Aquatic Invasions 2026 Volume 21, Issue 3: 167–184

Research Article

Field tests of trophic interactions between non-native European green crabs (*Carcinus maenas*) and non-native clams along an estuarine gradient

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Abstract

Estuaries are highly invaded ecosystems exhibiting many novel species interactions. This project addressed how predation from native and non-native crabs influences density of non-native clams along an estuarine gradient in Willapa Bay (Washington, USA). Recruitment of both Manila clams (*Ruditapes philippinarum*) and soft-shell clams (*Mya arenaria*) was greater up-estuary (south), likely from retention of locally-produced larvae. Three independent predator trapping efforts had higher catch of non-native European green crabs (*Carcinus maenas*) towards the ocean (north), setting up opposing predator and prey densities for exploration of top-down effects. Dungeness crabs (*Metacarcinus magister*) were 87% less abundant than green crabs and showed no regional difference in density in the single trapping effort where they were counted. Two field experiments investigated whether protection from nets impacted clam counts along the estuarine gradient. Excluding predators significantly increased survival of small Manila clams in both experiments, despite differences in duration, spatial scale, and whether clams were outplanted. Large Manila clams benefited only in the longer experiment. However, the protective effect of nets was unrelated to green crab catch, suggesting that the range of abundances observed in Willapa Bay during this study did not result in an additive mortality effect on clams. While abundances currently remain lower than other locations where impacts to clams have been documented, green crabs have increased rapidly in the past decade, and densities will likely continue to grow, particularly in the southern portion of the estuary. Thus, the lack of detected predation effects by green crabs in these experiments could be a transient phenomenon dwarfed by other post-recruitment losses of clams.

Academic editor: Yuriy Kvach
Received: 10 November 2025
Accepted: 20 May 2026
Published: 17 August 2026

Citation: Garcia L, Ruesink JL, Suhrbier A, Beugli D, Flannery R, Parker L, Grason EW (2026) Field tests of trophic interactions between non-native European green crabs (*Carcinus maenas*) and non-native clams along an estuarine gradient. Aquatic Invasions 21(3): 167–184. https://doi.org/10.3391/ai.2025.21.3.203309

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Key words: Aquaculture, intertidal flats, predation exclosure, recruitment, stress gradient

Introduction

Estuaries are highly invaded worldwide (Ruiz et al. 1997; Reise et al. 2023), which generates food web interactions among a novel complement of species. Introduced predators can have strong top-down effects on native species, particularly where evolutionary history has resulted in naivete to predators (Yli-Renko et al. 2022), but a recent review left open the case for top-down effects when both predator and prey are non-native, noting only that they may or may not share evolutionary history (David et al. 2017). Trophic impacts of non-native predators are expected to increase with population density and as they overlap susceptible prey (Parker et al. 1999; Jeschke et al. 2014). Therefore, environmental gradients could either heighten trophic interactions of non-native species, if predator and prey share responses to the gradient, or provide local refuges for prey outside the predator's suitable conditions (Silliman and He 2018). Here, along an estuarine gradient, we determine the extent to which economically valuable non-native clams are limited in production by a globally invasive non-native crab.

Clams are particularly vulnerable to crab predation when small, thin-shelled, near the sediment surface, in sediment without gravel, and in the absence of preferred alternative prey for crabs (Seitz et al. 2001; Thomson and Gannon 2013). In some cases, predator impacts increase with stressors, for instance, due to faster feeding at high temperature (Abbe and Breitburg 1992), or low salinity and low dissolved oxygen making clams more apparent to predators (Munari and Mistri 2012; Domínguez et al. 2021). By contrast, in consumer stress models, predators are more sensitive than prey to stressors such as low salinity (Jurgens et al. 2022). These biological traits may be more informative for understanding crab-clam interactions than a strict focus on their non-native status, particularly for generalist predators. Nevertheless, non-native crabs have been documented to harm native clams (Grosholz et al. 2000; Walton et al. 2002; Tan and Beal 2015; Young 2022; Prado et al. 2024), while native crabs can provide biotic resistance that keeps non-native clams in check (Byers 2002; Grason et al. 2024; Bissett et al. 2025).

Predation as a local process acts in a context of larger-scale recruitment patterns, which exhibit spatiotemporal variation in estuarine species with complex life cycles and a planktonic larval phase. Species with larvae retained in estuaries can recruit where water residence times are longer (Ruesink et al. 2014b; Kimbro et al. 2019), whereas those with longer larval durations or a period of near-ocean development may recruit close to estuary mouths from source populations in other estuaries (Banas et al. 2009). Species interacting via predation can have distinct spatial recruitment patterns that contribute to variability in top-down effects along gradients (Seitz et al. 2001; Daleo et al. 2015). Differential recruitment across trophic levels needs to be accounted for in field experimental studies of top-down effects; recruitment patterns could set up background conditions of different relative abundances of predators and prey, increasing the information content of testing top-down effects across multiple sites (Walton et al. 2002).

A novel predator, European green crab (EGC, *Carcinus maenas*), has strong global impacts on foundation species and could damage U.S. shellfish culture (Grosholz et al. 2011; Bissett et al. 2025). EGC have strong top-down effects on native clams in Europe, eastern and western North America, and Tasmania (Grosholz et al. 2000; Hiddink et al. 2002; Walton et al. 2002; Whitlow 2010; Tan and Beal 2015; Young 2022). In Willapa Bay (Washington, USA), the harvest of non-native Manila clams (*Ruditapes philippinarum*) dropped by about half during a period of steep increases in EGC density (Grason et al. 2024).

Willapa Bay also has established soft-shell clams (*Mya arenaria*), which are well-studied in their native range as showing low post-settlement survival with non-native EGC (Tan and Beal 2015). The role of non-native EGC in limiting these two species of non-native clams in Willapa Bay remains unclear; however, variability in their relative abundance, coupled with field exclosures, provides an opportunity to determine whether EGC variation across estuarine gradients may contribute to differences in clam survival.

To understand how non-native species interact trophically, we conducted a field study to gain insight into the interaction between two clam species and EGC in a northeast Pacific coastal estuary (Willapa Bay). We tested: 1) how crab populations (abundance and size structure) change along an estuarine gradient, and 2) how the predation effect from two exclusion experiments was related to EGC abundance. The overall aim was to determine conditions under which EGC may limit clam populations in the field, given complex food webs of species with and without coevolutionary histories.

Methods

Study site and species

Willapa Bay is a shallow estuary on the coast of Washington State, USA. About half the bay's area dries at low tide, and both oyster and clam aquaculture occur on these broad intertidal flats. The bay is a major contributor to U.S. shellfish production (Ruesink et al. 2006), primarily of non-native species (Pacific oysters, *Magallana gigas*; and Manila clams, *Ruditapes philippinarum*). The average depth is 3.2 m and mean tidal range is 1.9 m (Hickey and Banas 2003). Study sites were located on privately-owned commercial clam beds at elevations of 0.7 to 1.4 m relative to mean lower low water (Table 1). Crushed rock had been added as protection from predators. Study sites spanned 20 km along the western shore of the bay (Table 1, Fig. 1), a gradient that is typically warmer and less saline up-estuary (to the south) in summer (Ruesink et al. 2015). Despite this gradient, summer salinities exceed 25 PSU at all sites (Ruesink et al. 2015), whereas EGC can live and feed at much lower salinities (De Rivera et al. 2025). A northern and southern region are separated by a physical feature of the bay, known as the "fattening line," beyond which the water residence time shifts from ~1 week to ~1 month (Banas and Hickey 2005); sites were evenly divided between the two regions. Recruitment monitoring in 2023 and 2024 demonstrated substantial natural recruitment of non-native clams, especially up-estuary (Table 1, Grason et al. 2024).

Three introduced species at two trophic levels were the focus of this study. Manila clams were inadvertently introduced with Pacific oysters before the 1950s and now dominate commercial clam aquaculture in Washington State (Decker 2015; Grason et al. 2024). Soft-shell clams (*Mya arenaria*) arrived as aquaculture hitchhikers from the eastern U.S. and were intentionally planted in the late 1800s and were briefly abundant in many U.S. west coast estuaries (Carlton 2023). The two clams have similar summertime reproductive periods in Willapa Bay (Grason et al. 2024). Over their lifespan, Manila clams develop sturdy shells and are limited to surface sediments by their short siphons, whereas large soft-shell clams can bury deeply. European green crabs (*Carcinus maenas*) spread northward after their unintentional introduction to San Francisco Bay in the 1980s (Wonham and Carlton 2005), with a brief appearance in Willapa Bay in the late 1990s and more recent rapid increase (Yamada et al. 2025).

Table 1. Site descriptions where non-native clams and crabs were studied in Willapa Bay, Washington, USA, organized from north to south (ocean to up-estuary).

					Cumulative Manila clam recruitment per 0.015 m^2	
Site name (Code)	Geolocation (WGS84 decimal degrees latitude, longitude)	Distance from mouth (km)	Tidal elevation relative to MLLW (m)	Geolocation of nearest nets for commercial trial (Nov 2023-Nov 2024)	2023 (Grason et al. 2024) mean (SE, N = 5)	2024 mean (SE, N = 5) (Supplemental methods and results)
Stackpole S (STS)	46.5930, -124.0291	9.356	1.424	ST: 46.594, -124.026	36.6 (11.8)	33.58 (6.12)
Stackpole low (STC)	46.5913, -124.0249	9.591	1.14		–	21.27 (2.13)
Oysterville Duckpole (DP)	46.5543, -124.0140	13.644	0.724		14.2 (5.9)	9.60 (2.29)
Oysterville (OY)	46.5513, -124.0201	13.977	1.149	OY: 46.552, -124.019	39.8 (5.6)	26.25 (2.63)
Nahcotta Port (PO)	46.5030, -124.0275	19.340	1.121		170.4 (29.2)	57.15 (5.26)
Nahcotta Breakwater (BR)	46.4987, -124.0276	19.891	1.22	Mill Channel: 46.469, -124.023	155.0 (20.3)	93.95 (8.49)
Woody's low (WOL)	46.4288, -124.0152	27.687	0.783	WO: 46.437, -124.017	–	45.26 (4.03)
Woodys (WO)	46.4268, -124.0177	27.897	1.349		14.6 (1.6)	34.48 (6.40)

Predator gradient

Three trapping datasets were used to evaluate the patterns of relative abundance of predators across the Willapa Bay estuarine gradient. The first dataset was collected from a synoptic trapping effort conducted at the eight sites where clam recruitment (Table 1) and predator exclusion (small seeded plots, described below) took place. During this survey, predators were trapped with an overnight soak of baited traps from 2–3 August 2024. At each site, 10 traps were set during low tide, specifically five square Fukui traps (13 mm mesh) and five minnow traps (Gee-40, 50 mm diameter opening, and 6.35 mm mesh) alternating at 10-m intervals along a depth contour. All traps were baited using ~100–150 g Pacific mackerel (*Scomber japonicus*) and left on the mudflat overnight, for a 24-hour deployment period that included a night-time high tide. The traps were retrieved at low tide. During the trap retrieval, all organisms in the trap were identified to species and counted. For crabs other than EGC, size was measured as total carapace width at the widest point and sex determined on-site. Trap contents other than EGC were then released. Captured EGC were measured, sexed, and counted off-site, and they were subsequently euthanized.

Two other trapping-based EGC monitoring efforts currently occur in Willapa Bay and include sites spanning from Stackpole near the mouth to up-estuary sites in the southern part of the bay (Fig. 1, Suppl. material 1: table S1). We queried 2024 data from both of these programs to augment our interpretation of the spatial pattern of EGC. First, Washington Sea Grant (WSG) Crab Team is a regional participatory science monitoring program that engages community members and staff at partner organizations to conduct systematic trapping and molt surveys that target EGC (https://wsg.uw.edu/crabteam). Crab Team trapping protocols entail setting six traps at designated sites for a single overnight soak each month from April through September annually (Grason et al. 2018). Similar to the present study, this protocol includes two trap types, Fukui and minnow, set in alternating order at 10-m intervals, with the slight difference that minnow traps used in Crab Team surveys have a smaller opening (25 mm diameter). All WSG Crab Team monitoring sites in Willapa Bay occur in estuarine, stream-influenced, channels. Second, the Washington Department of Fish and Wildlife (WDFW) green crab

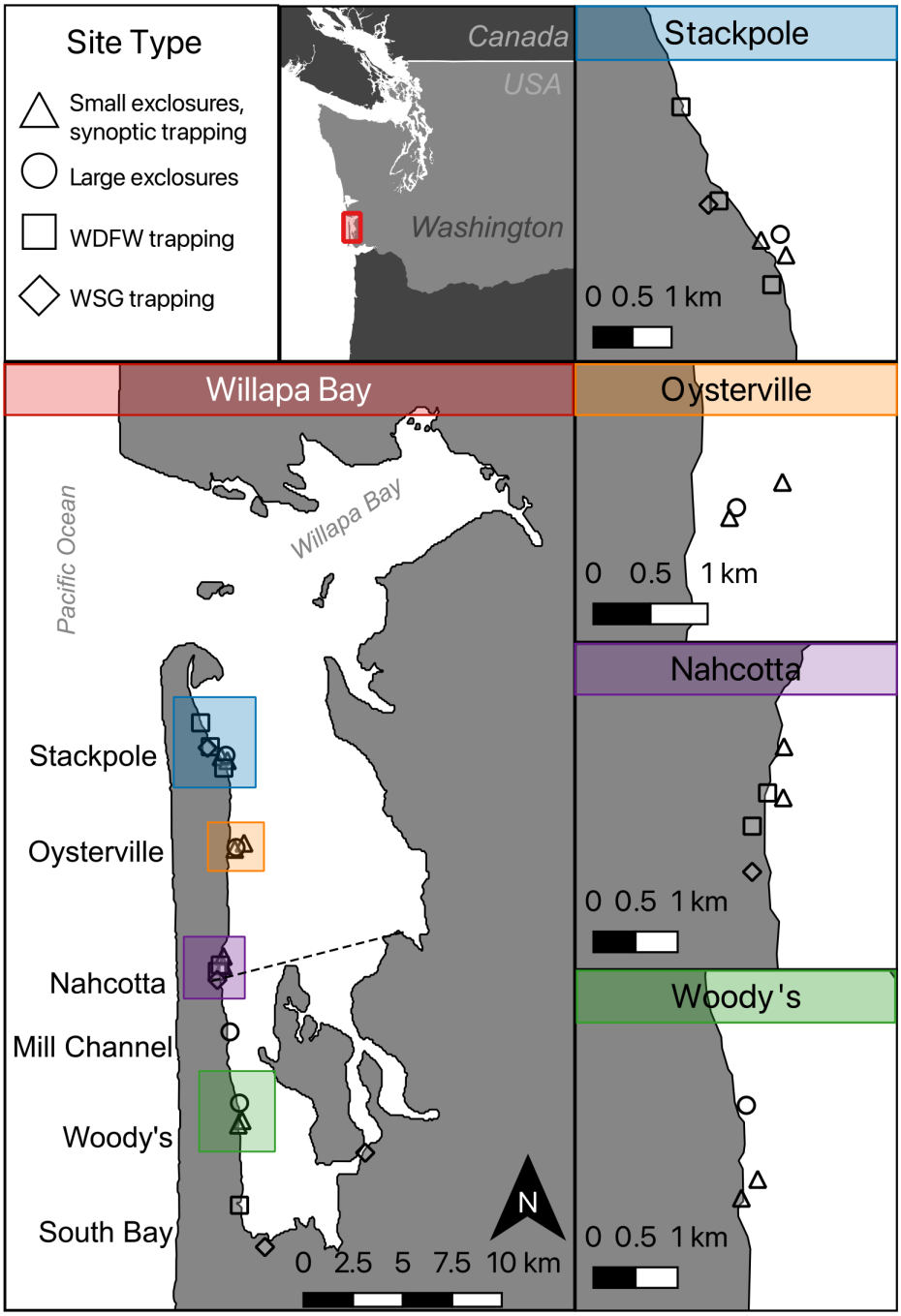

Figure 1. Map of study sites in Willapa Bay, Washington, USA. Insets indicated by colored, shaded boxes depict four regions of the bay with multiple sites at greater spatial resolution. Triangles indicate locations of predator exclusion experiment and synoptic crab sampling (8 sites), circles indicate locations of large clam net exclosures (4 sites), diamonds indicate locations of WSG Crab Team crab monitoring (4 sites), and squares indicate locations of WDFW crab monitoring (6 sites). The dotted line is the "fattening line" identified for the past century where there is a shift in water residence (1 wk down-estuary/ north, 1 mo up-estuary/ south).

management program initiated a similar monitoring effort for EGC in 2024. The WDFW EGC monitoring protocol utilizes three types of traps; in addition to Fukui and minnow (50 mm opening) traps, rigid box-style shrimp traps are used (Pro-Mar TR-244, 25 mm mesh size). Three traps of each type are arranged in a transect alternating trap type and placed 10-m apart. The six WDFW monitoring

sites in this study consist of salt marsh channels or edges of emergent marsh vegetation. While WDFW monitors monthly from April through October, not all sites were sampled every month. Thus, for this exploration, WDFW monitoring data were only used from April, May, and August 2024. While both programs also monitor at sites to the north of the mouth of the bay, data from those sites were not included in this investigation because no comparable clam survival observations were collected. Both programs use bait and data collection procedures consistent with the present study. Though trap, seasonal, and habitat-related differences in protocols make it difficult to compare absolute catch rates across these three trapping efforts, within-effort comparisons will still yield valid site-to-site comparisons of spatial/geographic patterns of relative abundance of EGC during 2024.

Predator exclusion experiment - small seeded plots

Predator access to clams was manipulated in a field experiment conducted at the same eight sites as above. All experimental units consisted of window-screen mesh boxes (20 × 20 × 10 cm; Suppl. material 1: fig. S1), dug into the sediment, and then local sediment was placed inside the unit. Each unit was covered by sewing Vexar mesh (1 cm mesh) to two sides at the top. Once sediment was added to exclosures in the field, the top was fully closed by connecting to the two remaining sides with zip-ties. The Vexar mesh of control units had two large cuts, 3 cm × 10 cm, allowing predators to enter and exit the unit. Before the units were sealed in the field, five large local Manila clams, ~40 mm, and 20 small hatchery-raised Manila clams (6.27 mm, SD 2.41, N = 25) were placed into each unit. Large clams were pushed into the sediment, while small clams were covered by additional substrate. The experiment was deployed 11–12 July and collected 23–24 August 2024 for a total of 6 weeks. At collection, units were sieved (to 2 mm) on the tidal flats to reduce the volume of sediment necessary to carry offsite. The remaining substrate was then sorted by hand, identifying and measuring all live clams, including Manila, soft-shell, and other clams.

Predator exclusion experiment - large nets

Large nets were installed by anchoring with rebar and digging the edges into the sediment, a commercial aquaculture method, at two northern and two southern sites (Table 1, Fig. 1). One net (14 × 5 m) per site with 6.35 mm mesh was installed in November 2023, and another with 12.7 mm mesh in April 2024; this larger-mesh net varied in size depending on grower preference: 12 × 6 m at ST and MC, 6 × 6 m at OY, and two 6 × 6 m nets at WO. Sampling for clams occurred in November 2023 (prior to small mesh installation), April 2024 (prior to large mesh installation), and November/December 2024 by digging 0.0929 m^2 cores to 10 cm depth and sieving material to collect any clams >5 mm length. All Manila clams in each sample were measured for shell length (nearest mm), which demonstrated a highly bimodal size frequency and enabled us to divide the clams into two size categories – small (<2.5 cm) and large (>2.5 cm). Counts in each size category were determined at each of the four sites for samples under the small-mesh net (N = 3), samples under the large-mesh net (N = 3), and reference samples. Reference samples were collected in a grid across the entire clam bed at each site (ST: 9,608 m^2, OY: 9,931 m^2, MC: 20,112 m^2, WO: 30,000 m^2). Each grid was divided into four quadrants, which we considered replicates of the treatment without nets, within which were 8–11 subsamples (on average, 9).

Data analysis

Each of the eight sites had an associated distance along the estuarine gradient based on their Northing geoposition, and an intertidal elevation determined by RTK-GPS (Table 1). Northing geoposition was adjusted to distance from the estuary mouth in km, so larger values represent distances further up-estuary. Separately, the sites were grouped into northern and southern regions.

Crab catch was compared across three model structures for each of two crab species separately. In each of the three model structures, the predictors represented different environmental gradients. Intertidal elevation represented a gradient of desiccation and access, given that Dungeness crabs (*Metacarcinus magister*) often move onto tidal flats to forage at high tide (Holsman et al. 2006). Distance from estuary mouth represented a suite of correlated thermal, hydrodynamic, and salinity changes characteristic of ocean-to-river gradients. North and South regions incorporated the residence time changes indicated by the "fattening line." These models were compared with Akaike Information Criterion (AICc, adjusted for small sample size): 1) Distance into estuary (km) + Intertidal elevation (m), 2) Distance into estuary (km), 3) North vs. South region as a categorical predictor. Response variables were the number of each of two crab species captured in traps (EGC and native Dungeness crabs). These analyses only included data from the trapping effort in August 2024 that precisely matched the predator exclusion sites. In all models of crab catch, the 10 traps from each of the 8 sites were nested as replicates within the site. We assumed a tweedie data distribution, which accommodates data with many zeros and occasional very large non-zero values; residuals were examined and found to meet assumptions. Relative abundance of EGC across the estuary as surveyed in the WSG Crab Team and WDFW green crab monitoring efforts was evaluated visually to assess whether patterns were consistent with those found in synoptic sampling.

Analysis of the predation experiment (small-scale) was focused on determining if site-level EGC catch predicted the treatment effect of excluding predators. Inherently, this question addresses the EGC x Treatment interaction effect, rather than the main effects of EGC catch or predator exclusion treatment. This two-factor analysis was carried out on the response variable of live Manila clam count per experimental unit at the end of the experiment. As in the analysis of EGC spatial patterns, only EGC data from the synoptic trapping effort in August 2024 was used for this analysis. Site was considered a random effect to account for the physical set-up of the study design. Small and large clams were analyzed separately. Some of the final counts of small clams exceeded the number initially added, which reflects that clams were already present from the 2023 recruitment season when we added local sediment to the experimental units. Soft-shell clams, all of which would have been added with the local substrate at the time of experimental setup, were similarly analyzed for EGC x Treatment, with site as a random effect. Data were initially assumed to have a poisson distribution; however, gaussian provided better residuals in the analysis of small Manila clams.

Analysis of the predation experiment (large nets) was done separately for large (>2.5 cm) and small clams (<2.5 cm) for data collected in November/December 2024. (Earlier dates are visualized in Suppl. material 1: fig. S2.) Each of the four sites had two nets (except for one site with three: WO) and four quadrants of the clam bed sampled outside the net. This strategy provided two or three true replicates of predator exclusion and four open areas at each site. Manila clam counts were the response variable, and site, netting, and their interaction were fixed effects,

with a group factor as a random effect to account for multiple subsamples per net or quadrant. Data fit assumptions with a negative binomial distribution for both size classes of clams.

All statistical models were built with the package glmmTMB (Brooks et al. 2017) and residuals tested with the package DHARMa (Hartig 2016) in R version 4.5.1 (R Core Team 2025).

Results

Predator gradient

In the synoptic baited trapping effort at the eight sites, catch rate of crabs differed across the estuarine gradient for EGC but not for Dungeness crab (Suppl. material 1: table S2). For EGC, highest catch on these mid-intertidal flats was in the northern region towards the mouth of Willapa Bay, with fewer in the southern region (Fig. 2). The continuous north-to-south distance predictor was statistically significant, but the model with north vs. south region provided a better fit.

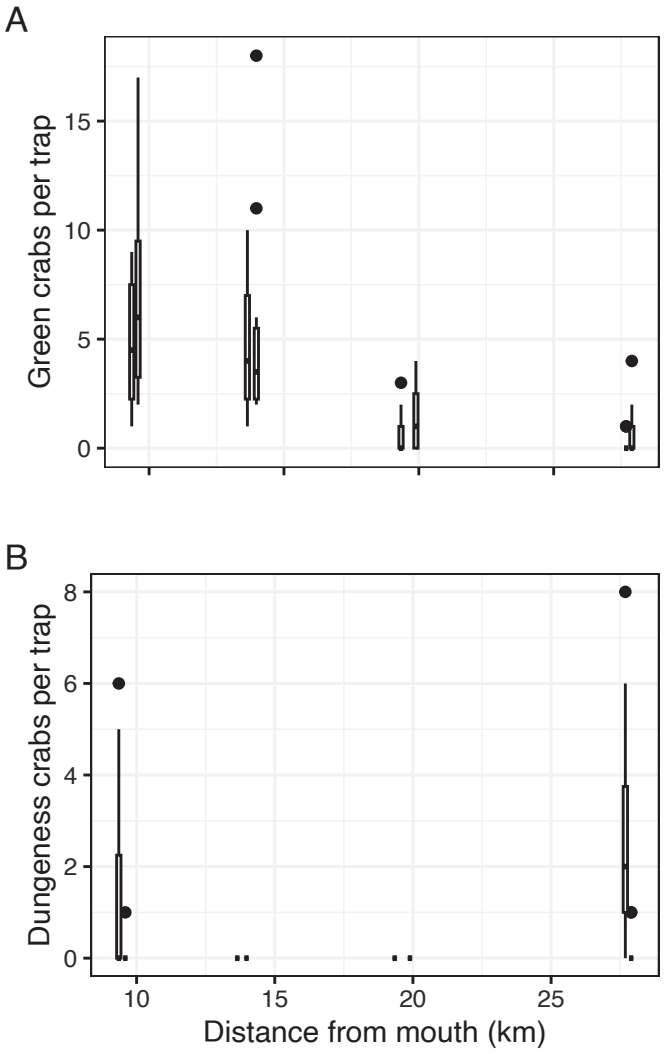

Figure 2. Catch of **A.** European green crabs (*Carcinus maenas*) and **B.** Dungeness crabs (*Metacarcinus magister*) based on distance from the estuary mouth. Crabs were trapped overnight at eight sites in Willapa Bay, Washington, 2–3 August 2024. Boxplots show the result for 10 traps at each site.

Therefore, the regional catch pattern for EGC was opposite the recruitment pattern for clams (Suppl. material 1: table S2, figs S3, S4). Dungeness crabs (*Metacarcinus magister*) were 87% less abundant than green crabs and showed no regional difference in density (Suppl. material 1: table S2). Elevation did not significantly improve model fit for either crab species over the range of elevations trapped.

The size of both species of crabs varied predictably across the estuarine gradient, but in opposite directions (Suppl. material 1: fig. S5). Notably, we observed clear size differentiation of Dungeness crabs at the two sites where they were abundant; crabs were generally 70–120 mm carapace width at the site closest to the mouth of the estuary, but ranged from 40–80 mm at the furthest up-estuary site. By contrast, EGC were smaller near the mouth of the estuary; most small crabs (<60 mm) were caught at northern sites, and most large crabs (>60 mm) were caught at southern sites.

Two other trapping programs also showed spatial variability in the catch of EGC (Fig. 3). Sites further up-estuary than our southernmost had very low catch rates, only rarely trapping EGC. Sites near Nahcotta, which grouped with the southern part of the bay in our analyses, had a high EGC catch rate in the WSG Crab Team data, but lower catch rates compared to northern sites in the WDFW monitoring.

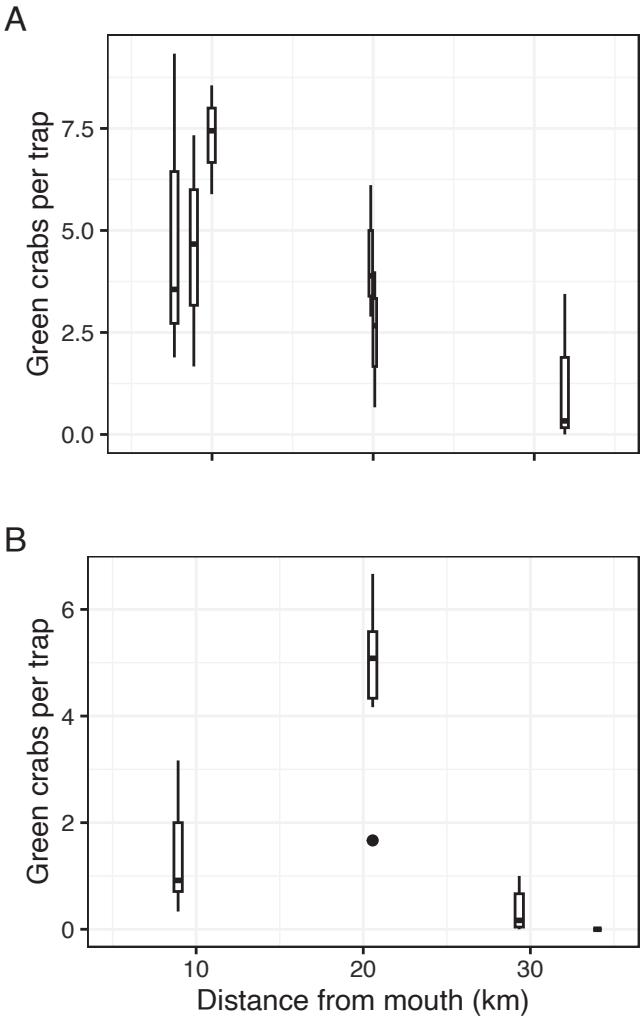

Figure 3. Catch of European green crabs (*Carcinus maenas*) trapped from two monitoring programs in Willapa Bay Washington, USA in summer 2024. **A.** Washington Department of Fish and Wildlife (n = 27 per site) and **B.** Washington Sea Grant Crab Team (n = 36 per site). Boxplots show number of crabs per trap for each monthly sample based on site distance (km) from the estuary mouth.

Predator exclusion experiment - small seeded plots

Although 20 small Manila clams were added to each experimental unit, exclosures in the south part of the bay had more than 20 recovered after six weeks, which we interpret to mean that small clams were already present in the local sediment added to each unit. In the experimental analysis, the statistical interaction of EGC catch and exclosure treatment was not significant for small clams ($Z(1,74)=0.24$, $P = 0.81$). This means that the effect of predation at a site did not depend on how many EGC were trapped there (Fig. 4). The main effect of EGC was significant ($Z=-3.7$, $P < 0.001$), which simply reflects an inverse relationship between small Manila clams and crab density. The treatment effect was also significant, with open treatments on average having 8 fewer clams than in exclosures, or a survival of 60% of the original 20 clams (Fig. 4A, $Z=-4.5$, $P < 0.001$). By contrast, no factors were significant for large clams (Suppl. material 1: table S3). Large clams were found at the end of six weeks at essentially equivalent densities to the start of the experiment, indicating that they were not susceptible to mortality sources in summer in these graveled

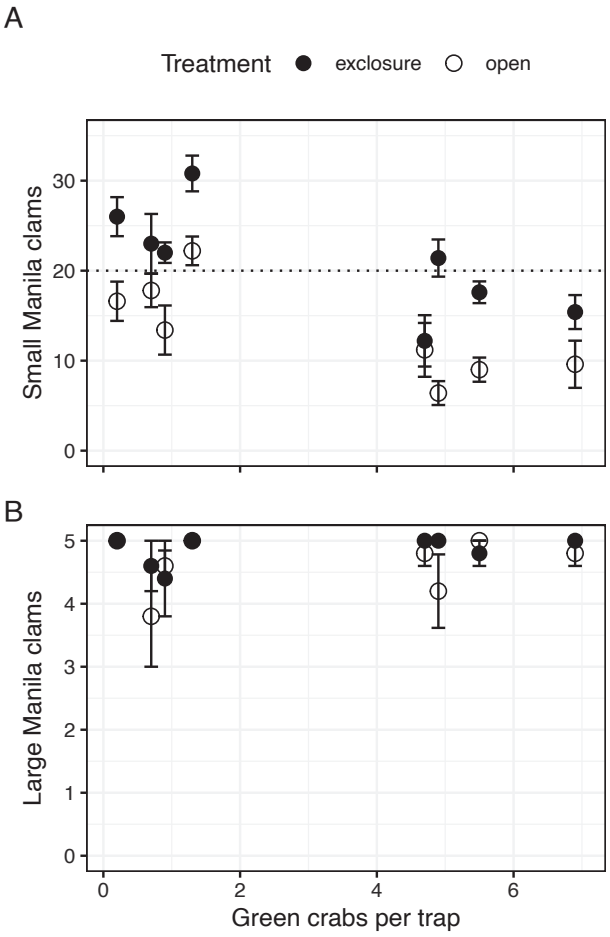

Figure 4. Manila clams (*Ruditapes philippinarum*) of **A.** Small and **B.** Large size classes remaining in experimental units after a six-week experimental manipulation of predator access, across the green crab catch rate (catch per unit = mean number per trap) at eight sites in Willapa Bay, Washington. Each unit was seeded with 20 small and 5 large clams on 11–12 July 2024. Each point represents the mean remaining on 23–24 August 2024, with the standard error (N = 5). From left to right, the sites are: WOL, PO, WO, BR, DP, STS, OY, STC.

clam beds (Fig. 4B). Soft-shell clams, which were not deliberately added, were found at low densities in both open and exclosure units, mostly <1 clam per unit except at the two sites near Nahcotta with 3 clams per unit, but no factors were significant (Suppl. material 1: table S3).

Predator exclusion experiment - large commercial nets

Densities of large Manila clams were enhanced by about 50% by netting for 8–12 months at all four sites, with a non-significant trend for this enhancement to be less at the site farthest up-estuary (Woody's; Fig. 5B, Suppl. material 1: table S4). The results for small clams were much more variable across sites, with two showing order-of-magnitude increases in small clam densities under nets – at the extreme ends of the estuarine gradient (Stackpole, Woody's) – and little effect in the middle (Fig. 5A; Suppl. material 1: table S4). The small clams that were enhanced by netting were collected at a minimum size of 5 mm; these clams must have settled in 2023 several months prior to net placement, since the 2024 cohort would still be <2 mm by December (Ruesink et al. 2014a).

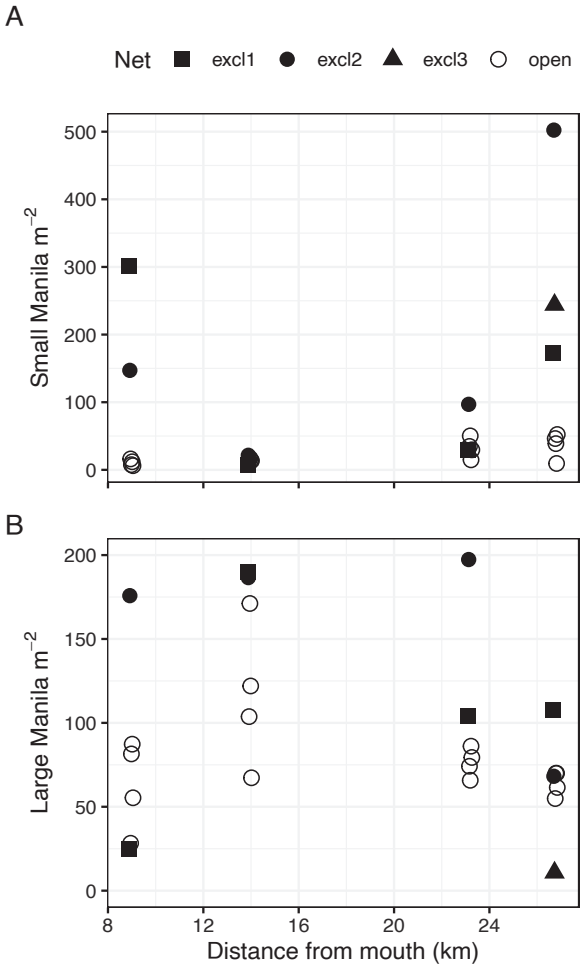

Figure 5. Manila clams (*Ruditapes philippinarum*) of **A.** Small (<2.5 cm) and **B.** Large (>2.5 cm) size classes naturally-occurring under (filled symbols) and outside nets (open symbols) at four sites in Willapa Bay, Washington. Data are from Nov/Dec 2024, when nets had been present for 8 (exclosures 2 and 3: ½ inch-mesh) or 12 months (exclosure 1: ¼ inch-mesh). Each point is the average of 3–11 subsamples. For data analysis, subsamples were appropriately nested (169 samples in 25 groups).

Discussion

The productivity of non-native clams within the study system was measurably improved by protecting seed clams (ca. 1 cm Manila clams) from predation by netting, even on graveled clam beds. This predation effect was not related to the abundance of a non-native predator and became less important as clams grew. Therefore, the outcome of predator-prey interactions among non-native species was not a straightforward function of their abundance. We were unable to attribute clam losses to EGC because, over the range of EGC densities along the estuarine gradient, the effect of predator access on clam survival did not change predictably with crab density. Instead, more clams were present at sites with low relative abundance of EGC due to inverse recruitment patterns. Our experimental setup inadvertently demonstrated the critical importance of recruitment along this estuarine gradient in supporting Manila clam productivity; baseline densities of naturally recruited small clams were higher in the south region, despite similar predator effects experienced by clams across the Willapa Bay gradient. The lack of evidence identifying EGC as an influential predator on Manila clam survival could be a transient phenomenon, disappearing as EGC populations continue to increase within Willapa Bay. At the early stages of invasions, novel species interactions can be difficult to detect, particularly in systems where strong predation effects already occur; for instance, prior to EGC invasion in Willapa Bay and elsewhere regionally, post-settlement clam mortality in ungraveled sediments was on the order of 99% (Williams 1980; Ruesink et al. 2014a).

Distribution of predators and prey across an estuarine gradient

The estuarine gradient helped explain distributions of non-native clams and EGC, for which larval ecology rather than physical factors per se (i.e. temperature, salinity) provides an underlying mechanism for their inverse relationship. Clam larvae are likely produced and retained within the bay, therefore settling disproportionately in the southern region of long water residence time (Banas and Hickey 2005). By contrast, at the present stage of the ongoing invasion of Willapa Bay, the majority of EGC larvae likely originate in other bays along the coast where green crabs are currently more abundant (e.g. Oregon, California and British Columbia, Canada) and transit coastal ocean waters before settling in Willapa Bay (Banas et al. 2009), hence showing higher catches in the north region of the bay, which has strong ocean influence (Banas and Hickey 2005). It is expected that as EGC continue to expand their population into the southern region of Willapa Bay, this pattern will shift, as, similar to clams, long water residence time will favor retention of crab larvae released by adults further into the estuary. Thus, the current gradient in relative abundance of EGC could be a transient phenomenon.

Other predators are likely to be contributing to the clam mortality observed along the entire estuarine gradient, such that we could not predict clam losses from EGC alone. Nevertheless, clam loss did not vary predictably with Dungeness crabs, which were the other crab predator abundant at our trapping elevations. Like EGC, Dungeness crabs also have an extended pelagic development phase, resulting in densities that decline away from estuary mouths for both intertidal recruitment and 1+-year crabs in channels (Armstrong et al. 2003; Dumbauld et al. 2021). Therefore, the pattern observed from intertidal traps, in which Dungeness crab densities were elevated at both ends of the estuarine gradient, was unexpected. Other possible drivers include recent trapping, distance to channel, and foraging opportunities (Armstrong et al. 2003; Holsman et al. 2006; Lewis et al. 2021), but trapping sites with few Dungeness crabs were not markedly distant from channels (pers. obs.).

Although uncommon in the traps in this study, native red rock crabs (*Cancer productus*) were caught at low intertidal elevations where large outplanted clams suffered high mortality in previous field experiments in Willapa Bay (Grason et al. 2024). Overall, our results reinforce the challenge of detecting novel predator effects within a complex food web in which clams across life stages are eaten by many taxa.

Green crabs as clam predators

EGC abundance was not a significant predictor of the predation effect on clams in our study. This conclusion is complicated by a generally negative relationship between Manila clams and crabs in the small-plot experiment, which we interpret as having added small clams along with locally sourced sediment. The key outcome is the lack of statistical interaction between predation treatment (open vs. exclosure) and EGC relative abundance. Open units lost small clams during the experiment, suggesting top-down control in aggregate; however, this predation effect did not increase with greater EGC catch. Similarly, larger nets improved densities of large clams regardless of position along the estuarine gradient, while small clam densities increased dramatically under nets only at the two ends of the gradient.

These field experiments at multiple sites caution against generalizing field impacts of EGC from their demonstrated capacity to consume clams. Laboratory feeding trials, along with enclosures of EGC with specific prey, show their predatory potential, especially when the crabs are large relative to prey. EGC were less likely to damage 40-mm Manila clams than juvenile oysters when held in tanks (Anaya et al. 2025), and EGC recruiting into bags of clams were associated with reduced survival of seed clams, while adult EGC were able to consume >36-mm Manila clams (Grosholz et al. 2011). Additionally, previous diet analysis from Willapa Bay showed that Manila clam consumption by EGC was extremely rare (Fisher et al. 2024), supporting the inference that EGC are not yet exerting a significant population-level impact on Manila clams. Similar to our study, in five estuaries to the south of Willapa Bay, no correlation arose between predation intensity and local EGC density, although in that study predation varied while EGC catch was unrelated to salinity (de Rivera et al. 2025). While the role of EGC in top-down effects on clams currently appears small, substantial evidence has accumulated that native crabs limit clam production in the northeast Pacific region by consuming juvenile clams (Dudas et al. 2005; Dethier et al. 2019). In comparison to laboratory feeding trials, field studies allow EGC to encounter impediments with buried clams, as well as alternative prey.

Several possible explanations exist for a lack of detectable predation impact of EGC in the current study. First, abundances of EGC in Willapa Bay may not yet be high enough to yield detectable effects even on small clams; for instance, catch per trap was below levels that have previously been suggested to result in top-down effects on clams (Grosholz et al. 2011). Second, substrate at all sites had been augmented by gravel, an effective commercial intervention for clam growers (Ruesink et al. 2014a) that might have conferred protection on small clams from EGC even in open treatments. Third, it is also possible that crab sampling, though synoptic and consistently implemented, did not sufficiently characterize EGC abundance across the 6-week predator exclosure deployment. For example, if additional population suppression trapping occurred shortly before or after our predator assessment at one or several of the sites, it could have biased our estimates of relative abundance with respect to what clams experienced in the experiment. The consistency of the spatial pattern in EGC catch among the three efforts reported here makes this last issue less likely. Nevertheless, the invasion appears still to be in the growth phase in Willapa Bay, and it therefore seems likely that predation by EGC will become increasingly important and costly.

Conclusions

Globally, Manila clam production requires protection from a suite of predators, including crabs (Munroe et al. 2015). In the current study, protection by large-scale nets augmented densities of commercial-sized (large) clams but only markedly improved recruitment at two of four sites. Given the position of these sites at the extreme ends of the estuarine gradient, EGC did not provide an explanation for recruitment enhancement due to nets. The Dungeness crab distribution was more consistent with results but does not explain the relatively low recruitment densities, whether or not protected, at the two mid-estuary sites. More broadly for aquaculture in Willapa Bay, growers depend on natural settlement, which did not always generate a new cohort, followed by graveling for post-settlement protection. Outplanting seed clams in the small-scale experiment improved our ability to determine survival rates despite the probabilistic settlement of marine organisms with planktonic life stages.

The current lack of top-down effects of EGC on non-native clams is probably not due to their lack of coevolutionary history. Even taxa that have not coevolved can detect and respond: prey that have not coevolved with a predator can still use general risk cues of injured conspecifics (Grason 2017). A co-evolutionary history is shared for EGC and native clams in Europe, where top-down effects are documented (Hiddink et al. 2002). For all other novel predator-prey combinations involving EGC, studies have documented strong top-down effects (Cigarrıia and Fernández 2000; Grosholz et al. 2000; Walton et al. 2002; Tan and Beal 2015). Additionally, Manila clams in their native range are affected by native crab predators (Sun et al. 2018), and non-native Manila clams in the Mediterranean have been reduced by another non-native crab (Chiesa et al. 2025). The broader picture shows that crabs can affect clams regardless of coevolutionary history; therefore, relative abundance, access, and availability of alternative prey all require consideration in evaluating EGC impacts.

Author contribution

Lidia Garcia: conceptualization, data curation, investigation, methodology, writing – original draft: review & editing. Jennifer L. Ruesink: conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision, visualization, writing – original draft, review & editing. Andy Suhrbier: funding acquisition, investigation, writing – review & editing. David Beugli: funding acquisition, investigation, writing – review & editing. Rachel Flannery: data curation, writing – review & editing. Lindsey Parker: data curation, writing – review & editing. Emily W. Grason: conceptualization, formal analysis, investigation, methodology, resources, visualization, writing – original draft, review & editing.

Acknowledgments

The study was carried out on private tidelands, and we appreciate access granted by Ken Wiegardt (Jolly Roger Oyster Company), Northern Oyster Company, John Heckes, Warren Cowell, and Andrea Randall. Field assistance was provided by Lucie Reizan, Athena Webster, and Anthony Garcia. The contents of this document do not necessarily reflect the views and policies of the Washington Department of Fish and Wildlife.

We thank the editor and an anonymous reviewer for their efforts that improved this paper. Data from this project are available at DOI: 10.5061/dryad.qnk98sfwg

Funding declaration

This project was funded in part by funding from the Washington Department of Fish and Wildlife (23-24088 and 24-24805).

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary material.

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Supplementary material 1

Supporting analyses of non-native crab effects on non-native clams

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Data type: docx

Explanation note: Field methods and results are presented for recruitment of two non-native clams (Manila clams Ruditapes philippinarum and soft-shell clams Mya arenaria) in 2024 in Willapa Bay, Washington, USA. Statistical analyses are provided for data collected across sites, including clam densities in two experiments (completed in Aug 2024 and Nov 2024) and crabs trapped in August 2024.

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Link: https://doi.org/10.3391/ai.2025.21.3.203309.suppl1