Limb Loss as an Indicator of Biotic Resistance

Against the Non-native European Green Crab (Carcinus maenas) in Coos Bay, Oregon

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Kimberly Sims

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[1] Male, European green crab missing limbs was collected near the Salmon River, Oregon. Photo taken by Carmel Finley.

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ABSTRACT

The presence of predators and competitors can offer biotic resistance against the establishment of non-native species, including the European green crab, *Carcinus maenas*, (EGC) in the estuary of Coos Bay, Oregon. It has been suggested that limb loss, or autotomy of the EGC will increase in areas that include populations of larger native crabs such as the red rock crab, (*Cancer productus)* and Dungeness crab (*Metacarcinus magister*). To test this hypothesis, we analyzed data from a long-term monitoring program collected by researchers from Oregon State University and South Slough National Estuarine Research Reserve (SSNERR). From this data set we examine the patterns of limb loss as functions of size and location and extract indicators of the relative population density of EGC and other native crab species. This manuscript also includes an additional component that evaluates the policy implications of the EGC and offers additional societal and cultural context to further address this wicked problem.

STATEMENT OF THE PROBLEM

Biotic assemblages of marine communities provide a vast array of food resources for the EGC to consume. Not only are mollusks and bivalves prey items for the green crab (*Carcinus maenas*), but also benthic macroalgae, small fishes, and native crabs can serve as nourishment. The estuary located in Coos Bay, Oregon is predisposed to colonization by non-native species (Rumrill 2007) such as the EGC.

Coos estuary is a vital coastal industrial center because of its shipping port that provides a commercial route to San Francisco, Puget Sound and other major ports located throughout the Pacific Rim. As a result of commercial shipping, non-native species in the form of hitchhikers may be transported to other regions attached to a ship’s hull or in contaminated ballast waters acquired from other regions. This movement of ballast water from region to region via global shipping routes results in all shipping ports being ecologically connected (Keller et al. 2015). Not only do the commercial shipping activities increase the exposure of Coos Bay to several non-native species but also the varied habitats, such as the vast intertidal sand, mudflats and eelgrass beds, are preferred by the EGC. These types of habitats can become colonized and established with large populations of EGC. The spread and establishment of non-indigenous species (NIS), especially the European green crab, can cause irreversible ecological changes and significant economic damages as NIS spread to new environments (Andersen et al. 2004).

INTRODUCTION

This manuscript is the product of a multi-disciplined approach seeking to thoroughly investigate the impacts and management options for controlling unwanted populations of the non-native European green crab (EGC), (*Carcinus maenas*) in Coos Bay, Oregon. Therefore, it contains two separate components in an effort to provide a comprehensive scope for a deeper understanding of this wicked problem. The first component includes research collected from scientific literature, and the examination of a long-term data set. In the aspirations to develop a process to identify areas with EGC that would benefit from targeted management actions we explored how limb loss may be used as an indicator for the presence of biotic resistance. The risk analysis of invasive species is an interdisciplinary issue that involves ecology, economics and mathematics; and therefore, the second component of this manuscript approaches the EGC as a societal problem and offers small-scale management actions for controlling the EGC population in Coos Bay, Oregon.

Aquatic nuisance species (ANS) are acknowledged as organisms that can disrupt ecology and trophic food webs of aquatic systems. ANS can have a negative financial impact on the commercial fisheries of several economically important species (Grosholz and Ruiz 1996). The non-indigenous green crab (*Carcinus maenas*) has been introduced to the coastal waters of the Pacific Northwest (PNW) and provides competition against the juvenile Dungeness crab (*Metacarcinus magister*) for resources in their nursery habitat. The commercial harvesting of Dungeness crab is the largest and most valuable fishery in Oregon (ODFW 2020 Dec 21). According to the Oregon Dungeness Crab Commission website, commercial Dungeness crab landings for 2019 exceeded 19 million pounds and were valued at $73 million dollars (ODCC 2020). Not only are the Dungeness crab fisheries at risk, but also farmed mollusks such as oysters and clams are susceptible to predation. Bivalves are a highly desired food of choice for the green crab, and therefore, both wild and cultivated shellfish farms are potential targets for the green crab incursion. Consequently, the green crab has significant potential to drastically alter coastal ecosystems, aquatic environments, and estuaries if population numbers continue to increase and become established (Behrens Yamada and Gillespie 2008).

Analysis of an 18-year-old data set compares six different sites located within the estuary of Coos Bay in an effort to identify areas that may provide a biotic resistance. This data set, collected as part of the monitoring efforts of the EGC populations located throughout the PNW, provides the basis for our investigation and analysis (Behrens Yamada and Schooler 2020).

Autotomy, which results in limb loss, is an important survival mechanism commonly utilized by wild crustacean species (Juanes and Smith 1995; Mariappan et al. 2000). The autotomy of limbs, especially that of claw appendages (chelipeds), can have significant consequences for growth, survival, and reproduction for the green crab (Sekkelsten 1988; Abelló et al. 1994; Juanes and Smith 1995; Delaney et al. 2011; Flynn et al. 2015). Review and analysis of data collected from individual EGC with limb loss may provide insight regarding predation/competition pressures for areas currently being monitored for the green crab populations.

HISTORICAL ECOLOGY OF COOS BAY, OREGON

Coos Bay is an estuary that has a winding access to the ocean. It is located at the midway point between the Strait of Juan de Fuca and San Francisco Bay. It is the second largest estuary in Oregon and the sixth largest along the western coastline.

Historically, estuaries such as Coos Bay, have offered a plethora of natural resources for indigenous people, such as timber for building, shellfish such as Dungeness crabs, clams, mussels and oysters including a variety of fish species such as salmon for harvesting (Good 2000; Losey et al. 2004). The Coos estuary was used for local transportation and trading and continues to remain a vital component for today's commerce. After the North Bend sawmill closed in 1989, Coos Bay entered a period of time referred to as deindustrialization. More recently, areas located in Coos Bay such as the Boat Basin, have become more gentrified and economic revenues are derived from hospitality services as a shift from natural resources (Robbins 2006).

BACKGROUND AND LITERATURE REVIEW

GREEN CRAB LIFE HISTORY, ECOLOGY AND BIOLOGY

The green crab is considered to be a generalist for both habitat and feeding preferences. Some researchers have labeled the green crab as an "ecological engineer" because it has been known to disturb eelgrass beds in the search for food which alters habitat structures. Additionally, the green crab is able to tolerate a wide range of water quality, salinity, and temperatures. Not only is the EGC able to persist in a wide variety of habitats, but it can also tolerate the exposure to air for up to 60 days if provided a shelter consisting of damp seaweed. EGC can endure starvation for up to three months (Behrens Yamada 2001). This phenotypic plasticity enables the green crab to persist and thrive in a variety of habitats and conditions.

The green crab is an aggressive species with high fecundity. Depending upon the size and age, a small adult female (34mm CW) can release approximately 185,000 - 200,000 eggs from a single brood (Broekhuysen 1937). EGC, from a population in Maine, have been documented to breed two to three times during a female's life span (Berrill 1982). In Oregon, EGC can reach sexual maturity in about one year of age (Behrens Yamada et al. 2005), and comparatively females from the Maine population are sexually mature around two to three years old (Berrill 1982).

The green crab has a two-stage life cycle that begins as a free swimming planktonic larval form and then matures into a benthic adult. As such, tiny larvae are easily distributed via ocean currents to other distant areas (Jamieson 2000; Behrens Yamada et al. 2005; Brasseale et al. 2019). Warming temperatures of sea water and strong ocean currents facilitate the dispersal of EGC larvae and can spread episodically along the coast. With an appetite preference for carnivory which increases as the green crab matures, EGC pose a substantial threat to wild and cultivated bivalve species (Ropes 1968). The lifespan of the EGC has been reported to be five to seven years for native European populations (Carlisle 1957), but appears to be around six years for EGC populations in Oregon (Behrens Yamada et al. 2001). For the PNW region, prevention and population control are important in order to avoid potentially devastating results, such as the situation experienced by the Atlantic coast (Grosholz and Ruiz 1996).

GEOGRAPHIC DISTRIBUTION

NATIVE REGIONS AND POTENTIAL RANGE EXPANSION

The green crab is native to the Atlantic shores of Europe, from the Baltic Sea in the north extending south to the northwestern coast of Africa (Behrens Yamada et al. 2001).

Warm water temperatures during the winter have been correlated with strong year classes of the green crab. Generally, water temperatures of 10° C or colder negatively impact survivorship and juvenile recruitment, so warmer temperatures result in more favorable conditions for the EGC (Ropes 1968). Therefore, the effects from climate change and warmer water temperatures can lead to an increase of EGC surviving throughout the winter. Strong coastal water currents moving northward, which are indicative of El Niño Southern Oscillation (ENSO) are also a strong factor for expanding the EGC range farther northward (Behrens Yamada and Kosro 2010; Behrens Yamada et al. 2015).

Range expansion of the EGC reached Oregon in 1997 and afterwards to other regions along the Pacific coast (Jamieson 2000) as larvae were transported via strong ocean currents

(Behrens Yamada et al. 2005). More recently, the EGC has colonized embayments of Oregon, northward to the coastal regions of Washington, the Salish Sea and coastal areas of British Columbia (Eissinger 2010; Behrens Yamada et al. 2021). Additionally, populations are established along the coast of South Africa, Australia, Tasmania, Japan and Patagonia, Argentina (for details see Behrens Yamada et al. 2021).

INVASION ACTIVITY

HISTORY OF INVASIVENESS

The European green crab has been established along the North American Atlantic coast for more than 200 years. The oldest founder population of EGC was established sometime before the year 1817 (Say 1817). Research indicates that the EGC has had severe negative economic impacts on the shellfish industry of the eastern coast of the US for an average cost of $22.6 million dollars per year (Lovell et al. 2007).

From the late 1940's into the early 1950's, the eastern coast of the US experienced a warming trend resulting in winter temperatures becoming the highest on record from 36° to 38°F. Some researchers believe this warming trend facilitated the EGC to expand its range from southwestern Maine to northeastern part of the state, and to New Brunswick and Nova Scotia (Glude 1955). Freezing temperatures had previously regulated the populations of EGC and limited its range. Five experimental soft-shell clam farms in Maine failed during 1950-1951 and those failures can be directly traced to predation events from the EGC (Glude 1955). Other factors, such as disease, overfishing and parasites, may have contributed to the decline of the shellfish industry along the Atlantic coast. However, research has also indicated that several mollusk species along the Atlantic coast have been negatively impacted from the presence of the green crab (Ropes 1968; Grosholz and Ruiz 1996; Lovell et al. 2007).

In 1998, the green crab was deemed as an aquatic nuisance species and was the first marine organism to be listed on the federal Aquatic Nuisance Species Task Force (ANSTF) (Kern et al. 2002). The biomass of the green crabs found in North America is greater than the biomass of green crabs found in its native region. As a result this "global invader" exhibits increased performance in novel regions and therefore, the EGC is considered to be a successful invader (Torchin et al. 2001).

POTENTIAL OR REPORTED ECOLOGICAL AND ECONOMIC IMPACTS

The EGC preying and feeding on mollusk species can have cascading effects. Wild and cultivated oysters, both native and non-native species are at risk of predation in Coos Bay. Bivalves, such as oysters provide important ecosystem services (Poirier et al. 2017). Some of the benefits provided by bivalves include the filtration of particles and nutrients from the water column which improves water quality, and oyster reefs can also alter the hydrodynamic conditions (Nelson et al. 2004). Denitrification is also an important process that occurs from the harvesting of bivalves (Rice 2001). Rice (2001) determined that for every kilogram of shellfish meat harvested removed on average 16.8g of nitrogen. These benefits are considered to be important to marine habitats and can prevent symptoms of eutrophication (Jackson et al. 2001).

Seagrasses, such as eelgrass *Zostera marina,* also provide valuable ecosystem services by oxygenating the water through photosynthesis, improving water quality from nutrient uptake, capturing excess carbon from the environment, providing essential habitats and shelter for other organisms, reducing erosion and increasing the stability of the coast (Costanza et al. 1997; Hemminga and Duarte 2000). The decline of eelgrass has been attributed to the presence of the EGC. When EGC are foraging for prey and digging for shelter, the rhizomes of eelgrass can become damaged from these behaviors (Matheson et al. 2016).

When populations of EGC become too dense, larval forms of marine organisms such as barnacles, urchins and bivalves are unable to settle; and therefore are unable to become established within the environment (Welch 1968). Not only has the EGC demonstrated competition for resources and living space, but it also has been shown to prey upon the native shore crab *Hemigrapsus oregonensis* (Grosholz and Ruiz 1996). The EGC has been associated with the decline in population abundance of *H. oregonensis* in California (Grosholz et al. 2000). For example, Bodega Harbor located in San Francisco, has been identified as having a decrease abundance of clam and native crab species because the EGC has reached a density of 0.2 crabs/m^2 (Grosholz et al. 2000). As a result, a large population of green crabs can significantly reduce the biodiversity of an area which can lead to an “invasion meltdown”. “Invasion meltdown” occurs when NIS alter habitats that causes significant changes such as the reduction of biodiversity, and therefore can initiate a chain reaction. For example, the non-native quagga mussels in the Great Lakes depleted the water column of nutrients. The lack of nutrients caused the benthic algae to bloom out of control, and then die off in massive quantities. The dying and decomposition of the algae depleted the available oxygen from the system, and created favorable conditions for botulism to spread in the ecosystem and contaminate food webs (Ricciardi 2001).

FACTORS DRIVING ESTABLISHMENT AND SPREAD

There are three major factors that are required for the successful establishment of NIS in novel ranges (Torchin et al. 2003).

- Reduced competition
- Better environmental conditions
- Absence of predation

Better environmental conditions can include an increase of food resources, a suitable opening within a habitat, water quality and/or temperatures that are more suitable for the invader and results in successful reproduction. Additionally, for the green crab, the effects of weather conditions such as ENSO and El Niño, creating strong and warm northward shelf currents have been correlated with the success of transporting EGC larvae to other regions of the PNW. The green crab's planktonic larval stage in combination with strong ocean currents can rapidly transport EGC larvae to novel regions (Behrens Yamada and Kosro 2010; Behrens Yamada et al. 2015).

Due to the EGC ability to tolerate a wide range of water quality, conditions and salinity concentrations, microhabitats within estuaries may provide refuge and act as "incubators" for the green crab (Cohen et al. 1995). Therefore, estuaries such as Coos Bay may provide refuge for the green crab to establish and develop self-reproducing populations.

ENEMY/PREDATOR RELEASE HYPOTHESIS

The predator release hypothesis suggests that the lack of natural predators to prevent NIS populations from dominating an ecosystem can be a significant factor for NIS becoming permanently established. Introduced species can reach unusually high population densities and outcompete native species for resources and reduce their population abundances (Grosholz et al. 2000; Torchin et al. 2003). The absence of natural predators includes the lack of native parasites seeking out the EGC as a host. In the green crab's native range, parasites have been identified as the primary factor responsible for regulating the natural population. Currently, researchers speculate that parasites and hosts share a life history and co-evolve together. Therefore, parasites of a novel region may not recognize the green crab as a potential host due to the lack of co-evolution and previous parasite/host interactions (Torchin et al. 2001; Torchin et al. 2003; Blakeslee et al. 2015). However, new research reveals the lack of coevolution may also demonstrate a higher potential of susceptibility to parasitic infections in the EGC populations along the US Atlantic coast (Blakeslee et al. 2020).

LIMB MORPHOLOGY AND FUNCTIONS OF AUTOTOMY

MAJOR AND MINOR CHELAE

The chelipeds of the EGC are heterochelous resulting in differentiated morphology between the two chelae as a major and minor claw appendage. The major chela is primarily used for agonistic behaviors and encounters. The major chela, also referred to as the crusher claw, is lined with molariform teeth formations and is effective for crushing mollusk shells. The major chela has more force and strength compared to the minor.

The minor chela is equipped with cutting teeth. Also known as the cutter claw, the minor chela is used to capture prey and grooming functions. The cutter claw is overall slender, longer and thinner than the stout crusher claw (see Figure 1).

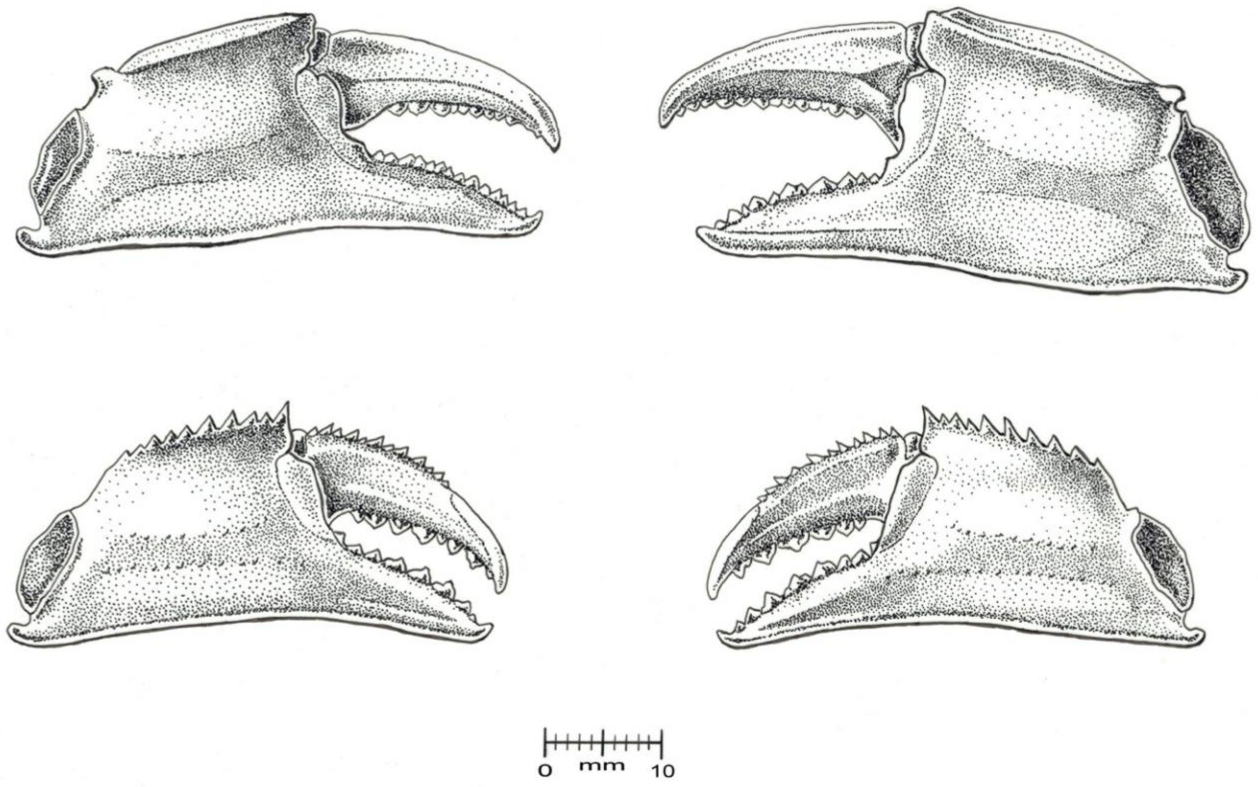

Figure 1: Showing heterochelous claws of Carcinus maenas (top) compared to monomorphic claws of Metacarcinus magister (bottom). The minor or cutter claw of C. maenas (top left) is smaller than the major or cutter claw (top right). Both claws represent similar sized crabs ~110g. Figure used with permission and taken from Behrens Yamada et al. (2010).

Not only are the claws of EGC heterochelous but are also sexually dimorphic. Studies have shown that different growth strategies are utilized to regenerate chelae between males and females. Accelerated growth occurs when a male EGC is regenerating a major chela in the development of reverse handedness (Juanes et al. 2008). The chelae of male EGC tend to be larger than that of their female counterparts (Mariappan et al. 2000). Additionally, these physiological differences in chelae are less stark in females "*… where both chelae are more cutter-like."* (Elner 1980).

Stronger claws enable crabs to consume more prey at a faster speed, and EGC chelae have a competitive mechanical advantage over *M. magister* chelae of similar sized individuals (McDonald et al. 2001). *M. magister*, also referred to as Dungeness crabs, have monomorphic claws that are thinner and have a mechanical advantage of 0.26 compared to EGC heterochelous mechanical advantage of 0.26 for the minor and 0.36 for major chela (Warner et al. 1982). Researchers have found that the duality of EGC claws may provide a competitive advantage to consume a wider range of prey compared to the weaker monomorphic claws of the Dungeness crab (Behrens Yamada et al. 2010).

Growth in crustaceans is discontinuous and requires the shedding of the highly mineralized exoskeleton, referred to as ecdysis (molting). Generally, green crabs can molt multiple times (10-11 times) before reaching their first year of age, and can regenerate a missing limb in a single molt (Crothers 1968). After the first year of age, molting may occur as often as twice a year in warm water conditions (Carlisle 1957). The frequency of molting is directly linked to limb regeneration. The regeneration of missing limbs may take at least three separate molting events for older EGC (Carlisle 1957; McVean and Findlay 1979). Therefore, limb loss serves as a record of an attack for at least two subsequent molts (Smith and Hines 1991; Torchin et al. 2001) Additionally, if an appendage is lost after anecdysis (terminal molt) has occurred, then limb regeneration cannot occur and the lost appendage is a permanent condition (Carlisle 1957; Emberts et al. 2019). EGC found in their native ranges have been recorded as reaching terminal molt when the measurement of their carapaces' width is between 70-75mm (Carlisle 1957; McVean 1976). After reaching anecdysis, it stands to reason that limb loss will continue to accumulate until the death of the crab. Furthermore, older crabs are unable to regenerate limbs as frequently compared to juvenile crabs (Carlisle 1957). Therefore, limb loss would increase with the size of carapace width.

AGONISTIC BEHAVIORS AND INTRASPECIFIC INTERACTIONS

Behavioral encounters, such as highly ritualized mating sequences, often include the use of chelae movements. Communication amongst crustaceans include the display and movement of chelae and antennae (Mariappan et al. 2000). Therefore, the loss of a chela may result in a handicap for finding a mate (Sekkelsten 1988; Mariappan et al. 2000). The display and possession of the major chela can trigger aggression in males and has been speculated to result in the loss of appendages (Mariappan et al. 2000). However, some researchers believe that intraspecific interactions are highly ritualized and almost never result in autotomy (McVean 1982; Abelló et al. 1994). Chelae were not observed to be lost/injured as a result from intraspecific EGC male competitions that were conducted during laboratory studies by Abelló et al. (1994). Modeling experiments conducted by Lee and Seed (1992) stated that EGC display their major chela, and the size of the chela was a visual indicator for establishing dominance amongst the male competitors. The utilization of visual display occurs throughout the animal kingdom, such as observed in peacocks and a vast array of other species in lieu of physical combat. For example, posturing and the visual display of chelipeds of fiddler crabs typically do not result in injurious combat (Crane 1966). The major chela is the most important appendage used for signaling and sexual selection (Mariappan et al. 2000). As a result, visual displays and demonstrations of chelae size may not result in injurious outcomes as frequently as once predicted, and therefore may not be a significant cause for limb loss in EGC.

Courtship behavior and the mating of EGC include a period of time when the female crab has recently molted, and her shell is still soft. At this time, the female crab is the most vulnerable and depends upon the protection from the male while her shell is hardening (Carlisle 1957; Lee and Seed 1992). Researchers observed handicapped EGC males, individuals missing a cheliped, experienced difficulty holding females in a pre-copula position. Additionally, field studies indicated a higher frequency of intact males mating with females, rather than handicapped males (Sekkelsten 1988). Limb loss due to intraspecific encounters are presumed to be rare events because limb loss, especially that of a cheliped, reduces a male crabs' fitness (McVean 1982). Loss of one or both chelipeds is equivalent to genetic mortality for adult male EGCs resulting in a significant decreased ability and likelihood to reproduce.

LIMB AUTOTOMY IN CRABS

Limb autotomy is defined as the self-amputation of an appendage that occurs at a predetermined breakage point (Wood and Wood 1932; McVean 1982). Autotomy in crustaceans can occur for the following three reasons:

- Escape from predation
- Non-predatory entrapment

- Wound limitation

Escape from predation is the primary premise behind the evolution of the mechanism for autotomy. The sacrificing of a limb is a highly evolved predator avoidance and defense mechanism.

Non-predatory entrapment refers to other conditions that do not include a predator responsible for the confinement. Most common example is an arthropod experiencing difficulty crawling out of an old exoskeleton during the molting process. Occasionally, arthropods may experience an unsuccessful molt where a limb may become stuck (Maginnis 2008). The EGC has been observed autotomizing three legs to free itself from a molt gone poorly (Wood and Wood 1932).

Self-amputation of a damaged limb can also reduce the cost of injury, possibly death and/or prevent blood loss and infection by limiting the effects of the wound (McVean 1982; Emberts et al. 2019). After a limb has been severed, a valve on the remaining tissue is able to minimize the loss of bodily fluid. Additionally, stopping the flow of bodily fluid also eliminates the spread of water-borne cues that can attract other predators (McVean and Findlay 1979). Sacrificing a limb can provide the EGC with an instantaneous benefit of escape, but with a longer-term cost of energy and resources needed for limb regeneration. Chelipeds can account for more than 30% of a green crab's total body weight; and therefore, may require a significant amount of energy diverted towards the regeneration efforts of the limb (Lee and Seed 1992). Researchers propose that regeneration of lost chelipeds require additional energy input and are referred to as "regeneration load" (Mariappan et al. 2000).

Other impacts to the green crab as a result of limb loss include the following: an increase in vulnerability to both inter and intraspecific species interactions, challenges in mating success and/or communication, and the reduction in foraging efficiency (Sekkelsten 1988). The loss of a cheliped has been observed to alter foraging and feeding behaviors (Delaney et al. 2011; Flynn et al. 2015; Emberts et al. 2019). The loss of a chela can reduce the foraging efficiency and potentially leave the crab handicapped until a new chela can be regenerated. Moreover, crustaceans with missing chelipeds have been observed to feed upon smaller, soft bodied and easily accessible prey when compared to intact crabs not missing a cheliped (Flynn et al. 2015).

Chelae are not only used for foraging and feeding behaviors but are also essential for defense and attacking engagements. Chelae can be used to shield the crab from an attack or pinch an attacker/prey when necessary. When a predator seizes a crab by an appendage, that limb can be autotomized to facilitate the crabs escape (Wasson and Lyon 2005). Predators can become preoccupied with handling and feeding upon the sacrificed limb and may not resume the pursuit of the crab (Emberts et al. 2019).

Injured EGC, such as those individuals missing chelipeds, are thought to have fewer ecological and economic impacts directly on the ecosystem. Research demonstrates that green crabs with missing limbs exhibit reduced feeding consumption by 21% (Delaney et al. 2011). The loss of the major chela has a negative impact on the EGC ability to feed upon hard shelled prey such as oysters, demonstrating around 98-100% reduced feeding rate. The lower feeding rates were compared to intact or crabs missing only the minor chela (Flynn et al. 2015). However, Flynn et al. (2015) found that feeding rates on soft-shell clams were reduced for only the first 24-hour period for EGC missing a major chela. Therefore, Flynn et al. (2015) suggested that the green crabs are able to prey upon clams despite the loss of the crusher claw. Other researchers have found that chelae loss did not have a substantial impact on the EGC ability to capture mussels or other soft-shelled prey because EGC are able to handle prey with their mandibles (Behrens Yamada et al. 2010).

BIOTIC RESISTANCE

Communities that are rich in species diversity may provide a stronger biotic resistance to NIS becoming established as a result from reduced availability of a limiting resource (e.g. shelter and food) (Stachowicz et al. 1999), or an abundant population of native predators and/or resilient competitors (Crawley et al. 1999). These types of interactions and the various factors that determine the “invasiveness” (e.g. spread, population abundance, condition of the environment, demographic rates) of NIS remains to be resolved (DeRivera et al. 2005).

Population densities of EGC are higher in microhabitats that lack a stable presence of larger native crabs (Hunt and Behrens Yamada 2003; Jensen et al. 2007). Green crabs are found residing in marginal microhabitats located higher on the shore in the estuaries of Oregon, Washington, and the west coast inlets along Vancouver Island. Comparatively, larger native crabs such as *Metacarcinus magister* (Dungeness), *Cancer productus* (red rock), *Cancer antennarius* (brown rock) and *Cancer gracilis* (graceful) do not reside in these microhabitats due to intolerances of low salinity and warmer temperatures. The lack of biotic resistance, in the form of large native crabs, provides a habitat and opportunity for the EGC to exploit.

Research conducted by Hunt and Behrens Yamada (2003) identified areas where populations of red rock crab overlapped with EGC. Red rock crabs provide a natural biotic resistance which has the capacity to reduce the abundance of the EGC. During their laboratory trials, Hunt and Behrens Yamada (2003) observed that the survival rate of the green crab was poor in the presence of a larger sized red rock crab. Additionally, during these trials, EGC lost claws and legs (Hunt and Behrens Yamada 2003).

In this study we investigated whether limb loss can be used as an indicator of interspecific competition and predation in order to identify areas that may be exhibiting biotic resistance. By identifying areas with biotic resistance, Coos Bay managers can then make decisions regarding recreational and commercial harvesting limits to maintain a sustainable population of native crabs, and therefore reduce the numbers of EGC.

HYPOTHESIS

Previous research has indicated that large-sized native crabs such as *Cancer productus* and *Metacarcinus magister*, prey on smaller EGC individuals (Hunt and Behrens Yamada 2003; McDonald 2006; Jensen et al. 2007). Therefore, we expect the incidence of autotomy in the EGC to be positively correlated with populations of large native crabs as a result of the increased probability of interspecific interactions. We also expect to find some evidence of autotomy in dense populations of EGC as a result from intraspecific interactions. However, previous research indicates that intraspecific interactions among EGC rarely result in limb loss, and intraspecific displays of aggression are typically for mating contests. Therefore, we hypothesize that areas with high densities of EGC will have less autotomy than areas with high densities of other crab species. Additionally, we expect to find a positive relationship of limb loss to increase with carapace width (CW) of the EGC as found in previous research studies.

METHODS

DATA COLLECTION

Working as part of a research team located in Coos Bay, Oregon, we set traps and collected crabs from the intertidal zone. For this study, we collected green crabs from several different collection sites located in Coos Bay from the year 2002 to 2020. Remnants of fish were placed into plastic bait containers and were added to the Fukui traps. Fukui traps (measuring 63x46x23 cm) have mesh openings of 1.6cm. There are two separate entry points into the trap located at opposite ends of the trap. The two openings of the trap are expandable slits that measure 46cm in length. These traps were used to collect adult sized crabs having a minimum of 40mm CW. Modified minnow traps, also referred to as crayfish traps, have a 6cm opening (measuring 21x37cm) and 0.5cm mesh were used to collect "young-of-the-year" or "age zero" green crabs. Traps were set during low tide and allowed to soak for a 24-hour period before retrieval. Collection efforts occurred predominantly during the summer months of June, July, and August and spanned across the course of a five-day period of each month. This collection method is replicated for each of three months during the summer. “Young-of-the-year” green crabs were collected at the end of their first growing season, during September or early October using crayfish/minnow traps instead of the Fukui traps.

After collection, all crabs were processed, and individual characteristics were recorded. The details of each individual crab (e.g., CW, weight, sex, color, and missing limbs) as well as the water temperature and salinity for each collection site were also recorded. The majority of the data used in this analysis (n= 5116, representing 94% of total data) was collected during the years 2016-2020. Data from the year 2002-2015 was also included in this analysis; however, the number of green crabs collected was smaller (n=325) for this period.

ANALYSIS

We focused on data from sites that were located within Coos estuary from 2002-2020 that were collected by Sylvia Behrens Yamada, Shon Schooler and others. In addition to the data set compiled for 2020, other information used in this analysis was retrieved from the annual technical reports (Behrens Yamada et al. 2018; Behrens Yamada et al. 2019; Schooler et al. 2020). The annual technical reports are generated from the dataset that is accumulated annually and can be retrieved from ScholarsArchive@OSU (Behrens Yamada et al. 2019; Behrens Yamada et al. 2020). Microsoft Excel and Pivot Table software were used to facilitate the data analysis and generate the graphs presented in this study. Statically significant differences between the regions in the estuary were found using an ANOVA performed by the R statistical package, followed by Tukey’s Honest Significant Difference (Tukey’s HSD).

Total number of EGC evaluated for this study n=5441, of which 3963 (72.8%) were male and 1478 (27.2%) were female. All EGC were grouped into size classes in increments of 5.0mm, and only size classes that had at least 10 EGC were included in the regression analysis.

For the graphs reflecting biotic resistance (Figures 3, 4 and table 5), we conducted our analysis by using the mean catch per unit effort (CPUE) located in the annual EGC monitoring technical report created by the South Slough National Estuarine Research Reserve (SSNERR) (Behrens Yamada et al. 2018; Behrens Yamada et al. 2019; Schooler et al. 2020). We analyzed the limb loss data of the green crab (Behrens Yamada et al. 2020) in association with the bycatch of native crabs (*C. productus, M. magister, H. oregonensis, and H. nudus*) from collection sites located within Coos Bay. We focused on six specific sites in Coos Bay from the last three years

(2018-2020) because these sites had data for every year and sufficient numbers of EGC for our analysis. This includes two from each region of the estuary reflecting upper, middle and lower regions. Coos History Museum and Isthmus Slough are in the upper regions of the estuary. Trans Pacific Lane and Joe Ney are located in the middle regions, and the lower regions are Indian Point North and Metcalf Marsh. The delineation regarding the classification of upper, middle, and lower estuary regions were taken directly from the annual monitoring technical report of 2020 provided by SSNERR (Schooler et al. 2020). These locations are shown on the map as Figure 2.

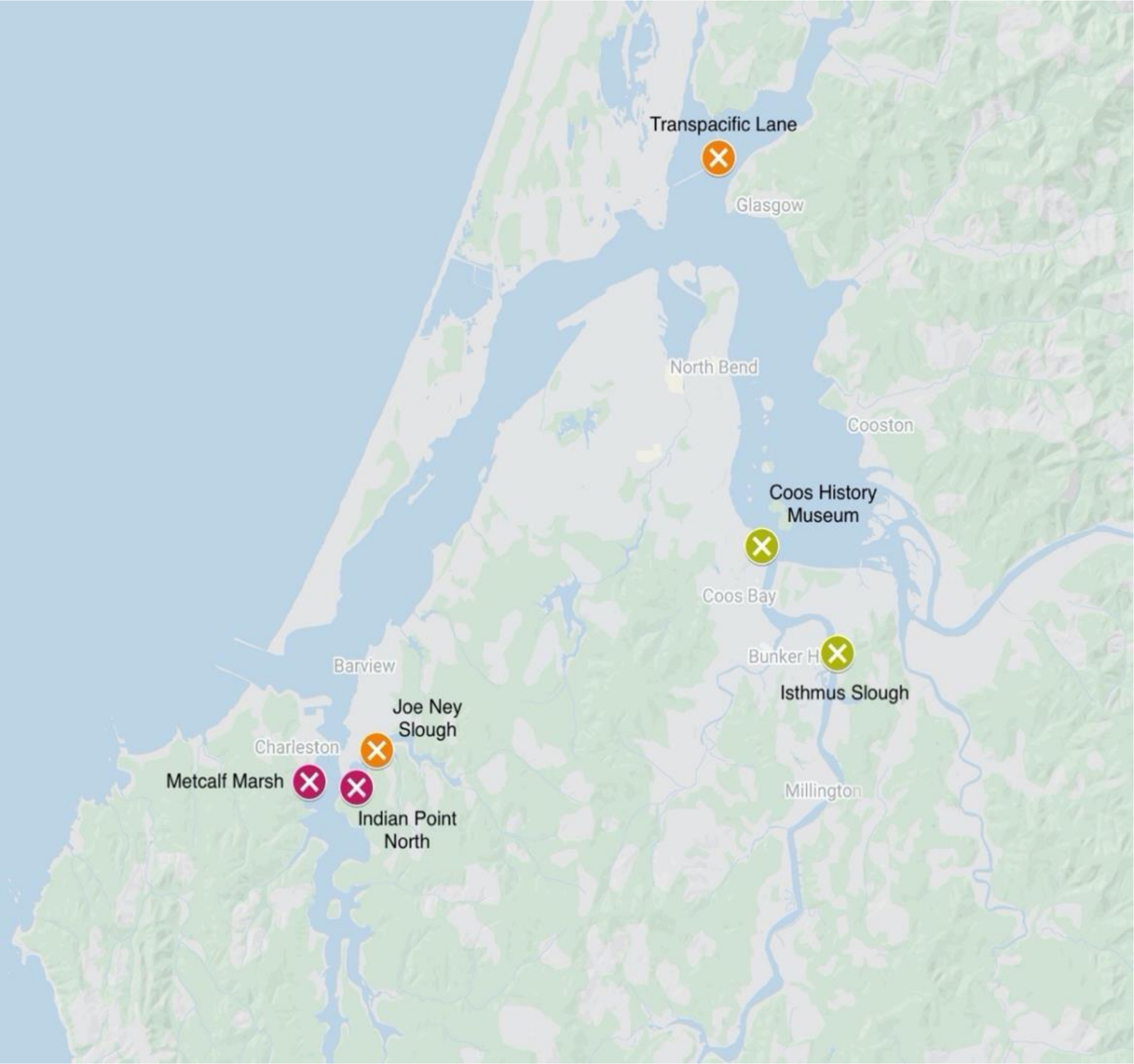

Figure 2: Red markers indicate the highest incidence of EGC limb loss. Orange markers indicate moderate incidence of limb loss and green markers indicate the lowest incidence EGC limb loss. See table 6 for details.

RESULTS AND DISCUSSION

LIMB LOSS AS BIOTIC RESISTANCE INDICATOR

A statistical analysis of variance was conducted for the regions classified as upper, middle, and lower estuary for comparing the averages of limb loss. This shows statistically significant differences in EGC limb loss between all three regions of Coos estuary. The difference between middle and lower was 16.7% ($p<0.05$), between upper and lower regions was 22.6% ($p<0.05$) and between upper and middle regions was 5.9% ($p<0.05$). Different regions exhibit different incidences of EGC limb loss. To further investigate these differences, we compared the percentage of EGC limb loss to the percentage of EGC caught at each site. These results are represented in Figure 3.

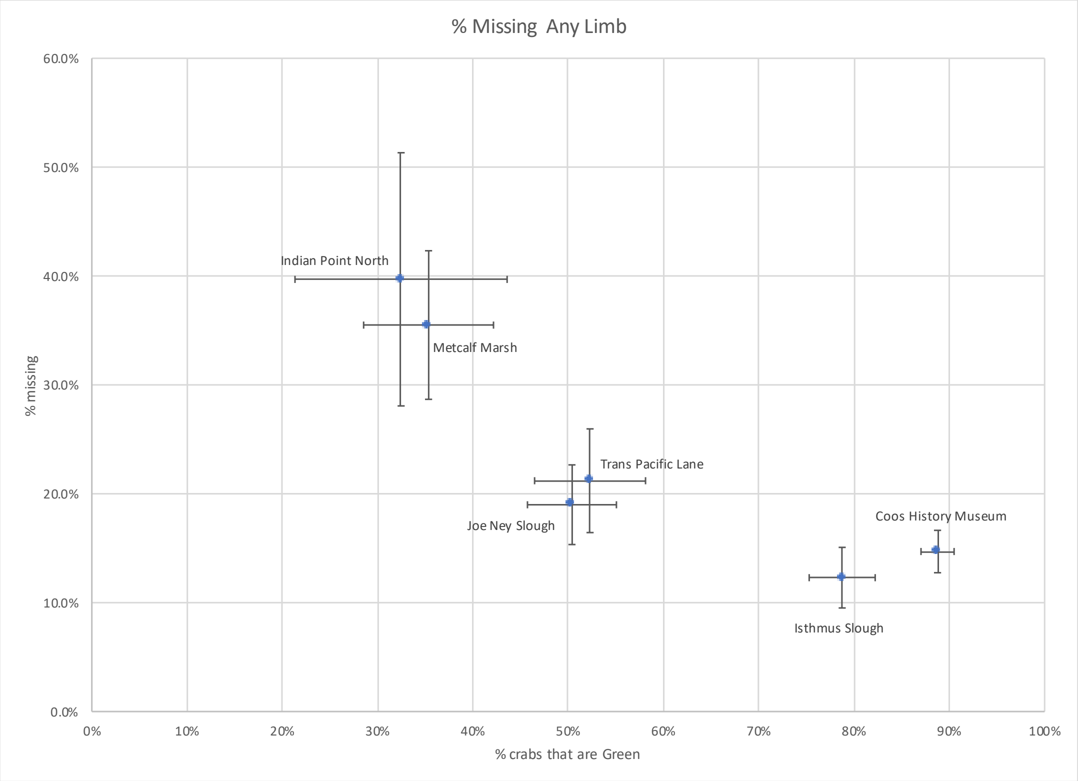

Figure 3: Percentage of EGC missing any limbs vs the percentage of crabs caught that were EGC. Indian Point North and Metcalf Marsh are considered lower to middle estuary and native crabs are caught as bycatch. Coos History Museum and Isthmus Slough are middle and upper parts of the estuary and exhibit a higher population of EGC with fewer native crabs. Error bars represent 95% confidence intervals.

From our data analysis we found a higher incidence of limb loss in areas where other native crabs such as *C. productus* and *M. magister* were caught as bycatch and therefore exhibit a stronger presence of biotic resistance. Additionally, the areas that have higher densities of EGC, such as Coos History Museum and Isthmus Slough have fewer native crabs and demonstrated a lower incidence of limb loss. To further investigate, we also compared the percentage of EGC limb loss to CPUE for green crabs (as a measure of EGC population) for each site. These results are shown in Figure 4.

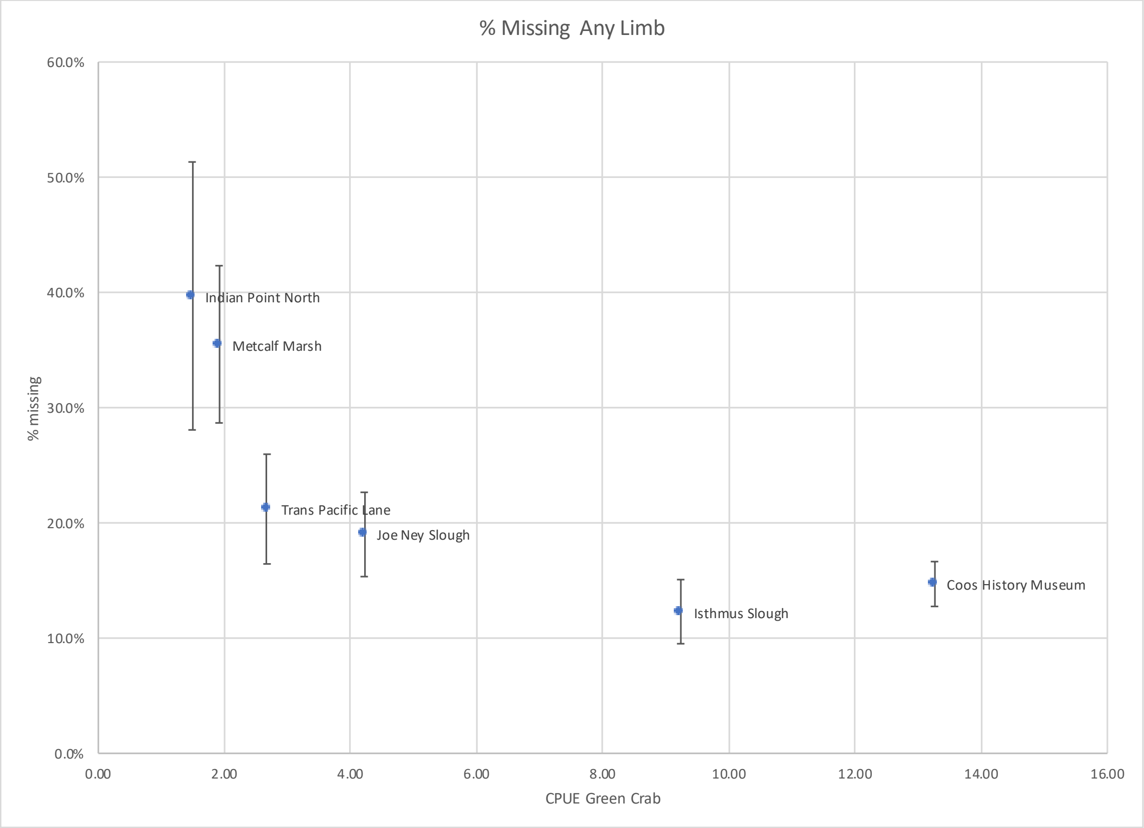

Figure 4: Percentage EGC limb loss versus the CPUE of EGC. Highest incidences of limb loss occur in lower parts of the estuary which are Indian Point North and Metcalf Marsh. Error bars represent 95% confidence intervals

Location	total # crabs	CPUE Green	%Green (vs native crabs)	% Missing Any Limb
Indian Point North	68	1.49	32.5%	39.7%
Metcalf Marsh	189	1.92	35.3%	35.5%
Trans Pacific Lane	283	2.67	52.3%	21.2%
Joe Ney Slough	441	4.22	50.4%	19.0%
Coos History Museum	1269	13.26	88.8%	14.7%
Isthmus Slough	536	9.24	78.8%	12.3%

Table 5: CPUE of EGC vs native crabs. Percentage of limb loss is reflected for EGC only. This includes CPUE data from the years 2018-2020 taken from SSNERR reports.

Lower regions of the Coos estuary, namely Indian Point North and Metcalf Marsh have a higher CPUE of other native crabs at 67.5% and 64.7% respectively when compared to the upper regions such as Coos History Museum and Isthmus Slough 11.25% and 21.2% respectively. Native crabs, such as *Cancer productus* generally prefer a higher concentration of salinity and most individuals are found in the lower regions of the estuary (Hunt and Behrens Yamada 2003). Additionally, these two locations also have the highest incidence of EGC limb loss at 39.7% for Indian Point North and 35.5% for Metcalf Marsh. This strongly supports our hypothesis that limb loss of EGC increases in areas that include other native crabs such as *C. productus* and *M. magister* as a result from predation and competition events. Additionally, we can infer that the population density of EGC for Coos History Museum and Isthmus Slough were not dense enough to result in significant intraspecific confrontations to result in a high incidence of limb loss. The middle regions of the estuary, Trans Pacific Lane and Joe Ney Slough have CPUE of roughly half EGC and half native crabs, and therefore demonstrate an intermediate percentage of limb loss.

PATTERNS OF AUTOTOMY

From our analysis we are able to predict the percentage of limb loss associated with the CW of the EGC using our regression formula:

$\%\text{limb loss} = 0.0023 * (\text{CWmm})$

Autotomy in smaller EGC individuals was observed less frequently possibly because predation attacks probably resulted in mortality instead of limb loss (Delaney et al. 2011). It is reasonable and plausible that smaller crabs are easily preyed upon whereas larger crabs may escape predation and suffer limb loss from predators. This supports our findings that EGCs measuring 35mm or smaller have roughly <10% limb loss. Additionally, previous research also supports that smaller crabs (less than one year of age) may be able to regenerate a complete limb in a single molt (Carlisle 1957). The frequency of autotomy of the EGC is predominately the result of predation and competition events that can be measured as a form of interspecific pressures at a community level (Smith and Hines 1991; Delaney et al. 2011).

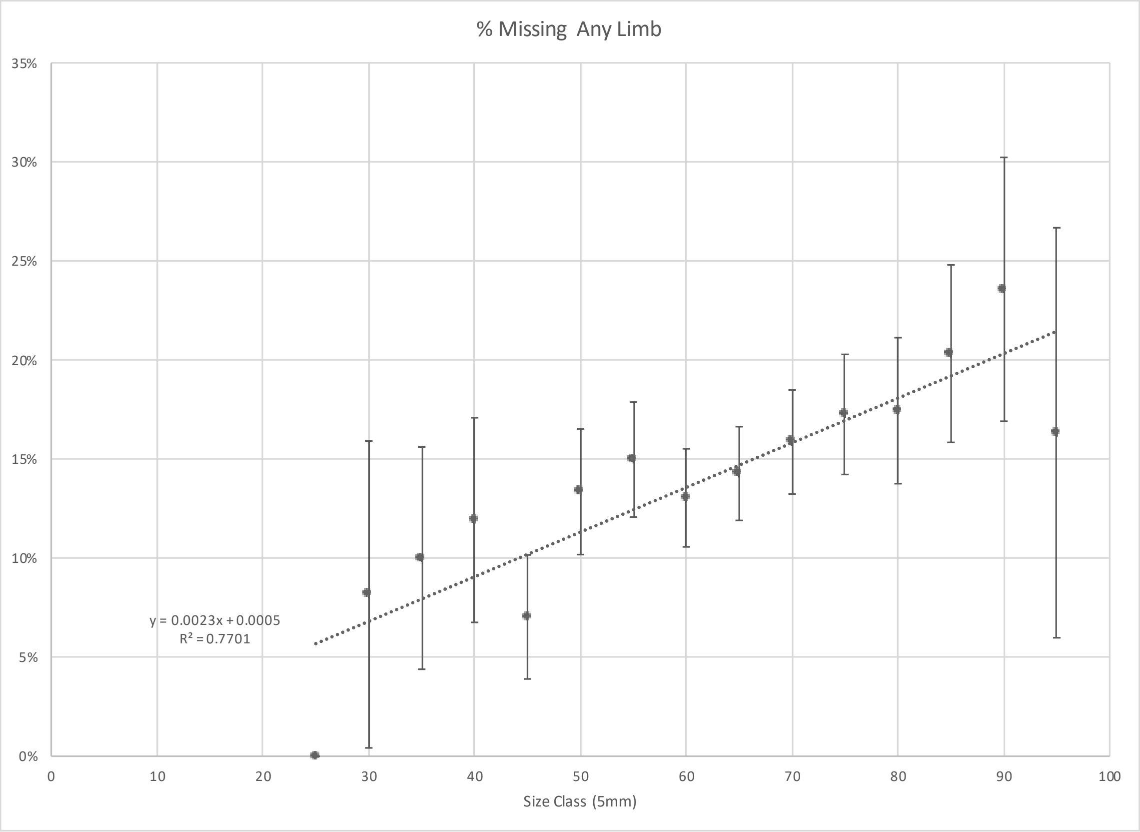

Figure 6: Linear regression for EGC CW and percentage of limb loss. Error bars represent 95% confidence intervals.

FUTURE SCIENTIFIC RESEARCH

Predation pressure experiments that focus upon quantifying the various mechanisms would help to understand these mechanisms more thoroughly. Additional research to determine how dense an EGC population needs to be to result in limb loss from intraspecific interactions may also be useful. This would assist researchers in comprehending the limits for intraspecific competition and allow for better utilization of limb loss as an indicator for biotic resistance. Additional work taking a biogeographical experimental approach would also be informative. According to the literature review, there is a substantial amount of observational biogeographical research, and more experimental work is needed to address some knowledge gaps. Embedding research programs within a broader cultural context can open up more possibilities for solutions and prevent singular mindedness and extreme reductionism.

POLICY IMPLICATIONS

Currently there is no federal legal legislation for addressing and managing harmful non-indigenous species (NIS), which leaves a regulatory void (Keller et al. 2015). For example, the Endangered Species Act and the Lacey Act provide legal frameworks for addressing issues regarding illegal poaching and provide protections for population segments of endangered species. However, there is not a comparable legal legislation equivalent for managing and regulating NIS at the national level. The lack of a broad and legal framework, that spans across multiple sectors such as aquaculture and fisheries, poses challenges for implementing a comprehensive and cohesive policy for controlling and managing NIS. The purpose of a legislation would enable researchers and wildlife managers to work together to address NIS as a single general problem as a nation instead of a series of local and regional issues working independently. Organization at a national level would allow for funding to enlist smaller community organizations to assist in managing and controlling NIS.

During the 1990’s, Coos county experienced a high rate of unemployment between 7-9% (Huppert et al. 2003) and was a symptom of deindustrialization after the North Bend sawmill closed. There was also an increased proportion of residents in Coos county receiving transfer payments, such as Social Security, pensions, and other forms of revenue from non-wages or non-salary incomes from 22-28% to 42-52% (Huppert et al. 2003). This indicates that many of the residents of Coos Bay are retired, or not part of the workforce. The lack of employment opportunities for the younger population forces them to move into other areas with more opportunities. Additionally, Huppert et al. (2003) research indicated the residents of Coos Bay considered economic issues to be more important priorities than environmental threats. These values may be the direct result of inadequate employment opportunities available to the residents of the Coos Bay. Therefore, providing some type of economic incentive to the general public of Coos Bay to assist in environmental issues would be beneficial to all parties and stakeholders and encourage more public participation.

SUGGESTIONS FOR MANAGEMENT AND CONTROL

Increasing public awareness is the first step to addressing NIS. While researchers, state fish and wildlife managers, and federal agency officials are familiar with the potential negative impacts from NIS becoming pests, the majority of the general public remain uninformed. From a personal observation communicating with the local residents of Coos Bay, many of them believe that the native red rock crab is an invasive species. Efforts to change that perception and focus on the EGC would increase public awareness. Social media platforms, such as *TikTok* and YouTube videos are effective and cost-efficient methods for disseminating critical information to a wider audience regarding the status and potential impacts from NIS. In order to engage and inform the younger members of society, an increase in digital outreach efforts is required. Engagement and involvement at the community level encourages members of society to participate and take ownership- not only for their personal actions but also for their environment.

Current management plans for Coos Bay could benefit from an increase of direct help from volunteers and citizens for detecting, monitoring, and culling of the EGC. For example, using volunteers has allowed invasive lionfish management to occur on a larger scale and is more cost-efficient then using scientists and managers alone (Anderson et al. 2017). Currently, the state of Washington has an organized team of volunteers to assist in monitoring and early detection of EGC (WSG 2020).

In response to the lionfish invasion, culling derbies were held to assist in the removal of lionfish from key areas (Green et al. 2012). These types of events can bring a community together and empower individuals to take ownership of their actions and environment. Additionally, more details and data on the EGC population can be collected during the derbies. Having large events can raise, promote and increase public awareness regarding not only the EGC situation but also inform the general public regarding other current/potential threats and risks to environmentally sensitive habitats. As indicated from our study culling derbies would provide the most impact in areas such as Coos History Museum and Isthmus Slough where fewer native crabs are found. Snorkeling and diving efforts should be incorporated into the culling efforts to ensure as many EGC are removed as possible.

Economic incentive could be in the form of prizes offered to individuals collecting the most green crabs, or the biggest crab in the form of a competition contest. Prizes offered could be presented in cash or a product form procured from local businesses and corporate donations, and/or complimentary shellfish collecting permit/license from Oregon Fish and Wildlife Department. Other incentives include hosting a green crab boil using the collected EGC to provide participants with an opportunity to taste the EGC since it is considered a delicacy in other countries and cultures (Klassen and Locke 2007). A movement called “invasivore” is gaining momentum and is one example of maximizing the benefits from the establishment of invasive species. For example, a grant was awarded to a marine nonprofit organization in Maine to develop a green crab fishery (Chase 2018 Sep 19).

These types of incentives help to engage and bring additional awareness to the entire community. Encouraging local residents to care is the first step to having people take ownership and responsibility for their environment. As a result from public engagement, removal and culling events have been effective in reducing population numbers and densities of the invasive lionfish. Green et al. (2017) determined that culling derbies were responsible for reducing lionfish densities by 52%.

Creating and deploying brooding traps designed to provide a secluded maternity habitat for ovigerous females may be a useful control method (Behrens Yamada 2001). These traps can be placed in strategic areas where ovigerous females have been located previously and monitored a couple of times a week during breeding seasons. Research indicates that the developing eggs of EGC are less tolerant of low salinities and need temperatures between 18°-10°C (Broekhuysen 1937; Crothers 1968) which are factors to consider when deploying brooding traps. By removing ovigerous females from the population before the eggs can hatch will help to destabilize reproducing colonies of EGC in specific and vulnerable areas such as Coos History Museum and Isthmus Slough. This strategy may be useful to keep the population of EGC under control by potentially removing thousands of larvae before they hatch and disperse.

Additional management and control strategies include temporary restrictions and additional limitations on recreational and commercial harvesting of native crab species, such as *C. productus* and *M. magister* in Coos Bay. Currently in Oregon, the bag limit for recreational harvesting of red rock crabs is set at 24 crabs of any size and sex (ODFW 2019 Dec 6) which is significantly greater than neighboring states (BC 4, WA 6 and AK 0), except for California has a bag limit of 35. Implementing a more conservative bag limit on native crabs, particularly in areas that have populations overlapping with EGC, namely Indian Point North, Metcalf Marsh, Trans Pacific Lane, and Joe Ney will help protect the larger native crabs. Large crabs grow slowly

(Behrens Yamada and Groth 2016), and therefore protecting those older individuals is critical for maintaining a biotic defense against EGC. Protecting large *C. productus* males which tend to be more aggressive, will facilitate a stronger presence of competition for both resources and the utilization of habitat space. Native crab species can limit the distribution of the EGC (DeRivera et al. 2005), and therefore require careful management of recreational and commercial harvesting activities. By temporarily suspending the harvesting activities on these two native crab species will facilitate the increase of the natural population levels to provide a stronger natural biotic resistance against the EGC invasion.

More importantly, the management of NIS needs to be applied as a steady and constant pressure especially in the situation of the EGC. Enlisting a dedicated and organized team of volunteers can facilitate this process. Management and control efforts can be undermined from re-invasion around the periphery of managed areas. In addition, linkages to landscape that enhances structural or functional connectivity from one ecotone to another can facilitate biodiversity (Glen et al. 2013). For example, increasing structural habitat to facilitate a stronger population of the native shore crab, *Hemigrapsus oregonensis*, would also increase the natural biotic resistance in the microhabitats. These smaller shore crabs not only will compete for resources against similar sized EGC but will also prey upon the smaller green crabs. Encouragement of native species such as shorebirds in these microhabitats would also provide additional biotic resistance, since small EGC can serve as prey.

FINAL SYNTHESIS

The worldwide spread and dispersal of non-native species are the result from anthropomorphic activities (DeRivera et al. 2005); such as globalization, building of canals to connect waterways, and the multitude of alterations that humans have utilized and modified the environment to better suit our needs (industrialization, agriculture, natural resource extraction, etc.). Globalization has connected continents and countries and bypassed geographical barriers that previously kept many species segregated. It is inaccurate to refer to NIS as “invaders or invasive species” because we (humans) have brought them here regardless of our intentions.

As the effects from climate change increase and become more urgent and evident, we can expect to encounter an increase in wicked problems, such as more NIS becoming more prevalent. If we could snap our fingers and magically eradicate the EGC populations of the PNW, it would only serve as a temporary band-aid. New larvae of EGC would drift in via ocean currents from other established populations from the south such as San Francisco Bay, and serve as new propagules to re-seed populations. Unless water temperatures are reduced, and freezing temperatures are returned with some kind of frequency- then we need to acknowledge the simple truth that EGC are here to stay. Unfortunately, there is not a magic silver bullet to easily remedy the problem, nor is there a single solution. Wicked problems such as NIS require a multi-faceted strategy for management and control. However, there are several accessible and affordable small-scale operations that when combined together can be effective options to control and manage the EGC population.

In closing, NIS becoming pests and causing negative environmental and economic impacts are a symptom of a bigger problem. Climate change is having a serious impact on the planet. Rapidly changing ecosystems, as a result from anthropogenic activities are occurring too quickly for individual organisms to adapt and too many drastic changes for most species to evolve. Addressing the bigger picture of climate change will help to rectify a series of other wicked problems, such as the declining wild salmon population and out-of-control wildfires- just to name a few. It is important to remember how the butterfly effect occurs in sensitive and complex non-linear systems.

REFERENCES

Abelló P, Warman CG, Reid DG, Naylor E. 1994. Chela loss in the shore crab *Carcinus maenas* (Crustacea: Brachyura) and its effect on mating success. Marine Biology. 121(2):247–252. doi:10.1007/BF00346732. https://doi.org/10.1007/BF00346732.

Andersen MC, Adams H, Hope B, Powell M. 2004. Risk assessment for invasive species. Risk Analysis: An International Journal. 24(4):787–793.

Anderson LG, Chapman JK, Escontrela D, Gough CL. 2017. The role of conservation volunteers in the detection, monitoring and management of invasive alien lionfish. Management of Biological Invasions. 8(4):589–598.

Behrens Yamada S. 2001. Global invader: the European green crab. Oregon Sea Grant, Corvallis.

Behrens Yamada S, Davidson TM, Fisher S. 2010. Claw morphology and feeding rates of introduced European green crabs (*Carcinus maenas* L, 1758) and native Dungeness crabs (*Cancer magister* Dana, 1852). Journal of Shellfish Research. 29(2):471–477.

Behrens Yamada S, Dumbauld BR, Kalin A, Hunt CE, Figlar-Barnes R, Randall A. 2005. Growth and persistence of a recent invader *Carcinus maenas* in estuaries of the northeastern Pacific. Biological Invasions. 7(2):309–321.

Behrens Yamada S, Gillespie GE. 2008. Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? ICES Journal of Marine Science. 65(5):725–729.

Behrens Yamada S, Gillespie GE, Norgard TC, Thomson RE. 2021. Range Expansion of the European Green Crab, *Carcinus maenas* Along the Pacific Coast of North America. Can ocean indicators predict their success? manuscript in preparation

Behrens Yamada S, Groth SD. 2016. Growth and longevity of the Red Rock crab *Cancer productus* (Randall, 1840). Journal of Shellfish Research. 35(4):1045–1051.

Behrens Yamada S, Kalin A, Hunt C. 2001. Growth and longevity of the European green crab *Carcinus maenas*, in the Pacific Northwest.

Behrens Yamada S, Kosro PM. 2010. Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas*. Biological Invasions. 12(6):1791–1804.

Behrens Yamada S, Peterson WT, Kosro PM. 2015. Biological and physical ocean indicators predict the success of an invasive crab, *Carcinus maenas*, in the northern California Current. Marine Ecology Progress Series. 537:175–189.

Behrens Yamada S, Schooler S, Heller R, Donaldson L, Takacs GT, Randall A, Buffington C. 2020. Dataset for Status of the European Green Crab, Carcinus maenas, in Oregon and Washington coastal Estuaries in 2019. https://doi.org/10.7267/028712995

Behrens Yamada S, Schooler S, Heller R, Donaldson L, Takacs GT, Randall A, Buffington C, Akmajian A. 2019. Status of the European Green Crab, *Carcinus maenas*, in Oregon and Washington coastal Estuaries in 2019. https://ir.library.oregonstate.edu/concern/technical_reports/xk81js14x

Behrens Yamada S, Yednock B, Schooler S, Carson C, Prickett J, Randall A. 2019. Dataset for Status of the European Green Crab, Carcinus maenas, in Oregon and Washington coastal Estuaries in 2018. https://doi.org/10.7267/tt44pt057

Behrens Yamada S, Schooler S, Yednock B, Carlson C, Prickett J, Randall A. 2018. Status of the European Green Crab, *Carcinus maenas*, in Oregon and Washington Coastal Estuaries in 2018. https://ir.library.oregonstate.edu/concern/technical_reports/vt150q47j

Berrill M. 1982. The life cycle of the green crab *Carcinus maenas* at the northern end of its range. Journal of Crustacean Biology. 2(1):31–39.

Blakeslee A, Ruocchio M, Moore C, Keogh C. 2020. Altered susceptibility to trematode infection in native versus introduced populations of the European green crab. Aquatic Invasions. 15(1):177–195.

Blakeslee AM, Keogh CL, Fowler AE, Griffen BD. 2015. Assessing the effects of trematode infection on invasive green crabs in Eastern North America. PloS one. 10(6).

Brasseale E, Grason EW, McDonald PS, Adams J, MacCready P. 2019. Larval Transport Modeling Support for Identifying Population Sources of European Green Crab in the Salish Sea. Estuaries and Coasts. 42(6):1586–1599.

Broekhuysen GJ. 1937. On Development, Growth and Distribution of *Carcinides maenas* (L.). Archives néerlandaises de zoologie. 2(1):257–400. doi:10.1163/187530137X00104.

Carlisle D. 1957. On the hormonal inhibition of moulting in decapod Crustacea. II. The terminal anecdysis in crabs. Journal of the Marine Biological Association of the United Kingdom. 36(2):291–307.

Chase C. 2018 Sep 19. Marine nonprofit awarded NOAA grant to develop green crab market. Seafood Source. https://www.seafoodsource.com/news/environment-sustainability/maine-nonprofit-awarded-noaa-grant-to-develop-green-crab-market.

Cohen AN, Carlton J, Fountain M. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology. 122(2):225–237.

Costanza R, d'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'neill RV, Paruelo J. 1997. The value of the world's ecosystem services and natural capital. nature. 387(6630):253–260.

Crane J. 1966. Combat display and ritualization in fiddler crabs (Ocypodidae, genus Uca). Philosophical Transactions of the Royal Society of London Series B, Biological Sciences. 251(772):459–472.

Crawley MJ, Brown SL, Heard MS, Edwards GR. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters. 2(3):140–148.

Crothers J. 1968. The biology of the shore crab, *Carcinus maenas* (L.). 2. The life of the adult crab. Field Stud. 2:579–614.

Delaney DG, Griffen BD, Leung B. 2011. Does consumer injury modify invasion impact? Biological Invasions. 13(12):2935–2945. doi:10.1007/s10530-011-9975-0. https://doi.org/10.1007/s10530-011-9975-0.

DeRivera CE, Ruiz GM, Hines AH, Jivoff P. 2005. Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology. 86(12):3364–3376.

Eissinger A. 2010. Puget Sound Marine Invasive Species Volunteer Monitoring Program. Final summary report and program analysis. Olympia, WA: WA Dept Fish and Wildlife, Aquatic Invasive Species Unit.

Elner RW. 1980. The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). Marine & Freshwater Behaviour & Phy. 7(1):15–24.

Emberts Z, Escalante I, Bateman PW. 2019. The ecology and evolution of autotomy. Biological Reviews. 94(6):1881–1896.

Flynn PST, Mellish CL, Pickering TR, Quijón PA. 2015. Effects of claw autotomy on green crab (*Carcinus maenas*) feeding rates. Journal of Sea Research. 103:113–119.

Glen AS, Pech RP, Byrom AE. 2013. Connectivity and invasive species management: towards an integrated landscape approach. Biological Invasions. 15(10):2127–2138.

Glude JB. 1955. The effects of temperature and predators on the abundance of the soft-shell clam, *Mya arenaria*, in New England. Transactions of the American Fisheries Society. 84(1):13–26.

Good JW. 2000. 3.3 Summary and Current Status of Oregon’s Estuarine Ecosystems. Salem, OR.

Green SJ, Akins JL, Maljković A, Côté IM. 2012. Invasive lionfish drive Atlantic coral reef fish declines. PloS one. 7(3): e32596.

Grosholz ED, Ruiz GM. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. Biological Conservation. 78(1–2):59–66.

Grosholz ED, Ruiz GM, Dean CA, Shirley KA, Maron JL, Connors PG. 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology. 81(5):1206–1224.

Hemminga MA, Duarte CM. 2000. Seagrass ecology. Cambridge University Press.

Hunt CE, Behrens Yamada S. 2003. Biotic resistance experienced by an invasive crustacean in a temperate estuary. Marine Bioinvasions: Patterns, Processes and Perspectives.:33–43.

Huppert DD, Johnson RL, Leahy J, Bell K. 2003. Interactions between human communities and estuaries in the Pacific Northwest: Trends and implications for management. Estuaries. 26(4):994–1009.

Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA. 2001. Historical overfishing and the recent collapse of coastal ecosystems. science. 293(5530):629–637.

Jamieson G. 2000. European green crab, *Carcinus maenas*, introductions in North America: differences between the Atlantic and Pacific experiences. p. 301–316.

Jensen GC, McDonald PS, Armstrong DA. 2007. Biotic resistance to green crab, *Carcinus maenas*, in California bays. Marine biology. 151(6):2231–2243.

Juanes F, Lee K, McKnight A, Kellogg K. 2008. Claw allometry in green crabs, *Carcinus maenas*: heterochely, handedness, and sex. Marine Biology. 153(4):523–528.

Juanes F, Smith LD. 1995. The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. Journal of Experimental Marine Biology and Ecology. 193(1–2):197–223.

Keller RP, Cadotte MW, Sandiford G, Keller RP, Cadotte MW, Sandiford G. 2015. Invasive species in a globalized world: ecological, social, and legal perspectives on policy. Chicago: The University of Chicago Press.

Kern F, Grosholz E, Ruiz G. 2002. Management plan for the European green crab. Aquatic Nuisance Species Task Force http://www anstaskforce gov/GreenCrabManagementPlan pdf.

Klassen GJ, Locke A. 2007. A biological synopsis of the European green crab, *Carcinus maenas*. Fisheries and Oceans Canada Moncton, New Brunswick, Canada.

Lee SY, Seed R. 1992. Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. Marine Ecology Progress Series. 84(2):151–160. [accessed 2020 Nov 10]. http://www.jstor.org.ezproxy.proxy.library.oregonstate.edu/stable/24829550.

Losey RJ, Yamada SB, Largaespada L. 2004. Late-Holocene Dungeness crab (*Cancer magister*) harvest at an Oregon coast estuary. Journal of Archaeological Science. 31(11):1603–1612.

Lovell SJ, Besedin EY, Grosholz E. 2007. Modeling Economic Impacts of the European Green Crab. http://ageconsearch.umn.edu/record/9765/files/so07lo01.pdf.

Maginnis TL. 2008. Autotomy in a stick insect (Insecta: Phasmida): predation versus molting. Florida Entomologist. 91(1):126–127.

Mariappan P, Balasundaram C, Schmitz B. 2000. Decapod crustacean chelipeds: an overview. Journal of biosciences. 25(3):301–313.

Matheson K, McKenzie C, Gregory R, Robichaud D, Bradbury I, Snelgrove P, Rose G. 2016. Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. Marine Ecology Progress Series. 548:31–45.

McDonald PS. 2006. Biotic Resistance and Other Factors Affecting the Distribution, Habitat Use, and Potential Impacts of Invasive European Green Crab, *Carcinus maenas,* in the Northeastern Pacific. UW.

McDonald PS, Jensen GC, Armstrong DA. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. Journal of Experimental Marine Biology and Ecology. 258(1):39–54. doi:10.1016/S0022-0981(00)00344-0. http://www.sciencedirect.com/science/article/pii/S0022098100003440.

McVean A. 1976. The incidence of autotomy in *Carcinus maenas* (L.). Journal of Experimental Marine Biology and Ecology. 24(2):177–187.

McVean A. 1982. Autotomy. The biology of Crustacea. 4:107–132.

McVean A, Findlay I. 1979. The incidence of autotomy in an estuarine population of the crab *Carcinus maenas*. Journal of the Marine Biological Association of the United Kingdom. 59(2):341–354.

Nelson KA, Leonard LA, Posey MH, Alphin TD, Mallin MA. 2004. Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. Journal of Experimental Marine Biology and Ecology. 298(2):347–368.

ODCC. 2020. Oregon Dungeness Crab Commission. Oregon Dungeness. https://oregondungeness.org/crabbers/.

ODFW. 2019 Dec 6. Oregon Department of Fish and Wildlife. Oregon Shellfish Regulations. https://myodfw.com/articles/oregon-shellfish-regulations.

ODFW. 2020 Dec 21. Oregon Department of Fish and Wildlife. Economic Impact. https://www.dfw.state.or.us/agency/economic_impact.asp.

Poirier LA, Symington LA, Davidson J, St-Hilaire S, Quijón PA. 2017. Exploring the decline of oyster beds in Atlantic Canada shorelines: potential effects of crab predation on American oysters (*Crassostrea virginica*). Helgoland Marine Research. 71(1):13.

Ricciardi A. 2001. Facilitative interactions among aquatic invaders: is an" invasional meltdown" occurring in the Great Lakes? Canadian journal of fisheries and aquatic sciences. 58(12):2513–2525.

Rice MA. 2001. Environmental impacts of shellfish aquaculture: filter feeding to control eutrophication. p. 77–86.

Robbins WG. 2006. Hard Times in Paradise: Coos Bay, Oregon. REV-Revised, 2. Seattle: Seattle: University of Washington Press.

Ropes JW. 1968. The feeding habits of the green crab, *Carcinus maenas* (L.). Fishery Bulletin. 67(2):183–203.

Rumrill SS. 2007. The Ecology of the South Slough Estuary: Site Profile of the South Slough National Estuarine Research Reserve. Oregon Department of State Lands.

Say T. 1817. An account of the Crustacea of the United States. Journal of the Academy of Natural Sciences of Philadelphia. 1:65–80.

Schooler S, Behrens Yamada S, Andreasen K. 2020. Status of Green Crabs in Coos Bay: Monitoring Report 2020. SSNERR. https://www.oregon.gov/dsl/SS/Documents/Green_Crab_report_2020_Coos_Bay_SSNERR.pdf

Sekkelsten GI. 1988. Effect of handicap on mating success in male shore crabs *Carcinus maenas*. Oikos.:131–134.

Smith LD, Hines AH. 1991. Autotomy in blue crab (*Callinectes sapidus* Rathbun) populations: geographic, temporal, and ontogenetic variation. The Biological Bulletin. 180(3):416–431.

Stachowicz JJ, Whitlatch RB, Osman RW. 1999. Species diversity and invasion resistance in a marine ecosystem. Science. 286(5444):1577–1579.

Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM. 2003. Introduced species and their missing parasites. Nature. 421(6923):628–630.

Torchin ME, Lafferty KD, Kuris AM. 2001. Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions. 3(4):333–345.

Warner G, Chapman D, Hawkey N, Waring D. 1982. Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). Journal of Zoology. 196(4):431–438.

Wasson K, Lyon BE. 2005. Flight or fight: flexible antipredatory strategies in porcelain crabs. Behavioral Ecology. 16(6):1037–1041.

Welch HE. 1968. Relationships between assimilation efficiencies and growth efficiencies for aquatic consumers. Ecology. 49(4):755–759.

Wood FD, Wood HE. 1932. Autotomy in decapod Crustacea. Journal of Experimental Zoology. 62(1):1–55.

WSG. 2020. WSG Crab Team. WSG University of Washington. https://wsg.washington.edu/crabteam/.