Recruitment of soft-shell clams, blue mussels, and green crabs at two intertidal sites in Taunton Bay, Franklin, Maine (April-November 2022)

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Introduction

Soft-shell clams, *Mya arenaria* L., are a commercially-important bivalve that inhabits soft-bottom intertidal areas along the coast of Maine and, during 2022, were ranked third of all marine resources in terms of dockside dollar value ($16.68 million) behind lobsters and elvers that ranked first and second, respectively (ME-DMR 2023a). Clams have a diphasic life history that begins typically in spring/summer (mid-May to early June) with adults spawning, an activity that results in the release of gametes into the water column where external fertilization occurs followed by a two- to three-week planktonic (larval) phase. Larvae begin life at ~as a fertilized egg 70 µm in diameter, and settle to the benthos at shell lengths between 250-300 µm (0.25-0.300 mm; or, 0.009-0.012 inches). During the larval (swimming) phase, gills, feet, and other organs such as those that form the digestive system, develop. Upon settlement to the benthos (the end of the swimming period), clams undergo a rapid period of metamorphosis and become more sedentary, although individuals can be moved by tidal and wind currents until they are approximately 10-15 mm in shell length. Clams are susceptible to predation by larval fish and other temporary or permanent members of the plankton community during their swimming phase, but few studies have focused on this earliest life-history stage (Hiebert 2015).

Once clams have settled, they are susceptible to a variety of predators, the most important today is the invasive European green (or shore) crab, *Carcinus maenas* (L.) (Beal 2006; Beal et al. 2020a,b; Tan and Beal 2015). Green crabs were first noticed in North America around 1817 in Long Island Sound where they arrived as accidental hitchhikers in the ballast of ships from the British Isles (Young and Elliott 2020), and have called Maine "home" since at least 1905 when a population was discovered in Casco Bay (Rathbun 1905). In time, mostly due to boat commerce prior to WWII, green crabs moved north and east along the Maine coast (the opposite direction of coastal currents) reaching Hancock County in the early 1930s, and to the easternmost towns of Lubec and Eastport, in Washington County, by 1951 (Carson 1955; Glude 1955). Green crabs have a catholic diet that includes items such as the seeds and above-ground portions of eelgrass, *Zostera marina* (Neckles 2015; Infantes et al. 2016), polychaete worms, snails, barnacles, fish, and insects, but prefer bivalve mollusks such as blue mussels and soft-shell clams (Ropes 1968).

While green crabs are susceptible to predation by ducks, fish, gulls, other crustaceans, and even by conspecifics (cannibalism), their populations are not regulated by these or any other predators in North America (Beal 2023). Instead, green crab populations are regulated by abiotic conditions that are related mostly to the severity of the winter (Glude 1955; Welch 1968; Beal et al. 2020a; Young and Elliott 2020). That is, during periods when ice forms and stays for weeks at a time in the intertidal zone, green crab populations decline precipitously because this species is physiologically unable to combat the cold weather. During the past 50 years, a warming trend in the Gulf of Maine (GoM) has been occurring (Pershing et al. 2015). For example, from 1982 to 2013, sea surface temperatures in the GoM taken daily from satellites rose at a rate of 0.03ºC per year compared with the global mean rate of 0.01ºC per year. Beginning in 2004, the warming rate in the GoM increased by a factor of ~7 to 0.23ºC per year, which is faster than 99% of the global ocean (Pershing et al. 2015). In addition, wintertime (1 January to 31 March) warming in the GoM increased at a rate of 0.034ºC per year from 1965 (1.355ºC) to 2015 (3.103ºC) (Beal et al. 2020a).

These historic sea surface temperatures signal a dire warning to those managing Maine's soft-shell clam fishery. That is, management schemes that may have worked to sustain or enhance the fishery during times when ocean temperatures were cooler than today (1960s & 1970s) such as "brushing" (Beal et al. 2020b), fallowing (i.e., "conservation closures"), rotating open and closed flats, and other measures should be reassessed in terms of the current climate conditions. While ocean warming continues annually, commercial soft-shell clam landings in Maine have declined by ~84% over the 45 years between 1977, when record catches of soft-shell clams were recorded (38.4 million pounds), and 2022, when landings were at historic lows (6.1 million pounds). While no concerted effort to measure green crab population densities exist on the scale of the Maine coast, observations by scientists and clammers suggests that green crab numbers have exploded recently, and that the record low clam landings reflect these observations.

Beginning in 2020, researchers at the Downeast Institute reached out to nine coastal communities from Sipayik to Wells that resulted in the formation of a monitoring network for young-of-the-year soft-shell clams (otherwise known as 0-yr class individuals, or recruits). A technical report outlining results from first two years is available online at:

https://downeastinstitute.org/research/soft-shell-clams/soft-shell-clam-recruitment-monitoring-network/. One group engaged with the monitoring network is the Frenchman Bay Regional Shellfish Conservation Commission. Two tidal flats within the greater Frenchman Bay region – Raccoon Cove (Lamoine) and Hog Bay (Franklin) – have been the focus of monitoring soft-shell clam recruitment.

Here, a collaborative study with the Friends of Taunton Bay is described that was conducted at two intertidal mudflats in Taunton Bay, Franklin, Maine from April to November 2022 to measure recruitment behavior of soft-shell clams and green crabs. Soft-shell clam "recruitment boxes" (sensu Beal et al. 2018) were used to assess clam and crab densities across two tidal heights at both sites. The wooden-framed boxes are passive collectors that are initially empty and are anchored to the mudflat surface prior to clam spawning (typically mid-May/early June). A piece of fine mesh (rectangular aperture = 0.9 mm x 1.7 mm, or 1.53 mm^2) is stapled to the top of each frame and a piece of woven landscape fabric is similarly affixed to the bottom of each box frame. Clams and crabs both have early life histories that depend on a successful planktonic period (2-3 weeks for soft-shell clams; 3-4 weeks for green crabs). Once animals have completed their larval period, clams settle to the benthos at sizes between 250-300 µm and can easily fall/swim/get swept through one of the thousands of small apertures that comprise the top of each box. (Approximately 30 clams could fit side-by-side in the space of one aperture when settlement size is 250 µm, and 15 clams could fit in the same space at a settlement size of 350 µm.) Green crabs can enter boxes possibly at two different times of year. These crustaceans settle to the benthos at a size of ~1 mm carapace width between July and October depending on water temperatures and can enter the boxes directly via settlement from the water column. Late settling crabs may not grow much at all during the fall and winter and may be capable of entering boxes in the spring up to carapace widths of 1.9 mm. In that event, crabs would likely become trapped after shedding to a larger size, and, when clams begin to settle, they may begin consuming them when the clams reach a size that suits the metabolic requirements of the crabs. The boxes give an excellent method to measure green crab growth since initial carapace width can only vary between 1-1.9 mm when they enter the boxes.

The study specifically assessed a number of factors that may be related to soft-shell clam and/or green crab recruitment dynamics. These include location (the study sites were two tidal flats within Taunton Bay – Karlson Point vs. Dwelley Point), tidal height (mid intertidal vs. low intertidal), and type of configuration of the recruitment boxes (see Methods). In addition, the experimental design accounted for the possibility of spatial variation in recruitment densities of clams and crabs within a tidal height at a given site. Finally, this study was designed as complementary to another in the same area that focused on monitoring seawater regularly for eDNA associated with green crabs. That is, the present study was designed to estimate recruitment densities of green crabs at the two sites, whereas the eDNA study was designed to test for presence/absence of this invasive species using DNA naturally released or shed by green crabs in membrane-bound forms as individual cells or organelles, or as extracellular DNA (Danziger et al. 2022).

Methods

To estimate recruitment of wild soft-shell clams and green crabs, an investigation was initiated on 17 April 2022 near the mid- and low intertidal zone at two intertidal flats in Taunton Bay in the town of Franklin, Maine. Wooden frames (1-ft x 2-ft x 2.5-inches deep) constructed of white spruce (*Picea glauca*) provided the primary structure for "recruitment boxes" (Beal et al. 2018). Two types of boxes were used. Half ("control" boxes) used wooden laths on top to secure a fine mesh (PetScreen®, a vinyl coated polyester material with a rectangular aperture – 0.9 mm x 1.7 mm) that was stapled to the top of the frame (Fig. 1). The use of laths increased the height of each box by approximately 0.75 inches compared with the other half of the boxes that were without top laths. For those boxes, the PetScreen® was stapled to the side of a box and a wooden lath was affixed to the side of a box to cover the staples. The bottom of all boxes was covered with a piece of woven polypropylene fabric that is used as agricultural or landscaping ground cloth for weed control. The ground cloth was supported by a piece of 1-inch vinyl-coated trap wire that also was affixed to the bottom of each box.

Empty boxes were deployed approximately three feet apart in groups (blocks) of two (one of each configuration). Three blocks (six boxes) were established at each tidal height at each study site, with 10-ft between adjacent blocks. Boxes were placed on the surface of the mudflat at

Karlson Point (clammers refer to it as “Tink’s”; 44º34’26.36”N, 68º15’44.29”W) and Dwelley Point (44º34’54.32”N, 68º14’36.77”W). To anchor boxes in place, a 22-inch lath was pushed into the mud at each of the short ends of each box so that they were at the same height as the top of the box. Two galvanized trap nails were pounded through the top of each lath and into the side of the box. (All boxes were recovered at the end of the experiment in the place each had been deployed.) This experimental design is referred to a randomized complete block design (RCBD; Neter et al. 1990), as there is a single replicate of box type within a block or group. In addition to deploying boxes, six benthic (bottom) core samples (Area = 0.1963 ft^2, or 0.01824 m^2) were taken at each tidal height and site to establish initial density and size-frequency distribution of clams and other infaunal organisms. The contents of each core sample were washed through a 1 mm sieve, and the shell length (SL – greatest anterior-posterior linear distance) of all live clams was measured to the nearest 0.01 mm using digital calipers.

Boxes remained at each site and tidal height until 6 November (204 days) when each was retrieved and the contents of each washed through a 1 mm sieve. All soft-shell clams, blue mussels, and green crabs were enumerated. When counts for a given species in a box were less than 20, all individuals were measured to the nearest 0.01 mm using digital calipers; otherwise, a representative sample was taken and a maximum of 20 individuals were measured. Shell length was recorded for clams and mussels, whereas carapace width (CW) – greatest distance between the longest lateral spines – was measured for crabs. In addition to retrieving boxes, six benthic (bottom) core samples (as described above) were taken at each tidal height and site. Core samples were processed and all counts and measurements of fauna were made as described above.

In addition to Karlson Point and Dwelley Point, recruitment boxes configured similarly to those with the laths on the sides of boxes were deployed on the same date (17 April 2022) in eight groups of two boxes each near the mid intertidal zone at Hog Bay (44º34’27.19”N; 68º13’35.95”W). Boxes within each group were identical in terms of their construction. The Hog Bay site is one of two in the Frenchman Bay region that has served as a soft-shell clam monitoring site since 2020 (see: https://downeastinstitute.org/research/soft-shell-clams/soft-shell-clam-recruitment-monitoring-network/). The other site is located at that same tidal height at Raccoon Cove in Lamoine, Maine.

Data from recruitment boxes at Karlson Point and Dwelley Point was analyzed to test for potential differences between the two types of boxes as well as spatial variability within and between tidal heights using the following linear model:

$$Y_{ijkl} = \mu + A_i + B_j + AB_{ij} + C_k + AC_{ik} + BC_{jk} + ABC_{ijk} + D(AB)_{l(ij)} + CD(AB)_{kl(ij)}$$

Where:

Y_{ijkl} = Dependent variable (soft-shell clam, blue mussel, and green crab density and size);
μ = Theoretical mean that is estimated by the overall, or grand, sample mean;
A_i = Location ($i = 1$ to $a = 2$; Karlson Point vs. Dwelley Point – factor is fixed);
B_j = Tidal Height ($j = 1$ to $b = 2$; mid-tide vs. low-tide – factor is fixed);
C_k = Box Type ($k = 1$ to $c = 2$; boxes with top laths vs. those without – factor is fixed); and,
D_l = Block ($l = 1$ to $d = 3$; blocks are unique to a location and tidal height – factor is random).

This was designed as a Randomized Complete Block Design (RCBD); hence, there is no true replication. F-statistics were calculated by following the Cornfield-Tukey rules (Silverstein and Mohan 1963). All means are presented with their 95% confidence interval.

Results

Core samples

Core samples (n = 6) taken on 17 April 2022 revealed no clams from the mid intertidal at Dwelley Point and 0.85 ± 2.18 individuals/ft^2 at the low intertidal. A single clam was sampled from the low intertidal that measured 87.61 mm SL. At Karlson Point, core sampling revealed a density of 1.69 ± 2.76 ind/ft^2 at the lower intertidal and 3.39 ± 2.76 ind/ft^2 at the mid intertidal. Clams ranged in SL from 9.39-75.85 mm at Karlson Point. Samples (n = 6) taken on 6 November 2022 from Dwelley Point demonstrated soft-shell clam densities of 3.40 ± 4.47 individuals/ft^2 at the mid intertidal; however, two of the four clams from those samples were not 0-yr class individuals (e.g., 31.1 mm and 53.97 mm SL). No clams occurred in cores taken at the low intertidal at Dwelley Point. Soft-shell clam densities were identical at the two tidal heights at Karlson Point (0.85 ± 2.18 ind./ft^2), and one of the two clams sampled was not a recruit from 2022 (49.7 mm SL). Combining data from both sites, soft-shell clam recruit density in November 2022 was 0.64 ± 0.97 ind./ft^2 (n = 24).

Recruitment boxes – Soft-shell clams
No statistically significant differences were observed in mean number of soft-shell clam recruits between the two sites (Karlson [2.51 ± 1.07 individuals/ft^2, n = 12] vs. Dwelley [1.69 ± 1.44 ind./ft^2, n = 12]) or between tidal heights at either site (Table 1; Fig. 2). Overall mean density (pooling all factors) was 2.10 ± 0.84 ind./ft^2 (n = 24). This recruitment rate was significantly higher than that observed over the same period in boxes deployed at Hog Bay where an average of 0.73 ± 0.47 ind./ft^2 (n = 16) was observed ($t_{obs} = 2.96$, df = 33, $P = 0.006$). Clam recruits ranged in size from 1.8-22.4 mm SL at Karlson Point and from 2.04-22.1 mm at Dwelley Point (Fig. 3). No significant effect of box configuration, site, or tidal height on mean SL was observed ($P \geq 0.21$).

Recruitment boxes – Green crabs
Green crabs were discovered in some recruitment boxes at both sites (Fig. 4); however, the pattern was complicated. For example, at Dwelley Point, crabs occurred in both types of boxes only in the lower intertidal, and only in boxes with the laths on top at the mid intertidal. At Karlson Point, crabs were found at both tidal heights, but only in boxes with laths on the side of the box. The highest mean density of green crabs occurred in boxes with laths on top near the mid intertidal at Karlson Point (1.67 ± 1.43 individuals/box, or 1.03 ± 0.88 individuals/ft^2; n = 3). At Dwelley Point, eight green crabs (CW size range = 19.72-50.86 mm) were found across six of twelve boxes, and no live soft-shell clam recruits were found in boxes containing one or more green crabs.

Clams (2-10/box) occurred in all six boxes at Dwelley Point that did not contain green crabs (mean density in these six boxes was 3.38 ± 2.19 individuals/ft^2 (n = 6). At Karlson Point, green crabs were discovered in 5 of 12 boxes, and in the boxes without crabs, mean soft-shell clam recruit density was 3.51 ± 1.08 ind./ft^2 compared with 1.11 ± 1.57 ind./ft^2 in boxes with one or more green crabs. This difference (2.41 ± 1.65 ind./ft^2) was statistically significant (two-tailed t-test: $t_{obs} = 3.37$, df = 10, $P = 0.01$). In the five boxes containing green crabs at Karlson Point, two contained large green crabs (one box contained an individual that was 34.0 mm CW, and the other contained two individuals that measured 30.9 mm and 22.9 mm CW). The three other boxes containing green crabs also contained soft-shell clam recruits (crabs measured 3.9 mm, 3.4 mm, and 14.9 mm CW). Combining data from both sites, in boxes containing no green crabs, mean soft-shell clam recruit density was 3.45 ± 0.95 ind./ft^2 (n = 13) as compared with a density of 0.50 ± 0.66 ind./ft^2 (n = 11) in boxes with ≥ 1 green crab(s). This difference (2.951 ± 1.10 ind./ft^2) was statistically significant using a two-tailed, two-sample t-test ($t_{obs} = 5.58$, df = 22, $P < 0.0001$). In the boxes, mean clam mortality due to crabs was estimated at 85.5% ($100\% - [\frac{0.50}{3.45}]$). Comparing densities of clams in boxes without green crabs to ambient conditions estimated from core samples, clam mortality was estimated at 81.4% ($100\% - [\frac{0.64}{3.45}]$).

A significant negative relationship existed between number of green crabs and number of soft-shell clam recruits ($r^2 = 0.444$, $P = 0.0004$; Fig. 5). A lack-of-fit test was conducted to determine if the addition of a quadratic term to a linear model would explain significantly more of the variation in clam recruits. A quadratic relationship did improve the fit ($r^2 = 0.568$; F = 6.02, df = 1, 21, $P = 0.023$). To explore further the possible linkage between green crabs and soft-shell clam recruits, we examined the relationship between the maximum size green crab/box and number of soft-shell clam recruits in the same box. This, too, demonstrated a negative relationship (Fig. 6). A lack-of-fit test determined that a linear model was appropriate ($r^2 = 0.525$, $P = 0.012$), as the addition of a quadratic term to the linear model did not improve the fit significantly ($P = 0.0623$).

Recruitment boxes – Blue mussels

Blue mussels, *Mytilus edulis*, were the most abundant macrofauna in recruitment boxes at both sites. Most were found byssed to the wooden frame adjacent to the PetScreen®, or directly to the underside of that material. Overall mean density (pooled across all factors) of blue mussels in recruitment boxes was 10.97 ± 4.91 individuals/ft^2 (n = 24), or nearly 5× the overall mean density of soft-shell clams. ANOVA on mean number per ft^2 indicated two statistically significant interactions (e.g., Site × Tidal Height [$P = 0.0034$] and Treatment × Tidal Height [$P = 0.0083$; Table 2). The significant Site × Tidal Height interaction occurred because at Karlson Point, blue mussel recruit densities were similar between the two tidal heights but the same pattern did not exist at Dwelley Point where mean density was higher in the mid- vs. low tide boxes (Fig. 7). The significant Treatment × Tidal height interaction source of variation (Table 2) occurred because the relationship between mean number per ft^2 of blue mussel recruits and box configuration (i.e., laths on top of box vs. sides of box) differed across tidal heights. At mid tide levels, more blue mussels were sampled from boxes with laths on top of the frame than on the side of the frame, while at low tide levels the opposite was true (Fig. 8).

Upon sampling in November 2022, blue mussels ranged in size from 2.1-33.7 mm SL at Dwelley Point, and from 3.9-33.8 mm at Karlson (Fig. 9). ANOVA on the mean size of *Mytilus* per box (Table 3) demonstrated a significant Site × Tidal height effect ($P = 0.032$) as well as a significant effect due to the box configuration ($P = 0.017$; Table 3). Mussels were similar in mean size (shell length) at both tidal heights at Karlson Point; however, individuals averaged ~50% larger in the mid (15.3 ± 3.6 mm, $n = 6$) vs. low intertidal at Dwelley Point (10.2 ± 4.9 mm, $n = 5$; Fig. 10). Mean SL of blue mussels pooled across tidal heights, sites, and blocks indicated that mussels in boxes with laths on top were ~25% longer (18.3 ± 3.2 mm, $n = 11$) than those growing in boxes with laths on the sides (13.4 ± 2.9 mm, $n = 12$).

No significant relationship was found between number of blue mussels per box and number of green crabs per box ($r^2 = 0.154$, $P = 0.057$); however, a strong, negative relationship was discovered between number of blue mussels per box and the maximum size of the green crab in the same box ($r^2 = 0.605$, $P = 0.0048$, $n = 11$; Fig. 11).

Discussion/Summary

This study answered several questions regarding recruitment of clams, mussels, and green crabs. First, green crabs occur in Taunton Bay. This may be surprising given that this species had not been recorded from recruitment boxes placed in the mid intertidal zone at nearby Hog Bay during 2021 & 2022 (crab density was ~1.3 individuals/ft^2 in recruitment boxes in 2020; Table 4) (Beal et al. unpublished data; see technical reports from 2020 and 2021 at: https://downeastinstitute.org/research/soft-shell-clams/soft-shell-clam-recruitment-monitoring-network/). Recruits (0-yr class individuals) of soft-shell clams, blue mussels, and green crabs were found in recruitment boxes at the two soft-bottom intertidal sites in Taunton Bay during 2022.

Boxes were deployed in spring (17 April) prior to clam spawning (Snelgrove et al. 2023) when seawater temperatures are typically less than 10ºC (50ºF), and remained in the field until well after the pelagic (swimming) stage of these three species had ceased (6 November). Densities of soft-shell clams in these boxes did not vary significantly between sites or tidal heights, and overall mean abundance recorded in the boxes was quite low (2.1 ± 0.84 individuals/ft^2, n = 24) compared with results from Raccoon Cove (Lamoine – Frenchman Bay), and other eastern Maine locations (Beal et al. unpubl.). This estimate came from boxes both with and without green crabs, which have been shown to be an important consumer of soft-shell clams (Glude 1955; Beal 2006; Tan and Beal 2015). Combining data from both sites, tidal heights, and box configurations, crabs occurred in 11 of 24 boxes, and in those boxes, soft-shell clam recruit density was 0.50 ± 0.66 ind./ft^2 as opposed to 3.45 ± 0.95 ind./ft^2 in boxes without green crabs – a nearly 7-fold difference. A similar comparison using information from core samples taken at the two Taunton Bay sites in November suggests a similar negative effect of green crabs on soft-shell clam recruits. That is, although green crab density also was low (the mean varied between 1.69 and 2.51 crabs/ft^2 [n = 12] in recruitment boxes), we observed significantly more soft-shell clam recruits in boxes without crabs than in boxes with crabs. We discovered a weak, negative relationship between number of clams and number of green crabs per box as well as a stronger negative relationship between number of clams and the largest size green crab per box. Similar relationships between maximum crab size and number of recruits have been observed in other Maine coastal communities (Beal et al. unpublished data).

Because green crabs are invasive, many think they have no predators. They do, and the list is large but not limited to fish, ducks, gulls, lobsters, horseshoe crabs, rock and Jonah crabs, and green crabs. That is, green crabs have many predators; however, even collectively, these predators cannot keep green crab populations in check as long as wintertime seawater temperatures remain relatively warm. Cold winters provide the necessary combination of environmental conditions that have a negative (lethal) effect on green crab physiology, so that its thermal tolerance capacity is challenged. Green crabs appear to show greater heat tolerance than other temperate species of crabs and lobsters with which they share their environment, and they also tolerate cold temperatures of 0ºC or below (Tepolt and Somero 2014). Long term exposure to freezing air and cold seawater temperatures that produce large ice floes in rivers, embayments, and coves is what limits green crab populations (Welch 1968), and these conditions have not been seen along the Maine coast in over a decade. Instead, average wintertime temperatures have been increasing steadily for nearly a half century (Fig. 12).

Seawater temperatures in Maine were higher, on average, during the early 1950s than they are today (Fig. 12), and at that time, green crabs decimated soft-shell clam populations from one end of the Maine coast to the other (Smith and Chin 1951; Smith et al. 1955; Glude 1955). Commercial populations of soft-shell clams dropped precipitously during the 1950s reaching an all-time low, until then, of 7.1 million pounds in 1959. This record was broken in 2020 when 6.6 million pounds were harvested (Fig. 13), only to be broken again in 2022 when 6.1 million pounds were landed (worth $16.7 million) (ME-DMR 2023b).

With increasing seawater temperatures and increasing green crab populations, how do soft-shell clams survive, how does a commercial fishery exist under these conditions, and where are commercial populations located? Soft-shell clams survive in many marine environments where one of two conditions exist in places where: 1) it is difficult for green crabs to survive because they have few refuges (hiding places) and are easily targeted by their predators; and, 2) clams have a spatial refuge from green crab attack, such as the upper intertidal. As an example of the latter, Beal et al. (2001) manipulated the density of juvenile soft-shell clams (12 mm SL) across three tidal heights in experimental units that were divided evenly between those that allowed predators to attack clams and those that deterred predator attack using flexible netting (6.4 mm aperture) over 248 days (6 April to 13 December 1996). In the lower intertidal, clam survival was enhanced by ~60% as a result of deterring predators; however, at the upper intertidal, survival was enhanced by only ~10% in units with deterrent netting. Why? Because waterborne predators such as green crabs have two advantages in preying on clams and other fauna in the lower intertidal. First, predators have more time to search, find, and consume prey on flats at/near the low water mark because these lower tidal levels are inundated with seawater longer the further they are from shore. Second, sediments near the upper shore typically are less muddy and more gravelly than sediments along the lower intertidal, and this makes excavating prey such as soft-shell clams more difficult and time-consuming for predators. These two conditions explain why most commercial populations of clams in Maine mudflats today are located in high intertidal areas or in areas where great distances exist between the mouth of a river and the upper reaches of that river system. That is, clams survive best along the upper shore – an area exposed for the most time during every tidal cycle – since green crabs are less effective/efficient predators in excavating their soft-shell clam prey during periods when the tide exposes sediments to the air. As the tide recedes from the upper shore, sediments become more compact and more difficult to penetrate.

Few soft-shell clams are found anymore at/near the middle and lower tidal heights; rather, most commercial clam populations occur at/near the upper intertidal, which gives clammers 3-5 hours to work a single tide. The practical problem for clammers and the fishery is that clams do not grow very fast in those upper intertidal habitats, and therefore cannot replace themselves at a rate that is faster than the rate at which they are being consumed collectively by non-human and human predators. That is, in many places along the Maine coast today, the subsidy of clams in the upper reaches of flats, rivers, embayments, and coves is where the bulk of the commercial fishery now exists. Historically, these clams would have been left alone to spawn contributing to the next generation of clams. In a colder environment, green crab populations are depressed, as was the case during the 1960s (Welch 1968) when clams thrived and individuals occurred throughout the intertidal zone that spreads out fishing effort rather than concentrating it.

Results from this study suggest that the current rate of clam recruitment at these two tidal flats (within the mid and low intertidal zones) in Taunton Bay is insufficient for a successful commercial fishery given the effects of green crabs and other predators. While clamming today is centered/focused mostly on upper intertidal populations of soft-shell clams that are slow-growing, it is likely that if seawater temperatures continue trending in the same direction they have for the past 50 years, that fewer and fewer commercial clammers will be able to support themselves as clam populations continue to decline. Clammers, clam managers, and others in the fishery such as buyers, shippers, wholesalers, and retailers should be concerned about these trends, and what they mean for the future of this fragile fishery. As commercial landings reflect population trends, fewer clams for public consumption means that alternative bivalve species such as oysters, mussels, and quahogs will become more widely used in commercial settings. Clams will become more difficult for the public to acquire as prices may increase beyond a point consumers are willing to pay, prompting the use of other less expensive alternatives. Traditional techniques once used to sustain or enhance clam populations (closing/fallowing flats; brushing [Beal et al. 2020b]; limiting licenses; moving clams from the upper to lower intertidal to increase growth rates; etc.) are no longer effective. Unless a fundamental change occurs in how soft-shell clams are managed, the commercial clam fishery in Maine will soon become a "thing of the past" like ice skating on grandma's pond on Thanksgiving Day.

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Table 1. Analysis of variance on the mean number of soft-shell clam recruits in two configurations of recruitment boxes (those with vs. those without top laths; labeled as "Treatment" in the table) at two locations (Karlson Point and Dwelley Point in Taunton Bay, Franklin, Maine), and two tidal heights (mid- vs. lower intertidal) arranged in three blocks (~ 4m^2) at both tidal heights.

Source of Variation	DF	Sum of Squares	Mean Square	F Value	Pr > F
Site	1	4.03502662	4.03502662	0.97	0.3536
Tide height	1	7.62872219	7.62872219	1.83	0.2127
Site x Tide height	1	2.26970247	2.26970247	0.55	0.4813
Treatment	1	7.62872219	7.62872219	3.10	0.1162
Site x Treatment	1	6.30472909	6.30472909	2.56	0.1480
Tide height x Treatment	1	1.57618227	1.57618227	0.64	0.4465
Site x Tide height x Treatm	1	9.07880988	9.07880988	3.69	0.0909
Block(Site, Tide height)	8	33.28896958	4.16112120	.	No test
Treatm x Block(Site, Tide)	8	19.67075475	2.45884434	.	No test
Total	23	91.48161904			

Table 2. Analysis of variance on the mean number of blue mussel recruits per ft^2 in two types of recruitment boxes (i.e., labeled as "Treatment" in the table; those with vs. those without top laths) at two locations (Karlson Point and Dwelley Point in Taunton Bay, Franklin, Maine), and two tidal heights (mid- vs. lower intertidal) arranged in three blocks (~ 4m^2) at both tidal heights.

Source of Variation	DF	Sum of Squares	Mean Square	F Value	Pr > F
Site	1	317.8213932	317.8213932	9.64	0.0146
Tide height	1	219.4676195	219.4676195	6.66	0.0326
Site x Tide height	1	557.0858621	557.0858621	16.89	0.0034
Treatment	1	133.4080675	133.4080675	2.51	0.1518
Site x Treatment	1	354.6410111	354.6410111	6.67	0.0325
Tide height x Treatment	1	643.1454141	643.1454141	12.10	0.0083
Site x Tide height x Treatm	1	197.7163041	197.7163041	3.72	0.0899
Block(Site, Tide height)	8	263.7898650	32.9737331	.	No test
Treatm x Block(Site, Tide)	8	425.1909296	53.1488662	.	No test
Total	23	3112.2864612			

Table 3. Analysis of variance on the mean SL of blue mussels at both sites (a = 2; Dwelley Point vs. Karlson Point), tidal heights (b = 2; mid vs. low intertidal), in both recruitment box configurations (c = 2; laths on top of box vs. sides of box; this factor is labeled as "Treatment" in the table), and blocks (d = 3; factor is nested within the combination of site and tidal height). Blue mussels were found in 23 of 24 recruitment boxes. No clams occurred in a single recruitment box (Dwelley Point, mid intertidal, box with laths on the side); hence, the data were unbalanced and Type III sums of squares were used.

Source	DF	Sums of Squares	Mean Square	F Value	Pr > F
Site	1	154.7090984	154.7090984	29.46	0.0006
Tide height	1	20.0855009	20.0855009	3.82	0.0862
Site x Tide height	1	35.1829738	35.1829738	6.70	0.0322
Treatment	1	116.5482043	116.5482043	9.83	0.0165
Site × Treatment	1	38.8302545	38.8302545	3.27	0.1133
Tide height × Treatment	1	8.6162883	8.6162883	0.73	0.4222
Site x Tide height× Treatm	1	66.1627010	66.1627010	5.58	0.0502
Block(Site x Tide height)	8	42.0138774	5.2517347	.	No test
Treatm x Block(Site, Tide)	7	83.0192887	11.8598984	.	No test
Total	22	565.1668723			

Table 4. Results of deploying soft-shell clam recruitment boxes in Hog Bay, Franklin, Maine for 2020-2022 (N = 16). Densities are presented from recruitment boxes and are in number of individuals per square foot. Values in parentheses represent 95% CI for µ. SL – shell length (in mm); CW = carapace width (in mm). n = number of individuals measured. Note: this information is taken from a larger study involving 9 (2020-2021) and 12 communities (2022) (see: https://downeastinstitute.org/research/soft-shell-clams/soft-shell-clam-recruitment-monitoring-network/).

Year	Clam Density	Mean SL	n	Green Crab Density	Mean CW	n
2020	1.38 (1.05)	9.1 (0.79)	54	1.27 (1.21)	30.7 (3.12)	4
2021	13.60 (1.70)	6.7 (0.80)	294	0.00 (0.00)	.	.
2022	0.73 (0.47)	9.9 (1.69)	19	0.00 (0.00)	.	.

Figure Legends

Figure 1. Soft-shell clam "control" recruitment box (wooden frame: 1-ft x 2-ft x 3-inches) with laths on top that help secure a piece of PetScreen® (aperture = 0.9 mm x 1.7 mm). Box bottoms were lined with a piece of woven, agricultural ground cloth/weed barrier constructed of vinyl coated polyester material. Boxes were deployed empty, and act as passive collectors for organisms that have a planktonic early life history and settle to the benthos at sizes typically less than 1 mm (clams and mussels settle at a size ~250 μm [0.25 mm] in shell length; green crabs settle at a size ~ 1,000 μm [1 mm] in carapace width).

Figure 2. Mean (+ 95% CI) number of soft-shell clam recruits per square foot from boxes established at Karlson Point and Dwelley Point in Franklin, Maine (Taunton Bay) from 17 April to 6 November 2022 (204 days). Red lines are the sample means from both sites (Dwelley Point: 1.69 ± 1.44 individuals/ft^2, n = 12; Karlson Point: 2.51 ± 1.07 individuals/ft^2, n = 12). No significant difference was observed in means between tidal heights within a given location or between locations. Overall mean was 2.10 ± 0.84 recruits/ft^2 (n = 24).

Figure 3. Size-frequency distribution of soft-shell clam recruits from two intertidal heights at Dwelley Point and Karlson Point (Franklin, Maine) on 6 November 2022. "N" represents the number of individuals measured from the six boxes at both tidal heights and sites.

Figure 4. Mean number of green crabs in recruitment boxes by site, tidal height, and treatment ("laths on top" refers to boxes with laths on the top of the wooden frame that increases the height of the box by approximately 0.75 inches compared with boxes where the laths are "on the side" of the box). ANOVA indicated a significant 3-way interaction (i.e., Site × Tide Height × Box type, P = 0.0093), which was the result of finding no green crabs in boxes with the laths on top at Karlson Point.

Figure 5. Relationship between number of soft-shell clam recruits per box and number of green crabs per box. A lack-of-fit to a linear equation ($r^2 = 0.444$) was significant (P = 0.023), and suggested that fitting a quadratic model to the same data would improve the fit, which it did ($Y = 5.62 – 7.49X + 2.59X^2$, $r^2 = 0.568$, n = 24). Values in parentheses indicate the number of data points that exist at that particular point in the graph.

Figure 6. Relationship between number of soft-shell clam recruits per box and the size of the largest green crab (maximum carapace width) in the same box. The equation associated with the line-of-best-fit (black line; least-squares regression line) is $Y = 3.40 – 8.864X$ ($r^2 = 0.525$, P = 0.012, n = 11). The blue concave lines represent the 95% confidence interval associated with the least-squares regression line.

Figure 7. Site × Tidal Height interaction plot. Mean (+95% CI) number of blue mussel recruits per square foot from boxes established at Karlson Point and Dwelley Point in Franklin, Maine (Taunton Bay) from 17 April to 6 November 2022 (204 days). Red horizontal bars represent means for each site pooled across tidal heights (Dwelley Point: 14.61 ± 9.34 individuals/ft^2; Karlson Point: 7.32 ± 3.91 individuals/ft^2; n = 12).

Figure 8. Treatment × Tidal Height interaction plot. Mean (+95% CI) number of blue mussel recruits per square foot from boxes established Karlson Point and Dwelley Point in Franklin, Maine (Taunton Bay) from 17 April to 6 November 2022 (204 days). Red horizontal bars represent means for each tidal height pooled across box configuration (Mid: 13.99 ± 9.28 individuals/ft^2; Low: 7.94 ± 4.47 individuals/ft^2; n = 12).

Figure 9. Size-frequency distribution of blue mussels from the mid and low intertidal zone at both Dwelley Point and Karlson Point (6 November 2022). "N" represents the number of mussels that were measured from the six boxes at both tidal heights and sites. ANOVA on the mean SL of blue mussels per recruitment box indicated a significant Site × Tide height interaction as well as a significant effect due to the box configuration (see Table 3).

Figure 10. Interaction plot – Site x Tidal height – for mean shell length of blue mussels in recruitment boxes at the mid and low intertidal at Dwelley Point and Karlson Point, Taunton Bay, Franklin, Maine. The interaction was statistically significant (P = 0.032; Table 3).

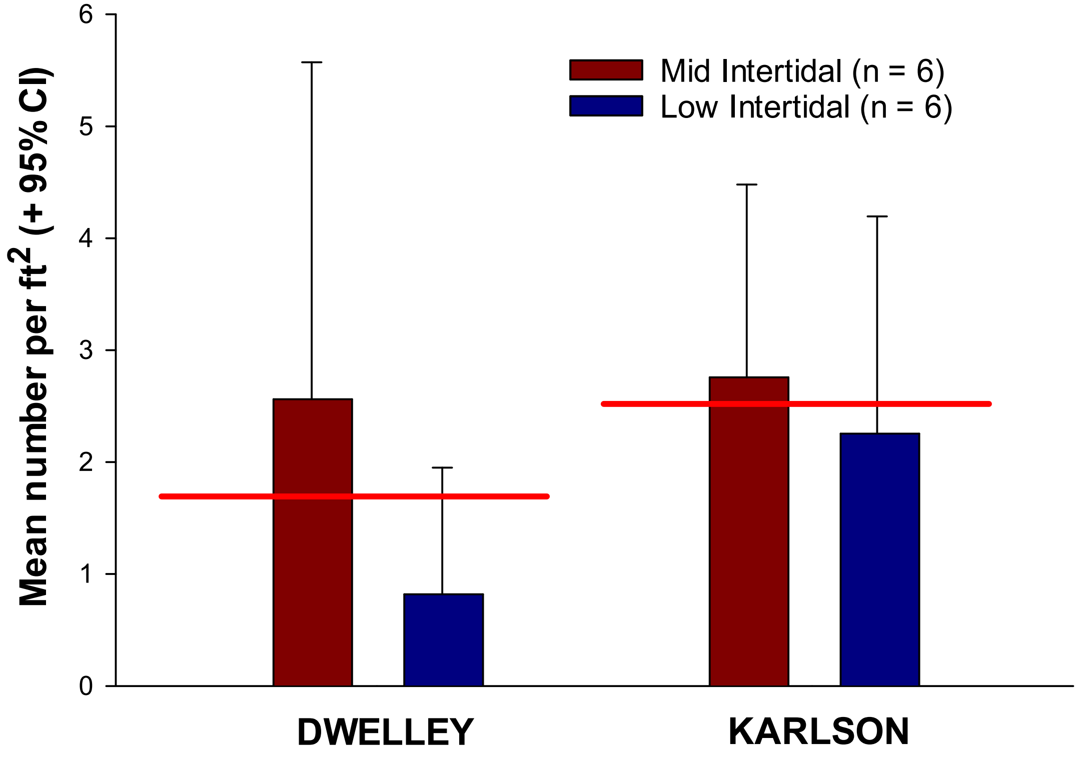
Figure 11. Relationship between number of blue mussel recruits per box and the size of the largest green crab (maximum carapace width) in the same box. The equation associated with the line-of-best-fit (black line; least-squares regression line) is $Y = 22.54 – 0.474X$ ($r^2 = 0.605$, $P = 0.0048$, $n = 11$). The blue concave lines represent the 95% confidence interval associated with the least-squares regression line.

Figure 12. Wintertime (1 January to 31 March) sea surface temperature taken in Boothbay Harbor, Maine from 1941 to 2019 (see: https://www.maine.gov/dmr/science/weather-tides/boothbay-harbor-environmental-data). Red triangles depict mean decadal temperature.

Figure 13. Commercial landings (millions of pounds) and value (millions of dollars) of soft-shell clams in Maine (1950-2021).

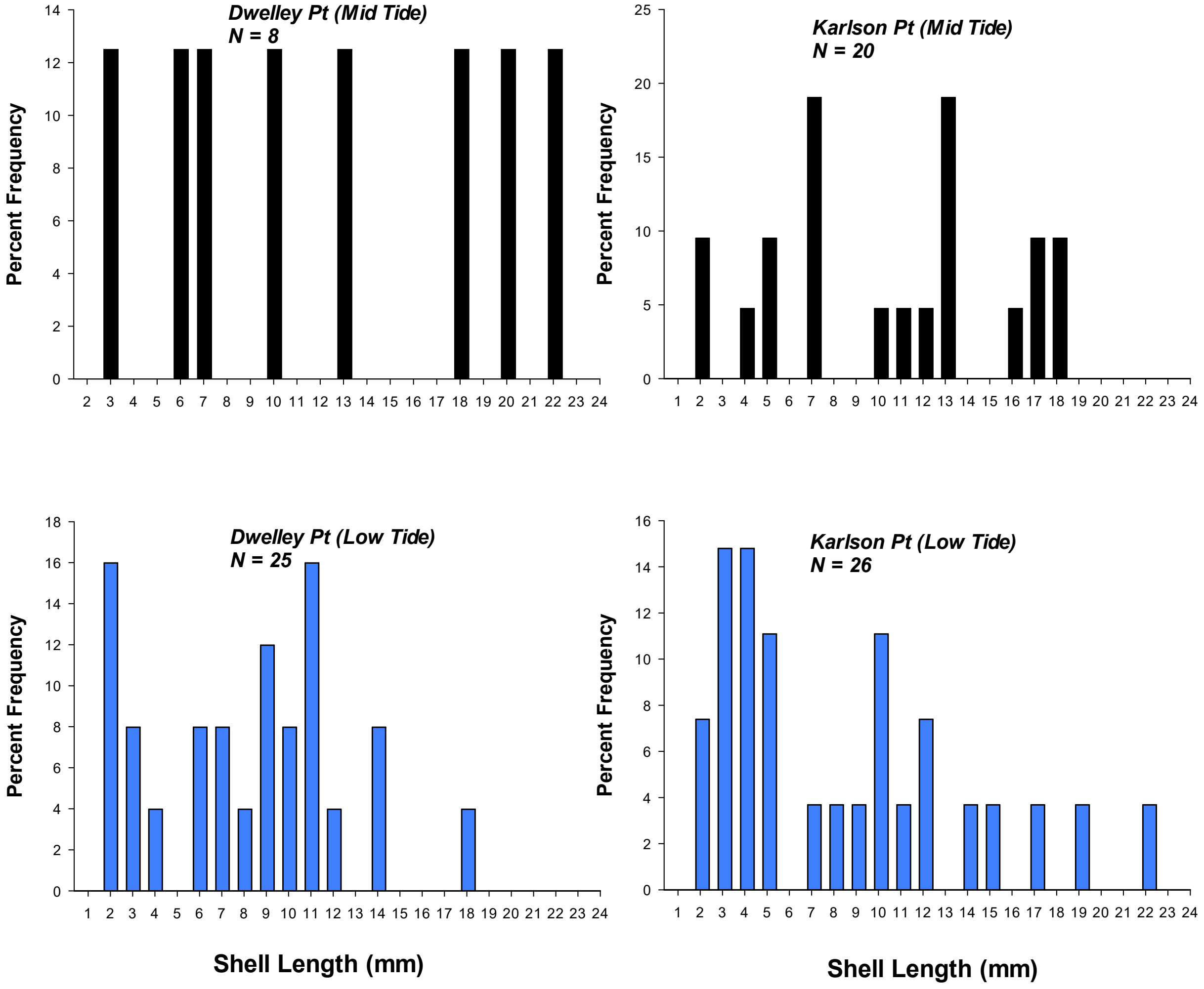
Figure 1.

Figure 2.



Mean number per ft^2 (+ 95% CI)
0
1
2
3
4
5
6
Mid Intertidal (n = 6)
Low Intertidal (n = 6)
DWELLEY
KARLSON

Figure 3.



Dwelley Pt (Mid Tide)
N = 8
Karlson Pt (Mid Tide)
N = 20
Dwelley Pt (Low Tide)
N = 25
Karlson Pt (Low Tide)
N = 26
Percent Frequency
Shell Length (mm)
0 2 4 6 8 10 12 14
0 5 10 15 20 25
0 2 4 6 8 10 12 14 16 18
0 2 4 6 8 10 12 14 16
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24

Figure 4.

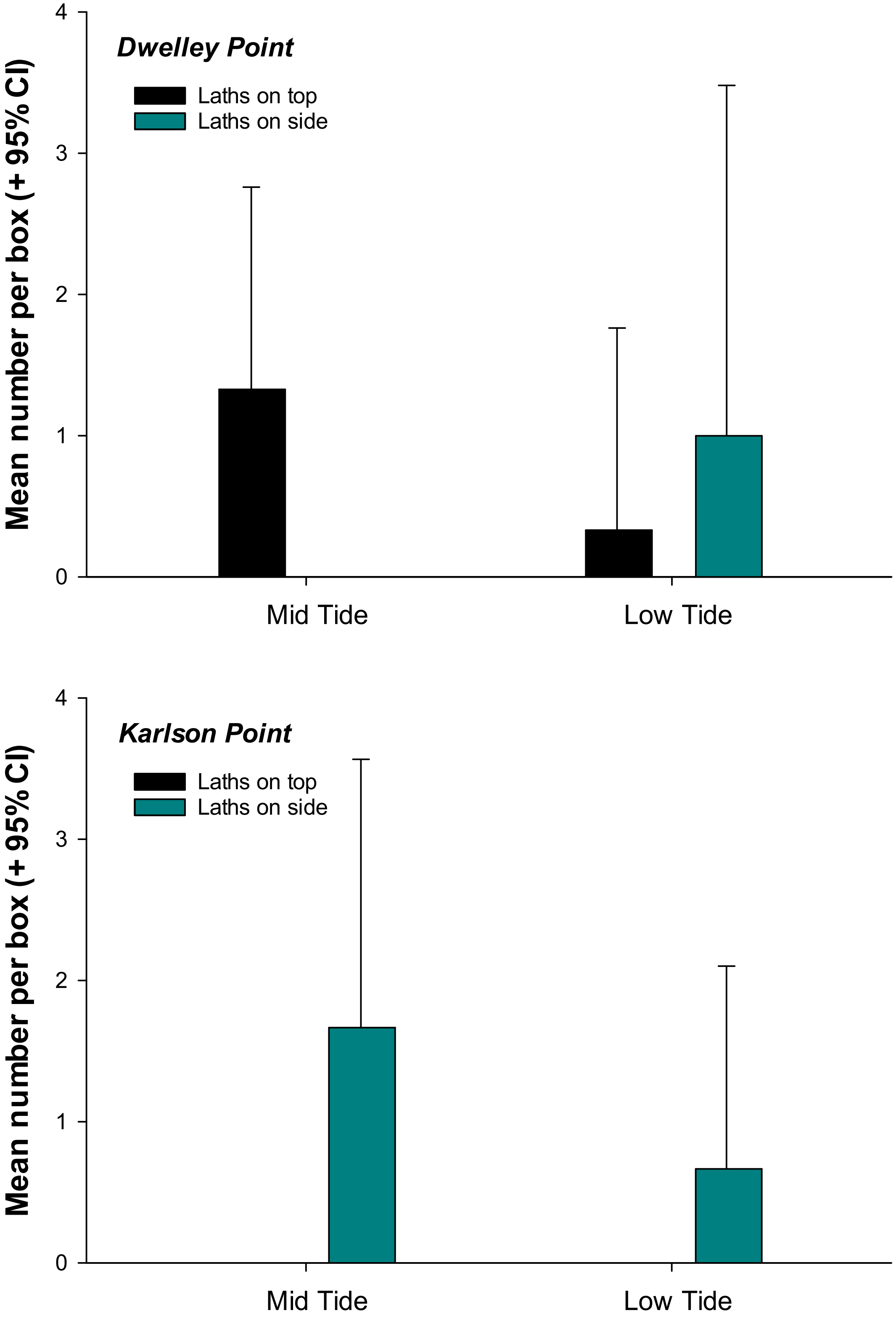

Dwelley Point
Laths on top
Laths on side
Mean number per box (+ 95% CI)
0
1
2
3
4
Mid Tide
Low Tide
Karlson Point
Laths on top
Laths on side
Mean number per box (+ 95% CI)
0
1
2
3
4
Mid Tide
Low Tide

Figure 5.

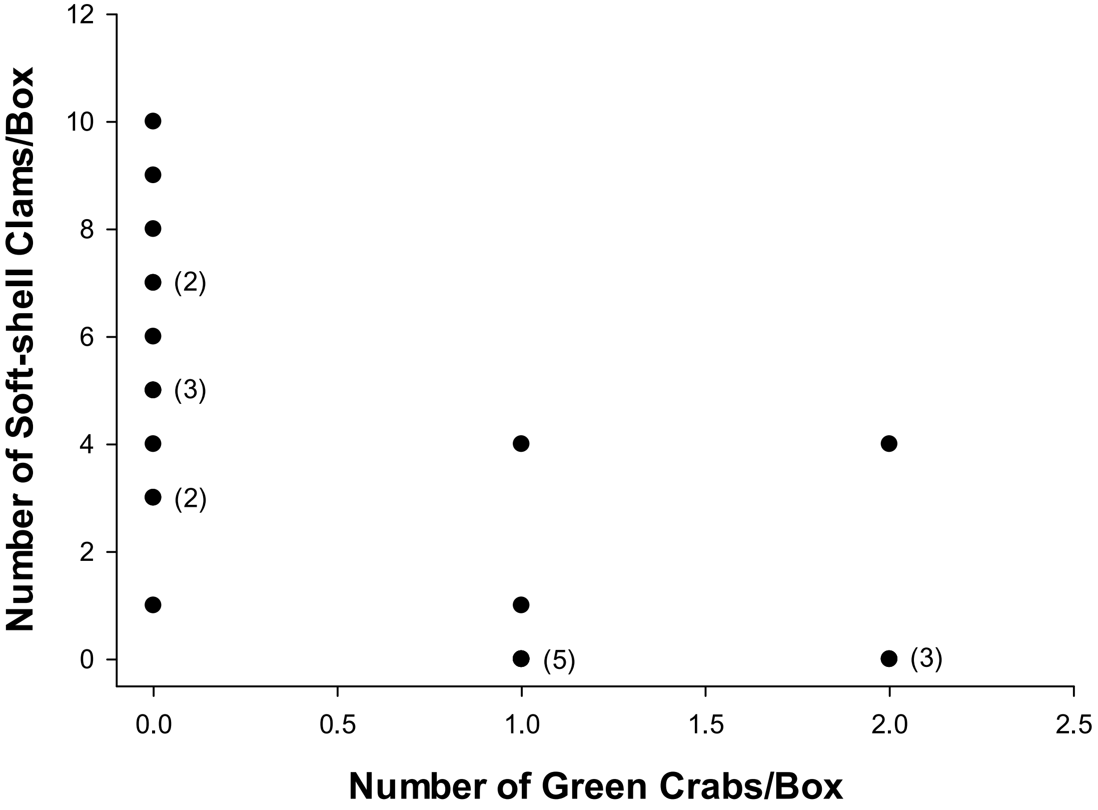

12
10
8
6
4
2
0
0.0
0.5
1.0
1.5
2.0
2.5
(2)
(3)
(2)
(5)
(3)
Number of Soft-shell Clams/Box
Number of Green Crabs/Box

Figure 6.

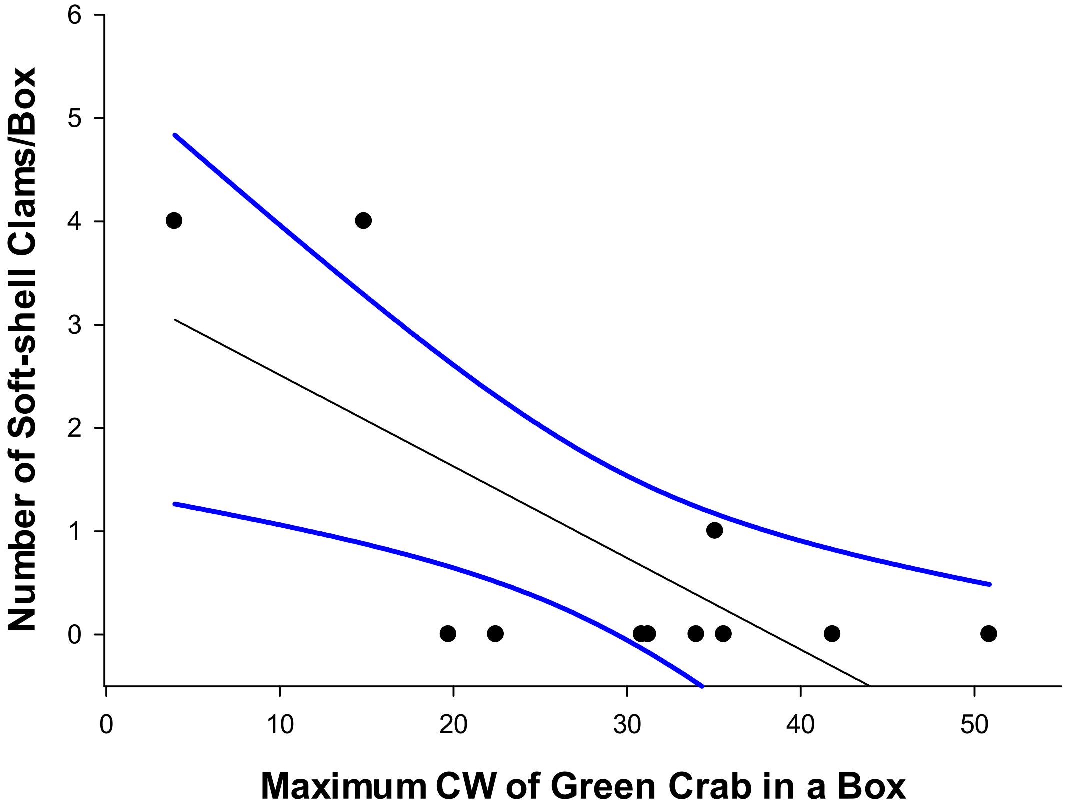

6
5
4
3
2
1
0
0
10
20
30
40
50
Number of Soft-shell Clams/Box
Maximum CW of Green Crab in a Box

Figure 7.

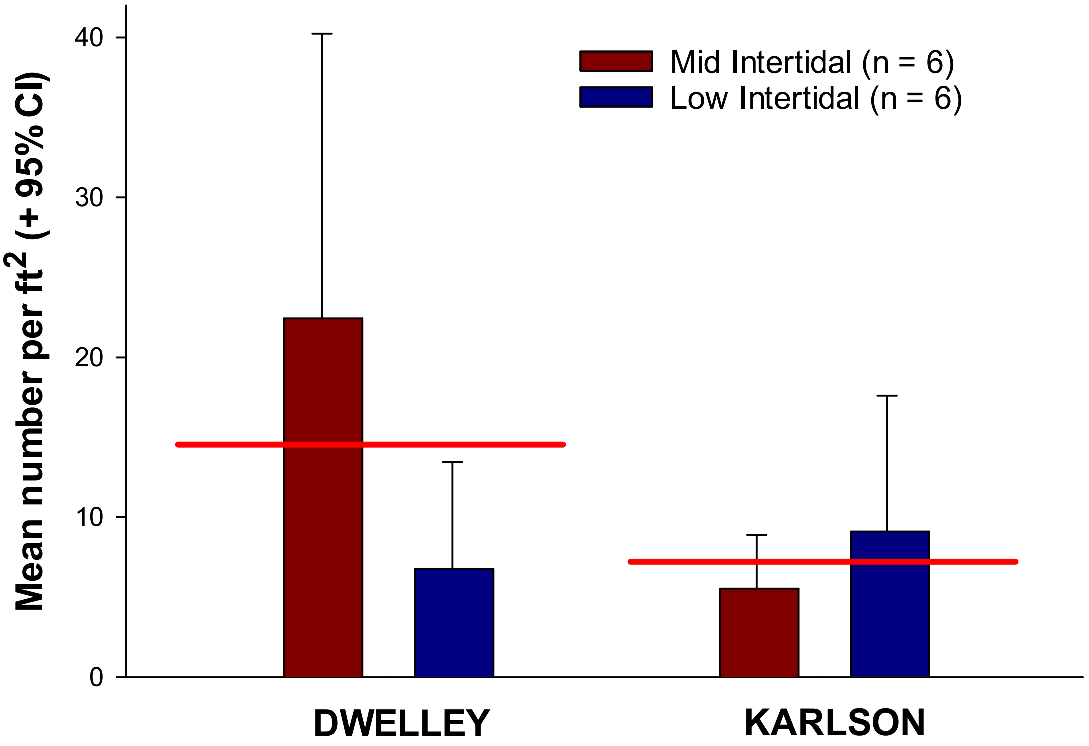

Mid Intertidal (n = 6)
Low Intertidal (n = 6)
Mean number per ft^2 (+ 95% CI)
0
10
20
30
40
DWELLEY
KARLSON

Figure 8.

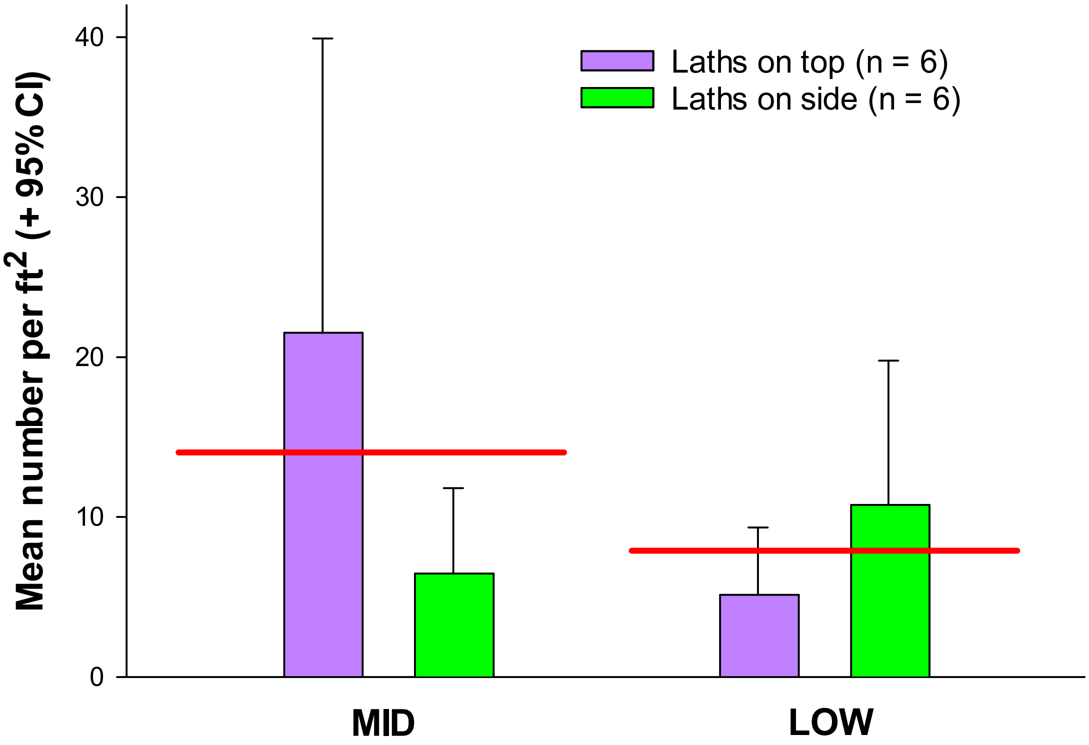

Mean number per ft² (+ 95% CI)
40
30
20
10
0
Laths on top (n = 6)
Laths on side (n = 6)
MID
LOW

Figure 9.

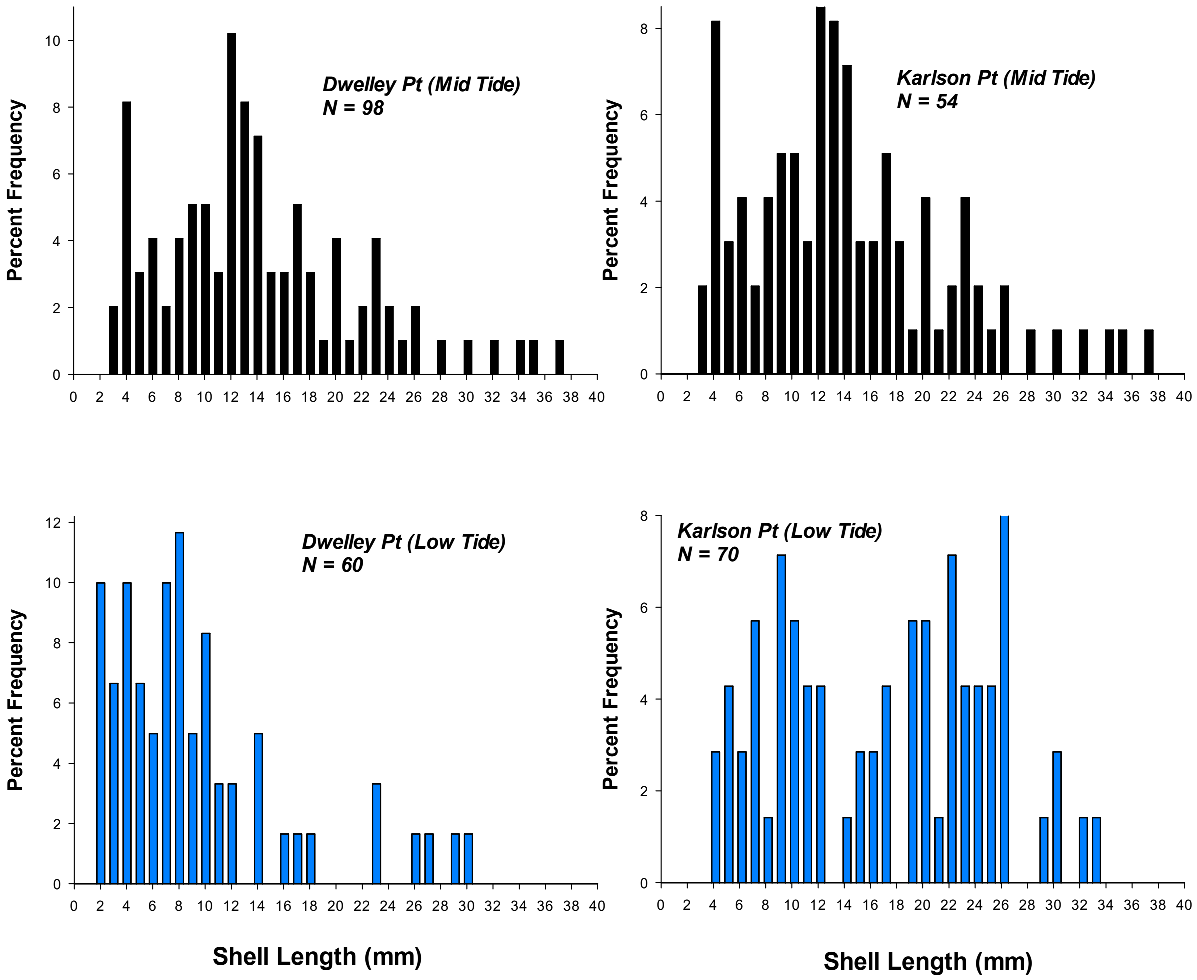

Dwelley Pt (Mid Tide)
N = 98
Karlson Pt (Mid Tide)
N = 54
Dwelley Pt (Low Tide)
N = 60
Karlson Pt (Low Tide)
N = 70
Percent Frequency
Percent Frequency
Percent Frequency
Percent Frequency
0
2
4
6
8
10
12
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Shell Length (mm)
Shell Length (mm)

Figure 10.

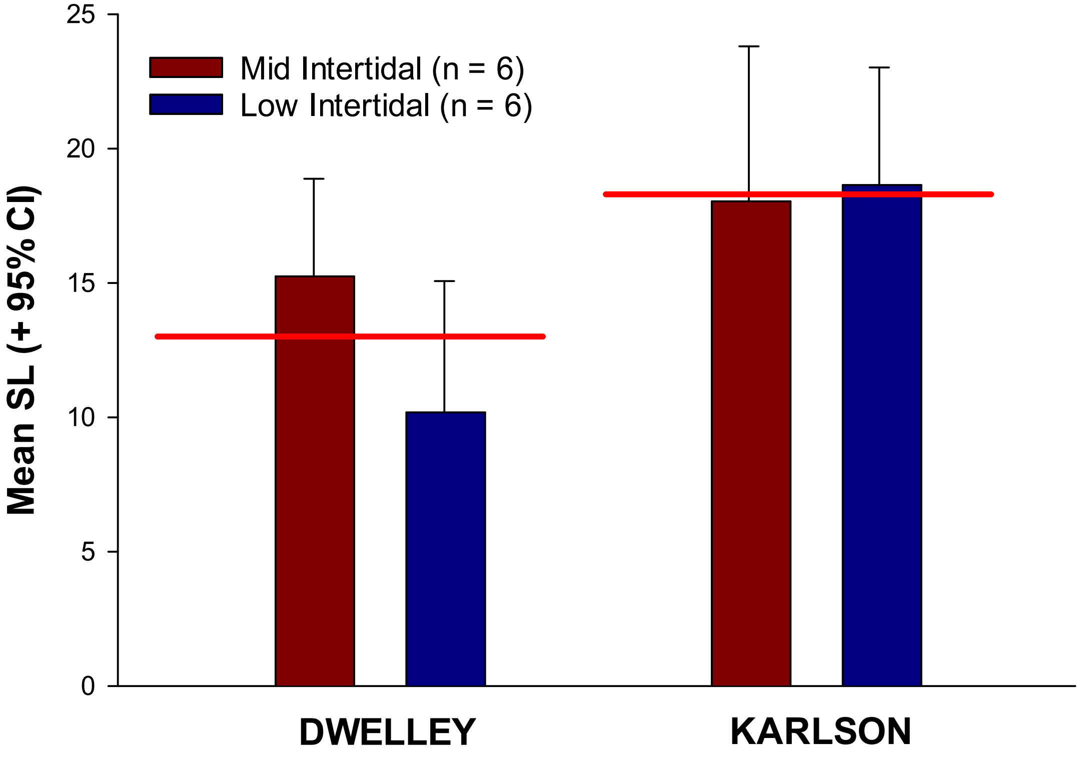
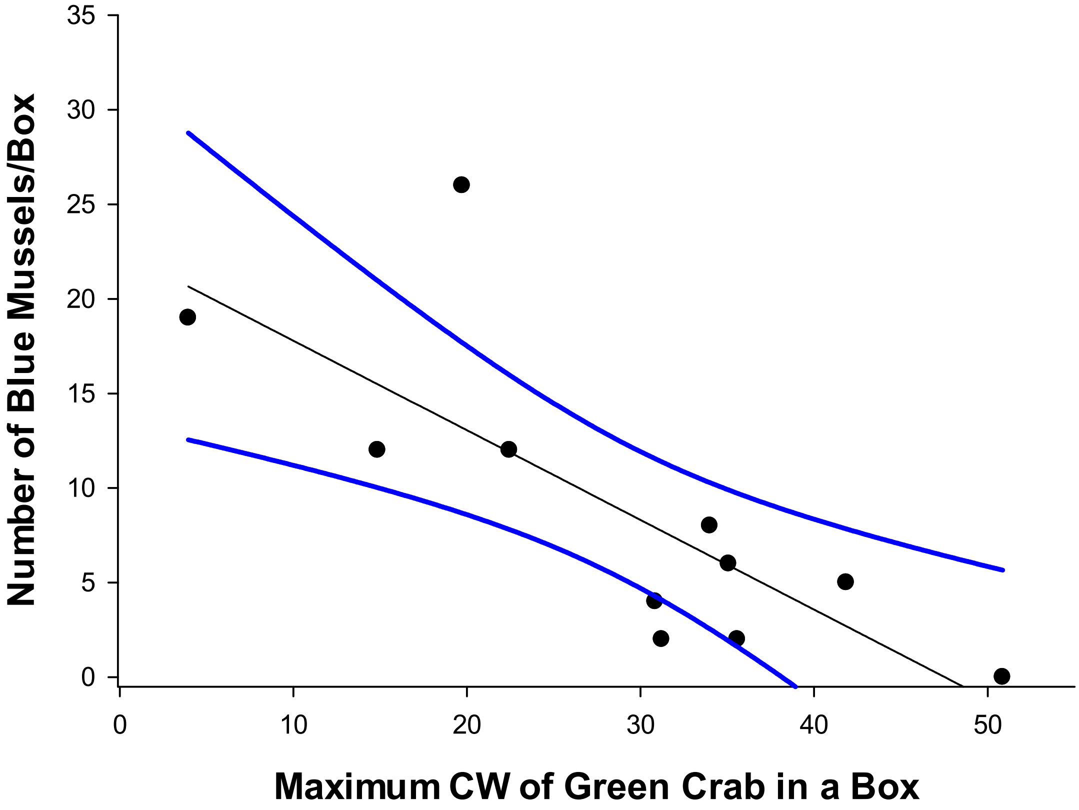

25
20
15
10
5
0
Mean SL (+ 95% CI)
Mid Intertidal (n = 6)
Low Intertidal (n = 6)
DWELLEY
KARLSON

Figure 11.



35
30
25
20
15
10
5
0
0
10
20
30
40
50
Number of Blue Mussels/Box
Maximum CW of Green Crab in a Box

Figure 12.

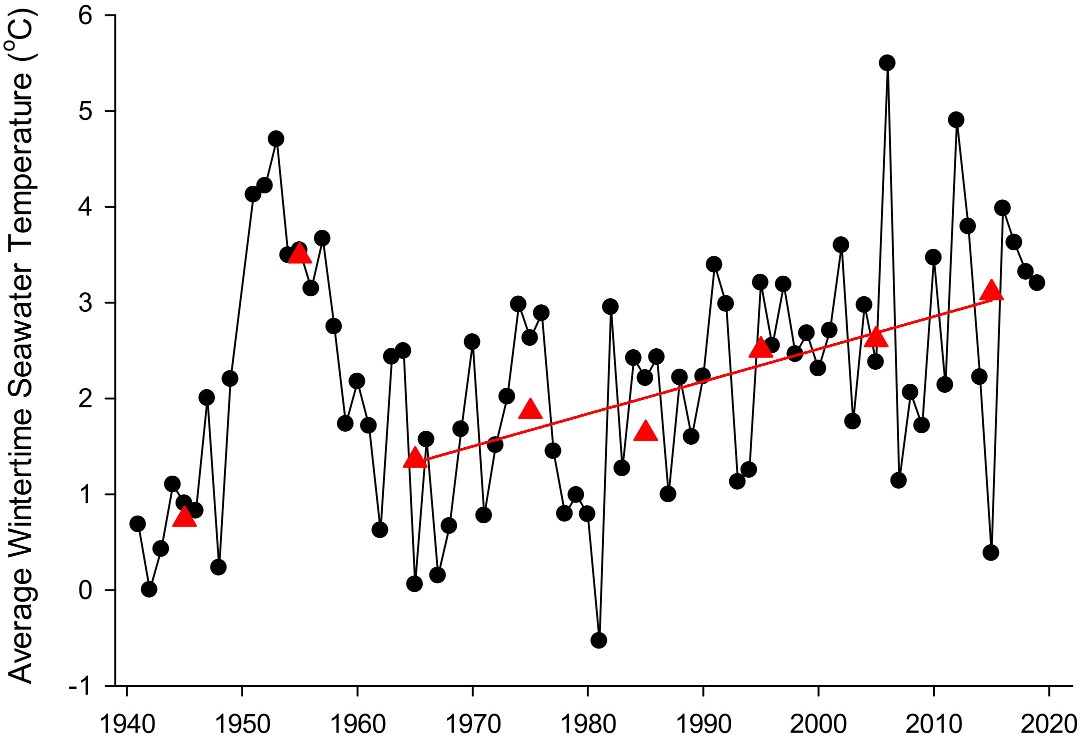
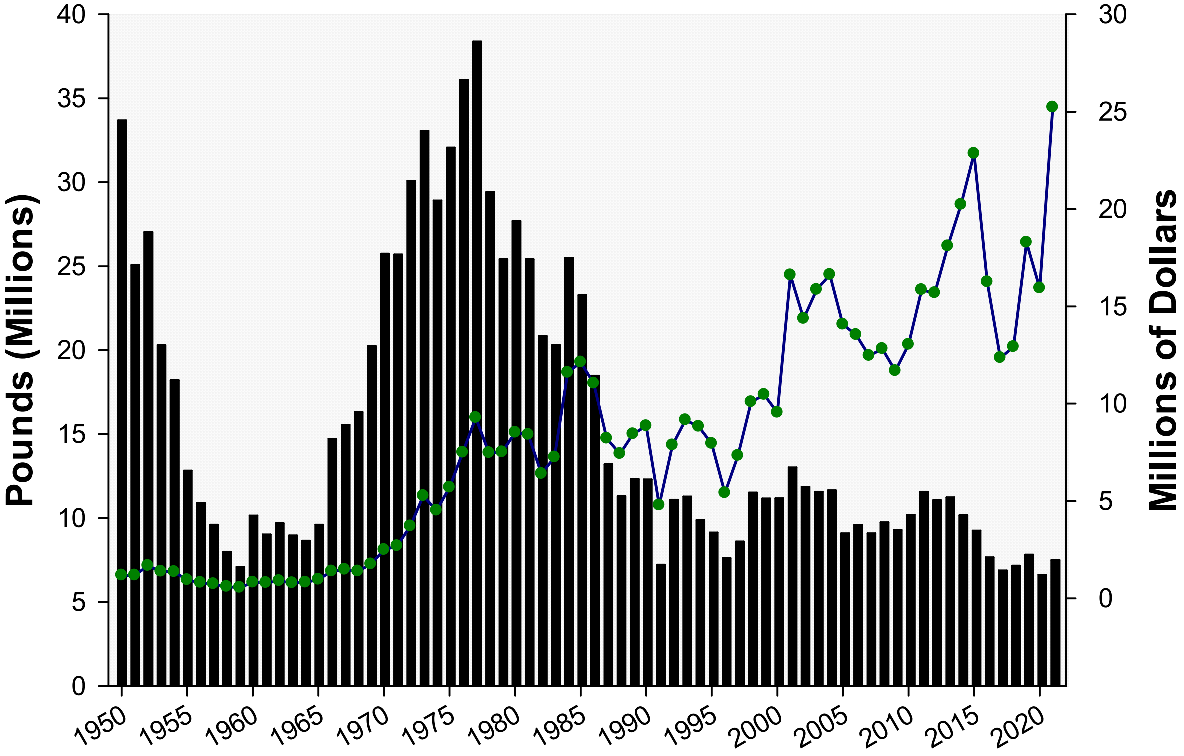

Average Wintertime Seawater Temperature (°C)
6
5
4
3
2
1
0
-1
1940
1950
1960
1970
1980
1990
2000
2010
2020

Figure 13.


Pounds (Millions)
Millions of Dollars
0
5
10
15
20
25
30
35
40
0
5
10
15
20
25
30
1950
1955
1960
1965
1970
1975
1980
1985
1990
1995
2000
2005
2010
2015
2020