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Effect of increasing size on the ability of green crab (*Carcinus maenas*) to manipulate and eat commercially and ecologically important species in the Pacific Northwest

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Abstract—We sought to determine the potential effect of invasive green crab (*Carcinus maenas*) on commercially and ecologically important species in the Pacific Northwest through choice and no-choice assays conducted with green crab of different sizes. We looked at the feeding behavior of green crab in relation to various prey choices, including adult Manila clam (*Ruditapes philippinarum*), adult Pacific oyster (*Crassostrea gigas*), young Pacific oyster as spat on shell, and native eelgrass (*Zostera marina*). No-choice assays were modeled with a negative binomial regression, and choice assays were modeled with a logistic regression. Results from the no-choice model reveal that the interaction of claw size and prey type was significant, and green crab of all sizes fed on spat of Pacific oyster on shells. Results from the choice model indicate that sex was not significant in predicting whether green crab consumed any prey type. In our study, green crab that fed exclusively on 1 prey type chose spat on shell or eelgrass over adult prey items. On the basis of the data, we suggest that growers focus on protecting spat of Pacific oyster from all sizes of green crab over protecting adult Pacific oyster if resources are limited.

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Invasive species can cause major changes to aquatic ecosystems and economies (Havel et al., 2015). Specifically, aquatic invasive species may consume or displace fish and benthic invertebrate species, activity that could cut into aquaculture yields (Gallardo et al., 2016). As a whole, aquatic invasive species may cause damages equal to $345 billion worldwide, with invertebrate species causing 62% of the damage reported (Cuthbert et al., 2021).

The green crab (*Carcinus maenas*) is on the Global Invasive Species Database's list of the worst invasive species (Lowe et al., 2000; GISD, 2025). Like many invasive species, the green crab is a pest with a wide-ranging diet and a high potential to damage ecosystems and habitats through direct and indirect competition (Ens et al., 2022). The first report of green crab on the Atlantic coast of the United States was made in the early 1800s, and this species arrived in San Francisco Bay in 1989 (Cohen et al., 1995). Since that time, currents and climate patterns have brought larvae north into Oregon, Washington, and British Columbia (See and Feist, 2010), and green crab were found in Alaska in 2022 (Du et al., 2024).

On the Pacific coast of North America, green crab can directly and indirectly compete with native crab species, such as the Dungeness crab (*Metacarcinus magister*) and shore crab (*Hemigrapsus* sp.), by preying on them, having similar prey, and occupying or changing their habitat (Ens et al., 2022). Of particular concern to growers of bivalve species in coastal Washington is the effect of green crab on shellfish aquaculture, particularly in Willapa Bay and Grays Harbor. In those locations, mature green crab are being removed by shellfish growers at rates significantly higher than in other parts of the state; in 2023, 95% of all green crab removed in Washington were from

Grays Harbor and Willapa Bay (Turner[1]). Green crab have been found to spend most of their time moving and sheltering in areas with high aquaculture activity and seem to prefer aquaculture structures, in contrast to the distribution of native Dungeness crab (Roegner et al.[2]), and they could be preying on shellfish grown in commercial operations in those areas.

There has been substantial research on the ability of green crab to prey on bivalves. During some studies in which exclusion cages were used in estuarine environments, the presence of green crab was correlated with predation of some shellfish species. For example, in Maine, declines in abundance of softshell clam (*Mya arenaria*) have been associated with large populations of green crab, and in Tasmania, Australia, declines in abundance of the clam species *Katelysia scalarina* (Veneridae) have been associated with increasing populations of green crab (Walton et al., 2002; Young, 2022). Green crab feed readily on mussels in their native and invasive ranges and have been reported to have preferred them in choice assays (Yamada et al., 2010; Bleile and Thieltges, 2021). Using field exposure experiments and physical gut content analysis, researchers have found that the population of green crab on the Pacific coast eats mostly bivalves and other crabs and to a lesser extent polychaetes and green algae (Grosholz and Ruiz, 1996). Mature green crab (40–75 mm in carapace width) are capable of feeding on adult Pacific oyster (*Crassostrea gigas*) (Ens et al., 2021). Results from other research indicate that green crab with a carapace width of at least 75 mm can feed on large oyster (with shell lengths of 55–60 mm), although they will feed on a greater percentage of available prey items if given oyster of a smaller size (Dare et al., 1983).

The feeding behavior of green crab in relation to littleneck clam (*Leukoma staminea*) and Manila clam (*Ruditapes philippinarum*) is similar (Curtis et al., 2012), and large green crab (>50 mm in carapace width) generally can feed on adult littleneck or Manila clam but have preferred other prey items in laboratory experiments (Palacios and Ferraro, 2003; Cohen et al., 1995; Grosholz et al., 2001). Both the Manila clam and the Pacific oyster are species that have been introduced to coastal waters of Washington for commercial fishing, but a native species of oyster, the Olympia oyster (*Ostrea lurida*), is the focus of small commercial fishing operations and some conservation efforts particularly in the Puget Sound area (Blake and Bradbury, 2012). Results from some research indicate that the Olympia oyster can be a preferred food source for green crab over larger species (Palacios and Ferraro, 2003). In feeding trials, a mature green crab with a claw length of 29 mm ate all the mussels in its cage before feeding on Olympia oyster but was still capable of feeding on them (Yamada et al., 2010).

Significant research has been conducted to examine the ability of green crab to feed on and affect commercially important shellfish, but most work has focused on one size class of juvenile or adult crab. We wanted to understand how different sizes of green crab, as defined by the size of their crusher claw, could prey on commercially and ecologically important species in coastal waters of Washington, where the green crab first invaded the state and the populations are significantly larger, as of publication, than the populations in Puget Sound. We also explored, on the basis of claw size, the ability of green crab to prey on Pacific oyster in immature *spat-on-shell* life stages in order to evaluate potential management measures for protection of bivalves in the state's largest shellfish industry that is concentrated in Willapa Bay and Grays Harbor. We attempted to include Olympia oyster but ran into challenges with green crab feeding on barnacles instead of crushing shells.

We evaluated the potential effect of green crab on bivalves and native eelgrass (*Zostera marina*) in the Pacific Northwest through no-choice and choice assays. We used a negative binomial model to evaluate the effect of increasing crusher claw size (hereafter referred to as *claw size*) on prey consumption by green crab. With data from the choice assays, we used a logistic regression model to examine the effect that sex and claw size may have had on prey choice in our experiment.

Materials and methods

Collection of green crab

We collected green crab from 2 separate sources, depending on their size class. Mature green crab were gathered by shellfish growers from baited traps they set in Willapa Bay as part of their regular removal efforts. Weekly, we were given about 150 mature green crab with a roughly equal sex ratio that were delivered in a large crab cage (76×76 cm) at a dock near Nahcotta Port. Only healthy green crab were selected for our experiment on the basis of the following standards: even claw size (claw regrowth was rejected), females were not gravid, crab had all appendages intact, crab were capable of feeding (based on standardized fish-feeding stage), and crab had to be alive and reactive. Crab that were red in color, indicating that they were about to molt, crab that did molt during the experiment (the color of some juveniles did not morph), and any crab that did not feed on the anchovy fish (Engraulidae) during the standardized fish-feeding period were removed from the experiment. To be clear, all crab included in the experiment fed on anchovy prior to a period of starvation, demonstrating that they were capable of feeding. Each green crab was used for one feeding experiment before being euthanized.

Juvenile or young-of-the-year crab were collected by our partners at the Washington Department of Fish and

[1] Turner, B. C. 2024. European green crab quarterly progress report—winter 2023 (October 1 to December 31, 2023), 26 p. Wash. Dep. Fish Wildl., Olympia, WA. [Available from website.]

[2] Roegner, G. C., Z. Forster, and D. Beugli. 2023. Habitat utilization by European green crab in Willapa Bay as measured with acoustic telemetry: a pilot study. NOAA Contract Rep. NMFS-NWFSC-CR-2023-08, 35 p. [Available from website.]

Wildlife (WDFW) during efforts to monitor and remove green crab along shorelines and in shellfish beds in Willapa Bay. Green crab were collected by using modified minnow traps (openings expanded to 25 mm), fukui traps (Fukui multispecies marine traps), and shrimp traps (rigid frame with 2.5-cm mesh). Traps were placed at low tide in pools and channels containing at least 6 cm of water to minimize desiccation of trapped organisms. Traps were checked after 24 h, all green crab were retained, and all other organisms released. Trap number, type, and deployment pattern varied greatly across collection efforts. Specimens were collected under WDFW scientific take permit 23-159A.

After collection, sex was determined for juvenile specimens of green crab, and carapace width was measured at the widest point to the nearest millimeter. Juvenile (<45 mm in carapace width) males and females and adult (≥45 mm in carapace width) females with undamaged limbs were housed in a seawater-fed tank at the WDFW Ocean Park Duty Office. The size classes of crab were separated by barriers within the tank, and water temperature was consistently 13°C throughout their containment. Green crab were transferred to the study facility weekly.

Study facility

Taylor Shellfish Inc. generously donated space in their hatchery at Bay Center, Washington, for the duration of the experiment from August through late November in 2023. The hatchery tanks were circular, 2.13 m in diameter, and 1 m deep. We filled tanks weekly with water taken from Willapa Bay, using a pump system located at Bay Center during high tide, and passed through a sand filter; after filtration, the water was held in a reservoir until it was needed to fill tanks. Bubblers supplied oxygen to green crab throughout the experiment. Tanks were filled with at least 56,785 L (1500 gal) of water or until cages holding green crab were completely submerged and covered by 5 cm of water. Temperature could not be controlled in this facility; therefore, we tracked temperature using 6 waterproof HOBO Pendant Temperature/Light 64K Data Loggers[3] (UA-002-64, LI-COR Environmental, Bourne, MA) of which 2 failed.

Green crab were housed in bins, with one crab in each bin, within the hatchery tanks. The black plastic bins had lids and the following dimensions: 51.0×38.0×17.8 cm. We drilled 2 holes on each side of the lids and bins to create hinges made with reusable zip ties that held the bins closed. A large square (18 cm^2) was cut from each lid and was covered by a black plastic marine mesh that had a 1-cm grid and was secured with zip ties. The mesh in the lids allowed water exchange and green crab to still see overhead sunlight despite having a cage with opaque, black sides to live in during the week.

Six bins were placed in each hatchery tank. Water within each tank was shared among all the bins. The most important factors that influence habitat suitability for green crab, in order from most to least important, are threat of predation, depth of water, and turbidity of water (Cosham et al., 2016). The threat of predation by larger crab is controlled for through the use of opaque black bins; individual green crab, each housed in its own bin, cannot see each other and feel safe. The depth and turbidity of water in the bins was standardized. Each tank held crab of only one sex to reduce distraction from potential sex pheromones, alternating the sex of crab as male-female-male-female-male-female in the tanks along the length of the facility and then switching the sex in the tanks to female-male-female-male-female-male every other week. In total, the facility contained 24 tanks, although we used only 14–20 each week. Depending on the healthy number of crab available each week, we had from 72 to 102 green crab per prey treatment each week, half male and half female.

Experimental procedure

At the start of each week, new green crab were delivered from Nahcotta Port to the facility in Bay Center and were evaluated for health. Healthy crab were measured and individually placed into a bin in a hatchery tank. They were each given an anchovy (about 24–30 cm long) to feed ad libitum for 24 h, followed by a 72-h starvation period. If crab did not feed on the anchovy during the feeding period, they were removed from the experiment. Finally, each green crab was fed either 1 prey species for no-choice assays or 2 different prey species for choice assays. Prey were removed from tanks after 24 h and investigated for evidence of feeding. Evidence of feeding included shellfish being fully open with meat missing or pieces of shellfish having an area longer than 4 mm and a crescent moon shape where some feeding on the interior meat was visible. If crab used a claw to cause minor damage to the edge of a shell (the damaged section was less than 4 mm long) without visible feeding on the shellfish meat inside, it did not count as evidence of feeding because the shellfish could recover from the minimal damage through shell regrowth.

Data are presented as the number of single intact shellfish eaten or as the proportion of individual shellfish eaten, depending on the table or figure. For adult Pacific oyster, Manila clam, and Olympia oyster, we gave each individual 4 intact shellfish. In the case of spat on shell, we counted the total number of spat on shells (2 shells were given to each green crab) and recorded the proportion as the total spat on shell eaten divided by the total spat on shell counted before putting the spat on shell into the bins with each crab each week. It was easy to tell when spat on shell was eaten because the thin shells would be either open and flapping or removed entirely, revealing a pearly white, concave bottom shell. In one part of our experiment, we compared the standard 2-month-old Pacific oyster spat on shell with the 5-month-old Pacific oyster spat on shell

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

and classified each type of spat as *small* and *large*, respectively. Adult Pacific oyster had an average shell length of 60.25 mm (standard deviation [SD] 5.07). For Manila clam, average shell width was 43.96 mm (SD 1.77), and for small spat of Pacific oyster, average shell width was 19.69 mm (SD 7.85). For eelgrass, we gave each blue crab 30 cm of eelgrass, anchored with a rubber band to a stone, with all juvenile amphipods and mollusks removed from eelgrass blades.

Ideally, the prey needed to conduct all treatments for which data were to be compared would be supplied in the same week, but with the quantity of shellfish required each week coming from different producers in the state, it was too challenging to coordinate (Table 1).

Statistical analysis

Analysis was carried out in statistical software R (vers. 4.4.2; R Core Team, 2024) with the stats package. The choice assays, which involved 310 green crab (153 females, 157 males), were analyzed by using a logistic regression model and by using a Wald test to assess significance. The response was a binary variable indicating that at least 1 prey type was eaten. We created a categorical variable, *prey type combination*, indicating the 2 prey types in the tank, and this variable was used as a predictor. *Claw size* (in millimeters) and *sex* were included as additional fixed-effect predictors. The observations in which at least 1 of the prey types was consumed were further analyzed. Both carapace width and claw size were initially considered together in the model but were extremely correlated (P=0.91). The difference in Akaike information criterion between models that included *carapace width* or *claw size* was 0.2. Because of research interests, only *claw size* was kept in the model. Only the main effects of *claw size* and *prey type combination* were included. We identified and counted the green crab that exclusively ate 1 type of prey, allowing comparison of preference between prey types for which different measurement units were used.

The no-choice assays, which involved 278 green crab (135 females, 143 males), were analyzed by using a negative binomial regression model. The quantity of prey eaten was the response variable, and *prey type*, *claw size* (in millimeters), *carapace width* (in millimeters), and *sex* were used as predictors. An expanded model including the interaction between *claw size* and *prey type* was chosen because of a reduction in the Akaike information criterion. Eelgrass is not discrete; therefore, it was omitted from this model. The experiment was done over several weeks, but the variation in average temperature among weeks was minimal (15°C–18°C), and temperature data were omitted from the model. Predictive intervals were generated to estimate normal ranges for the quantity of prey eaten.

Table 1

Details about the experiment conducted from August through November 2023 at a hatchery in Bay Center, Washington, during which green crab (*Carcinus maenas*) were given either 1 type of prey (no-choice assay) or 2 different prey types (choice assay). Green crab were collected from Willapa Bay, Washington. The dates are those on which green crab were first put into tanks and initially fed an anchovy (Engraulidae). Average water temperatures in the tanks are provided. A dash indicates that no second prey type was used because a no-choice assay was done that week or that temperature data were not available. The prey types are Manila clam (*Ruditapes philippinarum*), adult Pacific oyster (*Crassostrea gigas*), 2-month-old (small [S]) and 5-month-old (large [L]) spat of Pacific oyster, Olympia oyster (*Ostrea lurida*), and native eelgrass (*Zostera marina*). In a week during which a choice assay was done, we also included 1 tank with 6 individuals for a no-choice assay to compare proportions of feeding across weeks.

Date	Temp. (°C)	Prey type 1	Prey type 2	No. of crab
2023-08-10	–	Manila clam	–	74
2023-08-17	–	Pacific oyster spat S	–	57
2023-08-24	20.83	Adult Pacific oyster	Pacific oyster spat S	84
2023-08-31	18.33	Pacific oyster spat L	Pacific oyster spat S	64
2023-09-07	17.22	Eelgrass	–	54
2023-09-14	18.61	Adult Pacific oyster	Eelgrass	66
2023-09-14	18.61	Adult Pacific oyster	–	6
2023-09-21	16.35	Manila clam	Eelgrass	61
2023-09-21	18.33	Manila clam	–	6
2023-09-28	16.11	Adult Pacific oyster	–	65
2023-10-05	17.20	Manila clam	–	64
2023-10-12	15.56	Olympia oyster	Pacific oyster spat S	44
2023-10-12	15.56	Pacific oyster spat S	–	6
2023-10-19	15.56	Adult Pacific oyster	Olympia oyster	48
2023-10-26	10.83	Adult Pacific oyster	Olympia oyster	39

Results

No-choice assays

The majority of green crab tested did not eat all pieces of prey items given to them within the 24-h feeding period. For eelgrass, it was difficult to quantify feeding behavior separately from clipping behavior. In our experiment, 30% of observed green crab manipulated the native eelgrass in some way that was not easily distinguishable, leading us to remove this prey type from the negative binomial regression model for the no-choice assays in which proportion data were used. We did include data for eelgrass in the logistic regression analysis of the choice assays.

In Figure 1, the relationship of the number of individual bivalve consumed in a 24-h period and claw size of green crab estimated with the model is depicted. The inclusion of an interaction term between *claw size* and *prey type* lowered the Akaike information criterion value from that for the main-effect model, although not all interaction terms were significant (significance level=0.05) when analyzed individually. The sex of green crab is assumed to be male for this model. Although for adult Pacific oyster *prey type* was not significant in the negative binomial regression model (coefficient [coef.]: −1.0, P=0.10), *prey type* was significant for both Manila clam (coef.: −3.5, P<0.001) and small spat of Pacific oyster (coef.: 1.3, P=0.0005). The difference in coefficient makes sense when looking at the graphs in this figure. Green crab generally ate fewer adult Pacific oyster and Manila clam than Pacific oyster spat on shell. A crab with a bigger claw size will eat more of any type of food, an outcome we would expect as energy needs increase with size of crab.

Claw size by itself is not statistically significant (P=0.20), but the interaction term between *claw size* and *prey type* for Manila clam is statistically significant despite an estimated coefficient (coef.: 0.08, P=0.008) that is relatively low compared to the coefficient for the same interaction term for adult Pacific oyster. An increase in claw size is associated with a small increase in the rate of consumption of Manila clam relative to that of adult Pacific oyster. When consumption rates for adult Pacific oyster and small spat of Pacific oyster are compared, the interaction of *claw size* and *prey type* is not statistically significant (P=0.286). This relationship is clear when looking at the modeled predictions and at the differences in the slope between these 2 models (in Figure 1). The predicted ability of green crab to feed on adult Manila clam and Pacific oyster increases when the claw size reaches a large size (25 mm), but the predicted ability of green crab to prey on small spat of Pacific oyster increases much more gradually despite increasing claw size.

Choice assays

We used a logistic regression to predict which type of prey, of the 2 types provided, each green crab would eat (Table 2). It appears that *claw size* was not a significant predictor in the presence of prey type combinations. Data from the experiment when the prey type combination was large and small Pacific oyster spat on shell were omitted from the model because all 64 green crab fed on both of these prey types. A positive coefficient value means that crab in choice assays were more likely to eat at least 1 prey type, and a negative value indicates that they were less likely to eat at least 1 prey type. When presented with

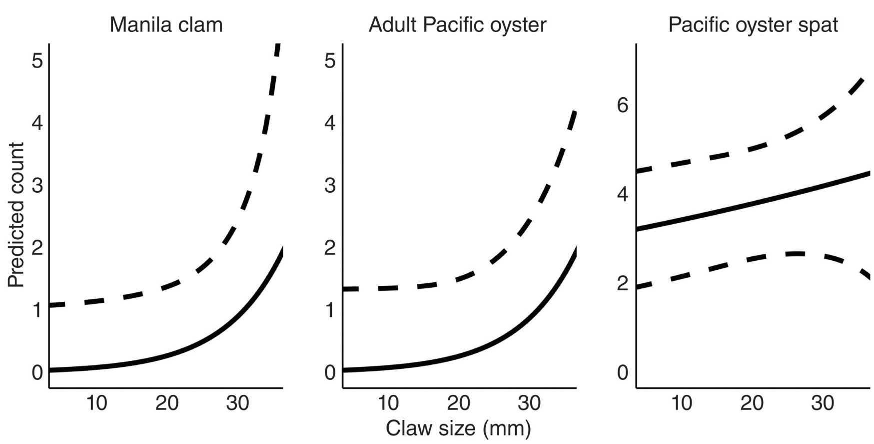

Figure 1

Predicted number of Manila clam (*Ruditapes philippinarum*), adult Pacific oyster (*Crassostrea gigas*), and small (2-month-old) spat of Pacific oyster consumed in a 24-h period by green crab (*Carcinus maenas*) in relation to the size of the crusher claw of green crab. A negative binomial regression model was fit to data from an experiment conducted from August through November 2023 with green crab held in hatchery tanks. The sex of crab was assumed to be male. Green crab were collected from Willapa Bay, Washington. The dashed lines indicate the 95% prediction intervals.

Table 2

Summary of results from the logistic regression used to predict the probability that a green crab (*Carcinus maenas*) would eat at least 1 type of prey, of the 2 types provided, during a choice assay. A categorical variable, *prey type combination*, which indicates the 2 prey types provided, was used as a predictor in the regression model. The other fixed-effect predictors are *claw size* (specifically of the crusher claw) and *sex* (assumed to be male [M] for this analysis). The prey types are Manila clam (*Ruditapes philippinarum*), adult Pacific oyster (*Crassostrea gigas*) (AdultPO), small (2-month-old) spat of Pacific oyster (POSpatS), and eelgrass (*Zostera marina*). Green crab were collected from Willapa Bay, Washington, and held in tanks for an experiment conducted between August and November 2023 at a hatchery in Bay Center, Washington. *P*-values from analysis with the Wald test are provided, along with mean estimates and standard errors of the mean (SEs).

Predictor	Estimate	SE	*P*-value
Manila clam vs. AdultPO	–2.91	0.835	<0.001
AdultPO vs. POSpatS	2.22	0.586	<0.001
Eelgrass vs. AdultPO	1.02	0.539	0.058
Eelgrass vs. Manila clam	–0.64	0.522	0.217
Claw size	–0.01	0.030	0.875
Sex (M)	0.15	0.374	0.694

either adult Manila clam or adult Pacific oyster, green crab were less likely than average to feed on either prey type, resulting in a large, significant, and negative estimate (coef.: –2.91, P<0.001). When spat of Pacific oyster were introduced, as in crab were given a choice of adult Pacific oyster versus small spat of Pacific oyster, green crab were significantly more likely to feed. We were surprised to see that *sex* was not significant in this model. Although claw sizes of females were on average smaller than those of males, the considerable overlap in claw size distributions led us to include both covariates in the model. Equally surprising, *claw size* was not statistically significant in the logistic regression model. This means that prey type combination is more likely than claw size to affect which prey a crab eats.

The proportion of prey consumed varied depending on whether the green crab were presented with a choice of or no choice of prey items (Table 3). It is notable that when green crab were presented with either large or small spat of Pacific oyster in a choice or no-choice assay, they ate higher proportions of prey than when they were presented with adult Manila clam or adult Pacific oyster. Green crab ate a greater proportion of prey when presented with no choice than when given a choice of prey items.

Comparing the discrete prey types (Manila clam, adult Pacific oyster, or spat of Pacific oyster) and the continuous

Table 3

The average proportion of prey consumed by green crab (*Carcinus maenas*) collected from Willapa Bay, Washington, and held in hatchery tanks during choice and no-choice assays conducted in August–November 2023. The prey types listed in the first column are the prey consumed by green crab: adult Pacific oyster (*Crassostrea gigas*) (AdultPO), Manila clam (*Ruditapes philippinarum*), small (2-month-old) spat of Pacific oyster (POSpatS), and large (5-month-old) spat of Pacific oyster (POSpatL). The names of prey that appear at the top of the other columns are the alternative prey provided in the choice assays, except when the prey type in the first column matches the prey type at the top of a column, the proportion given is from the no-choice assays. A dash indicates that that particular prey type combination was not included in the choice assays.

Prey type	AdultPO	Manila clam	POSpatS	POSpatL
AdultPO	0.1567	0.0000	0.1158	–
Manila clam	0.0192	0.0670	–	–
POSpatS	0.2130	–	0.3321	0.2680
POSpatL	–	–	0.3047	–

prey type (eelgrass) was difficult. The counts of green crab that consumed exclusively 1 prey item are compared in Table 4. Eelgrass was considered to have been consumed if there was any visible damage. In line with the analyses described herein previously, green crab had a strong preference for spat of Pacific oyster. In addition, they marginally preferred the larger of the 2 types of spat, 5-month-old Pacific oyster spat over the 2-month-old spat of Pacific oyster. Starved green crab in our experiment did considerable damage to eelgrass but made limited attempts to feed on protein-rich adult Manila clam and adult Pacific oyster.

Discussion

We found that *claw size* of green crab alone was not a statistically significant predictor in the model for the no-choice assays. Our data differ from that of past work that indicates a strong correlation between claw size and feeding proportion when the provided prey sizes were smaller (Dare et al., 1983). In our analysis, there was no statistically significant interaction between *claw size* and *prey type* for adult Pacific oyster relative to the interaction of *claw size* and *prey type* for spat of Pacific oyster (Fig. 1). Even small green crab (with claw sizes <20 mm) are capable of feeding on relatively high quantities of Pacific oyster spat on shell. Our findings, along with those from Dare et al. (1983), indicate that protecting spat of Pacific oyster, and potentially juveniles of other shellfish species, will be critical to efforts to support aquaculture by managing the effects of the invasive green crab. Shellfish growers in Willapa Bay are concerned about a decline in natural set for Manila clam (L. Kraft, personal commun.), and further

Table 4

Counts of green crab (*Carcinus maenas*) used in choice assays conducted between August and November 2023, the total numbers of crab in the assays (including those that fed on both prey types, which are not included in the counts in subsequent columns), the numbers of crab that consumed prey type 1 without feeding on prey type 2, and the numbers of crab that consumed prey type 2 without feeding on prey type 1. Crab were offered the following types of prey: adult Pacific oyster (*Crassostrea gigas*) (AdultPO), small (2-month-old) spat of Pacific oyster (POSpatS), eelgrass (*Zostera marina*), Manila clam (*Ruditapes philippinarum*), and large (5-month-old) spat of Pacific oyster (POSpatL). Crab were collected from Willapa Bay, Washington, and held in tanks at a hatchery for the experiment.

Prey type combination	Count		
	Total	Consumed prey 1	Consumed prey 2
AdultPO vs. POSpatS	82	6	41
Eelgrass vs. AdultPO	64	41	5
Eelgrass vs. ManilaClam	61	21	3
Manila clam vs. AdultPO	39	2	0
POSpatL vs. POSpatS	64	12	9

research is needed to determine if the growing invasion of green crab plays some part in that decline.

It seems that adult Pacific oyster and adult Manila clam experienced predation by green crab at a similar rate in the no-choice assays (Fig. 1), with a large claw size (>20 mm) needed to get into those food resources as indicated by results for the interaction term between *claw size* and *prey type* in our model. Because resources to manage green crab are limited, we suggest that growers focus on protecting their spat on shell and other juvenile life stages from all life stages of green crab. There may be a size at which each of 2 types of prey, adult Manila clam and adult Pacific oyster, are less damaged by green crab and, therefore, at which resources for management could be reduced for beds utilized by clam and oyster of those sizes. However, more research is needed to find the specific size at which adults of shellfish species can escape most predation by green crab.

We had intended to compare green crab feeding on the prey items described in the results to feeding on native eelgrass and Olympia oyster, but we ran into significant issues with our methods. For eelgrass, we measured the same length of eelgrass to put into each bin that held a green crab (30-cm length, including about 2.5 cm of root per shoot) and wanted to measure the proportion eaten on the basis of how much length was eaten. Remember that we carefully scraped all juvenile mollusks and amphipods off the eelgrass for this study, and note that those soft, easily accessible sources of protein may attract green crab to eelgrass in the wild (Howard et al., 2019). In our experiment, green crab sometimes ate eelgrass or sometimes merely clipped it and ate nothing. In the analysis of the choice assays, we included eelgrass damage, defined as feeding or clipping behavior or both, because each equally reduces a plant's ability to photosynthesize. Even eelgrass with all proteinaceous amphipods removed was eaten or clipped at relatively high rates. We did not see a statistically significant effect of either claw size or sex on eelgrass feeding or clipping behavior (P=0.495); therefore, again, even small green crab may need to be managed to reduce damage to eelgrass beds. Currently, the literature outlines burrowing behavior as causing the most significant damage in eelgrass beds (Matheson et al., 2016; Howard et al., 2019), where high densities of green crab have been associated with a 73%–81% loss of eelgrass shoots (Howard et al., 2019). Eelgrass shoot clipping, in addition to burrowing, by green crab has been reported to have caused significant damage to transplanted and existing beds in some experiments (Davis et al., 1998; Garbary et al., 2014).

In past studies, mature green crab have been found to feed readily on adult Olympia oyster (Palacios and Ferraro, 2003; Yamada et al., 2010). In our experiment, Olympia oyster arrived with barnacles on their shells. We noted immediately that green crab ate barnacles instead of attempting to open adult Olympia oyster, when removing prey items for the first assay with Olympia oyster. Each of the 72 green crab in the experiment were given 4 adult Olympia oyster to eat, but only 1 crab ate such an oyster: a female with a carapace width of 76 mm and a claw size of 17 mm, when the water temperature in the tank was 15.5°C or well within normal feeding temperatures. This result is strikingly different from data from Yamada et al. (2010) indicating that green crab fed on oysters at a much higher rate of 0.7 individuals/d. We think the barnacles found on Olympia oyster growing in Puget Sound may serve as a protection for these native oyster, with green crab, although capable of feeding on them, instead more likely to feed on barnacles first, especially when this invasive species is at low population levels. More research should be done to determine the density threshold at which green crab will begin to prey on Olympia oyster when other thin-shelled or shell-less high-protein resources are abundant, and such information may help to develop management tools that could trigger actions to limit the effect of this invasive species on commercial shellfish operations.

It is interesting that we found no statistically significant difference in feeding behavior of green crab between the sexes. Looking at the data, we might have expected to see large males with large claws feeding more than smaller females, but the feeding proportions look nearly equal between the sexes. This result may be due to increased energetic costs being spent by females on egg laying, although none of the females we tested were gravid. More research to specifically investigate feeding behavior of males and females may yield more information on differences in feeding proportion between the sexes.

The results of this study build on those of a larger body of work through which researchers have been trying to understand the effect that green crab will have on the ecology and economic output of shellfish growing areas in the Pacific Northwest. More research on the size of individuals of shellfish species in locations where they are protected from predation by green crab will be helpful in development of management recommendations for shellfish growers and operators in the region. However, such research has been focused on visible green crab with claw sizes of at least 6 mm. Some researchers working on the Atlantic coast of the United Sates, where the invasion of green crab is further along, are warning that major ecological effects of this species may exist at earlier life stages (Grosholz and Ruiz, 1996; Young, 2022). More research on green crab in late larval stages, often called *megalopae*, and on recently settled individuals will also be necessary to understand the larger ecological picture of how green crab may affect our coastline and how to best manage this invasive species to protect commercially important shellfish and recreational bivalve fishing and to maintain ecological services in our estuaries.

Conclusions

Green crab are capable of feeding on each of the economically and ecologically relevant types of prey included in our experiment. Claw size on its own did not determine how much food a green crab ate but did influence prey choice when an interaction term was included in the model. Green crab had a preference for Pacific oyster spat on shell, as expected. Sex did not influence feeding behavior in the choice assays; still, more research is needed to better evaluate, or refute, this claim. If given native eelgrass, green crab in our study both clipped and fed on it, behavior that is reportedly typical for this species. In the comparison of claw sizes, we found no significant difference in the feeding on or clipping of eelgrass by green crab; therefore, again, it is possible that even small green crab (with claw sizes <20 mm) may damage eelgrass as much as large green crab. Although Olympia oyster have been a preferred food source in some previous studies, the Olympia oyster we provided to green crab in our study had barnacles attached to their shells, and the green crab ate the barnacles instead of the meat of Olympia oyster. More research is needed to understand which resources in an estuary may be eaten first and which may be preferred as the size of populations of green crab grow and the most-preferred food sources become scarcer. On the basis of this research, we recognize that the shellfish industry in the Pacific Northwest is at risk of economic decline from the invasion of green crab. We suggest that managers of this invasive species begin to focus on all sizes of green crab, not just adults, given the ability of small juveniles (with claw sizes >8 mm) to eat significant proportions of Pacific oyster spat on shell. Growers of Pacific oyster should preferentially protect juvenile shellfish resources from all sizes of green crab.

Resumen

Tratamos de determinar el efecto potencial del cangrejo verde invasor (*Carcinus maenas*) sobre especies comercial y ecológicamente importantes en el noroeste del Pacífico mediante ensayos de elección y no elección realizados con cangrejos verdes de diferentes tamaños. Observamos el comportamiento alimentario del cangrejo verde en relación con varias presas elegidas, como la almeja de Manila adulta (*Ruditapes philippinarum*), la ostra del Pacífico adulta (*Crassostrea gigas*), las poslarvas de la ostra del Pacífico asentadas en la concha y la hierba marina nativa (*Zostera marina*). Los ensayos de no elección se modelaron con una regresión binomial negativa, y los ensayos de elección se modelaron con una regresión logística. Los resultados del modelo de no elección revelan que la interacción entre el tamaño de las tenazas y el tipo de presa fue significativa, y que el cangrejo verde de todos los tamaños se alimentó de poslarvas de la ostra del Pacífico asentadas a la concha. Los resultados del modelo de elección indican que el sexo no fue significativo para predecir si el cangrejo verde consumía algún tipo de presa. En nuestro estudio, el cangrejo verde que se alimentaba exclusivamente de un tipo de presa eligió las crías de concha o la hierba marina en lugar de los bivalvos adultas. Basándonos en estos datos, sugerimos que los acuicultores protegen las poslarvas de la ostra del Pacífico de todos los tamaños de cangrejo verde en lugar de proteger a la ostra adulta del Pacífico si los recursos son limitados.

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