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Research Article

Recruitment and Losses through the Life Cycle for Intertidal Clams in Willapa Bay, Washington

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When bivalve aquaculture production relies on natural recruitment, yields may decline due to density-independent constraints at multiple life stages. These life stage transitions include larval settlement, which is typically variable with rapid losses of newly settled individuals and the additional mortality from predation or abiotic factors (e.g., temperature, desiccation, and physical disturbance) as the bivalves grow. Recruitment monitoring and outplants were used to evaluate the potential limiting factors affecting different life stages in two nonnative clam species, Manila clams, *Ruditapes philippinarum*, and softshell clams, *Mya arenaria* in Willapa Bay, Washington, USA. Recruits (250–500 μm) did not differ in cumulative abundance in 2023 relative to prior years of monitoring (five recruitment seasons between 2011 and 2017). Recruits surviving to the end of the summer represented 12% or less of those that had arrived, but still showed spatial patterns consistent with rates of arrival. Manila clams outplanted across an elevation gradient suffered high mortality below mean lower low water regardless of size class (small: 8 mm and large: 20 mm), where native rock crabs (*Cancer productus*) were abundant. Clam growth declined at higher tidal elevations consistent with inundation time. European green crabs (*Carcinus maenas*) were relatively abundant at midtidal levels where commercial clam aquaculture typically occurs in the bay and where small clams were particularly reduced without predator protection from mesh. While these data support that green crabs may be reducing survival of 1-year-old clams at midintertidal elevations, they also identify earlier bottlenecks to repopulating commercial clam beds, which point out why seeding clams is used to maintain consistent production. Further exploration is needed before green crabs can be singled out as a new limit on clam yields relative to the roles of predation across the size classes of clams in Willapa Bay.

1. Introduction

Aquaculture practices are exerting increased control over all life cycle phases of cultivated species, yet farmers continue to rely on natural recruitment for many benthic species with pelagic larval stages. Accordingly, when yields fall, the question arises of what portion of the life cycle creates a bottleneck before a market-sized product is reached. Additionally, economic market factors can influence how much effort is put into harvesting. Determining causality for harvest declines has been challenging and requires data on both environmental conditions and performance [1, 2, 3] as well as harvest effort. Different datasets may be necessary to distinguish among multiple hypotheses for reduced yields, which can include periods of low recruitment and novel sources of postrecruitment mortality. Indeed, there are long-standing debates on whether pre- or postrecruitment factors limit marine benthic species [4]. A paradigm in soft-sediment systems is that biological interactions are more important than arrival of propagules for adult densities [5]. Exceptions, of course, have been documented [6]. Also, pre-and postsettlement processes both occurr prior to recruitment, which tends to be operationally defined at a life stage later than propagule arrival [7].

Two species of nonnative clams provide much of the intertidal clam recruitment in Willapa Bay, Washington, USA. In surveys, Manila clams (*Ruditapes philippinarum* (Adams and Reeve)) were 86% and softshell clams (*Mya arenaria* L.) were 9% of intertidal clams in summer 2011, based on 4,526 clams in 101 0.25 m^2 quadrats ([8]; unpublished data). Manila clams are commercially harvested from privately owned or

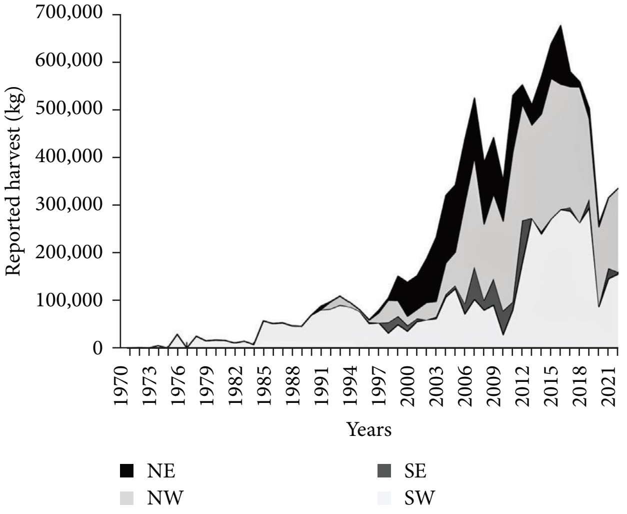


Figure 1: Reported harvest of Manila clams (*R. philippinarum*) as fresh whole weight from four regions of Willapa Bay, Washington, USA, from 1970 to 2022. Legend abbreviations refer to quadrants of the bay as follows: NE, northeast; NW, northwest; SE, southeast; SW, southwest. Data retrieved from Washington Department of Fish and Wildlife.

leased intertidal beds. Annual reported harvests rose from the late 1990s through 2016, but are now at half of peak levels (Figure 1). Clam recruitment has tended to be higher in the southern portion of the bay [9, 10], which has a longer water residence time than the northern portion closer to the ocean [11, 12].

Manila clams, native to the western Pacific ocean, were first reported in Willapa Bay in the 1950s, whereas softshell clams were introduced from the Atlantic ocean in the late 1800s [13]. Manila clams can reproduce at water temperatures of 14°C [14], and successful larval development over 2.5–3 weeks occurs at 18−28°C [15]. Spawning temperatures for softshell clams are lower (10−15°C) and reported development times more variable (10–35 days; [16]). For both species, however, an extended reproductive period occurs from late spring to early fall, and in some cases, two spawning peaks appear as water warms and then cools through a suitable temperature range [16, 17, 18, 19, 20, 21]. Interannual variation in recruitment (clams < 1 mm) can reach an order of magnitude in Manila clams [19] or softshell clams [22]. This recruitment variability underscores the importance of irregular strong year-classes for persistence of natural populations, as well as motivates the seeding of aquaculture beds with hatchery-produced clams [23]. Even if larval recruitment in benthic species is often coupled with adult reproductive output [24], spawning can differ in timing or amount each year, contributing to observed recruitment variability.

High mortality characterizes the first year postsettlement in clams, including Manila and softshell clams [22, 25]. This early mortality can be caused by abiotic stressors or predation; nevertheless, densities of year-1 individuals are often enhanced when natural set is protected from epibenthic predators [8, 26]. Predation remains a limiting factor for clams after the first year, and crabs can be particularly damaging [27]. Mortality due to crabs typically declines as clams grow larger, along with a shift from crushing to prying or chipping as a handling strategy [28, 29]. Thus, overall predation on clams will be influenced both by size structure and growth rates of clams, and by the community and population structure of crabs present. In Willapa Bay, two large species of cancrid crab, red rock crab (*Cancer productus*) and Dungeness crab (*Metacarcinus* (previously *Cancer*) *magister*), likely exert predation pressure on clams, particularly at lower intertidal and shallow subtidal elevations. Additionally, an invasive crab predator, European green crab (*Carcinus maenas*, hereafter green crab), has become increasingly abundant in Willapa Bay after 2015 [30], and could augment top-down control of intertidal clams.

Limiting factors on Willapa Bay's clam beds could be: (1) Insufficient recruitment through the summer, particularly in the southern portion of the bay that historically was supported by natural sets; (2) insufficient accumulation of surviving recruits by the end of the summer, pointing towards constraints very early in the benthic portion of the life cycle; and (3) poor survival of 1st and 2nd year clams before they reach harvestable size. Figure 2 schematically depicts these stages. To address the first potential limiting factor, summer recruitment patterns were compared between 2023 and five of the prior 12 years across multiple sites in the bay. To address the second potential limiting factor, the number of clams at the end of the season was compared to the cumulative number recruited. To address predation as a potential limiting factor of seeded clams, experimental exclusion of predators was conducted across tidal elevations, which generated a metric of predator impact. Patterns of predation were examined for correlation with the intertidal distribution of native crabs and green crabs sampled by trapping.

2. Methods

2.1. Study Sites. Willapa Bay is a shallow coastal estuary of extensive intertidal flats, located on the Pacific coast of Washington State, USA. Average depth is 3.2 m, diurnal tidal range is 3.2 m, and about half of the bay's total area dries on extreme low tides [32]. These tidal flats have been used for more than a century for oyster culture around mean lower low water (MLLW). More recently, clam aquaculture has been developed on beds at midtide levels about 1–2 m above MLLW. In summer 2023, clam recruitment was measured at these midlevel elevations at seven sites spanning 20 km on the west side of the bay (Figure 3 and Table S1). All sites were current clam beds, except the most northern site that was not in active use. The Breakwater (BR) site toward the middle of Willapa Bay was selected for a predator exclusion experiment across tidal elevations, coupled with a survey of predator densities by trapping.

2.2. Clam Recruitment. Clam recruitment was monitored with a standard bag (15 cm × 10 cm) made of window screen (1 mm mesh) and filled with pea gravel. One set of five bags per site was replaced monthly, and another set was placed at the beginning of the summer and retrieved at the end. Bags were set at 10 m intervals at a consistent elevation at each

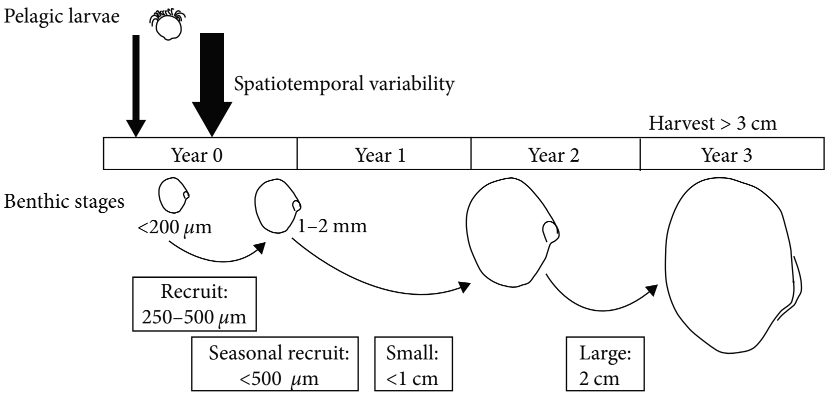


Figure 2: Schematic diagram of life history stages for clams where harvest depends on natural recruitment. Shell dimensions are typical for Manila clams in Willapa Bay, whereas softshell clams can reach >5 cm in 1 year and move substantially deeper in the sediment [31]. Boxed size–class stages correspond loosely to ages and were operationally defined for monitoring and experimental work in this study.

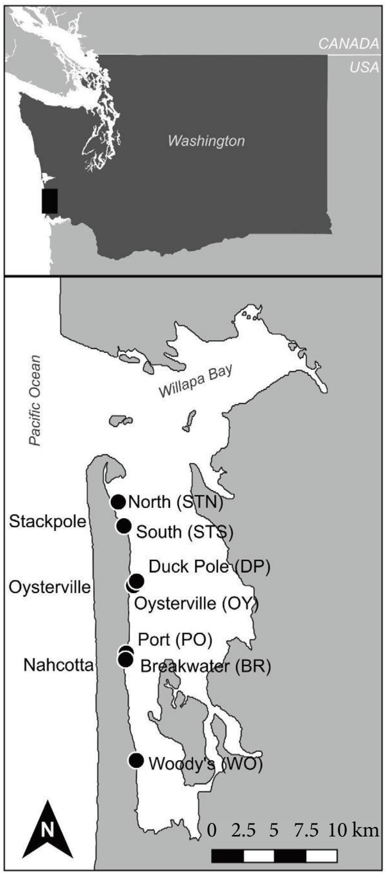


Figure 3: Map of study sites in Willapa Bay, Washington, USA. In top panel, the solid black square indicates map extent of lower panel. Abbreviations used for each site are indicated in parentheses.

site. Bags were deployed initially on 4 June 2023, with the monthly bags replaced on 20 June, 14 July, and 18 August 2023. The final set of monthly bags and the seasonal bags, which were present all summer, were collected on 17 September 2023.

Once collected, contents of each recruitment bag were sorted through a sieve series, with sieve sizes of 2,000, 500, and 250 μm. Gravel and other large sediment in the 2,000 μm sieve were set aside. The sediment in the 500 and 250 μm sieves was then poured into separate petri dishes to be sorted under a dissecting microscope (10–30x). After being separated from the fine sediment, clams were identified and recorded by species and the sieve they were found in. Softshell (*M. arenaria*) and Manila (*R. philippinarum*) clams were counted and identified, whereas other clams were counted but not identified to species. Only those clams on the 250 μm sieve were considered recruits in that month.

2.3. Clam Predation Experiment. An experiment to test predation on Manila clams was set up at the BR site at four tidal elevations: subzero (−0.23 m MLLW), low (+0.66 m MLLW), mid (+1.2 m MLLW), and high (+1.59 m MLLW). The mid zone corresponded with recruitment monitoring surveys. At each elevation, two treatments were established, one of which excluded predators and the other allowing access. At each elevation, six control and six exclusion replicates were set out in an alternating pattern 0.5 m apart. This experiment was deployed from 7 July 2023 to 15 August 2023.

Clams were placed into square mesh boxes that consisted of a side and base of window screen (1 mm mesh size), 20 cm on a side and 10 cm tall (Figure S1). The top of each experimental unit consisted of vexar mesh (1 cm mesh size). The top of the exclusion cages was complete, but for the open controls, two larger (3 cm × 10 cm) holes were cut to allow predator access while accounting for flow effects of the mesh. The boxes were dug into the sediment so the tops were flush with the sediment surface and were then filled with the excavated substrata. This substrate consisted of sand and mud with gravel at the three higher elevations and with shell at the lowest elevation. Substrate was not sieved to remove any live clams that were already present.

Two size classes of Manila clam were used in this experiment. Small clams were obtained from a commercial hatchery and were initially 8.6 mm (maximum dimension, $N = 30$). Large clams were sourced from the public tideland near Long Island in Willapa Bay and were between 20 and 30 mm maximum shell dimension. In each box, 20 small clams and five large clams were buried under the surface level of the substrate. Once the clams were buried, the tops on the exclusion boxes, which had been sewn to the box on two sides, were then zip tied on the open, unsewn sides to complete the exclusion top.

At the end of the experiment, the contents of each box were placed in a labeled bag in the field and sorted by hand in the lab. On sorting, Manila clams were separated from other species and separated into the two size classes that had been initially placed into each box. Clams larger than 40 mm were not counted, as they would have been inadvertently included with local sediment. Small clams were measured (nearest 0.01 mm) with digital calipers.

2.4. Crab Trapping. To assess the association of predatory crabs with clam mortality, baited traps were used to collect mobile epibenthic fauna along an elevation gradient at the same site where predator exclosures were deployed (BR). At each of four tidal elevations adjacent to the predator exclosures, sets of 10 traps were deployed in horizontal transects. Each transect consisted of five cylindrical minnow traps (Gee-40, 50 mm diameter opening, and 6.35 mm mesh; Figure S2) and five folding square fukui-style fish traps (13 mm mesh; Figure S2), alternating trap type and each trap separated by 10 m. Traps baited with ca. 100 g of Pacific mackerel (*Scomber japonicus*) were set on a morning lower-low tide (14 July 2023), allowed to soak through the overnight higher-high tide, and retrieved on the following day's lower-low tide (15 July 2023). Though this amounted to a deployment time of ~24 hr, soak time of traps decreased with increasing elevation and ranged from ~8.5 hr at the shallowest elevation to nearly 24 hr at the deepest elevation. While this soak time range is substantial, traps at all elevations were fishing for a nighttime high tide, which is the primary period during which crabs are foraging and enter traps. Moreover, this variability in soak time accurately reflects the difference in time tidal flats are available to crabs for foraging based on elevation, that is, the differential exposure to crab predators by elevation.

All organisms in traps were identified to species and counted. All crabs were measured to the nearest mm carapace width and totaled by sex and species for each trap (Figure S3). Green crabs were retained and euthanized, and all other catch was returned on site immediately.

2.5. Data Analysis

2.5.1. Hypothesis 1: Change in Recruitment. All seven sites in 2023 were included in a comparison of clam recruitment between the regions of the bay that differ in residence time. However, only three of these sites had data from prior years for a comparison of interannual recruitment. Each clam species was analyzed separately. For the seven sites in 2023, monthly counts of clams caught on the 250-*μm* sieve were used as a response variable. Predictor variables were collection day of year (DOY) and region (north (short residence time) and south (longer residence time)), and DOY × region interaction. Site was a random effect (four sites in the north and three in the south). Analyses were carried out with generalized linear mixed models and required a data distribution that accommodated zero counts as well as wide ranging counts when clams were present (tweedie distribution).

The three sites with recruitment data in prior years were Oysterville (OY), Port (PO), and Woody's (WO) (Figure 3). Oysterville and Woody's had 2 years of prior data (2016–17), and Port had 3 years (2011–2013; Table S2). In 2011–2013, the material collected from bags was sieved to 147 *μ*m rather than 250 *μ*m. As in 2023, recruitment bags were replaced monthly, but the total time when bags were out ranged from 57 to 153 days, while 2023 duration was in the middle of this range (105 days). The response variable, cumulative recruitment, was the sum across months for counts of each clam species caught on the 147- or 250-*μ*m mesh. In 2 years (2017 and 2023) counts were summed from bags replaced in the same position on the tidal flat, but in earlier years bag position was not tracked, and the sums were across a random bag choice for each month. Predictor variables were time period (current vs. prior) and site, since only three sites had prior data (too few to include as a random effect). Year was included as a categorical random variable to account for multiple prior years. It was not possible to include statistical interactions. Model framework was a generalized linear mixed effects model (Gaussian error, for log-transformed cumulative recruitment).

2.5.2. Hypothesis 2: Early Mortality. Early mortality of clams was tested across four sites with sufficient data, that is, all monthly bags and the bags left in place from June to September were recovered. The sum of monthly bags (counts on 250 *μ*m sieve) provided an index of cumulative recruitment through the summer. Cumulative recruitment was based on the specific position where a bag was placed (and replaced) within each site, and the counts were added across the four collection timepoints ($N = 5$ per site). Seasonal bags collected at the end of the summer represented the net outcome of recruitment and mortality. Net recruitment and mortality, from seasonal bags, was the count on the 500-*μ*m sieve at the end of summer. Seasonal counts were tested for correlation with cumulative recruitment (Pearson's r, $N = 4$ sites), and the fraction calculated as an index of early postsettlement survival.

2.5.3. Hypothesis 3: Predator Impacts across Tidal Elevations. Intertidal elevation and predator exclusion were evaluated for three response variables of Manila clams: number of small clams, size of small clams, and number of large clams. Elevation was included as a categorical factor for clam numbers since its influence could be nonlinear. Two-factor linear models were built, including the elevation × predation interaction, and distributions of residuals were examined and allowed a gaussian assumption for all responses.

To evaluate the variability of the predator community across the tidal gradient, the relative abundance of each crab species in traps was compared by tidal elevation. The effect of predation on clams at each elevation was estimated separately for each size class of clams at each elevation as the effect size (sample mean difference, Hedge's G; [33]) of the predator exclosure treatment on the number of clams remaining in each replicate at a given elevation.

All analyses were conducted using the R statistical software [34]. Models were built with the glmmTMB package

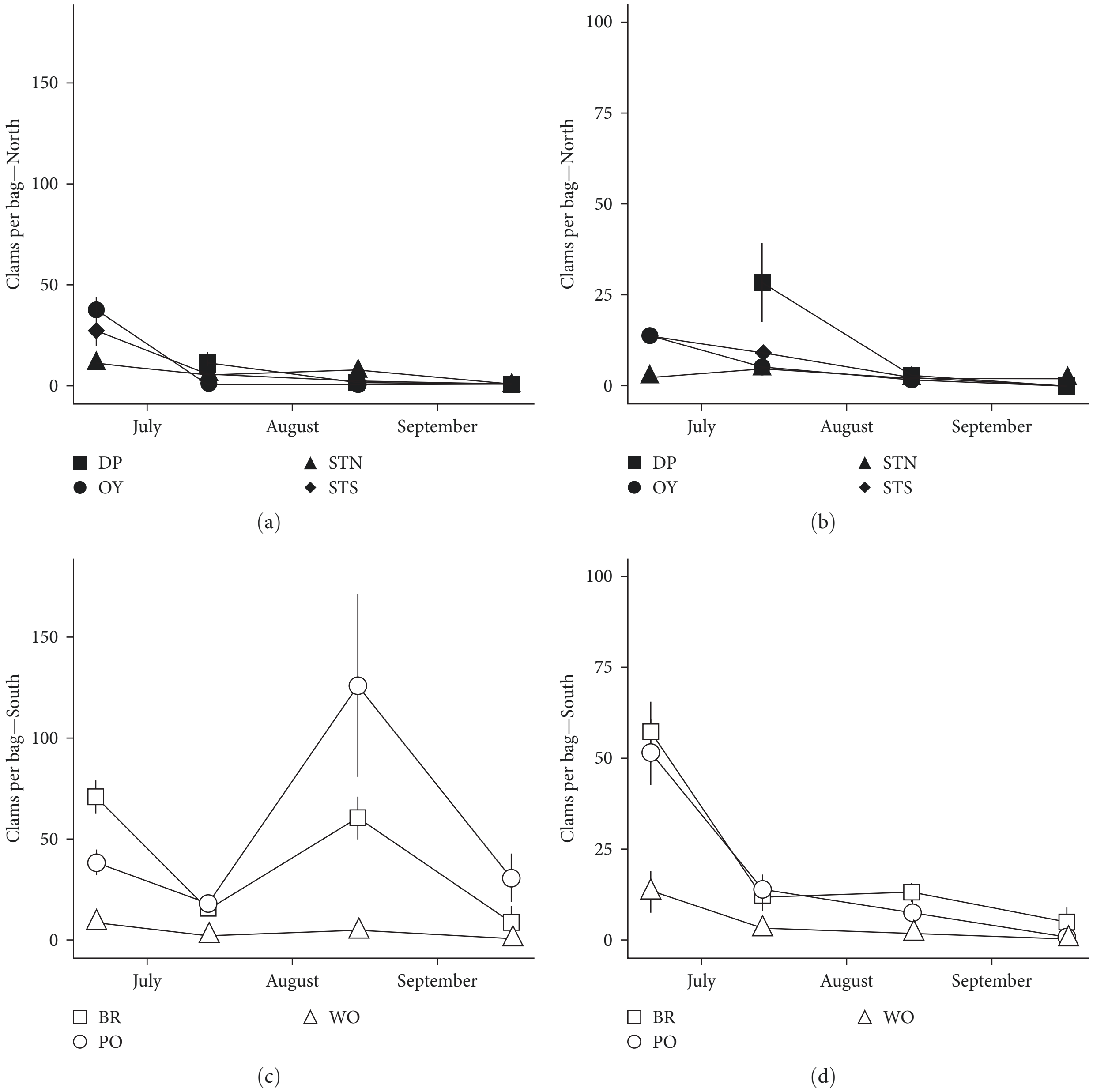


Figure 4: Monthly recruitment of intertidal clams at seven sites in Willapa Bay, Washington, USA, in 2023. (a) Manila clam, *R. philippinarum* northern sites; (b) softshell clam, *M. arenaria* northern sites; (c) *R. philippinarum* southern sites; and (d) *M. arenaria* southern sites. Note different y-axis scales by species. Bags were 15 cm × 10 cm in size, constructed of 1 mm mesh, and filled with pea gravel. Clams were counted from a 250-μm sieve. Dates on x-axis are collection dates. Error bars show standard error ($N = 5$). Site codes are in Figure 3.

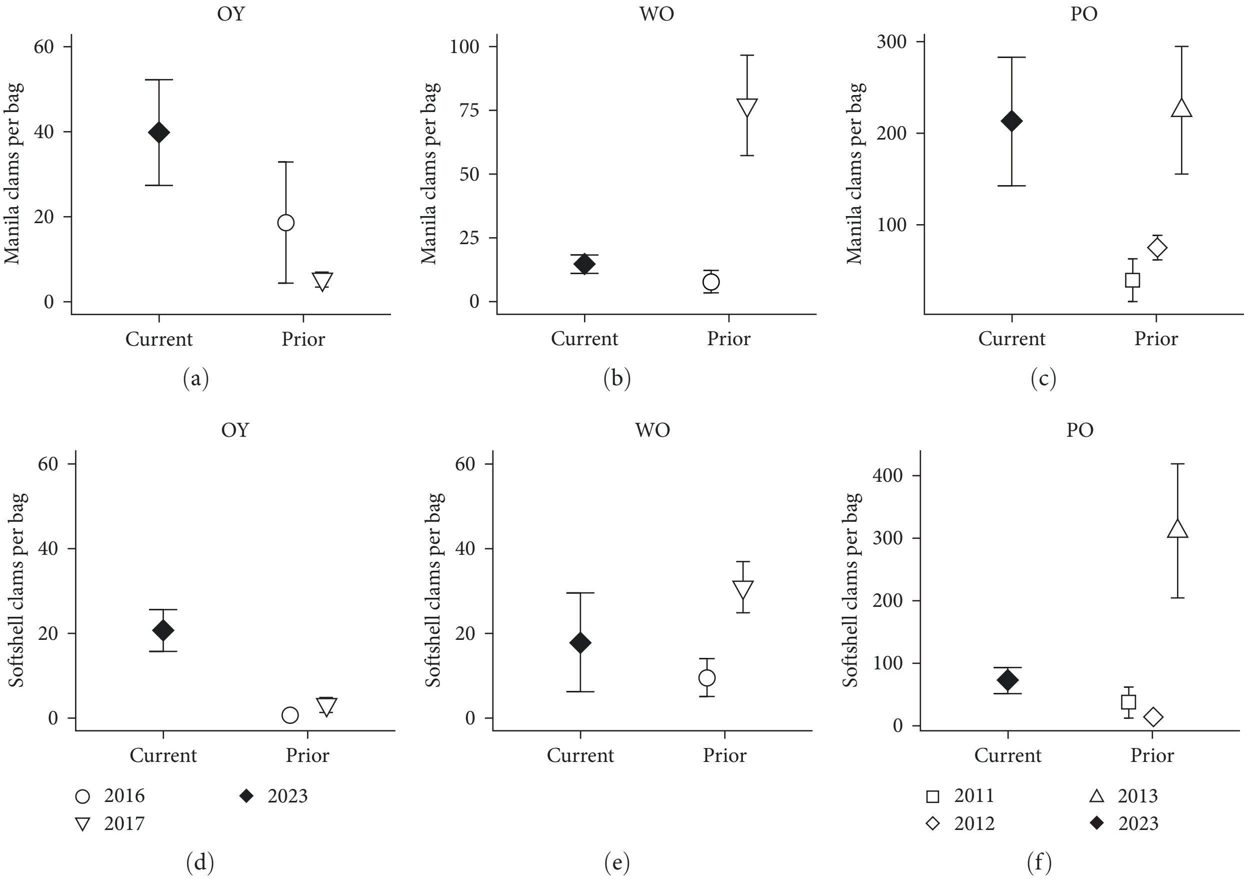
[35], residuals analyzed with the DHARMa package [36], and effect sizes calculated with the metafor package [33].

3. Results

3.1. Hypothesis 1: Change in Recruitment. In 2023, recruitment of Manila clams showed a significant spatiotemporal interaction effect, in which recruitment declined through the summer in the northern region but was more consistent in the southern region (day of year × region interaction: Z (1,122) = 5.6, $P < 0.001$). Nevertheless, the southern region overall had higher recruitment than the northern region (S: 127 (SE 51), N: 29 (SE 7) cumulative recruitment). For softshell clams, recruitment declined through the summer (Z (1,122) = −11.9, $P < 0.001$), while the main effect of region was not significant (Z (1,122) = 1.3, $P = 0.2$, Figure 4).

At the three sites where monthly recruitment of clams had been measured in previous years, recruitment in 2023 occurred at similar amounts (Figure 5). For Manila clams, 2023 was not distinguishable from prior years (Z (1,45) = −1.5, $P = 0.12$). For softshell clams, 2023 also was not distinguishable (Z (1,45) = −0.7, $P = 0.5$). For both clam species, recruitment differed by site (Port > Woody's > Oysterville).

3.2. Hypothesis 2: Early Mortality. The count of clams alive at the end of the summer recruitment period was positively



(a) (b) (c)

(d) (e) (f)

Figure 5: Cumulative recruitment of intertidal clams in several years between 2011 and 2023 at three sites in Willapa Bay, Washington, USA. (a–c) Manila clam, *R. philippinarum*, (d–f) softshell clam, *M. arenaria*. Three sites were: (a and d) Oysterville, (b and e) Woody's, and (c and f) Port. Note different *y*-axis scales. Bags were 15 cm x 10 cm in size, constructed of 1 mm mesh, and filled with pea gravel. Counts were from a 250-μm sieve (147 μm for prior years at the Port site). Error bars show standard deviation ($N = 2$ in 2012, $N = 3$ in 2013, $N = 8$ in 2017 and $N = 5$ in 2011, 2016, and 2023).

related to the cumulative number recruiting for Manila clams ($r = 0.96$, t (1,2) = 5.1, $P = 0.03$) but not significant in Eastern softshell clams ($r = 0.85$, t (1,2) = 2.3, $P = 0.15$). For Manila clams, the seasonal bags contained 11.4% of the cumulative count (5.3% SE, $N = 4$), and this survival index was also low for Eastern softshell clams (12.0%, 3.8% SE; Figure 6).

3.3. Hypothesis 3: Predator Impacts Across Tidal Elevations.

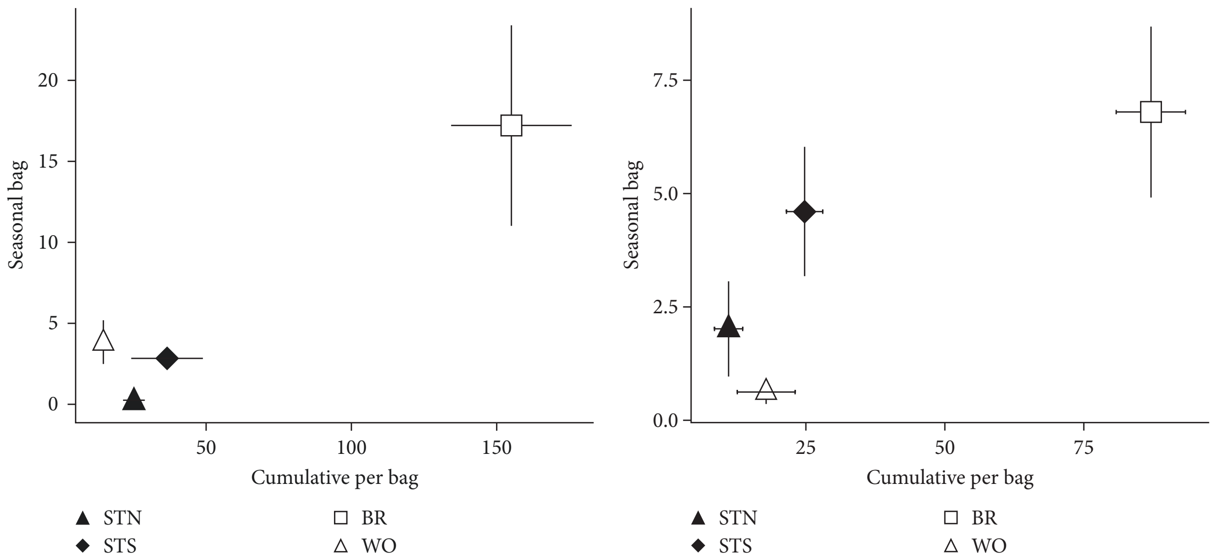
The importance of elevation and predators on clam survival in the predation experiment depended on the size class of clam deployed (Figure 7). Manila clam survival was poor at the lowest (subzero) tidal elevation for both small and large clams. At the three intertidal elevations, similar numbers of clams were found at the end of the 6-week experiment as were added initially.

Predator access reduced small clam numbers across all elevations (main effect of predator exclusion treatment). Statistically, for count of small clams as a response variable, the interaction of elevation × predation did not improve model fit. Small Manilla clam counts were higher where predators were excluded regardless of elevation (Z (1,40) = 3.8, $P < 0.001$). Small clam counts also differed by elevation (Z (1,40) = −9.4, $P < 0.001$) and were particularly low in the subzero zone.

By contrast, predator exclusion had the greatest effect on large clam numbers at the subzero elevation (interaction effect; Figure 7). The response variable of large clam count included the elevation × predation interaction in the best model, with predator exclusion having a larger effect at the subzero than other elevations (Z (1,37) = 2.23, $P = 0.03$; Figure 7).

Growth of small clams declined at higher tidal elevations, especially when elevation was included as a continuous variable (Z (1,29) = −2.7, $P = 0.006$) but did not differ by predator treatment (Z (1,29) = 0.32, $P = 0.75$; Figure 8). The interaction term was nonsignificant (elevation × predator treatment Z (1,29) = −0.43, $P = 0.67$).

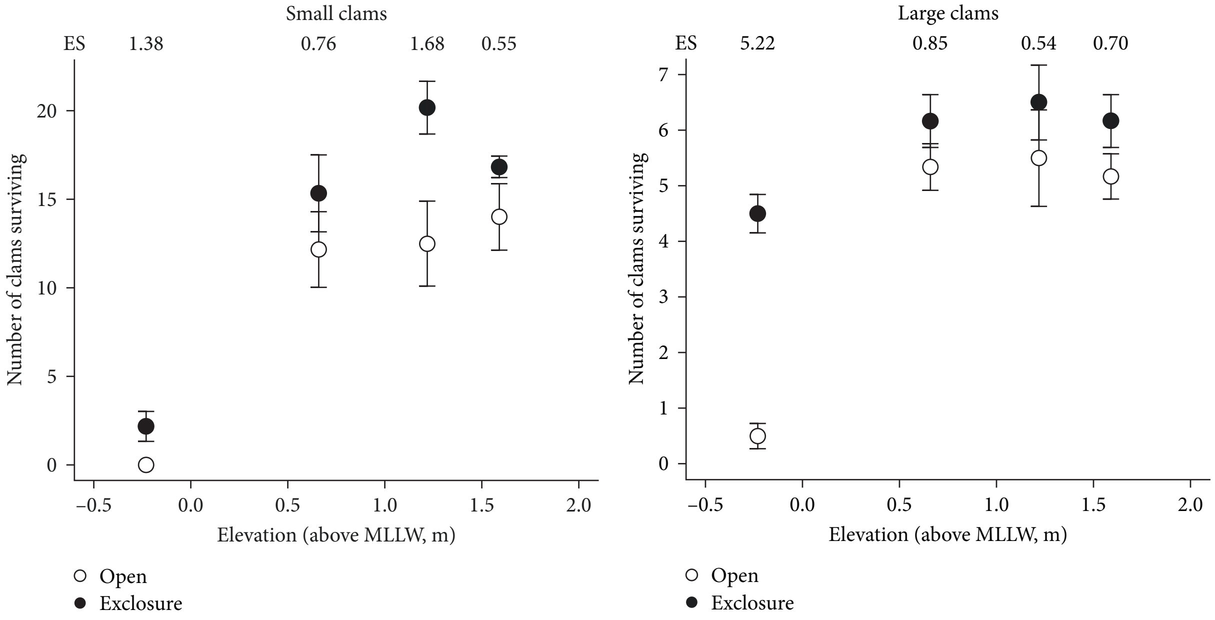
Crabs differed in abundance and size across tidal elevations (Figure 9 and Figure S3). Red rock crabs (*C. productus*) were predominant at the deepest (subzero) tidal elevation, where large clams disappeared from the open experimental units, corresponding to the largest effect size of exclosures on large clam survival (5.22). By contrast, small clams also survived poorly at the lowest elevation, but this occurred regardless of whether or not they were in an exclosure (ES = 1.38). Green crabs (*C. maenas*) peaked in abundance at the mid-intertidal elevation, where they exceeded the combined abundance of all other crab species. This was also the elevation



(a)

(b)

Figure 6: Recruitment of intertidal clams at four sites in Willapa Bay, Washington, USA, in 2023, comparing the count of clams still alive at the end of summer (seasonal bag) to the cumulative number recruiting. (a) Manila clam, *R. philippinarum*, (b) softshell clam, *M. arenaria*. Bags were 15 cm × 10 cm in size, constructed of 1 mm mesh, and filled with pea gravel. Error bars show standard error ($N = 5$).



(a)

(b)

Figure 7: Number of small (a) and large (b) Manila clams (*R. philippinarum*) retrieved from open (empty points) and exclosure (filled circles) experimental units at the end of the 6-week predation experiment across tidal elevations in 2023 at the Breakwater site in Willapa Bay, Washington, USA. Twenty small (8 mm) clams and five large (20 mm) clams were initially added to each experimental unit, which were also filled with local sediment. Error bars show standard error ($N = 6$). Bold numbers above plots indicate calculated effect size (SMD) for effect of exclosure at that elevation.

where the effect size of exclosures on small clam survival was greatest. Dungeness crabs (*M. magister*) were relatively most abundant at the deepest two elevations, but did not dominate the traps numerically at either. At the low elevation, they were present in traps at similar abundances as green crabs, but slightly larger in size. Native shore crabs (*H. oregonensis*) were extremely scarce at all elevations, including the highest elevations sampled. For both clam size classes, the effect sizes of exclosures were lowest at the highest elevation, where all crab species were rarely observed in traps.

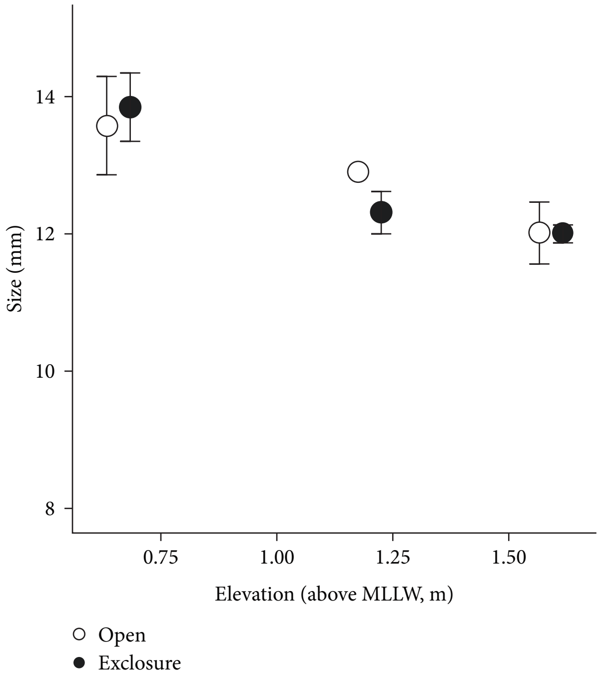


Figure 8: Shell size of small Manila clams, *R. philippinarum*, retrieved from open (empty points) and exclosure (filled circles) experimental units at the end of the 6-week predation experiment across tidal elevations in 2023 at the Breakwater site in Willapa Bay, Washington, USA. Average initial size was 8.1 mm. Size was averaged per experimental unit, and visual display is the average across experimental units, with error bars showing standard error ($N = 6$). The lowest tidal elevation is excluded due to few surviving clams. Points are jittered slightly along the *x*-axis for visibility.

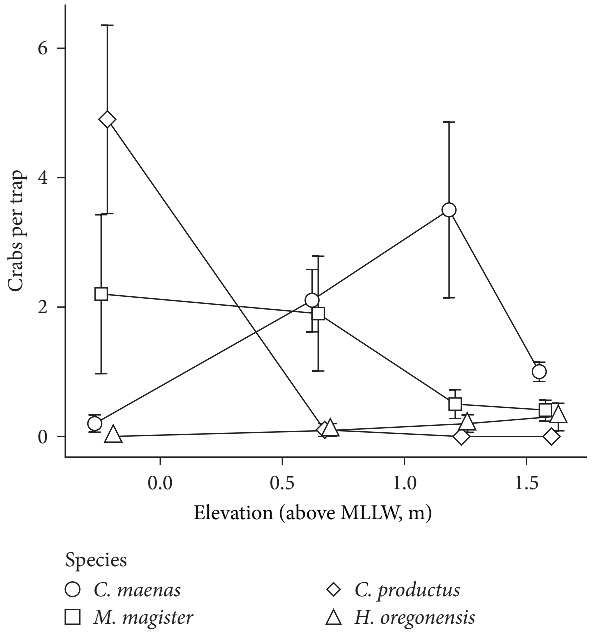


Figure 9: Average number of crabs per trap by species (European green crabs, *C. maenas*; red rock crab, *C. productus*; hairy shore crab, *Hemigrapsus oregonensis*; and Dungeness crab, *M.* (= *Cancer*) *magister*) captured in trapping across tidal elevations. Points are jittered slightly along the *x*-axis for visibility. Error bars show standard error ($N = 10$).

4. Discussion

A general feature of benthic soft-sediment species with pelagic larval stages is that the numbers of settling larvae are highly variable interannually [7], and these small benthic individuals are highly vulnerable to mortality ([37]; Figure 2). The life-stage-specific data collected in the present study on Manila and softshell clams aligned with these more general patterns. In the present study, even though recruitment was measured monthly and did not count early mortalities, year-to-year recruitment variability was high. By contrast, spatial patterns of clam recruitment were maintained over time, as recruitment tended to be greater with longer water residence time (Figures 4 and 5; [9]). By the end of summer, losses of newly recruited clams reached nearly 90%, even when surrounded by 1-mm protective mesh and gravel (Figure 6). Recruitment was not statistically worse in 2023 than in the previous decade (Figure 5), while the rapid drop in clam numbers shortly following settlement has been observed previously in Willapa Bay [8]. The time series lacks data for 2018–2022 that could determine if several years of recruitment failure underlies the recent drop in harvested Manila clams (Figure 1); if recruitment or survival were low in 2018–2022, that would be consistent with observed harvest declines. Of course, the most dramatic drop occurred in 2020, when a global pandemic affected market demand, and the aquaculture industry in general suffered [38]. Tradeoffs between predation risk and growth were evident across tidal elevations in the experimental study of Manila clams at one site (Figures 7, 8, and 9). A novel source of top-down control has appeared with the invasion of green crabs, particularly for ca. 1-year-old Manila clams, and additional work will be necessary to quantify their role in limiting market-sized clams. It is clear, however, that these two species overlap in mid-intertidal elevations, as this is the predominant elevation at which commercial clams are grown in Willapa Bay.

Mechanisms have been explored that address why settlement varies, and how this variability might influence post-settlement survival. For instance, more than half of available datasets for marine benthic taxa show correlations between the number of spawned larvae and settlement magnitude [24]. For clams with extended settlement seasons, postsettlement survival can differ by arrival time. Early settlers have more time to grow and acquire resources prior to challenging winter conditions. In northern Europe, early settlers of softshell clams are also advantaged by preceding cold winters, which delay the arrival of predators [39]. Late-settling clams are at an advantage in eastern US bays because they arrive after seasonal declines of predators [31]. In the present study, data were not collected to test a relationship between recruitment timing or magnitude and early postsettlement survival. By contrast, across sites, recruitment at the end of the season was improved by numbers arriving during the season, with some standout sites in the high-water-residence portion of the bay (PO and BR). Similarly, spatial variation in settlement of clams is related to water circulation and properties within bays [40, 41, 42] and can show consistent patterns across bays despite temporal recruitment variability [10].

Survival of bivalves immediately following metamorphosis and settlement is often low in benthic marine species, with losses of 95%–99% not uncommon over a few days to weeks [25, 43]. The small numbers of live clams in the seasonal bags relative to cumulative recruitment are in keeping with this general pattern of high mortality shortly following settlement (Figure 6). Small mesh can protect clams of 3–6 mm size based on field outplant experiments [44], and still smaller clams disappear more rapidly outside than inside mesh bags [8]. Physical stressors such as low tide-related heat or drying, or accumulation of fine particles and interference with feeding, could result in mortality of newly recruited clams. Some predators of clams have body sizes that would allow them to access clams within mesh bags [26], consistent with our observations of feeding holes in many dead clams at the end of the summer (Figure S4). Evidence does not point towards any of these factors only recently becoming problematic. It is nevertheless worth noting that losses of clams within a few months, even within the recruitment monitoring bags, could contribute to the failure of clams to recruit to a visible size for farmers to see on their beds.

The impacts of predators on infaunal bivalves depend on attributes of the bivalve (burrowing depth and shell strength) as well as environment (inundation time and sediment type; [45]). Predation rates typically decline for larger clams [46, 47]. Crabs are less likely to kill clams as clams grow, in part due to extended handling time as crabs utilize crushing to open small clams and prying to open large clams [29]. All four crab species detected by trapping are known to consume clams [28, 48, 49, 50] but only two species, native red rock crab (*C. productus*) and invasive European green crab (*C. maenas*), were notable at elevations where clam loss occurred due to predation in the field experiment.

The establishment of European green crabs in Willapa Bay constitutes a novel top-down pressure on mid-intertidal clams, which is the major zone for commercial aquaculture. In other regions where green crabs have invaded, field studies demonstrate that they can reduce infaunal densities of small softshell clams [51] and change community structure [52, 53]. The predator exclusion experiment was consistent with green crabs reducing the abundance of ca. 1 cm Manila clams. The larger size class of clams, however, only experienced significant predation at elevations where red rock crabs (*C. productus*) were most abundant, suggesting a size refuge for adult clams from other crab species. This occurred notwithstanding the abundance of large green crabs (>70 mm carapace width) at multiple elevations (Figure S3), which have previously been shown to be capable predators of a wide size range of both Manila (>36 mm; [54, 55]) and softshell [56] clams.

Based on gut contents of green crabs analyzed via diet DNA, consumption of Manila clams by adult green crabs in Willapa Bay is rare, while consumption of softshell clams is comparatively more frequent [57]. Therefore, the additional contribution of green crabs to top-down control of intertidal clams is not yet resolved. Any effect of green crabs needs to be placed in a context of the existing community of predators. For instance, red rock crabs were clearly implicated as considerable predators of clams below MLLW in the current study, and agonistic competition among crab species might alter feeding behavior [58, 59, 60]. Moreover, because green crabs reduce populations of native shore crabs (*Hemigrapsus* spp.; [61], Rubinoff et al. in prep), the net effect of green crab presence could include an indirect benefit for <1-year-old clams.

Protection from predators is a reliable way to increase aquaculture yields [62] although crabs also can recruit into mesh bags in aquaculture and subsequently cause high mortality [55, 63]. All monitoring sites, including Breakwater, where the experiment was carried out, were clam beds amended with gravel to protect against predators. Therefore, additional predator protection was provided by the net used in the predation experiment (1 cm mesh) over and above graveling. It is possible that the larger holes in the open treatments allowed clams to leave, so some of the losses might not be from predation. Even in the predator exclusion treatment, clams were lost at the lowest tidal elevation, where red rock crabs may have been particularly capable of removing small clams through the net. Alternatively, clams might have been dislodged through the mesh, which was slightly larger than the maximum shell dimension at outplant.

This study points out three environmental limitations to clam production when farmers depend on wild set to repopulate their beds (Figure 2). First, the growth rates of clams decline at higher tidal elevations within the range used for clam farms (Figure 8), which could generate longer crop cycles under restricted growth. Second, a strong tradeoff exists at low elevations where no size-escape existed against predators, meaning that faster growth could not compensate for strong top-down control. Finally, netting protected clams from predation even when placed on graveled tidal flats that likely already deter clam predators (Figure 7). While our data support that green crabs may be reducing survival of 1-year-old clams at mid-intertidal elevations, they also identify earlier bottlenecks to repopulating commercial clam beds, which point out why seeding clams is a method for evening out production [23]. The relative roles of predators across size classes of clams in Willapa Bay, including those that could cause losses within small-mesh bags, need further exploration before green crab can be singled out as a new limit on clam yields.

Data Availability

Data supporting the study presented here are published via Mendeley: https://doi.org/10.17632/mfsz6zpjkm.1.

Disclosure

The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA (National Oceanic and Atmospheric Administration) or any of its sub-agencies. WDFW provided Manila clam landings data.

Conflicts of Interest

The authors declare that there is no conflict of interest regarding the publication of this article.

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Supplementary Materials

Two tables of study site locations and clam recruitment (2011–2023), and four figures showing sizes of trapped crabs, and photographs of experimental exclosures, trapping materials, and clam recruits. (*Supplementary Materials*)

References

[1] X. de Montaudouin, I. Arzul, N. Caill-Milly et al., “Asari clam (*Ruditapes philippinarum*) in France: history of an exotic species 1972–2015,” *Bulletin of Japan Fisheries Research and Education Agency*, vol. 42, pp. 35–42, 2016.

[2] C. N. Glaspie, R. D. Seitz, M. B. Ogburn, C. F. Dungan, and A. H. Hines, “Impacts of habitat, predators, recruitment, and disease on soft-shell clams *Mya arenaria* and stout razor clams *Tagelus plebeius* in Chesapeake Bay,” *Marine Ecology Progress Series*, vol. 603, pp. 117–133, 2018.

[3] M. Toba, J. Kakino, K. Tada, Y. Kobayashi, and H. Tsuchie, “Production of asari (Manila) clams, *Ruditapes philippinarum*, during the period of harvest decrease in the, 2000s, in the Banzu tidal area, Tokyo Bay,” *Aquatic Living Resources*, vol. 33, Article ID 14, 2020.

[4] H. L. Hunt and R. E. Scheibling, “Role of early post-settlement mortality in recruitment of benthic marine invertebrates,” *Marine Ecology Progress Series*, vol. 155, pp. 269–301, 1997.

[5] E. B. Olafsson, C. H. Peterson, and W. G. Ambrose, “Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post-settlement processes,” *Oceanography and Marine Biology: An Annual Review*, vol. 65, pp. 65–109, 1995.

[6] F. Van de Meutter, O. Bezdenjesnji, N. De Regge et al., “The cross-shore distribution of epibenthic predators and its effect on zonation of intertidal macrobenthos: a case study in the river Scheldt,” *Hydrobiologia*, vol. 846, no. 1, pp. 123–133, 2019.

[7] S. Fraschetti, A. Giangrande, A. Terlizzi, and F. Boero, “Pre- and post-settlement events in benthic community dynamics,” *Oceanologica Acta*, vol. 25, no. 6, pp. 285–295, 2002.

[8] J. L. Ruesink, N. Freshley, S. Herrold, A. C. Trimble, and K. Patten, “Influence of substratum on non-native clam recruitment in Willapa Bay, Washington, USA,” *Journal of Experimental Marine Biology and Ecology*, vol. 459, pp. 23–30, 2014.

[9] J. L. Ruesink, K. van Raay, A. Witt et al., “Spatio-temporal recruitment variability of naturalized Manila clams (*Ruditapes philippinarum*) in Willapa Bay, Washington, USA,” *Fisheries Research*, vol. 151, pp. 199–204, 2014.

[10] J. N. Kobelt, D. S. Yiu, M. N. Dethier, and J. L. Ruesink, “Spatiotemporal variation in clam recruitment among beaches in Washington State (USA),” *Marine Ecology*, vol. 45, no. 3, Article ID e12790, 2024.

[11] N. S. Banas, P. S. McDonald, and D. A. Armstrong, “Green crab larval retention in Willapa Bay, Washington: an intensive Lagrangian modeling approach,” *Estuaries and Coasts*, vol. 32, no. 5, pp. 893–905, 2009.

[12] N. S. Banas and B. M. Hickey, “Mapping exchange and residence time in a model of Willapa Bay, Washington, a branching, macrotidal estuary,” *Journal of Geophysical Research: Oceans*, vol. 110, no. C11, Article ID C11011, 2005.

[13] M. J. Wonham and J. T. Carlton, “Trends in marine biological invasions at local and regional scales: the northeast Pacific Ocean as a model system,” *Biological Invasions*, vol. 7, no. 3, pp. 369–392, 2005.

[14] M. Delgado and A. Pérez Camacho, “Influence of temperature on gonadal development of *Ruditapes philippinarum* (Adams and Reeve, 1850) with special reference to ingested food and energy balance,” *Aquaculture*, vol. 264, no. 1–4, pp. 398–407, 2007.

[15] Z. Huo, Y. Li, M. Golam Rbbani, Q. Wu, and X. Yan, “Temperature challenge on larvae and juveniles of the Manila clam *Ruditapes philippinarum*,” *Aquaculture Research*, vol. 49, no. 4, pp. 1727–1731, 2018.

[16] P. V. R. Snelgrove, B. F. Beal, and V. S. Kennedy, “Reproduction and larval biology of the soft-shell clam *Mya arenaria*,” in *The Soft-Shell Clam Mya arenaria: Biology, Fisheries, and Mariculture*, pp. 51–87, American Fisheries Society, Bethesda, Maryland, 2023.

[17] J. Humphreys, R. W. G. Caldow, S. McGrorty, A. D. West, and A. C. Jensen, “Population dynamics of naturalised Manila clams *Ruditapes philippinarum* in British coastal waters,” *Marine Biology*, vol. 151, no. 6, pp. 2255–2270, 2007.

[18] A. C. Jensen, J. Humphreys, R. W. G. Caldow, C. Grisley, and P. E. J. Dyrynda, “Naturalization of the Manila clam (*Tapes philippinarum*), an alien species, and establishment of a clam fishery within Poole Harbour, Dorset,” *Journal of the Marine Biological Association of the United Kingdom*, vol. 84, no. 5, pp. 1069–1073, 2004.

[19] D. Munroe and R. S. Mckinley, “Effect of predator netting on recruitment and growth of Manila clams (*Venerupis philippinarum*) on soft substrate intertidal plots in British Columbia, Canada,” *Journal of Shellfish Research*, vol. 26, no. 4, pp. 1035–1044, 2007.

[20] Y. Ren, B. Xu, Y. Guo, M. Yang, and J. Yang, “Growth, mortality and reproduction of the transplanted Manila clam (*Ruditapes philippinarum* Adams and Reeve 1850) in Jiaozhou Bay,” *Aquaculture Research*, vol. 39, no. 16, pp. 1759–1768, 2008.

[21] M. J. Uddin, H.-S. Yang, K.-J. Park, C.-K. Kang, H.-S. Kang, and K.-S. Choi, “Annual reproductive cycle and reproductive efforts of the Manila clam *Ruditapes philippinarum* in Incheon Bay off the west coast of Korea using a histology-ELISA combined assay,” *Aquaculture*, vol. 364-365, pp. 25–32, 2012.

[22] J. A. Commito, “Population dynamics of the soft-shell clam Mya arenaria,” in *The Soft-Shell Clam Mya arenaria: Biology, fisheries, and Mariculture*, pp. 167–192, American Fisheries Society, Bethesda, Maryland, 2023.

[23] P. Becker, C. Barringer, and D. C. Marelli, “Thirty years of sea ranching Manila clams (*Venerupis philippinarum*): successful techniques and lessons learned,” *Reviews in Fisheries Science*, vol. 16, no. 1–3, pp. 44–50, 2008.

[24] S. G. Morgan, "Coupling and decoupling of reproduction and larval recruitment," *Estuaries and Coasts*, vol. 45, no. 1, pp. 272–301, 2022.

[25] J. G. Williams, "Growth and survival in newly settled spat of the Manila clam, *Tapes japonica*," *Fishery Bulletin*, vol. 77, no. 4, pp. 891–900, 1980.

[26] B. F. Beal, "Predators and competitors of the soft-shell clam Mya arenaria," in *The Soft-Shell Clam Mya arenaria: Biology, Fisheries, and Mariculture*, pp. 193–270, American Fisheries Society, Bethesda, Maryland, 2023.

[27] A. Meira, J. E. Byers, and R. Sousa, "A global synthesis of predation on bivalves," *Biological Reviews*, vol. 99, no. 3, pp. 1015–1057, 2024.

[28] M. N. Dethier, K. Dobkowski, A. Noreen, M. Yun, and A. Moosmiller, "Vulnerability of juvenile clams to predation by shore crabs," *Aquaculture*, vol. 506, pp. 350–354, 2019.

[29] Y. Sun, F. Wang, X. Su, D. Liu, and S. Dong, "Size matters for predator-prey relationships: the case of swimming crab *Portunus trituberculatus* preying on Manila clam *Ruditapes philippinarum*," *Aquaculture*, vol. 479, pp. 638–644, 2017.

[30] S. B. Yamada, C. Royer, S. Schooler, R. Flitcroft, M. Vance, and A. Randall, "Status of the European green crab, *Carcinus maenas*, (aka 5-spine crab) in Oregon estuaries. Report for 2022," Oregon State University, Corvallis, Oregon, 2023, https://www.oregon.gov/dsl/ss/Documents/CarcinusMaenas_report_2022.pdf.

[31] R. D. Seitz and A. H. Hines, "Ecology of the soft-shell clam *Mya arenaria*," in *The Soft-Shell Clam Mya arenaria: Biology, Fisheries, and Mariculture*, pp. 139–165, American Fisheries Society, Bethesda, Maryland, 2023.

[32] B. M. Hickey and N. S. Banas, "Oceanography of the U.S. Pacific northwest coastal ocean and estuaries with application to coastal ecology," *Estuaries*, vol. 26, no. 4, pp. 1010–1031, 2003.

[33] W. Viechtbauer, "Conducting meta-analyses in R with the metafor package," *Journal of Statistical Software*, vol. 36, no. 3, pp. 1–48, 2010.

[34] R Development Core Team, "R: A language and environment for statistical computing," 2023.

[35] M,E. Brooks, K. Kristensen, K,J,van Benthem et al., "glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling," *The R Journal*, vol. 9, no. 2, pp. 378–400, 2017.

[36] F. Hartig, "DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models," 2022.

[37] L. A. Gosselin and P. Y. Qian, "Juvenile mortality in benthic marine invertebrates," *Marine Ecology Progress Series*, vol. 146, pp. 265–282, 1997.

[38] M. C. Mangano, M. Berlino, L. Corbari et al., "The aquaculture supply chain in the time of COVID-19 pandemic: vulnerability, resilience, solutions and priorities at the global scale," *Environmental Science and Policy*, vol. 127, pp. 98–110, 2022.

[39] J. J. Beukema and R. Dekker, "Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat," *Marine Ecology Progress Series*, vol. 513, pp. 1–15, 2014.

[40] C. Dang, X. de Montaudouin, M. Gam, C. Paroissin, N. Bru, and N. Caill-Milly, "The Manila clam population in Arcachon Bay (SW France): can it be kept sustainable?" *Journal of Sea Research*, vol. 63, no. 2, pp. 108–118, 2010.

[41] N. Hasegawa, H. Abe, T. Onitsuka, and S. Ito, "Association between the planktonic larval and benthic stages of Manila clam *Ruditapes philippinarum* in eastern Hokkaido, Japan," *Fisheries Science*, vol. 84, no. 2, pp. 237–249, 2018.

[42] R. J. H. Herbert, J. Willis, E. Jones et al., "Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam, *Ruditapes philippinarum*, in the UK," *Journal of Biogeography*, vol. 39, no. 3, pp. 585–599, 2012.

[43] B. F. Beal, C. R. Coffin, S. F. Randall et al., "Spatial variability in recruitment of an infaunal bivalve: experimental effects of predator exclusion on the softshell clam (*Mya arenaria* L.) along three tidal estuaries in Southern Maine, USA," *Journal of Shellfish Research*, vol. 37, no. 1, pp. 1–27, 2018.

[44] M. N. Dethier, J. Kobelt, D. Yiu, L. Wentzel, and J. L. Ruesink, "Context-dependence of abiotic and biotic factors influencing performance of juvenile clams," *Estuarine, Coastal and Shelf Science*, vol. 219, pp. 201–209, 2019.

[45] R. D. Seitz, R. N. Lipcius, A. H. Hines, and D. B. Eggleston, "Density-dependent predation, habitat variation, and the persistence of marine bivalve prey," *Ecology*, vol. 82, pp. 2435–2451, 2001.

[46] R. W. Elner, "The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.)," *Marine Behaviour and Physiology*, vol. 7, no. 1, pp. 15–24, 2009.

[47] M. E. Sanchez-Salazar, C. L. Griffiths, and R. Seed, "The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.)," *Journal of Experimental Marine Biology and Ecology*, vol. 111, no. 2, pp. 181–193, 1987.

[48] E. G. Boulding, "Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time," *Journal of Experimental Marine Biology and Ecology*, vol. 76, no. 3, pp. 201–223, 1984.

[49] S. E. Dudas, I. J. McGaw, and J. F. Dower, "Selective crab predation on native and introduced bivalves in British Columbia," *Journal of Experimental Marine Biology and Ecology*, vol. 325, no. 1, pp. 8–17, 2005.

[50] T. E. Smith, R. C. Ydenberg, and R. W. Elner, "Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.)," *Journal of Experimental Marine Biology and Ecology*, vol. 238, no. 2, pp. 185–197, 1999.

[51] T. Floyd and J. Williams, "Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern gulf of St. Lawrence," *Journal of Shellfish Research*, vol. 23, pp. 457–463, 2004.

[52] V. Lutz-Collins, R. Cox, and P. A. Quijón, "Habitat disruption by a coastal invader: local community change in Atlantic Canada sedimentary habitats," *Marine Biology*, vol. 163, no. 8, Article ID 177, 2016.

[53] A. V. Malyshev, P. Tummon Flynn, R. Cox, C. Duarte, P. A. Quijón, and M(Gee) G. Chapman, "Community disruption in small biogenic habitats: a coastal invader overcomes habitat complexity to alter community structure," *PLOS ONE*, vol. 15, no. 10, Article ID e0241116, 2020.

[54] E. Grosholz and P. Olin, "Predation by European green crabs on Manila clams in central California," *Journal of Shellfish Research*, vol. 19, pp. 631–631, 2000.

[55] E. D. Grosholz, P. Olin, B. Williams, and R. Tinsman, "Reducing predation on Manila clams by nonindigenous European green crabs," *Journal of Shellfish Research*, vol. 20, pp. 913–919, 2001.

[56] K. Matheson and C. H. Mckenzie, "Predation of sea scallops and other indigenous bivalves by invasive green crab, *Carcinus*

maenas, from Newfoundland, Canada," *Journal of Shellfish Research*, vol. 33, no. 2, pp. 495–501, 2014.

[57] M. C. Fisher, E. W. Grason, A. Stote, R. P. Kelly, K. Litle, and P. S. McDonald, "Invasive European green crab (*Carcinus maenas*) predation in a Washington State estuary revealed with DNA metabarcoding," *PLOS ONE*, vol. 19, no. 5, Article ID e0302518, 2024.

[58] C. E. Hunt and S. B. Yamada, "Biotic resistance experienced by an invasive crustacean in a temperate estuary," *Biological Invasions*, vol. 5, pp. 33–43, 2003.

[59] G. C. Jensen, P. S. McDonald, and D. A. Armstrong, "East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp." *Marine Ecology Progress Series*, vol. 225, pp. 251–262, 2002.

[60] P. S. McDonald, G. C. Jensen, and D. A. Armstrong, "The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana," *Journal of Marine Biology and Ecology*, vol. 258, pp. 39–54, 2001.

[61] C. E. de Rivera, E. D. Grosholz, and G. M. Ruiz, "Multiple and long-term effects of an introduced predatory crab," *Marine Ecology Progress Series*, vol. 429, pp. 145–155, 2011.

[62] D. Munroe, J. Kraeuter, B. Beal, K. Chew, M. Luckenbach, and C. P. Peterson, "Clam predator protection is effective and necessary for food production," *Marine Pollution Bulletin*, vol. 100, no. 1, pp. 47–52, 2015.

[63] S. B. Yamada, H. Metcalf, and B. C. Baldwin, "Predation by the pygmy rock crab, *Cancer oregonensis* (Dana, 1852) inside oyster trays," *Journal of Shellfish Research*, vol. 12, pp. 89–92, 1993.