mariculture practices in addition to building rock walls, designed specifically to increase clam productivity (Woods and Woods 2005; Haggan et al. 2006). Altering the intertidal substrate is one of several ancient mariculture practices practiced by coast First Nations to increase productivity of clams. Substrate type is a defining characteristic of clam gardens – they are observed to be higher in gravel and shell hash (Haggan et al. 2006; Harper et al. 1995). *L. staminea* are known to be found on beaches with coarse sand or fine gravel mixed with mud, stones or shells (Fraser and Smith 1928; Fitch 1953). Hul'qumi'num knowledge holders report returning crushed and whole clam shells to clam gardens as management practice (Parks Canada 2011). The substrate type is also important in settlement and recruitment in oyster aquaculture (Bayne 1969; Turner et al. 1994), suggesting that parental shell is an important settling cue (Tamburri et al. 1992; Butman et al. 1988). Other reports of substrate modifications include the Heiltsuk First Nation, "We put gravel in the garden to increase the number of clams" (Wilson 2012). This may aid in aerating the sediments and reduce fine silts and clays that are known to smother newly settled *L. staminea* larvae (Fraser and Smith 1928). The act of aerating beach sediments by rolling rocks, or "turning over beaches" is also commonly reported (Woods and Woods 2005; Turner 2005; Parks Canada 2011) and aims to reduce anoxic conditions that can reduce productivity.

Of course other types of management were used in concert with building clam garden terraces, and these were aimed at manipulating the intertidal ecology to benefit bivalves, such as reducing density dependence, excluding competitors and predators. Turner (2005) reports that clam gardens were “thinned,” reducing densities of large adult clams via harvest, and giving smaller clams the space and resources to grow, thus increasing overall yields (Peterson and Beal 1989). We also hypothesize that managed gardens would benefit from increased predator removal for predators such as *Pycnopodia helianthoides*, *Pisaster spp.*, *Metacarcinus magister* and small terrestrial mammals, decreasing both direct predator mortality and negative non-lethal predator effects on clam productivity (Nakaoka 2000; Smee and Weissburg 2006).

Clam gardens, like clam harvesting beaches more broadly, would have been embedded in traditional systems of governance and tenure. Building and maintaining clam gardens were intentional acts, clearly showing cultural investment. Such systems delineated access rights to the land and sea, likely including clam gardens (Trosper 2002; Turner 2005; Trosper 2009). “Only certain families owned clam gardens and the whole family would look after it.” (Wilson 2012). Territorial access rights, via family-based proprietorship, established a governance system over common pool fisheries resources that granted resilience to societies on the Northwest coast for millennia (Trosper 2009). Similarly, empirical evidence from contemporary fisheries management highlights the importance of designating access rights to sustainability (Ostrom 2009; Pinkerton and Silver 2011).

4.2. Enhancing Food Security Confers Resilience to Social Ecological Systems

Increased appreciation of the coupling between ecosystems and human well-being has triggered a paradigm shift in the applied ecological sciences towards a focus on understanding the dynamics of coupled social-ecological systems (SES), and linked systems of people and nature (Berkes et al., 2000; Haggan et al. 2006). In marine systems, current management approaches have demonstrably failed to halt or reverse fisheries declines (Pauly et al. 2002), in part due to the inadequate recognition of the strong links between social and ecological processes (Gelcich et al. 2010; Horan et al. 2011). Ancient clam gardens and their governance by

coastal communities is an example of an adaptive strategy that enhanced regional food security and thus conferred resilience to this coupled human-coastal ocean ecosystems.

Our observations on the variation in this ancient form of mariculture also highlight key aspects of resilient social ecological systems learning and functional redundancy. It appears that the height of clam garden wall and clam garden terraces were engineered to target specific intertidal heights. Although most clam garden sites we surveyed extended the optimal tidal range for *L. staminea*, we found two clam gardens that fell outside of this range. Alternative hypotheses can be invoked to explain the presence of these outliers. They could be engineering errors and thereby represent evidence of learning, or be built during different time periods of differing sea levels. Alternatively these features may have been built to target other species or may have had purposes other than shellfish harvest.

Clam gardens were not the only resource management technique used to increase local food security among coastal indigenous people of the past. Other examples of ancient engineering strategies used for traditional marine resource management include stone fish traps of the Pacific Northwest (Haggan et al. 2006); stone fish ponds of Polynesia (Costa-Pierce 1987); complex wooden fish weir configurations of the Pacific Northwest and Brittany (Haggan et al. 2006; Langouët and Daire 2009); and cleared clam beaches of Pacific Northwest Nations (Caldwell et al. 2012). In addition to direct environmental manipulations, evidence of size selective harvest, beach harvest rotations, partial beach harvest and multiple years of leaving beaches unharvested suggest complex resource management (Turner 2005; Cannon and Burchell 2009; Parks Canada 2011). These examples advocate that harvesting of many marine resources by coastal First Nations was far from a passive activity. It appears to include intensive management and ingenuity, rejecting the notion that these people were simple hunter-gatherers (Turner and Deur 2005; Lepofsky and Lertzman 2008; Cannon and Burchell 2009; Caldwell et al. 2012).

Food security is not only a contemporary issue. It has motivated ingenuity and development of civilizations throughout time. Along the coast of Pacific Northwest, ancient people developed a suite of practices (i.e. landscape engineering, substrate modification, restricted access) in addition to stewardship practices in effort to increase cultural resilience and secure stable food production. Investigations of how ancient clam gardens work will provide

information on possible solutions to local food security and economic resiliency to coastal communities. Based on our clam surveys on Quadra Island, densities of *L. staminea* and *S. giganteus* are elevated on average by 151% and 300%, respectively, within clam gardens (Table S2). Clam garden biomass of *L. staminea* and *S. giganteus* is then elevated on average by 68% and 253%, respectively (Table S2). Additionally, clam gardens within optimal habitat experimentally enhanced growth rates of *L. staminea* on average by 89%, meaning that clams reach harvestable size at a faster rate (Table S2). The archaeological record is clear, abundant shellfish have supported large populations of people on the Northwest Coast through history (Cannon et al. 2008; Cannon and Burchell 2009); we clearly have lessons to learn from the past. This new evidence helps to lay the foundation for the incorporation of traditional management techniques into future strategies of sustainable solutions, contributing to local food security efforts globally.

4.3. *Governance of Ocean Spaces*

The occurrence and distribution of clam gardens indicates a long history of strategic clam cultivation and management by indigenous people on the northwest coast, and their revitalisation and reinstatement of use has the potential to enrich First Nations community's social and ecological resources. In Canada, intertidal space is by default under the regulation of the Department of Fisheries and Oceans, including beaches that border treaty land, unless specifically negotiated. Communities do not have neither management over nor unrestricted access to their traditional clam beaches and gardens. Ancient clam garden walls and fish weir stakes are not recognized as signs of ownership and access rights by Canada's contemporary government, as they were traditionally in the past (Turner 2005; Haggan et al. 2006). As a result, communities struggle to assert their local values and management within their traditional territories and upon their traditional resources, to maintain social-ecological systems (Pinkerton and Silver 2011). Clam garden walls clearly highlight areas of traditionally concentrated shellfish harvesting effort, and their documentation lends support to claims of rights and title within traditional territories.

4.4. *Informing Contemporary and Future Marine Management*

Finding a solution set to meet ecologically sound food production for the growing demands is a global effort, even though successful remedies may be locally adapted. Local food production is essential to community food security and autonomy (Menezes 2001). Autonomous economies have been found to, out of necessity, value the recognition of ecological limits, and tend towards protecting biological, cultural and social diversity (Starr and Adams 2003). Many issues with some of today's clam aquaculture practices include decreasing the biodiversity of nearshore systems, destabilizing sediments, and facilitating introductions of invasive species (Palmer et al. 2000; Whiteley and Bendell-Young 2007). Ecosystem impacts of modern harvest techniques that do not prioritize conservation of ecosystem biodiversity as well as productivity undermine nearshore ecosystem resilience (Gunderson and Pritchard 2002). These are very real concerns for coastal First Nations who remember relying upon locally gathered clams as a staple food source. Coastal First Nations communities who historically managed their local resources for millennia are the most concerned about and impacted by current declining nearshore resilience, but no longer have the rights to manage their local marine resources.

This study confirms that ancient mariculture and engineering practice of First Nations' clam gardens can successfully provide a local, stable and reliable food source year-round by increasing potential harvests of *L. staminea* and *S. giganteus*, while maintaining overall shellfish productivity. We provide evidence through *in situ* surveys and experiments that past traditional aquaculture techniques were extremely successful in increasing yields. The implications of these findings and the traditional knowledge of the first Nations elders are important to the success of food security plans for the Pacific Northwest coastal communities and are easily translated to coastal peoples around the globe.

5. Tables

Table 1. The effect of clam gardens (Beach Type) on the responses of biomass and density (per survey transect, 0.027m³) of *L. staminea* (littleneck clam), *S. giganteus* (butter clam), *V. philippinarum* (Japanese littleneck clam), *Macoma* spp (macoma clams) and total clams. * designates significant p-values ($p \leq 0.05$).

	Fixed Effect		Random Effect	
Response variable	Beach Type		Site (Beach Type)	
Density	<i>z</i>	<i>p</i>	Variance	StdDev
<i>L. staminea</i> (All)	-2.24	0.03*	0.60	0.78
<i>S. giganteus</i>	-2.25	.03*	2.38	1.54
<i>V. philippinarum</i>	-0.69	0.49	4.66	2.16
<i>Macoma</i> spp.	0.05	0.96	1.51	1.23
TOTAL clam	-1.01	0.32	0.53	0.73
<i>L. staminea</i> (1-13mm)	-2.49	0.01*	0.61	0.78
<i>L. staminea</i> (14-26mm)	-2.76	<0.01*	0.77	0.87
<i>L. staminea</i> (27-39mm)	-2.11	0.04*	0.73	0.86
<i>L. staminea</i> (40-52mm)	-1.06	0.29	1.12	1.06
<i>L. staminea</i> (53-65mm)	0.18	0.86	3.70	1.92
Biomass	<i>t</i>	<i>p</i>	Residual	
<i>L. staminea</i>	-1.16	0.26	0.10	
<i>S. giganteus</i>	-1.77	0.09	0.24	
<i>V. philippinarum</i>	-1.23	0.24	0.03	
<i>Macoma</i> spp.	1.41	0.17	0.04	
TOTAL clam	-0.20	0.85	0.33	

TABLE 2. The effects of clam gardens (Beach Type), oceanographic context (Waiatt Bay vs. Kanish Bay), and Tidal Station on the biomass and density of surveyed *L. staminea*, *S. giganteus*, *V. philippinarum*, *Macoma spp.*, and total clams (per survey transect, 0.027m³). * designates significant p-values (p≤0.05).

Response variable	Fixed Effect						Random Effect			
	Beach Type		Bay		Tidal Station		Beach Type x Tidal Station		Site	
	z	p	z	p	z	p	z	p	Variance	StdDev
Density										
<i>L. staminea</i> (All)	-5.78	<0.01*	-0.21	0.83	-3.47	<0.01*	10.34	<0.01*	0.60	0.77
<i>S. giganteus</i>	-4.72	<0.01*	-0.52	0.96	-4.29	<0.01*	7.14	<0.01*	2.38	1.54
<i>V. philippinarum</i>	-0.32	0.75	-0.40	0.69	-3.47	<0.01*	-1.16	0.25	4.61	2.15
<i>Macoma</i>	-2.69	0.01*	-0.87	0.39	0.12	0.91	15.97	<0.01*	1.46	1.21
TOTAL clam	-4.50	<0.01*	-0.55	0.58	-4.03	<0.01*	18.21	<0.01*	0.53	0.73
<i>L. staminea</i> (1-13mm)	-3.02	<0.01*	0.59	0.56	0.90	0.37	1.93	0.05*	0.62	0.79
<i>L. staminea</i> (14-26mm)	-5.63	<0.01*	0.32	0.75	-3.62	<0.01*	6.17	<0.01*	0.77	0.88
<i>L. staminea</i> (27-39mm)	-4.96	<0.01*	1.48	0.14	-3.18	<0.01*	6.13	<0.01*	0.67	0.82
<i>L. staminea</i> (40-52mm)	-2.74	<0.01*	-1.72	0.09	-0.06	0.95	3.57	<0.01*	0.92	0.96
<i>L. staminea</i> (53-65mm)	-1.19	0.23	0.94	0.35	0.77	0.44	2.81	<0.01*	3.59	1.90
Biomass	t	p	t	p	t	p	t	p	Residual	
<i>L. staminea</i>	-2.77	0.01*	-0.71	0.49	-0.59	0.55	3.92	<0.01*	0.10	
<i>S. giganteus</i>	-2.59	0.02*	1.05	0.31	-0.89	0.37	2.21	0.03*	0.24	
<i>V. philippinarum</i>	-2.16	0.04*	-1.45	0.17	-3.03	<0.01*	1.83	0.07	0.03	
<i>Macoma spp.</i>	-0.92	0.37	-1.56	0.14	-0.62	0.53	4.14	0.00	0.04	
TOTAL clam	-0.83	0.42	-0.56	0.58	0.60	0.55	1.36	0.17	0.33	

Table 3. Parameters for the modeled responses of biomass (kg/0.018m³ +/- SE), density (count/0.018m³ +/- SE), and growth (mean +/-SE) of surveyed and transplanted *L. staminea* (*L.s.*) as a function of intertidal height. Each response was predicted by modeling a gaussian curve to the data, $y = a \cdot \exp(-0.5 \cdot ((x-\mu)/\sigma)^2)$, where y =response, x =intertidal height, a =height, μ =mean, and σ =standard deviation.

Predictive Gaussian Curves, 3 parameter: $y = a \cdot \exp(-0.5 \cdot ((x-\mu)/\sigma)^2)$							
	Bay	Type	Response	a (height)	μ (mean)	σ (variance)	R²
Ecological Surveys	Kanish	NW	<i>L.s.</i> Density	5.000	1.126	0.286	0.327
	Kanish	CG	<i>L.s.</i> Density	10.913	1.613	0.222	0.380
	Waiatt	NW	<i>L.s.</i> Density	5.219	1.065	0.487	0.291
	Waiatt	CG	<i>L.s.</i> Density	13.640	1.038	0.167	0.323
	Kanish	NW	<i>L.s.</i> Biomass	0.226	1.125	0.207	0.315
	Kanish	CG	<i>L.s.</i> Biomass	0.231	1.564	0.155	0.258
	Waiatt	NW	<i>L.s.</i> Biomass	0.216	0.015	0.882	0.398
	Waiatt	CG	<i>L.s.</i> Biomass	0.274	1.009	0.144	0.322
Experiment	Waiatt	NW	<i>L.s.</i> Growth	0.065	1.209	0.566	0.362
	Waiatt	CG	<i>L.s.</i> Growth	0.088	1.027	0.331	0.283

Table 4. The effects of clam gardens (*beach type*) and tidal station on the growth and survivorship of transplanted *L. staminea*. * designates significant p-values ($p \leq 0.05$).

Response variable	Fixed Effect								
	Beach Type			Tidal Station			Beach Type x Tidal Station		
Growth Rates	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Growth rate (All sizes)	1,9	8.79	0.02*	1,666	22.05	<0.01*	1,666	8.62	<0.01*
Growth rate (11-16mm)	1,9	1.57	0.242	1,87	3.90	0.05*	1,87	0.38	0.54
Growth rate (17-22mm)	1,9	<0.01	0.980	1,197	0.13	0.720	1,197	0.08	0.78
Growth rate (23-28mm)	1,9	0.23	0.646	1,125	1.30	0.256	1,125	0.01	0.92
Survival	<i>SE</i>	<i>z</i>	<i>p</i>	<i>SE</i>	<i>z</i>	<i>p</i>	<i>SE</i>	<i>z</i>	<i>p</i>
Survivorship (All sizes)	1.53	-0.98	0.33	0.31	-1.28	0.20	0.47	0.77	0.44
Survivorship (11-16mm)	0.95	-1.92	0.05*	0.14	-2.66	<0.01*	0.27	1.19	0.23
Survivorship (17-22mm)	0.81	-2.50	0.01*	0.14	-4.15	<0.01*	0.20	2.73	<0.01*
Survivorship (23-28mm)	1.18	-0.01	0.99	-0.48	0.20	0.02*	0.32	0.07	0.95

6. Figures



Figure 1. A) Ancient clam gardens on Quadra Island, BC, Canada, are intertidal beach terraces built by humans by constructing B) a rock wall at low tide typically between 0.7-1.3m above chart datum. C, D) Quadra clam gardens range in size and shape but generally create shallow sloping intertidal terraces encompassing tidal heights of 0.9-1.5m above chart datum.

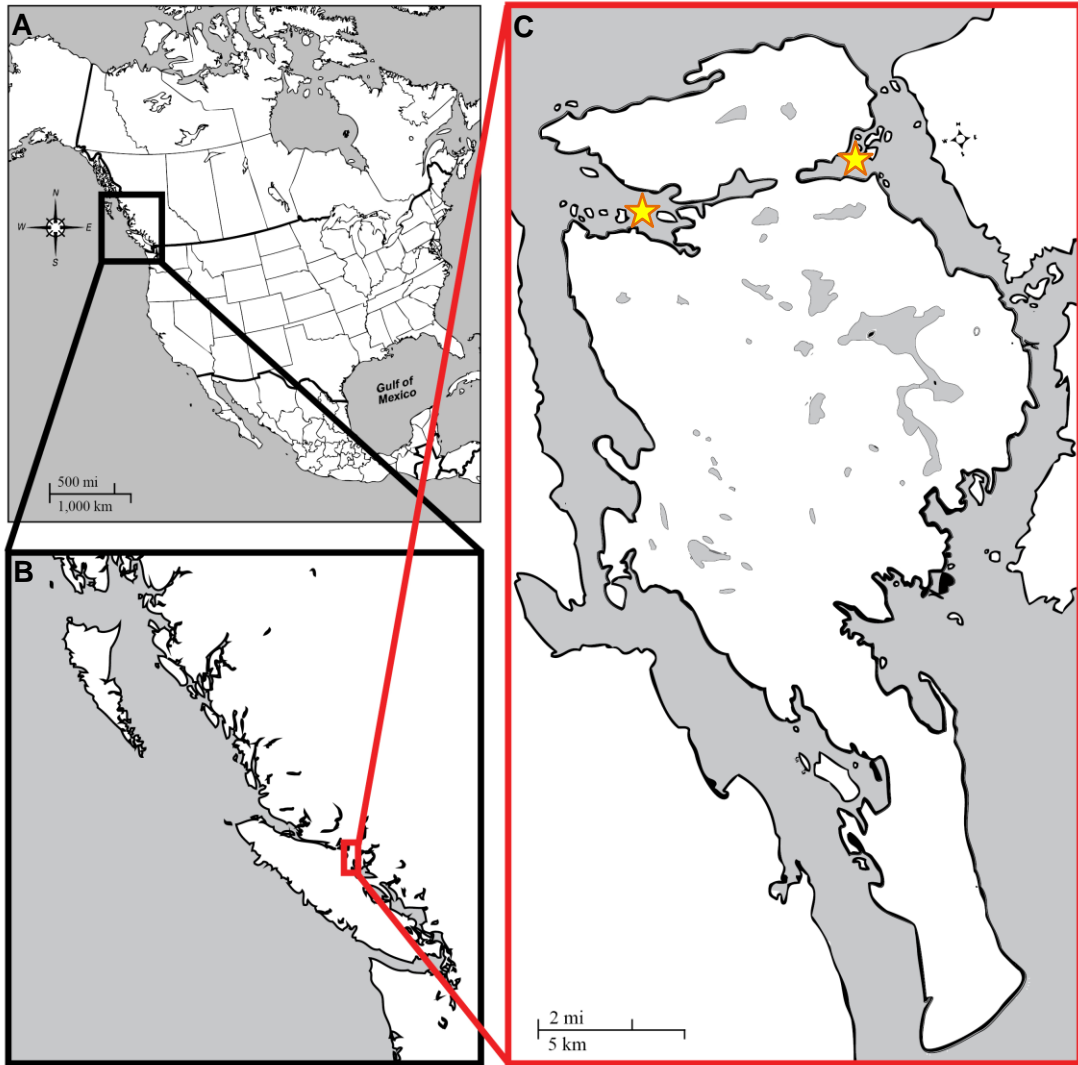


Figure 2: This research was conducted on A) the west coast of British Columbia, Canada, in the Inside Passage between B) Vancouver Island and the mainland on the northern end of C) Quadra Island, in Kanish Bay (West, starred) and Waiatt Bay (East, starred).

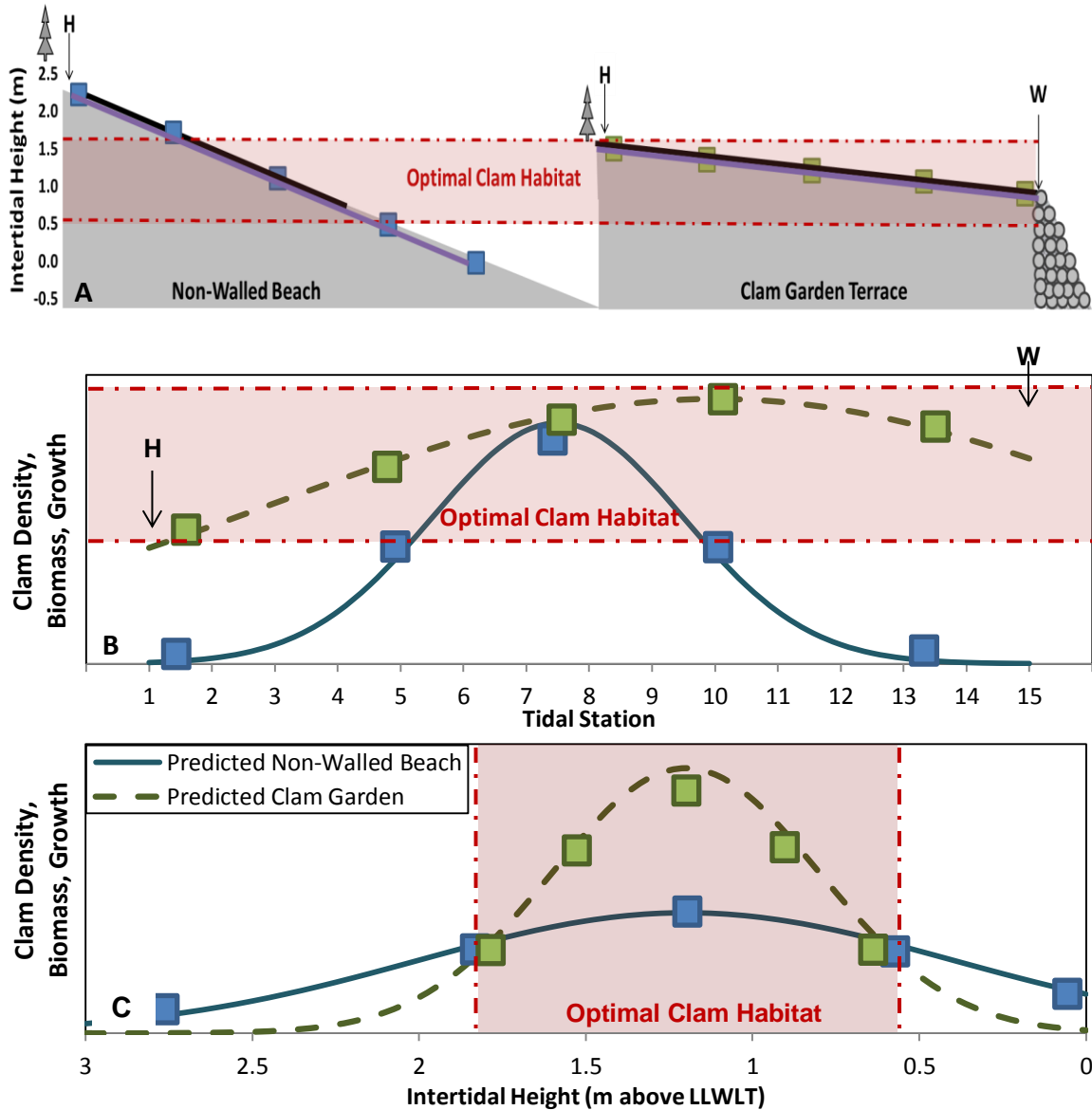


Figure 3. A) Survey Design: We surveyed clams at 15 randomly stratified tidal stations across a vertical transect (purple line) from the top of clam habitat (H) to ~0.75m in 10 Non-Walled Beaches (Left) and to the edge of the rock wall (W) in 11 Clam Gardens. **Experimental Design:** Five experimental clam transplant bags (blue and green colored squares), were buried at 5 evenly stratified tidal stations across a vertical transect (black line) from the top of clam habitat (H) to ~0m in 5 Non-Walled Beaches (Left) and to the edge of the rock wall (W) in 6 Clam Gardens (Right). **B) Hypothesis 1:** predicted clam productivity as a function of tidal station. Tidal station 1 = top of clam habitat, tidal station 15 = top of clam garden wall in clam gardens or ~0m tidal height in non-walled beaches. **C) Hypothesis 2:** Predicted clam productivity as a function of intertidal height.

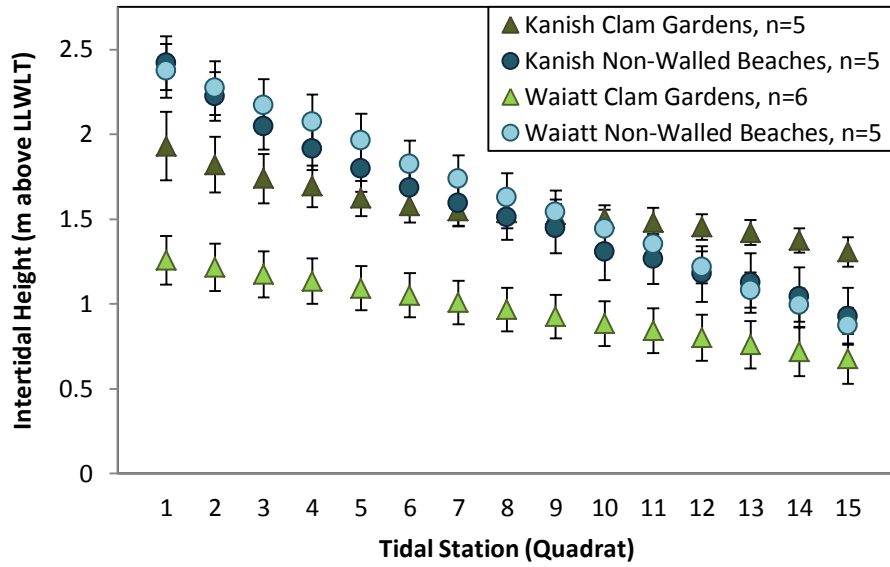


Figure 4. Intertidal height (mean +/-SE) and visualized slope ($\Delta y/\Delta x$) from top of clam habitat (tidal station = 1) to top of rock wall feature in clam gardens and ~0.75m above LLWLT in non-walled beaches (tidal station = 15).

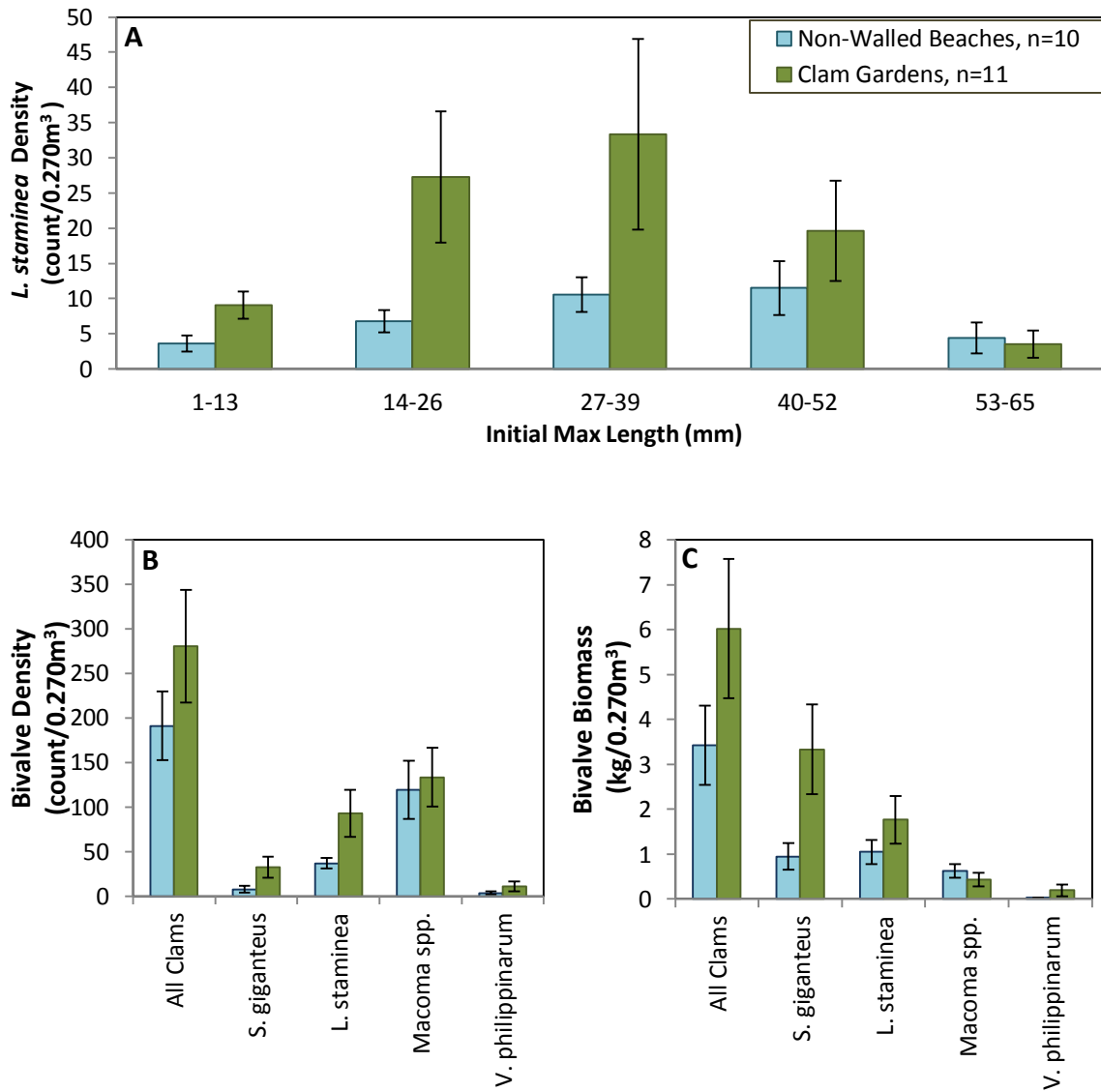


Figure 5. A) *L. staminea* density (count/0.270m³ +/-SE) of 5 size classes; B) Density (count/0.270m³ +/-SE) and C) Biomass (kg/0.270 m³ +/-SE) of four most abundant bivalve species in Clam Gardens and Non-Walled Beaches.

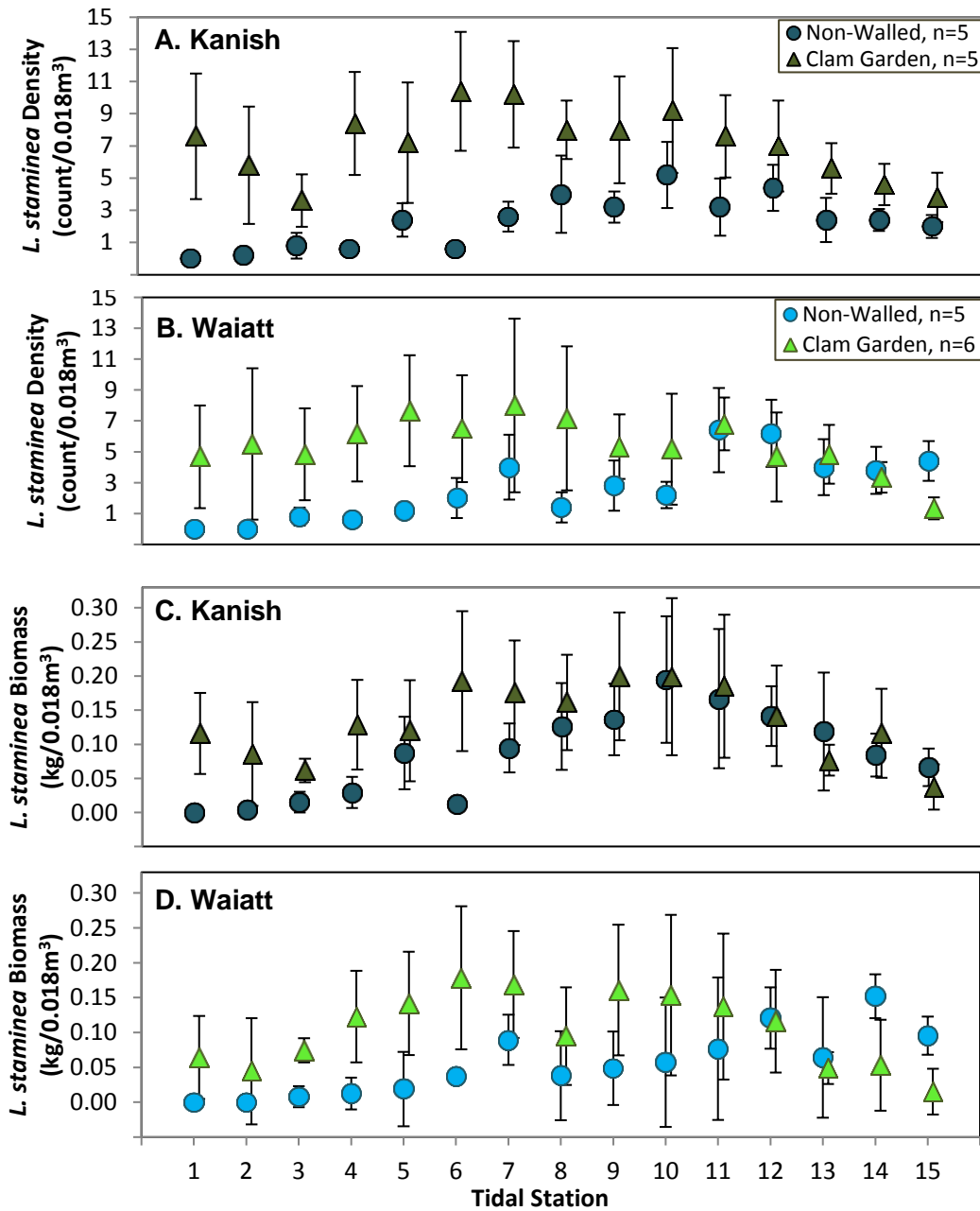


Figure 6. Surveyed A&B) density (count/0.018m³ +/- SE) and C&D) biomass (kg/0.018m³ +/- SE) and of *L. staminea* as a function of bay (Kanish or Waiatt), site type (Clam Garden or Non-Walled Beach), and tidal station (1=top of clam habitat, 15= top of clam garden wall or ~0.75m intertidal height in non-walled beaches).

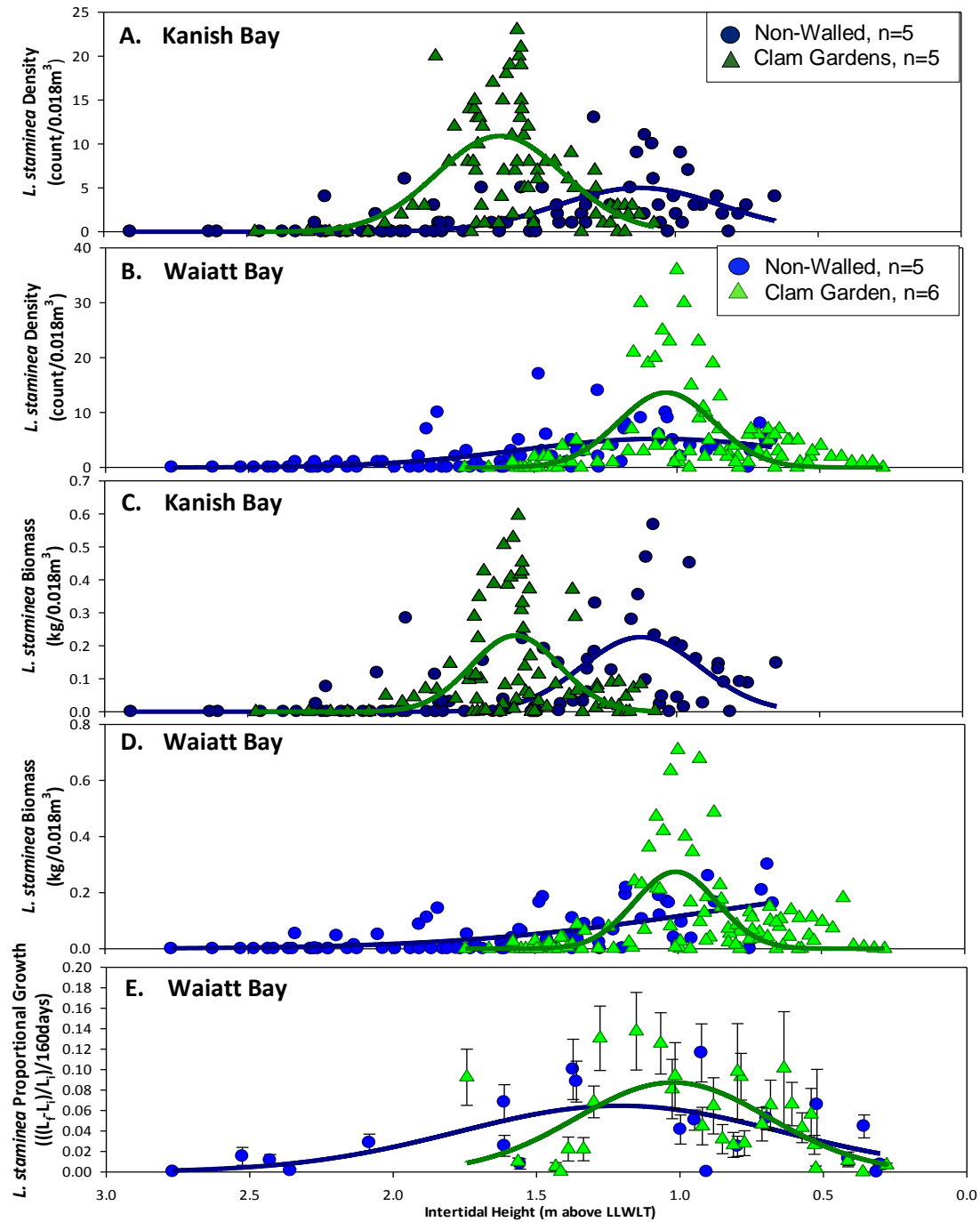


Figure 7. Actual and predicted A&B) density (count/0.018m³ +/- SE) C&D) biomass (kg/0.018m³ +/- SE) and E) growth (mean +/-SE) of surveyed (A-D) and transplanted (E) *L. staminea* as a function of intertidal height (m above LLWLT) in clam gardens (green triangles) and non-walled beaches (blue circles) in Kanish and Waiatt bays, British Columbia, Canada.

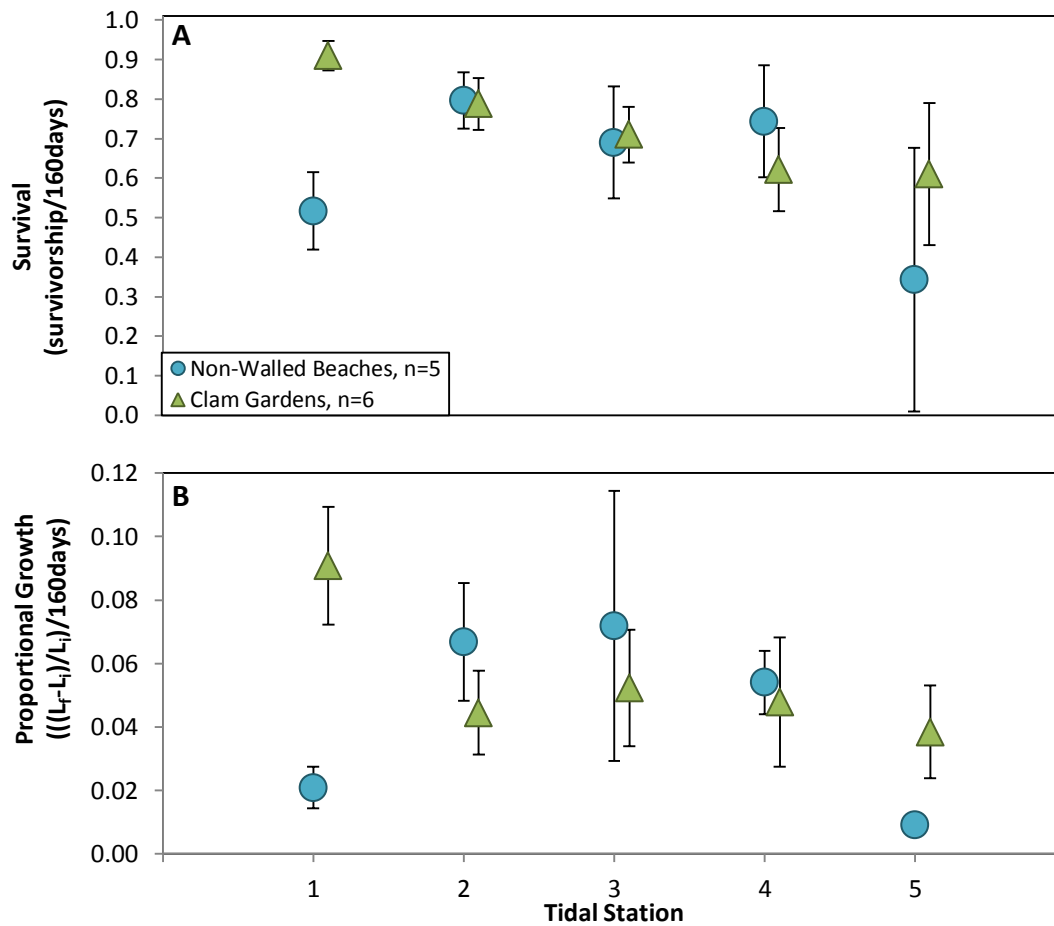


Figure 8. A) Survival and B) growth rates (+/-SE) of transplanted *L. staminea* as a function of tidal station. Tidal station 1 was anchored at top of clam habitat and tidal station 5 was located at the top of the rock wall feature in clam gardens, and at ~0m below LLW in non-walled beaches.

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Appendices

Appendix A.

Supplementary Figures

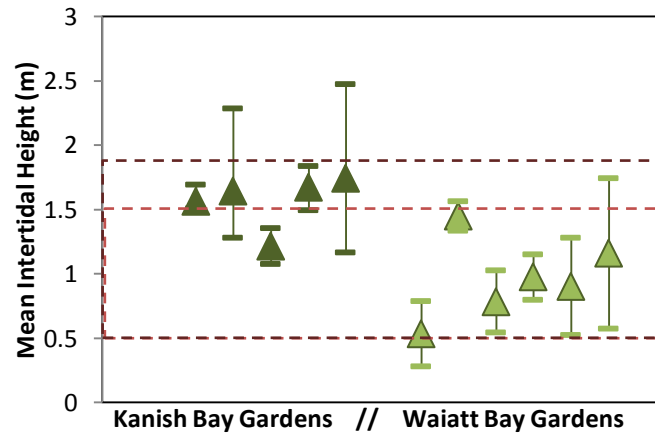


Figure S1. Mean Intertidal Height (+/- min and max terrace height) of eleven clam garden Waiatt Bay and Kanish Bay, British Columbia, Canada. $n=6$. Dashed lines represent optimal tidal height for *L. staminea* in Kanish Bay (darker line, 0.7-1.9m) and Waiatt Bay (lighter line, 0.6-1.6m) as determined by our survey data of *L. staminea* density experimental growth rates of non-walled beaches (Fig. S4a&b).

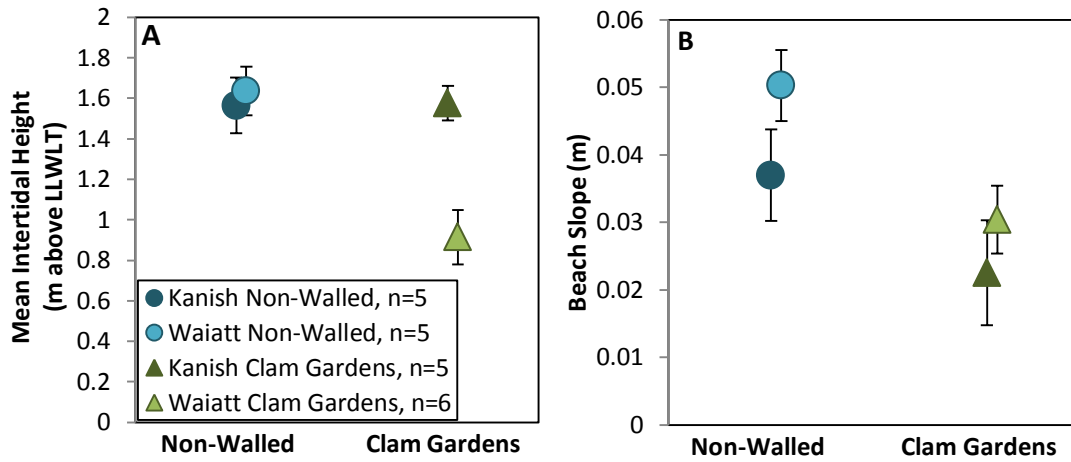


Figure S2. A) Mean intertidal height (m above LLWLT +/- SE) and B) slope ($\Delta y/\Delta x$ +/-SE) across survey transects spanning from the top of clam habitat to top of clam garden wall within clam gardens, and to ~0.75m intertidal height within non-walled beaches in Waiatt and Kanish Bay, British Columbia, Canada.

Table S1. Means and standard errors of all measured site characteristics by site type and bay.

Site Characteristics	Site Type	Kanish Bay			Waiatt Bay		
		Mean	SE	n	Mean	SE	n
Mean Intertidal Height (m above LLWL)	Non-Walled	1.565	0.138	5	1.636	0.121	5
	Clam Garden	1.569	0.093	5	0.968	0.129	6
Beach Slope ($\Delta y/\Delta x$)	Non-Walled	0.037	0.007	5	0.050	0.005	5
	Clam Garden	0.023	0.008	5	0.030	0.005	6
Top of Habitat (m above LLWL)	Non-Walled	2.420	0.159	5	1.929	0.202	5
	Clam Garden	2.373	0.159	5	1.259	0.143	6
Rockwall Height (m above LLWL)	Clam Garden	1.306	0.087	5	0.676	0.148	6

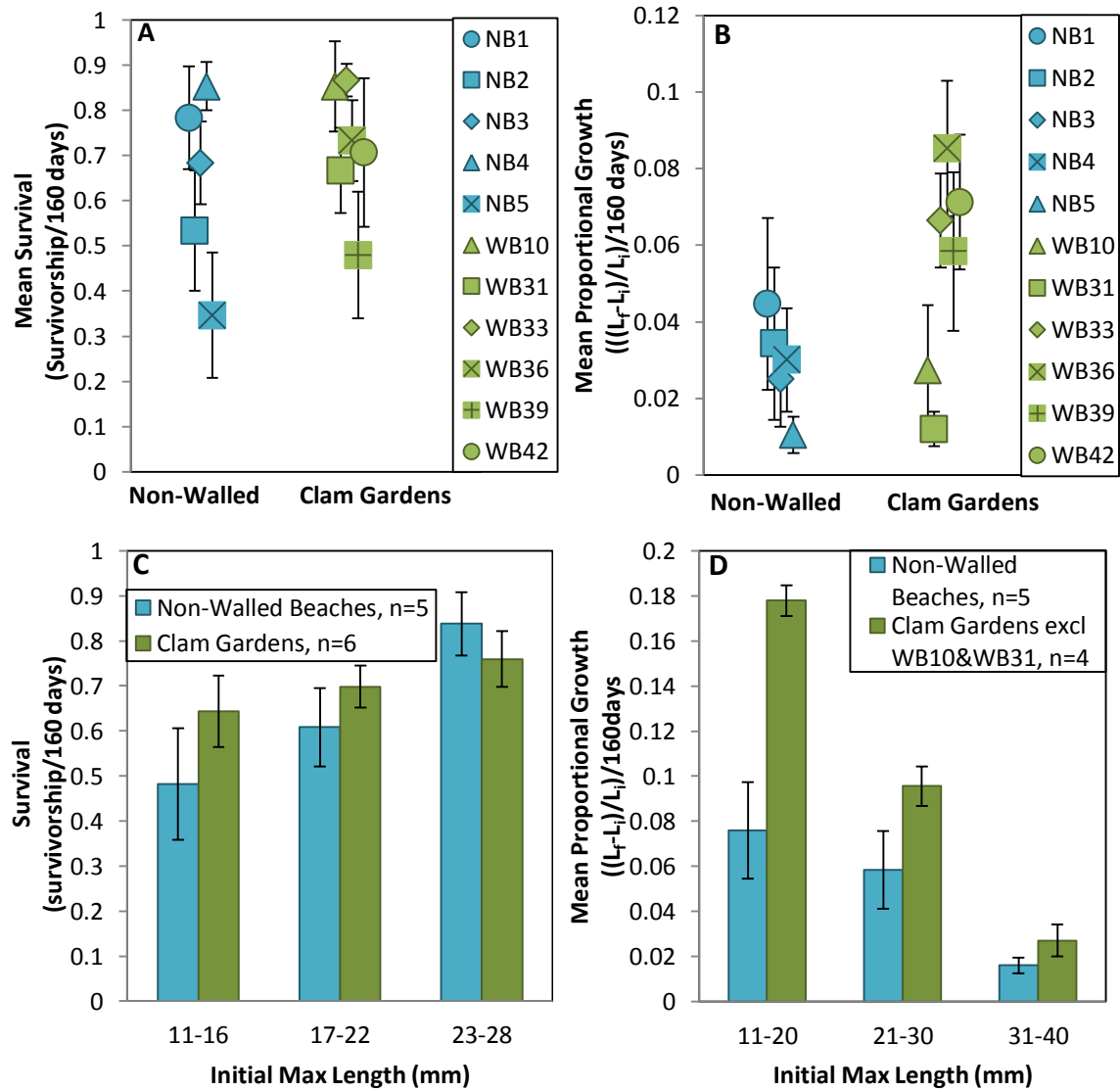


Figure S3. A,C) Survival (+/-SE) and B,D) growth (+/-SE) of transplanted *L. staminea* (n=15 individuals/outplant bag) over 160 days in clam gardens (n=6) and non-walled beaches (n=5). Note: D) includes gardens WB33,36,39,42 and excludes WB10 and WB31.

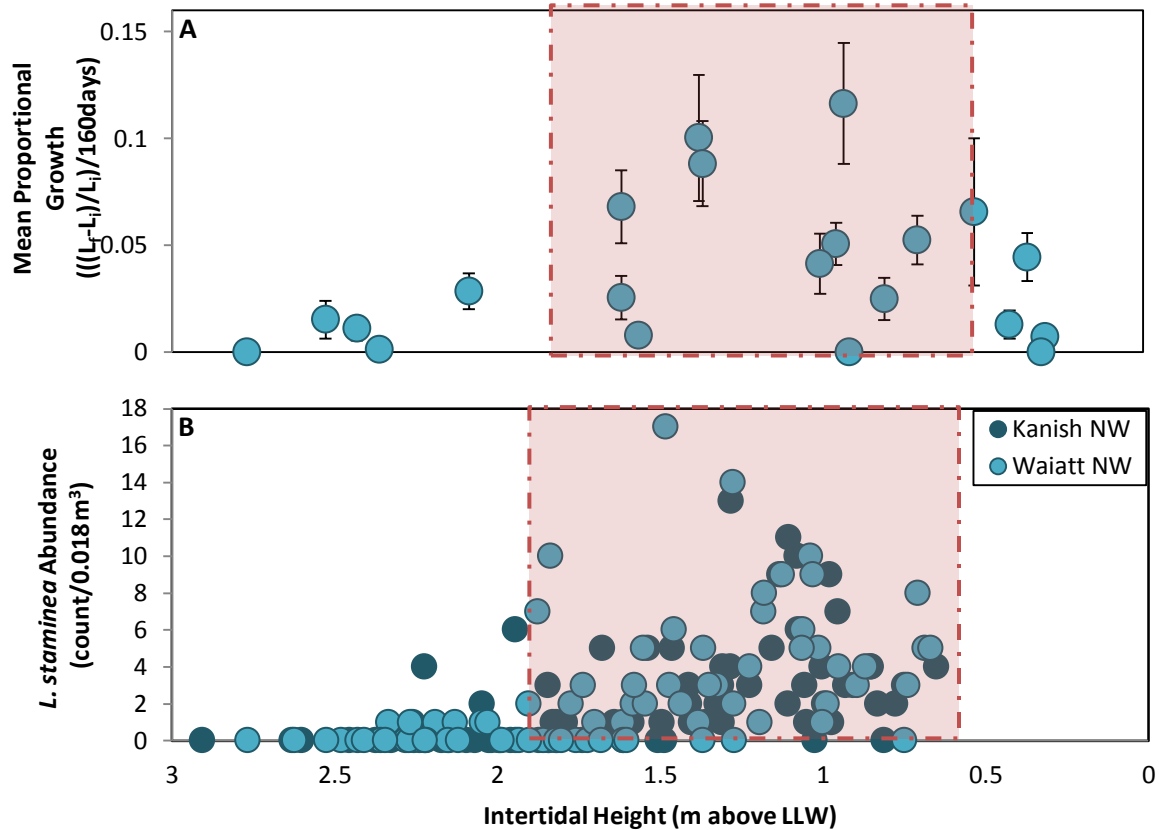


Figure S4. A) Proportional Growth (+/-SE) of transplanted *L. staminea* over 160 days by Intertidal Height of each experimental outplant bag in Non-Walled beaches. Bag n= 15 individuals. Shaded area designates intertidal zone of highest growth. B) *L. staminea* Abundance (count/0.018m³ +/-SE) by intertidal height (m above LLW) of each survey core of non-walled beaches. Site n=15. Shaded area designates intertidal zone of highest abundance.

Table S2: Means and standard errors for all measured response variables of bivalve productivity by site type.

Response variable	Site Type					
	Non-Walled Beaches			Clam Gardens		
	Mean	SE	n	Mean	SE	n
Density (count/0.270m³)						
<i>L. staminea</i> (All)	37	6	10	93	26	11
<i>S. giganteus</i>	8	4	10	32	12	11
<i>V. philippinarum</i>	4	2	10	11	5	11
<i>Macoma</i> spp.	119	32	10	133	33	11
ALL clams	191	39	10	281	63	11
<i>L. staminea</i> (1-13mm)	4	1	10	9	2	11
<i>L. staminea</i> (14-26mm)	7	2	10	27	9	11
<i>L. staminea</i> (27-39mm)	11	2	10	33	14	11
<i>L. staminea</i> (40-52mm)	12	4	10	20	7	11
<i>L. staminea</i> (53-65mm)	4	2	10	4	2	11
Biomass (kg/0.270m³)						
<i>L. staminea</i>	1.049	0.267	10	1.763	0.536	11
<i>S. giganteus</i>	0.944	0.299	10	3.332	1.005	11
<i>V. philippinarum</i>	0.028	0.010	10	0.192	0.128	11
<i>Macoma</i> spp.	0.624	0.152	10	0.428	0.149	11
ALL clams	3.428	0.884	10	6.019	1.552	11
Growth Rates $((L_f - L_i)/160\text{days})$						
Growth rate (All sizes)	0.037	0.011	5	0.053	0.011	6
Growth rate (11-16mm)	0.076	0.021	5	0.130	0.031	6
Growth rate (17-22mm)	0.058	0.017	5	0.072	0.016	6
Growth rate (23-28mm)	0.016	0.003	5	0.020	0.006	6
Growth rate (All sizes) (excluding WB10,WB31)	0.037	0.011	5	0.070	0.006	4
Growth rate (11-16mm) (excluding WB10,WB31)	0.076	0.021	5	0.178	0.007	4
Growth rate (17-22mm) (excluding WB10,WB31)	0.058	0.017	5	0.096	0.009	4
Growth rate (23-28mm) (excluding WB10,WB31)	0.016	0.003	5	0.027	0.007	4
Survival (survivorship/160days)						
Survivorship (All sizes)	0.640	0.091	5	0.718	0.058	6
Survivorship (11-16mm)	0.482	0.124	5	0.644	0.079	6
Survivorship (17-22mm)	0.608	0.087	5	0.698	0.047	6
Survivorship (23-28mm)	0.838	0.071	5	0.760	0.062	6

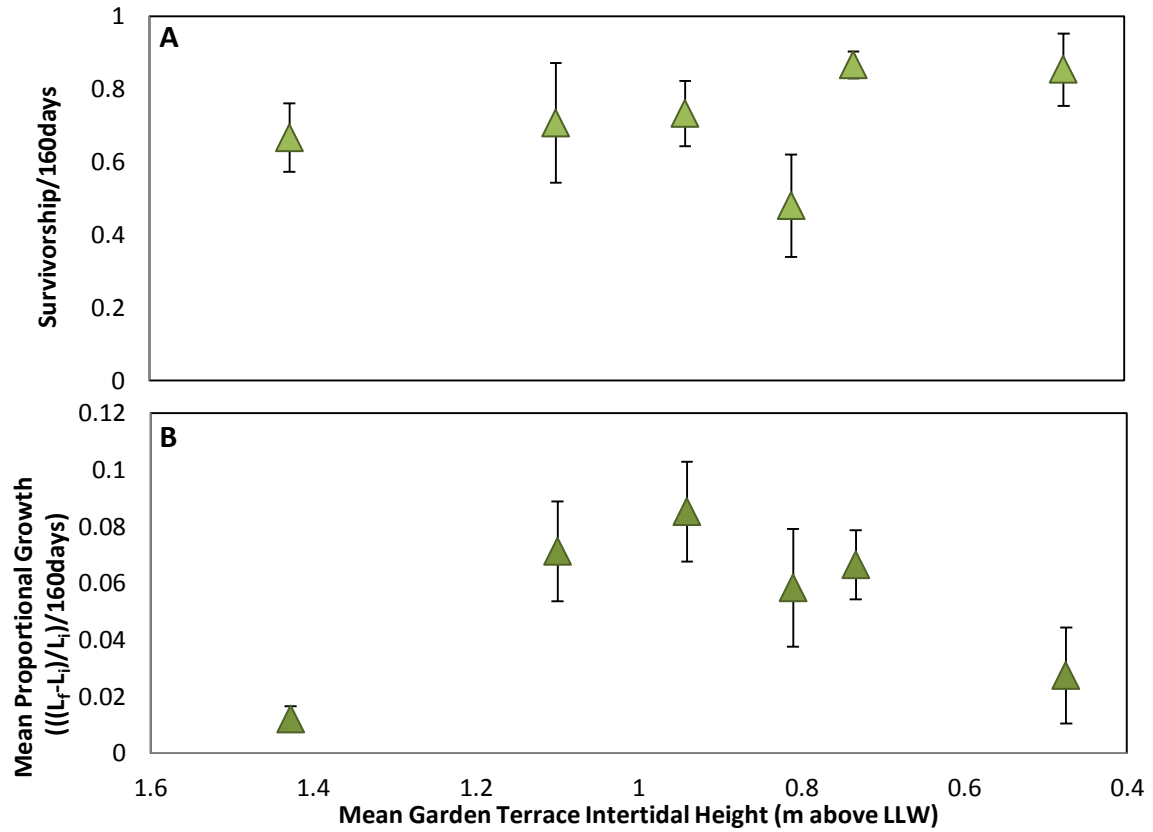


Figure S5. A) Survival and B) growth rates (+/-SE) of transplanted *L. staminea* by mean Intertidal Height of each experimental clam garden terrace.

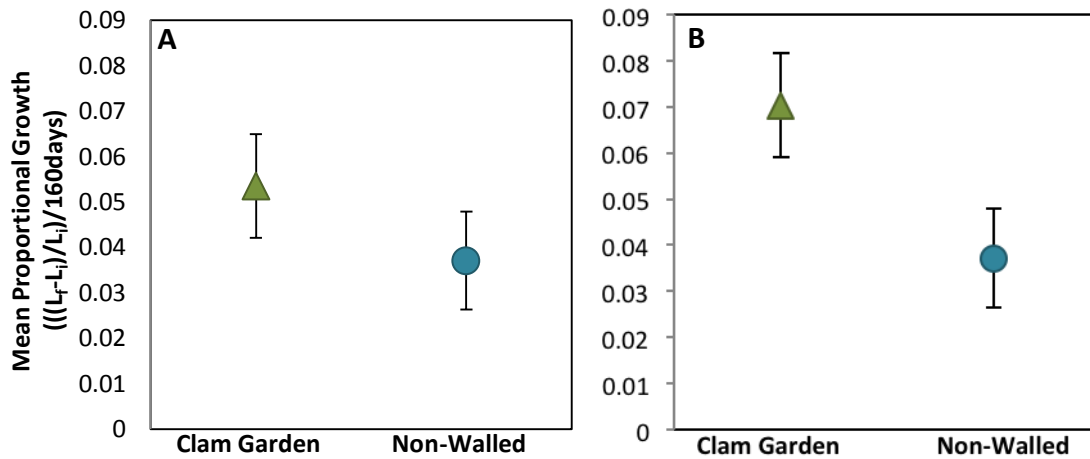


Figure S6. A) Proportional growth (mean of site means \pm SE) of transplanted *L. staminea* over 160 days in Clam Gardens ($n=6$ sites, $n_{\text{site}}=5$) and Non-Walled Beaches ($n=5$, $n_{\text{site}}=5$) ($F_{(4,9)}=1.576$, $p=0.241$). and B) growth excluding outlier gardens WB10 and WB31 ($F_{(4,7)}=11.947$, $p=0.011^*$).

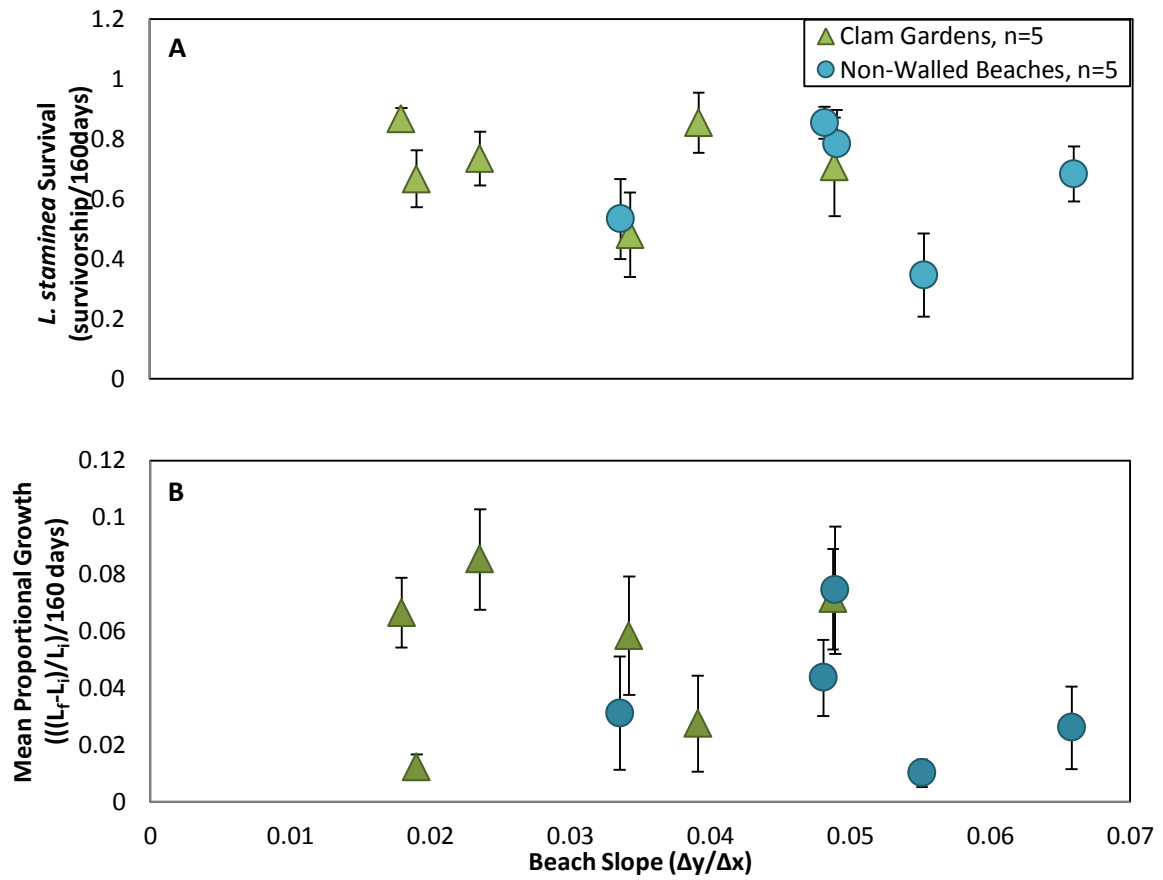


Figure S7. A) Survival and B) growth rates (+/-SE) of transplanted *L. staminea* in Waiatt bay as a function of beach slope (rise/run) at each experimental site.

Table S3. The effects of clam gardens (Beach Type) on experimentally transplanted *L. staminea* survivorship and growth. Analysis of GLMMs with Beach Type as a fixed effect (i.e. clam garden vs. non-walled beach) and Site as a random effect. * designates significant p-values ($p \leq 0.05$).

Response variable	Fixed Effect		
	Beach Type		
Survival	<i>SE</i>	<i>z</i>	<i>p</i>
Survivorship (All sizes)	0.610	-0.563	0.573
Survivorship (11-16mm)	0.582	-1.506	0.132
Survivorship (17-22mm)	0.497	-0.569	0.569
Survivorship (23-28mm)	0.574	0.376	0.707
Growth Rates	<i>df</i>	<i>F</i>	<i>p</i>
Growth rate (All sizes)	1,9	1.576	0.241
Growth rate (11-16mm)	1,9	1.598	0.238
Growth rate (17-22mm)	1,9	0.025	0.879
Growth rate (23-28mm)	1,9	0.221	0.650
Growth rate (All sizes) (excluding WB10,WB31)	1,7	11.947	0.011*
Growth rate (11-16mm) (excluding WB10,WB31)	1,7	10.399	0.015*
Growth rate (17-22mm) (excluding WB10,WB31)	1,7	1.705	0.233
Growth rate (23-28mm) (excluding WB10,WB31)	1,7	1.991	0.201

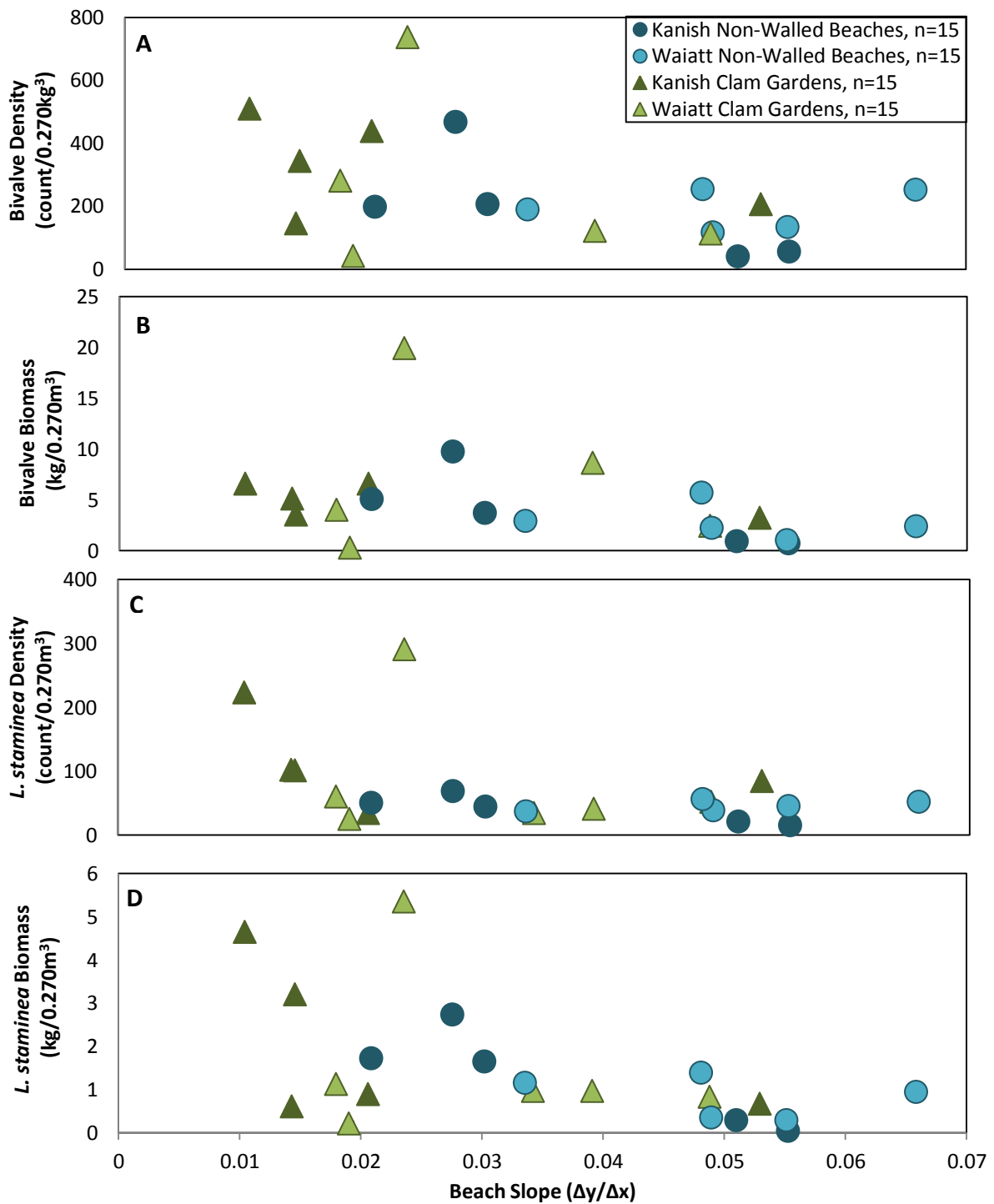


Figure S8. A) Clam Biomass (kg/0.270m³ +/-SE), B) Clam Density (count/0.270m³ +/-SE), C) *L. staminea* Biomass (kg/0.270m³ +/-SE, and D) *L. staminea* Density (count/0.270m³ +/-SE) as a function of beach slope (rise/run) at each survey site.