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The Impacts of the Introduced European Green Crab, Carcinus Maenas, on Selected Bivalves and Meiofaunal Communities

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THESIS APPROVAL

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ABSTRACT

An abstract of the thesis of Zasha A. Bassett for the Master of Science in Biology presented July 6, 2000.

Title: The Impacts of the Introduced European Green Crab, *Carcinus maenas*, on Selected Bivalves and Meiofaunal Communities

This thesis examines the potential impact of the invasive green crab, *Carcinus maenas,* in Yaquina Bay, Oregon. I sampled the current extent of crab colonization in the intertidal zone of Yaquina Bay using a standardized trapping regimen in selected intertidal sites in August and September 1999. I also evaluated the potential impacts of *C. maenas* on the commercially important bivalve, *Crassotrea gigas. Carcinus'* preferred size ranges of *C. gigas* and other species were experimentally determined. Additionally, *Carcinus* species preference for *C. gigas* was examined in relation to two common bivalves, *Mytilus trossolus* and *Macoma nasuta.* Experiments were also conducted to see if *C. maenas* distinguished between two mussels species, *M. trossolus*, the native mussel found in natural populations in Oregon, and *M. galloprovincialis*, a popular aquaculture species in the Pacific Northwest. I also examined the potential impacts of *C. maenas* on meiofauna assemblages in a manipulative field experiment.

Evidence from the trapping regimen indicated that the majority of *C. maenas* present in Yaquina Bay were second year class and were capable of persisting in Yaquina. Size and species preference experiments indicated that *C. maenas* generally preferred bivalves in the 10-20 mm size range for all species tested and preferred *M. trossolus* over *C. gigas* and *M. nasuta*. Results also suggested that *C. maenas* showed no preference between size classes *M. trossolus* (except in post-hoc analysis where medium-sized mussels (20 mm±2 mm) to small-sized mussels (10 mm±2 mm) and preferred medium-sized (20 mm±2 mm) *M. galloprovincialis*. Mitigation recommendations for aquaculture are discussed. Enclosure experiments conducted during August and September 1999 at intertidal sandflats showed that *C. maenas* significantly reduced amphipod (*Corophidae*) densities and Cumacea (*Nannastacidae*). This suggests that *C. maenas* may significantly alter community structure in embayments of western North America.

THE IMPACTS OF THE INTRODUCED EUROPEAN GREEN CRAB, *CARCINUS MAENAS*, ON SELECTED BIVALVES AND MEIOFAUNAL COMMUNITIES

by

ZASHA A. BASSETT

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INTRODUCTION

Invasion Biology:

Biological invasions present a serious threat to the integrity of natural communities and to the preservation of endangered species (Carlton, 1996). Such invasions have a broad range of impacts from significant ecological consequences to substantial economic gains or losses. Traditionally, invasion studies have focused on terrestrial and freshwater systems where an invasive species have had a catastrophic effect on native biota (Carlton and Geller, 1993). Examples include the starling, *Sturnus vulgaris*, which was introduced in the eastern, US in the 1890s. The starling has expanded its range across most of North America (Kruger, *et. al*, 1989). Starlings have had significant negative impacts through their roosting and feeding behavior on human activities such as farming, cattle production, and industry and starlings have been shown to displace native bird species (Feare, 1984). The zebra mussel, *Dreissena polymorpha*, introduced in the Great Lakes region in 1988, is a biofouling organism capable of attaching to solid surfaces in high densities. It can hinder the performance of equipment exposed to lake or river waters (e.g. intake pipes, cooling systems and boat hulls) and smother aquatic organisms (Johnson and Padilla, 1996). Furthermore, its ability to actively pump water makes it an extremely efficient filter feeder. This filtering capacity gives it the ability to profoundly reduce phytoplankton communities and consequently, drastically alter the path of energy flow in aquatic food webs which can lead to changes in zooplankton and pelagic fish abundances (Johnson and Padilla, 1996).

One of the difficulties of studying invasions in any ecosystem has been determining which species possess characteristics that enable them to successfully invade a new region. Invasions often occur long after dispersal corridors have been established and scientists have generally responded to invasive crises in a piecemeal fashion (Carlton, 1996). Specific invasions have been studied in great detail but only a few scientists have attempted to understand the general patterns of invasions and the characteristics of successful invaders (Vermeji, 1996). For example, it is not known whether successful invaders possess a particular set of biological qualities that give them distinct advantages when expanding their range or whether only those new species that are significantly different from those already present in a community are likely to become established (Vermiji, 1996).

The most well known description of invaders is Baker's description of the "ideal weed." In summary, the ideal weed is a plastic perennial that can germinate in a wide range of physical conditions, grow quickly, flower early, is self-compatible, produces many seeds that disperse widely, reproduces vegetatively, and is a good competitor. No one species is likely to have all these characteristics, nor are they all required for a species to be a successful invader, however, possession of one or a few of these features may contribute to its ability to invade successfully (Noble, 1989). For example, the South African shrub, *Chrsanthemoides monilifera*, is displacing *Acacia longifolia* in coastal dunes in Australia. Suprisingly, *C. monilifera* has a lower light assimilation rate per unit leaf area and lower drought tolerance than *A. longifolia*.

However, when grown together, the invader seedlings outgrow those of the native species because of their more efficient arrangement of photosynthetic tissue (Noble, 1989).

A simple demographic advantage (lower mortality rate) may also be an important characteristic of invaders. Byers and Goldwasser (1999) demonstrated in a theoretical model that *Batillaria attramentaria*, an introduced intertidal mud snail on the US West Coast, overwhelmed the native species, *Cerithidea californica*, simply by having a demographic advantage. In their model, parameters such as competitive and parasitism resistance factors enjoyed by this invader were controlled, but *B. attramentaria* still outgrew *C. californica*.

Another factor that may contribute to the success of invaders is an increase in the population size in a donor region, so more individuals are available for transport or range expansion. For example, the southern California spider crab, *Pyromania tuberculata*, was introduced into San Francisco Bay in the 1960s (Carlton, 1979) from Japan and soon thereafter was introduced to Korea and then New Zealand. Each successive "jump" was made after the species established itself in a new area (Carlton, 1996). New donor regions can become available so the species is available for transport, or different ports may make different genetic stocks available, that have greater invasive potential.

Beyond those qualities specific to the invader, there may also be interrelated processes that can be useful in explaining *why* invasions occur in certain communities.

Understanding these processes may improve our ability to predict which target communities may be specifically at risk for invasion (Carlton, 1996).

A variety of factors in a recipient community can make it more susceptible than other communities to invasions. Von Broembsen (1989) pointed out that isolated environments with a low diversity of native species tend to be differentially susceptible to invasion. When opportunities for colonization are equal, historically depauperate insular regions often acquire more invading species than non-isolated, species-rich areas (i.e. Hawaii and New Zealand have more exotic birds than North America and Australia). Specifically, communities that are poor in species or that are missing key members may be more likely to be invaded. Additionally, communities that have high connectance may be more difficult to invade than those with low connectance (Pimm, 1989).

Invaders may also enjoy greater success in recipient regions where their populations are not limited by natural predators or competitors (Vermiji, 1996 and Pimm, 1989). Invasions may be enhanced by similarity in the physical environment between the source and recipient areas (Van Broembsen, 1989). Furthermore, invasions may occur in specific "windows," when unique biological and physical conditions occur leaving an opening for an invader to enter a new region successfully (Carlton, 1996).

Changes in recipient regions that lead to altered ecological, biological, chemical, or physical conditions, can also lead to increased susceptibility of the region for invasions (Carlton, 1996). For example, Nichols *et. al.*, (1990) observed that the successful invasion of the Asian clam, *Potamocorbula amurensis*, in San Francisco Bay, may be due in part to the depression of native biota after a major flooding episode. Vermiji (1996) also suggests that biotic interchange is more common in communities where prior extinctions have occurred (through natural causes or overexploitation).

Opportunity is a vital component of invasion processes. It is well known that European insects have successfully invaded many other regions more frequently than species from those regions have invaded Europe. This may not be due to the inherent superiority of European species or the size of invader inoculations but rather simply because more European species have historically been transported to other regions than vice versa (Simberloff, 1989). Thus, stochastic inoculation events where large numbers of a species are released into a region are another essential process for invasion. For example, one vessel with hundreds of millions of *Dreissena* larvae picked up in ballast water in the Black Sea and released in the Lake St. Clair, in the Great Lakes Region may have facilitated the successful establishment of zebra mussels in that region (Johnson and Padilla, 1996). Changing dispersal vectors such as size, speed, and quality (such as larger, faster ships) can lead to an increase in inoculant species diversity, increased numbers of invasive species, and an increase in the number of post-transport 'fit' individuals that are available to invade a donor region (Carlton, 1996).

Finally, it is essential to consider what ecological and evolutionary impacts an invader has on a recipient biological community. Invaders have a wide range of direct and indirect impacts on communities they invade. For example, direct predation by the brown tree snake, *Boiga irregularis*, has lead to extirpation of eight of the eleven endemic forest bird species on the island of Guam (Silva-Krott *et. al*, 1998). The *B. irregularis* introduction also has led to radical reductions in Guam's lizard populations after avian food sources became scarce (Gordon and Fritts, 1992). The introduction of the grazing snail, *Littorina littorea*, on the East coast of the United States led to reductions in algal canopy species in the intertidal regions. These algal canopies have strong direct positive effects in the high rocky intertidal communities by enhancing organism recruitment, growth, and survival. Reduction of the canopy by *L. littorea* predation, however, offsets these mitigating effects for intertidal species that depend on them (Bertness, *et. al.*, 1999).

Byers (1999) showed *Batillaria attramentaria*, an introduced intertidal mud snail on the US West Coast, competitively excludes the native snail *Cerithidea californica* in estuaries when the two species compete for the same shared, preferred food resource - epipelic diatoms. The introduction of four cordgrass species *(Spartina alterniflora, S. anglica, S. patens, and S. densiflora)* in several estuaries along the Pacific coast of North America has been shown to reduce open mud-flat feeding habitats of shorebirds, as well as competitively displace native salt marsh vegetation (Daehler and Strong, 1996). Morrison *et. al.* (2000) showed that sediment disturbance by the invasive round goby, *Neogobius melanostomus*, led to changes in the chemical dynamics and food web structure of Lake Erie.

Such ecological consequences of an invader may not be detectable immediately after an introduction. It can take many years before the ecological impacts of an invasive species are recognized and by then it may be too late to take action to mitigate these consequences. For example, Byers (1999) showed that the range of coexistence time for *B. attramentaria* and *C. californica* was 55-68 years before *C. californica* was competitively excluded in some areas. Evolutionary impacts are even more difficult to demonstrate. If invasions occur on a small scale, the resulting evolutionary changes may be minor. However, if newcomers arrive from far away as the result of large-scale alterations in the geography or climate, the change in selective regime and subsequent evolutionary responses could be more dramatic (Vermiji, 1996).

Historically, invasions in marine ecosystems have received less attention than freshwater or terrestrial invasions (Carlton and Geller, 1996). However, the rate of introduction of non-native species through human-mediated vectors in coastal regions of the world appears to be increasing at the close of the 20th century (Carlton, 1996). This may be due in part to the successful transport and release of ships' ballast water and sediments (Carlton and Geller, 1993). Although several other vectors for various invasive species have been identified, information about non-indigenous species such as their time of arrival, rate of spread and distribution is often poorly resolved (Grosholz and Ruiz, 1996).

Studies of marine invasions tend to focus on a few regions that have been heavily invaded, such as San Francisco Bay, or on invasions by "pest" species, such as the invasion of *Spartina spp.* on the Pacific coast of the United States. *Spartina* restricts open mudflats in the intertidal zone and consequently, can disrupt aquaculture production (Daehler and Strong, 1996). Given these consequences, the focus of these studies is often on mitigation and management of the species. Quantitative studies that document the effects of marine invasions on communities, using experiments and long-term data to distinguish effects of an introduction from natural variation, are rare (Allmon and Sebens, 1988).

This thesis focuses on the relatively recent introduction of the marine European green crab, *Carcinus maenas*, into Yaquina Bay in Oregon. In particular, I will address the potential impacts of this species on commercial and native bivalves, as well as, potential implications for soft sediment invertebrate communities. It is important, however, to first understand aspects of the species biology such as, how it is dispersing from the point of origin, and the perceived ecological consequences that have been observed to date.

Green crab biology:

The European green crab is a medium-sized intertidal brachyuran crab (ranging from 40-90 mm carapace width). It is an aggressive species that feeds on a wide variety of prey (Ropes, 1968; over 150 genera of plants and animals are listed by Cohen *et. al.*, 1995). It feeds on bivalves particularly (Juanes, 1992; Cohen *et. al.*, 1995, and Elner, 1981), other crabs (Ropes, 1968) and conspecifics (Klein Breteler, 1975). The green crab has remarkably broad physiological tolerances; adults are euyhaline to 4% salinity and larvae to 17% salinity (Jamieson *et. al.*, 1998) and they can overwinter at water temperatures less than 0°C (Jamieson *et. al.*, 1998). Under favorable conditions, the green crab can reach sexual maturity within a year (Grosholz and Ruiz, 1995). The species is able to occupy a wide range of habitat types including open sand/mudflats, shell, cobble, and algal, as well as, rocky intertidal habitats (Jamieson *et. al.* 1998). In the Atlantic, green crabs have been observed making diel and seasonal migration from sub to intertidal zones (Hunter and Naylor, 1993). They migrate into the intertidal on the flood tide and returns to subtidal zones on the ebb. It has commonly been found 'stranded' between tides.

Green crabs have been shown to exert predatory control over species abundance and community structure, particularly on bivalves (Jensen and Jensen, 1985) and to compete with and displace certain crabs and shrimp when foraging (Jamieson *et. al*, 1998). In its native range, the green crab has a significant impact on populations of molluscs such as the mussel, *Mytilus edulis*, and the predatory snail, *Nucella lapillus*, (Grosholz and Ruiz, 1996b) and green crab predation has been demonstrated to be a causal mechanism for spatial and temporal variability in *Macoma balthica* and *Cerastoderma edule* clam populations (Richards *et. al.*, 1999). Although poorly documented, the introduction of the green crab into Maine, USA coincided with extensive reduction in the beds of the soft-shell clam, *Mya arenaria* Linneaus

(Jamieson *et. al*, 1998). Furthermore, Vermiji (1982) suggested the green crab has acted as a strong selective source in the evolution of shell size and shape in the snail *Nucella lapillus.*

Understanding the physical limits of the green crab may help predict the potential range and distribution of this species in the northeastern Pacific. While adult green crabs have broad physiological tolerances, they are unable to survive in areas with strong wave action and, as a result, spend most of their life in sheltered estuaries. Additionally, conditions for reproduction and development are more stringent than for survival of adult crabs; eggs develop normally at 10° C and only in salinities greater than 26% (compared to larvae which can tolerate salinities as low as 17%) and adults will not breed in temperature of 14-26° C (Jamieson *et. al*, 1998). Despite these limitations, Cohen *et. al.* (1995) estimated that suitable conditions exist that may enable the green crab to colonize sheltered areas of the west coast of North America from the Aleutian Islands to Baja, California. As the first crab in the family Portunidae to be introduced into the northeastern Pacific, the green crab may have adaptations that allow it to exploit currently unoccupied niches in the region. For example, of the few crab species that occur in West Coast estuaries, only one species, *Hemigrapsus oregonensis*, typically reproduces in the low salinity habitats that green crabs may be able to colonize. West Coast estuaries may be especially vulnerable to invasions because they have few brackish water species and it is these lower diversity systems that may be more easily invaded, although there is no empirical evidence as of yet to support this (Jamieson *et. al*, 1998).

Green crab introductions world-wide:

Green crabs are native to temperate waters in the Mediterranean Sea and the eastern Atlantic from Mauritana to Norway (Jamieson *et. al*, 1998). The crab was accidentally introduced into the western Atlantic in the early 1800s, into Australia in the 1850s in Philip Bay, Melbourne, into South Africa in 1983, from Australia to Tasmania around 1990, and into San Francisco Bay in 1989-1990. Other invasions may have occurred, but little is known about them either because they were not successful or they were poorly documented in the scientific literature. The introduction of the species into Australia is poorly documented, possibly because marine ecological studies were not as wide-spread in the early part of the 20th century as they are today or possibly because the species has had little impact in that area (Jamieson *et. al*, 1998).

More information is available on the invasion in the western Atlantic, possibly because the invasion was correlated with the decline of bivalve fisheries. Several studies indicate that the green crab is a significant predator on wild and cultured bivalves although it is able to prey on a wide variety of species (Ropes, 1968 and Dare, *et. al*, 1983). Green crab invasion also led to changes in nematode community structure through predation and modification of the sediment (Schratzberger and Warwick, 1999) in studies conducted in the western Atlantic.

On the east coast of North America, the green crab ranges over 1,000 km of coast, from Virginia to Cape Breton, Nova Scotia. It is believed that the northern end of the species range is still slowly being expanded (Jamieson *et. al*, 1998). While predatory impacts are well known, competitive interactions with other species have been more difficult to determine through controlled experiments. The crab has been become well-established in protected embayments throughout this region on both soft and hard substrate and is even able to colonize some hard substrate regions of the outer coast, although this distribution is more limited (Grosholz and Ruiz, 1996).

In South Africa, the green crab first became established at Table Bay Docks, Cape Town and has expanded its range over 100 km of shore, mostly northward. Range expansion has ceased and green crabs are currently found only in Table Bay and a few lagoons to the north (Sylvia Yamada, personal communication, 2000). There is concern that the predatory impact of this species may negatively impact bivalve culture but this has not been documented as of yet (Griffiths *et. al.* 1992). The crab has not been shown to be a significant competitor of native crabs, probably due to limited habitat and dietary overlap with those crab species (LeRoux *et. al.*, 1990). In South Africa, the green crab has been able to establish itself on both hard and soft substrates in protected areas and has colonized the rocky intertidal regions of the outer coast to some extent (Grosholz and Ruiz, 1996).

Green crabs were first identified on the West Coast of North America in San Francisco Bay in 1989 (Ricketts *et. al.* (1985) documented a single green crab in

Willapa Bay, Washington several decades earlier in 1961 although this sighting may have been an error). The introduction in San Francisco, was actually thought to have occurred earlier than 1989, however, as the San Francisco populations were well-established and breeding by the time they were discovered and since search efforts have been sporadic and uncoordinated on the West Coast (Yamada and Hunt, 1999). Several potential vectors for the initial introduction have been suggested including ballast water, fouled pipe systems of ocean going vessels, the packing materials of commercial fisheries products, or through accidental release from private or research aquaria (Cohen, *et. al.* 1995). The green crab spread northward from San Francisco Bay rapidly, traveling an average of 25 km/yr. from 1993-1996 (Grosholz, 1996). The crab was discovered in Humboldt Bay, California in 1995. It was found in Coos Bay, Oregon (300 km north of Humboldt Bay, which was thought to be the northern end of its range in 1996) in 1997 (Jamieson, *et. al*, 1998). In 1998, the green crab was discovered simultaneously in seven major estuaries in Oregon (including Yaquina and Tillamook bays), as well as in Willapa Bay and Grays Harbor in Washington State. In 1999, it was found on Vancouver Island, Canada (Yamada and Hunt, 1999).

Three possible mechanisms have been suggested for the appearance of *C. maenas* in Pacific Northwest estuaries; transplantation of oysters, ballast water discharge, and larval transport on ocean currents. While oyster growers in Oregon and Washington frequently import seed oysters and market size oysters from other growing areas such as Humboldt Bay, CA, shellfish culture is not well correlated with the appearance of the 1998 invasion of several estuaries (Yamada and Hunt, 1999). Ballast water discharge in Oregon is limited to Coos Bay and Yaquina Bay since these large estuaries are the only ones receiving cargo ships on the coast of Oregon. Thus ballast water discharge can only partially account for the invasion into the state. Furthermore, if ballast water were a major vector along the West coast, it seems likely that green crabs would already be established in Vancouver Harbor and Burrard inlets (Yamada and Hunt, 1999). This pattern suggests that ballast water is also unlikely to be a primary mechanism for the spread of *Carcinus* in the Pacific Northwest.

The northward expansion of the green crab has not been a steady progression, but rather a series of jumps from one bay to another, sometimes with several years in between (Grosholz and Ruiz, 1995). This suggests that larvae rather than adults are colonizing the new areas. This theory is supported by data showing that newly-established populations are generally in the same age cohort. Furthermore, the El Nino ocean conditions from September 1997 to April 1998 were extremely favorable for larval transport from California. Typically, surface currents along the Oregon coast generally move south from April to October and north from October to April. Currents typically occur in a narrow 10-20 km strip close to shore, moving at 10-20 km/day. In 1997/1998, the northward currents were greater in duration and magnitude than normal. In September 1997, a northward current of 10 km/day was measured off Newport. Currents recorded off Crescent City, CA and Coos Bay, OR were over 40 km/day (Yamada and Hunt, 1999). These high currents lasted until April 1998 and drifters off Newport, OR traveled to the West Coast of Vancouver Island at an average of 50 km/day until the spring of 1998. Thus, it is feasible that *C. maenas* larvae from the San Francisco Bay area could have seeded Oregon, Washington, and Vancouver Island estuaries between September 1997 and April 1998 (Yamada and Hunt, 1999).

Potential ecological implications of the green crab invasion in the North Pacific:

Although the invasion has occurred rapidly, some information is available about the impacts of the green crab on native fauna in the north Pacific. Prior to green crab colonization, Grosholz and Ruiz (1995) had established a 10-year database on the abundance and distribution of benthic invertebrates and shorebird predators in Bodega Harbor. These data, combined with observations about green crab habitat preferences and biology in Bodega Harbor, together with field and lab experiments have allowed initial evaluation of the impact of the green crab on the California coast.

Green crabs established quickly in Bodega Harbor. They appeared to prefer soft substrata, with less evidence of rocky habitat colonization as seen in its native habitat (Grosholz and Ruiz, 1995). Average size for green crab populations in Bodega Harbor was larger than documented size ranges in their native range (Grosholz, and Ruiz, 1996). The green crab may alter community function in intertidal benthic communities. Field experiments have shown significantly reduced densities of abundant taxa, including the bivalves *Transnella confusa* and *T. tantilla* (Grosholz and Ruiz, 1995). These preliminary data indicated that these changes, at least thus far, have not translated into changes in the abundances of wintering shore birds in this area that depend on these invertebrates for food. This suggests that the invasion of the green crab may impact only a single trophic level (Grosholz and Ruiz, 1996b).

During the spring and summer of 1998, Yamada and Hunt (1999) described size frequency and growth data for green crabs in several bays in Oregon, including Yaquina Bay. The average carapace width of this new year class reached 47 mm by September of that year. Mark and recapture studies indicated that growth ceased during the winter and resumed in early spring. By the end of the second summer, crabs that were trapped averaged 70 mm and crabs were found on both soft and hard substrates.

To summarize, the current data on the invasion suggests that colonization in the Pacific differs in some major ways from green crab colonization in the Atlantic. In the Pacific, green crabs appear to reach a larger size, are more likely to colonize soft substrate, and may be able to affect the relative abundances of a variety of invertebrates as well as alter community function in benthic areas.

Green crabs may have important economical and ecological impacts in the North Pacific. Commercial aquaculture of *Crassotrea gigas*, the Pacific oyster, and *Venerupis philippinarum*, the Manila clam, and the mussel, *Mytilus galloprovincialis* are economic mainstays, particularly in Washington state. The culture of Pacific oysters is also common in Oregon, contributing $761,810 (21,766 gallons) to the economy in 1999 (Korn, 1999). Green crab predation has had serious negative impacts in northern California. Some Manila clam growers have experienced losses as high as 50% (Ted Grosholz, personal communication, 1998). The degree of impact from green crab predation may rest in part on the type of culture method used to grow bivalves. In the Puget Sound region and in parts of Oregon, "on-bottom" culture is the most common strategy used to grow both Pacific oysters and Manila clams. This method consists of building low concrete dikes to partition off many acres of mud flats, which are leveled; the idea is to retain water so growing oysters are never exposed. To avoid smothering the oysters in mud, bits of shell are scattered on the surface and the young oysters called "spat" are scattered over the surface and attach to the shell (Ricketts, *et. al.*, 1985). This differs from the "bag" culture commonly used in Bodega Bay for Manila clams, where bags of young clams are spread on protected areas of intertidal mud flats. Another type of culture that is becoming more popular is "floating culture" particularly for mussels and to some extent, oysters. In this method, bivalves are grown in bags that hang along lines near the surface of the water column in subtidal areas. Young bivalves can also be grown in trays placed in the intertidal region. I know of no research at this time that has evaluated whether the degree of green crab predation differs between these methods. However, if green crabs actively select habitat, either for refuge or high prey abundance, the practice of habitat modification for on bottom and bag cultures may need to be altered or growers may need to consider alternate culture practices to avoid losses from green crab predation.

Other bivalve species such as: the cockle *Clinocardium nuttallii*; the native littleneck clam, *Protothaca staminea*; and the gaper clam, *Tresus spp.*, are not cultured but are commercially and recreationally harvested in Oregon (Johnson and Wood, 1996). These species may also be at risk. These bivalve species all settle at microscopic sizes and grow through a size range that makes them vulnerable to crab predation. The addition of another crab predator may further impact their survival.

Existing crab predators have already caused dramatic declines in the densities of small clams. *Nutricola spp.* clam densities have been documented to decline from 100-100,000 m^{-2} to<1 m^{-2} during episodic Dungeness crab, *Cancer magister*, recruitment events (Jamieson *et. al.*, 1998). Green crabs may also prey on other bivalve predators such as young Dungeness and the shore crab, *Hemigrapsus oregonensis*, but whether or not this will negate direct green crab predation is unknown (Grosholz and Ruiz, 1996; Chris Hunt, personal communication, 1999).

Research on the implications of green crab invasion in Oregon is important for several reasons. First, it will provide a perspective on the degree of impact to the shellfish industry and it will allow the development of mitigation recommendations, if necessary. Second, the introduction of the green crab provides a rare opportunity to observe invasion processes and gather information about how a new species impacts native communities.

The purpose of this thesis was three-fold. First, it is important to know the distribution and abundance of the green crab in order to determine its ecological impacts. As part of a larger, on-going effort to map the species invasion in Oregon (Yamada, unpublished data), I gathered baseline data about green crab distribution and abundance from specific sites in Yaquina, Bay. These data will be submitted to S. Yamada as part of that larger effort. Second, I gathered essential information on the green crabs' potential impact on Oregon's most commercially important species, the Pacific oyster, *C. gigas,* by examining the crab's preferred size and species preferences. Although the green crab is known to prey on *C. gigas*, preferred size ranges are unknown and the degree of impact may depend to some extent on whether or not the green crab prefers the oyster or some other native species commonly found in soft-sediment habitats. This information can be used to direct further research or make management recommendations to mitigate the predatory impacts of the green crab.

Finally, I addressed the potential implications of the green crab on the meiofauna of soft-sediment communities through disturbance and/or predation. Disturbance and predation are significant mortality sources in many assemblages, and thus are important forces in shaping community structure (Dayton, 1971 and Menge, 1976). Bell (1980) showed clear evidence that macrofaunal organisms exert control over meiofaunal communities through a variety of mechanisms. In particular, a variety of macrofaunal crustaceans, as well as some fish, have been shown to impact meiofauna either by direct predation or sediment modification during their foraging activities (Palmer, 1988, Marinelli and Coull, 1987, and Martin *et. al.*, 1989). Many organisms in these communities are thought to influence the turnover and availability of nutrients and to act as food sources for native organisms (Grosholz and Ruiz, 1995). Thus, if *Carcinus* significantly reduces the abundance of organisms or alters the relative proportions of these organisms, community function may be altered. Coull and Palmer (1984) recommend a controlled experimental approach to examine the impacts of macrofaunal species on benthic infauna. Therefore I used a caging experiment to evaluate the impacts of the green crab on meiofaunal communities.

METHODS

Trapping regime:

Four sites (NW Natural Gas Tank, HMSC Pumphouse, Sawyer's Landing and Idaho Point) in Yaquina Bay, Oregon were monitored for green crabs (Figure 1). I used minnow traps, which had been modified by widening the trap entrance to 5 cm, between August 10, 1999 through September 9, 1999. The traps were baited with chicken legs and were left in the water for 24 hours. I recorded the carapace width (CW) and sex of all green crabs caught in the traps. Temperature and salinity data (using a hydrometer to measure salinity) were also recorded. Native crabs were released and green crabs were held in the EPA laboratory. Sylvia Yamada and Chris Hunt (Oregon State University) had monitored the four intertidal sites selected for this study the previous year with a similar trapping regime. However, since these researchers were trapping at other subtidal locations in Yaquina Bay, I continued to monitor these four sites in order to provide continuous record.

Each of the sites had rip-rap on the outermost edge along with smaller rocks along the upper intertidal edge that were colonized by common intertidal species (barnacles, mussels, etc.). All the traps were deployed along this upper intertidal zone. Sawyer's Landing was the site farthest upriver that was monitored (Figure 1). The HMSC pumphouse was the most saline site.

Feeding Preference Experiments:

Feeding experiments were conducted to determine *Carcinus maenas'* selectivity for different prey sizes and species. Ten male *C. maenas*, 52-62 mm in carapace width, were collected from Yaquina Bay, Oregon and brought back to the EPA laboratory in Hatfield Marine Science Center in April and May of 1999. The crabs were housed individually in plastic Ziploc sandwich boxes and held in a flow-through circulating seawater system with a 14 hr. light: 10 hr. dark cycle. During the trials, the water temperature ranged from 11.5° to 15° C. The crabs were maintained on pieces of fish or squid, but were starved for 48 hours prior to each trial to standardize hunger levels. The same ten crabs were used in all of the trials.

Size selection tests were performed on four prey species found in Yaquina Bay: *Crassotrea gigas*, the Pacific oyster; *Mytilus trossolus*, an abundant native epifaunal mussel; *Mytilus galloprovincialis*, an exotic mussel used in aquaculture production, and *Macoma nasuta*, a common thin-shelled clam in Oregon bays. The Pacific oyster is the largest commercial aquaculture species in the state of Oregon. The oysters were purchased from Oregon Oyster farm located in Newport, Oregon and the exotic mussels were provided by an aquaculture facility in Washington state. The other two species were collected from the bay. The prey items were classified into three size-classes, small (10 mm±2 mm), medium (20 mm±2 mm), and large (30 mm±2 mm). I used preference-selection tests for this study. In each size-preference test, a single crab was presented with three different size classes of a species and allowed to "choose" the preferred prey size. Size preference tests for each species were conducted seperately.

In the species preference tests, each crab was presented with a two different combinations of species, the first combination was as follows: Pacific oysters (*Crassotrea gigas*), the bent-nosed clam (*Macoma nasuta*), and the native mussel, (*M. trossolus*). In the second species preference test, two mussel species *M. trossolus* and *M. galloprovincialis* were offered. Separate offerings (or consumption tests) of each size class were not conducted as the objective was to determine which size ranges were the most vulnerable to predation. "Preference rankings" in separate-offering tests can be confused because a sub-optimal size class or species may be consumed at a higher rate to compensate for other factors (such as low nutrient value), when no other choice is offered (Elner and Hughes, 1978).

Prey Size Selection:

The prey items were classified into three size categories; small (10 mm ± 2 mm), medium (20 mm ± 2 mm), and large (30 mm ± 2 mm), according to bivalve length. For each prey species, ten of each size-class was offered simultaneously to a crab in a 40-L aquaria with a constant supply of fresh seawater. The epifaunal species, mussels and oysters, were randomly scattered across the bare floor of the tank.

Macoma nasuta prey were offered in aquaria containing 15 cm of sand (dried and sieved through a 1 mm mesh to remove all potential prey items) from Yaquina bay and allowed to bury for 12 hours before the start of the experiment. Fifteen cm is the average maximum depth at which these sizes of *M. nasuta* are found (Ricketts *et. al*, 1985). After the prey items were established in the aquaria, a single crab was added to the center of the tank and allowed to feed until an estimated 1/2 of the preferred size-class was consumed. The number of prey consumed was calculated by subtracting the number of unbroken prey items in each size class remaining from the number offered at the beginning of the experiment. Crabs that did not eat during a trial were excluded from the analysis.

Prey Species Choice Experiment:

Two prey choice experiments were conducted after size tests demonstrated that crabs generally preferred prey items in the small and medium size classes (see results below). Since the crabs either preferred the medium size class or did not distinguish between medium and other size classes, the medium size class was used for this experiment. The first test was conducted to determine the relative vulnerability of the commercial Pacific oyster, *C. gigas*, in the presence of two common bay species *M. nasuta* and *M. trossolus*. Mussels are commonly found attached to oyster bags, cultch, or, in trays at culture sites and the clam *Macoma* is a very common soft-sediment species found near culture sites in Yaquina Bay. For this trial, 15 cm of sieved sand (prepared as described above) was added to the aquaria. Twenty *M.*

nasuta were randomly spread across the sand 12 hours before the experiment began and allowed to bury naturally. Then 20 mussels and oysters were randomly scattered across the top of the sediment. A crab was placed in the center of each tank and allowed to feed until an estimated 1/2 of the preferred prey items had been consumed. Ten crabs were used in the experiment. The number of prey consumed was calculated by subtracting the number of unbroken prey items for each species remaining after the experiment was stopped from the number offered. Crabs that did not eat, as well as crabs that consumed all of one prey species item, (consumption rates varied substantially in this experiment) were excluded from the statistical analysis.

Mussel-Preference Test:

I tested preference between two mussel species, *Mytilus galloprovincialis*, a commercially important species in Washington State, and the native species, *Mytilus trossolus*. These two species have similar morphologies and can be reliably distinguished only by using genetic analysis (Cohen *et. al.*, 1995). However, studies indicate that some predator species do distinguish between the two species. Specifically, *Nucella spp.* has been shown to prey preferentially on *M. trossolus* over *M. galloprovinicialis* in field studies (M. Worham, personal communication). *Mytilus trossolus* is the dominant mussel species found in natural communities in Oregon and throughout most of the Pacific Northwest coast-line (McDonald and Koehn, 1988). *Mytilus galloprovincialis* has become the preferred species for aquaculture, however, because its higher growth rate allows this species to reach market size more quickly than the indigenous *M. trossolus* (Gosling, 1992). If *Carcinus* showed a preference for *M. galloprovincialis* over *M. trossolus,* then this preference would need to be considered in the development of mitigation measures for aquaculture. If *Carcinus* preferred *M. trossolus* over *M. galloprovincialis*, that information has important consequences for the persistence of *M. trossolus* in Pacific Northwest estuaries and the potential replacement *of M. trossolus* by *M. galloprovincialis.* Preference tests were conducted to determine if Carcinus did show a preference between these two species. *M. trossolus* species were gathered from Yaquina bay and a sub-sample sent to Marjorie Worham at the University of Washington to confirm their identification. *M. galloprovincialis* was provided by Kalmilche Sea Farms in Washington and were assumed to be exclusively *galloprovincialis.*

To determine whether *Carcinus* shows a preference for either of the two mussel species, crabs were presented with a choice of 10 (medium-size class) of each mussel scattered randomly across the bare floor of the aquaria. The mussels were marked along the shell hinge using a non-toxic paint, *M. galloprovincialis* was marked with a small "o", and *M. trossolus* individuals marked with a small "t". *Carcinus* were added to the tank and allowed to feed until an estimated 1/3 to 1/2 the prey items were consumed.

Genetic Analysis:

M. trossolus species were gathered from Yaquina Bay and analyzed using the protocol outlined below. DNA was extracted from the gonad tissue of 66 mussels (approximately 10% of the number used in the experiment) using the methods described by Geller *et. al* (1993). DNA samples were sent to Marjorie Worham at the University of Washington for genetic analysis. Analysis was conducted on only 19 of these samples because several of the samples were destroyed when the freezer in which they were held malfunctioned.

After extraction, length variations found in a non-repetitive region of DNA that codes for adhesive foot proteins were used to diagnose species (Inoue *et. al*, 1995). Specifically, Me-15 and Me-16 PCR primers (which amplify the non-repetitive part of the gene that codes for the protein) were used to produce species-specific lengths of 180, 168, and 126 bp for *M. edulis*, *M. trossolus*, and *M. galloprovincialis*, respectively. Then, following the protocol outlined by Suckanek *et. al.* (1997), PCR amplifications were conducted in a total volume of 25 µl using 10 mM Tris (pH = 8.3), 50 - mM KCL, 0.01% Triton-X 100, 0.01% gelatin, 0.01% NP-40, 200 µM dNTPs, 1.5 - mM $MgCl_2$, 0.3% Taq DNA polymerase, 25 - pmol of each primer. 0.5 - µl DNA template and autoclaved ultrapure water. Cycling conditions were: 30 s at 98° C followed by 30 cycles of 10 s at 95° C, 30 s at 54° C and 30 s at 72° C. For all amplifications, 10 µl of the PCR product were run on 3% agarose gels, stained with ethidium bromide, and visualized under UV light. Band lengths compared to those of known species.

Statistical Analysis:

The Friedman test, a non-parametric alternative to the one-way repeated measure ANOVA, was used to test differences in crab consumption of the three size classes and then the different species. This test was chosen because the repeated use of the same ten crabs undergoing different treatments is a repeated-measures design since the crabs individual preferences may influence the results. Additionally, I could not show normality in the small sample distribution, which necessitated a non-parametric test (Winer, 1962). Post-hoc Wilcoxon sign-rank tests were used to further test differences among size classes (and species groups). I used a Wilcoxon sign-rank test to evaluate size differences between the two mussel species.

Field Enclosure Experiment:

To examine the short-term impact of *Carcinus maenas* on the benthic invertebrate community of Yaquina Bay, I conducted enclosure experiments beginning on August 26, 1999. I adopted the methods used by Grosholz and Ruiz (1995). I enclosed one male *Carcinus* (60-67 mm CW) in each of 11 replicate square enclosures (0.25-m length x 0.1m height with an additional 0.15 m buried in the sediment). The enclosures were made of galvanized hardware cloth mesh (1.25 cm). The crabs were captured from Yaquina Bay in minnow traps or provided by Chris Hunt. Crabs were maintained in the laboratory on a diet of squid. The crabs were placed into the enclosures after a 24-hour starvation period to standardize hunger levels. Eleven identical enclosures without crabs served as controls. I deployed experimental and control cages alternately along a transect line (approximately 2.2 ft MLLW) with 5 m between cages.

The crabs remained in the cages for 12 days. During the course of the experiment, one crab molted and so this replicate was excluded from statistical analysis. At the end of the experiment, I removed the crabs and took a single core sample (10 cm, 5-cm depth) from the center of each experimental and control enclosure. I sieved all the cores in the laboratory through a 0.5 mm sieve and preserved the retained organisms in 10% buffered formalin. After two weeks, the samples were transferred to a 70% ethanol solution. Samples were sorted under a dissecting microscope and the taxa identified to family for enumeration (with the exception of nematodes, which could only be identified to the phyla taxonomic level).

Community evenness was calculated for each enclosure using Hill's modified ratio, which is:

$$E=\frac{(1/\lambda)-1}{e^{H'}-1}$$

where λ = Simpson's Index and H' is Shannon's diversity index (Ludwig and Reynolds, 1988). I chose this evenness index because it is not as sensitive to species richness as other indexes (such as Pielou's 'J). Furthermore, this particular evenness calculation remains relatively constant under different sampling variations and thus tends to be independent of sample size (Alatalo, 1981; Hill, 1972; Ludwig and Reynolds, 1988). Finally, as Hill's modified ratio approaches zero, a single species becomes more and more dominant, which is a useful characteristic of an evenness index (Alatalo, 1981).

In this experiment, families that made up less 0.005% of the total community abundance were excluded from the analysis.

Statistical Analysis:

To examine differences in community evenness between control and treatment groups, I conducted a one-way ANOVA (SPSS 8.0). The dependent variable was the evenness index per core. The calculated evenness indexes were normally distributed as is often the case with diversity and evenness indices (Magurran, 1988). I also conducted a one-way ANOVA on the number of individuals in each of the eight abundant families in the cores. Prior to these ANOVAs, I conducted a Levene's test of equality of error variances to insure my data met the assumption of homogenetiy of variances for an ANOVA. I conducted a Q-Q plot (SPSS) to evaluate normality in the data. The number of individuals data was not normally distributed so I transformed the data using square root (+0.5) transformation to normalize the data and to remove heteroscedicity (Sokal and Rohlf, 1981). It seems illogical that the distribution for the number of individuals in each family was not normal while the evenness index indexes were distributed normally (since evenness is calculated from the number of individuals in each family). However, evenness indexes are calculated using all the family groups data (i.e. the numbers for the whole community) and so the indexes can be normally distributed even when the number of individuals in family is not. A Kruskal-Wallis test was used to evaluate differences in total community abundance because of the severe departure from normality (Sokal and Rohlf, 1981).

RESULTS

Carcinus Abundance at Four Sites:

The four sites in Yaquina Bay were monitored for the presence of *Carcinus* using the trapping regimen described above. Few crabs were caught at these four sites. The NW Natural Gas Tank site had the highest average daily CPU of 0.25 crabs caught per day, followed by the HMSC Pumphouse with a CPU of 0.097 crabs caught per day. Sawyer's Landing and Idaho Point had CPUs of 0.65 and 0.061 respectively (Figure 2).

The percent of male *Carcinus,* 82%, that were trapped at all of these locations was higher than females, 18% (Figure 3). Crabs caught ranged in size from 46 mm-71 mm and were assumed to be a second year class. Crabs were separated into 5 mm size classes. The 61-65 mm size-class had the highest frequency, followed by the 66-70 mm size-class. Larger and smaller crabs were less frequent (Figure 4).

Air temperature at the four sites ranged from 21-24° C during the trapping regime. Salinity varied from 28 % to 34%. Idaho Point and the HMSC Pumphouse generally had slightly higher salinities than the NW Natural Gas Tank Site and Sawyer's Landing, which usually had the lowest salinity.

Feeding Preference Experiments:

The results of the experiments to evaluate *Carcinus* preferences for prey size and species are outlined below.

Genetic Analysis:

The genetic analysis conducted by M. Worham on the 19 mussels confirmed that they all had band lengths approximately 168 bp and, therefore, were all *M. trossolus*. This supports the data from K. Brooks (1992) that Yaquina's mussel populations are primarily *M. trossolus* (with a few *M. trossolus-galloprovincialis* hybrids) and so it is reasonable to assume all the mussels collected from Yaquina Bay and used in this experiment were *M. trossolus*.

Size Experiments:

Carcinus size preferences of M. trossolus:

Carcinus consumed all three size classes of *M. trossolus* but not at a different rate (Table 1) (p=0.06, N=10). However, a post-hoc pair-wise comparison of the three size classes showed that green crabs consumed more medium than small mussels (Table 2) (p=0.02, N=10). All other comparisons yielded non-significant results.

Carcinus size preferences of C. gigas:

Carcinus showed a significant preference for medium and small size classes of *C. gigas* (Table 3) (p=0.001, N=10). Post-hoc pair-wise comparison of *Carcinus*' consumption supported this result. Significant differences were found between the small and large size classes (p=0.005, N=10), as well as between the medium and large size classes but not between small and medium size classes (Table 4) (p=0.005, N=10).

Carcinus size preferences of M. nasuta:

Carcinus also distinguished between the three size classes of *M. nasuta* (Table 5) (p=0.002, N=9). *Carcinus* showed a preference for small and medium-sized *Macoma nasuta* over large-sized *Macoma* (Table 6) (p=0.01, N=9) but did not distinguish between the small and medium classes (Table 6) (p=0.14, N=9).

Carcinus size preferences of M. galloprovincialis:

Green crabs preferred different sizes of *M. galloprovincialis* than *M. trossolus*. *Carcinus* distinguished between the three size classes of the exotic mussels *M. galloprovincialis* (Table 7) (p=0.01, N=10). Specifically, *Carcinus* showed a distinct preference for medium-size mussels over small (p=0.04, N=10) and large *M. galloprovincialis* (Table 8) (p=0.007, N=10). *Carcinus* did not distinguish between large and small mussels (Table 8) (p=0.55, N=10). In the *M. trossolus* size-choice experiments, *Carcinus* did not distinguish between medium and large sized prey (p=0.13, N=10) but did choose medium sized mussels over small ones (Table 2) (p=0.02, N=10).

Prey Species-Choice Experiments:

Carcinus species preferences of M. trossolus, M. nasuta, and C. gigas:

When offered a choice of *C. gigas*, *M. trossolus*, and *M. nasuta*, *Carcinus* distinguished between the three species (Table 9) (p=0.04, N=6). *Carcinus* preferred the mussels to the Pacific oyster, *C. gigas*, (p=0.04, N=6) and the clam, *M. nasuta*, (p=0.05,N=6) and did not distinguish between *C. gigas* and *M. nasuta* (Table 10) (p=0.41, N=6). In this experiment, two of the crabs did not eat and were excluded from the statistical analysis. Additionally, two crabs consumed all 20 of the mussels in the tank before the experiment was stopped. One of these crabs stopped eating after consuming all the mussels in the aquaria and the other consumed all 20 mussels, two oysters and one clam. These two crabs were eliminated from statistical analysis because once they had consumed all the mussels, that "choice" was eliminated. However, the fact that green crabs consumed all the mussels offered (and in one case the crab stopped eating after all the mussels were consumed) supports the notion that *Carcinus* strongly prefers mussels over the other two species under these conditions.

Carcinus species preferences between M. trossolus and M. galloprovincialis:

When offered a choice of medium-size *M. trossolus* and *M. galloprovincialis*, *Carcinus* did not distinguish between the two mussel species and consumed both in equal amounts (Table 11) (p=0.46, N=9).

Field Experiment:

I found 14 families (not including the Nematoda phyla) in the field enclosures. The five most common taxa, Corophidae, Paratanidae, Foxcephalidae, and Nannastacidae, and Nematoda, comprised over 80% of the total organisms (Figure 5). Eight families were included in evenness calculations and abundance analysis. The remaining taxa were too numerically insignificant (numbering only a few individuals) to warrant their inclusion in the analysis. Green crabs significantly reduced the evenness of meiofauna communities (p=0.036), the control group had an average evenness index of 0.7562 while the treatment group had an average evenness index of 0.6928. (Table 12).

Paratanidae proportions increased from 34.1% in the control to 42.0% in the treatment. Paratanidae also showed a trend of increasing in number although the difference was not significant (Figure 5 and Table 13). The amphipod, Foxocephalidae's, relative abundance increased from 14.4% to 32.0% and the densities were slightly higher in the experimental than the control group, but this difference was not statistically significant ($p=0.35$). The tube building amphipod, Corophidae declined from 26.9% to 8.0% of the community make-up and dramatically decreased in numbers ($p<0.001$) when crabs were present. The Cumacea, Nannastracidae (primarily *Cumella vulgaris*) also declined from 6.9% to 1.5% in the presence of *Carcinus* and the differences in number of individuals per cage was statistically significant ($p=0.001$). The Nannastracidae and Corophidae families exhibited statistically significant decreases in the number of individuals as well as relative decreases in the presence of *Carcinus*. Capitellidae, Nematodes, and Supionidae were abundant in both treatment and controls and did not show significant change in either their numeric or relative abundances. The family Tellinidae (largely *Macoma spp.*) declined from 1.2% to 0.7% of the relative community abundance, but this difference was not significant (Figures 5 and Table 13). Total community abundance was not affected ($p=0.48$) (Figure 6).

DISCUSSION

Distribution of Carcinus maenas in Yaquina Bay:

Relatively few crabs were caught in these intertidal regions when compared to the subtidal trapping efforts conducted by Chris Hunt in Yaquina Bay. In his study approximately 600 crabs were caught between June and September in 1999 (C. Hunt, personal communication, 1999). This suggests that the adult crabs had moved from primarily intertidal to subtidal regions. Data collected in this study, however, indicated that crabs do still occupy intertidal regions to some extent and thus the crabs may migrate to the intertidal to forage at high tide while otherwise occupying subtidal regions as was observed by Hunter and Naylor (1993) in their native range. Size-frequency data was similar between the two studies, with most crabs between 60-70 mm CW, and presumably a second year class.

No first year size classes were recorded in my study, previous studies indicated that earlier year-classes tended to be found the intertidal regions through September of the previous year (Sylvia Yamada, personal communication, 1999). Temperatures in Yaquina were lower than normal in the summer of 1999, which may have led *Carcinus* to delay breeding. No first year class crabs were detected until late September in 1999 (S. Yamada, personal communication, 1999). Despite delays, the population in Yaquina Bay is capable of reproduction. Furthermore, crabs trapped in the spring 2000 ranged from 30-45 mm carapace width and were assumed to represent the 1999 year class, which again indicated that crabs are breeding successfully in

Yaquina Bay (S. Yamada, personal communication, 1999). This information combined the continued presence of green crabs in both subtidal and intertidal regions (and the discovery of the young of the year, despite its delayed appearance) suggests that *Carcinus* will be able to persist in Yaquina bay. However, the 1999 year class did not replace the parental one. If this pattern persists, the green crab in Yaquina bay could die out in approximately 3-4 years (based on growth and life history measurements) and these populations may not be self-perpetuating and populations will still rely on larval transport from the south (Sylvia Yamada, personal communication, 2000). However, the next El Nino may continue to seed Yaquina Bay with green crabs.

Carcinus Prey Preferences:

Prey Size Preferences:

Green crabs consume commercially important bivalve species in, addition to native epifaunal and infaunal bivalves. *Carcinus* preferentially consumed the small and medium size classes of *Crassotrea gigas* and *Macoma nasuta* when offered a choice between the three different size classes of each species. This suggests that the smaller size classes are more vulnerable to predation and that the larger individuals may have a size refuge from predation. Dare, *et. al.* (1983) also found higher consumption rates of smaller prey, but noted that crabs of 55 mm can consume oysters up to 45 mm in length, although the predation rate on large oysters was low, approximately one per day. Because these experiments were conducted in a laboratory setting, the number of prey eaten per day may be somewhat higher than could be expected in oyster cultures in the field. However, my test results, along with the information collected by Dare *et. al.*, indicate that mitigation efforts should be targeted at oyster seed in the 10-20 mm size range, when they are most vulnerable to attack by the green crab.

The size and species preferences of the green crab have potentially important implications for the ecological community. First, new bivalve recruits will be favored as prey by the green crab and the number of recruits may decline as a result of crab predation. Second, the size refuge of large individuals may favor rapid growth rates and thicker shells in bivalve populations. Finally, the size refuge of large individuals suggests that bivalve populations are likely to be sustained, provided a sufficient number young recruits escape predation long enough to grow large enough to become "crab-proof." Mussels have a similar size refuge from *Nucella* predation and *Piaste*r (Hunt and Scheibling, 1999 and Paine, 1976). Furthermore, on the East Coast of the US, green crab predation limits (but does not eliminate) mussel densities in the understory of algal canopies (Bertness, *et. al*, 1999).

For commercial ventures, preferences for smaller sizes may impact the number of individuals that survive to harvest size and may significantly increase costs if crab densities reach extremely high densities. Mitigation recommendations to minimize these potential impacts are discussed below.

When offered *M. trossolus* in different sizes, *Carcinus* did not distinguish between large and medium (although it did prefer medium to small sized mussels). This suggests that the crab is able to prey readily on all three size classes. Interestingly, *Carcinus* did show a significant preference for medium-size *M. galloprovincialis* over both the large and small size-classes.

Since the green crab did not appear to distinguish between the two species of mussel, I expected similar proportions of each size class to be consumed in both species. One potential explanation for these results is that there may be a slight difference in shell thickness or shape in the two species that led to lower predation rates on by *Carcinus* on larger *M. galloprovincialis* than were observed for *M. trossolus*. This may have important consequences in areas where the two species coexist as it indicates that the predatory effect on the *M. trossolus* is greater than on *M. galloprovincialis* which reaches a size refuge more quickly than the native species. There is a possibility that *M. galloprovincialis* could replace *M. trossolus* in locations where *Carcinus* predation *on M. trossolus* was sufficiently high.

Another possible explanation for the observed preference of medium-sized *M. galloprovincialis* is the order in which the experiments were conducted. The size preference test for *M. galloprovincialis* was conducted after the test for *M. trossolus* but the same green crabs were used in both trials. This could have been "controlled" by offering each crab the species in a random order. However, this was not possible because the water in the tanks that contained the exotic mussel, *M. galloprovincialis*, had to be treated with chlorine before it was released into the bay. Thus, it was necessary to conduct the all the trials with *M. galloprovincialis* at the same time. It is possible that the crabs' prior experience with *M. trossolus* influenced their choice in the experiment with *M. galloprovincialis*. In studies with intertidal snails, green crabs have been shown to improve their foraging efficiency with experience (Cunningham and Hughes, 1984). *Carcinus* has been shown to forage optimally. When selecting between different-sized mussels, crabs choose the size that offers the most energy relative to handling time - the time it takes to open and consume a prey item) (Elner and Hughes, 1978).

It is also possible, that after the first experience with mussels, the crabs were able to more readily identify "optimal" size class thus accounting for the slight differences in the two mussel experiments. The design of the experiments may also have insufficient power, repeating the tests may yield slightly different results each time. Increasing the number of replicates, or offering a larger number of mussels to each crab may give better results. In any case, the data from the mussel tests indicates that all three size classes of mussels tested are highly susceptible to *Carcinus* predation. Further testing must be conducted to determine at what size mussels become "crab-proof."

Species Preference Tests:

Species preference tests were conducted to match as closely as possible, natural conditions surrounding oyster culture in Yaquina bay. *Carcinus* showed a distinct preference for mussels, *M. trossolus*, over both the Pacific oyster, *C. gigas*, and the infaunal clam *Macoma* in this trial. This is consistent with studies by Dare *et. al.* (1983) in which *Carcinus* consumed a higher number of mussels than oysters in all size classes (no choice was offered). Thus, it appears that mussel culture in Oregon and throughout the Northwest may be more vulnerable to crab predation than Pacific oyster culture. In this experiment, two crabs that consumed all the mussels were excluded from the statistical analysis as explained in the above results section. These results, however, strongly support the notion that the green crab prefers mussels over the other two species. Particularly because one individual stopped eating after all the mussels had been consumed.

M. galloprovincialis and *M. trossolus* populations may also have different impacts due to crab predation. Since *M. galloprovincialis* has a higher growth rate, it may be able to reach a size refuge more quickly than *M. trossolus*. As demonstrated by this study and the work of Dare *et. al.* (1993), *Carcinus* is able to prey readily on Pacific oysters and oyster cultures are likely to be impacted by crabs and mitigation recommendations should be considered. As mentioned above, *Carcinus* exerts predatory control over mussel populations in its native range and may impact Yaquina populations in a similar manner.

Carcinus also chose mussels over the clam *Macoma nasuta*. Although I noted that *Macoma* has a thin-shell that is easily opened by the green crab when the clams are offered to the crabs without a refuge, the sediment refuge may protect *Macoma* from predation, at least in the presence of small mussels. In a study with the other native species, the native oyster, *Ostrea lurida* and an infaunal clam, *Cryptomya californica*, *Macoma* was not the preferred species (Kelly Chapin Palacios, personal communication, 1999). Thus, it is difficult to predict the precise nature of the impact that *Carcinus* predation may have on *Macoma* populations. Clearly, *Carcinus* is able to prey on this species, however, further investigation including field experiments are necessary to understand the degree of impact the green crab may have on this species.

In the preference experiments, the statistical results may have been affected by the exclusion of crabs that did not eat during the trials since these crabs demonstrated "no-preference". However, since they did not consume prey items, the proportions of different size classes and species remain the same regardless of the exclusion of these individuals. Another potential source of error in the preference experiments was that I was the only observer present to determine when the crabs had consumed approximately have of the preferred prey item. In future experiments, more than one person should be used to determine when experiments should be stopped in order to prevent observer bias.

Management Recommendations:

The prey size and species preferences described provide information that is essential for developing mitigation recommendations for aquaculture. As noted above, oysters are most vulnerable to crab predation before they reach 30 mm in length. Therefore, growers may be able to minimize seed losses by focusing on protection of oyster seed below that size. A variety of methods are available including; protective netting to cover seed, and active hand removal of crabs from culture beds. However, these strategies are often time intensive and have varying degrees of success (Jamieson *et. al.*, 1998).

A more effective strategy may be to establish different seasonal and life-history stages of out-planting. For example, early field placement would allow maximal growth prior to annual green crab settlement. Alternatively, cultch could be maintained in protected areas until they reach approximately 30 mm. These management strategies also apply to mussel culture, as mentioned above mussels will need to be held until they are larger than 30 mm to be protected from crab predation.

Growers might also consider offering preferred prey items in their culture areas to deter crab predation. For example, oyster growers that use tray, bag or bottom culture, may consider maintaining mussels in their oyster beds/bags/trays since *Carcinus* has a demonstrated preference for mussels over this Pacific oysters. This may mitigate, to some extent, crab predation on oysters. However, many oyster growers consider the presence of mussels a nuisance and thus a cost-benefits analysis of this strategy (along with quantitative studies of its effectiveness) are needed before the practice could be widely recommended. Furthermore, experiments need to be conducted to insure that the presence of mussels does not attract green crabs to oyster beds. At best, it could be a partial solution that may help deter crab predation when combined with the other strategies mentioned such as timed out-planting.

Impacts of meiofauna communities:

This study demonstrated that *Carcinus maenas* alters the composition of the estuarine meiofauna communities in Yaquina Bay. It is unclear whether *Carcinus* is impacting the meiofauna community through disturbance or predation or some combination of both. The activity of *Carcinus* decreased the evenness of the meiofaunal community. Evenness is defined as the relative abundance of species in a community. These changes resulted from changes in the relative abundances of a few species rather than the removal of a few dominants. Warwick *et. al.* (1990) observed similar changes in community evenness when examining the impacts of soldier crabs, *Mictyris platycheles*, on meiobenthic community structure. In particular, the relative abundance of Foxicephalidae and Paratanidae increased in enclosures with *Carcinus*, while Nannastacidae (primarily *Cumella spp.*) and Corophidae (primarily *Corophium spp.*) showed marked decreases in both their relative and numerical abundances. However, the total number of individuals in the community (irrespective of changes in composition) remained relatively unaffected. These results indicated that Foxocephalidae and Paratanidae become more dominant, with those two families comprising 74% of the total community abundance in enclosures containing crabs compared to 48.5% of the overall community make-up in the control cages. Communities in more complex habitats have a more even abundance distributions than those in simpler habitats (Cotgreave and Harvey, 1994). Therefore, *Carcinus* may be modifying, to some extent, the physical complexity of the meiofaunal environment through disturbance. In addition to their increases in relative abundance, both families showed an increased trend of individuals present in enclosures with crabs. A follow-up study that measured the relationship between habitat complexity and predator disturbance could help clarify this result.

One important result was the dramatic decline of Corphidae and Nannastacidae observed in the enclosures containing crabs. These declines suggest that these two families may be severely negatively impacted by the addition of *Carcinus* in their environment. Again, it is not possible to conclude whether the regulatory effect is predation or disturbance. Palmer (1988) demonstrated that disturbance accounted for 30-55% of predator-associated declines in copepods. These effects were significantly increased when water flow was increased. I have observed that Corophidae and Nannastacidae are highly mobile, fast swimmers that were frequently observed actively swimming in the water column, rather than hiding among the tanaid tubal mats when observed live in the laboratory. This may increase their susceptibility to predator induced drift, particularly in the presence of strong hydrodynamic flow. It is also possible that such behavior increases these organisms vulnerability to direct predation by *Carcinus*, although this explanation seems less likely given their ability to swim rapidly. Furthermore, it is possible that some of the small crustaceans escaped through the 1.25 cm mesh in order to avoid crab disturbance.

Of particular interest is the fact that tanaids (Family: Paratanidae) (primarily *Leptochelia dubia*) was not negatively impacted in this experiment. In a similar experiment, Grosholz and Ruiz (1995) observed significant reductions of tanaids in experimental enclosures with *Carcinus*. Furthermore, tanaid declines have been correlated with large settlement periods of *C. magister* in Bodega Harbor (Grosholz and Ruiz, 1995). These declines were followed by changes in the composition of the invertebrate community. In addition to this evidence, I expected that tanaid density would decrease because they are the most abundant species present at the site. It seemed likely that they would be impacted by random *Carcinus* activity (either accidental ingestion or dislocation), even if they were not the primary target of foraging activities. In my experiment, however, tanaids did not decline in experimental treatments. In fact, tanaids increased in relative abundance in this study.

Tanaids are numerically abundant and functionally important in embayments from California to Washington (Grosholz and Ruiz, 1995). These organisms build tubes that can alter both the physical and chemical characteristics of sediments and provide a habitat for other organisms (Woodin, 1974). Thus, they are an important component of the benthic community. It is important to understand why similar experiments are suggesting different impacts on this important taxon.

Several explanations may account for differences in tanaid impacts although there is no empirical evidence available to support them. First, it is possible that some physical characteristic of the environment may exist at my site, which provides tanaids with a mechanism to escape the negative impacts of crab activity demonstrated by Grosholz and Ruiz (1995). For example, perhaps different sediment grain sizes may affect the quality of the tubes tanaids construct, although I did not measure sediment grain size in this experiment. Woodin (1978) demonstrated that these tube-like structures provide important refuges from biological and physical disturbances. However, Bell and Woodin (1984) showed variable refuge effects of macrofauna on meiofauna under varying conditions. If the sites for the two experiments had different grain sizes, which in turn affected the quality of their tubes, perhaps tanaids at the Yaquina site were able to escape the deleterious impacts of *Carcinus* through building a more "crab-proof" habitat. Other species abundances and community composition did change in the enclosures containing crabs and so it is clear crabs may have impacted the physical environment, which may include the tanaid tubes. However, it seems possible that some physical characteristic in the environment (such as more "crab-proof" tubes) minimized the impacts of *Carcinus* on tanaids.

An alternate explanation may be that differing complexities of the tube habitat influenced crab-feeding activity. Marinelli and Coull (1987) found that "high complexity" habitats can promote mortality for meiofauna in the presence of fish predators. Although this result seems counter-intuitive, they proposed two potential explanations for their result that may apply to my experiment: 1) The interaction of prey within the refuge element may occur so they become more vulnerable; 2) the high complexity of the habitat allows predators to forage more efficiently among the structure (Marinelli and Coull, 1987). If different habitat complexities do affect predation rates, then it is possible that the species composition and physical environment different led to a "lower" complexity habitat in my experiment than that of Grosholz and Ruiz (1995) which led to *Carcinus* having decreased foraging efficiency on tanaids in my experiment.

A second potential explanation is that the crabs feeding activity differed in the two experiments. I used larger crabs in this experiment than those used in the Grosholz experiment. Ropes (1969) indicated that young crabs are more likely to prey on small crustacean prey while larger crabs prey mainly on macrofauna. This may account for the lack of predation on tanaids in my sample, although the explanation is questionable since other taxa were affected by the presence of the crab and since there was very little macrofaunal available in the enclosures. A more likely reason is that crab feeding activity on *Transennella spp.* (an abundant bivalve) in the experiment conducted by Grosholz and Ruiz (1995) lead to increased physical disturbance of the sediment which contributed to the decline of tanaids in that experiment. Schratzberger and Warwick (1999) observed that the degree to which *Carcinus* impacted nematode assemblages depended on the level of disturbance (via sediment modification) caused by feeding activity which differed depending on the quality of prey items available and the sediment type. Thus, it seems possible that the lack of a preferred prey item, such as *Transennella* species, led to a change in *Carcinus'* foraging strategy and this in turn led to a lower disturbance rate for tanaids. To fully understand the effects of *Carcinus* on tanaids and the proximate mechanisms behind those effects, further investigation is necessary. A laboratory examination of the potential effects of foraging activity levels with different combinations of meiofaunal prey items may help explain how and why *Carcinus* affects tanaids differently under varying conditions.

It is difficult to predict with certainty what, if any, indirect impacts may result in this community from the introduction of *Carcinus*. Grosholz and Ruiz (1996b) anticipated that *Carcinus* effects on benthic infauna may indirectly lead to changes in seabird populations, which rely on infaunal species for food, but so far these impacts have not been detected. The lack of observed impacts on seabirds may be due to the short-term nature of the studies used to evaluate the effect of *Carcinus* on North Pacific estuarine communities. Most ecological studies are conducted over a relatively short time period, less than five years (Brosnan and Menassee, unpublished review of papers in Ecology). Thus, it is possible that the introduction of *Carcinus* into estuaries and its subsequent impacts on meiofaunal communities may lead to changes beyond a single-trophic level, but the impacts may be difficult to detect unless long-term experiments are carried out. In addition to seabirds, microphytobenthos, such as diatoms, are a significant food source for several species of amphipods in the family Corophidae (Peletier, 1996). The negative impact of *Carcinus* on Corophidae may lead to reduced grazing intensity on diatoms as Corophidae are reduced.

Carcinus did not have significant impacts on polycheate or nematode assemblages in this experiment which is unsurprising since these organisms generally make up a relatively small percentage of *Carcinus*' diet (Ropes, 1968). The presence of the crab also did not appear to affect bivalves in the Tellinidae family (*Macoma* *spp.*). However, this may be due to the relatively low number of bivalves present in the samples since prey preference results in this thesis indicate that *Carcinus* is able to prey on species in the Tellinidae family.

There are some sources of error that may have effected this experiment. The systematic spatial arrangement of the enclosures may have biased the results, however, this is unlikely because meiofaunal communities exhibit spatial heterogeneity rather than periodicity (Mathieson and Nienhuis, 1991). Additionally, I was the only observer that counted the number of individuals for each family in the field experiment. This may have resulted in slightly skewed counts if, for example, I was more accurate at counting one taxa than another. Whenever possible, counts should be repeated by more than one observer to insure accuracy, however, this was not possible in this experiment.

One interesting result that was not adequately explained is the increasing number of Paratanaidae and Foxocephalidae in the enclosures with crabs compared to controls. Although, numeric increases were not significant, it seems possible that these the presence of the crab may lead to increased colonization of these species when the crab is present. It may be that the number of replicates in this experiment was too small to detect statistical differences or that increasing the length of the experiment to allow the species more time to colonize might yield clearer results. Further investigation is needed to properly evaluate proximal and ultimate causes for the impacts of *Carcinus maenas* on meiofaunal assemblages in Pacific Northwest estuaries.

CONCLUSION

The invasion of the green crab in Oregon may have important ecological and economic impacts. The green crab's biological plasticity, including its tolerance of a broad range of physiological conditions and its ability to produce large numbers of offspring with wide dispersal capabilities closely match Baker's description of the "ideal weed." In short, the green crab possesses many of the characteristics of a good invader and these qualities have allowed the green crab to expand its range around the world including into the North Pacific. Furthermore, the arrival and spread of the green crab on the West coast of the United States is similar to spread of the California spider crab previously described where the species "jumped" to new areas after establishing itself in a donor region. The increases in populations in donor regions in California and subsequent jumps northward along the Pacific coast strongly support the idea that the green crab arrived in Oregon through shifts in donor regions. Furthermore, the lack of brackish water crab species in Pacific estuaries as described by Jamieson *et. al.* (1998) supports the model put forth by Van Broembsen (1989) that recipient regions lacking key incumbents are more susceptible to invasion.

This study suggests that the green crab has the potential to persist in Yaquina Bay, and suggests that green crab predation is likely to impact *M. trossolus* populations and the commercially produced *M. galloprovincialis*, although this species may less vulnerable than the native species. *Macoma nasuta* may also be affected by the introduction of the green crab, although the degree of impact on this species remains unclear. Finally, the lucrative Pacific oyster aquaculture industry may be impacted if crabs reach high densities in Oregon estuaries.

The results of my study demonstrated that the presence of *Carcinus* impacts the evenness and relative composition of meiofaunal community through predation and/or disturbance. These preliminary results suggest that impacts on the meiofaunal community may be determined, to some extent, by the physical environment. These results should be interpreted cautiously as they may reflect current low numbers of *Carcinus* but as crab density increases, impacts may be more severe. Further studies should be conducted to determine the precise nature of *Carcinus* impacts on meiofauna before community compositions are permanently altered.

TABLE 1. Results of a Friedman test on *C. maenas* consumption of three different size classes of *M. trossolus* in prey size preference tests. (N=10).

Size class of *M. trossolus*	Mean N/ crab (±1 SE)	Friedman Chi-square	p
Small (10 mm ±2 mm)	1.2 (± 0.51)	5.556	0.06
Medium (20 mm ±2 mm)	3.0 (± 0.39)		
Large (30 mm ±2 mm)	1.9 (± 0.48)		

TABLE 2. Results of Wilcoxon sign test as a post-hoc to test for differences between pairs of three size classes for *M. trossolus* in prey size preference tests. (N=10).

Size classes compared	Z value	p
Small and Medium	2.235	0.02
Medium and Large	1.491	0.13
Large and Small	0.914	0.36

TABLE 3. Results of a Friedman test on *C. maenas* consumption of three different size classes of *C. gigas* in prey size preference tests. (N=10).

Size class of *C. gigas*	Mean N/crab (±1 SE)	Friedman Chi-square	p
Small (10 mm ±2 mm)	4.8 (±0.57)	14.973	0.001
Medium (20 mm ±2 mm)	3.8 (± 0.69)		
Large (10 mm ±2 mm)	0.4 (± 0.16)		

TABLE 4. Results of Wilcoxon sign test as a post-hoc to test for differences between pairs of three size classes for *C. gigas* in prey size preference tests (N=10).

Size classes compared	Z value	p
Small and Medium	-0.914	0.36
Medium and Large	-2.673	0.008
Large and Small	-2.812	0.005

TABLE 5. Results of a Friedman test of *C. maenas* consumption of three different size classes of *M. nasuta* in prey size preference tests. (N=9).

Size class of *C. gigas*	Mean N/crab (± 1 SE)	Friedman Chi-square	p
Small (10 mm ±2 mm)	3.1 (±0.79)	12.563	0.002
Medium (20 mm ±2 mm)	2.0 (± 0.33)		
Large	0.2 (± 0.15)		

TABLE 6. Results of Wilcoxon sign test as a post-hoc to test for differences between pairs of size classes for *M. nasuta* in prey size preference tests. (N=9).

Size classes compared	Z value	p
Small and Medium	-1.452	0.14
Medium and Large	-2.558	0.01
Large and Small	-2.530	0.01

TABLE 7. Results of a Friedman test of *C. maenas* consumption of *M. galloprovincialis* for prey size preference between three size classes. (N=10).

Size class of *M. galloprovincialis*	Mean N/crab (± 1 SE)	Friedman Chi-square	p
Small (10 mm ±2 mm)	2.7 (±0.39)	8.176	0.01
Medium (20 mm ±2 mm)	4.2 (± 0.51)		
Large (30 mm ±2 mm)	2.2 (± 0.44)		

TABLE 8. Results of Wilcoxon sign test as a post-hoc to test for differences between pairs of size classes for *M. galloprovincialis* in prey size preference tests.

Size classes compared	Z value	p
Small and Medium	-1.995	0.04
Medium and Large	-2.699	0.007
Large and Small	-0.604	0.55

TABLE 9. Results of a Friedman test for *C. maenas* species preference of three species in Yaquina Bay, Oregon, (N=6).

Species	Mean N/crab (± 1 SE)	Friedman Chi-square	p
M. trossolus	8.8 (±3.09)	6.100	0.04
C. gigas	1.1 (± 0.98)		
M. nasuta	0.5 (± 0.34)		

TABLE 10. Results of Wilcoxon sign test as a post-hoc to test for differences between pairs of different species in preference tests.

Species compared	Z value	p
M. trossolus and *C. gigas*	-2.023	0.04
M. trossolus and *M. nasuta*	-1.897	0.05
M. nasuta and *C. gigas*	-0.816	0.41

TABLE 11. Results of a Wilcoxon sign test of *C. maenas* preference tests between two mussel species (N=9).

Two species of mussels	Mean N/ crab (± 1 SE)	Z-value	p
M. trossolus	3.4 (±0.65)	-0.744	0.46
M. galloprovincialis	3.0 (± 0.86)		

Table 12. Evenness index mean values (+ 1 SE) and treatment factor in a one-way ANOVA for the field enclosure experiment in Yaquina Bay (N=10, treatment, N=11, control).

Experimental (n=10)	Control (n=11)	F value	p
0.6928 (0.019)	0.7562 (0.020)	5.096	p=0.036

Table 13. Abundance of taxa in cores in field-enclosure experiment. For each taxa the number for each core (±1 SE) are given along with the effect of the treatment factor in a one-way ANOVA (N=10, treatment, N=11, control).

Taxon	Experimental	Control	F-value	p
Crustacea				
Tanaidacea				
Paratanaidae	329.7 (67.41)	281.7 (32.41)	0.508	0.486
Cumacea				
	11.0 (5.37)	49.5 (5.21)	10.761	0.001
Nannastacidae				
Amphipoda	218.9(24.18)	143.0 (30.83)	0.887	0.358
	61.7 (23.65)	242.3 (32.65)	26.051	0.000
Foxocephalidae				
Corophidae	58.1 (17.13)	91.5 (40.17)	0.778	0.389
Nematodes				
Annelidia	38.2 (7.16)	27.0 (4.21)	1.545	0.229
Polychaeta	36.6 (8.90)	58.6 (8.83)	3.690	0.70
Capitellidae				
Supionidae				
Mollusca	5.8 (1.90)	11.4 (1.61)	0.792	0.385
Bivalvia				
Tellinidae				

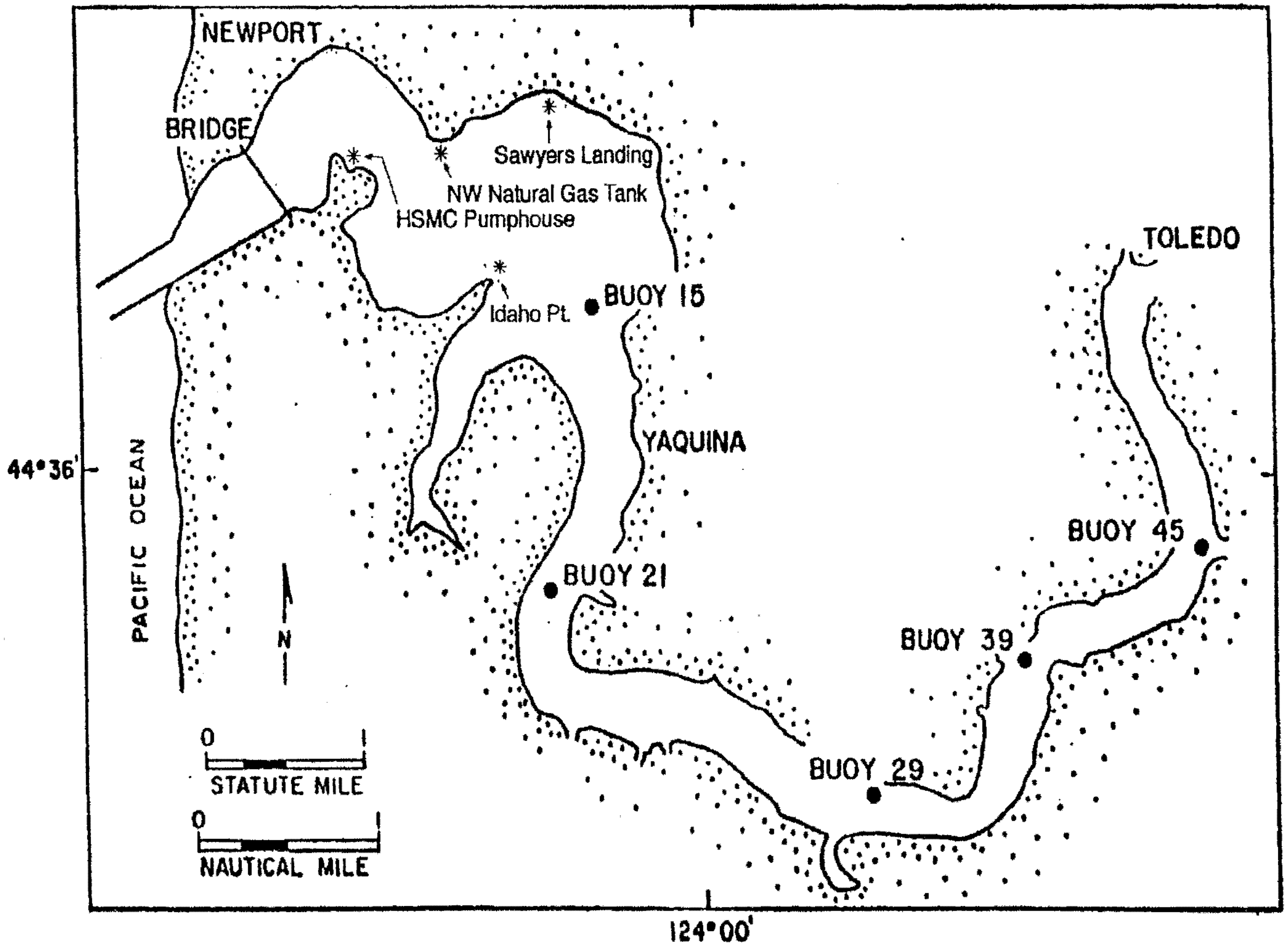


Figure 1. Location of trapping sites in Yaquina Bay

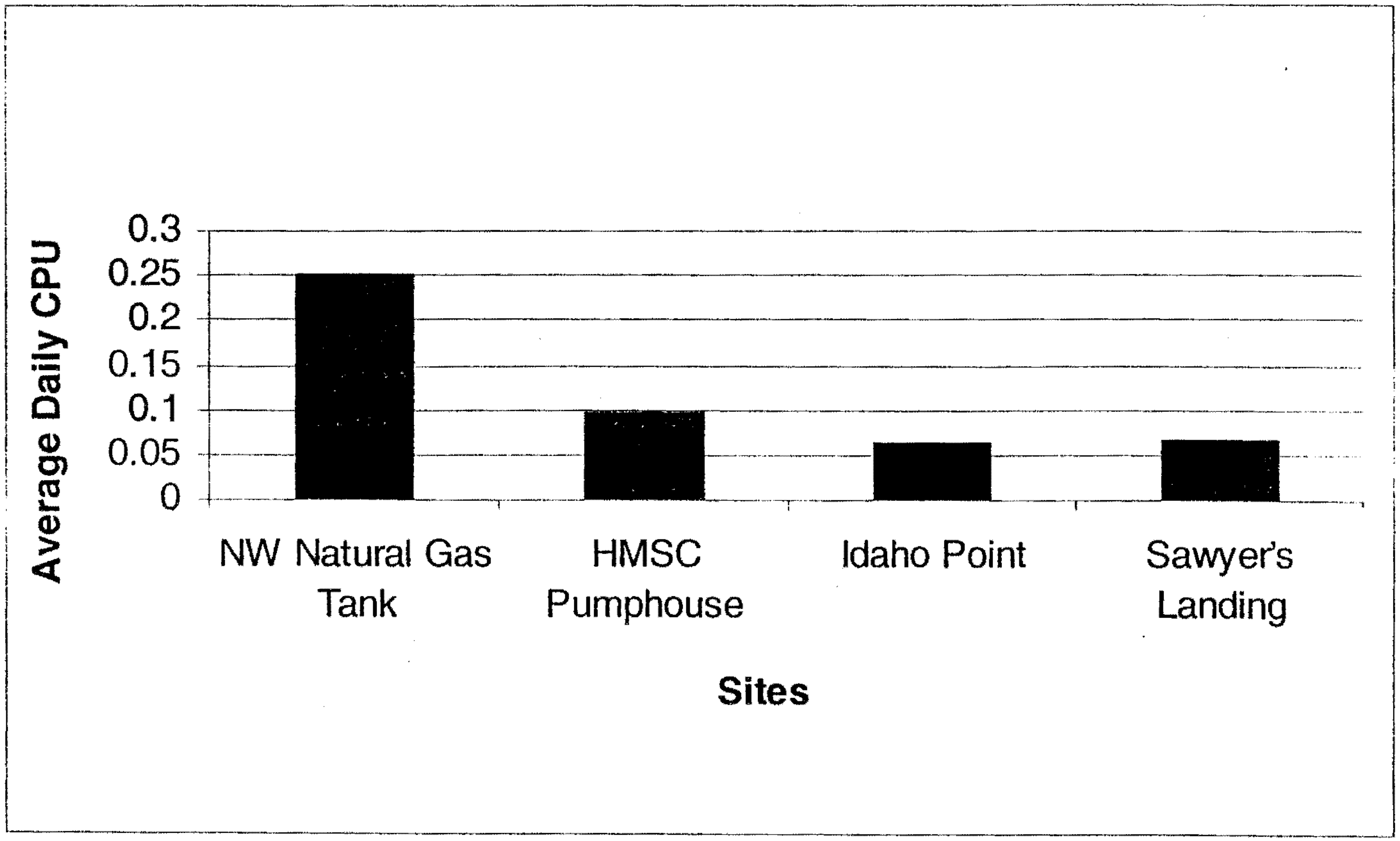


FIGURE 2. Daily average catch per unit (CPU) of *C. maenas* at four intertidal trapping sites from August 10, 1999 through September 9, 1999 using modified minnow traps.

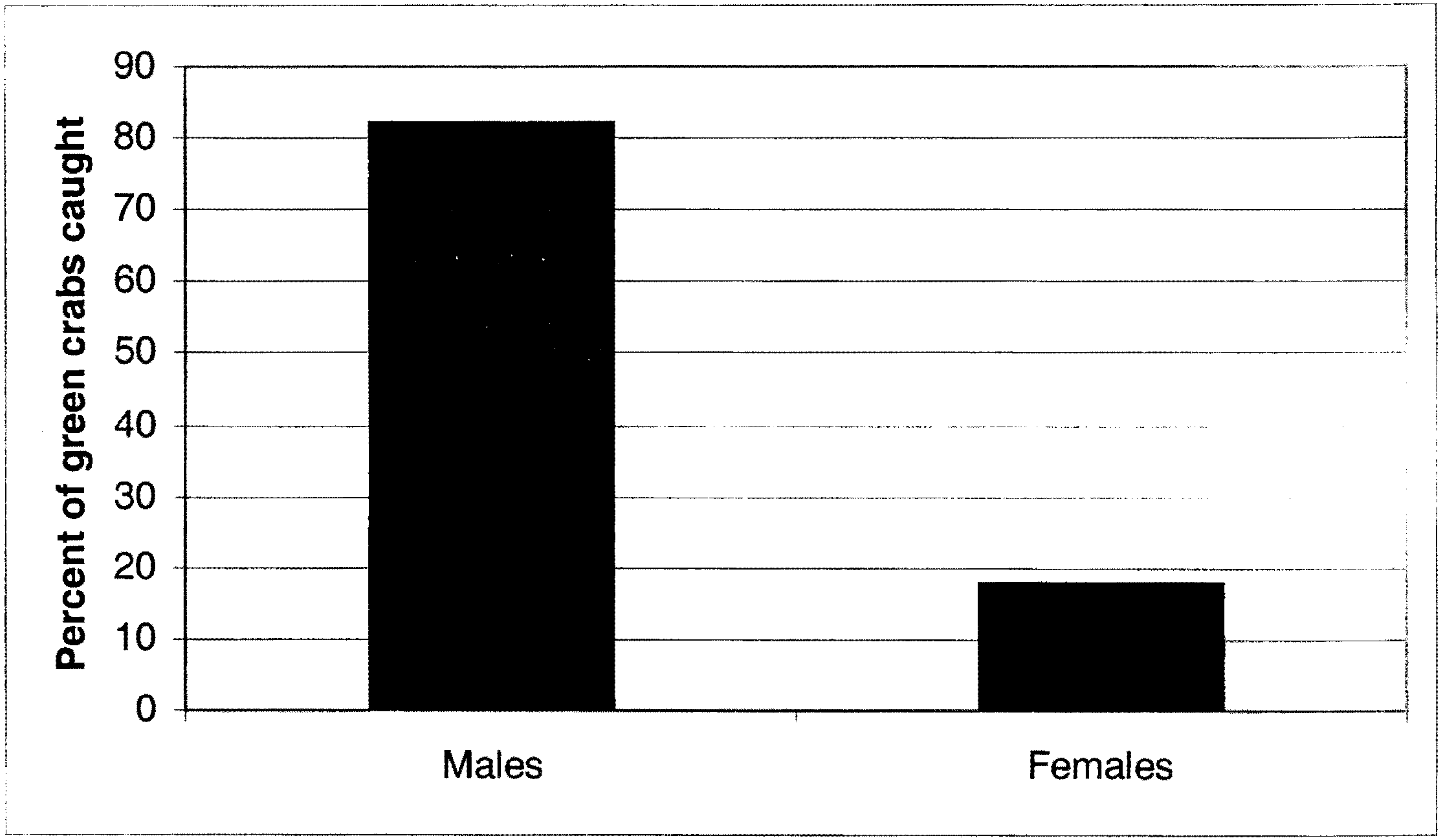


FIGURE 3. Sex ratio of *C. maenas* caught in four intertidal trapping sites in Yaquina Bay, Oregon from August 10, 1999 through September 9, 1999.

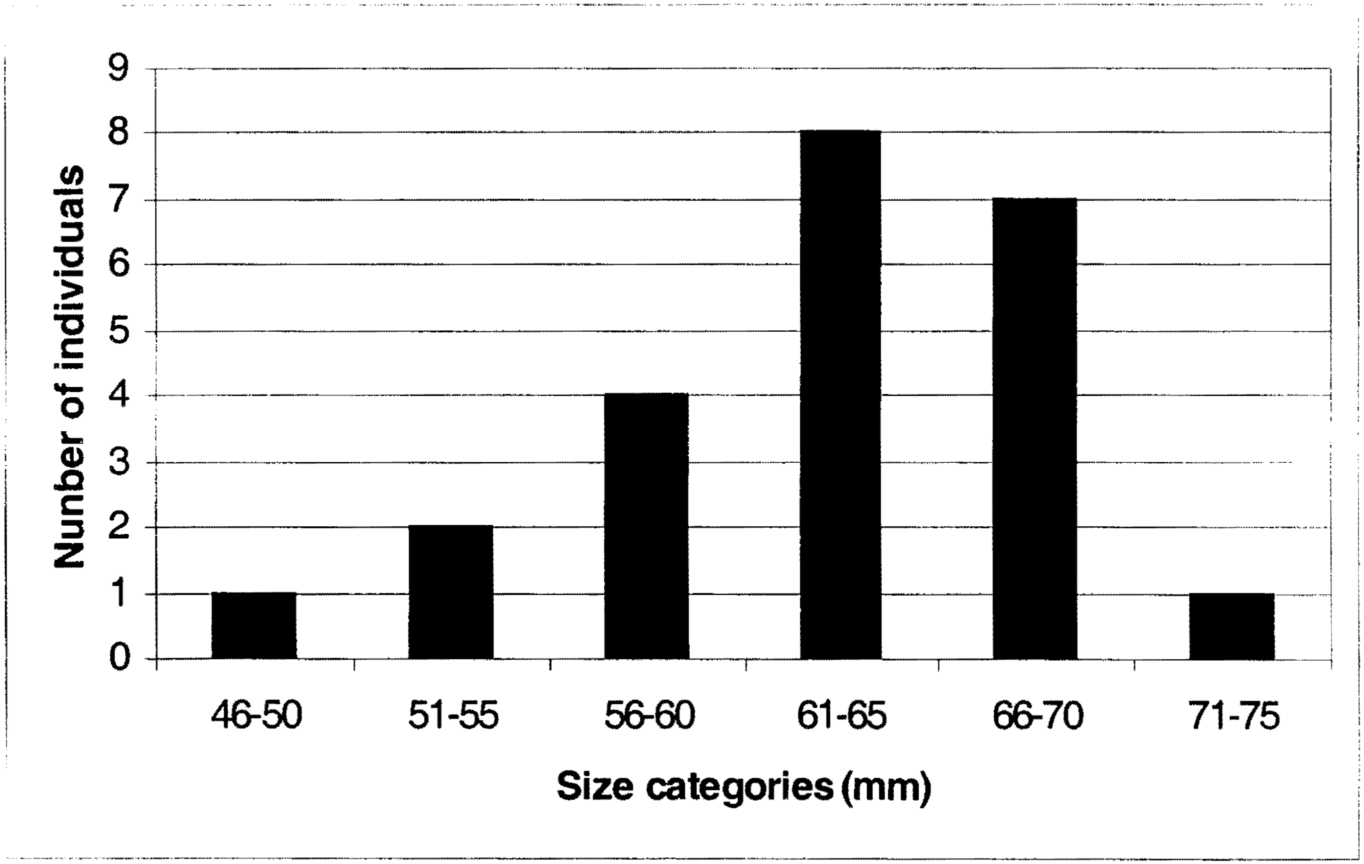
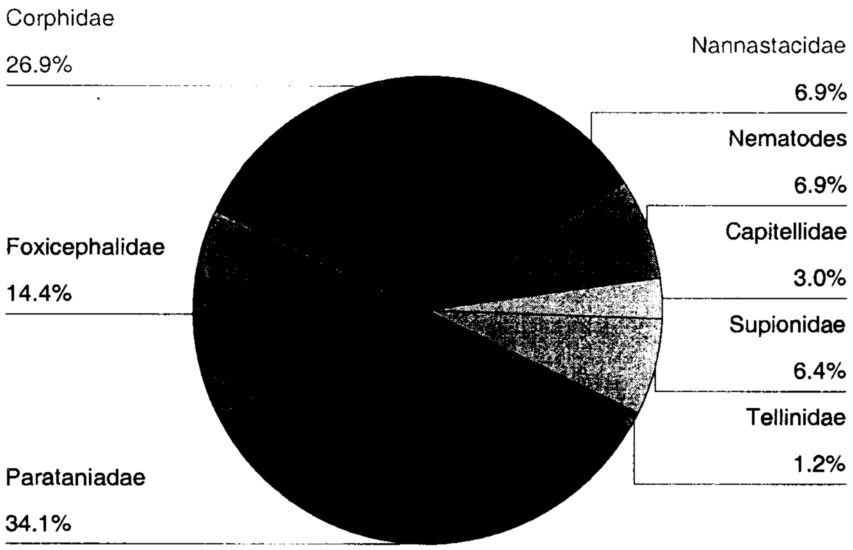


FIGURE 4. Size frequency distribution of *C. maenas* caught at four intertidal trapping sites in Yaquina Bay, Oregon from August 10, 1999 through September 9, 1999.

Species composition in control plots.



Species composition in treatment plots.

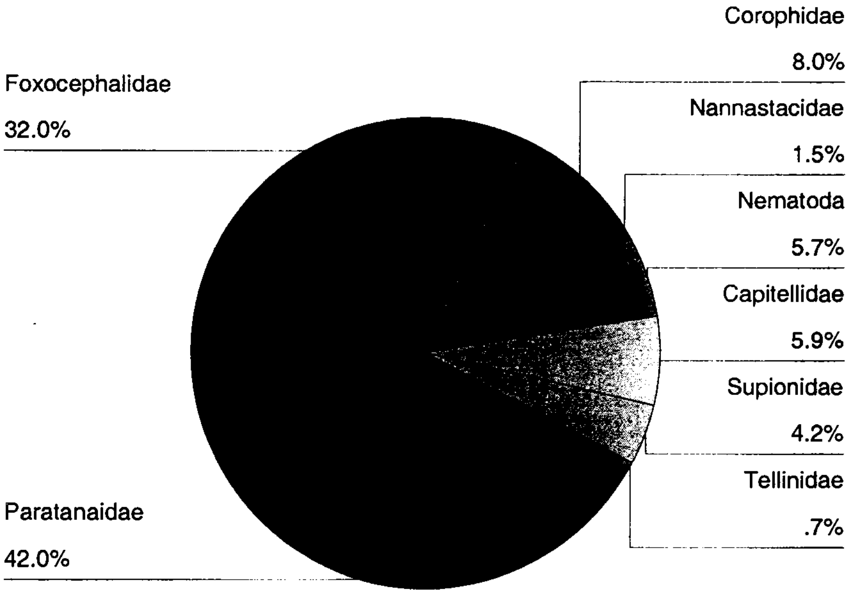
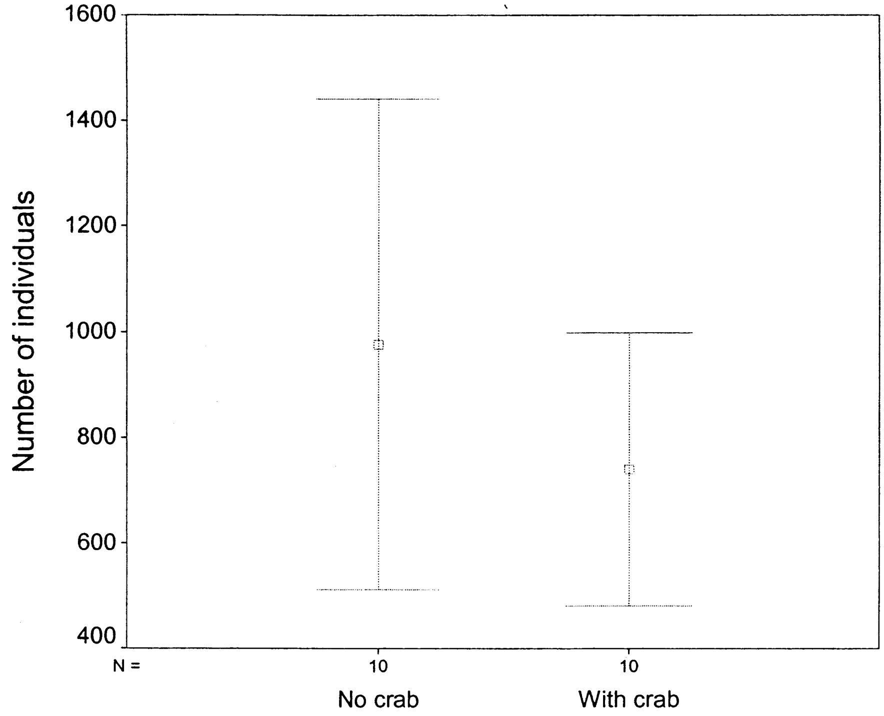


FIGURE 5. Meiofauna community composition in control and treatment groups for *Carcinus* field enclosure experiment.

FIGURE 6. Total meiofauna community abundance in field enclosure experiments. Results of Kruskal-Wallis (Chi-square=0.496, p=0.48)(N=10 treatments, 11 controls).



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