



Biotic resistance experienced by an invasive crustacean in a temperate estuary

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Abstract

Communities high in species diversity tend to be more successful in resisting invaders than those low in species diversity. It has been proposed that the biotic resistance offered by native predators, competitors and disease organisms plays a role. In Yaquina Bay, Oregon, we observed very little overlap in the distribution of the invasive European green crab, *Carcinus maenas*, and the larger red rock crab, *Cancer productus*. *C. productus* dominates the more saline, cooler lower estuary and *C. maenas*, the less saline, warmer upper estuary. Because caged *C. maenas* survive well in the lower estuary, we decided to test the hypothesis that *C. productus* prey on *C. maenas* and thus contribute to their exclusion from the more physically benign lower estuary. A laboratory species interaction experiment was designed to determine whether *C. productus* preys on smaller *C. maenas* 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 *C. maenas* and *C. productus* of various sizes. When conspecifics were paired, mortality was less than 14%, even in the presence of larger crabs. Smaller *C. productus* survived well in the presence of larger *C. maenas*, but the reverse was not true. When small *C. maenas* (60–67 mm carapace width) were matched with medium and large *C. productus*, their mortality increased to 52% and 76%, respectively. A less dramatic pattern was observed for medium *C. maenas* (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, *C. productus*, has the potential to reduce the abundance of *C. maenas* in the more saline and cooler lower estuaries.

Introduction

One of the most difficult questions facing invasion biologists is: why do exotic species invade some communities and not others? It has been proposed that islands and disturbed habitats are especially prone to invasions because the species-poor native communities lack predators, competitors, and disease organisms and thus offer little biotic resistance (Stachowicz et al. 1999). The success of goats on oceanic islands and the establishment of the Asian clam *Potamocorbula amurensis*

in disturbed temperate estuaries are two examples that support this view (Coblentz 1978; Nichols et al. 1990; Cohen and Carlton 1998).

It may be possible to test the biotic resistance hypothesis, by comparing the success of a global invader in ecosystems differing in species diversity. The European green crab, *Carcinus maenas*, with its long invasion history is a good candidate for such a comparison. This species became established on the Atlantic coast of North America and the southeast coast of Australia prior to 1900 and recently appeared in

South Africa, Tasmania and on the Pacific coast of North America (Say 1817; Fulton and Grant 1900; Le Roux et al. 1990; Cohen et al. 1995; Grosholz and Ruiz 1995). Like many invasive species, *C. maenas* is a physiological and ecological generalist, tolerating air exposure, starvation and wide ranges in temperature and salinity (Behrens Yamada 2001). It consumes prey from over 150 genera including molluscs, crustaceans, worms, algae and marsh vegetation (Cohen et al. 1995). In its native habitat and on the Atlantic coast of North America, *C. maenas* inhabits estuarine tidal marshes, mudflats, cobble beaches, as well as rocky shores on both wave-protected and semi-exposed shores (Crothers 1970; Menge 1983; Grosholz and Ruiz 1996). When *C. maenas* is abundant, young mussels, urchins, cockle beds and barnacles cannot establish themselves (Kitching et al. 1959; Muntz et al. 1965; Jensen and Jensen 1985; Beukema 1991; Leonard et al. 1999). On the Atlantic coast of North America, the build up of *C. maenas* densities (up to 500/m²) has been correlated with a dramatic decline in the landings of the soft-shelled clam, *Mya arenaria* (Glude 1955; MacPhail et al. 1955; Welch 1968).

While *C. maenas* is considered a pest on the Atlantic coast of North America, its presence in southeastern Australia causes little concern. Natural enemies, including predators, competitors and parasites, appear to keep densities low and impact small. Native Australian predators include the heavily armored crab *Ozius truncatus*, the aggressive swimming crab *Portunus pelagicus*, skates and rays (Zeidler 1997; Center for Research on Introduced Marine Pests information sheet). Sinclair (1997) found that seven species of native grapsid crabs were not adversely affected by the invader. While we lack information on the early invasion process of *C. maenas* in Australia, it appears that the resistance offered by the diverse native fauna, including other crabs, may prevent *C. maenas* from becoming a pest.

If the biotic resistance hypothesis applies to *C. maenas*, we might expect this invader to exert less of an impact on marine communities on the Pacific coast of North America than on the Atlantic coast. Jamieson et al. (1998) points out that 23 native brachyuran crabs species occur on the Pacific compared to only nine on the Atlantic coast. In our surveys of Oregon estuaries we typically find 10 native crabs within the distributional range of *C. maenas*. The most common are the grapsids, *Hemigrapsus oregonensis* (Oregon shore crab) and *H. nudus* (purple shore crab) and the cancrids, *Cancer productus* (red rock crab) and juvenile

Cancer magister (Dungeness crab). Both species of *Hemigrapsus* are small omnivorous crabs that rarely attain a carapace width of over 30 mm. They possess relatively weak monomorphic claws with fine denticles and mechanical advantages of 0.28. (Mechanical advantage is the ratio of a claw's lever arms: the distance from the fulcrum to the attachment of the closer muscle and the distance from the fulcrum to the tip of the moveable finger.) The two species of *Cancer* are much larger, attaining carapace widths of over 160 mm for *C. productus* and over 190 mm for *C. magister*. While *C. magister* attains a larger size, its slender claws exhibit a mechanical advantage of only 0.25. *C. productus*, on the other hand, has very powerful claws for its size with a mechanical advantage of 0.39 (Behrens Yamada and Boulding 1998). *C. maenas*, with a carapace width of over 90 mm, is a medium sized crab compared to *Hemigrapsus* spp. and *Cancer* spp. Adult *C. maenas* possess claws of different sizes. The larger crusher claw has a mechanical advantage of 0.36 while the more slender cutter claw, 0.26 (Warner et al. 1982). This dual tool set may allow *C. maenas* to exploit a larger food spectrum than *Hemigrapsus* spp. and *Cancer* spp. with their monomorphic claws.

While surveying Oregon estuaries for the status of the *C. maenas* invasion during the summer of 1998, we noted very little overlap in the distribution of *C. maenas* and *C. productus*. *C. maenas* was the dominant crab in the warmer, less saline upper estuary and *C. productus*, in the cooler, more saline low estuary. A similar pattern was observed in Bodega Bay Harbor, California. *C. maenas* was restricted to the shallow mudflats inside the harbor while the brown rock crab, *Cancer antennarius*, and *C. productus* occupied the rocky shore close to the mouth of the harbor (Grosholz and Ruiz 1996; McDonald et al. 1998). When five *C. maenas* were caged on a rocky shore near the mouth of an Oregon estuary, they survived well (authors' unpublished data). This observation suggests that physical factors are not responsible for keeping *C. maenas* out of the lower estuary. Since *C. productus* has a reputation as a voracious predator on mollusks and other crabs, including smaller members of their own species (Daley 1981; Boulding and Hay 1984; Robles et al. 1989; Behrens Yamada and Boulding 1996), we suspected that *C. productus* predation may limit the distribution of *C. maenas* to the upper estuary. The goal of our study was twofold: (1) to document the distributional relationships between *C. maenas* and common native crabs, and (2) to test the hypothesis that predation by the native *C. productus* limits the distribution

and abundance of nonindigenous *C. maenas*. These objectives were accomplished by systematically trapping crabs along a temperate Oregon estuary and by setting up laboratory arenas to elucidate the interactions between *C. maenas* and *C. productus* of various sizes.

Materials and methods

Distribution study

In order to document the distributional patterns between *C. maenas* and common native crabs, we sampled 10 stations, representing a range of habitat types, along the Yaquina estuary (Figure 1, Table 1). Since vandalism of traps was a problem, we focused

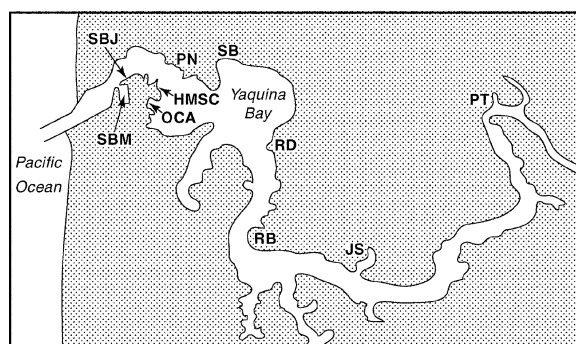


Figure 1. Map of Yaquina Bay, Oregon, showing locations of the ten trapping sites. For abbreviations and characteristics of sites see Table 1.

our efforts on five permanent sites that were relatively secure from public interference: Port of Toledo docks, Riverbend Marine on Oneatta Point, Roberts' private dock by Weiser Point, a mudflat near the Oregon Coast Aquarium (OCA) and South Beach Marina. These sites were trapped daily for 90 days from June to September 1999 while five less secure sites were trapped for only 18 days.

All but one of the study sites possess rock shelters in the form of rip-rap close to the trapping sites. The OCA site, a tidal flat intersected by a channel, lacks rock cover. Temperature and salinity measurements were taken whenever traps were checked. Air and water temperatures were measured with a field thermometer and salinity of the surface water, with a temperature-compensated refractometer. Tidal levels of the traps were estimated from tide tables using the observed low tide mark as a reference point.

Two trap designs were used to collect a range of crab sizes. The collapsible Fukui fish trap (60 cm × 45 cm × 20 cm) is covered with 2 cm plastic mesh and possesses two expandable slit openings (45 cm) at each end. This design allows even the largest crabs to enter. The box trap is a modified 2 cm mesh stainless steel cage (60 cm × 60 cm × 30 cm) with conical meshed openings (8–9 cm in diameter) on each of the four sides. A commercial bait container, filled with fresh salmon backbone and flesh, was added to each trap each day. Two to three traps of each type were used at each of the sites. Traps were placed near the 0 m tidal level, except at the Sally's Bend mudflat where traps were set at the 0.5 m level. Traps were allowed to soak for a

Table 1. Description of the physical features of each of the 10 trapping sites. Permanent sites with more than 208 trap days each are indicated by an asterisk.

Site	River mile	Salinity range (ppt)	Temperature range (°C)	Estimated slope	Habitat type
Port of Toledo, PT*	12.5	14–24	19–21	20–70°	Upper intertidal <i>Scirpus</i> , adjacent to rip-rap.
Johnson Slough, JS	7.4	16–28	15–18	10–30°	Upper intertidal <i>Scirpus</i> , adjacent to rip-rap.
Riverbend, RB*	5.5	21–35	14–16	30–50°	Rip-rap finger jetty, adjacent to river channel and tidal flat.
Roberts' Dock, RD*	4.6	28–36	11–19	10–45°	Intertidal <i>Zostera</i> on tidal flat, adjacent to rip-rap.
Sally's Bend, SB	3.1	15–30	13–20	<10°	Large tidal flat with upper intertidal <i>Scirpus</i> .
Oregon Coast Aquarium, OCA*	2.2	28–36	14–20	<10°	Upper intertidal <i>Scirpus</i> , minor rip-rap. Sea-water from aquarium outfall constantly drains into a channel that intersects a mudflat.
Port of Newport, PN	1.9	25–32	12–15	<10–45°	Rip-rapped shoreline adjacent to tidal flat.
Pumphouse, HMSC	1.8	23–30	12–14	10–45°	Rip-rapped finger jetty entering lower intertidal <i>Zostera</i> and sandy subtidal.
South Beach Marina Jetty, SBJ	1.3	28–34	12–16	10–45°	Rip-rapped shoreline adjacent to intertidal <i>Zostera</i> tidal flat.
South Beach Marina, SBM*	1.3	22–36	13–16	<10–45°	Rip-rapped shoreline entering subtidal sand and fine sediments.

day before they were checked. All trapped crabs were identified to species and sex and any injuries or parasite infections noted. Maximum carapace width, including protruding spines, was measured using vernier calipers. For example, *C. maenas* was measured between the tips of their 5th antero-lateral spines and *C. productus*, between the tips of their 10th anterior-lateral spine. Catch per unit effort (CPUE) was calculated for each site by averaging the number of crabs caught per trap per day.

Laboratory predation experiment

Since we observed an inverse distributional relationship between *C. maenas* and *C. productus*, we set up pair-wise laboratory trials to determine whether the native *C. productus* preys on smaller *C. maenas* at a greater rate than on similar sized crabs of its own species. In order to set up a fair interaction trial between two crabs, we used only healthy crabs that had not molted recently or were not about to molt soon. We collected healthy male crabs of both species with intact limbs, weighed and measured them and derived regression equations of mass on carapace width:

$$\begin{aligned} C. maenas \quad \text{Log}_{10}(\text{Mass}) \\ = \text{Log}_{10}(3.12\text{CW} - 3.83) \quad R^2 = 0.96 \end{aligned}$$

$$\begin{aligned} C. productus \quad \text{Log}_{10}(\text{Mass}) \\ = \text{Log}_{10}(2.93\text{CW} - 3.73) \quad R^2 = 0.98 \end{aligned}$$

These regressions allowed us to identify animals that did not fall within the predicted 95% confidence interval of the regressions. Thus, crabs that were about to molt soon (heavy for their CW) or had recently molted (light for their CW) could be discarded. Three distinct weight classes of crabs were chosen: small (52–78 g), medium (85–125 g) and large (166–214 g). *C. maenas* from the abundant 1997/1998 year class were divided into small (60–67 mm CW) and medium (73–80 mm CW) size classes. Since *C. productus* reaches a maximum size twice that of *C. maenas*, three size classes were chosen: small (71–77 mm), medium (91–98 mm) and large (103–109 mm). Although still not approaching the maximum size (>190 mm) for *C. productus*, the large size class (103–109 mm) was used to determine if size plays a factor in the species interactions.

Upon entering the laboratory each healthy male crab was put into a conspecific community tank (120 cm × 43 cm × 30 cm) and fed mussels. Three days prior

Table 2. Experimental design for the *C. maenas*–*C. productus* species interaction experiment. S, M and L refers to small medium and large crabs. Each of the 14 pairings was run 50 times.

	<i>Carcinus</i> (S)	<i>Carcinus</i> (M)	<i>Cancer</i> (S)	<i>Cancer</i> (M)
<i>Carcinus</i> (S)	50			
<i>Carcinus</i> (M)	50	50		
<i>Cancer</i> (S)	50	50	50	
<i>Cancer</i> (M)	50	50	50	50
<i>Cancer</i> (L)	50	50	50	50

to starting an experiment, crabs were chosen at random, weighed and placed into individually numbered containers and starved. This allowed us to standardize hunger level and to randomly pair crabs from appropriate size classes. Small and medium *C. maenas* and small, medium and large *C. productus* were each paired with *C. maenas* and *C. productus* of various sizes. We did not run the interaction between two large *C. productus* as this interaction was not the focus of our study. Each of the 14 pairings was replicated 50 times (Table 2).

Experimental arenas consisted of 3.8 liter rectangular plastic Sterilite® boxes (15.8 cm × 30 mm × 8 cm) with secured plastic lids. Filtered seawater (minimum flow of 2 l/h) entered via the top and exited via six out-flow holes along the sides. Thus, each arena had its own water source. No sediment was added to the arenas in an attempt to avoid possible variation due to sediment type. The salinity ranged from 32 to 37 ppt, and temperature from 11 °C to 14 °C. Each pair of crabs was placed simultaneously at opposite ends of an arena (Figure 2). Seven arenas were placed into each of eight fully drained outdoor aquariums with a semi-opaque lids and sides. Four replicates of each of the 14 treatments were run concurrently to minimize variation through time (day length, salinity, and temperature). Each day, for seven days, crabs were checked for limb loss and predation events.

Results

Distribution study

The ten study sites in Yaquina Bay reflect the typical habitat diversity and physical factors found in temperate estuaries (Figure 1, Table 1). As expected, the Port of Toledo in the upper estuary exhibited the lowest salinities and highest temperatures while sites near

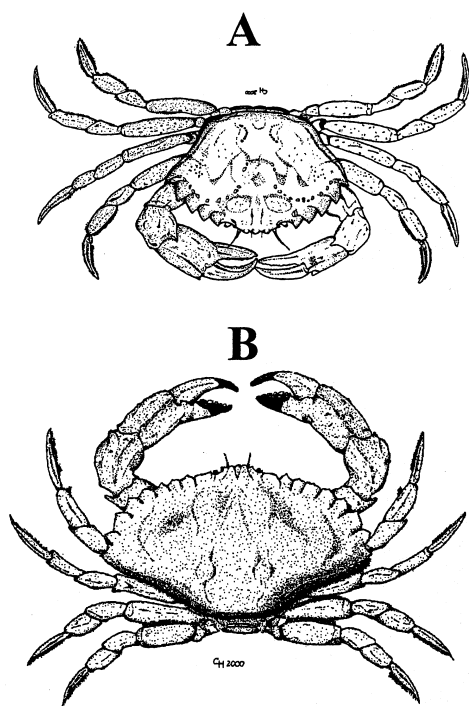


Figure 2. Top view of an experimental arena showing a medium *C. maenas* (A) paired with a medium *C. productus* (B).

the mouth of the estuary, the highest salinities and lowest temperatures. Sally's Bend with its extensive shallow mudflat exhibited salinities as low as 15 ppt and temperatures as high as 20 °C. The greatest variability in temperature was observed in the mid-estuary, reflecting the movement of upper and lower estuarine waters during the tidal cycle.

While crabs were trapped at all ten study sites, species diversity increased toward the cooler, high saline lower estuary (Table 3). *C. maenas* and the native crabs *C. productus*, juvenile *C. magister* and *H. oregonensis* were the most frequently trapped crabs. The native crabs *H. nudus*, *C. antennarius* and *Pugettia producta* occasionally entered traps in the lower estuary. The euryhaline *H. oregonensis* occurred throughout the estuary while the nonindigenous brackish water crab, *Rhithropanopeus harrisi* was only trapped at the Port of Toledo.

While crab species showed different preferences for the two trap types, the distributional patterns for the crabs remained the same. *C. maenas* entered box traps twice as often as the Fukui fish traps, while *C. magister* exhibited the opposite preference (Table 3). *H. oregonensis* was present at all 10 sites. The juveniles

Table 3. CPUE for the four most frequently caught crabs at the ten sites using Fukui fish traps (A) and box traps (B). CPUE is given as number of crabs per trap per day.

Site	<i>Carcinus maenas</i>	<i>Cancer productus</i>	<i>Cancer magister</i>	<i>Hemigrapsus oregonensis</i>
A. Fukui fish trap CPUE				
Port of Toledo, PT*	–	–	–	0.204
Johnson Slough, JS	0.869	–	1.986	0.331
Riverbend, RB*	0.742	0.017	0.922	0.104
Roberts Dock, RD*	0.551	0.008	1.884	1.045
Sally's Bend, SB	0.5780	–	–	0.154
Aquarium, OCA*	0.813	0.066	0.206	2.180
Port of Newport, PN	–	0.958	0.152	0.030
Pumphouse, HMSC	0.269	1.418	1.038	0.090
South Beach Jetty, SBJ	0.159	3.347	1.068	–
South Beach Marina, SBM*	–	5.857	0.222	0.148
B. Box trap CPUE				
Port of Toledo, PT*	–	–	–	0.056
Johnson Slough, JS	1.517	–	0.032	0.570
Riverbend, RB*	2.809	0.009	0.080	0.044
Roberts Dock, RD*	1.337	–	0.050	0.350
Sally's Bend, SB	1.050	–	–	0.011
Aquarium, OCA*	2.337	–	0.131	4.279
Port of Newport, PN	–	1.549	–	0.056
Pumphouse, HMSC	0.024	2.083	0.057	0.328
South Beach Jetty, SBJ	0.625	2.133	0.010	0.084
South Beach Marina, SBM*	–	4.477	0.099	–

of the commercial Dungeness crab, *C. magister*, ranged throughout the estuary, but were absent from the two sites where salinities dropped to 15 ppt and temperatures rose to 20 °C. *C. maenas* was most abundant between River Mile 2 and 7.4 but was noticeably absent from the Port of Toledo where salinities were the lowest and from the Port of Newport and South Beach Marina near the mouth of the estuary. *C. productus* was

Table 4. Correlation of CPUE of *C. maenas* with three of the most common native crabs using Fukui fish traps (A) and box traps (B). The Pearson correlation coefficient is based on nine study sites. The Port of Toledo was eliminated from the analysis, as salinities there are too low to support most crab species.

Green crab vs. native species	Pearson correlation coefficient	Probability
A. Fukui fish trap		
<i>C. maenas</i> vs. <i>C. productus</i>	-0.747	0.021
<i>C. maenas</i> vs. <i>C. magister</i>	0.368	0.330
<i>C. maenas</i> vs. <i>H. oregonensis</i>	0.515	0.156
B. Box trap		
<i>C. maenas</i> vs. <i>C. productus</i>	-0.746	0.021
<i>C. maenas</i> vs. <i>C. magister</i>	0.421	0.259
<i>C. maenas</i> vs. <i>H. oregonensis</i>	0.471	0.200

the most abundant crab in the lower estuary from River Mile 1–2.

Correlations of *C. maenas* catches with those of each of the three common native species indicates no significant correlation with juvenile *C. magister* and *H. oregonensis* but a significant negative correlation in the distribution pattern with *C. productus* (Table 4). This negative correlation is observed with both trap types and is particularly dramatic for the five permanent study sites (Figure 3).

Laboratory predation experiment

Theoretically, the pairing of any two crabs could result in a predation event occurring in either direction. When conspecific crabs were paired, mortality was less than 14%, even in the presence of larger crabs (Figure 4). Smaller *C. productus* survived equally well in the presence of larger green crabs, but the reverse was not true. When small *C. maenas* were matched with medium *C. productus*, they experienced a 52% mortality. When matched with large *C. productus*, mortality increases even further to 76%. A similar pattern was found when medium *C. maenas* were matched with medium and large *C. productus*. Mortality increased to 32% and 46%, respectively. Chi-squared tests on the effect of *C. productus* size on the survival of *C. maenas* were highly significant (small *C. maenas*: $\chi^2 = 42.00$, $df = 2$, $P = < 0.0005$; medium *C. maenas*: $\chi^2 = 25.84$, $df = 2$, $P = < 0.0005$). Thus, the larger the asymmetry in size in favor of *C. productus*, the greater the mortality experienced by *C. maenas*.

Discussion

Distributions

Crab species diversity along a temperate Oregon estuary decreased with distance from the mouth. In Yaquina Bay, we observed the native crabs *H. oregonensis*, *H. nudus*, *Pachygrapsus crassipes*, *Lophopanopeus bellus*, *Cancer oregonensis*, *C. magister*, *C. productus*, *C. antennarius*, *Cancer gracilis* and *P. producta* in the saline, cooler lower estuary, but only *H. oregonensis* and the nonindigenous brackish water specialist, *R. harrisi* at the Port of Toledo at River Mile 12.5. The distance crabs penetrate up an estuary is dictated by their physiological tolerances. For example, *H. oregonensis* is the most tolerant of the native crabs to sedimentation, and to a wide range of temperatures and salinities (Dehnel and Carefoot 1965; Daley 1981) and consequently thrives at all sites along the estuary from South Beach Marina at River Mile 1.3 to the Port of Toledo at River Mile 12.5. Juvenile *C. magister* and adult *C. maenas* appear to be slightly less tolerant in that they penetrate the estuary up to Johnson Slough at River Mile 7.4. In contrast, *C. productus*, with its narrow physiological tolerances, is only found in the lower estuary where salinities remain above 25 ppt, temperatures below 15°C and fine sediment is absent (Daley 1981). This species thrives on gently sloping shores with boulder shelters but is absent from tidal marshes and mudflats.

While marginal physical factors set the distributional limit of crab species in the upper estuary, species interactions become more important in the physically benign lower estuary. Although *C. maenas* is physiologically able to tolerate the habitat type and physical conditions in the lower estuary, its densities decrease near the mouth. *C. maenas* is present at South Beach Jetty but not inside South Beach Marina where *C. productus* is most abundant. The strong inverse correlation in catches of *C. maenas* and *C. productus* suggest that large male *C. productus* prey on smaller *C. maenas*. Large male *C. productus* are voracious predators that prey not only on molluscs but also on other crabs, including their own species (Daley 1981). Robles et al. (1989) have shown that female and smaller male *C. productus* do not leave their shelters when large male *C. productus* are foraging. Our unpublished observations suggest that small *C. productus* will not enter a trap if a large male *C. productus* is

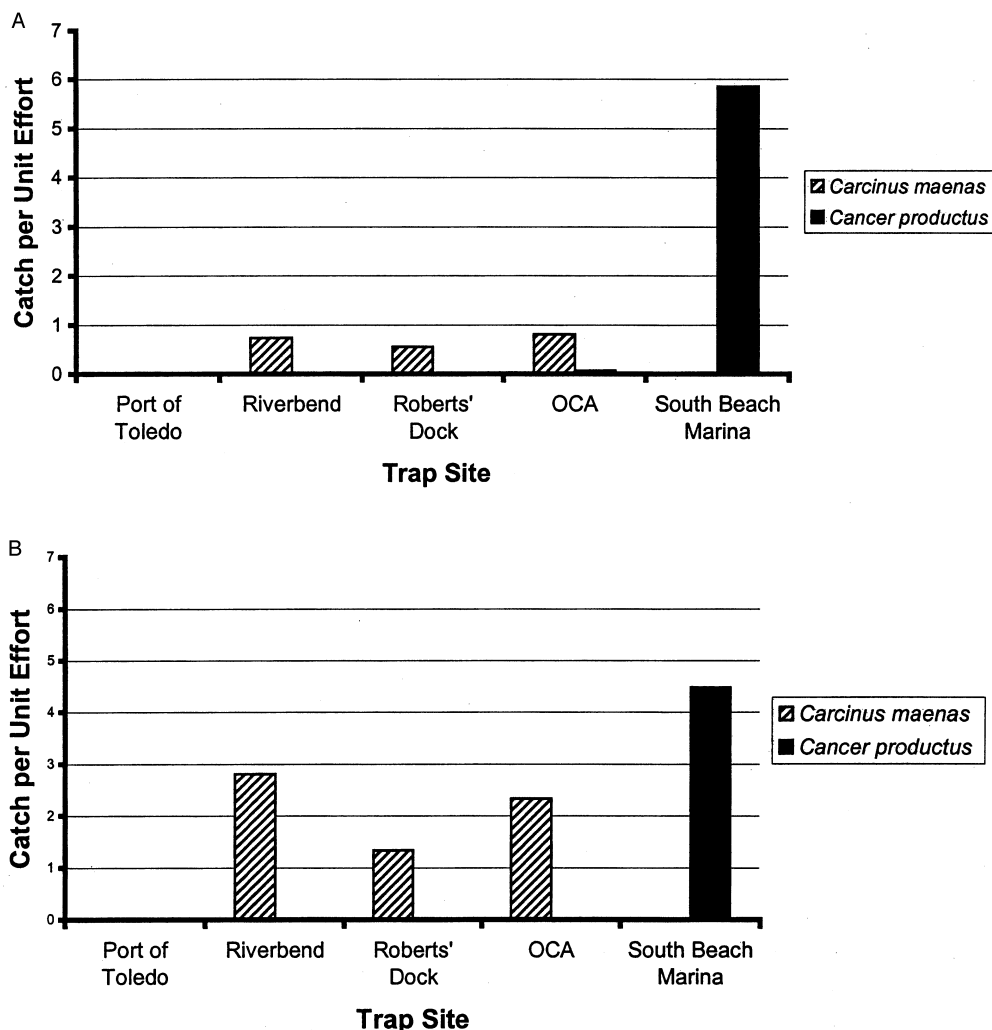


Figure 3. Primary site comparison: CPUE of *C. maenas* and *C. productus* at the five permanent trapping sites using Fukui fish traps (A) and box traps (B).

already present. It is conceivable that *C. maenas* exhibits similar avoidance behavior to the presence of larger *C. productus*. Thus, physiological tolerances prevent *C. productus* from exploiting the upper estuary while intraguild interactions play a role in excluding *C. maenas* from the more benign lower estuary.

Species interactions

Both species of crabs exhibited a low rate of cannibalism (14%) when confined to the arenas for seven days. 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, including *C. maenas* and *C. productus* (Elner 1981; Kurihara and Okamoto 1987; Anger 1995; Beck 1997; Lovrich and Sainte-Marie 1997; Moksnes et al. 1997). Cannibalism can regulate population size, reduce intra-specific competition, and supplement the diet with a nitrogen rich food source (Klein Breteler 1975; Kneib et al. 1999).

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

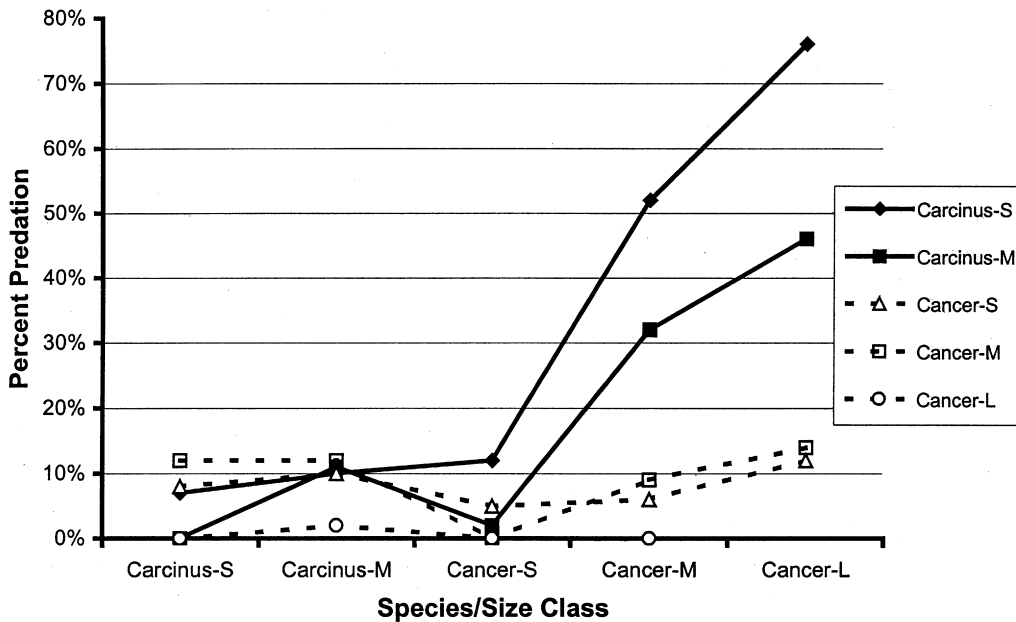


Figure 4. Percent predation experienced by crabs in the legend when paired with crabs on the x-axis. Cancer refers to *C. productus* and S, M and L to small medium and large crabs. See text for details.

risk of injury for the larger antagonist. Predation on conspecifics, however, did not increase with size in our arenas. Even small *C. productus* survived well when matched with large conspecifics. Small *C. productus* survived well in the presence of medium *C. maenas* but the reverse was not true. Larger *C. productus* preyed significantly more on smaller *C. maenas* than on conspecifics. The greater the size difference, the greater the predation rate. Small *C. maenas* experienced 12%, 52% and 76% predation respectively when matched with small, medium and large *C. productus*. Even medium *C. maenas* survived poorly when matched with similar sized *C. productus*. It appears that *C. maenas* with only one crusher claw with a mechanical advantage of 0.36 is no match for *C. productus* with two strong claws with a mechanical advantage of 0.39. Our laboratory trials demonstrate that direct predation by larger *C. productus* males can explain the low abundance or absence of *C. maenas* in our study sites near the mouth of the estuary.

Predictions

It is difficult to predict the eventual distribution, densities and impact of *C. maenas* on the Pacific shores of North America. With maximum densities of only 0.04–0.4/m² (Grosholz et al. 2000), this species has

not reached the densities observed in its native range or on the Atlantic coast of North America. Currently, the species appears to be recruitment limited. The next El Niño event, however, could result in another density increase and range expansion (Behrens Yamada and Hunt 2000; Behrens Yamada 2001).

The results from our study suggests that at least one member of the native community, *C. productus*, is offering biotic resistance to the invasive *C. maenas* on the Pacific coast of North America. Direct predation, or the threat of predation, by larger *C. productus* appears to keep *C. maenas* out of habitats where dense populations of larger *C. productus* thrive: wave-protected rocky shores and gently sloping bolder beaches in cool, saline waters. On those beaches *C. maenas* larvae may settle high on the shore but as the young crabs mature and migrate down, they will encounter resistance from the larger *C. productus*. While large male *C. productus* spend most of their time in the subtidal, they do migrate into the intertidal with the tide to forage (Robles et al. 1989; Walker and Behrens Yamada 1993; Behrens Yamada and Boulding 1996). We predict that the native community on those beaches, where *C. productus* dominates, will not be heavily impacted by *C. maenas* and thus will retain much of their current species diversity.

The impact of *C. maenas* will be most intense in the estuaries and bays with soft sediment. Studies indicate that the native oyster (*Ostrea conchaphila*), mussels (*Mytilus trossulus*), thin shelled clams (e.g. *Nutricula* spp.) and *H. oregonensis* will be adversely affected (Bassett 2000; Grosholz et al. 2000; Palacios and Ferraro 2001). It is also feared that *C. maenas* predation and competition will reduce the abundance of the commercial Dungeness crab, *C. magister*, and flatfish that use estuarine mudflats as nursery habitat (Lafferty et al. 1996). Juvenile *C. magister* and small *H. oregonensis* appear to offer little resistance to the more aggressive *C. maenas* in the upper estuary. Jensen et al. (2000) and McDonald et al. (2001) set up laboratory competition trials in which individual *C. maenas* were matched with *C. magister* or *H. oregonensis* of similar size. Crab pairs were introduced into arenas with either a food or oyster shells for shelters. *C. maenas* was a better competitor for food and shelter than similar sized *C. magister*. Claw size and mechanical advantage undoubtedly played a role in these interactions. Those of *C. magister* are much smaller and weaker than the crusher claw of similar sized *C. maenas* (Hauck 2000). While *C. maenas* won the food competition, *H. oregonensis* won the shelter competition (Jensen et al. 2000). Size for size adult *H. oregonensis* males have larger claws than juvenile *C. maenas* but young *C. maenas* have a higher metabolic rate and consume more food than *H. oregonensis* of similar size (S. Mahaffy, unpub. student report).

It is too early to predict the eventual densities, range and impact of *C. maenas* on the Pacific coast of North America. It is also too early to test the biotic resistance hypothesis that high crab species diversity on the Pacific coast will prevent *C. maenas* from becoming less of a pest than on the Atlantic coast where crab species diversity is low (Jamieson et al. 1998). The biotic resistance hypothesis, however, does apply on a smaller geographic scale. We observed that the species-poor community in the upper estuary is more prone to invasions by exotic crabs than the species rich community in the lower estuary. The brackish water crab, *R. harrisii*, from the Atlantic coast of North America was introduced to the Pacific coast in the 1930s, most likely with oyster transplants (Carlton 1979). It is now established in uppermost estuary of some California and Oregon estuaries where it encounters only one native species: the euryhaline *H. oregonensis*. Jordan (1989) found that the larger and more aggressive native *H. oregonensis* preys on juvenile *R. harrisii* and may

force this invader to move into lower saline waters than in its native habitat. The invasive *C. maenas* thrives in the upper estuary where it coexists with *H. oregonensis* and juvenile *C. magister* but not in the species rich lower estuary where it encounter resistance from the aggressive *C. productus*.

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