

Beyond Predation: Invasive Green Crab (*Carcinus maenas*) Alters Juvenile Pacific Oyster
(*Magallana gigas*) Function and Survival Across Environmental Gradients

by

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A thesis submitted in partial fulfillment of the
requirements for the degree of

Master of Science
in
Environmental Science and Management

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Portland State University
2026

Abstract

The establishment of the invasive green crab, *Carcinus maenas*, creates ecological and economic impacts in estuaries, particularly through predation on bivalves and alteration of species interactions. This thesis evaluates the direct predation, non-consumptive predator presence, and spatial management implications of *C. maenas* impacts on filtration rate of juvenile Pacific oysters, *Magallana gigas*, across laboratory, field, and GIS-based vulnerability mapping approaches. In laboratory conditions, clearance rates of *M. gigas* were measured over 72 hours across two temperatures (14°C and 18°C) and predator treatments including *C. maenas*, Pacific rock crab (*Romaleon antennarium*), both predators together, and a predator-free control. Predator effect was tested across three phases: an acclimation phase to temperature and chemical cues, a non-consumptive phase with crabs with banded chelae, and a consumptive phase with unrestrained crabs. *M. gigas* clearance rates were influenced by both predator presence and phase, with *C. maenas* treatments suppressing clearance the most, even without direct predation. *Carcinus maenas* consumed more *M. gigas* than both the native *R. antennarium* and mixed treatments, indicating stronger predation pressure on juvenile *M. gigas* spat. Unlike *R. antennarium*, which showed a positive foraging association with size, *C. maenas* consumed *M. gigas* across a broader size range, suggesting less size selectivity within our sample of juvenile *M. gigas* spat.

Field experiments in Netarts Bay, Oregon, examined how habitat, prey size, vertical position, and predator assemblages influenced juvenile *M. gigas* survival. *M. gigas* were tethered in eelgrass (*Zostera marina*) and adjacent mudflat habitats across multiple sites and monitored for predation under natural conditions. Additional experiments tested the effects of *M. gigas* size and elevation above the substrate in areas with high *C. maenas* abundance. *M. gigas* survival was

generally lower in mudflats, and predation patterns suggested greater vulnerability in areas with higher *C. maenas* abundance. Larger *M. gigas* and elevated *M. gigas* had higher survival, indicating that habitat structure and prey context mediate vulnerability to predation.

To extend these experimental findings into an estuary-scale management context, a GIS-based Resource Vulnerability Index (RVI) was developed for Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay. The RVI integrated habitat and resources to identify areas where suitable *C. maenas* conditions and vulnerable estuarine resources overlap. Observed *C. maenas* CPUE did not show a simple linear correlation with RVI, indicating that trap catch, and resource vulnerability inform management in different ways. Areas with both high RVI and observed *C. maenas* CPUE may represent high priority zones for trapping or monitoring, while high RVI areas with limited CPUE may indicate potential monitoring gaps. Together, these findings suggest that *C. maenas* affects *M. gigas* performance through both direct predation and non-consumptive effects on feeding, with outcomes shaped by temperature and habitat. By linking laboratory mechanisms, field predation patterns, and spatial vulnerability mapping, this thesis shows that *C. maenas* impacts are both biological and spatially structured. This work highlights the importance of considering both trophic and non-trophic impacts from invasive species in estuarine systems that can create ecosystem-level effects. It has implications for invasive species management, *M. gigas* aquaculture, shellfish restoration, and spatially targeted monitoring across Oregon estuaries.

Acknowledgements

I would like to express my sincere gratitude to the many people who supported me throughout this thesis and my graduate studies. This project would not have been possible without the guidance and encouragement of my mentors, collaborators, friends, and family. First, I would like to thank my advisor Dr. Catherine de Rivera for supporting my M.S. research and development as a scientist every step of the way. Thank you for helping me develop this project and grow as both a researcher and writer. I am also grateful for my committee members, Dr. Amy Larson and Dr. Paola López-Duarte, for their thoughtful feedback and expertise throughout this project. Thank you to Dr. Elise Granek for generously lending me the tank set up for the clearance rate laboratory experiment. Additionally, I would like to thank Max Wiegardt and Whiskey Creek Oyster Hatchery for donating the Pacific oysters used in this study. I am also grateful to the U.S. Fish and Wildlife Service for funding that supported this work through the 2023 and 2024 Oregon Aquatic Nuisance Species Management Plan Implementation grants through Dr. Catherine de Rivera. I would also like to thank the members of the de Rivera lab and everyone who helped with field work, lab experiments, crab collection, and troubleshooting along the way. I especially want to thank Kyle Swanson, Jen Riddle, Keria Moritsugu-Vandehey, Blanca Hidalgo, Hannah Roy, Destiny Hazeri, and Sebastian Pacheco-Thompson for their assistance with sampling and data collection. Finally, I would like to thank my parents Dr. David Mize and Marguerite Mize for inspiring me to continue my educational journey and for encouraging me to shape that path around my own passions and curiosities. Thank you to my fiancé, Austin Gonzalez for every early morning and late night spent with me throughout this project, for your constant support along the way, and bringing me a coffee when I locked myself out of the wet lab.

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Introduction

Estuaries are among the most productive and ecologically important habitats in coastal regions worldwide (Barbier 2011). These biodiverse environments support nursery habitat for commercially and ecologically important fishes and invertebrates, promote nutrient cycling, and contribute to shoreline stabilization (Montagna et al. 2018; Magel et al. 2022). Estuaries also provide abundant food resources, sheltered conditions, and structurally complex habitats that can enhance survival during vulnerable juvenile stages for species, particularly through foundation habitats such as eelgrass (*Zostera marina*) beds (Fernandez et al. 1993; Weihrauch & McGaw 2024; Beck et al. 2001). These habitat forming species contribute to estuarine ecosystem function by supporting diverse food webs, increasing habitat availability, and facilitating processes such as benthic-pelagic coupling and water clarification (Marks et al. 2024; zu Ermgassen et al. 2013). As highly dynamic systems, estuaries are characterized by fluctuating salinity, temperature, and nutrient flow, which can favor stress-tolerant invader species (Crooks et al. 2011; McKnight et al. 2021). These variable conditions may exclude more specialized species, while high connectivity to human mediated transport pathways and disturbances to native communities can create opportunities for invaders to establish (Crooks et al. 2011; de Rivera et al. 2025). Estuaries are both functionally important coastal systems and environments where shifts in species interactions can have large ecological consequences.

Oysters are foundational ecosystem engineers in estuarine environments, where their accumulated shells create complex physical habitat that supports estuarine species (Kreeger et al. 2018; Marks et al. 2024). The shell beds provide refuge from predation and physical stress, while also increasing habitat availability for invertebrates and juvenile fishes and crabs (Ens et al. 2021; Jensen et al. 2002). As suspension feeders, oysters contribute to water filtration and clarification

by removing particulate matter from the water column. Therefore, they reduce turbidity and increase light availability for submerged aquatic vegetation, such as *Z. marina* (zu Ermgassen et al. 2013). Additionally, through filtration, oysters facilitate nutrient cycling and benthic-pelagic coupling by depositing material onto the sediment surface (Kreeger et al. 2018). This fertilization of the sediment can support benthic macroinvertebrate communities and broader estuarine food webs (Marks et al. 2024; zu Ermgassen et al. 2013). Through these combined roles, oysters contribute to estuarine function by stabilizing sediments and supporting local biodiversity (Marks et al. 2024). The Pacific oyster (*Magallana gigas*, formerly *Crassostrea gigas*) is an economically and ecologically important species that will be the study focus of this thesis (Holsman et al. 2006; Rosa et al. 2018). Since *M. gigas* influences both physical habitat structure and water-column processes, reductions in its survival may alter ecosystem functions that extend beyond the loss of individual oysters.

Non-native green shore crabs (*Carcinus maenas*) are among the world's most impactful marine invaders and have become a major ecological concern to the U.S. Pacific Northwest coastline due to their ecological and economic impacts (Jamieson et al. 1998; See & Feist 2010; Yamada et al. 2015). Native to the Atlantic Coasts of Europe and northern Africa, from Norway to Mauritania, *C. maenas* has expanded globally due anthropogenic vectors such as ballast water discharge and movement of aquaculture materials (Fulton et al. 2013; Ens et al. 2021). First detected on the U.S. West Coast in the San Francisco Bay in 1989, *C. maenas* reached Oregon estuaries by the late 1990s (Jamieson et al. 1998; Bassett 2000). Their rapid spread northward was likely facilitated by warm El Niño events, which carried viable larvae along coastal currents (Yamada & Gillespie 2021). Although early invasion was successful along the Pacific Northwest coast, with populations appearing in multiple estuaries, their abundance varied over time, and

consistent, self-sustaining *C. maenas* populations did not appear until 2015 (Yamada et al. 2015). The West Coast population shows a genetic relationship with the East Coast North American population, suggesting that *C. maenas* in Oregon likely originated from a secondary invasion from the East Coast rather than directly from the founding European population (Tepolt et al. 2009).

The success of *C. maenas* in estuarine systems is strongly tied to their physiological flexibility. Following dispersal, its broad tolerance of salinities ranging from 5 to 50 ppt and near-freezing temperatures allows it to establish across a wide range of estuarine environments, from cooler, saltier deep waters to areas influenced by freshwater input (Weihrauch & McGaw 2024). This euryhaline and eurythermal flexibility helps explain why *C. maenas* is so successful in highly variable estuarine environments (Weihrauch & McGaw 2024). In Oregon and the broader PNW this physiological flexibility may further advantage *C. maenas* where there are few medium to large native brackish-water crab specialists (Hunt & Yamada 2003).

The establishment of *C. maenas* in Oregon estuaries has the potential to cause major ecological impacts. *Carcinus maenas* can alter the physical habitat structure across *Z. marina* beds when foraging (Fernandez et al. 1993; Thayer et al. 1984). Due to its ability to physically modify its habitats, it has been considered an ecosystem engineer, whose disturbance reduces overall habitat quality (Bassett 2000). When eelgrass is present, *C. maenas* not only tears blades but also burrows under rhizomes and roots, breaking or uprooting them (Malyshev and Quijón 2011, Garbary et al. 2014). Although eelgrass may persist in invaded areas, the disturbances can reduce the structural complexity that eelgrass provides for shelter and foraging habitat for juvenile crabs and other native species (Fernandez et al. 1993; Thayer et al. 1984). Because of *C. maenas*' broad physical tolerances and flexible behavioral traits, they can be particularly disruptive to estuarine environments (Weihrauch & McGaw 2024). They are omnivorous, opportunistic feeders that prey

on a wide variety of more than 150 species, including mollusks, crustaceans, polychaetes, algae, eelgrass, and smaller conspecifics (Baeta et al. 2006; MacDonald et al. 2018; Fisher et al. 2024). Their diet changes seasonally based on availability and they have high foraging rates, which allows them to outcompete native species (Baeta et al. 2006; Leignel et al. 2014). As a result, they can disrupt local food webs and dominate habitats shared with native species (Matheson & McKenzie 2014; Baillie & Grabowski 2019). Their predation on native clams and other bivalves directly increases pressure on commercial fisheries and aquaculture operations (Yamada et al. 2020).

The ecological effects of *C. maenas* extend beyond direct predation alone. In addition to consumptive impacts on the ecosystem through prey removal, *C. maenas* may also generate non-consumptive effects that alter prey behavior, habitat use, and ecological function (Palacios & Ferraro 2003). For suspension feeding bivalves, such as *M. gigas*, predator presence may influence feeding activity even in the absence of direct consumption, as prey respond to predator cues through energetically costly defensive behaviors that can reduce filtration and growth (Marks et al. 2024). These non-consumptive impacts may be especially important because changes in oyster feeding can affect broader estuarine functions, including water filtration and nutrient cycling (Marks et al. 2024; Rosa et al. 2018). Hunt & Yamada (2003) showed that interactions between *C. maenas* and the native red rock crab (*Cancer productus*) can shape crab distributions in Oregon estuaries, suggesting that invasive and native cancrid predators differ in ecological effects. Nonconsumptive impacts may also therefore differ based on predator identity, as invasive *C. maenas* and native Pacific rock crabs (*Romaleon antennarium*) occupy different ecological roles and may expose prey to different levels of risk, and *R. antennarium* was selected for this study over *Cancer productus* as the more abundant native crab in the study system. In structured habitats such as *Z. marina* beds, vegetation may mediate predator-prey interactions by altering refuge

availability, predator foraging efficiency, and the balance between invasive and native predator effects (Holsman et al. 2006; Fernandez et al. 1993). Temperature may intensify both consumptive and non-consumptive impacts by increasing crab metabolic demand and foraging activity, while reducing the ability of *M. gigas* to maintain effective defensive responses (DeRoy et al. 2022; Matheson & McKenzie 2014). Since *C. maenas* can affect estuarine communities through both trophic and non-trophic pathways, understanding their ecological role requires consideration of their impacts through direct predation, non-consumptive effects, and habitat context in which these interactions occur.

Despite decades of research on *C. maenas*, important knowledge gaps remain regarding how this invasive predator influences the feeding behavior of suspension-feeding bivalves under realistic ecological conditions. Most studies of *C. maenas* impacts on bivalves have focused solely on survival, while comparatively less attention has been given to how the isolated presence of this predator alters bivalve behavior (Kimbrow et al. 2020; Howard et al. 2022). As a result, relatively little is known about how the presence of *C. maenas* alters *M. gigas* filtration behavior through non-consumptive effects, such as through chemical cue driven reductions in feeding (Howard et al. 2022; Marks et al. 2024). Additionally, comparing the behavioral impacts of invasive *C. maenas* with those of native crab species under varying temperature conditions, particularly *R. antennarium*, as a larger, more aggressive species that holds some biotic resistance to *C. maenas* (Yamada et al. 2020; Hunt & Yamada 2003). Comparing how *C. maenas* interact with different habitat types compared to native predator assemblages would be beneficial to understanding how refuge and foraging dynamics shift across vegetation, especially in structured estuarine habitats such as eelgrass, where refuge availability and predator foraging efficiency may differ from more open environments (Holsman et al. 2006). Temperature may further modify these interactions by

increasing crab metabolic demand and foraging activity, while also reducing the ability of *M. gigas* to maintain effective defensive responses under physiological stress (DeRoy et al. 2022; Yang et al. 2016). Addressing uncertainties in *C. maenas* effects on *M. gigas* compared to native predator context and across habitat and environmental conditions is important for informing shellfish recovery, aquaculture, and management under continued climate change and pressure from marine invaders.

Understanding *C. maenas* impacts also requires linking species effects to spatial management priorities. Laboratory and field experiments can identify mechanisms of impacts and localized observations of impacts, but management also requires identifying where vulnerable resources and suitable *C. maenas* conditions overlap across estuaries. Since catch per unit effort (CPUE) monitoring describes observed catch but does not directly identify resource vulnerability, GIS-based vulnerability mapping can complement trapping data by highlighting areas where shellfish resources, seagrass habitat, salinity conditions, and native crab context may create elevated management concern.

This thesis investigates the direct (predation), non-consumptive (presence), and broader interaction-mediated ecological impacts of *C. maenas* on juvenile *M. gigas* under varying biotic and abiotic conditions. Chapter one examines how predator identity and temperature shape *M. gigas* clearance rates and survival in a controlled laboratory experiment, comparing the effects of invasive *C. maenas*, native *R. antennarium*, mixed-predator treatments, and predator-free controls. This chapter evaluates both non-consumptive and consumptive effects by measuring *M. gigas* clearance rates during phases with predator cues alone and phases allowing direct predation across two temperature treatments. Chapter two evaluates predation on juvenile *M. gigas* in the field across eelgrass and unvegetated habitats, site-level predator assemblages, prey size classes, and

vertical refuge treatments. Chapter three extends these laboratory and field findings into an applied management context by developing a GIS-based Resource Vulnerability Index for Oregon estuaries with documented *C. maenas* presence. This chapter integrates habitat, shellfish resources, seagrass, salinity, and native crab CPUE to identify areas where suitable *C. maenas* conditions and vulnerable estuarine resources overlap. Together, these chapters assess how *C. maenas* effects on *M. gigas* vary across predator context, habitat structure, temperature, and spatial vulnerability, providing a broader understanding of how invasive predators alter estuarine ecological function, shellfish vulnerability, and management priorities.

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Chapter One: Non-consumptive and consumptive effects of invasive green crab (*Carcinus maenas*) on Pacific oyster (*Magallana gigas*) clearance rates under varying temperature conditions

Introduction

Estuaries are among the most productive and ecologically important habitats in coastal regions worldwide (Barbier et al. 2011). These biodiverse systems support nursery grounds for commercially important fish and invertebrates, promote nutrient cycling, and provide shoreline stabilization (Montagna et al. 2018; Magel et al. 2022). Suspension-feeding bivalves such as the Pacific oyster (*Magallana gigas*) play an important ecological role in these environments by filtering suspended particles from the water column (Gray and Langdon 2017; Mach and Chan 2014). Through this feeding activity, oysters remove organic and inorganic particles from the water column, improving water clarity by reducing turbidity (Marks et al. 2024; zu Ermgassen et al. 2013). This filtration also transfers material between the water column and sediment surface, contributing to benthic-pelagic coupling and influencing nutrient exchange in estuarine food webs (Rosa et al. 2018). Changes in oyster feeding behavior may affect ecological processes beyond the individual organism, with consequences for broader estuarine function. Since these functions depend partially on oyster performance, invasive predators such as the European green crab (*Carcinus maenas*) may influence oyster survival and feeding behavior.

Estuarine systems are increasingly affected by multiple stressors, including climate-driven temperature change and biological invasions (Crooks et al. 2011; de Rivera et al. 2011). These environments experience highly variable salinity, temperature, and nutrient conditions, which often favor stress-tolerant invasive species (Crooks et al. 2011). Along the Pacific Northwest coast, this environmental variability can create space for opportunistic invaders while altering species

interactions and ecological function (Bailey et al. 2020). For *M. gigas*, performance may be shaped not only by abiotic conditions, but also by how invasive predators respond to those same conditions. Among these stressors, warming and invasion are especially important, as both can alter the strength and outcome of predator-prey interactions.

One of the most impactful marine invaders in temperate estuaries worldwide is the European green crab (*Carcinus maenas*). Native to the Atlantic coasts of Europe and northern Africa, *C. maenas* has expanded globally through anthropogenic transport mechanisms such as ballast water discharge, aquaculture transfers, and other maritime vectors (Fulton et al. 2013; Ens et al. 2021). The ecological impact of *C. maenas* is driven by its opportunistic feeding behavior as a generalist predator, allowing it to consume a wide range of plant and animal prey (Jamieson et al. 1998; Baeta et al. 2006; Fisher et al. 2024). Their dietary flexibility, combined with high foraging rates, allow them to outcompete native species and disrupt food webs in invaded ecosystems (Baillie & Grabowski 2019; Matheson & McKenzie 2014). *Carcinus maenas* commonly target bivalves, can alter habitat structure, and predator presence may also alter prey behavior through nonconsumptive pathways, extending their effects beyond direct predation (Palacios & Ferraro 2003; Kimbro et al. 2020).

In estuarine environments, bivalves are among the most frequently targeted prey, making shellfish populations particularly vulnerable to *C. maenas* predation (Ens et al 2021; Fisher et al. 2024). Compared with native crab predators, *C. maenas* may exert stronger effects on *M. gigas* survival under similar conditions. Previous studies have shown that *C. maenas* can consume more *M. gigas* than the native red rock crab (*Cancer productus*) when prey densities are low, suggesting that invasive predator identity may strongly influence bivalve survival in estuarine systems (Ens et al. 2021). Predation in early life stages is especially important, as *C. maenas* often target juvenile

stages of bivalves or *M. gigas* spat on shell, which can limit population reproduction through bottlenecks (Anaya 2025; Grason & Miner 2012). Native cancrid crabs may differ from *C. maenas* in both ecological effects and environmental associations. *Cancer productus* is a larger native cancrid crab that also preys on *M. gigas* and may contribute to biotic resistance against *C. maenas* in Oregon estuaries (Grosholz et al. 2011; Yamada et al. 2020). Although many previous studies have focused on *Cancer productus*, the Pacific rock crab (*R. antennarium*) provides a relevant native comparison because it is also a native cancrid crab in the same subfamily, Cancrinae (WoRMS Editorial Board, 2026; ITIS, 2026). *Romaleon antennarium* was formerly placed in the genus *Cancer*, further supporting its use as a closely related native predator comparison (WoRMS Editorial Board, 2026; ITIS, 2026). *Romaleon antennarium* also has robust, black-tipped chelae typical of rock crabs, making it a biologically relevant native crab predator comparison (ODFW, 2024). *Romaleon antennarium* differ from *C. maenas* in habitat associations and environmental tolerances with *R. antennarium* less tolerant of the brackish conditions that *C. maenas* found in (ODFW, 2024; Hunt & Yamada, 2003). Comparing these predators therefore provides a way to assess whether oyster responses differ between invasive and native crab contexts.

While much research has focused on the direct predation impacts of *C. maenas*, predators can also influence prey species through indirect or non-consumptive effects (Trussell et al. 2003; Trussell et al. 2004). In aquatic environments, chemical cues released by predators or injured prey can alter the behavior of nearby organisms (Smee et al. 2008). These cues can signal predation risk and trigger behavioral responses such as reduced movement or decreased feeding in oysters and other bivalves (Howard 2022). In crabs, chemical signals can influence activity, aggression, and feeding behavior; therefore, mixed-predator treatments may expose oysters to a more complex olfactory environment than single-species treatments. In this study, these pathways were separated

experimentally using a chemical cue phase, a non-consumptive phase with crabs' present but chelae banded, and a direct predation phase with chelae unbanded. Understanding these non-consumptive effects is important because predator-driven reductions in oyster feeding may influence both oyster performance and the broader habitat functions that oysters provide in estuarine ecosystems (Marks et al. 2024). Non-consumptive effects may also extend beyond feeding suppression, as predator chemical cues may reduce recruitment of larval settlement, even in the absence of direct predation (Kimbrow et al. 2020). These studies suggest that predator effects on oysters may operate through multiple behavioral pathways, which may catalyze *C. maenas* presence.

Environmental conditions such as temperature may further modify predator-prey interactions. Temperature influences metabolic rates, activity levels, and feeding behavior in many marine organisms, including *C. maenas* (DeRoy et al. 2022). Although metabolic demand and feeding rates often increase with warming, these responses are elevated only up to a species-specific thermal optimum, after which performance typically declines (Gray & Langdon 2017). Since *C. maenas* has a relatively broad thermal tolerance, it may maintain strong foraging performance across a wider temperature range than other predators or their prey (Weihrauch & McGaw 2024). Warmer temperatures can therefore increase predator metabolism and consumption rates, potentially intensifying predator impacts on prey populations, while predator-free clearance rates in *M. gigas* also rise with warming and peak near 20°C before declining at higher temperatures (Howard et al. 2022; Gray & Langdon 2017). Elevated temperature can alter oyster physiological performance and survival, suggesting that thermally stressed oysters may have less capacity to maintain effective defensive or feeding responses under elevated temperature conditions (Yang et al. 2016; Li et al. 2022). Temperature may also alter the persistence of

chemical cues in marine environments through faster microbial degradation (Kimbrow et al. 2020). These mechanisms suggest that warming may alter not only the strength of predation, but also how oysters perceive and respond to predation risk.

Despite decades of research on *C. maenas*, important knowledge gaps remain regarding how this invasive predator influences the feeding behavior of suspension-feeding bivalves. Most studies have focused on direct predation impacts, while relatively little is known about how the presence of *C. maenas* alters oyster filtration behavior through non-consumptive effects. Additionally, few studies have compared the behavioral impacts of invasive *C. maenas* with those of native crab species under varying temperature conditions. To evaluate the effects of invasive *C. maenas* on oyster feeding and survival, this chapter examines both the consumptive and non-consumptive predator impacts under varying biotic and abiotic conditions. A multi-phase experiment was used to evaluate how *C. maenas* influences *M. gigas* clearance rates and survival through cue-mediated indirect effects and direct predation. Non-consumptive effects were measured by quantifying *M. gigas* clearance rates in the presence of *C. maenas* with temporarily immobilized claws, allowing predator cues without mechanical predation, while consumptive effects were assessed following removal of claw constraints.

To determine whether these effects were more pronounced for the recently introduced, euryhaline predator *C. maenas*, than for a native cancrinid crab with narrower tolerances, such as *R. antennarium*, both species were tested using the same experimental framework. Outcomes were compared among two native *R. antennarium* alone, two *C. maenas* alone, and a mixed-species treatment with one individual of each species. predator-prey interactions may shift under changing environmental conditions, including estuarine gradients in salinity and temperature (de Rivera et al., 2025). Specifically, a multi-phase experimental approach was used to assess how the presence

of crabs alters *M. gigas* clearance rates and survival through indirect mechanisms, such as chemical cues, behavioral cues, and physical disturbance, as well as through direct predation. Experiments were conducted at two temperatures selected to compare ambient collection conditions with a warmer summer-relevant condition for Oregon estuaries (NCEI, n.d.). The study tested the hypothesis that crab presence would reduce *M. gigas* feeding, reflected in lower *M. gigas* clearance rates, and that crabs would affect *M. gigas* through both trophic effects (direct consumption) and non-trophic effects (predator cues and physical interactions without consumption). These effects were further predicted to vary with predator treatment and temperature. The presence of *C. maenas* was hypothesized to exert greater non-consumptive effects on oyster feeding and reduce survival more strongly than the native crab treatment given the broad thermal tolerance of *C. maenas* and its high foraging rates of bivalves. Warmer temperatures were hypothesized to strengthen *C. maenas* impacts, such that both direct predation and indirect behavioral effects would persist or intensify under thermal stress. The mixed species predator treatment was predicted to have relatively weaker consumptive and non-consumptive effects on *M. gigas* than the two *C. maenas* treatment due to interspecific crab interactions. Together, these interactions were predicted to result in stronger combined effects of the invasive predators and abiotic stressors than temperature alone.

Methods

A three-phase laboratory experiment was conducted from May 31st to July 3rd, 2025, to assess indirect and direct ecological effects of *C. maenas* and *R. antennarium* on juvenile *M. gigas* spat across controlled environmental conditions. The experiment manipulated predator exposure and temperature, while measuring *M. gigas* spat feeding responses through algal clearance rates and survival.

Experiments were performed in aerated, static 55 liter tanks maintained under controlled laboratory conditions. Tanks operated as closed systems with individual recirculating pumps that maintained continuous water movement and filtration within each tank. Salinity was standardized to 28 PSU using instant Ocean synthetic sea salt. Tanks were randomly assigned to one of two temperature treatments and four predator treatments (predator-free control, two *C. maenas*, two *R. antennarium*, or one of each crab). Water was replaced between trials to eliminate residual chemical cues from previous trials. Tanks were maintained under a controlled photoperiod designed to mimic natural light conditions on the Oregon coast in June, the time of collection and the experiment, with lighting programmed to follow daily sunrise and sunset times.

Temperature treatments were selected to represent a cooler estuarine reference condition and a warmer summer-relevant condition for Oregon estuaries. The 14°C treatment reflected conditions close to those measured during organism collection in Netarts Bay, where water temperature averaged $14.8 \pm 1.4^\circ\text{C}$. Additionally, National Centers for Environmental Information coastal water temperature averages for Oregon coastal stations show summer values ranging from approximately 12–18°C depending on location and month, with some averages approaching 18°C in late summer (NCEI, n.d.). The 18°C treatment represented a warmer condition relevant to summer estuarine warming and potential future warming scenarios along the Oregon coast.

Each predator by temperature treatment combination was replicated seven times ($n = 7$), resulting in a total of 56 experimental tanks. Trials were conducted in sequential blocks due to tank availability, with one or two trials running simultaneously. During the third block, a tank system shutdown required several treatments to be repeated during a fourth experimental block to maintain consistent replication across treatments. In addition, ten algae-only control trials were conducted

across temperature treatments to account for background changes in algal concentration unrelated to oyster filtration.

For each crab pair, one individual was selected from a smaller and one from a larger size class, with an average difference of ~30 mm carapace width. Across treatments, the larger crab averaged at 79.5 mm width and the smaller 51.7 mm width. In the two *C. maenas* treatments, crabs ranged from 27 to 88 mm carapace width. In mixed *R. antennarium* and *C. maenas* treatments, crabs ranged from 26 to 95 mm and *R. antennarium* was always the larger crab in mixed-species pairs. In the two *R. antennarium* treatments, crabs ranged from 35 to 107 mm. This size difference was intended to allow for potential interspecific or intraspecific competition during the direct interaction phase (Figure 1.1). Each tank contained two empty clam or oyster shells and two rocks to provide structural complexity.

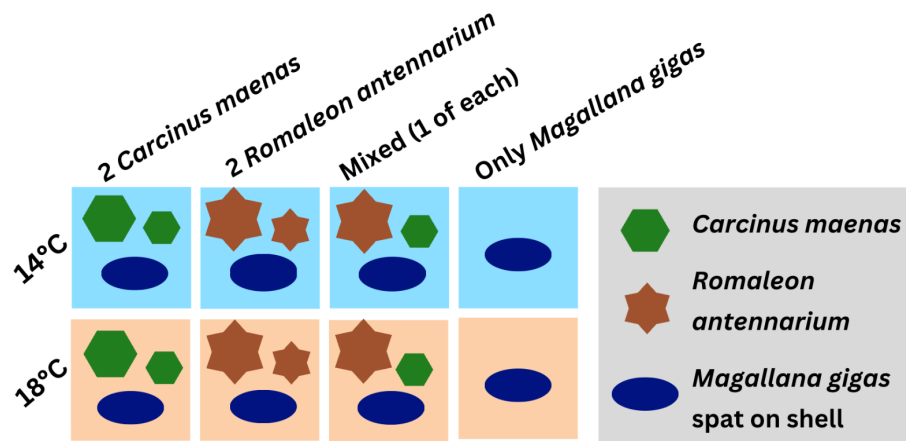


Figure 1.1 Predator treatment experimental design. Diagram of the four predator treatments and two temperature treatments. Treatments were randomly assigned across tanks, and each treatment was conducted 7 times.

All crabs were collected from Netarts Bay, OR during low tide on the following dates: May 30, June 12, June 16, and June 30, 2025. *Romaleon antennarium* individuals were collected at the mouth of the bay adjacent to the boat launch site (45.429851, -123.946323). *Carcinus maenas* were collected primarily by an outfall pipe near a key shellfish reserve site in the bay that is known for a high abundance of the crab (45.414545, -123.934275) except on May 30th, when they were collected near a different outfall pipe closer to the mouth of the bay, (45.430456, -123.946930) by the boat launch. Crabs were not re-used between trials.

Following collection, crabs were transported to a wet laboratory facility at PSU's Science and Research Technology building, maintained in flow-through seawater tables 28ppt and 16°C and fed between 18:00-19:00 on collection day. Phase 1 of the experiment began 36 hours after feeding to standardize hunger levels.

Juvenile Pacific oysters (*M. gigas*) were donated by Whiskey Creek Hatchery on May 30. *M. gigas* spat ranged from 9-57mm in length (median = 26 mm). Shells with attached spat were selected randomly from the flow-through water tables where they were held. If a selected shell had fewer than five spat, an additional shell was pulled and added to that treatment. Each tank contained between 6-21 juvenile spat (median = 9). Variation in spat number resulted from the natural density of hatchery-set oysters on selected shells. All spats were measured at the start of the experiment, and surviving spat were re-measured at the conclusion of Phase 3.

Clearance rates were calculated using the standard formula to identify the volume of water cleared of algae particles per unit of time for filter feeders (Kreeger et al. 2018; Rosa et al. 2018): $CR = (V / nt) * \ln(C_0 / C_t)$ where CR is clearance rate, V is chamber volume in liters, n is the number of individuals, t is the duration of the sampling interval, C_0 is the initial particle concentration in cells per mL, and C_t is the particle concentration at time t in cells per mL.

Clearance rate was measured across each phase. For each phase, C_0 was the algal concentration measured from the 30 minute post-dosing water sample, and C_t was the algal concentration measured from the water sample collected 24 hours later marking the end of that phase. Water samples were processed one at a time in random order. Samples were refrigerated when not in use but counted on the day of collection. Algal concentrations were quantified using a two-chamber Fuchs–Rosenthal counting slide. For each tank sample, four total hemocytometer counts were subsampled from the same 1 mL water sample. Both chambers were fully filled with sample water, and algae were allowed to settle for approximately one minute before examination under a compound microscope at 100× magnification. This was conducted twice. The chamber contains 16 one square millimeter areas, and 8 of the 16 were counted, consistent with the manufacturer’s recommended counting approach (Hausser Scientific, n.d.). This count was doubled to estimate total algal abundance per subsample. Algal concentrations were determined for each subsample chamber count, then averaged by tank. The mean algal concentrations were used for statistical analyses.

The experiment was structured to separate predator effects into three increasingly direct exposure pathways. Each experimental phase lasted 24 hours, resulting in a total experimental duration of 72 hours. Phase 1 tested whether chemical cues alone affected *M. gigas* clearance rates while crabs were physically isolated from *M. gigas*. Phase 2 tested whether predator presence and physical contact, without mechanical predation, further altered clearance rates. Phase 3 tested whether direct crab interactions, with allowed full consumptive interactions, affected both clearance rates and survival. This structure allowed non-consumptive and consumptive effects to be evaluated within the same experimental framework.

Phase 1: Chemical Cue Exposure and Temperature Acclimation

Phase 1 aimed to determine whether crab chemical cues alone would affect oyster feeding rates. To establish baseline algal concentrations, 1mL of Shellfish Diet 1800 was added to each tank and allowed to circulate for 30 minutes. Continuous recirculating water flow helped keep algae suspended and promoted a relatively uniform distribution throughout the tank. After 30 minutes, a 1mL water sample was collected from each tank after circulation and used as the initial algal concentration for Phase 1. Following algae dosing, oysters were placed at the base of each tank, and each crab treatment, which included two crabs, each housed in separate perforated container within the tank to prevent them from physically interacting with the oysters while their chemical cues circulated in the tank water. Both oyster shells and predator by temperature treatment were randomly selected per tank. At the start of Phase 1, crab carapace width, sex, and visible injuries (such as missing legs) were recorded along with the number and size of oyster spat in each tank.

During this phase, tanks and their oysters and crabs were gradually acclimated to their assigned water treatment. All tanks began at 16°C to match the holding water table. Temperatures were adjusted by 1°C every 12 hours (7:00 and 19:00) until the target temperature was reached (14°C for the cool treatment, 18°C for the warm treatment). This gradual adjustment aimed to minimize thermal stress and allow sufficient time for temperature equilibration of the full 55-L water volume.

Up to twelve hours before Phase 2, crabs were removed individually, and claws were temporarily immobilized using small rubber bands before being returned to the perforated containers in their original treatment tanks (Figure 1.2). Twenty-four hours after Phase 1 began, a

second water sample was collected from each tank to estimate algal density, and therefore clearance rates, from this olfactory cue phase. The experiment then advanced to Phase 2.

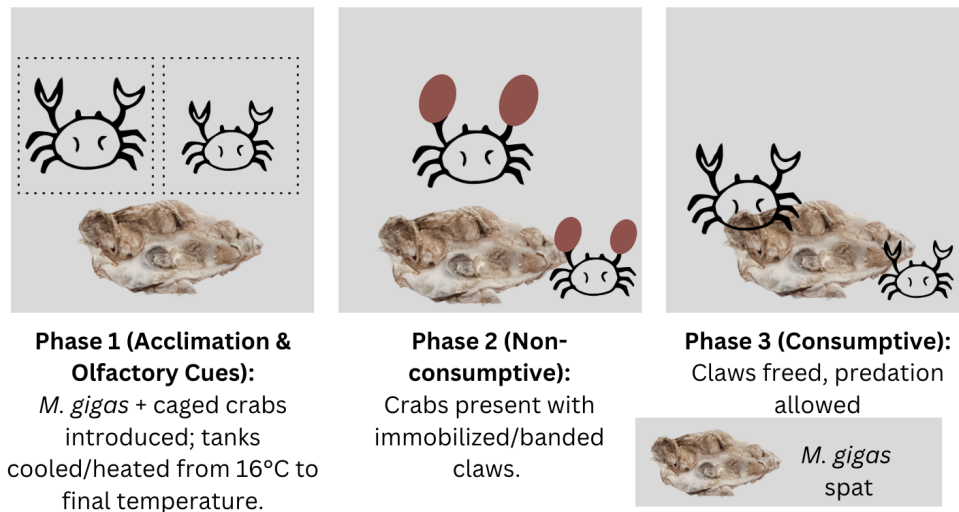


Figure 1.2 Experimental phase design. *Diagram of the three sequential 24 hour experimental phases. Clearance rates were measured from algae concentration at the start and end of each phase, and *M. gigas* predation was assessed at the end of the experiment.*

Phase 2: Indirect Effects

Phase 2 aimed to determine whether the presence of crabs, without direct predation, would affect oyster feeding rates through indirect interactions such as chemical and tactile cues, excluding mechanical predation. Phase 2 started 24 hours after Phase 1 by redosing tanks with 1 mL of Shellfish Diet 1800 and then releasing the banded crabs from their enclosures. After a 30-minute circulation period, a 1 mL water sample was collected from each tank and used as the initial algal concentration for phase 2. After 24 hrs, a second 1 mL water sample was collected from each tank at the end of the phase.

Phase 3: Direct Effects

Phase 3 aimed to determine how direct crab-oyster interactions, including predation, affected oyster feeding rates and survival. Following completion of Phase 2, crab claw bands were removed, allowing full direct interaction between crabs and oysters for the final 24-hour phase of the experiment. All other experimental conditions remained unchanged. Crabs were allowed to interact freely with oysters and with each other for the duration of Phase 3. At the start of Phase 3, tanks were again dosed with 1mL of Shellfish Diet 1800 and allowed to circulate for 30 minutes before a 1 mL water sample was collected from each tank as the initial algal concentration for the phase. A second 1 mL water sample was collected 24 hours later at the end of the phase. Phase 3 and the water sampled at 30 min and 24 hrs to calculate the change in density. Oyster survival and crab injury were assessed at the conclusion of Phase 3. For tanks with consumption events during Phase 3, the number of individuals (n) in the clearance rate equation was adjusted to reflect the reduced number of surviving oysters remaining at the end of the phase.

Statistical Analysis

Clearance rate data were initially evaluated for distributional assumptions and were strongly right skewed. To improve normality and meet model assumptions, clearance rates were transformed using a Box-Cox transformation ($\lambda = 0.3434$) then an addition of a small constant (+0.158) to ensure all values were positive. Clearance rate was analyzed using a linear model with temperature, predator treatment, and experimental phase as fixed effects, including all interaction terms. Random effects for tank and experimental day were initially included to account for variation among tanks and sampling days, but they were removed from the final model because they explained negligible variance. Algae-only tanks were analyzed separately to evaluate whether background algal concentrations changed over the same 24-hour intervals used to calculate

clearance rates. Since the experiment was structured to separate chemical cue exposure, non-consumptive predator exposure, and direct predator-prey interactions, phase-specific ANOVAs were also used to evaluate temperature and predator treatment effects within each experimental phase. Post-hoc contrasts were used to identify treatment differences. Total *M. gigas* consumption during Phase 3 was compared among predator treatments using a Kruskal-Wallis test. To evaluate whether crab size influenced prey-size patterns, linear regression was used to test the relationship between mean crab claw size and consumed *M. gigas* size within each predator treatment. Statistical approaches are summarized in Table 1.1.

Table 1.1 Statistical analyses for *M. gigas* clearance rate and consumption analysis. *Summary of statistical approaches used to test how predator treatment, temperature, and experimental phase affected juvenile *M. gigas* clearance rates and consumption. Analyses were structured around the three phase experimental design to distinguish chemical cue exposure, non-consumptive predator exposure, and direct predator-prey interactions.*

Question	Data subset	Statistical approach	Independent variables	Dependent variables
Do algae concentrations change over the same sampling intervals used to calculate clearance rates?	Algae-only tanks samples within the 24 hour blocks and across the full 72 hours.	Paired t-test (start to end)	Sampling time, temperature	Algal concentration
Do predator treatment, temperature, and exposure affect <i>M. gigas</i> clearance rates across the experiment?	Clearance rates from all experimental tanks Phases 1-3	Linear model using Box-Cox transformed clearance rates	Predator treatment, temperature, experimental phase, interaction terms	<i>M. gigas</i> clearance rate
Do predator treatment, temperature, and exposure affect <i>M. gigas</i> clearance rates in each phase?	Clearance rates from all experimental tanks for each Phases 1-3	Phase-specific ANOVA with post-hoc contrasts	Predator treatment, temperature, predator treatment by temperature	<i>M. gigas</i> clearance rate
Does predator identity affect direct <i>M. gigas</i> consumption?	Total number of <i>M. gigas</i> spat	Kruskal-Wallis test	Predator treatment	Number of <i>M. gigas</i> consumed

	consumed per tank during Phase 3			
Does crab claw size predict the size of <i>M. gigas</i> consumed?	Consumed <i>M. gigas</i> spat from predator treatments during Phase 3	Linear regressions by predator treatment, interaction test across treatments	Mean crab claw size, predator treatment, claw size by predator treatment	Size of consumed <i>M. gigas</i>

Results

The final algal concentration was lower, but not significantly lower, than the initial concentration in algae-only procedural control tanks ($t_{11} = -1.94$, $p = 0.08$; Table 1.2). Although mean concentration declined by about 5.5 units, this change was small relative to the overall algal concentrations (average starting concentration: 272 cells/mL) and did not indicate a clear shift in the stock algae (Shellfish Diet 1800) over the course of the experiment. The algae control tanks were also evaluated from the start to end of each 24 hour block to match the redosing intervals used in experimental tanks. Algae concentrations did not differ significantly within any block: 0-24 hour block ($t_{11} = 0.06$, $p = 0.95$); 24-48 hour block ($t_{11} = -1.92$, $p = 0.08$); 48-72 hour block ($t_{11} = 0.57$, $p = 0.58$). Algae change also did not differ by temperature, time block, or their interaction. This suggests that background algae change was limited over the intervals used for the clearance rate calculations.

Table 1.2 Statistical summary of *M. gigas* clearance rates. *Summary of statistical analyses for *M. gigas* clearance rates, consumption, and *M. gigas* size consumed. Clearance rate analyses tested the effects of predator treatment, temperature, experimental phase, and their interactions. Consumption and consumed-size analyses tested whether direct predation and prey-size patterns differed among predator treatments. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p < 0.10$.*

Analysis	Explicit test	df	MS	Statistic	P-value	Sig.
Control tanks testing algae stability	Change in algae concentration from beginning to end of the experiment	11	—	t = -1.94	0.0787	.
Clearance rate: overall model	Treatment	3, 144	12.48	F = 16.04	4.754e-09	***
	Temperature	1, 144	0.08	F = 0.10	.752	
	Phase	2, 144	8.24	F = 10.60	5.109e-05	***
	Treatment by temperature	3, 144	1.60	F = 2.05	0.110	
	Treatment by phase	6, 144	1.30	F = 1.67	0.133	
	Temperature by phase	2, 144	3.26	F = 4.19	0.0170	*
	Treatment by temperature by phase	6, 144	1.05	1.35	0.239	
	Residuals	144	0.78			
Clearance rate: Phase 1	Temperature	1, 48	1.03	F = 1.21	0.2764	
	Treatment	3, 48	1.68	F = 2.00	0.13	
	Temperature by Treatment	3, 48	2.74	F = 3.22	0.0309	*
	Post-hoc, 14°C: <i>C. maenas</i> + <i>C. maenas</i> vs <i>M. gigas</i>	48	—	t = -3.11	0.0161	*
	Temperature contrast within <i>C. maenas</i> + <i>C. maenas</i> , 14 vs 18°C	48	—	t = -1.97	0.0542	.
	Temperature contrast within mixed (<i>R. antennarium</i> + <i>C. maenas</i>), 14 vs 18°C	48	—	t = 2.23	0.0304	*
	Residuals	48	0.85	—	—	
Clearance rate: Phase 2	Temperature	1, 48	3.66	F = 5.67	0.0214	*
	Treatment	3, 48	8.67	F = 13.40	1.77e-06	***
	Temperature by Treatment	3, 48	0.78	F = 1.20	0.3203	
	Post-hoc, 14°C: <i>C. maenas</i> + <i>C. maenas</i> vs <i>M. gigas</i>	48	—	t = -5.02	<0.0001	***
	Post-hoc, 14°C: <i>C. maenas</i> + <i>C. maenas</i> vs <i>R. antennarium</i> + <i>R. antennarium</i>	48	—	t = -2.41	0.0883	.
	Post-hoc, 14°C: <i>M. gigas</i> vs mixed (<i>R. antennarium</i> + <i>C. maenas</i>)	48	—	t = 4.92	0.0001	***

	Post-hoc, 14°C: <i>M. gigas</i> vs <i>R. antennarium</i> + <i>R. antennarium</i>	48	—	t = 2.61	0.0564	.
	Post-hoc, 18°C: <i>C. maenas</i> + <i>C. maenas</i> vs <i>M. gigas</i>	48	—	t = -2.54	0.0668	.
	Post-hoc, 18°C: <i>M. gigas</i> vs mixed (<i>R. antennarium</i> + <i>C. maenas</i>)	48	—	t = 2.86	0.0311	*
	Temperature contrast within <i>C. maenas</i> + <i>C. maenas</i> , 14 vs 18°C	48	—	t = -2.23	0.0308	*
	Temperature contrast within mixed (<i>R. antennarium</i> + <i>C. maenas</i>), 14 vs 18°C	48	—	t = -1.81	0.0771	.
	Residuals	48	0.65	—	—	
Clearance rate: Phase 3	Treatment	3, 48	4.74	F = 5.66	0.0021	**
	Temperature	1, 48	1.91	F = 2.28	0.1374	
	Temperature by Treatment	3, 48	0.18	F = 0.22	0.8855	
	Post-hoc, 14°C: <i>M. gigas</i> vs <i>R. antennarium</i> + <i>R. antennarium</i>	48	—	t = 2.63	0.0540	.
	Post-hoc, 18°C: <i>M. gigas</i> vs mixed (<i>R. antennarium</i> + <i>C. maenas</i>)	48	—	t = 2.83	0.0333	*
	Post-hoc, 18°C: <i>M. gigas</i> vs <i>R. antennarium</i> + <i>R. antennarium</i>	48	—	t = 2.50	0.0735	.
	Residuals	48	0.84	—	—	
Total <i>M. gigas</i> consumption	Predator treatment	3	—	H = 15.96	<0.001	***
<i>M. gigas</i> size consumed	Mean claw size by predator treatment interaction	2, 49	—	F = 2.49	0.094	.

To test whether predator effects on *M. gigas* feeding changed as exposure became more direct, clearance rates were compared across predator treatments, temperatures, and experimental phases. Clearance rate varied significantly among predator treatments and experimental phases, and the effect of experimental phase differed between temperatures (Table 1.2). Mean clearance

patterns across predator treatments, temperatures, and phases are shown in Figure 1.3. In the full model, predator treatment ($F_{3,144} = 16.04$, $p < 0.001$), phase ($F_{2,144} = 10.59$, $p < 0.001$), and temperature by experimental phase interaction ($F_{2,144} = 4.19$, $p = 0.02$) were significant. Temperature alone was not significant, but the significant temperature by phase interaction indicates that temperature influenced clearance rates differently across experimental phases. Overall, predator-free tanks maintained the highest clearance rates across phases, and the strongest reductions in *M. gigas* feeding were associated with predator treatments containing *C. maenas*, particularly the two *C. maenas* and mixed species predator treatments. Estimated marginal means ($\pm 95\%$ CI) showed that no-predator tanks consistently exhibited the highest clearance rates across phases, while predator treatments suppressed feeding activity, particularly during the non-consumptive predator exposure phase (Figure 1.3). Overall, predator presence had a stronger effect on clearance rates than temperature alone, but temperature still shaped how clearance rates changed across experimental phases.

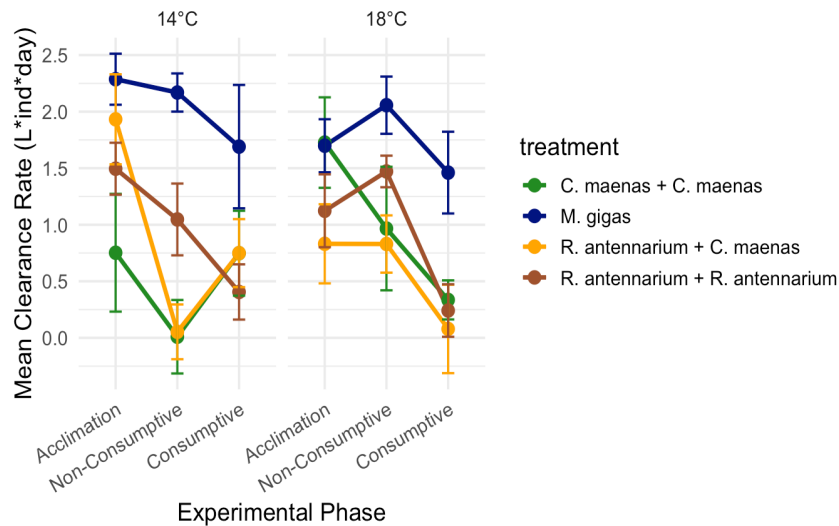


Figure 1.3 *M. gigas* clearance rates across experimental phases. Mean *M. gigas* clearance rates ($\pm 95\%$ confidence intervals) across experimental phases under 14°C and 18°C temperature treatments. The no predator controls maintained the highest clearance rates across phases,

whereas predator treatments generally reduced clearance rates, particularly during the non-consumptive phase.

To further examine how temperature and predator treatment affected *M. gigas* clearance rates within each experimental phase, separate ANOVAs were conducted for each phase (Table 1.2). In Phase 1, clearance rates showed a significant temperature by predator treatment interaction effect ($F_{3,48}=3.22$, $p = 0.03$), indicating that early responses to predator context differed between temperature treatments. At 14°C, predator-free control tanks had higher clearance rates than the tanks holding two *C. maenas* ($t = -3.11$, $p = 0.02$). This shows that feeding suppression was detectable during the chemical cue/acclimation phase at 14°C, but no treatment contrasts were significant at 18°C. The mixed-species predator treatment also differed significantly between temperatures, with lower clearance rates at 18°C than at 14°C ($t = 2.23$, $p = 0.03$). The two *C. maenas* showed a similar visual trend, but the temperature contrast was marginally significant ($t = -1.97$, 0.0542).

Phase 2 showed the clearest evidence of non-consumptive effects on *M. gigas* clearance rates. Temperature ($F_{1,48} = 5.66$, $p = 0.02$), and predator treatment ($F_{3,48} = 13.40$, $p < 0.001$) were significant, while temperature by predator treatment was not ($F_{3,48} = 1.20$, $p = 0.32$). At 14°C, predator-free control tanks had significantly higher clearance rates than tanks containing two *C. maenas* ($t = -5.02$, $p < 0.001$) and higher clearance rates than the mixed-species group ($t = 4.92$, $p < 0.001$). These were the strongest pairwise contrasts in the clearance rate analysis, showing that non-consumptive feeding suppression was the most pronounced when *C. maenas* was present. Within the two *C. maenas* treatment, clearance rates were lower 14°C than at 18°C ($t = -2.23$, $p = 0.03$). Together, these results indicate that predator presence had a non-consumptive negative

effect on *M. gigas* clearance rates during Phase 2, although the strongest pairwise evidence for feeding suppression occurred in treatments containing *C. maenas*.

In Phase 3, clearance rates continue to differ among predator treatments ($F_{3,48} = 5.66$, $p < 0.01$), while temperature ($F_{1,48} = 2.28$, $p = 0.12$) and the temperature by predator treatment interaction ($F_{3,48} = 0.22$, $p = 0.87$) were not significant. Post-hoc comparisons detected one significant contrast at 18°C, where predator-free control tanks had higher clearance rates than mixed-species treatments ($t = 2.83$, $p = 0.03$). A similar contrast between predator-free control tanks and two *R. antennarium* treatments at both 14°C and 18°C was marginally significant ($p < 0.10$). Overall, predator treatment effects persisted into the consumptive phase.

Predator treatments differed in both the amount and distribution of *M. gigas* spat consumption during the direct predation phase. Tanks containing two *C. maenas* consumed more than twice as many *M. gigas* spat on average as either the mixed species and two *R. antennarium* treatments (Table 1.3). Consumption was also more variable in tanks containing two *C. maenas*, with high-consumption events reaching 7–8 *M. gigas* spat per tank, while the tanks with mixed species and two *R. antennarium* treatments generally consumed 0–3 *M. gigas* (Figure 1.4). Total *M. gigas* consumption differed significantly among predator treatments, indicating that predator identity directly influenced predation (Kruskal-Wallis $H_3 = 15.96$, $p < 0.001$; Table 1.2).

Table 1.3 Statistical summary of *M. gigas* consumption. Summary statistics are reported per tank for each predator treatment. Each treatment included 14 tanks.

Treatment	Mean consumed	SD	Median	Max	Tanks with no consumption
<i>C. maenas</i> + <i>C. maenas</i>	2.07	2.46	1.0	8	3
<i>R. antennarium</i> + <i>C. maenas</i>	0.86	1.03	0.5	3	7
<i>R. antennarium</i> + <i>R. antennarium</i>	1.00	1.41	0.0	4	8

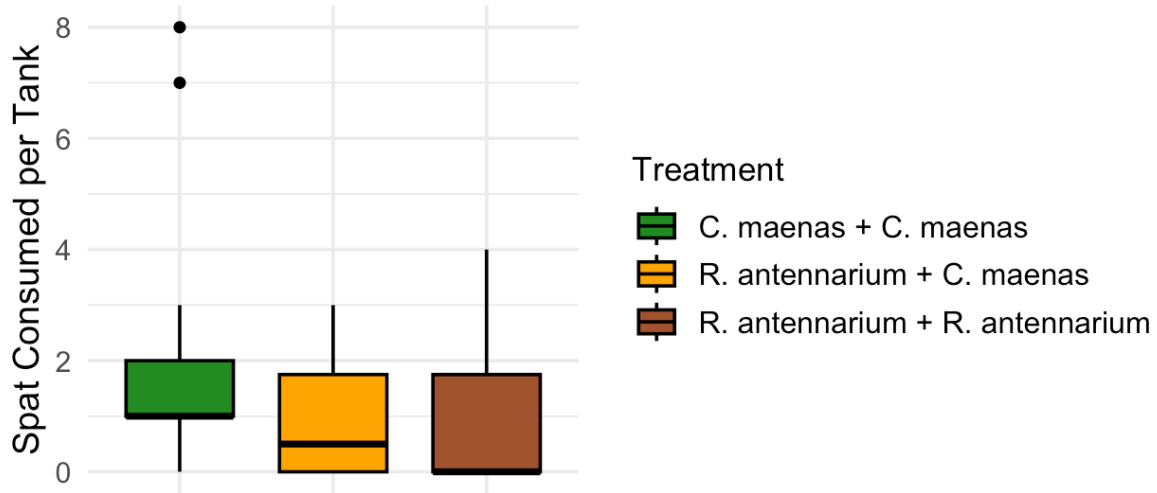


Figure 1.4 *M. gigas* consumption by predator treatment. Mean number of *M. gigas* spat consumed per tank by predator treatment. Boxes show the interquartile range, horizontal lines show medians, whiskers show the spread of the data, and points show high-consumption observations. Tanks containing two *C. maenas* had the highest maximum consumption and the highest mean number of spat consumed.

The size of consumed *M. gigas* varied across predator treatments and mean claw sizes. Larger crabs generally consumed larger *M. gigas*, in the predator treatment containing two *R. antennarium*, where mean claw size significantly and positively predicted consumed *M. gigas* size ($F_{1,12} = 6.48$, $p = 0.03$; Table 1.4). This positive relationship is shown visually in Figure 1.5, where consumed *M. gigas* size increased with mean claw size most clearly in the two *R. antennarium* treatments. In contrast, the two *C. maenas* predator treatment consumed a wider range of *M. gigas* sizes across crab sizes, indicating weaker size selectivity (Figure 1.5). This pattern was supported by the non-significant claw-size relationship in the two *C. maenas* predator treatment ($F_{1,27} = 0.03$, $p = 0.87$; Table 1.4). Across treatments, mean claw size weakly predicted consumed *M. gigas*, with a marginal claw size by predator treatment interaction ($F_{2,49} = 2.49$, $p = 0.09$; Table 1.2).

Table 1.4 Crab claw size and consumed *M. gigas* size regressions. *Linear regression results testing the relationship between mean crab claw size and the size of consumed *M. gigas* spat. Regressions are shown separately by predator treatment to evaluate whether prey-size selectivity differed between *C. maenas*, mixed-species, and *R. antennarium* predator contexts.*

Treatment	Slope (β)	F	df	p-value	R ²
<i>C. maenas</i> + <i>C. maenas</i>	0.039	0.03	1, 27	0.870	0.001
<i>R. antennarium</i> + <i>C. maenas</i>	-0.216	0.55	1, 10	0.475	0.052
<i>R. antennarium</i> + <i>R. antennarium</i>	0.813	6.48	1, 12	0.026	0.351

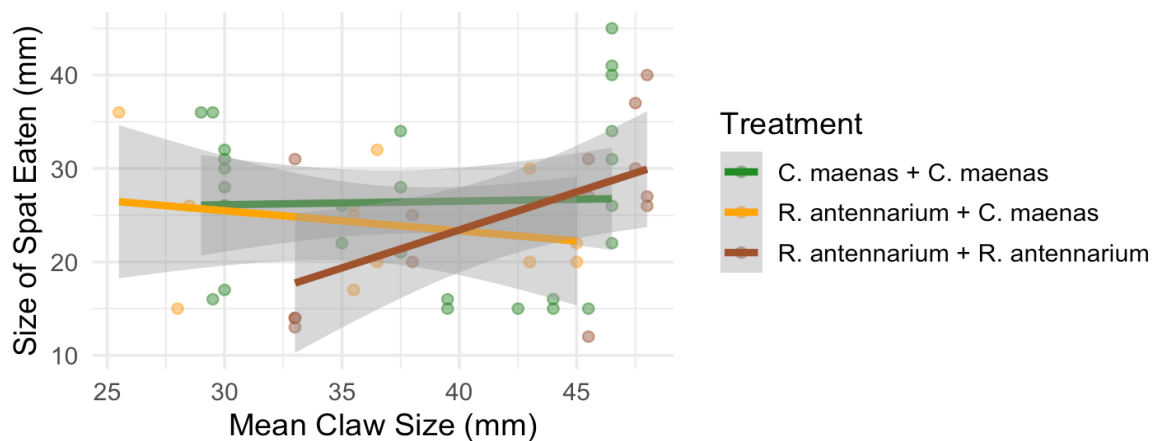


Figure 1.5 Relationship between crab claw size and consumed *M. gigas* size. *Relationship between mean crab claw size and the size of consumed *M. gigas* spat across predator treatments. Points show individual consumed spat, lines show treatment-specific linear regressions, and gray bands show 95% confidence intervals. The relationship was strongest in the *R. antennarium* treatment, while *C. maenas* consumed a wider range of oyster sizes across crab claw sizes.*

Discussion

Crab presence reduced *M. gigas* feeding and survival, and these effects occurred through both consumptive and non-consumptive pathways. Across experimental phases, predator presence significantly suppressed *M. gigas* clearance rates, with the strongest reductions occurring in treatments containing two *C. maenas*. Predator identity also influenced *M. gigas* survival, with *C. maenas* consuming more *M. gigas* spat on average than native *R. antennarium*. Temperature had

comparatively weaker effects overall, although its influence varied across experimental phases. Together, these findings support the predictions that crab presence suppresses *M. gigas* feeding, that both trophic and non-trophic pathways contribute to these effects, and that treatments containing *C. maenas* generally exert stronger impacts than the native crab treatment. By contrast, support for temperature-driven strengthening of predator effects was more limited and phase dependent, and the mixed-species treatment did not weaken effects as strongly as predicted.

Reduced *M. gigas* clearance rates were one of the clearest responses to predator presence. The strongest suppression of clearance rates occurred during the non-consumptive phase, when crabs were present but unable to feed on *M. gigas* directly. *Magallana gigas* likely responded behaviorally to predator-associated cues by reducing filtration activity in response to perceived predation risk. Bivalves initiate valve closure and reduction of activity as defensive behaviors (Kimbrow et al. 2020). For suspension-feeding bivalves, such reductions may represent a tradeoff between defense and long-term energetic costs (Domínguez et al. 2021). These behavioral changes allow prey to detect risk without direct contact but can also reduce feeding efficiency and growth over time (Kimbrow et al. 2020). Rather than requiring direct predation, predator presence alone was sufficient to suppress *M. gigas* clearance rates, indicating that *M. gigas* reduced feeding in response to perceived predation risk. By Phase 3 however, the cue environment was likely more complex because direct predation could have released alarm cues from injured or consumed conspecifics. Reduced clearance rates during this consumption phase may therefore reflect not only predator presence, but also *M. gigas* responses from other damaged conspecifics. Bivalves respond to the presence of a predator by closing their valve, which can be an energetically costly response impacting both feeding and ventilation (Domínguez et al. 2021; Gray & Langdon 2017). These results suggest that predator-driven behavioral suppression reduces *M. gigas* feeding even

without direct consumption and extends that idea by showing that non-consumptive predator effects may influence ecosystem function of estuaries through reduced filtration.

Both trophic and non-trophic pathways contributed to reduced *M. gigas* clearance, but predator identity strongly shaped the magnitude of these effects. Treatments containing *C. maenas* produced the strongest reductions in *M. gigas* clearance rates and the highest levels of *M. gigas* consumption across all three phases, indicating that these invasive predators affected *M. gigas* through both indirect and direct pathways. This distinction is important because predator effects on *M. gigas* may occur even when *M. gigas* are not consumed. During non-consumptive exposure, reduced clearance rates suggest that *M. gigas* altered feeding behavior in response to predator-associated cues or physical predator presence. If similar responses occur in the field, *M. gigas* in areas with high crab abundance may experience reduced feeding time, lower energy intake, slower growth, or reduced condition, even when direct mortality is limited. At larger spatial scales, suppression of *M. gigas* clearance rates could also reduce the filtration capacity provided by oyster populations in areas where green crabs are abundant.

Predator identity further shaped these direct and indirect effects. Invasive *C. maenas* may impose stronger negative effects on *M. gigas* than native *R. antennarium* under similar conditions. This difference may reflect the feeding ecology of *C. maenas*, which can consume oysters even at low prey densities, and disproportionately targets juvenile oysters and spat on shell (Ens et al. 2021; Grason & Miner 2012). Differences in predator identity may therefore shape not only direct oyster mortality, but also the intensity of non-consumptive stress experienced by *M. gigas*. If sustained in the field, these non-consumptive effects could reduce feeding time, lower filtration rates, and potentially affect oyster growth or condition in areas with high crab abundance. Compared with the native *R. antennarium*, *C. maenas* may exert stronger effects through its broad

tolerance of shallow estuarine habitats, high foraging activity, and flexible feeding on vulnerable bivalve life stages (Yamada & Gillespie 2008). These traits suggest that *C. maenas* may influence *M. gigas* differently than native crabs not only through consumption, but also through persistent presence in habitats where *M. gigas* and other juvenile bivalves are vulnerable. In this study, that prediction was supported for the native comparison species tested here, suggesting that the invasive *C. maenas* can exert stronger direct and indirect effects than *R. antennarium* under similar laboratory conditions.

The presence of *C. maenas* in a predator treatment appeared sufficient to modify the risk environment experienced by *M. gigas*. During the non-consumptive and consumptive phase, clearance rates in the mixed-species treatment were reduced similarly to the treatment with two *C. maenas*, suggesting that non-consumptive impacts persisted whenever *C. maenas* was present. With the native and invasive crab together, it is unclear whether this response was driven primarily by *C. maenas* itself or by the more complex cue environment by both crab species. Chemical cues can provide information about predator activity, condition, competitive context, or foraging behavior, rather than predator presence alone (Baillie and Grabowski 2019; Domínguez et al. 2021). This suggests that *M. gigas* responses in the mixed treatment may reflect the combined cue environment generated by both crab species.

By Phase 3, reduced clearance rates may also have reflected active predation, physical disturbance, and cues from injured or consumed conspecifics rather than predator presence alone. Bivalves can respond to chemical cues from predators and damaged conspecifics by reducing feeding activity or increasing anti-predator behavior (Castorani & Hovel 2016; Poulin et al. 2018). These findings are relevant to field settings, although the magnitude of cue mediated effects may be reduced by currents, tidal exchange, and turbulence moving chemical cues away from *M. gigas*.

During low-flow periods around low tide, *M. gigas* in shallow intertidal areas may still receive and retain predator associated cues. Repeated exposure to these cues in areas with frequent *C. maenas* activity could therefore reduce feeding even when direct predation does not occur, although field responses are likely to be more variable than responses observed in static tanks.

Temperature effects were not uniform across the experiment, but they did vary across experimental phases and therefore partially support the prediction that warming would strengthen *C. maenas* impacts on *M. gigas*. In the overall model, temperature alone did not significantly affect clearance rates, but the significant temperature by phase interaction indicated that warming influenced *M. gigas* responses differently depending on the experimental context. This pattern was especially evident in Phase 1, where the significant temperature by predator treatment interaction suggests that *M. gigas* responses depended on both predator identity and temperature context. Temperature effects were clearest in Phase 2, where temperature had a significant main effect on clearance rates, and in the two *C. maenas* predator treatment, where clearance rates differed between 14 and 18°C. These results suggest that warming was most important during cue-mediated phases, rather than during direct predation. One possible explanation is that the tested temperature range was not large enough to generate consistently strong differences in predator-prey dynamics relative to the effect of predator treatment alone. A 4°C difference may have altered metabolic demand, feeding motivation, or cue responsiveness, but not strongly enough over a 72-hour period to consistently override the larger effect of predator identity. In a longer-term experiment, sustained warming could have increased predator energetic demand, increased cumulative feeding pressure, or amplified the energetic consequences of reduced *M. gigas* clearance rates over time. Since reduced clearance represents reduced feeding opportunity, even modest behavioral

suppression could have stronger consequences if maintained over longer periods or under more intense warming.

Temperature may also have influenced how predator cues were produced, perceived, or maintained in the water column. Warmer water can also accelerate chemical degradation and microbial breakdown of dissolved cues, potentially reducing the strength or duration of predator signals available to prey, and alter the persistence of predator-associated chemical cues in marine environments (Nagelkerken et al. 2019). Therefore, warming may affect non-consumptive interactions multiple ways. It may increase predator activity or metabolic demand while also changing the persistence or detectability of predator associated cues. If predator cues degrade more rapidly under warmer conditions, *M. gigas* may receive weaker signals of predation risk even as predators become more metabolically active. Conversely, bivalves under thermal stress may be less able to respond effectively to those cues, while predators experiencing higher metabolic demand may prioritize foraging responses more strongly. Temperature was least important when direct predation was allowed, which may reflect the fact that crabs had already experienced an initial starvation period followed by two days in tanks with *M. gigas* present but inaccessible. Under those conditions, hunger may have overridden differences in metabolic demand across the 4°C treatments once direct feeding became possible. Rather than consistently increasing predation across all phases, temperature appeared to alter the context in which oysters responded to predator risk. The warming hypothesis was only partly supported, with the strongest evidence for temperature effects occurring during cue-mediated or behavioral phases rather than during direct consumption within this thermal range.

Differences in predator identity were also reflected in patterns of *M. gigas* consumption. Predator size influenced patterns of *M. gigas* consumption, with larger crabs tending to consume

larger *M. gigas*, particularly in two *R. antennarium* tank treatments. Size-selective predation is common in crab–bivalve systems, where predators choose prey based on shell thickness, energetic return, and the mechanical ability to crush or open shells (Palacios & Ferraro 2003; Matheson & McKenzie 2014). In this study, *R. antennarium* appeared to have a more size-limited prey handling relative to *C. maenas*, which consumed a wider range of *M. gigas* size. There is evidence *C. maenas* prefer prey with shorter handling times but also have greater mechanical capabilities (Hunt & Yamada 2003; Anaya 2025). These differences are consistent with the contrasting feeding morphology of the two species where *C. maenas* uses one smaller claw for slicing and manipulating prey and one crushing claw while *R. antennarium* have two larger, crushing claws (Ens et al. 2021). Together these results support the broader finding that predator identity influenced *M. gigas* mortality and suggest that differences in claw morphology and prey handling may help explain why *C. maenas* affected *M. gigas* differently than the native crab treatment.

Invasive predators may influence *M. gigas* through both direct mortality and indirect suppression of feeding behavior. In this study, *C. maenas* not only consumed more *M. gigas* spat, but also reduced *M. gigas* filtration even without direct predation. These results suggest that the ecological effects of these invasive predators extend beyond prey population removal to include changes in how foundation species function within estuarine ecosystems. Since oysters play an important role in water filtration and nutrient cycling in estuarine systems, predator-driven reductions in feeding behavior may have consequences that scale beyond the individual prey response to broader ecosystem functioning (zu Ermgassen et al. 2013; Marks et al. 2024). By reducing filtration, predator presence may diminish oysters' capacity to remove suspended particles from the water column, potentially limiting their contributions to water clarification and nutrient processing (Kimbrow et al. 2020). *Carcinus maenas* may alter the overall estuarine

ecosystem functioning not only by consumption of *M. gigas*, but by also reducing their effectiveness at performing their ecological roles.

This study was conducted under controlled laboratory conditions, which allowed predator identity and temperature effects to be isolated but may not fully capture the complexity of natural estuarine environments. In the field, predator associated cues are likely to be more variable because tidal exchange, currents, turbulence, and water-column mixing can dilute or redistribute cues over short timescales. Cue environments may also be more complex in natural habitats for *M. gigas* due to exposure of chemicals from multiple predators, injured conspecifics, other prey species, and organic background matter. Habitat structure may further alter cue movement by retaining water and signals in some areas, while others may be flushed more frequently. Therefore, the non-consumptive responses observed in the laboratory setting indicate that *M. gigas* can respond to predator-associated cues, but the strength and duration of these responses in the field may depend on the local environment. Future work could examine these predator-driven behavioral responses in field settings and across broader temperature ranges. Understanding how invasive predators alter both *M. gigas* survival and filtration behavior will be important for predicting ecosystem responses to biological invasions and climate change.

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Chapter Two: Predation on juvenile Pacific oyster (*Magallana gigas*) by green crab (*Carcinus maenas*) across habitats and size gradients

Introduction

Predation is a primary driver of survival during the early life stages of marine invertebrates, and habitat structure can strongly shape predator-prey interactions in estuarine environments (Fernandez et al. 1993; Holsman et al. 2006; Jensen et al. 2002). Estuaries function as highly productive nursery habitats for fish, crustaceans, and shellfish because they provide abundant food resources, sheltered conditions, and complex refuge during vulnerable juvenile stages (Fernandez et al. 1993). These conditions also support shellfish mariculture, including oyster cultivation, linking estuarine habitat quality to both natural recruitment and aquaculture production (Whitfield 2017). Within estuaries, physical structure is especially important because it can reduce predator encounter rates, provide refuge, and increases access to food (Gunderson et al. 1990; zu Ermgassen et al. 2013). Habitat forming species, such as eelgrass (*Zostera marina*) are important in this context as they create three-dimensional structure that can reduce predator efficiency, increase search and handling time, and buffer vulnerable species from both biological and physical stressors (Holsman et al. 2006; Gelling 2024; Grason & Miner 2012). Eelgrass beds also support recruitment efforts by providing settlement surfaces, microhabitats, and environmental conditions more favorable for newly settled individuals (Jensen et al. 2002; Howard et al. 2019; zu Ermgassen et al. 2013). As a result, estuarine nursery habitats contribute to broader ecosystem function by supporting biodiversity and enhancing trophic linkages (Kreeger et al. 2018; Bassett 2000). Many commercially and ecologically important species rely on *Z. marina* habitats early in life, making habitat quality closely tied to fisheries productivity and food web stability (Howard et al. 2019; Garbary et al. 2014). As a result, the quality of structured estuarine habitats can shape not only

early survival, but also broader patterns of recruitment, fisheries productivity, and food web stability.

Within estuaries, *Z. marina* beds are often associated with reduced predation risk due to their dense vegetative structure providing refuge for small-bodied prey (Magel et al. 2022; Holsman et al. 2006). *Z. marina* creates vertical and horizontal complexity that lowers encounter rates between predators and prey (Holsman et al. 2006). In contrast, unvegetated mudflat habitats generally provide less structural refuge, leaving prey more visible and accessible, and therefore allowing epi-benthic predators to forage more efficiently (Fernandez et al. 1993). Although some species may use burial strategies in soft sediment as a secondary refuge strategy, mudflat habitats typically expose juvenile shellfish and other prey to higher predation pressure than vegetated habitats (Palacios & Ferraro 2003). Evaluating differences in survival of ecologically important prey species between *Z. marina* and unvegetated mudflats is especially important in invaded estuaries, where changes in predator identity and habitat use may modify the refuge value of structured habitats (Fulton et al. 2013). This question is especially important as *Z. marina* habitats within estuaries are increasingly threatened by multiple interacting stressors, including habitat degradation, climate-driven changes in temperature and salinity, and invasive predators (Duarte 2002; Magel et al. 2022). Invasive species can alter both the quality of the habitat and balance of predator-prey interactions that take place within (Baillie & Grabowski 2019; Howard et al. 2019). Understanding how predation differs between *Z. marina* beds and adjacent mudflats is therefore important in invaded estuaries, where habitat degradation and changing predator communities may alter the refuge value of structured habitats.

The invasive green crab (*Carcinus maenas*) is particularly important to estuarine nursery habitats because it can both prey on vulnerable juvenile populations, and alter the habitat features

that would otherwise provide refuge (Howard et al. 2019; Garbary et al. 2014). As a generalist predator and one of the most impactful marine invaders globally, *C. maenas* has documented ecological and economic consequences in estuarine ecosystems (Jamieson et al. 1998; See & Feist 2010; Yamada et al. 2015). As an opportunistic predator *C. maenas* can exert strong predation pressure on a wide range of invertebrate prey, altering local food webs through direct consumption and interaction with other predators (Baeta et al. 2006; Matheson & McKenzie 2014). Its foraging behavior is influenced by habitat structure, with increased efficiency in low-complexity environments such as mudflats and bare sediment, where prey are more exposed (Fernandez et al. 1993). *Carcinus maenas* not only forages within *Z. marina* habitats, but can actively degrade it through digging, pitting, and bioturbation (MacDonald et al. 2018). Although eelgrass may persist in invaded areas, the disturbances can reduce the structural complexity that eelgrass provides for shelter and foraging habitat for juvenile crabs and other native species (Thayer et al. 1984). *Carcinus maenas* is often most abundant in warmer, shallower, and less saline areas of estuaries, while larger native predators may dominate cooler, more saline habitats, producing heterogeneous predator assemblages across sites (Fulton et al. 2013; Yamada et al. 2020). These spatial differences are important because predation pressure on juvenile shellfish may depend on predator identity, relative abundance, and interactions among predators within the community.

Juvenile Pacific oysters (*Magallana gigas*) are particularly vulnerable to predation during early life stages, when small body size, relatively thin shells, and limited defensive capacity increase their susceptibility to crab predation (Grason et al. 2024; Bassett 2000). Their vulnerability is strongly size dependent, with smaller *M. gigas* available to a broader range of crab sizes while larger individuals may begin to experience a partial size refuge as increased shell size and strength reduce handling success (Grason & Miner 2012; Anaya et al. 2025). As a result,

predation during early post-settlement stages for juveniles can create an important bottleneck in survival and recruitment (Mach & Chan 2014). This bottleneck is especially relevant in estuaries, where *M. gigas* occur in shallow intertidal habitats that are also used by *C. maenas* populations, including areas associated with benthic shellfish culture (See & Feist 2010; Anaya et al. 2025). Since *C. maenas* forage in these habitats and have been shown to prey on *M. gigas*, spatial variation in predation risk may have both ecological and economic consequences (Palacios & Ferraro 2003; Jamieson et al. 1998; Mach & Chan 2014). Understanding how predation risk varies across habitat and predator context is critical for predicting *M. gigas* survival and understanding the broader ecological impacts of invasive predators in estuarine systems.

While previous work has shown that habitat complexity can mediate predation risk, less is known about how multiple sources of variation combine to shape predation outcomes in estuaries. Predation in these systems is mediated not only by structural refuge such as *Z. marina*, but also by predator identity and the interaction of multiple factors within habitat types (Jensen et al. 2002; Grason & Miner 2012). It remains unclear how habitat type, predator assemblage, prey size, and vertical position interact to influence *M. gigas* survival under natural estuarine conditions. This uncertainty is especially relevant in invaded estuaries where spatial variation in *C. maenas* abundance across estuarine gradients may influence *M. gigas* consumption (Hunt & Yamada 2003). *Carcinus maenas* and native crabs may dominate different portions of estuaries, creating predation landscapes associated with salinity, temperature, and habitat type (Grason et al. 2024). The role of structure through vegetation and vertical position in the water column should therefore be explored in combination with these factors. Although prey size influences vulnerability, the extent to which this effect changes across habitat types and predator gradients remains unclear

(Bassett 2000). These unresolved factors limit understanding of how multiple sources of variation interact to influence juvenile *M. gigas* survival across estuarine habitats.

A series of field tethering experiments was conducted to quantify the predation on juvenile *M. gigas* with natural predator assemblages. *Magallana gigas* were deployed in paired eelgrass and mudflat habitats across multiple sites to evaluate habitat-specific predation rates under contrasting levels of structural refuge. Tethering provides a useful approach for estimating relative predation risk across habitat types by exposing prey under natural conditions, although it may alter prey escape behavior and therefore may not reflect natural predation rates the same way (Fernandez et al. 1993; de Rivera et al. 2005). Even so, experiments conducted under natural predator assemblages can help distinguish how native and invasive predators contribute to observed predation patterns (Grason et al. 2024). Three complementary experimental designs were used to isolate different sources of variation in predation risk. First, clustered spat of various sizes attached to shell were deployed to assess size level variation in predation. Then, individual *M. gigas* spat were placed on dowels to examine site-level predation. Lastly, a combined height experiment with both clustered spat of shell and individual *M. gigas* spat tested how raised position of the spat above the seafloor influences predation risk in areas with high *C. maenas* abundance. Together these experiments were structured to test how habitat type, site level predator assemblage, prey size, and vertical position interacts to shape overall predation risk for juvenile *M. gigas* in the field.

We tested four hypotheses about how habitat, predator context, prey size, and vertical position shape crab predation on *M. gigas*. First, predation on juvenile *M. gigas* was expected to be higher in mudflat habitats than in eelgrass given that the reduced structural refuge in unvegetated habitats should increase exposure for benthic predators (Holsman 2006; Gelling

2024). Sites with higher *C. maenas* abundance were expected to have increased *M. gigas* consumption, reflecting the invasive predator's role in shaping predation pressure (Grosholz et al. 2011). Third, smaller *M. gigas* were expected to experience higher predation rates as they are more accessible to a broader range of crab sizes and have not yet reached size refuge (Anaya et al. 2025; Bassett 2000). Fourth, elevating *M. gigas* above the substrate was expected to reduce consumption by decreasing access for benthic predators and increasing spatial separation from crab foraging activity (Gelling 2024; Holsman et al. 2006). Together these expectations suggest that habitat structure, predator abundance, prey size, and vertical position interact to determine overall predation risk for juvenile *M. gigas*.

Methods

Field experiments were conducted in Netarts Bay, Oregon, in July 2025. This field study extended the laboratory experiment in Chapter one by testing whether *M. gigas* vulnerability varied across natural habitat and predator assemblage conditions. Netarts Bay is a temperate estuary characterized by high marine exchange during each tidal cycle, extensive *Z. marina* beds, unvegetated mudflats, active *M. gigas* aquaculture operations, and wild shellfish harvest areas. Sites were selected based on the presence of accessible eelgrass habitat paired with the nearest adjacent mudflat habitat along the more marine half of the estuary. Each site was defined as a paired eelgrass–mudflat location, with paired habitats generally separated by approximately 15 m and a maximum separation of 42 m at Site 1. A total of 10 sites were included across three experiments; Sites 1–7 were sampled during initial trials, and Sites 8–10 were added in later experiments to expand spatial coverage and increase overlap with areas of higher *C. maenas* abundance (Figure 2.1). All deployments were conducted in intertidal habitats exposed during low tide.

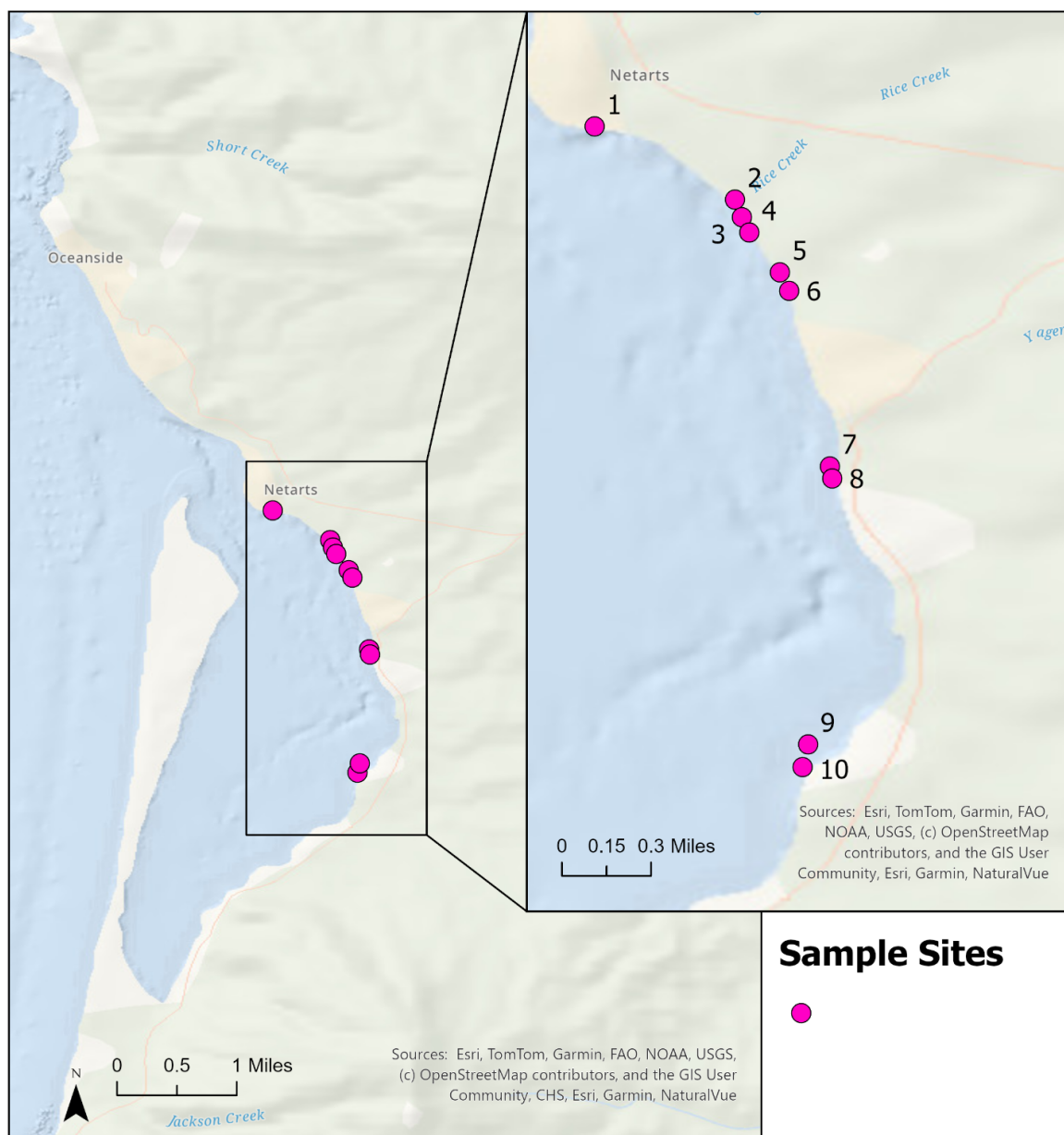


Figure 2.1 Netarts Bay field sampling sites. *Pink points indicate paired eelgrass and mudflat sampling locations across Sites 1-10. Sites are ordered from the mouth of the estuary toward the Upper Bay. Map created in ArcGIS Pro using Esri basemap data.*

To quantify the predation on juvenile *M. gigas* under natural predator assemblages, three complimentary field tethering experiments were conducted using tethered *M. gigas*. Each deployment lasted approximately 24 hours to encompass one tidal cycle. These were designed to

isolate the effects of habitat type, prey size, and vertical position in the water column on predation risk. *Magallana gigas* survival was assessed upon retrieval, and missing *M. gigas* were assumed to be consumed unless clear evidence of tether failure or other non-predation related loss. Together, the three field experiments were designed to separate different components of juvenile *M. gigas* vulnerability under natural predator assemblages. The clustered spat on shell experiment tested how *M. gigas* size and habitat structure influenced consumption across paired eelgrass and mudflat habitats. The individual spat on dowel experiment standardized *M. gigas* size to isolate habitat and predator assemblage effects on a smaller more vulnerable size class. The height experiment then tested whether moving *M. gigas* 20 cm above the substrate reduced access by benthic predators in areas where *C. maenas* abundance was highest. This sequence allowed for predation risk to be evaluated across prey size, habitat structure, predator assemblage and vertical refuge.

Experiment 1: Benthic clustered spat on shell deployment

To assess site-level variation in predation and assess size consumption across a broader size range of juvenile *M. gigas*, clustered spat attached to shells were deployed at sites 1-7. Each shell contained multiple naturally settled *M. gigas* spat of varying sizes, with an average of 22 spat per shell and a median spat size of 26 mm. Each experimental unit consisted of six shells arranged in a line and deployed for 24 hrs. One line set per habitat per site, with one unit deployed in eelgrass and one in a paired mudflat area of a similar depth. Shells were individually drilled and attached to monofilament line, and each line was secured to a vertical stake inserted into the substrate. Experimental units were staked just below the lower low tide line for the 24 h deployment period so that the shells rested directly on the substrate and were available to benthic or demersal predators. This design allowed individual *M. gigas* within clustered shell units to be measured and evaluated for size-dependent predation.

Experiment 2: Benthic individual spat on dowel deployment

To examine predation on a smaller and more standardized *M. gigas* size class, individual *M. gigas* spat were deployed on wooden dowels at the same sites (sites 1-7). Twenty individual *M. gigas* spat between 7mm and 15mm in width along their longest end were glued to a 0.914m dowel, 2.54 cm apart, secured by a stake on either side. Dowel units were deployed in paired eelgrass and mudflat habitats for approximately 24 hours. By standardizing *M. gigas* size and spacing, this experiment emphasized habitat-level differences in predation while minimizing variation associated with *M. gigas* size.

Experiment 3: Elevated and benthic spat refuge experiment

To evaluate how vertical position in the water column influences predation rates a combined experiment was conducted at Sites 7-10, where *C. maenas* abundance was highest. This experiment included both one shell containing clustered *M. gigas* on shell and one dowel containing individual *M. gigas* spat. These were stacked at two heights above the sediment: benthic (0 cm above the sediment) and elevated (20 cm). Again, these were deployed in paired eelgrass and mudflat habitats for 24 hours. The ‘double-decker’ design allowed comparison of predation risk at different heights under the same local environmental conditions and tested whether elevation could provide refuge from benthic predators.

For each experiment, *M. gigas* survival was recorded at the end of each deployment. Each individual spat on the clustered shells were measured in millimeters along its longest end before and after deployment. In the individual spat experiments, *M. gigas* size was smaller and more uniform, allowing for comparison within the same size class. Consumption was measured as a binary response (consumed/survived) for individual *M. gigas*.

To characterize predator communities at each site, Fukui-style collapsible box ($60 \times 45 \times 20$ cm) and minnow traps ($42\text{--}44 \times 23$ cm, with openings widened to 4-7 cm diameter) were deployed at the same spots as the *M. gigas* spat 24-48 hours after each experiment and retrieved 24 hours later. Captured organisms were identified to species, or to genus for some non-crustaceans, and crabs were noted for sex, carapace size, and visible injury. Catch per unit effort (CPUE) was calculated for each species at each site as the number of individuals captured per 24-hour box-trap deployment. CPUE was calculated for each species at each site as the number of individuals captured per 24-h box-trap deployment. For predator assemblage analyses, only box-trap catches were used because box traps were more likely to capture the larger benthic predators capable of consuming *M. gigas* spat. This metric was used to evaluate spatial variation in predator assemblages and to assess the relationships between *C. maenas* abundance and *M. gigas* consumption.

Predator assemblages were simplified to the four crab species known to consume *M. gigas* (*Romaleon antennarium*, *Cancer productus*, *Metacarcinus magister*, and *Carcinus maenas*). Other organisms captured in the box and minnow traps were identified and recorded but were not included in predator assemblage analyses because they were not considered likely predators of the deployed *M. gigas* spat. Differences in CPUE among crab species were tested using Kruskal–Wallis tests followed by Holm-adjusted Dunn’s post-hoc comparisons, and paired habitat differences were evaluated with Wilcoxon signed-rank tests. Predator assemblage was categorized as invasive only when only *C. maenas* were caught and mixed when both *C. maenas* and native crabs were present.

Statistical approaches for *M. gigas* consumption were selected based on model structure and assumption checks (Table 2.1). When site-level consumed data met ANOVA assumptions,

ANOVA was used. When individual *M. gigas* fate was available, consumption was modeled as a binary response using binomial GLMs. When initial binomial models showed overdispersion, quasibinomial GLMs were used for final inference. Predictor variables included vegetation type, predator assemblage, spat size, height above the substrate, and relevant interactions depending on the experimental design.

Table 2.1 Statistical model overview for *M. gigas* consumption field experiments. *Summary of statistical models used to test drivers of juvenile *M. gigas* consumption in field experiments. Predator assemblage was categorized as invasive only when only *C. maenas* were caught and mixed when both *C. maenas* and native crabs were caught. Vegetation by predator assemblage and vegetation by height interactions were tested where relevant and retained only when included in the final model.*

Question	Data subset	Statistical approach	Independent variables	Dependent variable
Do <i>M. gigas</i> size, habitat, and predator assemblage affect consumption of clustered spat on shell?	Experiment 1: six clustered spat on shell deployed at Sites 1-7 in paired eelgrass and mudflat habitats.	Binomial GLM	<i>M. gigas</i> size, vegetation type, predator assemblage, vegetation by predator assemblage	Individual <i>M. gigas</i> consumption status
Do habitat and predator assemblage affect consumption of smaller, more uniform <i>M. gigas</i> individual spat on dowels?	Experiment 2: 20 individual spat on one dowel deployed at Sites 1-7 in paired eelgrass and mudflat habitats	Two-way ANOVA; assumptions were met for site-level percentage consumed	Vegetation type, predator assemblage, vegetation by predator assemblage	Percent of <i>M. gigas</i> consumed
Do <i>M. gigas</i> size, habitat, and elevation affect consumption of spat-on-shell in <i>C. maenas</i> abundant area?	Experiment 3a: one clustered spat on shell deployed at Sites 7-10 at 0 cm and 20 cm above the substrate.	Binomial GLM	<i>M. gigas</i> size, vegetation, height above substrate, vegetation by height	Individual <i>M. gigas</i> consumption status

Do habitat and elevation affect consumption of individual spat on dowels in <i>C. maenas</i> abundant area?	Experiment 3b: 20 individual spat on one dowel deployed at Sites 7-10 at 0 cm and 20 cm above the substrate.	Quasibinomial GLM used after initial binomial model showed overdispersion	Vegetation type, height above the substrate	Percent of <i>M. gigas</i> consumed
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Results

Results are presented from predator context to *M. gigas* response. First predator CPUE patterns are described to establish the spatial and habitat context for predation. Consumption results are then presented by experiment, moving from size-variable clustered spat on shell, to smaller individualized spat, and finally to the height experiment testing vertical refuge.

Predator assemblages varied across sites and habitats in Netarts Bay. CPUE differed significantly among crab species (Kruskal–Wallis $\chi^2 = 9.58$, $df = 3$, $p = 0.02$). Post-hoc Dunn’s tests (Holm-adjusted) indicated that *C. maenas* exhibited significantly higher CPUE than *R. antennarium* ($p = 0.02$), while differences among native crab species were not significant. Across the sampled predator assemblage, *C. maenas* was the dominant crab species captured in traps, especially at mudflat sites and at sites farther up the estuary (Figure 2.2). This pattern establishes that juvenile *M. gigas* were deployed across a predator landscape where invasive crab abundance was spatially uneven rather than uniformly distributed across the bay.

CPUE also varied by vegetation type. Paired comparisons between eelgrass and mudflat habitats revealed significantly higher total CPUE in mudflats than in eelgrass (Wilcoxon signed-rank test: $V = 0$, $p < 0.01$), and *C. maenas* CPUE was also higher in mudflat habitats ($V = 2$, $p = 0.01$; Figure 2.2). The $V = 0$ statistic for total CPUE indicates that total predator CPUE was consistently greater in mudflat habitats across paired sites. Together, these results indicate that relative predator abundance, particularly *C. maenas* catch rates, was greater in mudflat habitats

than in eelgrass habitats. Because mudflat habitats also generally provide less structural refuge than eelgrass, this CPUE pattern suggests that mudflats combined higher predator availability with greater prey exposure. This predator and habitat context provides the basis for interpreting the *M. gigas* consumption experiments below.

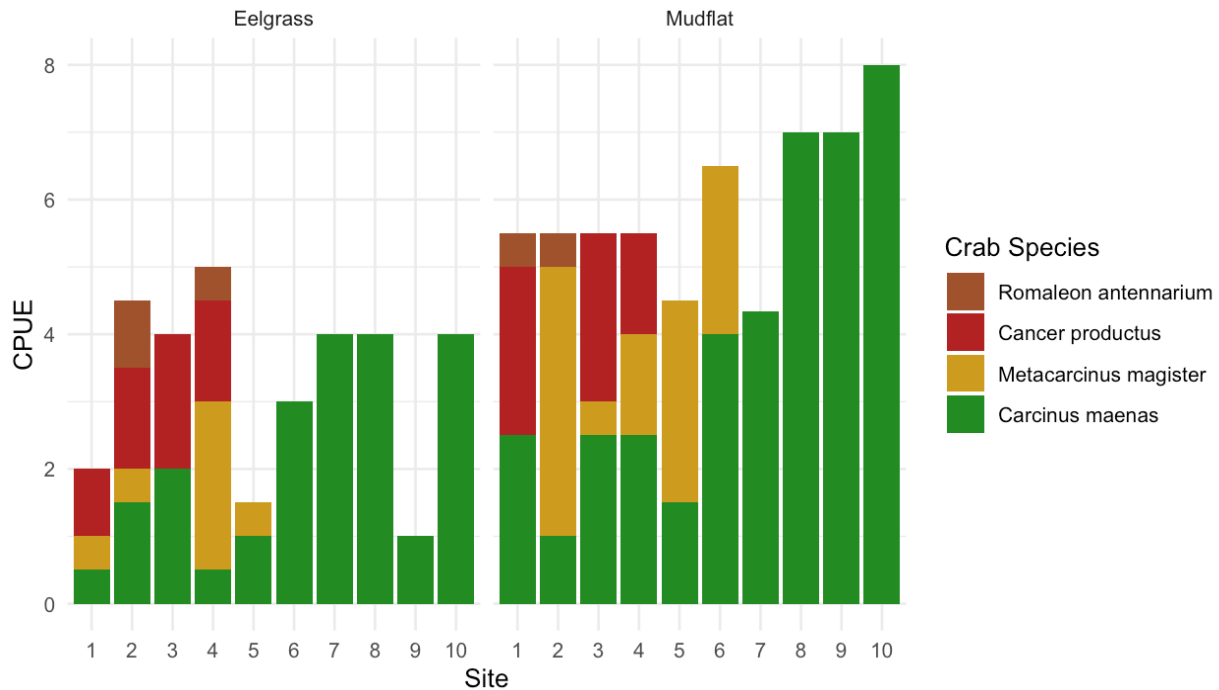


Figure 2.2 Predator crab CPUE across sites and habitats. Catch per unit effort of *M. gigas*-consuming crab species caught in box traps across sites in eelgrass (left set of bars) and mudflat (right bars) habitats. Stacked bars show the number of *Carcinus maenas* (green, bottom), *Metacarcinus magister* (yellow), *Cancer productus* (red), or *Romaleon antennarium* (brown, top) crabs caught. Sites are ordered from mouth (1) to farthest up the estuary, about two-thirds of the way to the head (10), as shown in Figure 2.1.

The clustered spat on shell experiment tested whether *M. gigas* size, habitat type, and predator assemblage jointly predicted consumption when *M. gigas* were deployed in natural size clusters. A binomial GLM indicated that juvenile *M. gigas* spat size, vegetation type, and predator assemblage significantly predicted *M. gigas* consumption (Table 2.2). *Magallana gigas* spat size was a significant predictor of consumption, with smaller spat being more likely to be consumed than larger *M. gigas* ($\chi^2 = 4.79$, $df = 1$, $p = 0.04$; Table 2.2). This size-based pattern is shown in

Figure 2.3, where the model-predicted probability of consumption declined with increasing *M. gigas* size. Consumption risk declined from roughly 25% for *M. gigas* smaller than 15 mm to below 10% for the largest size classes.

Table 2.2 Binomial GLM for clustered spat on shell consumption. *Summary of binomial generalized linear model analysis for the clustered spat on shell experiment testing effects of *M. gigas* size, vegetation, and predator assemblage on juvenile *M. gigas* consumption. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p < 0.10$.*

Analysis	Explicit test	df	Statistic	P-value	Sig.
Clustered spat on shell consumption	Size	1	$\chi^2 = 4.27$	0.0387	*
	Vegetation	1	$\chi^2 = 8.17$	0.0043	**
	Predator assemblage	1	$\chi^2 = 21.05$	< 0.001	***
	Vegetation by predator assemblage	1	$\chi^2 = 2.32$	0.1279	

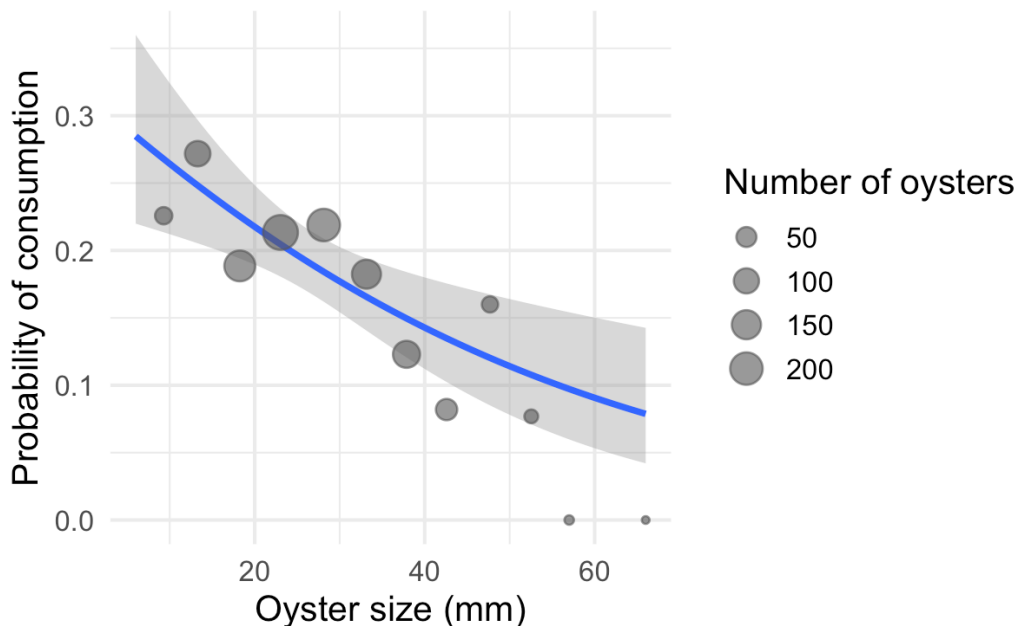


Figure 2.3 Predicted probability of *M. gigas* consumption by size. *Predicted probability of *M. gigas* consumption related to *M. gigas* size. Points represent the observed proportion consumed*

within *M. gigas* size bins, with point size scaled to the number of *M. gigas* in each bin. The solid line shows the model-predicted probability of consumption, and the gray shaded band indicates the 95% confidence interval around the fitted relationship.

Vegetation type was also significant, with higher consumption in mudflat habitats than eelgrass habitats ($\chi^2 = 8.17$, $df = 1$, $p < 0.01$; Figure 2.4). Predator assemblage was the strongest predictor in this model, with consumption differing between invasive-only and mixed predator assemblage areas ($\chi^2 = 21.05$, $df = 1$, $p < 0.001$). Although predator assemblage was statistically important, the percentage of crab CPUE represented by *C. maenas* did not show a simple linear relationship with *M. gigas* consumption when plotted directly (Figure 2.5). In the clustered spat on shell experiment, mudflat sites showed a weak positive visual trend, while eelgrass sites showed little relationship. The vegetation by predator assemblage interaction was not significant ($\chi^2 = 2.32$, $df = 1$, $p = 0.13$), indicating that the effect of predator assemblage did not differ significantly between the mudflat and eelgrass habitat types. Together, these results suggest that clustered spat on shell consumption was shaped by both *M. gigas* vulnerability, especially with size and habitat type, and broader predator assemblage context rather than by *C. maenas* dominance alone.

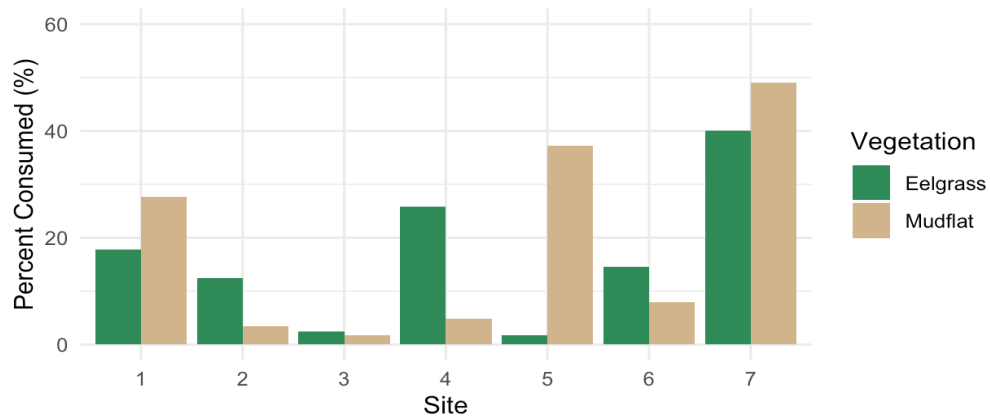


Figure 2.4 Clustered *M. gigas* consumption across sites. *Percentage of *M. gigas* consumed across sites 1-7 in eelgrass and mudflat habitats during the first deployment of the clustered spat on shell experiment. Green bars represent *M. gigas* deployed and consumed in eelgrass, whereas brown bars represent *M. gigas* deployed and consumed in mudflat habitats. Sites are ordered from the mouth of the estuary (Site 1) to farther up the estuary (Site 7, approximately halfway to the estuary head), as shown in Figure 2.1.*

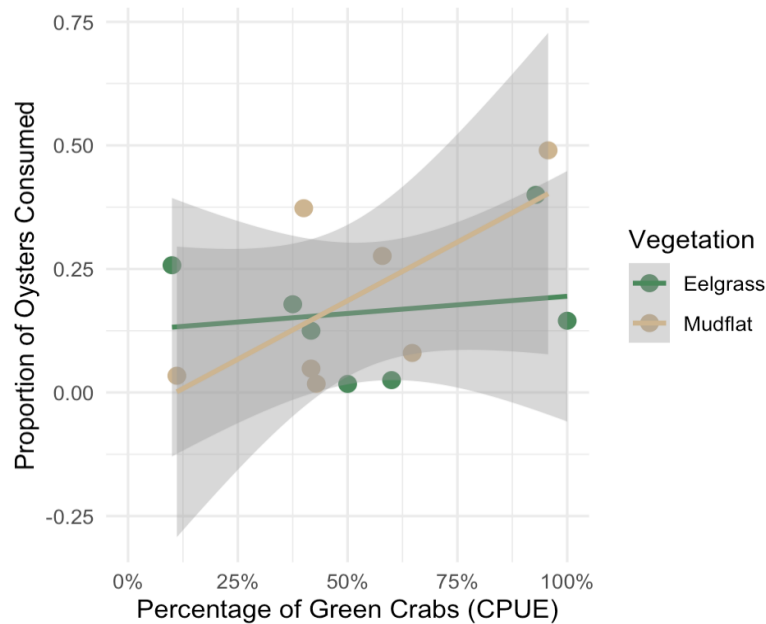


Figure 2.5 Clustered *M. gigas* consumption in relation to *C. maenas* abundance. *Percentage of *M. gigas* consumed in relation to the percentage of total crab CPUE represented by *C. maenas* for the clustered spat on shell experiment. Brown points represent *M. gigas* consumed at mudflat sites, and green points represent *M. gigas* deployed at eelgrass sites. The gray shaded band indicates the 95% confidence interval around the fitted relationship.*

The individual spat on dowel experiment tested whether habitat and predator assemblage still explain consumption when *M. gigas* size was smaller and more standardized. Vegetation type significantly predicted consumption, with higher *M. gigas* consumption in mudflat habitats than eelgrass habitats ($F_{1, 11} = 6.48$, $p = 0.03$; Table 2.3). This habitat pattern was visually consistent across most paired sites, with mudflat consumption exceeding eelgrass consumption at six of the seven sites (Figure 2.6). Predator assemblage did not significantly predict consumption ($F_{1, 11} = 0.25$, $p = 0.63$). Consumption was higher in mudflat habitats than eelgrass habitats, while the consumption was similar between mixed and invasive only predator assemblage categories. When viewed as the percentage of crab CPUE represented by *C. maenas*, *M. gigas* showed no clear relationship with either *C. maenas* catch in either eelgrass or mudflat habitats (Figure 2.7). Individual *M. gigas* spat used were smaller and more uniform than the clustered spat on shell, so size dependent predation could not be evaluated in this experiment. Together, these results suggest that when oyster size variation was minimized, habitat structure remained an important predictor of predation risk, while the broad predator assemblage category was less informative.

Table 2.3 ANOVA for individual spat on dowel consumption. *Summary of two-way ANOVA results for the individual spat on dowels experiment testing effects of vegetation, predator assemblage, and their interaction on juvenile M. gigas consumption. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p < 0.10$.*

Analysis	Explicit test	df	MS	Statistic	P-value	Sig.
Individual spat on dowel consumption	Vegetation	1, 11	0.15	F = 6.48	0.0272	*
	Predator assemblage	1, 11	0.01	F = 0.25	0.6293	
	Residuals	11	0.02	—	—	

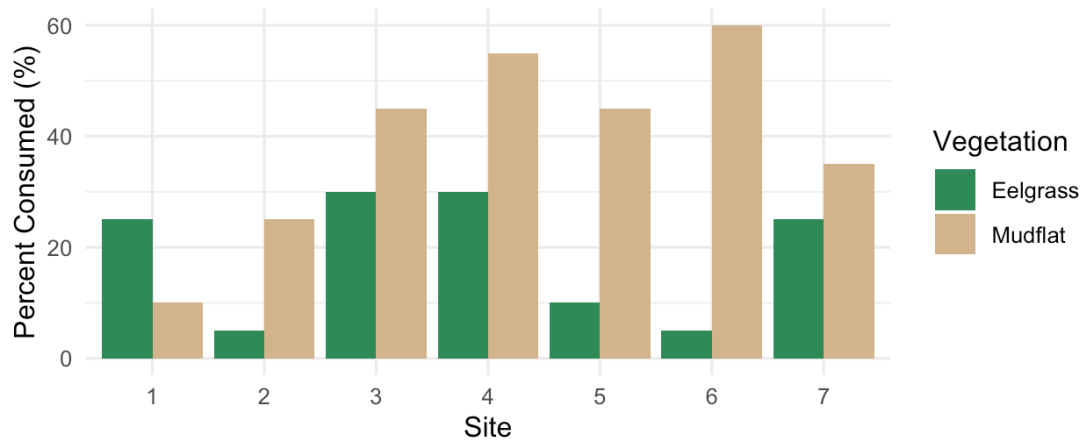


Figure 2.6 Individual *M. gigas* consumption across sites. *Percentage of *M. gigas* consumed across sites 1-7 in eelgrass and mudflat habitats for individually deployed *M. gigas* on dowels. Green bars represent *M. gigas* deployed and consumed in eelgrass, whereas brown bars represent *M. gigas* deployed and consumed in mudflat habitats. Sites are ordered from the mouth of the estuary (Site 1) to farther up the estuary (Site 7, approximately halfway to the estuary head).*

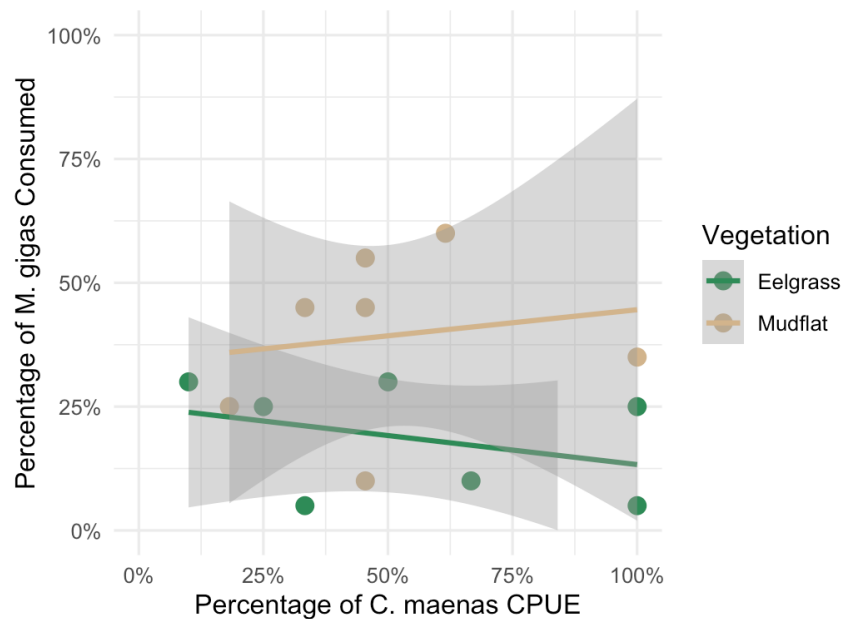


Figure 2.7 Individual *M. gigas* consumption in relation to *C. maenas* abundance. *Percentage of *M. gigas* consumed relating to *Carcinus maenas* abundance for the individual *M. gigas* spat on dowels experiment. Brown points represent *M. gigas* consumed at mudflat sites, and green points represent *M. gigas* deployed at eelgrass sites. The gray shaded band indicates the 95% confidence interval around the fitted relationship.*

The height manipulation experiment tested whether elevating *M. gigas* above the substrate reduced predation risk at four southern sites (7-10) with high *C. maenas* abundance; Separate GLMs were used for the individual spat on dowels and clustered spat on shell components of the height experiment (Table 2.4). For the individual spat on dowels height experiment, a quasibinomial model GLM was used because the initial binomial model showed overdispersion. Vegetation type did not significantly predict consumption ($F = 0.005$, $df = 1$, $p = 0.94$), but height was significant ($F = 5.99$, $df = 1$, $p = 0.03$; Figure 2.8). *Magallana gigas* placed 20 cm above the substrate experienced lower consumption than those placed at the benthos. In the boxplots, benthic dowel deployments showed the greatest spread and highest consumption values, while elevated dowel deployments were generally near zero or low across both habitats. Although the vegetation by height interaction could not be retained in the final reduced model due to small sample size and high variability, the Figure 2.8 suggests that the effect of elevation may have been stronger in mudflat habitats than in eelgrass.

Table 2.4 GLM analysis for height manipulation experiments. *Summary of generalized linear model analyses for the height experiment at Sites 7–10 testing the effects of vegetation, height, their interaction, and M. gigas size for the clustered set of spat on shells on juvenile M. gigas consumption. The individual spat on dowels model used a quasibinomial GLM because the initial binomial model showed overdispersion. The final reduced model did not include the vegetation by height interaction due to small sample size and high variability. The clustered spat on shell model used a binomial GLM. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, . $p < 0.10$.*

Analysis	Explicit test	df	Statistic	P-value	Sig.
Individual spat on dowels consumption	Vegetation	1	$F = 0.005$	0.9446	
	Height	1	$F = 5.99$	0.0294	*
Clustered spat on shells consumption	Size	1	$\chi^2 = 1.93$	0.1648	
	Vegetation	1	$\chi^2 = 0.22$	0.6408	
	Height	1	$\chi^2 = 15.24$	< 0.001	***
	Vegetation by height	1	$\chi^2 = 0.002$	0.9672	

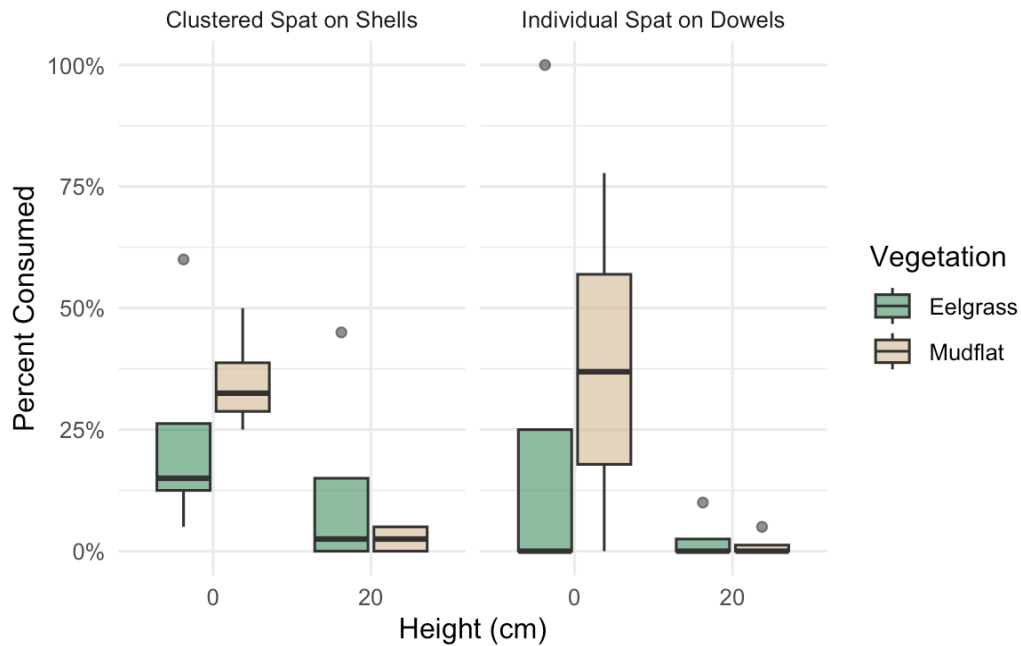


Figure 2.8 *M. gigas* consumption across height and habitat treatments. Percent of *M. gigas* consumed across height treatments (benthic, 0, versus 20 cm above the bottom) and habitat types (eelgrass, green boxplots, or mudflat, brown boxplots) for two field experiments conducted at Sites 7–10: clustered spat on shell (left) and individual spat on dowels (right). Each box shows the interquartile range, center lines show the median, whiskers extend to 1.5 times the interquartile range, and points indicate outliers.

For the clustered spat on shell height experiment, a binomial GLM indicated that height was the only significant predictor of consumption. *Magallana gigas* size was not significant ($\chi^2 = 1.93$, $df = 1$, $p = 0.16$), and vegetation type was not significant ($\chi^2 = 0.22$, $df = 1$, $p = 0.64$). Height significantly predicted consumption, with *M. gigas* elevated 20 cm above the benthos experiencing lower consumption than *M. gigas* placed at 0 cm ($\chi^2 = 15.24$, $df = 1$, $p < 0.001$). Vegetation by height interactions were tested but were not retained in the final models because they were not significant after model correction. Across both height experiment components, the strongest

supported pattern was that elevation above the substrate reduced consumption, indicating that vertical position can provide refuge from benthic predators even in high *C. maenas* areas.

Discussion

Overall, predation risk for juvenile *M. gigas* in Netarts Bay was shaped by multiple interacting factors, with habitat structure, prey size, and vertical position all important determinants of survival across experiments. In the clustered spat on shell experiment, small *M. gigas* were more likely to be consumed, consumption was higher in mudflat habitats, and predator assemblage significantly influenced consumption. Risk differed significantly between invasive only and mixed predator assemblage areas. In the individual spat on dowels experiment, ANOVA results also showed higher consumption in mudflat habitats, while predator assemblage did not significantly explain variation in consumption. Across both components of the height experiment, elevating *M. gigas* 20 cm above substrate reduced consumption, indicating that vertical refuge can reduce access by benthic predators, especially in mudflats. Several consistent patterns emerged across the experiments. Predation risk on juvenile *M. gigas* spat was generally greater in mudflat habitats than in eelgrass. Predator assemblages also varied spatially with predator assemblage context, and *C. maenas* catch was higher at southern sites than at sites closer to the mouth and in traps set in mudflat habitat than in eelgrass beds. Smaller *M. gigas* spat were more vulnerable than larger *M. gigas*, and elevating *M. gigas* above the substrate generally reduced consumption. Together, these results indicate that habitat structure, prey size, and vertical refuge all shape juvenile *M. gigas* survival in Netarts Bay under natural predator communities.

Habitat structure influenced juvenile *M. gigas* survival across experiments, although the strength of its effect varied among experimental designs. Mudflat habitats generally experienced higher predation than eelgrass, with vegetation significantly predicting consumption in both the

clustered spat on shell GLM and the individual spat-on-dowels ANOVA. In the clustered spat on shell experiment, *M. gigas* in mudflat habitats were more likely to be consumed than those in eelgrass, even after accounting for *M. gigas* size and predator assemblage. Similarly, in the individual spat on dowels experiment, *M. gigas* consumption was higher in mudflats than eelgrass in the site-level ANOVA. The higher CPUE observed in mudflat habitats, particularly for *C. maenas* suggests that mudflats provide less structural refuge for prey and offer more foraging opportunities for predators. Compared to native crabs, *C. maenas* may more readily utilize mudflats for intensive foraging (Baeta et al. 2006; MacDonald et al. 2018).

Eelgrass was expected to provide partial refuge by increasing predator search and handling time while reducing encounter rates for prey (Fernandez et al. 1993). Consistent with this expectation, predation was lower in eelgrass than in mudflat habitats in the benthic deployment experiments. Eelgrass likely reduced predation by increasing the search time required for predators to locate and access prey through its complex three-dimensional blades. These results are consistent with the idea that eelgrass functions as a partial refuge for prey, not providing complete protection, as predator access is reduced but not fully limited (Fernandez et al. 1993). Since predation still occurred in eelgrass, the refuge value of vegetation appears conditional and likely depends on predator abundance, habitat configuration, and whether predators are actively foraging within or moving through eelgrass.

In contrast, vegetation type did not significantly predict consumption in the height experiment once vertical position was included in the model. This does not necessarily contradict the earlier habitat results; instead, it suggests that elevation above the benthos may have provided a stronger or more direct refuge from benthic predators than vegetation structure under that experimental context. The height experiment was also conducted at Sites 7–10, where *C. maenas*

abundance was higher, and used a different, combined deployment design than the earlier benthic-only experiments. Therefore, the lack of a vegetation effect in this experiment may reflect the stronger influence of vertical refuge, differences in site context, or reduced power to detect vegetation effects under a smaller, more variable design. Further research would help determine whether suspending *M. gigas* cultivation reduces predation more effectively over open mudflat than within eelgrass beds.

Prey size significantly predicted predation risk in the clustered spat on shell experiment, with larger spat experiencing significantly lower consumption than smaller individuals. This finding indicates strong size-selective predation and suggests that juvenile *M. gigas* begin to gain protection as shell size increases, with only 1 in 10 of the spat eaten once they reach 55 mm along their widest dimension. Larger prey require more handling time, as greater crushing power or prying force is needed from crab predators (Matheson & McKenzie 2014; Grason et al. 2024). The clustered shell design made this pattern especially clear as each shell contained a broad range of spat sizes within the same local predator and habitat context. This finding suggests that prey size can strongly mediate survival alongside habitat and predator community context, and that size refuge may be an important mechanism in early *M. gigas* survival. In this context, the spat on shell experiment provides evidence that predation on juvenile *M. gigas* is not only habitat dependent, but also highly selective within juvenile size classes. However, size was not significant in the spat on shell height experiment, likely because elevation had a stronger effect on predator access, sample size was smaller, and the experiment was conducted in a different spatial context with higher *C. maenas* abundance. Together, these results suggest that size refuge can reduce risk, but its importance may depend on deployment context and predator access.

The individual dowel experiment, with a small *M. gigas* size class, showed a significant habitat-associated pattern, with higher *M. gigas* consumption in mudflat habitats than eelgrass. Predator assemblage did not significantly predict consumption, suggesting that the broad predator category, invasive-only versus mixed assemblage, explained less variation than habitat type in this experiment. Because the juvenile *M. gigas* spat in this experiment were smaller and more uniform in size than the spat on shell experiment, variation attributable to prey size was minimized. Vulnerability to consumption is consistent with studies finding that *C. maenas* target prey under 20 mm (Bassett 2000; Matheson & McKenzie 2014). The close spacing of individual spat should not itself generate a habitat effect, but it may still influence how predators interact with prey once a dowel is encountered. There is evidence that *C. maenas* can continue foraging effectively even when prey occurs at low densities (Ens et al. 2021). As a result, a single predator encountering a dowel can consume multiple spat during one feeding bout. Together, these results suggest that habitat complexity may be especially important for the smallest, most vulnerable juvenile *M. gigas*, when even small differences in accessibility can produce large differences in survival. The lower consumption observed in eelgrass suggests that eelgrass habitats may provide biologically meaningful refuge for early *M. gigas*, although this refuge was partial rather than complete. Given that *C. maenas* can disturb and degrade *Z. marina* habitat, the loss or reduction of structure could further increase risk (Howard et al. 2019; Garbary et al. 2014).

Elevation above the substrate reduced predation risk, supporting the idea that vertical position can function as an effective refuge from benthic crab predators. In the height experiment, *M. gigas* positioned 20 cm above the substrate experienced substantially lower predation risk than *M. gigas* placed benthically at 0cm. This pattern was strongest statistically in the clustered spat on shell experiment and was also significant in the individual spat on dowels experiment, indicating

that vertical refuge reduced predation across both deployment types. In this experiment, vegetation type was not a strong predictor of consumption, indicating that prey accessibility may have been more important than habitat type. Vegetation type was not a significant predictor in either height model, suggesting that prey accessibility above the substrate was more important than eelgrass versus mudflat habitat in this experimental context. Although Figure 2.8 suggests that the benefit of elevation may have been greatest in mudflat habitats, the final models did not support a significant vegetation by height interaction. Therefore, the strongest supported conclusion is that elevation reduced consumption across habitat contexts, rather than that the effect of elevation differed statistically between eelgrass and mudflat. This suggests that the benefit of vertical refuge can partially substitute for the natural structural refuge by moving prey out of the primary foraging zone of benthic predators. Raised oyster beds are a common strategy in aquaculture, particularly until they reach a size refuge to then can be out-planted (Bassett 2000; Jamieson et al. 1998). More broadly, these results reinforce that benthic predators are a major source of juvenile *M. gigas* mortality in estuarine systems.

Although *C. maenas* was clearly a prominent predator in Netarts Bay, its role must be interpreted within the broader context of strong site-level variation in predator community CPUE and species composition. *Carcinus maenas* had the highest CPUE overall and was especially associated with mudflat habitats. *Carcinus maenas* abundance also increased toward the head of the estuary, where *M. gigas* aquaculture and recreational shellfishing are concentrated. This spatial distribution supports the idea that invasive crabs contribute substantially to local predation pressure. At the same time, the relationship between predator context and consumption differed among experiments. Predator community significantly predicted consumption in the clustered spat on shell GLM but did not significantly predict consumption in the individual spat on dowels

ANOVA. Spatial structure within the estuary likely reflects differences in salinity tolerance and habitat use between *C. maenas* and native crab species (Yamada et al. 2020; Yamada & Gillespie 2008). Rather than acting as a consistent predictor across all field experiments, predator community CPUE appeared to interact with prey size, habitat exposure, and deployment structure to shape predation risk. The high abundance of *C. maenas* and its association with mudflat habitats indicate that this species is likely altering the landscape of predation risk for juvenile *M. gigas* throughout the bay, even if its effects are not uniform across sites, habitats, or deployment designs.

Predation outcomes varied across habitat types, sites, and predator assemblages, suggesting that juvenile *M. gigas* survival depends on both predator context and the refuge value of habitats. Because this was a field tethering study conducted under natural predator assemblages, the results are best interpreted as relative predation risk rather than direct measurements of predator specific attack rates. Together these findings indicate that predation on juvenile *M. gigas* is best understood as a process shaped by both physical refuge levels and variation in predator assemblages. The strongest supported patterns were that smaller *M. gigas* were more vulnerable in the clustered spat on shell experiment, mudflat habitats increased consumption in the main habitat experiments, predator assemblage mattered for clustered spat on shell but not individual spat on dowels, and elevation reduced consumption in both height experiment components. When interpreting these results, several limitations of the experimental design should be considered. Sites 1-7 were included in the clustered spat on shell and individual spat on dowel experiments, while the height experiment expanded sampling into the more southern portion of the estuary through sites 7-10. As a result, comparisons among experiments should be made with some caution, since the height experiment was conducted in a slightly different spatial and predator context than the other experiments. Tethering provided a useful way to compare relative predation across habitats and

deployment designs, but it did not allow definitive identification of the predator responsible for each consumption event. Expanding the height experiment across a broader range of sites would help determine whether native predators show similar responses to elevated prey and whether the refuge provided by elevation is consistent across different predator contexts.

This work has direct implications for both *M. gigas* aquaculture and estuarine habitat management. Since predation risk was generally higher in mudflats and for the smallest *M. gigas*, early out-planting stages may be especially vulnerable where *M. gigas* are exposed benthically. The height experiment suggests that raising juvenile *M. gigas* above the substrate can reduce predation where *M. gigas* overlap with *C. maenas* populations, regardless of whether *M. gigas* are deployed as individual spat on dowels or as clustered spat on shells. The clustered spat on shell results also suggests that allowing *M. gigas* to reach larger sizes before outplanting may reduce consumption risk. Beyond aquaculture, successful recruitment and survival of *M. gigas* also contribute greatly to estuarine functions such as water quality through water filtration, benthic-pelagic coupling, and growth promotion of *Z. marina* in estuarine systems, highlighting the need for maintaining seagrass beds and management of *C. maenas* around vulnerable recruitment times and shellfish growing areas (zu Ermgassen et al. 2013; Marks et al. 2024). Together, these findings highlight the importance of maintaining eelgrass beds, reducing *C. maenas* pressure near shellfish growing areas, and considering *M. gigas* size and vertical placement during vulnerable recruitment and outplanting stages.

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Chapter Three: Integrating Green Crab (*Carcinus maenas*) Risk and Estuarine Habitat Structure Using GIS-Based Resource Vulnerability Mapping

Introduction

The green crab (*Carcinus maenas*) is a globally invasive estuarine predator that can impact Oregon's coastal ecosystems through direct predation, indirect impacts, competition with native species, and alteration of structured habitats. Its impacts are especially relevant in estuaries, as these systems support shellfish diversity, eelgrass beds (*Zostera marina*), native crab communities, and productive intertidal habitats. *Carcinus maenas* is a generalist predator, and bivalves are among its most widely documented prey (Bassett 2000; Palacios & Ferraro 2003). Ecologically, shellfish contribute to filtration, habitat structure, and estuarine ecosystem function, so *C. maenas* impacts affect both management and ecosystem function (Grosholz et al. 2011; zu Ermgassen et al. 2013).

Through foraging and bioturbation, *C. maenas* can disturb sediments, affect infaunal communities, and damage *Z. marina* beds (Bassett 2000; Howard et al. 2019). *Zostera marina* and other seagrasses provide structural complexity that supports nursery habitat, refuge, and foraging grounds for estuarine organisms (Whitfield 2017). Because seagrass is both habitat and a vulnerable resource, its spatial distribution is relevant to *C. maenas* vulnerability mapping. Habitat complexity can mediate predator-prey interactions by altering refuge availability, encounter rates, and foraging success (Fernandez et al. 1993). Therefore, habitats such as eelgrass, algal beds, muddy shorelines, and mixed soft-sediment areas may be important both because they can support *C. maenas* occupancy and because they contain vulnerable ecological resources.

The distribution and impact of *C. maenas* are also shaped by physical gradients and biological interactions. Although *C. maenas* tolerates a wide range of estuarine conditions, its

abundance, activity, recruitment, and persistence can vary with salinity, temperature, habitat structure, prey availability, and regional oceanographic conditions (Yamada & Gillespie 2008; Yamada et al. 2015; MacDonald et al. 2018). In the Pacific Northwest, native crabs may also influence *C. maenas* distribution through competition, predation, or broader biotic resistance. Larger native crabs, including red rock crab (*Cancer productus*) and Dungeness crab (*Metacarcinus magister*), may contribute to this resistance, although the strength of these interactions likely varies by species, size, habitat, and estuarine position (Hunt & Yamada 2003; Hunt & Yamada 2003; Gillespie et al. 2015). In Oregon estuaries, *Cancer productus* has been shown to restrict *C. maenas* in some lower-estuary habitats, while broader studies show that native predators can limit *C. maenas* abundance and distribution in other invaded systems (Hunt & Yamada 2003; de Rivera et al. 2005). At the same time, *C. maenas* may persist in warmer, less salinated, or more protected areas where larger native marine crabs are less abundant or less physiologically suited (Hunt & Yamada 2003; Yamada et al. 2015). Resource vulnerability to *C. maenas* therefore depends on the combination of suitable habitat and abiotic conditions, such as salinity gradients that influence where *C. maenas* can persist, native crab assemblages that may limit its distribution, and the extent to which *C. maenas* habitat overlaps with vulnerable resources.

Carcinus maenas management often relies on monitoring catch per unit effort (CPUE), which provides valuable information about observed occurrence and relative abundance. However, CPUE does not directly identify where estuarine resources are most vulnerable to *C. maenas* impacts. Trap catch can also be influenced by sampling effort, trap type, season, bait, local movement, environmental conditions, site accessibility, and the availability of alternative food sources that may reduce trap attraction. As a result, areas with low CPUE may still be impacted if they contain vulnerable resources and suitable *C. maenas* habitat, while areas with high CPUE

may not always correspond to the most vulnerable resource areas. A spatial decision-support tool can therefore complement CPUE monitoring by identifying where multiple vulnerability factors overlap.

Vulnerability maps and indices are commonly used to translate complex ecological or risk factors into spatial decision-support tools. These products often combine multiple indicators, such as exposure, habitat condition, resource value, environmental sensitivity, or management capacity, and may assign weights to reflect the relative importance or vulnerability of each component. These approaches often combine spatial layers representing exposure, habitat condition, resource value, environmental suitability, or ecological sensitivity, and may use weighting schemes to reflect the relative importance of different components. For example, coastal vulnerability indices have integrated multiple physical and socio-environmental indicators in GIS-based frameworks, often using weighting schemes to reflect the relative importance of different components (Barzehkar et al. 2024). A similar approach is useful for *C. maenas* management because trap-based CPUE identifies where crabs have been captured, but not necessarily where vulnerable resources are most exposed to potential impacts. Because Oregon does not currently have an estuary-scale vulnerability map for *C. maenas*, this RVI provides a timely spatial framework for supporting statewide *C. maenas* management planning.

The objective of this chapter was to develop a GIS-based Resource Vulnerability Index (RVI) for four Oregon estuaries with documented *C. maenas* presence: Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay. The RVI integrates habitat, shellfish resource, seagrass, salinity, and native crab CPUE data into a single spatial framework. Specifically, this chapter aimed to map spatial variation in relative resource vulnerability within each estuary, compare mapped RVI values with observed *C. maenas* CPUE, and identify areas where additional trapping, monitoring,

or management may be useful. The RVI was designed as a decision support tool for identifying vulnerable areas where suitable *C. maenas* habitat, shellfish resources, seagrass, salinity conditions, and reduced native crab competitor pressure overlap, rather than a direct prediction of *C. maenas* abundance.

Methods: RVI Development

Spatial Data Sources and Map Preparation

Estuary polygons for Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay were created in ArcGIS Pro by digitizing available estuary and shoreline data from DLCD/OCMP-based spatial resources associated with the Oregon Coastal Atlas and Estuary Data Viewer (Table 3.1). Benthic habitat and seagrass layers were imported or digitized from transferred DLCD/OCMP-based GIS layers. Salinity zones were imported from the NOAA National Centers for Environmental Information Estuarine Salinity Zones dataset. Shellfish resource polygons were digitized from ODFW SEACOR and bay-specific public shellfish/clamming maps. Native crab and *C. maenas* CPUE records were compiled from monitoring reports and research datasets collected between 2019 and 2025. All spatial datasets were projected into a common coordinate system prior to analysis to ensure spatial alignment.

Table 3.1 Spatial data layers used to develop RVI *Summary of spatial datasets incorporated into the Resource Vulnerability Index (RVI) , including estuary boundaries, habitat, seagrass, salinity zones, shellfish beds, native crab catch per unit effort (CPUE), and C. maenas CPUE. This table identifies each data source and explains how each layer contributed to estimating spatial patterns of resource vulnerability and C. maenas invasion risk.*

Data Layer	Source	Year(s)	Role in RVI
Estuary boundaries	DLCD/OCMP-based spatial layers associated with Oregon Coastal Atlas and Estuary Data Viewer	Received/accessed 2025; original mapping year varies by estuary and layer	Digitized estuary and analysis boundaries
Habitat	DLCD/OCMP-based benthic habitat layers associated with Oregon Coastal Atlas and Estuary Data Viewer	Received/accessed 2025; original mapping year varies by estuary and layer	Used to assign habitat type scores for each polygon within estuaries
Seagrass	DLCD/OCMP-based seagrass layers associated with Oregon Coastal Atlas and Estuary Data Viewer	Received/accessed 2025; original mapping year varies by estuary and layer	Used to identify and score seagrass habitat presence
Salinity zones	NOAA National Centers for Environmental Information Estuarine Salinity Zones	1999; NCEI Accession 0127396	Used to assign salinity suitability scores
Shellfish beds	ODFW SEACOR shellfish maps and bay-specific public shellfish/clamming maps	Accessed 2025–2026; map dates vary by bay and map	Digitized to represent vulnerable shellfish resource areas
Native crab CPUE	Yamada 2019 PSMFC report and datasets from Eric Anderson, Shon Schooler, and Isabel Mize.	2019-2025	Used to estimate native crab competitor pressure
<i>C. maenas</i> CPUE	Yamada 2019 PSMFC report and datasets from Eric Anderson, Shon Schooler, and Isabel Mize.	2019-2025	Overlaid on final RVI maps to compare observed <i>C. maenas</i> CPUE with mapped vulnerability

Note. Years represent the year of data collection, publication, compilation, receipt, or access depending on available metadata. Estuary boundary, habitat, and seagrass layers were obtained as transferred DLCD/OCMP-based GIS layers associated with Oregon Coastal Atlas and Estuary Data Viewer resources. Because the transferred GIS layers did not contain consistent original collection dates for all estuaries and layer types, these layers are reported by access/receipt year and source rather than a single collection year. NOAA salinity zones were from the NCEI Estuarine Salinity Zones dataset, dated 1999 and archived as NCEI Accession 0127396. Shellfish polygons were digitized from ODFW SEACOR and bay-specific public shellfish/clamming maps. CPUE records were compiled from monitoring reports and research datasets collected between 2019 and 2025, including PSMFC/Yamada monitoring reports, unpublished datasets provided by Shon Schooler and Eric Anderson, and Isabel Mize’s 2025 thesis field collections. The most recent trapping year available was used for each site. Native crab CPUE and *C. maenas* CPUE were derived from the same compiled trapping dataset, but native crab CPUE was incorporated into the RVI as a competitor-pressure layer, whereas observed *C. maenas* CPUE was retained as an independent comparison layer.

Habitat, Resource, and Salinity Scoring

Each derived or digitized polygon from the habitat type, seagrass, shellfish resources, and salinity layers was assigned initial numeric suitability scores. Habitat types were scored from 1-6 based on relative suitability for *C. maenas* occupancy, foraging value, or expected use. Higher values reflected greater expected suitability. Habitat rankings were based on a combination of observed *C. maenas* patterns and published ecological studies on *C. maenas* habitat use, foraging behavior, salinity tolerance, and interactions with benthic resource impacts. Habitat scores were assigned to represent relative suitability for *C. maenas* occupancy, foraging, refuge, and movement rather than direct estimates of density (Table 3.2).

Table 3.2 Habitat suitability scores for the RVI Habitat suitability framework used to score mapped estuarine habitat types for the Resource Vulnerability Index (RVI). Habitat types were assigned scores from 1–6 based on mapped habitat characteristics and ecological interpretation of habitat structure, sediment type, tidal access, refuge availability, and likely foraging value for *C. maenas*. Higher scores indicate habitats expected to provide greater suitability for *C. maenas* occurrence or trapping.

Habitat Description	Score	Rationale
Aquatic Bed - Algal	6	Structured aquatic vegetation may provide refuge, foraging habitat, and benthic prey resources for <i>C. maenas</i> .
Aquatic Bed - Seagrasses	6	Structured aquatic vegetation may provide refuge, foraging habitat, and benthic prey resources for <i>C. maenas</i> .
Flat	3	Broad intertidal and subtidal flats may provide foraging habitat, but limited structure reduces value.
Flat - Sand - Mud	2	Mixed sand-mud flats may provide some foraging opportunity, but low structural complexity limits refuge value.
Flat-Mud	2	Mud dominated flats may provide some foraging opportunity, but low structural complexity limits refuge value.
Flat-Sand	2	Sand dominated flats may provide some foraging opportunity, but low structural complexity limits refuge value.
Shore	3	General shoreline habitat may provide moderate foraging or movement habitat.

Shore - Wood Debris - Organic	4	Organic debris adds physical structure that may increase refuge availability and foraging opportunities.
Shore-Mud	5	Muddy shoreline habitat may support benthic prey resources and provide suitable foraging habitat for green crabs.
Shore-Sand	4	Sandy shoreline habitat may provide moderate foraging habitat
Tidal Marsh - Fresh Marsh	1	Freshwater influence and low salinity likely reduce suitability for green crab persistence.
Tidal Marsh - High Salt Marsh	1	High marsh is less frequently inundated, limiting access and reducing suitability for aquatic crab use.
Tidal Marsh - Low Salt Marsh	3	Low salt marsh is more frequently inundated and may provide moderate refuge or foraging habitat when accessible.
Unconsol. Bottom - Sand-Mud	5	Mixed soft-sediment bottom may provide suitable foraging habitat and support benthic prey resources.
Unconsolidated Bottom	3	General soft-bottom habitat may provide moderate foraging opportunities, but suitability likely varies with sediment composition and depth.
Unconsolidated Bottom-Sand	2	Sand-dominated bottom has low structural complexity and may provide fewer refuge or prey resources than mixed or muddy sediments.
Cobble - Gravel	1	Coarse, high-energy substrate is expected to provide limited foraging suitability and reduced access to soft-sediment prey.
Shore Bedrock	2	Bedrock shoreline may provide limited refuge in crevices but generally offers low soft-sediment foraging value.
Shore Boulder	4	Boulder shoreline may provide structural refuge and crevice habitat, although foraging value may be lower than muddy habitats.
Shore - Cobble - Gravel	2	Coarse shoreline substrate may provide some structure but is expected to have limited soft-sediment foraging value.
Shell	2	Shell-dominated habitat may provide some structure, but high-energy conditions and limited soft sediment reduce expected suitability.
Unconsolidated Bottom - Shell	1	Shell-dominated bottom is expected to have low suitability due to limited soft-sediment foraging habitat.
Unconsolidated Bottom - Cobble - Gravel	2	Coarse unconsolidated bottom may provide limited structure but reduced suitability for benthic foraging.
Rock Bottom - Boulder	1	Hard-bottom boulder habitat is expected to have low suitability due to limited sediment-associated prey access.
Wood debris	2	Wood debris may provide localized structure, but suitability is limited when not associated with broader shoreline or soft-sediment habitat.

Structured habitats, including algal and seagrass beds, were generally assigned higher scores because habitat complexity can influence refuge availability, predator-prey interactions, and intertidal habitat use (Fernandez et al. 1993; MacDonald et al. 2018). Muddy shorelines and mixed soft-sediment habitats were also ranked highly as *C. maenas* forages on benthic invertebrates and can disrupt bivalve, sediment, and infaunal communities (Bassett 2000; Palacios & Ferraro 2003). Less suitable or more physically stressful habitats, including fresh marsh, high salt marsh, high-energy shell or gravel areas, and exposed rocky habitats, were assigned lower scores because these areas were interpreted as less accessible, lower in soft-sediment prey availability, or more physically stressful.

Seagrass, shellfish, and salinity variables were all scored on 1-3 scales. Higher seagrass scores represented greater structural habitat value and potential overlap with areas likely to be used by *C. maenas*. Seagrass was also included as a vulnerable estuarine resource layer because *C. maenas* foraging, movement, and sediment disturbance may affect structured benthic habitats and associated ecological communities (Howard et al. 2019; Garbary et al. 2014). Higher shellfish scores represented mapped shellfish resources that may be vulnerable to *C. maenas* consumption or disturbance, based on documentation of *C. maenas* consumption of bivalve prey (Bassett 2000; Palacios & Ferraro 2003).

Salinity scores were assigned using NOAA estuarine salinity zones, with higher values representing greater expected suitability for *C. maenas* persistence and activity. Physical estuarine conditions can influence *C. maenas* persistence and native crab distributions across estuarine gradients (Yamada & Gillespie 2008; Yamada et al. 2015). Lower salinity or more protected upper-estuary areas were scored higher for *C. maenas* where they were interpreted as favorable for *C. maenas* and potentially less dominated by larger native crabs. Though context dependent,

there is regional evidence that *C. maenas* can occur in warmer, lower-salinity upper-estuary habitats where some native cancrid crabs may be less abundant, although these patterns are context dependent (Hunt & Yamada 2003; Yamada & Gillespie 2008). Habitat, seagrass, shellfish, and salinity layers were combined using union operations, clipped to the estuary habitat extent, and converted to single-part features so that each polygon represented an individual spatial unit for RVI scoring after initial resource scoring.

Native Crab CPUE Processing

CPUE data for potential *C. maenas* competitors, including Dungeness crab (*Metacarcinus magister*) and red rock crab (*Cancer productus*), were imported as point features using latitude and longitude information. Native crab CPUE was included as a biotic context layer because native crab abundance may reflect potential competition, predation pressure, or biotic resistance affecting *C. maenas* distribution and impacts. Of the original 96 CPUE records, some were excluded because they lacked reliable spatial information or fell outside the mapped estuary boundaries. Remaining records were assigned to the nearest sampling site or polygon, and records occurring within the same spatial unit were averaged to represent localized competitor pressure. This process resulted in 83 final CPUE values used in the RVI.

Score Normalization and RVI Calculation

Raw input scores were normalized prior to calculating RVI values so that all variables contributed on a comparable 0–1 scale. Habitat scores were normalized from their original 1–6 scale, while seagrass, shellfish, and salinity scores were normalized from their original 1–3 scales. Competitor CPUE was normalized and inverted so that lower competitor abundance corresponded to higher vulnerability to *C. maenas*. RVI values were calculated at the polygon level using

weighted combinations of all available data layers. The equations used for normalization, competitor CPUE inversion, and full-data RVI calculation are provided in Table 3.3.

Table 3.3 Normalization equations for the RVI variables. Equations used to normalize input variables for the Resource Vulnerability Index (RVI). Habitat, seagrass, shellfish resource, and salinity scores were rescaled to a common 0–1 scale before index calculation. Native crab CPUE was inverted so that lower native competitor abundance corresponded to higher relative vulnerability.

Equation purpose	Equation	Notes
Habitat normalization	$HAB_{norm} = (HabitatScore - 1) / 5$	Used to normalize habitat scores from the original 1–6 scale to a 0–1 scale.
Seagrass, Shellfish, and Salinity normalization	$X_{norm} = (XScore - 1) / 2$	Used to normalize seagrass, shellfish, and salinity scores from their original 1–3 scales to a 0–1 scale, where X represents SG = Seagrass, SH = Shellfish, and SAL = Salinity
Competitor CPUE inversion	$COMP_{norm} = [1 - CP_CPUE / CP_{max}] + (1 - MM_CPUE / MM_{max}) / 2$	Used to invert normalized native crab CPUE so that lower competitor abundance corresponds to higher relative vulnerability. CP = <i>Cancer productus</i> ; MM = <i>Metacarcinus magister</i> . In this analysis, $CP_{max} = 29.625$ and $MM_{max} = 84.33$.
Full-data RVI calculation	$RVI = [SG_{norm} \times 0.25] + (HAB_{norm} \times 0.25) + (SH_{norm} \times 0.125) + (COMP_{norm} \times 0.25) + (SAL_{norm} \times 0.125) \times 10$	Used to calculate full-data RVI scores at the polygon level. Multiplication by 10 scaled scores from 0–1 to 0–10, with higher values indicating greater relative resource vulnerability.

Multiple RVI equations were applied depending on data availability by estuary and polygon. In the full data equation seagrass and habitat together represented half of the index weight, reflecting the importance of structured habitat and mapped habitat suitability (Table 3.4). Shellfish resources, salinity, and native crab CPUE provided additional resource, environmental,

and biotic context. In the full-data RVI, 75% of the index weight was assigned to habitat, resource, and salinity layers, while 25% was assigned to native crab competitor CPUE. This weighting emphasized areas where suitable *C. maenas* habitat and vulnerable estuarine resources overlap, while still accounting for potential biotic resistance from native crab assemblages. When a data layer was unavailable for a given estuary or scenario, the remaining weight was redistributed, preserving the 75:25 habitat/competitor structure as possible.

Table 3.4 Weighting scenarios for the RVI calculations. *Weighting scenarios used to calculate Resource Vulnerability Index (RVI) scores across alternative GIS data-layer combinations. Weights represent the relative contribution of each spatial layer to the final RVI score under different data-availability scenarios. Alternative scenarios were used to evaluate how index construction changed when salinity, native competitor CPUE, habitat type, or combinations of these layers were excluded. Dash symbols indicate that a layer was not included in each scenario.*

RVI Weighting Scenario	Habitat Type	Seagrass Presence	Shellfish Resource	Competitor CPUE	Salinity
Full dataset	0.25	0.25	0.125	0.25	0.125
Salinity excluded	0.30	0.30	0.15	0.25	—
Competitor CPUE excluded	0.25	0.25	0.25	—	0.25
Habitat type excluded	—	0.50	0.125	0.25	0.125
Habitat type and salinity excluded	—	0.50	0.25	0.25	—
Habitat and shellfish resource	0.40	0.40	0.20	—	—
Seagrass, shellfish resource, and salinity	—	0.50	0.25	—	0.25
Seagrass and shellfish resource	—	0.80	0.20	—	—

Mapping and Comparison of Observed *C. maenas* CPUE

Weights emphasized habitat structure and resource overlap as the primary driver of vulnerability while competitors contributed smaller but meaningful influence. Final RVI rankings allowed comparison among polygons despite differences in available data layers. RVI outputs were mapped with the available *C. maenas* CPUE data (compiled from the Sylvia Yamada 2019 PSMFC Report and datasets from Eric Anderson, Shon Schooler, and Isabel Mize) overlaid to visualize management prioritization and exploration within estuaries with established *C. maenas* populations. This observed *C. maenas* CPUE data was not used as a direct component of the RVI calculation but rather retained as an independent comparison layer to evaluate whether areas of high mapped vulnerability overlapped with known *C. maenas* captures. The combination may aid identification of areas where additional trapping or monitoring would be useful.

Results: RVI Outputs and Spatial Patterns

RVI values and observed *C. maenas* CPUE varied within and among the four Oregon estuaries, indicating that potential resource vulnerability to *C. maenas* impacts was spatially heterogeneous across Oregon estuaries. High RVI values were not distributed evenly across entire estuaries, but instead occurred in discrete areas where suitable habitat, vulnerable shellfish resources, favorable salinity conditions, and/or lower native crab competitor pressure overlapped. This spatial variability suggests that vulnerability is concentrated in specific portions of each estuary rather than distributed uniformly across invaded systems.

Across estuaries, observed *C. maenas* CPUE did not show a simple linear relationship with RVI (Figure 3.1). Some sites with higher RVI values also had observed *C. maenas* captures, indicating overlap between mapped vulnerability and current *C. maenas* occurrence. However, several sites with high observed CPUE occurred at moderate RVI values, and some high RVI sites

had low or no observed CPUE. Most observations were clustered at low to moderate RVI values, while the highest RVI values were represented by fewer sites. Netarts Bay included several high RVI observations with moderate CPUE, whereas Yaquina Bay included several of the highest CPUE observations at moderate RVI values.

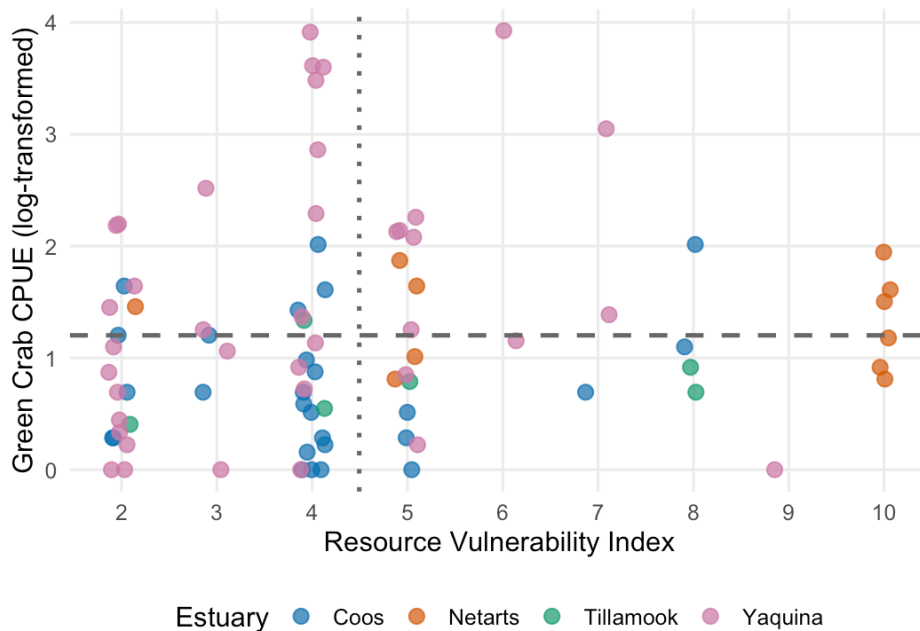
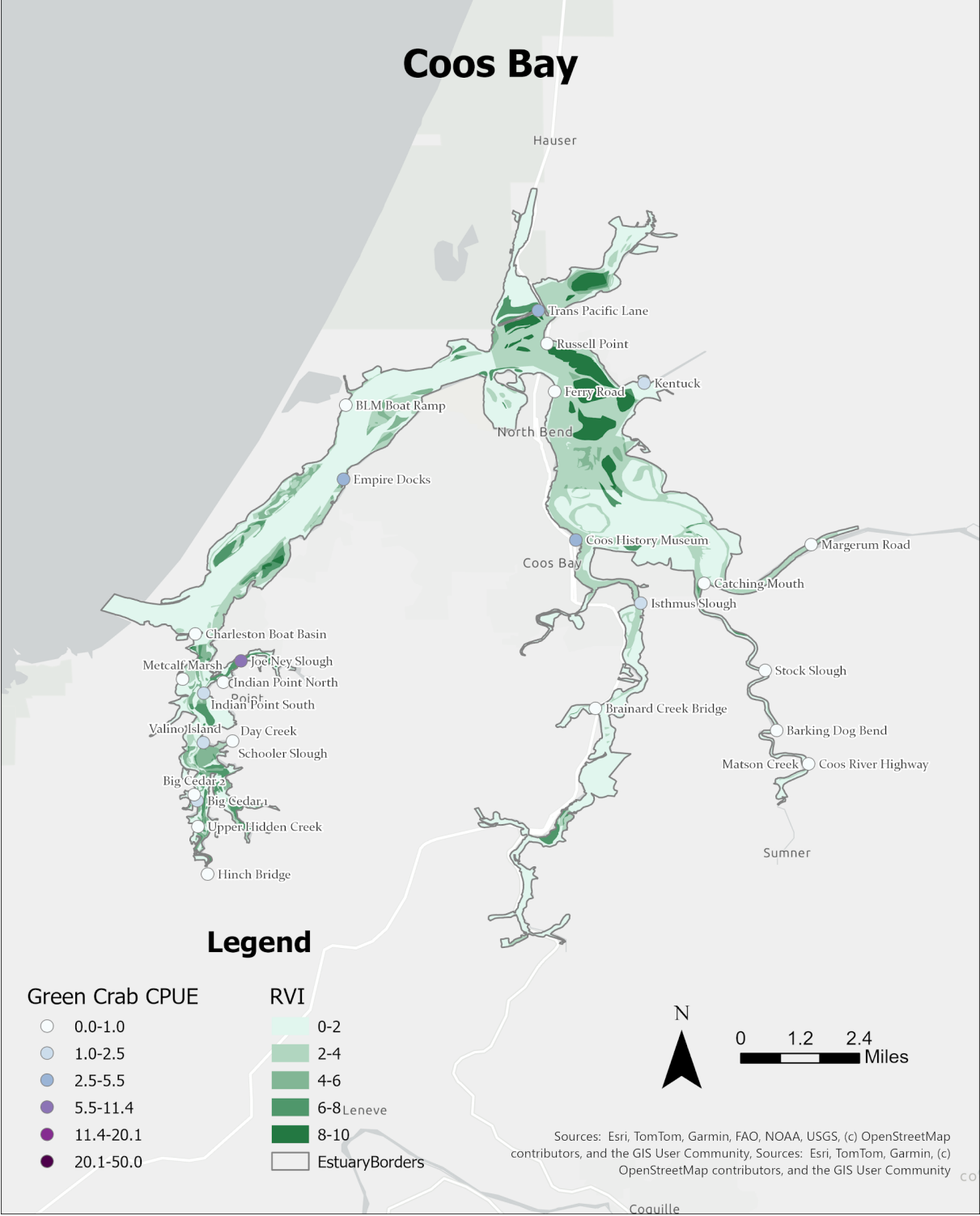


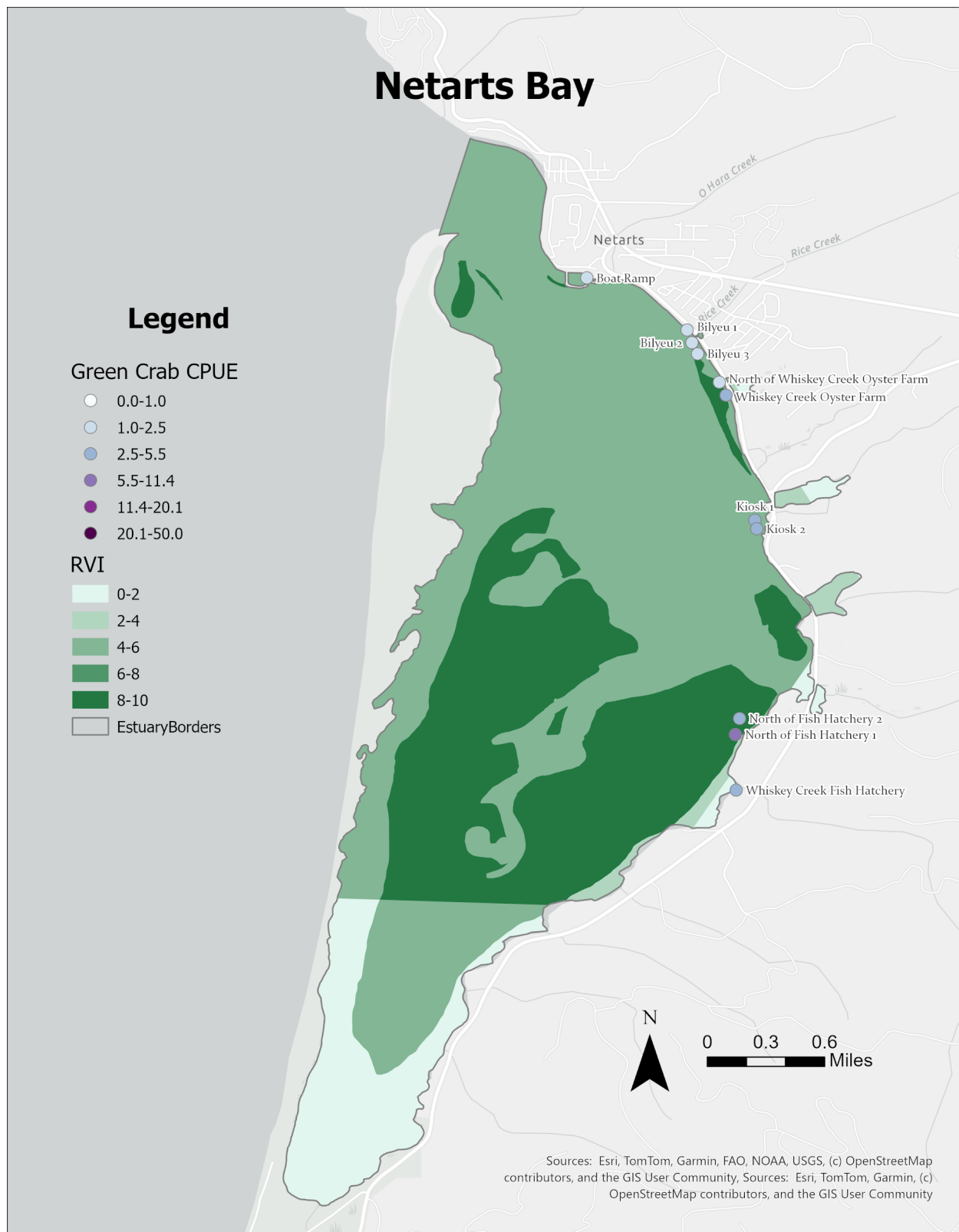
Figure 3.1 RVI and observed *C. maenas* CPUE relationship. *Resource Vulnerability Index (RVI) values and log-transformed *C. maenas* catch per unit effort (CPUE) across four Oregon estuaries: Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay. Points represent individual sampling observations and are horizontally jittered to improve visibility at discrete RVI values. The vertical dotted line represents mean RVI, and the horizontal dashed line represents log-transformed mean *C. maenas* CPUE. Because the RVI incorporates resource availability, habitat suitability, salinity, and native crab CPUE, it is intended as a relative vulnerability index rather than a direct predictor of trap catch.*

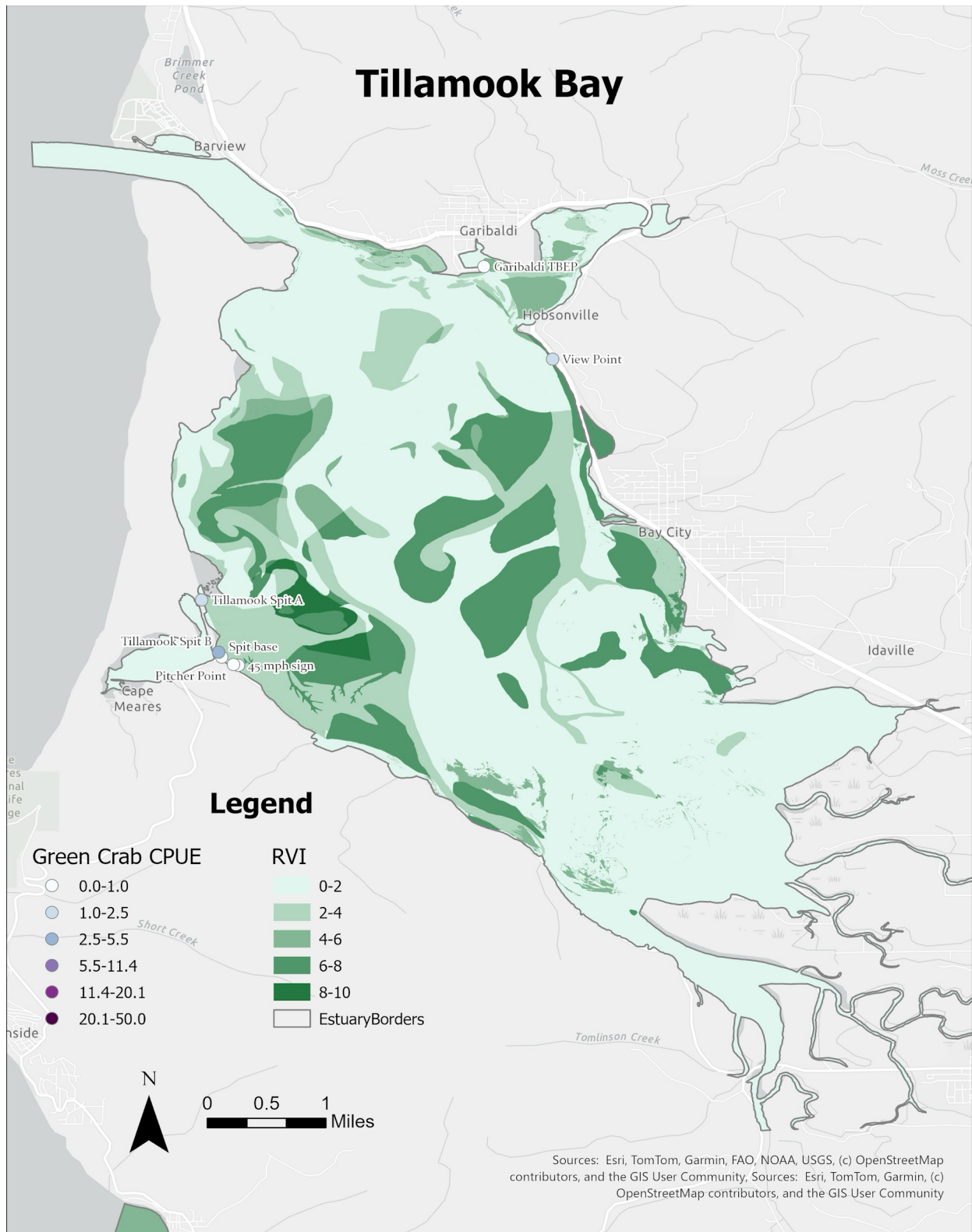
This mismatch is expected because RVI and CPUE measure different aspects of invasion risk. CPUE reflects observed catch at specific sampling locations and times, whereas RVI reflects mapped habitat suitability, resource vulnerability, salinity conditions, and native crab competitor

pressure. Therefore, Figure 3.1 provides a broad comparison between mapped vulnerability and observed catch, while the estuary maps show where those relationships occur spatially.

Mapped RVI outputs showed that potential vulnerability was spatially clustered within each estuary (Figure 3.2). RVI values identify areas where mapped resources and habitat characteristics may make an area more vulnerable to *C. maenas*, while CPUE points represent observed trap data at specific sampling locations. Some areas had both elevated RVI and observed *C. maenas* captures, suggesting overlap between mapped vulnerability and current *C. maenas* occurrence. Other areas had high RVI but low or limited CPUE observations, suggesting potential monitoring gaps or areas where green crabs were not captured during available surveys. Conversely, some areas had high observed CPUE but only moderate RVI, suggesting that *C. maenas* abundance may be influenced by factors not fully captured by the index, including local movement, microhabitats, trapping location, and sampling season.







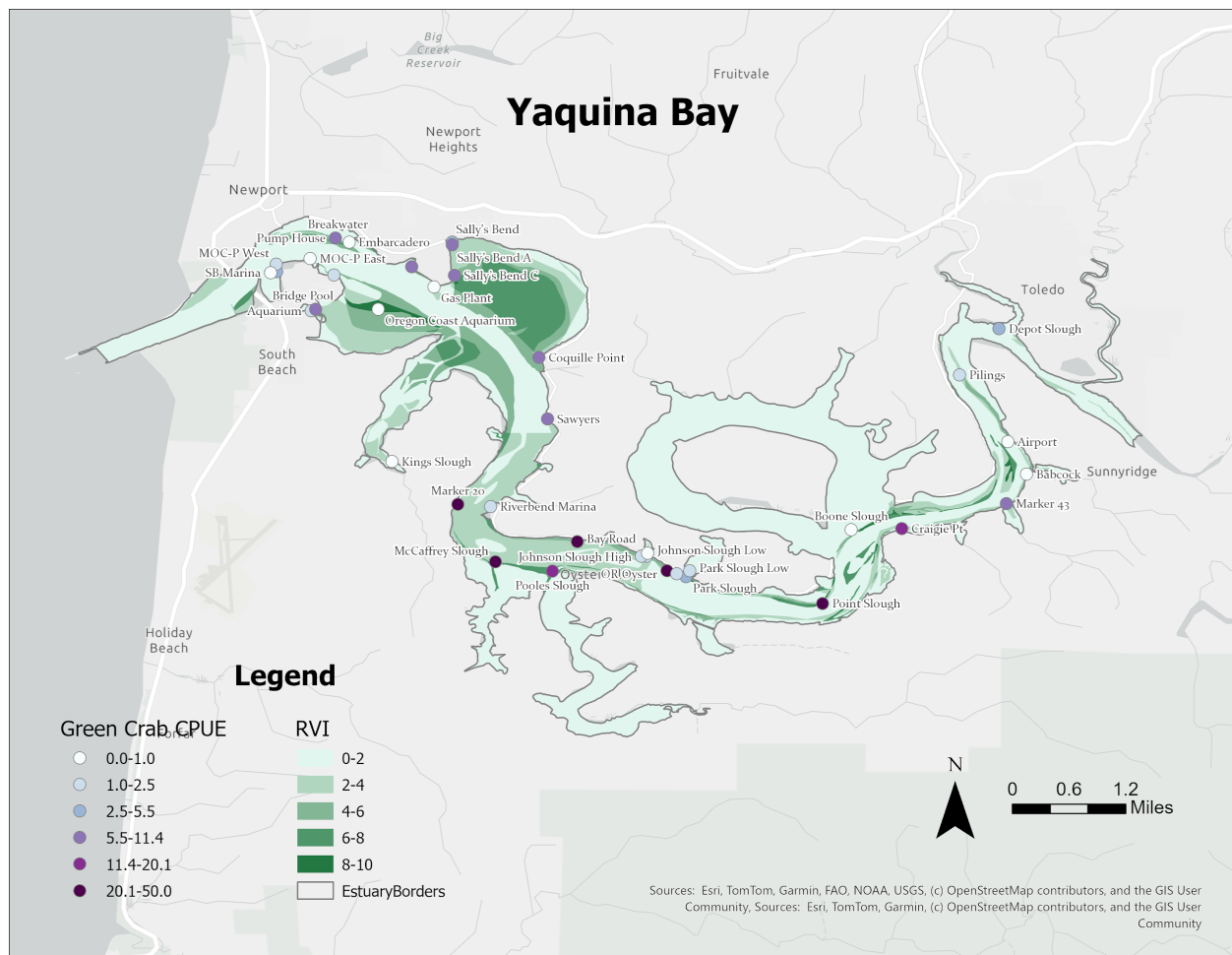


Figure 3.2 RVI scores and observed *C. maenas* CPUE maps. Maps show Resource Vulnerability Index (RVI) values and *C. maenas* catch per unit effort (CPUE) across four Oregon estuaries: A) Coos Bay, B) Netarts Bay, C) Tillamook Bay, and D) Yaquina Bay. More saturated colors indicate higher RVI scores and higher observed *C. maenas* CPUE. RVI values were calculated from habitat, seagrass, shellfish, salinity, and native crab competitor CPUE layers. Spatial data sources included the Oregon Estuary Habitat dataset, NOAA Estuarine Salinity Zones, ODFW shellfish bed maps, and *C. maenas* CPUE datasets compiled from Yamada et al. 2019, Eric Anderson, Shon Schooler, and Isabel Mize.

Coos Bay showed patchy RVI patterns across a large and spatially complex estuary. Higher RVI values were concentrated in several intertidal and shoreline areas, particularly around the western and central portions of the bay and within some slough and shoreline habitats. Many sample sites had low to moderate observed *C. maenas* CPUE, but several sites had higher catches

in areas with moderate to high RVI values. For example, Joe Ney Slough and Valino Island occurred near higher RVI areas and had observed *C. maenas* CPUE, suggesting overlap between mapped vulnerability and current *C. maenas* occurrence.

Several Coos Bay sites with observed *C. maenas* CPUE occurred in areas with moderate rather than high RVI. This indicates that while the RVI captured areas of potential resource vulnerability, observed *C. maenas* catch was not restricted to the highest RVI classes. In Coos Bay, this pattern may reflect the size and complexity of the estuary, variation in trapping locations, and the presence of *C. maenas* across multiple habitat contexts.

Netarts Bay contained some of the most extensive high RVI areas among the mapped estuaries. High RVI values were concentrated through the central and southern portions of the bay, with additional high-vulnerability areas along the eastern shoreline near several sampled sites. Observed *C. maenas* CPUE was present at multiple sites along the eastern margin of the estuary, including areas near Bilyeu, Whiskey Creek Oyster Farm, and North of the Whiskey Creek Fish Hatchery. Several of these sites occurred adjacent to high RVI polygons, suggesting broad spatial overlap between mapped vulnerability and observed *C. maenas* occurrence.

Because mapped habitat classification data were not available for Netarts Bay, RVI values for this estuary were calculated using modified equations based on the available structure, shellfish, salinity, and CPUE layers. As a result, Netarts Bay should be interpreted as a relative within-estuary vulnerability surface rather than directly compared to estuaries with complete habitat data. Even with this limitation, the map suggests that Netarts Bay contains broad areas where vulnerable resources and observed *C. maenas* occurrence overlap, making it an important estuary for continued monitoring and management attention. The concentration of high RVI values

may also reflect the overlap of recreational shellfish areas, oyster aquaculture, and seagrass habitat within the bay.

Tillamook Bay showed broad areas of low to moderate RVI, with higher RVI values concentrated in discrete intertidal and shoreline zones. High-vulnerability areas were especially apparent near portions of the western and central bay, including areas near the Tillamook Spit and some interior intertidal features. Observed *C. maenas* CPUE points were more limited in Tillamook Bay than in Coos Bay or Yaquina Bay, but *C. maenas* were captured at several sampled locations.

Some sampled sites, such as Pitcher Point and View Point, occurred near moderate to high RVI areas, suggesting possible overlap between mapped vulnerability and *C. maenas* occurrence. However, the relatively small number of CPUE sampling locations limits interpretation of the relationship between RVI and observed catch in this estuary. High RVI areas without dense CPUE coverage may represent useful targets for expanded trapping or monitoring, particularly where vulnerable shellfish resources and structured habitat are present.

Yaquina Bay showed strong spatial variation in both RVI and observed *C. maenas* CPUE. Higher RVI values were concentrated in parts of the lower and middle estuary, including areas near Sally's Bend, Coquille Point, Pooles Slough, Johnson Slough, and Point Slough. These areas generally corresponded with intertidal margins, sloughs, and shoreline habitats where mapped habitats and resource layers overlapped.

Observed *C. maenas* CPUE was also spatially variable in Yaquina Bay. Several high-CPUE sites occurred in the middle estuary, including Bay Road, Marker 20, McCaffrey Slough, Point Slough, and Oregon Oyster. Many of these sites occurred in or near moderate RVI areas rather than only in the highest RVI classes. In contrast, some higher RVI areas, such as portions

near the Oregon Coast Aquarium and nearby lower-estuary habitats, had low or zero observed CPUE in the compiled dataset. This pattern reinforces that RVI does not directly predict trap catch; instead, it identifies areas where vulnerable resources and suitable habitat conditions may overlap.

Across estuaries, observed *C. maenas* CPUE did not show a simple linear relationship with RVI (Figure 3.1). Some sites with high RVI also had observed *C. maenas* CPUE, indicating overlap between mapped vulnerability and current *C. maenas* occurrence. However, sites with high observed CPUE were often associated with moderate RVI values, while some high RVI sites had low or no observed CPUE. This mismatch is expected because RVI and CPUE measure different aspects of invasion risk. CPUE reflects observed catch at specific sampling locations and times, whereas RVI reflects mapped habitat suitability, resource vulnerability, salinity conditions, and native crab competitor pressure.

Overall, the RVI should be interpreted as a management prioritization layer rather than a *C. maenas* abundance model. Areas with both high RVI and observed *C. maenas* CPUE may represent short term priorities for continued trapping. Areas with high RVI but limited or low observed CPUE may represent locations where additional monitoring could be useful. Areas with high CPUE but moderate RVI may indicate established *C. maenas* activity in locations where vulnerability is driven by factors not fully represented in the current index value

Discussion

The GIS-based Resource Vulnerability Index showed that potential vulnerability to *C. maenas* impacts is spatially heterogeneous across Oregon estuaries. Rather than being distributed evenly across Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay, high RVI values were concentrated in areas where suitable habitat, vulnerable shellfish resources, favorable salinity conditions, and lower native crab competitor pressure overlapped. This spatial clustering is

important as it suggests that management may be more effective when targeted toward specific high-vulnerability areas rather than applied uniformly across entire estuaries. Estuaries provide valuable ecosystem services, including habitat provisioning, water filtration, shoreline protection, and support for fisheries and shellfish resources (Barbier et al. 2011). Identifying where these resources may be most vulnerable to *C. maenas* impacts can therefore help translate ecological risk into spatially explicit management priorities.

The highest RVI areas were not simply areas of *C. maenas* occurrence, but rather areas where multiple vulnerability factors overlapped. This distinction is important as the RVI was designed to represent resource vulnerability rather than abundance alone. The index gives greater weight to areas where suitable *C. maenas* habitat overlaps with mapped ecological or shellfish resources that could be affected by invasion. Shellfish beds were included because shellfish resources have ecological, commercial, and cultural value (Grosholz et al. 2011; Mach & Chan 2014). Previous studies have documented *C. maenas* predation on bivalves, including clams, mussels, and oysters (Bassett 2000; Palacios & Ferraro 2003). Since suspension-feeding bivalves contribute to filtration and estuarine ecosystem function, areas where mapped shellfish resources overlap with suitable *C. maenas* habitat may represent important management priorities (Zu Ermgassen et al. 2013; Marks et al. 2024).

Seagrass and structured habitats added another dimension of vulnerability. In the RVI, seagrass was treated as both a potential habitat structure and as a vulnerable resource that may be affected by *C. maenas* activity. Habitat complexity can influence prey refuge availability, predator-prey interactions, and foraging success (Fernandez et al. 1993). At the same time, *C. maenas* foraging and bioturbation can damage *Z. marina* beds, making seagrass relevant to management prioritization as a resource at risk (Howard et al. 2019). Therefore, high RVI values in areas with

seagrass, suitable foraging habitats, or shellfish resources should be interpreted as zones where *C. maenas* habitat suitability and resource vulnerability may coincide.

The lack of a simple relationship between RVI and observed *C. maenas* CPUE is expected because the two metrics represent different aspects of invasion risk. CPUE reflects observed trap catch at specific locations and times, while RVI reflects mapped habitat suitability, resource vulnerability, salinity conditions, and native crab competitor pressure. High CPUE at moderate RVI sites may indicate areas where *C. maenas* abundance is influenced by factors not fully captured in the index, such as microhabitat conditions, trap placement, seasonal activity, and prey availability. Conversely, high RVI areas with low or no observed CPUE may represent locations where trapping has been limited, *C. maenas* populations were not captured during the available surveys, or populations have not yet expanded into vulnerable habitat. This pattern is not necessarily a weakness of the RVI. Instead, it reflects that vulnerability and observed abundance are related but distinct management questions. A conservative tendency for the RVI to identify potentially vulnerable areas beyond known high CPUE sites may be useful for management because it can highlight possible monitoring gaps rather than only confirming known capture locations.

Native crab CPUE added an important biotic context layer to the RVI because salinity gradients may influence both *C. maenas* persistence and the distribution of potential native competitors or predators. Lower estuary habitats may support larger marine crabs, while upper estuaries may provide partial refuge for *C. maenas* from some native competitors or predators (Hunt & Yamada 2003; Yamada et al. 2015). *Metacarcinus magister* and other native species also vary across estuarine gradients, reinforcing the need to interpret native crab CPUE spatially across estuaries (Gunderson et al. 1990). Salinity is another important overlapping variable for

vulnerability mapping, as areas suitable for *C. maenas* may be especially viable where native crab competition is lower. Broader studies of biotic resistance also show that native predators can limit *C. maenas* abundance and distribution, supporting the inclusion of native crab context in the index (de Rivera et al. 2005). Competitor CPUE should be interpreted as a general spatial proxy for biotic resistance as abundance does not directly measure predation, competition, or behavioral exclusion.

Interpreting RVI and CPUE together provides a practical framework for management. Areas with both high RVI and observed *C. maenas* CPUE may represent near-term priorities because vulnerable resources and current green crab occurrence overlap. These sites may be appropriate for continued trapping, impact monitoring, or shellfish resource protection. Areas with high RVI but limited or low CPUE may represent potential monitoring gaps, especially where shellfish beds, seagrass, or structured habitat are present but trapping coverage has been sparse. In contrast, sites with high CPUE but moderate RVI may still be important for understanding *C. maenas* movement, local abundance, or spread pathways, even if mapped resource vulnerability is lower. This distinction helps answer a central management question: not only where *C. maenas* have been caught, but where additional trapping or monitoring may be needed because vulnerable resources are present.

The estuary specific results highlight why this type of spatial tool is useful. Coos Bay showed patchy vulnerability across a large and complex estuary, with high RVI areas concentrated in particular shoreline, slough, and intertidal habitats. Netarts Bay contained broad high RVI areas, especially where shellfish resources, seagrass, and observed *C. maenas* occurrence overlapped, although interpretation is limited by the lack of mapped habitat classification data. Tillamook Bay had fewer CPUE sampling locations, making high RVI areas useful candidates for future monitoring. Yaquina Bay showed the clearest mismatch between high observed CPUE and

moderate RVI values, suggesting that *C. maenas* catch in this estuary may be influenced by local conditions, movement pathways, or sampling patterns not fully represented in the current index. Together, these patterns reinforce that vulnerability is spatially structured and that CPUE alone does not capture all management relevant risk.

The index is a relative vulnerability ranking rather than a direct precision of *C. maenas* density, predation rate, or ecological impact. The spatial datasets used in the index vary in resolution and availability across estuaries and within estuary study boundaries. Habitat classifications, shellfish maps, seagrass layers, salinity zones, and CPUE records do not represent the same time period or spatial precision. CPUE data were compiled from multiple sources and may vary in survey objective, trap placement, and sampling intensity. Habitat scoring and variable weights involved ecological interpretation, so alternative weighting schemes could produce different vulnerability scores.

Additional variables could refine RVI scoring, such as temperature, freshwater inputs, tidal elevation, and seasonal trapping patterns. Despite limitations, the RVI framework developed here for *C. maenas* could be adapted to other regions or crustaceans if local data are available. The scoring system would need to be recalibrated to local habitat types, environmental conditions, species interactions, and management priorities. More broadly, the RVI demonstrates how spatial data can be used to complement trapping records and support targeted management for invasive estuarine predators.

Overall, GIS based vulnerability mapping can help connect ecological mechanisms to management action. The RVI does not replace CPUE monitoring but instead provides a complementary decision support layer for identifying where vulnerable resources and suitable *C. maenas* conditions overlap. By pairing the two, managers can better distinguish areas of current

C. maenas activity, areas of potential resource vulnerability, and locations where additional monitoring may be warranted.

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Appendix: Supplemental Table

Table A.1 RVI and *C. maenas* CPUE raw values. *Site-level Resource Vulnerability Index (RVI) values and observed *C. maenas* catch per unit effort (CPUE) are reported for sampled locations across Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay. Values were used to compare observed trapping records with mapped vulnerability patterns across the four Oregon estuaries.*

Estuary	Site	Green crab CPUE	RVI
Coos	Barking Dog Bend	0	4
Coos	Big Cedar	1.4	4
Coos	Big Cedar	1	7
Coos	BLM Boat Ramp	0	4
Coos	Brainard Creek Bridge	0.33	2
Coos	Catching Mouth	0.67	5
Coos	Charleston Boat Basin	1	2
Coos	Coos History Museum	4.17	2
Coos	Coos River Highway	6.5	4
Coos	Day Creek	0.8	4
Coos	Empire Docks	3.17	4
Coos	Ferry Road	0.33	2
Coos	Hinch Bridge	0.33	5
Coos	Indian Point North	1	4
Coos	Indian Point South	2.33	3
Coos	Isthmus Slough	2.33	2
Coos	Joe Ney Slough	6.5	8
Coos	Kentuck	1.67	4
Coos	Margerum Road	1	3
Coos	Matson Creek	0	4
Coos	Metcalf Marsh	0.67	4
Coos	Russell Point	0.25	4
Coos	Schooler Slough	0.17	4
Coos	Stock Slough	0.33	4
Coos	Trans Pacific Lane	4	4
Coos	Upper Hidden Creek	0	5
Coos	Valino Island	2	8
Netarts	Bilyeu 1	1.25	5
Netarts	Bilyeu 2	2.25	10
Netarts	Bilyeu 3	1.5	10
Netarts	Boat Ramp	1.75	5
Netarts	Kiosk 1	4.17	5
Netarts	Kiosk 2	5.5	5
Netarts	North of Fish Hatchery 1	6	10
Netarts	North of Fish Hatchery 2	4	10
Netarts	North of Whiskey Creek Oyster Farm	1.25	10

Netarts	Whiskey Creek Fish Hatchery	3.3	2
Netarts	Whiskey Creek Oyster Farm	3.5	10
Tillamook	Garibaldi TBEP	0.5	2
Tillamook	Pitcher Point	1	8
Tillamook	Spit base	0.73	4
Tillamook	Tillamook Spit A	1.2	5
Tillamook	Tillamook Spit B	2.8	4
Tillamook	View Point	1.5	8
Yaquina	Airport	0	2
Yaquina	Aquarium	2.5	5
Yaquina	Babcock	0	4
Yaquina	Bay Road	49.78	6
Yaquina	Boone Slough	0.4	2
Yaquina	Breakwater	0.25	5
Yaquina	Bridge Pool	8.57	5
Yaquina	Coquille Point	7	5
Yaquina	Craigie Point	16.5	4
Yaquina	Depot Slough	4.17	2
Yaquina	Embarcadero	0	2
Yaquina	Gas Plant	1	2
Yaquina	HMSC Pumphouse	1.5	4
Yaquina	Johnson Slough	1.34	5
Yaquina	Johnson Slough High	2.17	6
Yaquina	Johnson Slough Low	1.06	4
Yaquina	Kings Slough	0	3
Yaquina	Marker 20	31.56	4
Yaquina	Marker 43	8	2
Yaquina	Marina Bed	3.27	2
Yaquina	McCaffrey Slough	35.63	4
Yaquina	MOC-P East	0.56	2
Yaquina	MOC-P West	2	2
Yaquina	OR Oyster	49.11	4
Yaquina	Oregon Coast Aquarium	0	9
Yaquina	Park Slough	3	7
Yaquina	Park Slough High	2.11	4
Yaquina	Park Slough Low	1.39	2
Yaquina	Pilings	1.89	3
Yaquina	Point Slough	36.13	4
Yaquina	Pooles Slough	20.11	7
Yaquina	Pump House	7.41	5
Yaquina	Riverbend Marina	2.5	3
Yaquina	Sally's Bend	2.93	4
Yaquina	Sally's Bend A	11.4	3
Yaquina	Sally's Bend C	7.5	5
Yaquina	Sawyers	8.89	4
Yaquina	SB Marina	0.25	2
Yaquina	Turning Basin	7.89	2

Full Conclusions

The results of this thesis show that the impacts of the invasive European green crab (*Carcinus maenas*) on juvenile Pacific oysters (*Magallana gigas*) extend beyond direct consumption and depend strongly on ecological context. In Chapter one, *C. maenas* presence impacted *M. gigas* through both consumptive effects, through direct foraging activity, and non-consumptive effects, through chemical and tactile cues reducing *M. gigas* clearance rates. This demonstrates that predator effects can alter not only prey mortality but also *M. gigas* function (Kimbrow et al. 2020; Domínguez et al. 2021). In Chapter Two, the field experiments showed that predation risk was not uniform across Netarts Bay, but varied with habitat type, prey size, elevation above the substrate, and predator assemblage context. In Chapter three, these experimental findings were extended into a management framework by developing a GIS based Resource Vulnerability Index (RVI) to identify where suitable *C. maenas* habitat, vulnerable resources, and *C. maenas* abundance overlap across Oregon estuaries. Juvenile *M. gigas* survival is shaped by both direct predation and the broader risk environment in which *M. gigas* grow, including predator identity, habitat structure, and prey accessibility (Fernandez et al. 1993; Ens et al. 2021).

The laboratory experiment established the mechanistic basis for these interactions by showing that predator presence alone was sufficient to suppress *M. gigas* clearance rates, with the strongest effects often occurring in treatments containing *C. maenas*. Invasive predators may influence *M. gigas* populations not only through direct mortality but also by reducing filtration and therefore altering the ecological role *M. gigas* plays in estuarine ecosystems. Since *M. gigas* contribute to water clarification, nutrient cycling, and benthic pelagic coupling, these non-consumptive predator impacts have broader implications that extend beyond survival (Zu Ermgassen et al. 2013; Rosa et al. 2018; Marks et al. 2024).

In the field, predator effects are filtered through estuarine conditions. Across experiments predation was generally higher in mudflat habitats than in eelgrass, indicating that habitat structure can mediate access to juvenile *M. gigas*. In the clustered spat on shell experiment, prey size a significant predictor of predation risk, supporting the existence of a size refuge within juvenile *M. gigas* classes. In the height manipulation experiment, elevating *M. gigas* 20 cm above the substrate reduced predation, especially where baseline predation pressure was otherwise high. These findings indicate that prey accessibility, whether determined by habitat complexity, prey size, or vertical position, is a central feature of juvenile *M. gigas* survival in estuarine systems (Fernandez et al. 1993; Matheson & McKenzie 2014; Howard et al. 2019).

The laboratory and field experiments together provide a more complete picture of invasive predator effects than either approach alone. *Carcinus maenas* alter *M. gigas* function and behavior by suppressing feeding and increasing mortality through both trophic and non-trophic pathways. Field experiments show where and when those effects are more likely to shape survival in estuaries, with predation risk greatest where habitat refuge is reduced, prey are small, and benthic predators have easier access to *M. gigas*. Together, these findings suggest that even when *M. gigas* are not consumed, overlap with *C. maenas* may reduce *M. gigas* filtration through non-consumptive effects, while direct predation can further reduce survival in high-risk habitats. This thesis therefore supports a view of *C. maenas* impacts as both mechanistic and spatial. Invasive predators alter *M. gigas* function and survival, but the magnitude of those effects depends on local habitat and predator context. Because *C. maenas* impacts can affect shellfish resources and vary across invaded estuaries, spatially explicit management is important for identifying where vulnerable resources may be most at risk (Grosholz et al. 2011; Mach & Chan 2014; Yamada & Gillespie 2008).

The RVI developed in Chapter three extends these biological findings into an estuary scale management context. Chapters 1 and 2 showed that *C. maenas* can affect juvenile *M. gigas* through predation and non-consumptive effects on feeding activity. These impacts expand past just individual organisms and become relevant to management where vulnerable populations overlap spatially with suitable *C. maenas* habitat. By mapping these overlapping conditions across Coos Bay, Netarts Bay, Tillamook Bay, and Yaquina Bay, the RVI provides a way to identify areas where oyster and shellfish resources may be especially vulnerable to *C. maenas* impacts. The RVI does not replace CPUE monitoring but complements it by distinguishing areas of observed *C. maenas* activity from areas of potential resource vulnerability. This distinction is important because high CPUE does not always occur in the same places as high resource vulnerability, and high vulnerability areas with low or limited CPUE may still warrant monitoring if *C. maenas* populations expand.

These findings have direct implications for oyster aquaculture, restoration, and estuarine management. Early life stages appear to be most vulnerable when oysters are small, benthic, and exposed in habitats with limited structural refuge. Eelgrass can reduce predation risk under many conditions, but its refuge value is partial and conditional rather than absolute. Elevation above the substrate may also reduce predation where overlap with benthic crab predators is high, particularly over open mudflat. Management actions are therefore likely to be most effective when they reduce predator access during vulnerable life stages rather than treating predation risk as uniform across the estuary. This may include maintaining structured refuge habitats, reducing *C. maenas* pressure near shellfish resources, and using deployment strategies that limit access by benthic predators (Fernandez et al. 1993; Howard et al. 2019; Jamieson et al. 1998). At broader spatial scales, GIS based vulnerability mapping can help identify where those resources overlap with suitable *C.*

maenas habitat, salinity conditions, and lower native crab competitor pressure. In this thesis, Resource Vulnerability Index maps extend these experimental findings to the estuary scale and provide a framework for prioritizing monitoring and management across Oregon estuaries (Barbier et al. 2011; Grosholz et al. 2011; Yamada & Gillespie 2008).

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