AN ABSTRACT OF THE THESIS OF

Chris Hunt for the degree of Master of Science in Environmental Sciences presented on June 8, 2001. Title: The Role of Predation by the Red Rock Crab, Cancer productus, on the Invasive European Green Crab, Carcinus maenas, in Yaquina Bay, Oregon.

Abstract approved: ____________________

Sylvia Yamada

In Yaquina Bay, Oregon, I observed very little overlap in the distribution of the invasive green crab, Carcinus maenas, and the larger red rock crab, Cancer productus. Red rock crabs dominate the more saline, cooler lower estuary and green crabs, the less saline, warmer upper estuary. Because caged green crabs survive well in the lower estuary, I decided to test the hypothesis that red rock crabs prey on green crabs and thus contribute to their exclusion from the more physically benign lower estuary.

A laboratory species interaction experiment was designed to determine whether red rock crabs prey on smaller green crabs at a higher rate than on smaller crabs of their own species. Crabs of both species were collected and sorted by weight into three size classes: small, medium and large. Small and medium crabs of both species were paired with green crabs or red rock crabs of various sizes. Crab pairs were housed in individual arenas and allowed to interact for seven days. When conspecifics were paired, mortality was less than 15%, even in the presence of larger crabs. Smaller red rock crabs survived well in the presence of larger green crabs, but the reverse was not true. When small green crabs (60-67 mm carapace width) were matched with medium and large red rock crabs, their mortality increased to 52% and 76% respectively. A less dramatic pattern was observed for medium green crabs (73-80 mm) in the presence of medium and large C. productus. Thus on the West Coast of North America, the more aggressive red rock crab, Cancer productus, has the potential to reduce the abundance of Carcinus maenas in the more saline and cooler lower estuaries.

by

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INTRODUCTION

The European green crab, *Carcinus maenas* (Decapoda: Portunidae) (Figure 1) is endemic to the North Sea, the eastern Baltic Sea, and in the Atlantic extends from Mauritania to Norway, and southern Iceland (Crothers 1968). *C. maenas* is a very successful invader and was established in the northwestern Atlantic by 1817 (Say 1817), southern Australia prior to 1900 (Fulton and Grant 1900), South Africa prior to 1983 (Le Roux et al. 1990), Tasmania around 1990, and into the northeastern Pacific (San Francisco Bay) prior to 1989 (Cohen et al. 1995; Grosholz and Ruiz 1995).

The European green crab, *Carcinus maenas*, and the red rock crab, *Cancer productus*.

Figure 1. European green crab, *Carcinus maenas*, on the left, and the red rock crab, *Cancer productus*, on the right. Note the difference in carapace shapes between the two species.
*Carcinus maenas* was first detected along the eastern Pacific 70 km north of San Francisco Bay, in a gill net in Estero Americano, in May, 1989 (Cohen et al. 1995). In the same year, a well-established population was found in San Francisco Bay (Cohen et al. 1995). In 1993 it spread to Bodega Harbor, Bolinas Lagoon, Tomales Bay, Drakes Estero, and in 1995 it was discovered in Humboldt Bay (Grosholz and Ruiz 1995; Miller 1996). Larval transport via north-flowing currents was the most likely mechanism of this spread (Grosholz and Ruiz 1995).

The first reported specimen of *C. maenas* in Oregon was found by Heath Hampel on his oyster ground in Coos Bay, in late March, 1997 (Richmond 1998). By the end of fall 1997 nine crabs were found, ranging in size from 56-86 mm carapace width (CW), in over 200 hours of shore searching and 800 hours of trapping. Thus in 1997, green crabs were rare in Oregon. During the spring and summer of 1998, however, a strong new, year class of *C. maenas* appeared in seven Oregon estuaries as well as in two Washington bays and on Vancouver Island. We believe that the unusually strong northward flowing El Niño currents of the previous fall, winter, and spring could have transported planktonic larvae from established populations in California to Pacific Northwest shores (Behrens Yamada and Hunt 2000; Yamada et al. 1999).
Problem Definition

*Carcinus maenas* is one of the most extensively studied species of crab (Reid et al. 1997). Although its previous popularity with biologists was related to its ease of capture, ubiquity, and suitability for short-term laboratory studies (Reid et al. 1997), recent focus has centered on its economical and ecological impact as an invader (Cohen et al. 1995; Grosholz and Ruiz 1995; Grosholz 2000). Much of the concern surrounds its potential to impact the shellfish industry along the West Coast of the US, disrupting the natural community through predation, competition, and habitat alteration (Cohen et al. 1995).

The green crab is large compared to the native shore crabs (*Hemigrapsus* spp.) of the eastern Pacific coast, approaching a maximum carapace width of 100 mm ([P. --O. Moksnes, unpublished observation). It has been shown to consume prey items from 104 families and 158 genera in 5 plant and protist and 14 animal phyla (Cohen et al. 1995). Its presence can result in significant reductions of algae, marsh vegetation, crustaceans, mollusks, and to some degree young flat fish (Ropes 1968; Reise 1978; Scherer and Reise 1981; Elner 1981). McDonald (2000) found that *C. maenas* out-competes similar sized juvenile Dungeness crabs, *Cancer magister*, for both refuge and freshly killed clams within the lab. *Carcinus maenas* has broad physiological tolerances to reduced salinity, with adults tolerating short-term exposure of 4 to 54 ppt (Broekhuysen 1936; Crothers 1967; Muus 1967; Perkins et al. 1969), and larvae developing at 17 ppt (Rasmussen 1973). *Carcinus maenas*
occupies many different habitat types from open sand, mudflats, shell and cobble, rocky shoreline to algal communities (Rangeley and Thomas 1987).

The combination of its large size, generalized diet, and its broad salinity tolerance makes *Carcinus maenas* the largest crab species to inhabit and reproduce in brackish waters of Oregon estuaries. The other two estuarine crabs are the native *Hemigrapsus oregonensis* (maximum 32 mm), and another invasive crab, *Rithropanopeus harrisii* (maximum 19 mm). Because *Carcinus maenas* is the first portunid to establish itself in the northeastern Pacific, it may exploit resources not available to native crabs (Jamieson et al. 1998). The large native cancrids are restricted from the upper intertidal by their physiological tolerances. The smaller graspsids that inhabit the upper intertidal are much smaller than *Carcinus maenas* and are unable to prey on larger gastropods that are within the prey range for *Carcinus maenas*. The smaller size of these crabs also makes them vulnerable to predation by *Carcinus maenas* (Grosholz and Ruiz 1995). The presence of this new predator could alter established size, distribution, and zonation patterns of prey such as gastropods and graspsid crabs.

Cohen et al. (1995) suggest that there may be significant economic impacts due to the arrival of *Carcinus maenas*. In its native range *C. maenas* predation can limit the abundance of mussels, sea urchins, some species of crabs, dogwhelks and littorines (Ebling et al. 1964; Muntz et al. 1965; Dare and Edwards 1976; Janke 1990). *Carcinus maenas* predation has also been implicated in the decline of the soft-shell clam, *Mya arenaria*, along the coasts of New England and southeastern Canada.
Carcinus maenas can also be a significant crab predator, preying upon the native yellow shore crab, H. oregonensis, and juvenile Dungeness crab, Cancer magister, along the northeastern Pacific coast (Grosholz and Ruiz 1995).

Along the southwestern coast of Nova Scotia Carcinus maenas coexists in the same habitat as native cancrid species. Analysis of stomach samples showed that juvenile cancrids and green crabs both are prey items of adult green crabs (Elner 1981). Grosholz (2000) documented the reduced densities of the native clams, Nutricula tantilla and N. confusa, and the native crab Hemigrapsus oregonensis three years after green crabs invaded the soft-bottom community of Bodega Harbor.

As an intertidal migratory species, adult green crab forage in the upper intertidal at high tide and return to the lower intertidal or subtidal regions at low tide (Edwards 1958; Naylor 1958, 1962; Klein Breteler 1976; McGaw and Naylor 1992a; Hunter and Naylor 1993; Attrill and Thomas 1996; Burrows et al. 1999; Zeng et al. 1999). In Oregon estuaries green crabs are subject to predation from Western gulls, Larus occidentalis, Glaucous-winged gulls Larus glaucescens, and native adult crabs such as Cancer magister, and the red rock crab, Cancer productus (Figure 1) (personal observations). Among eastern Atlantic species, Elner (1981) found that adult lobsters and rock crabs, Cancer pagurus, an Atlantic species very similar to C. productus, both prey on adult green crabs. This observation suggests that predation may result in decreased abundance or even exclusion from certain “high predation zones” limiting the ability of C. maenas to exploit these regions.
Preliminary Findings

While trapping Oregon estuaries to document the arrival of *Carcinus maenas* during the summer of 1998, I noticed *C. maenas* was more abundant in the upper than in the lower estuary where the less physiologically tolerant cancrids dominate in Tillamook and Yaquina bays. This effort documented the arrival of a strong, new 1997/98 year class. By September, 1998, these crabs had reached adult size with a mean of 47 mm ± 5 mm (Figure 2).

Figure 2.
Size Frequency Distribution for *Carcinus maenas* in Yaquina Bay, Oregon, 1998 depicting the strong 1997/98 year class of *Carcinus maenas*. 
The native adult cancrids that inhabit the lower estuary include the Dungeness crab, *Cancer magister* up to 260 mm, the red rock crab, *Cancer productus* to 200 mm, the Pacific rock crab, *Cancer antennarius* to 178 mm, and the graceful crab, *Cancer graciliis* to 115 mm. These large *Cancer* crabs thus have a size advantage over *C. maenas*, which reaches a maximum carapace width of 100 mm. *C. productus*, *C. antennarius*, and *C. magister* adults have been confirmed to prey upon the smaller *C. maenas* (personal observation).

The most striking distinction in crab distribution was between *Carcinus maenas* and the red rock crab, *Cancer productus*. In Yaquina Bay, preliminary observations indicated that the catch per unit effort (CPUE) was highest for *C. maenas* where there were few or no *C. productus* present, and where the CPUE for *C. productus* was high, *C. maenas* was rare. Further, the areas of high *C. maenas* abundance were areas of fluctuating temperatures, fine sediment substrates, and low salinity at low tide. While *C. maenas* is able to persist under these conditions, *C. productus* has much lower tolerance for low salinities and high temperatures (Defur and McMahon 1984 a, b). *Cancer productus* prefers lower intertidal areas protected from wave action where it feeds upon a variety of prey, including decapod crustaceans (Robles et al. 1989). The distribution of *C. productus* throughout the Yaquina Bay estuary is determined by these physiological tolerances. This makes the habitat under variable conditions too stressful for *C. productus* to occupy. *Carcinus maenas* was physiologically able to tolerate the areas where CPUE for *C. productus* was high (Broekhuysen 1936; Crothers 1967; Muus 1967; Perkins et al. 1969), yet *C.
maenas was absent, or rare. The observation that five green crabs protected by a cage on a sloping rocky shore inhabited by red rock crabs survived for over a month (Behrens Yamada, unpublished data) suggests that species interaction may be limiting the abundance of C. maenas in this habitat.

Statement of Purpose

The goal of this study was to determine if the native red rock crab, Cancer productus, has a limiting effect on the distribution and abundance of the nonindigenous European green crab, Carcinus maenas within Yaquina Bay, Oregon. This was accomplished with two objectives; 1) to determine if the preliminarily observed negative relationship between Carcinus maenas and Cancer productus is real by sampling more intensely and 2) to determine whether heterospecific adult-adult interactions exhibit greater potential as a mechanism for localized population control than that for conspecifics under laboratory conditions. The specific questions addressed by this research included the following; (1) Is there a difference in CPUE in habitat suitable for both species within Yaquina Bay, Oregon? (2) Do adult C. productus prey upon C. maenas to a greater degree than on similar sized conspecifics?
Selected Case Histories of Biological Invasions

Nonindigenous species represent one of the greatest threats to the loss of natural diversity in ecosystems worldwide. Introduced fire ants, *Solenopsis invicta*, are known to kill amphibians, lizards, hatchling turtles, and alligator eggs in the southeastern United States (Culpepper, 1953; Hamman et al. 1986; Vinson and Sorenson 1986). The European starling, *Sturnus vulgaris*, first introduced into the United States in 1918, has reduced native cavity nesting birds such as the western bluebird and purple martin (Kessel 1957; Small 1974; Grabill 1977; Troetschler 1976). The cane toad, *Bufo marinus*, is displacing populations of native amphibians in Australia, Florida, US Virgin Islands, Guam, and Samoa (Stohler and Cooling 1945; Straughan 1966; Sabath et al. 1981). The gypsy moth, *Lymantria dispar*, was introduced into Boston around 1868, and has since dramatically reduced the once-dominant oak species in the eastern US through defoliation (Doane and McManus 1981; Ganser et al. 1987). The river tea tree, *Melaleuca quinquenervia*, was imported in 1906 and planted extensively to drain the Florida everglades, but is now expanding beyond control at 50 wetland acres each day (Morton 1966, 1976; Balciunas and Center 1991; Hoffsetter 1991). Saltcedar, *Tamarix* spp., with their extremely long tap roots have lowered water tables in regions of the western US and Great Basin where they have become locally abundant (Robinson 1965; Baum 1967;
Davenport et al. 1982; Brotherson and Field 1987; Busch et al. 1992). Purple
loosestrife, *Lythrum salicaria*, producing 2,700,000 seeds annually, is now present in
26 US states covering approximately 400,000 acres and costing $45 million annually
(Thompson et al. 1987; Anderson 1995; Notzold et al. 1997; Mullin 1998). These
types of introductions result in the annual loss of billions of dollars to local
economies and industries, and represent an immeasurable disturbance to native
communities across all types of habitats globally.

Two seminal works set the stage for the scientific study of invasion biology:
the compilation of studies edited in 1956 by William Thomas entitled *Man’s role in
Changing the Face of the Earth*, and the work by Charles Elton who wrote *The
Ecology of Invasions by Animals and Plants* (1958). These works recognized that
biological introductions were a threat to the stability of natural systems and could
lead to unpredictable “ecological explosions.” Since the time of these first
publications, biological introductions have become increasingly recognized as one
the greatest threats to native ecosystems. Not only have invasions been recognized as
a biological threat to natural diversity but recent examples have demonstrated their
potential for adverse economic impacts as well.

Intentional introductions of exotic species have been taking place for
centuries. When human populations moved across the globe they transported species
they were familiar with to their new destination, either as food resources or as
aesthetic symbols of their former land. Examples of this include the introduction of
The European Wild Boar, *Sus scrofa* (Frankenberger and Belden 1976), the
introduction of goats, *Capra hircus*, to islands worldwide (Yocum 1967; Coblentz 1978; King 1985), the introduction of starlings into North America (Kessel 1957), and the introduction of rabbits to Australia (Rolls 1969; Pickard 1991). But while each of these is an example of introduced species that thrived in their new environment, not all exotic species are invasive. We commonly move exotic plants around the world, but not all of these plants become established in their new habitat. Marigolds, lillies, mums, many rose species, and even cacti are non-native species imported into Oregon on a daily basis, yet their persistence, reproduction and dispersal appear restricted, and rarely extends beyond where intentionally planted, and may result in little or no effect upon the native fauna. We also introduce species accidentally, or have them “escape” from their initial introduction site, such as kudzu, Russian knapweed, yellow starthistle, and purple loosestrife, which expand beyond our control and establish themselves in unintended habitats with varied impacts to these new systems (Miller and Edwards 1982; Maddox et al. 1985; Thompson et al. 1987; Anderson 1995; Notzold et al. 1997; Mullin 1998; Ward 1998). Many times these species are presented with a new habitat similar to their own, but in the absence of their native predators, competitors, diseases and parasites enabling them to rapidly overwhelm and spread throughout this new range.

Although terrestrial and freshwater ecologists have long recognized that biological introductions pose a threat to natural communities, similar introductions in marine systems have undergone less study (Carlton and Geller 1993). With increasing global commerce, marine introductions are occurring at a large scale,
through mechanisms such as ballast water discharge, hull fouling, aquaculture transport, and intentional introductions (Carlton 1987, 1989, 1996 a, c, 1999; Ruiz et al. 1997). These introductions can lead to profound ecological changes in the structure and diversity of many coastal communities, including exposed rocky shores, sublittoral soft-bottom habitats, sandy beaches, marshes and estuaries (Carlton 1987, 1989, 1996 a, c, 1999; Carlton and Geller 1993; Ruiz et al. 1997; and Cohen and Carlton 1998).

The wooden hulls of early Viking sailing ships were likely covered with a large fouling community (Carlton and Hodder 1995). When these ships arrived in a new destination there was the potential for some of these fouling species to establish themselves into the new environment (Carlton and Hodder 1995; Carlton 1999). It is believed some of the greatest inoculations during these early periods occurred when the ship, in a state beyond repair, would be intentionally sunk in the new destination, complete with its fouling community (Carlton and Hodder 1995; Carlton 1999). While many of these nonindigenous species did not persist, some have become very successful invaders.

Within recent history these rates of habitat inoculations with nonindigenous species have occurred at a grander scale with the advent of ballast water in large ocean going vessels (Carlton 1985, 1987, 1989, 1999; Carlton and Geller 1993). Once again many of these exotic organisms did not establish themselves in the new environment, but some have, including the green crab, *Carcinus maenas* (Grosholz and Ruiz 1995), and the Asian clam, *Potamocorbula amurensis* (Carlton et al. 1990),
within US coastal and estuarine habitats, the Japanese seastar, *Asterias amurensis*
into Tasmania and Australia (Turner 1992; Morris and Johnson 1998), and the comb
jelly *Mnemiopsis leidyi* into the Black Sea (Harbison and Volovik 1994), among
many others.

Geographical barriers that historically isolated species are removed as a
function of human transport. The Erie Canal, once in place, allowed the Atlantic Sea
Lamprey, *Petromyzon marinus*, access to the Great Lake ecosystem from which it
was previously isolated (Smith 1971; Houston and Kelso 1991). The Rocky
Mountains prevented the establishment of smallmouth bass, *Micropterus dolomieui*,
to the west, yet now they may represent another of the many threats to west coast
salmonids (Linder 1963; Idaho Fish and Game 1990; San Joaquin River
Management Program 1995). The shear distance of the world’s oceans and
continents prevented the western Pacific shore crab, *Hemigrapsus sanguineus*, from
establishing itself along the shores of the western Atlantic, and now it may become
the most dominant crab along these shores (Casanova 1999; Gerard et al. 1999;
Lohrer et al. 2000). Many, many other examples exist where once unsurpassable
biogeographic barriers are breached through human activities, and ecosystems
evolved independently are blended together.

Other introductions can support industries and contribute to the stability of
costal economies. The Pacific oyster, *Crassostrea gigas*, a Japanese species, has
been intentionally introduced to supply the industry with a sustainable market
species to use as a foundation for a multi-million dollar shellfish industry around the
world (Ruiz et al. 1997). Although there is a high demand for this marketable species, it did not come without its costs. The Atlantic oyster, *Crassostrea virginica* had been intentionally introduced repeatedly into Pacific coast estuaries from 1869 through the first part of the twentieth century in an attempt to establish a shellfish industry (Ruiz et al. 1997; Carlton 1999). The attempt to establish commercial species, such as these, alters the structuring of the benthic community and results in the establishment of a number of exotics associated with them, including epibionts, disease, mudsnails, and oysterdrills (Ruiz et al. 1997; Carlton 1999).

With many of the marine introductions thought to be associated with ballast water or hull fouling (Carlton 1987, 1989, 1996a, 1999), it is not surprising that most of the marine exotics identified have come from areas with international ports (Ruiz et al. 1997). Chesapeake Bay receives >10,000,000 metric tons of foreign ballast water and the associated exotics annually, with many of these inoculations occurring from ships able to carry >150,000 metric tons of ballast water each (Ruiz et al. 1997). This volume creates the potential that on any given day 3,000 species are being transported globally in the ballast tanks of ocean going vessels (Carlton 1996a).

Cohen and Carlton (1998) demonstrated the dramatic rate at which San Francisco Bay is becoming colonized by exotic species with the current invasion rate greater than one newly established species every 14 weeks. The increasing evidence of the dramatic scale at which these introductions are occurring in marine systems suggests that we may lose much of our native species diversity within these systems.
Examples of Marine Nonindigenous Species

In 1993, the US congressional Office of Technology Assessment determined a minimum of 4,500 established nonindigenous species within the United States. This figure represents 2-8% of the taxonomic groups examined (Ruiz et al. 1997) and is likely an underestimate of the total number of nonindigenous species present. Of that number approximately 400 of the exotic species are established along the Pacific, Atlantic, and Gulf coasts (Mills et al. 1996; Cohen and Carlton 1998), and of that total 212 of these species are found within San Francisco Bay (Ruiz et al. 1997) and 97 found within Coos Bay, Oregon (J.T. Carlton, personal communication, 2000).

The northern Pacific seastar, *Asterias amurensis*, is a voracious predator, preying heavily on bivalves, impacting both the native benthic ecosystem and the shellfish industry (Mosig 1998; Ross and Johnson 1998). It is commonly found in the intertidal and shallow subtidal but has been reported at depths up to 200 meters (Goggin 1998). This seastar is native to the coastlines of China, Japan, Korea and Russia, and is also found in the Bering Sea along the shores of Alaska and northern Canada. *A. amurensis* is believed to been introduced to southeastern Tasmania in the late 1970’s and then, subsequently, invaded Port Phillip Bay, the location of Melbourne harbor in the state of Victoria, as recently as 1995 (Turner 1992; Byrne et al. 1997; CRIMP Tech. Report 15, 1998). The first discovery of a specimen in the
Derwent estuary, near Hobart, was discovered in 1986. Yet by 1998 estimated densities for the Derwent estuary suggested a population of 30 million seastars (Goggin 1998) which is thought to have contributed to the severe decline of bivalves within invaded regions (Grannum et al. 1996). Investigations of the physiology and reproductive nature of *A. amurensis* suggest that this species poses a threat from the east coast ports north of Newcastle to the west coast ports of Fremantle (Sutton and Bruce 1996; Morris and Johnson 1998). The source of the invading population has been proposed as ballast water taken up in Japan, but another possibility includes hull fouling (Bruce et al. in press).

The spiny water flea, *Bythotrephes cederstroemi*, a cladoceran native to northern Europe west of the Caspian Sea, was discovered at least as early as 1984 and possibly as early as 1982 in Lake Huron. It subsequently spread throughout the Great Lakes region by 1987 into more than 30 lakes in the United States and Canada (Bur et al. 1986; Lehman 1987; Evans 1988; Garton and Berg 1990; Johannsson et al. 1991; Yan et al. 1992; Yan and Pawson 1997). It is estimated that this introduction was facilitated by ballast water of ships which could have included adults or the egg resting phase (Lehman 1987; Sprules et al. 1990). Densities from samples within Batchawana Bay, Lake Superior in September, 1988, showed up to 122.8 individuals/m$^2$, although estimates vary (Garton and Berg 1990).

Females can either reproduce sexually or parthenogenically depending on environmental conditions. This makes them very successful invaders, and allows females to create 10 offspring every two weeks, asexually under optimal conditions.
This very fast way of reproducing allows *Bythotrephes cederstroemi* to explode in population, enabling it to exploit limited resources during favorable conditions. When conditions decline *B. cederstroemi* reproduce sexually which results in the female carrying “resting eggs” which can enter diapause. This resting egg phase can survive through adverse environmental conditions such as desiccation, and often be transported by passive currents (Evans 1988) and attached to fishing equipment from one location to another. These resting eggs are also able to survive being ingested by fish. Jarnagin et al. (2000) found that 94% of mature diapausing eggs consumed by fish were intact following excretion. These eggs were then hatched under variable conditions, which showed 41% hatch rate following recovery and hatching from fecal pellets. This demonstrates that fish may be an important vector contributing to the spread of *B. cederstroemi* during seasonal fish migrations between pelagic and sublittoral zones (Jarnagin et al. 2000).

Food web dynamics have been altered distinctly since its introduction. *Bythotrephes cederstroemi* preys upon Daphnia and other zooplankton which is in direct competition with juvenile fish in these systems. The increase in zooplanktivores has resulted in declines of the native zooplankton communities with *B. cederstroemi* becoming a dominant zooplankton component able to consume up to 20 smaller zooplankton each day (Schulz and Yurista 1995; Schulz and Yurista 1999). Further, *B. cederstroemi*’s large size (>1cm), long and sharp spines make it difficult for juvenile fish populations to swallow, depleting these fish of their zooplankton food source they are dependent upon, yet their size and abundance has
created a new food source for fish greater than two inches in length (Schulz and Yurista 1995, 1999). *B. cederstroemi*’s ability to explode in population in times of plenty far exceeds that of fish populations which it competes with for food and is therefore reducing fish numbers due to the limited abundance of a zooplankton food source (Schulz and Yurista 1995, 1999).

The fishhook water flea, *Cercopagis pengoi*, is native to the Aral, Azov, Black, and Caspian Sea basins (Rivier 1998). This species was discovered in the Baltic Sea in 1992, and has since spread to the Gulf of Finland, Gulf of Riga and Neva Estuary (Gorokova et al. 2000; Ojaveer and Lumberg 1995). Discovered 16 years later than *Bythotrephes cederstroemi* the relatively spiny Ponto-Caspian cladoceran *Cercopagis pengoi* was discovered in Lake Ontario (MacIsaac et al. 1999). They were discovered in 1998 on both the Canadian and United States shores of Lake Ontario, as a fouling organism on research nets and angler fishing lines, and were subsequently discovered in Lake Michigan one year later. The source for the North American population appears to be from ballast water or fouling communities transported from the Baltic Sea (Cristescu et al. 2001). In North America it is thought to have established populations within dozens of North American lakes, and is spreading rapidly throughout the region (Ricciardi and MacIsaac 2000).

*Cercopagis pengoi* is similar to *Bythotrephes cederstroemi* in that they are both in the family *Cercopagidae* which can reproduce either asexually, through parthenogenesis, or sexually, producing eggs that can enter diapause for years at a time, are tolerant of dessication, cool temperatures, and persist in both fresh and
brackish environments (Rivier 1998). MacIsaac et al. (1999) found that 92% of the *C. pengoi* collected in 1998 were parthenogenetic females, suggesting favorable environmental conditions. The presence of females with eggs suggest that this species is successfully established within Lake Ontario, but in July 1998 decreased to <10% of the 1998 170 individuals/m³ densities then exploding to densities >1,500 individuals/m³ by the fall (MacIsaac et al. 1999). This may suggest that there are resource limitations within invaded zooplankton communities, and that the lifecycle of *C. pengoi* is well suited to resource limited environments. As a smaller species it will likely be easier to fit into the food web, becoming prey for alewife, yellow perch, other fishes and zooplanktivores, including its predatory invasive cousin *B. cederstroemi*.

The Asian clam, *Corbicula fluminea*, is native to southeast China, Korea, and southeast Russia (Lachner et al. 1970). The earliest known North American record dates back to 1924 in Nanaimo, British Columbia (Counts 1981). They are thought to have established permanent populations in the Californian San Joaquin and Sacramento Rivers, and the Columbia River, bordering Oregon and Washington in the 1930’s and 1940’s (Ingram 1948). Although they can survive in both lotic and lentic, freshwater and brackish environments, in North America they appear to be most abundant in streams and rivers (Sinclair 1971; Carlton 1992). It’s ability to produce a crawling larvae, pediveliger, enables this species to colonize habitats upstream from the parent population (Britton and Morton 1986). Competition with *C. fluminea* for food and space may be a major contributor to the demise of native
freshwater mussel species. Densities have been reported as high as 25,000/m² (Sinclair 1971). These densities have altered the benthic substrate composition (Sickel 1986), and reduced the availability of organic resources to native organisms (Devick 1991).

_Corbicula fluminea_ is thought to be an important coupler between the benthic and pelagic communities, consuming organic matter from both the water column and the stream sediments (Sickel 1986; Hakenkamp and Palmer 1999). This coupling is important as it may concentrate a significant portion of energy within the system into a single organism. Clam predators such as crayfish, fish, and diving ducks have been the most successful candidates to access, and liberate, this converted energy source. In Florida alone, _C. fluminea_ is preyed upon by crayfish, and at least 11 different species of fish (Lachner et al. 1970; McMahon 1983).

The spiny Daphnia, _Daphnia lumholtzi_, is a dominant component of the zooplankton community in its native range of subtropical and tropical lakes in Africa, Australia, and India (Havel and Hebert 1993). Presumably introduced into a small lake in Texas along with the shipments of Nile Perch and Tilapia from Lake Victoria in 1983, it was not discovered until 1990, and has since spread to at least 56 rivers and lakes in at least 15 states, including its discovery in Lake Erie in 1999 (Havel and Hebert 1993; Stoeckel et al. 1996; Davidson and Kelso 1997; Havel et al. 2000; Muzinic 2000).

There is concern that this _Daphnia lumholtzi_ will out-compete native _Daphnia_ species and establish itself as a permanent zooplankter within freshwater
systems of North America (Jack and Gilbert 1994; Havel et al. 1995; Kolar et al. 1997; East et al. 1999). *D. lumholtzi* is thought to be more successful in avoiding predation, and produces larger and more numerous spines than species of *Daphnia* native to North America. It’s success in range expansion may be enhanced by this avoidance of heavy predation, and, indeed, no *D. lumholtzi* were discovered in fish stomach content analysis conducted in the Norris Reservoir, where it is established (Goulden et al. 1995; Havel et al. 1995; Work and Gophen 1999a). But there may be some evidence that there is resistance by the native community. Peaks of abundance of *D. lumholtzi* only occur during periods when native zooplankton assemblages are at their lowest levels (Work and Gophen 1999b). This may suggest that this exotic cladoceran has minimal impact on members of native zooplankton assemblages in the form of direct competition (Work and Gophen 1999b).

The zebra mussel, *Dreissena polymorpha*, is probably the most studied marine nonindigenous organism in the world. A native to the Caspian Sea region, it has spread throughout Europe and was discovered for the first time in North America in Lake St. Clair in the mid-1980’s, presumably via a ballast water introduction (Hebert et al. 1989; Roberts 1990). The subsequent spread to both lake and riverine systems throughout eastern North Americas has cost billions of dollars, with a large portion of this from it’s fouling of municipal water intakes (MacIsaac 1996). This figure becomes even more impressive when it is realized that the invasion by *D. polymorpha*, and the related *Dreissena bugensis*, may represent only 1% of all European mollusks transported and released into North America (Carlton 1996a).
The presence of *Dreissena polymorpha* has dramatically altered colonized habitats. Following the introduction of zebra mussels light penetration, benthic algal biomass, chlorophyll concentrations, and rates of benthic primary productivity have increased (Griffiths 1992; Lowe and Pillsbury 1995). Unionid bivalve mussel populations have declined, and their existence may be threatened (Schloesser and Nalepa 1994; Schloesser et al. 1996). Live Unionid bivalves have been found to be preferred over dead shells for *D. polymorpha* byssal thread attachment, with live Unionids having been found with up to 15,000 zebra mussels attached to their shells (Hebert et al. 1991; Mackie 1991; Hunter and Bailey 1992; Mackie 1992; Haag et al. 1993; Nalepa 1994; Nalepa et al. 1996). From 1993-1995 zebra mussel abundances on hard substrata averaged up to 17,000/m², and were responsible for large declines in phytoplankton biomass in the Hudson River (Strayer et al. 1998).

Although no negative effect has been detected within nonindigenous zebra mussel population dynamics, freshwater drum, carp, sturgeon, and diving ducks, among others, eat zebra mussels within North America (French and Bur 1993). Bottom-up effects, showing a positive influence on species that utilize *Dreissena polymorpha* as a food source, have not yet been detected, yet may become apparent after an undetermined lag time. Within its European distribution, there are estimated to be at least 200 species that prey upon, or parasitize, *D. polymorpha*, including birds, fish, copepods, coelenterates, leeches, crabs, crayfish, and rodents, with many of these potential predators also competing for food and space (Molloy et al. 1997). Yellow perch, *Perca flavescens*, grew larger and at an accelerated rate in the
presence of zebra mussels compared to treatments w/out zebra mussels (Thayer et al. 1997), yet there was no direct predation upon zebra mussels, rather there was an indirect effect involving zebra mussel induced changes in the benthic structure and biota (Thayer et al. 1997). This may be the result of creating greater structural heterogeneity. Habitats with mussels had an increase in oligochaetes, isopods and amphipods, and the result were more crustaceans in the diet of the perch in those with mussels (Thayer et al. 1997).

The Chinese mitten crab, *Eriocheir sinensis*, is native to Chinese and Korean rivers and estuaries between latitudes 26°N and 40°N. This catadromous crab was introduced into Germany in 1912 (Panning 1939), subsequently spreading through the region, including; Finland, Sweden, Russia, Poland, Netherlands, Belgium and France. North American discoveries include the Detroit River at Windsor, Ontario in 1965, Lake Erie in 1973 (Nepszy and Leach 1973), the Mississippi Delta in 1987 (Horwath 1989), and the 1992 discovery in San Francisco Bay (Cohen and Carlton 1997; Hieb 1997). The introduction into the San Francisco estuary is thought to either represent another ballast water-mediated introduction, or the deliberate release by individuals in the attempt to initiate a Pacific coast fishery, where these crabs sell for $27.50-$32.00 per kg (Cohen and Carlton 1997).

*Eriocheir sinensis* not only poses a threat to the regions ecosystems, fishing industries, and levies and dikes through their burrowing nature, reaching densities of 130 per 10 linear feet (Cohen and Carlton 1997; Veldhuizen and Standish 1999), but are also intermediate hosts for Asian lung flukes, the trematodes *Paragonimus*
The western Pacific shore crab, *Hemigrapsus sanguineus*, was discovered in New Jersey in 1988. As its name suggests *H. sanguineus* is native to western Pacific shores, including the Korean and Chinese coasts to Hong Kong and the shores of the Japanese archipelago. It is thought to have been introduced to the Atlantic coast from ballast water, and extended its range through larval dispersal (Epifanio et al. 1998). Within the last 12 years this crab has spread from this area north to Cape Cod, Massachusetts, and south to Chesapeake Bay (McDermott 1998). This omnivorous, intertidal to shallow subtidal crab is now displacing the European green crab, *Carcinus maenas*, a previous invader, from limited sheltered habitats (Casanova 1999; Gerard et al. 1999). One of the reasons for its success is thought to be the low overlap with native crabs within the western Atlantic shore communities (Lohrer et al. 2000). This new invader is now becoming the dominant crab species along the intertidal shores of the northwestern Atlantic shores (Lohrer and Whitlach 1997, Lohrer et al. 2000). Once again, the ecosystems along the shores of this region are subject to the pressures of a new generalist crab species. Similar to *C. maenas*, *H. sanguineus* preys upon mytilid bivalves, littorine snails, and algal communities, and

*Eurydice sinensis*, and *Paragonimus ringeri* (Ingle 1986). The diet of *E. sinensis* involves a consumption of vegetation as juveniles, switching to fish, and invertebrates as they grow in size and reach maturity (Veldhuizen and Stanish 1999). It is also important to recognize that these crabs have the potential to interact with endangered salmonid stocks if they spread north along the Pacific coast (Veldhuizen and Standish 1999).
has the potential to alter rocky intertidal communities in the northwestern Atlantic Ocean (Gerard et al. 1999; Larson 1999).

The Western Atlantic Comb Jelly, *Mnemiopsis leidyi*, a ctenophore, was discovered in the Black Sea in 1982, seasonally in the Sea of Azov since 1982, and also invaded the Caspian Sea by the mid-1990’s (Vinogradov et al. 1989; Shushkina and Musayeva 1990; Shushkina et al. 1990). Its rapid increase in abundance resulted in the demise of native planktonic communities, and the organisms that depended on them as a food resource and is now considered to represent 95% of the Black Sea biomass (Mutlu et al. 1994; Shiganova 1998). This included the collapse of native seal populations and the commercial anchovy fisheries, worth an estimated $250 million annually (Shushkina et al. 1990; Malyshev and Arkhipov 1992; Harbison and Volovik 1994; Mutlu et al. 1994), and the resulting total biomass of *Mnemiopsis leidyi* in 1995 to exceed the global fisheries landings (Mutlu et al. 1994).

It appears that the Mediterranean horse mackerel, *Trachurus trachurus*, a ctenophore, *Beroe ovata*, and the butterfish, *Peprilus triacanthus* (Kremer 1979) may prey heavily enough upon *Mnemiopsis leidyi* to allow for some recovery of the zooplankton community. *B. ovata*, is a comb jelly specializing in predation upon other comb jellies and not likely to prey-switch (Swanberg 1974). This trait suggests that it may apply selective pressures on *M. leidyi*, allowing the zooplankton communities some recovery.

The Asian green mussel, *Perna viridis*, is a four inch mussel native to marine and brackish systems of the Indo-Pacific and coast of India (Siddal 1980). *P. viridis*
was discovered in the Caribbean at Trinidad in 1990, the Golfo de Paria, Venezuela in 1993, and in Tampa Bay in 1999, all thought to have been ballast water-mediated introductions (Agard et al. 1992). This species of mussel is able to tolerate areas of high particulate matter, including pollutants, by producing massive amounts of mucous, consuming appropriate sized organic materials, including heavy metals, organochlorines, and petroleum hydrocarbons (Krishnakumar et al. 1990; Chidambaram 1991; Agard et al. 1992; Karunasagar and Karusanagar 1992), egesting indigestible components as pseudofeces (Morton 1987). *P. viridis* is displacing the brown mussel *Perna perna* along the shores of La Esmeralda, Guatapamare and El Morro de Chacopata, Sucre State and, by the end of 1995, also appeared along the Isla Margarita, Nueva Esparta State, Venezuela (Segrini de Bravo et al. 1998). *P. viridis* is also much more tolerant of harsh environmental conditions than the North American species such as *Mytilus edulis* with which there is direct competition for food and space which allows for the prediction to expand from its current distribution (Morton 1987).

The Asian mussel, *Musculista senhousia*, is a small, densely aggregating mussel native to the intertidal and subtidal communities of the northwestern Pacific (Morton 1974). *M. senhousia* was introduced to the shores of the eastern Pacific in the 1940’s, New Zealand during the 1970’s, and into Australia and the Mediterranean during the 1980’s (Willan 1987; Creese et al. 1997; Crooks 1998). Potential vectors for the invasive populations include ship ballast water or hull fouling (Willan 1987). The Asian mussel becomes reproductively mature within nine months of settlement.
(Crooks 1996b). Following settlement it commonly forms aggregations of 3,000 mussels per square meter, but has been reported to reach densities in the San Diego, California region of up to 15,000 mussels per square meter (Crooks 1992). When these dense aggregations occur, the mussels become tightly bound with their byssal threads, creating “mussel mats,” decreasing the availability of the benthic substrate to native species such as native eelgrass, Zostera marina, and species dependent on eelgrass as a resource (Crooks 1996a; Crooks 1998; Reusch and Williams 1998). The ability of M. senhousia to function as an efficient filter feeder has resulted in the decrease native species, both in competing for the available food and space resources, and with its direct predation on the planktonic stages of native species larval stages (Crooks 1998).

The Asian clam, Potamocorbula amurensis, native to subtropical and temperate waters of China, Japan, and Korea, was discovered in San Francisco Bay in 1986 (Carlton et al. 1990; Nichols et al. 1990; Thompson et al. 1991). Within a few years this clam had established itself as the dominant member of the estuarine benthic community, consistently reaching densities >10,000/m², and maximum densities of 48,000/m² (Carlton et al. 1990; Nichols et al. 1990; Peterson 1998; Carlton 1999). The density of this clam combined with its effective filtration rate has decreased plankton abundance and redistributed food web energetics significantly (Alpine and Cloern 1992; Thompson and Luoma 1999). Chlorophyll concentration decreased 5-fold, followed by reductions in three copepods, the mysid shrimp, Neomysis mercedis, and other fish prey species (Nichols 1990; Kimmerer 1998). P.
amurensis has become symbolic of the effects marine bioinvasions. This invasive clam now contributes significantly to an estuarine biomass that is 99% exotic (Nichols et al. 1990; Cohen and Carlton 1998).

While abiotic physical factors, such as the freshet-induced mortalities of 1995 (Peterson 1996), appear to determine its distribution, P. amurensis is not without biotic interactions. While some species such as pelagic predators and planktivorous species have declined as a result of the “over-grazing” achieved through filter feeding of Potamocorbula amurensis, other species have benefited (Thompson and Luoma 1999). Bottom feeding predators such as the white sturgeon, 

Asipenser transmontanous, and diving duck species have benefited from an “enhanced” food source (Thompson and Luoma 1999) which may increase their abundance.

MATERIAL AND METHODS

Distribution Study

In order to determine if there is a distributional relationship between Carcinus maenas and Cancer productus within Yaquina Bay, Oregon, habitat type had to be considered as it is an important variable in explaining crab distribution. Carcinus maenas can occupy habitat ranging from tidal marshes, mudflats, sandflats, cobble and shell, and rocky shores protected from wave action (Naylor 1962; Crothers 1969, 1970). Cancer productus is most abundant on high salinity shores
with rock or boulder shelter and is generally not found in tidal marshes, mudflats, and shores that experience temperatures above 15 °C and salinities below 25 ppt. (Rathbun 1930; Nations 1975).

Ten sites were chosen for the sampling study. The sites were chosen because they represent the general habitat of their respective region of the bay, and extend from the marine waters near the mouth of Yaquina Bay, up to the brackish waters at river mile 12.5 (Figure 3). Of these ten sites a subset of five permanent sites, and five minor sites were chosen. The permanent sites were sampled daily from June to September and received no less than 5,000 trap hours/site. They were selected as sites that were representative of the surrounding habitat, and yet were relatively secure from public interference, allowing for long-term trap deployment. The five permanent sites included: Port of Toledo docks at river mile 12.5; Riverbend Marine on Oneatta Point at river mile 5.4; Roberts private dock just downstream of Weiser Point at river mile 4.6; the Oregon Coast Aquarium (OCA) water outfall at approximately river mile 2.2; and the South Beach Marina at river-mile 1.2.
Figure 3.
Map of Yaquina Bay, Oregon. The ten sample sites include: 1) **Port of Toledo, 2) Johnson Slough, 3)** Riverbend, 4)** Roberts' Dock, 5) Sally’s Bend, 6)** Oregon Coast Aquarium outfall (OCA), 7) Port of Newport, 8) Hatfield Marine Science Center Pumphouse, 9) South Beach jetty, 10)** South Beach marina. (** 5 sites with > 5,000 trap hours each).

The five minor sites were also representative of the surrounding habitat types, but only received 1,000 trap hours/site. These sites were less secure from public interference and included: Johnson Slough at mile mark 7.4; Sally’s Bend at mile mark 3.1; Port of Newport office at mile mark 1.9; Hatfield Marine Science Center Pumphouse at mile mark 1.8; and the outer entrance to the South Beach Marina at mile mark 1.4 (Figure 3).
The Port of Toledo, located at river mile 12.5 on the north side of Yaquina Bay, has a shoreline dominated by rushes of the genus Scirpus, with the upper intertidal consisting of fine sediment, with few rocks or boulders greater than 100 cm diameter. The slope of the shore ranges from 20-70° for approximately 10 meters where it enters the river channel with a depth of 2.5 m below the zero tide line (D. Heinen, manager Port of Toledo).

Johnson Slough, located at river mile 7.4 on the north side of Yaquina Bay, is primarily a tidal channel with shorelines dominated by Scirpus rushes. On either side of the channel are bank-stabilizing areas constructed of rip-rap less than 2 m in diameter. The slope of the shore ranges from 10-30°. At high tide most of the slough is inundated with water, at low tide there are few isolated pools less than 3 m across and 1 m in depth.

Riverbend Marine is located at river mile 5.5 on the north side of Yaquina Bay. As a 30 m long finger jetty on the north side of the bay, it extends southward toward the river channel. The finger jetty is constructed of rip-rap ranging from 0.25-2 m in diameter. The east side of the finger jetty has an approximate slope of 40° down 1.5 m to a tidal mud flat of fine sediment, 0.3 m above the zero tide line. The west side of the finger jetty also has an approximate slope of 40° down 2 m into the bay at the zero tide line, and therefore has no tidal flat, but the sediment composition is comparable to the east side of the jetty. The southern tip of the finger jetty has an approximate slope of 50° down 4 m where it enters the river channel with a depth of 2 m below the zero tide line.
Roberts’ Dock is located at river mile 4.6 on the south side of Yaquina Bay. It has a shoreline dominated by rip-rap ranging from 0.25-1.0 m in diameter sloping down approximately 45° to a tidal mud flat 0.4 m above the zero tide line. The tidal flat has a slope <15° for 10-15 m where it increases to >45° entering a channel 1.5 m below the zero tide line.

Sally’s Bend, a large tidal mud flat located at river mile 3.1 on the north side of Yaquina Bay, has a shoreline dominated by Scirpus. The tidal flat extends from the high tide line >100 m toward the river channel with a slope of < 10°. The flat is dominated by fine particle sediment with an occasional 50 cm diameter rock, and a small tidal channel < 0.5 m below the tidal flat, which empties completely at low tide.

The Oregon Coast Aquarium outfall is located at river mile 2.2 on the south side of Yaquina Bay. The shoreline is dominated by Scirpus and rip-rap ranging from 0.25-2 m in diameter. The outfall consists of marine water exiting the aquarium and creating a permanent marine tidal channel with a depth < 0.1 m at low tide, through a sand flat 0.4 m above the zero tide line. The channel empties into a small permanent pool of 2 m depth at low tide. The channel exits the pool through the sand flat a few hundred meters before emptying into the bay.

The Port of Newport is located at river mile 1.9 on the north side of Yaquina Bay. The shoreline is comprised of rip-rap ranging from 0.25-2 m in diameter. It has a slope of approximately 45° where it enters a mud flat at 0.3 m above the zero tide
line. The mud flat then extends with a slope < 15° for 10 m where it drops off to 2 m below the zero tide line in the marina.

The Hatfield Marine Science Center (HMSC) Pumphouse is located at river mile 1.8 on the south side of Yaquina Bay. This site is comprised of a finger jetty, which extends northward into the bay. Running along the east side of the finger jetty is the marine water outflow from HMSC. The shore line is dominated by rip-rap of 0.25-2 m in diameter with an approximate slope of 45°, occasional 50 cm rocks, and sand. The tip of the jetty slopes down toward a benthos dominated by 50 cm rocks and sand at the 0.2 m above the zero tide line.

The South Beach Marina Jetty is located at river mile 1.3 on the south side of Yaquina Bay. This jetty runs along the eastern side of the entry point of the South Beach Marina. The shoreline is comprised of rip-rap of 0.25-2 m in diameter. The rip-rap slopes approximately 45° to where it reaches a sand flat 0.4 m above the zero tide line. The sand flat has a slight dome shape with the south side of the dome dominated by eel grass and an occasional 0.25 m rock, and the north side of the dome, nearest the bay, almost completely bare, with very few areas of eel grass or rocks.

The South Beach Marina is located at river mile 1.3 on the south side of Yaquina Bay. The rectangular marina is completely enclosed by rip-rap of 0.1-2 m in diameter except for the northwest corner that serves as the entry point into the bay. The slope of the rip-rap varies from 20-70°, intersects the fine sediment benthos at -0.1 m. The maximum depth of the marina is 3m below the zero tide line.
The ten study sites range from low salinity habitats, which physiologically limit the existence of crabs known to inhabit Oregon estuaries, except for the yellow shore crab, *Hemigrapsus oregonensis*, and the nonindigenous brackish water crab, *Rithropanopeus harrisii*, to the lower estuary where the salinity was high enough for all known Oregon crab species to persist. Except for the OCA entrance, each of the other sites included accessible cover in the form of rip-rap within 6 m or less of the trapping site. The OCA site was primarily a channel through a tidal flat with minimal submersed rock cover for hundreds of meters. At each station the following measurements were taken daily: temperature, salinity, sediment type and tidal level. Air and water temperature was measured with a field thermometer and salinity of the surface water was measured using a temperature-compensated refractometer. Sediment type was categorized by particle size. Tidal level was estimated from tide tables using the observed low tide mark as a reference point.
Site Specific Physical Data

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<th>Site</th>
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<th>Habitat Type</th>
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<td>15-18</td>
<td>1,2</td>
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<td>11-15</td>
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<td>22-36</td>
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Table 1.
Physical parameters of the ten trapping sites. The five primary sites that received a minimum of 5,000 trap hours are noted with **. The habitat type is explained by 1) fine, soft silt; 2) mud/clay; 3) sand; 4) coarse sand/fine gravel (to lady bug size); 5) gravel (to marble); 6) cobble (to baseball); 7) rock (to basketball); 8) boulders (to medicine ball); 9) large boulders (to car size); 10) bedrock.

Two trap designs were used, the Aquatic Ecosystems (AES) trap (63.5 cm x 46 cm x 23 cm) made of 20 mm plastic mesh, with expandable mesh openings at each end to allow the trapping of even the largest crabs, and the square mesh box trap, a square trap with 20 mm stainless steel mesh (60 cm x 60 cm x 30 cm) with four plastic meshed conical entries, approximately 80-90 mm in diameter. Each trap
held a plastic oval-shaped commercial baiter filled daily with salmon backbone, allowed to soak for a 24 hour period, and checked daily for a period of ninety days. Each site received two to three traps of each type. Traps were placed near the zero foot tidal range, but varied up to 0.5 m according to site. Each crab that entered a trap was checked for species, sex, carapace width, injury, and parasite infection. *Carcinus maenas* were measured between the tips of their 5th anterio-lateral spines, and *Cancer productus* at the tips of their 10th anterior-lateral spine, using Vernier calipers. Salinity, tidal height, weather condition, air temperature and water temperature were also taken daily at each site. All *C. maenas* were saved for the predation experiment or frozen.

**Laboratory Predation Experiment**

To test whether the presence of a *Cancer productus* is more detrimental to the survival of *Carcinus maenas* than to that of a conspecific, I set up a laboratory predation experiment. In this design there were two crabs per container, each a potential threat to the survival of the other. The shapes of the carapace for the two species are very different (Figure 1) therefore size classes were determined by mass. For both species, carapace width was compared to mass to determine appropriate crabs for the size classes. These graphs were used to determine which crabs carapace width to weight relationship did not fall within the predicted 95% confidence interval of a logged linear regression. This point was crucial for determining which crabs
were heavy for their carapace width (CW) (likely to molt soon) or light for their CW (a likely recent molt, see outlier Figure 4). This determination was important to avoid crabs molting during the experiment, usually followed by a predation event, as well as those that had recently molted, and are too weak, or not yet hard enough, to defend themselves. If some level of intermolt stage were not determined it could have resulted in an increase in observed variability (Lipcius and Hernkind 1982). Only these hard-shelled crabs were used, and trials in which either crab molted during the experimental time were not used in the analysis.

Figure 4.
Comparison of carapace width and mass for 200 male Cancer productus caught in Yaquina Bay, Oregon, 1999. These were used to determine crabs that either recently molted or are likely to molt soon. (Especially note the one outlier. This crab is likely a recently molted individual).
Each *Carcinus maenas* that was retained from the trapping study was brought back to the laboratory, weighed to the nearest gram, measured for carapace width to the next lowest millimeter using Vernier calipers, checked for weight to CW relationship using the regression data, and then put into a community tank containing conspecifics of the appropriate size classes. Only healthy male crabs with each limb intact were included in both the regression analysis and predation experiment. Two hundred male *Cancer productus* were also weighed and measured to determine the linear regression equation and 95% CI. Once the size classes were determined from this line only appropriate sized *C. productus* were retained from the trapping effort, and were treated similarly to *C. maenas*. After the *C. productus* were used for the predation experiment each was right-spine-clipped and returned to the bay. The right spine clip allowed for determination in the field of a crab previously used so that it would not enter the experiment more than once. At the end of an experimental run any surviving *C. maenas* were destroyed in accordance with the Oregon Department of Fish and Wildlife collection permit.

All crabs used were male to reduce between-sex variability. Two size classes of *Carcinus maenas* were chosen, one at the lower end of the abundant 1997/98 year class (small = 52-78g, 60-67 mm) and the other at the upper end of the year class (large = 85-125g, 73-80 mm). *Cancer productus* reaches a maximum size twice that of *C. maenas* so three size classes were chosen for this crab (small = 52-78g, 71-77 mm; medium = 85-125g, 91-98 mm; and large = 166-214g, 103-109 mm). Although still not approaching the maximum size for *C. productus*, this larger size class was
used to determine if large *C. productus* are more likely to prey upon *C. maenas* than medium *C. productus*. Each pairing was replicated 50 times against all other size classes and itself, except for the large *C. productus* vs large *C. productus*. The interaction between large *C. productus* could not be used to determine differences in heterospecific vs conspecific predation rates and was therefore excluded from the experiment.

Upon entering the laboratory each crab was put into the conspecific community tank (120cm x 43cm x 30 cm) and fed mussels. They were then chosen at random and put into individually numbered perforated containers. Each crab was starved for three days prior to entering the predation pairing experimental arena to standardize the hunger level. Crabs from appropriate size classes were paired (Table 1) using random numbers of their individual container number.

The experimental arenas consisted of 3.8 L. rectangular plastic Sterilite® boxes (158 mm X 300 mm X 80 mm, Figure 5) with a secured plastic lid. Filtered sea water (minimum flow of 2 liters/ hour) entered via the top and exited via six out-flow holes along the sides. No sediment was added to the container in an attempt to avoid possible variation due to sediment type. The salinity ranged from 32-37 ppt., and temperature from 11-14°C.
Experimental Predation Pairings

<table>
<thead>
<tr>
<th>Mass</th>
<th>Carcinus maenas</th>
<th>Cancer productus</th>
</tr>
</thead>
<tbody>
<tr>
<td>small</td>
<td>vs small Carcinus maenas</td>
<td>60 mm to 67 mm vs 71 mm to 77 mm</td>
</tr>
<tr>
<td>medium</td>
<td>vs medium Carcinus maenas</td>
<td>73 mm to 80 mm vs 91 mm to 98 mm</td>
</tr>
<tr>
<td>large</td>
<td>vs large Carcinus maenas</td>
<td>73 mm to 80 mm vs 103 mm to 109 mm</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mass</th>
<th>Carcinus maenas</th>
<th>Cancer productus</th>
</tr>
</thead>
<tbody>
<tr>
<td>small</td>
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<tr>
<td>medium</td>
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<td>73 mm to 80 mm vs 91 mm to 98 mm</td>
</tr>
<tr>
<td>large</td>
<td>vs large Cancer productus</td>
<td>73 mm to 80 mm vs 103 mm to 109 mm</td>
</tr>
</tbody>
</table>

Table 2.
Carapace width, mass, and pairings for Cancer productus and Carcinus maenas entering the predation experiment (large Cancer productus paired with large Cancer productus did not occur).

Each pair of crabs was placed simultaneously into the experimental container at opposite ends of the arena in an attempt to reduce stress (Figure 6). These containers were then placed into a fully drained outdoor opaque green aquarium with an opaque lid. This allowed for each of the containers to maintain their independence of water source, yet receive a reduced, yet constant light level that would not interfere with internal clocks based on time of day. After entering the predation
experiment, each crab was checked daily for limb loss and predation events for a period of one week. Replicates were run concurrently to avoid variation through time (day length, salinity, and temperature).

Pearson's Chi-squared test for independence was then used to detect differences in predation between species and size classes.

Figure 5. External view of the experimental design for the predation experiment, showing one top water entrance and six exit sites, three on each side.
Predation Arena; View From Above.

Figure 6.
Top view of the experimental container showing relative proportions between a pairing of similar sized *Carcinus maenas* and *Cancer productus* and their experimental surroundings.
RESULTS

Distribution Study

The physical factors that appear to be most significant in determining the abundance and distribution of crab species are salinity, temperature, and substrate type. Table 2 shows the location by river mile of each site, the variation in physical factors taken throughout the study at each site, and sediment size, ranging from fine silt to bedrock. As might be predicted, the sites with the lowest maximum salinities were the Port of Toledo with a range of 14-24 parts per thousand (ppt), followed by Johnson Slough with 16-28 ppt. The rest of the sites experienced a minimum salinity of over 21% with the exception of the shallow mudflat at Sally’s Bend, which ranged from 15-30 ppt (Table 2).

Temperature can also limit the habitat accessible to decapod crustaceans. The measurements within this study suggest that temperature was more indicative of river mile than salinity range. As would be predicted the temperatures at the Port of Toledo had the highest temperatures, ranging from 19-21°C, whereas the lowest temperatures were experienced at the lower river miles, ranging from 12-16°C at the South Beach Marina Jetty (Table 2). Also as might be expected from the tidal influence mixing marine and freshwater within mid-estuary habitat, temperatures at Roberts Dock had the greatest variability ranging from 11-19°C (Table 2).
Catch per unit effort (CPUE), standardized as the number of crabs per trap per day, was calculated for each trap type at each site (Tables 3 and 4). The only crab species caught at site 1, Port of Toledo, was the nonindigenous brackish water crab, *Rithropanopeus harrisii*, and the native yellow shore crab, *Hemigrapsus oregonensis*. While *R. harrisii* was only found at site 1, *H. oregonensis* was found at each site and was found to overlap with every species caught (Tables 3 and 4). Juvenile *Cancer magister* were found at every site where *Carcinus maenas* was found, with very little variation in abundance except for site 5, Sally's Bend (Tables 3 and 4, personal observations). *Cancer productus* was most abundant at sites 7, Port of Newport, 8, HMSC Pumphouse, 9, South Beach Marina Jetty, and site 10, South Beach Marina (Tables 3 and 4). *Carcinus maenas* was absent or rare at each of these sites (Tables 3 and 4). The only other site where *C. maenas* was absent was site 1 where increased temperature and decreased salinity, below the minimum 14 ppt is known to limit adult long-term survival, likely limited its ability to persist in that environment.

Comparing the CPUE for the two traps reveals selective capture differences between the two designs. At Riverbend *Cancer magister* had a 0.922 CPUE with the Aquatic Ecosystem trap, but only a 0.080 CPUE effort with the Box trap (Tables 3 and 4). The reverse trend was observed at the same site for *Carcinus maenas*, with a 0.742 CPUE with the Aquatic Ecosystem trap, and a 2.81 CPUE effort with the Box trap (Tables 3 and 4). There was no consistent trend of selective capture for *Cancer productus* (Tables 3 and 4).
### Catch Per Unit Effort; Aquatic Ecosystem Trap

<table>
<thead>
<tr>
<th>Site</th>
<th>Carcinus maenas</th>
<th>Cancer productus</th>
<th>Cancer magister</th>
<th>Hemigrapsus oregonensis</th>
<th>Rithropanopeus harrisii</th>
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</thead>
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<tr>
<td>Port of Toledo*</td>
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<td>-</td>
<td>-</td>
<td>0.20352</td>
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</tr>
<tr>
<td>Johnson Slough</td>
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<td>-</td>
<td>1.9862</td>
<td>0.33096</td>
<td>-</td>
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<td>Riverbend*</td>
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<td>Roberts Dock*</td>
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<td>Sally’s Bend</td>
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</tr>
<tr>
<td>South Beach Jetty</td>
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<td>-</td>
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<tr>
<td>South Beach Marina*</td>
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<td>5.8565</td>
<td>0.22248</td>
<td>0.14832</td>
<td>-</td>
</tr>
</tbody>
</table>

**Table 3.**

Catch per Unit Effort (CPUE) for crab species caught during the study at each of the ten sites using the Aquatic Ecosystems Trap (AES). CPUE is calculated by the number of crabs per trap day.
Although there is overlap in habitat between *Carcinus maenas* and juvenile to sub-adult *Cancer magister*, there is no inverse CPUE relationship for these two species of crab for either trap designs (Tables 3 and 4). The CPUE data suggests that there is a distributional relationship between *C. maenas* and *Cancer productus* for
both trap types (Tables 3 and 4). By looking at both trap types and comparing the CPUE it is determined that the observation is not an artifact of trap type but is related to species abundance. Simplifying the data to the 5 primary sites and comparing the CPUE for both *C. maenas* and *C. productus* shows an inverse relationship between the abundance of these two crabs (Figures 7 and 8). Tables 3 and 4 demonstrate that this pattern does not exist for abundances of the other brachyuran species in this study.

![Primary Site Comparison; Aquatic Ecosystems Trap.](image)

**Figure 7.**
Catch per Unit Effort (CPUE) of *Carcinus maenas* and *Cancer productus* at the five primary trapping sites using the Aquatic Ecosystems trap (AES).
Figure 8.
Catch per Unit Effort (CPUE) of *Carcinus maenas* and *Cancer productus* at the five primary trapping sites using the Box trap.

Laboratory Predation Experiment

Theoretically the pairing of any two crabs could result in a predation event occurring in either direction. Intraspecific predation for either species was less than 14% (Table 5). The most significant increase in mortality occurred when same-sized or larger *Cancer productus* were paired with same sized or smaller *Carcinus maenas*.
(Table 5). Small *C. productus* experienced 10% mortality in pairings with medium
*C. maenas*, yet 52% mortality was experienced by small *C. maenas* when paired with
medium *C. productus* (Table 5). The rate of mortality for small *C. maenas* increases
even further to 76% when paired with large *C. productus* (Table 5).

Percent Survival in Predation Pairings

<table>
<thead>
<tr>
<th></th>
<th>Carcinus maenas 52-78 g</th>
<th>Carcinus maenas 85-125 g</th>
<th>Cancer productus 52-78 g</th>
<th>Cancer productus 85-125 g</th>
<th>Cancer productus 166-214 g</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcinus maenas 52-78 g</td>
<td>93%</td>
<td>90%</td>
<td>88%</td>
<td>48%</td>
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<tr>
<td>Carcinus maenas 85-125 g</td>
<td>100%</td>
<td>89%</td>
<td>98%</td>
<td>68%</td>
<td>54%</td>
</tr>
<tr>
<td>Cancer productus 52-78 g</td>
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<td>90%</td>
<td>95%</td>
<td>94%</td>
<td>88%</td>
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<tr>
<td>Cancer productus 85-125 g</td>
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<td>98%</td>
<td>100%</td>
<td>91%</td>
<td>86%</td>
</tr>
<tr>
<td>Cancer productus 166-214 g</td>
<td>100%</td>
<td>98%</td>
<td>100%</td>
<td>100%</td>
<td>Did not test</td>
</tr>
</tbody>
</table>

Table 5.
Percent predation each species/size class experiences when paired with the others.
When paired with the species/size class in the column across the top this explains the
percent survival experienced by the species/size class along the rows.
For the most part, predation of two different size classes was as predicted with the larger crab surviving more often than the smaller crab (Table 5). Percent mortality was less than 14% for all pairings except for when small *Carcinus maenas* were paired with either medium or large *Cancer productus* (Table 5). The line graph describing percent mortality of *C. maenas* in the presence of *C. productus* (Figure 9) shows an increase in mortality with a decrease in size for *C. maenas* showing that predation rates increased with increasing asymmetry in size between predator and prey as expected.

**Percent Predation for Pairings of Male *Carcinus maenas* and *Cancer productus*.**

![Line graph](image)

*Figure 9.* Line graph explaining the percent predation experienced by the species/size class with its appropriate pair group.
The Pearson's Chi-squared test for independence used for each size of *Cancer productus* to determine if they prey more heavily on smaller *Carcinus maenas* than on larger *C. maenas* showed convincing evidence that both the medium and large *C. productus* demonstrated an increasing rate of predation with increasing size difference between heterospecifics. The test for independence of large (166-214g) *C. productus* predation, testing greater predation upon 52-78g *C. maenas* than on 85-125g *C. maenas*, gave a $X^2 = 9.46$ ($p < 0.0025$). There is convincing evidence that 166-214g *C. productus* prey more heavily upon the 85-125g *C. maenas* than on 85-125g *C. productus*, which gave a $X^2 = 7.31$ ($p < 0.01$). There is overwhelming evidence that 166-214g *C. productus* prey more heavily upon the 52-78g *C. maenas* than on 52-78g *C. productus*, which gave a $X^2 = 41.56$ ($p < 0.0005$).

The test for independence of medium (85-125g) *Cancer productus* predation, testing for greater predation upon 52-78g *Carcinus maenas* than on the 85-125g sized *C. maenas*, gave a $X^2 = 4.11$ ($p < 0.05$). There is convincing evidence that 85-125g *C. productus* prey more heavily upon the 85-125g *C. maenas* than on 85-125g *C. productus*, which gave a $X^2 = 7.29$ ($p < 0.01$). There is overwhelming evidence that 85-125g *C. productus* prey more heavily upon the 52-78g *C. maenas* than on 52-78g *C. productus*, which gave a $X^2 = 25.69$ ($p < 0.0005$).

Within the predation experiment very few non-lethal events such as carapace injury, claw loss or leg loss occurred (Table 6). A non-lethal loss such as a claw or leg was changed to a predation event if at the end of the week the injured crab was dead as a result of predation, but if it was still alive it was noted as a non-lethal
interaction. Combining Tables 5 and 6 suggests that the observed predation may represent an all-or-nothing event, once a crab is injured the other crab sensed vulnerability and took advantage of an easy food source.

Non-lethal Injuries Within Predation Pairings

<table>
<thead>
<tr>
<th></th>
<th>Carcinus maenas 52-78 g</th>
<th>Carcinus maenas 85-125 g</th>
<th>Cancer productus 52-78 g</th>
<th>Cancer productus 85-125 g</th>
<th>Cancer productus 166-214 g</th>
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</thead>
<tbody>
<tr>
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<td>Cancer productus 166-214 g</td>
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</tbody>
</table>

Table 6.
Non-lethal injuries occurring during the predation pairing study, indicating leg loss, claw loss, or carapace injury. When paired with the species/size class in the column across the top this explains the non-lethal interactions experienced by the species/size class along the rows (Cl = Claw Loss, L = Leg Loss, Cp = Carapace Injury).
DISCUSSION

Community structure and function within aquatic systems is tightly linked to predation (Paine 1966, 1980; Sih et al. 1985; Kerfoot and Sih 1987; Posey and Hines 1991). The highly mobile crabs, *Carcinus maenas* and *Cancer productus*, are both efficient predators that affect the distribution and abundance of prey species. The invasive *C. maenas*, has the potential to reduce both species diversity and species abundance within the newly invaded community. Reise (1978) found that juvenile *C. maenas* could prevent the development of cockle beds, thus altering the community structure. Jensen and Jensen (1985) found that in years of low *C. maenas* abundance, cockles are so dense that they reduce the survival and fertility of the tube building amphipod *Corophium volutator*. Thus a reduction in cockles through predation by *C. maenas* increased the productivity of *Corophium volutator*. Decreases in other bivalve populations have also been associated with predation by *C. maenas* (Virnstein 1977; Grosholz and Ruiz 1995). Evans (1983) found that the larger predators within a soft-bottomed ecosystem control the level of abundance of smaller epibenthic consumers and predators. Reise (1978) found that *C. maenas* was one of two species to strongly influence the continually changing community structure and composition within tidal flat communities of the Wadden Sea.

*Carcinus maenas* has become known as a successful marine invasive species having established populations on four continents. It is the largest and potentially most aggressive shore crab that currently exists within the upper estuarine habitats on the west coast of North America. Its abundance and exploitation of resources
along the shores of the Atlantic coast of North America following its 19th century invasion have concerned Pacific coast marine ecologists about the uncertain future of native organisms within the same habitat. Yet, while much of the research interest is focused on its range expansion and its role as a bivalve predator, relatively little is known how this new invader will fit into the guild of native crabs.

The distributions of Brachyuran crab species in estuaries are controlled by physical and biotic factors. These include physiological tolerances to desiccation, temperature, salinity, and fine particulates (DeFur and McMahon 1984a, b; Menge 1978a, b; Dayton 1984), and competition and predation (Muntz et al. 1965; Paine 1966; Virnstein 1977; Caswell 1978; Reise 1978, 1985; Peterson 1979 a, b; Evans 1983; Taylor 1984; Heck and Wilson 1987; Behrens Yamada and Boulding 1998). These estuarine habitat gradients may also explain differences in diet among or within populations of crabs (Paul 1981; Laughlin 1982; Norman and Jones 1992; Freire and González-Gurriarán 1995). The physiological limitations of Carcinus maenas and Cancer productus are very different. Carcinus maenas is more physiologically tolerant and was found at sites with salinities as low as 15 ppt, and water temperatures ranging as high as 20 °C, while C. productus was found above 21 ppt, and below 16 °C. The greatest CPUE for C. productus occurred at stations with the lowest temperatures and highest salinities. High temperatures, reduced salinity, and soft sediment without cover appear to exclude C. productus from the upper estuary. The shallow habitat at the OCA exhibited high salinity but was unsuitable
for *C. productus* because it lacked rock and boulder shelters and the water
temperatures rose to 20 °C.

The two most important biotic interactions influencing benthic populations
are predation and competition (Muus 1973; Rees et al. 1976, 1977; Evans 1983).
Competition and intraguild predation are important factors with both immediate and
long term affects for the structure and function of communities and ecosystems
(Polis 1988; Polis et al. 1989). Although *Carcinus maenas* is physiologically able to
tolerate the habitat type and physical conditions in the lower estuary, it appears that
the threat of predation by large male *Cancer productus* contributes to their exclusion.

Size is an important consideration in any interaction between two crabs.
Similar sized antagonists of the same species seldom kill each other (Huntingford et
al. 1995; Lee 1995). Aggressive behavior directed against substantially smaller
individuals, however, carries less risk of injury for the larger antagonist. This pattern
was demonstrated by both medium and large *Cancer productus* preying significantly
more heavily on smaller size class of *Carcinus maenas*.

These stage-structured interactions have a great potential to influence
population and community dynamics (Werner and Gilliam 1984). Cannibalism upon
the young by older members of the population is known to occur at some stage in the
life history of many animal species (Polis 1981), and is very common among crabs
(Elner 1981; Kurihara and Okamoto 1987; Wolcott 1988; Anger 1995; Perkins-
Green crabs of all sizes are vulnerable to cannibalism immediately after molting
Predation and cannibalism events can regulate population size, reduce inter- and intra-specific competition, and supplement the diet with a nitrogen rich food source (Klein Breteler 1975; Wolcott 1988, Wolcott and O'Connor 1992; Kneib et al. 1999).

Both interspecific and intraspecific predator-prey dynamics exist among crustaceans (MacKay 1942; Butler 1954; Macnae 1968; Gotshall 1977; Warner 1977; Botsford and Wickman 1978; Stevens et al. 1982; ap Rheinallt and Hughes 1985; ap Rheinallt 1986; Lovrich and Sainte Marie 1997; Kneib et al. 1999). Similar to other crab species, adult Cancer productus and Carcinus maenas preyed upon both conspecific and heterospecific juveniles under laboratory conditions, and as such, functioned as both cannibals and as potential intraguild predators (Polis et al. 1989; Kneib et al. 1999). The dramatic difference here is the low survival rate of adult C. maenas in the presence of similar-sized or larger adult male C. productus.

Hines et al. (1990) suggest that interspecific differences in aggregative behavior and resource utilization are the major causes of the patchiness observed in predator distribution. Their findings could explain why C. maenas was rare or absent in suitable sloping intertidal habitats such as the Port of Newport and South Beach Marina Jetty. While such habitats are utilized by C. maenas within its native and nonindigenous ranges, this was not the case in Yaquina Bay. Instead, these habitats support dense populations of Cancer productus. The predation study conducted within the lab suggests that there is more to the distributional pattern than
aggregative behavior, namely that intraguild predation of *C. maenas* by *C. productus* may exclude *C. maenas* from the lower estuary.

These experiments on the distribution of, and predation patterns between, a native and introduced epibenthic predator show: (1) an inverse distributional relationship between adult *Carcinus maenas* and adult *Cancer productus* within Yaquina Bay, Oregon, and (2) predation between the two species is generally unidirectional, with an increased rate of predation on *C. maenas* by larger *C. productus*. With the degree of interspecific predation greater than the rate of intraspecific predation (cannibalism), localized population regulation of *C. maenas* is not intraspecific, in the lower estuary, but regulated by other guild members.

The physiology of *Cancer productus* undoubtedly contributed to the limited number of sites where it was found. Although *Carcinus maenas* was physiologically able to tolerate conditions at all sites, except the upper extreme at the Port of Toledo, it was only discovered at sites with low CPUE of *C. productus*. Of the seven sites in which *C. maenas* was discovered, *C. productus* occurred in only three. In contrast, *C. maenas* overlapped with *Cancer magister* at six sites and with *Hemigrapsus oregonensis* at all seven *C. maenas* was discovered.

While physiological tolerance to physical factors determines the general distribution pattern of brachyuran crab species, predation gradient also appear to limit distributions. *Carcinus maenas, H. oregonensis*, and juvenile *C. magister* have greater tolerance to reduced salinity than *C. productus* and therefore persist farther up the estuary. A caging experiment demonstrated that *C. maenas* is able to tolerate
the lower estuarine habitats dominated by *C. productus* (S.B. Yamada, unpublished data). Further, *C. maenas* is found just outside of the South Beach Marina, but is absent within, where *C. productus* is abundant. It thus appears that physiological tolerances prevent *C. productus* from exploiting the upper estuary while intraguild predation plays a role in keeping *C. maenas* out of the more benign lower estuary.

It has been pointed out that active intraguild predation reduces the effects of resource partitioning (Cody 1974), and would therefore reduce the possibility of competitive exclusion of western Pacific shore crab populations (*Hemigrapsus* spp.) by *Carcinus maenas*. In this case it appears that *Hemigrapsus* species will benefit from the predatory nature of *C. productus* as a predator of their predator, i.e. “the enemy of your enemy is your friend.” *Cancer productus* is considered primarily a shallow subtidal predator, with adult males foraging intertidally at high salinities, with females and juveniles being restricted to sheltered habitats in the lower intertidal (Robles et al. 1989; Behrens Yamada and Boulding 1998; Smith et al. 1999). Areas where *C. productus* controls the abundance of *C. maenas* may provide refuges for the continued survival and reproduction of native species. One result of predation is the reduction of resource competition by keeping competing species at reduced densities, leading to increased diversity (Connell 1970; Dayton 1971; Paine 1974; Evans 1983). This may be good news for the Puget Sound and Pacific Northwest estuaries where *C. productus* is abundant within high salinity low temperature environments.
Aggressive predation by native adult crabs may be an important factor determining the survival of newly recruited *C. maenas* in Pacific Northwest estuaries. If they settle out of the plankton in regions of high marine salinities and low temperatures that support populations of adult *C. productus*, there is a much greater risk of predation by the larger red rock crabs. Those that settle out in the upper estuary would avoid the predator, and would effectively increase their chances of survival.

The direct predation by *Cancer productus* on *Carcinus maenas* may allow the diversity of the natural community to maintain a level that resembles the environment pre-invasion, while habitats in the upper estuary, out of the physiological range of *C. productus*, are exploited by *C. maenas*. This is comparable to some European shores where the upper boundary is dominated by *C. maenas*, the mid depths are dominated by *Cancer pagurus*, and below them the habitat is dominated by *Necora puber* (M. Torchin, personal communication). In these habitats *N. puber* is a highly mobile predator of *C. maenas*, and juvenile cancrids. Once again, the primary control of habitat exploited and occupied by each species is determined by physical conditions and physiological tolerances, but boundaries within suitable habitats may be explained by intraguild predation.

Not all interactions between *Carcinus maenas* and *Cancer productus* within the predation study resulted in direct predation events. Evidence for these interactions included carapace damage, limb damage, and limb loss. Within crab species claw damage resulting in claw loss has been shown to decrease the fitness of
the individual crab, reducing its ability of foraging for prey (Kuris and Mager 1975; McVean and Findlay 1979; Elner 1980; Abby-Kalio and Warner 1989; Smith 1995; Brock 1998; Lee and Seed 1992; Brock and Smith 1998) and compete successfully for reproductive females (Bennett 1973; Kaiser et al. 1990). Males with only one or no claws lose receptive females to healthy male crabs (Bennett 1973; Kaiser et al. 1990). The results of the interactions observed in this study between these two crab species may have localized implications for the reproductive population of *C. maenas* within Yaquina Bay. If interactions with *Cancer productus* only occur within the lower estuary, and these interactions reduce the fitness of lower estuarine *C. maenas* crabs, then the members of this population which reside in the upper estuary may contribute a greater proportion to the reproductive population than crabs in the lower estuary.
CONCLUSIONS

Many of the questions surrounding the introduction of *Carcinus maenas* to North American west coast habitats focus on whether this new predator will severely decrease the abundance of native estuarine species (Jamieson et al. 1998). For example, an increase in *C. maenas* was correlated with a decrease in the native yellow shore crab, *Hemigrapsus oregonensis* (Grosholz et al. 2000). Other species, such as the native red rock crab, *Cancer productus* may actually benefit from the presence of *C. maenas*. The intertidal migration exhibited by *C. maenas* (Naylor 1958; Naylor 1962; Klein Breteler 1976; McGaw and Naylor 1992a, 1992b; McGaw et al. 1992) suggest that adult crabs within the lower estuary will occupy the same habitat as adult *C. productus*, and have been shown to represent an available food source. If *C. maenas* becomes as abundant as in their native range, or the eastern U.S. coast, *C. productus* could benefit from this addition of a new food source within eastern Pacific ecosystems. The presence of *C. productus* would reduce levels of *C. maenas* abundance and thus would favor the persistence of native species. These regions may in effect become a "refuge" for native species that would otherwise see declines in abundance as a result of the introduction of *C. maenas*.

Should *Cancer productus* follow the observed predation rates upon, and inverse distributional relationship with *Carcinus maenas* it may prove to be the restrictive force for *C. maenas* distribution within the Pacific Northwest. Puget Sound with its cool temperatures and a more stable salinity profile than does
Yaquina Bay, Oregon, may ultimately determine if this intraguild predation is an important factor in habitat exploitation by *C. maenas* within Pacific Northwest estuaries. Within these waters the distribution of *C. productus* is not limited by decreased salinity and many of these areas support dense populations of *C. productus*. In these habitats adult *C. maenas* may be prevented from reaching the dense populations, which have been reported as adversely impacting Bodega Harbor and the San Francisco Bay estuary benthic communities.
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