

CLAW MORPHOLOGY AND FEEDING RATES OF INTRODUCED EUROPEAN GREEN CRABS (*CARCINUS MAENAS* L, 1758) AND NATIVE DUNGENESS CRABS (*CANCER MAGISTER* DANA, 1852)

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ABSTRACT Claw morphology and prey consumption rates of two estuarine crab species were compared: the introduced European green crab, *Carcinus maenas*, and the native Dungeness crab, *Cancer magister*. For crabs of similar weight, both the crusher and cutter claws of *C. maenas* were larger and exhibited higher mechanical advantage values of the claw lever system than *C. magister*. The mechanical advantages of *C. maenas* crusher and cutter claws are 0.37 and 0.30 respectively versus 0.25 for the claws of *C. magister*. To evaluate the feeding rates of similar-size crabs of each species on prey varying in shell thickness, we conducted laboratory feeding trials. Each crab was offered thin-shelled mussels (*Mytilus trossulus*, 30–40 mm) or thicker shelled native oysters (*Ostrea lurida*, 40–50 mm), and the number of consumed prey items was recorded. When offered mussels, subadult *C. magister* ate significantly more prey per day (7.2 prey/day) than adult *C. maenas* (5.4 prey/day). However, when crabs were offered harder shelled native oysters, *C. maenas*, with their more robust claws, were more capable of crushing them than *C. magister*, with their more delicate claws. Although *C. maenas* is competitively dominant to similar-size juvenile *C. magister*, the per capita feeding rate and predatory impacts of these 2 species depends on prey type.

KEY WORDS: *Carcinus maenas*, *Cancer magister*, claw morphology, prey consumption, feeding rates, mechanical advantage, *Mytilus trossulus*, *Ostrea lurida*, green crab, Dungeness crab

INTRODUCTION

Crabs are major predators of shellfish (Menzel & Hopkins 1955, Parsons 1974, Walne & Davies 1977, Dare et al. 1983). This is also true for the northwest coast of North America. Crab predators on hard-shelled prey include two species of small shore crabs: *Hemigrapsus* spp. and a number of *Cancer* species (Quayle 1988). Although newly planted shellfish are vulnerable to all these crabs species, larger *Cancer* crabs such as the red rock crab, *Cancer productus* (Randall, 1839), are capable of opening even market-size clams, mussels, and oysters (Boulding 1984, Smith et al. 1999). The recent arrival of the European green crab, *Carcinus maenas* (L. 1758), on the west coast of North America adds another shellfish predator to estuarine communities (Cohen et al. 1995, Grosholz & Ruiz 1995, Behrens Yamada & Gillespie 2008).

The European green crab, *C. maenas*, a native to Europe, southern Iceland, and North Africa, has established self-maintaining populations in South Africa, eastern Australia, Tasmania, Argentina, and on both coasts of North America (Say 1817, Le Roux et al. 1990, Cohen et al. 1995, Grosholz & Ruiz 1995, Ah Yong 2005, Hidalgo et al. 2005). Its success as a global invader can be traced to its wide tolerances to temperature, salinity, and desiccation, as well its ability to thrive on a diversity of prey organisms and substrate types (Wallace 1973, Eriksson et al. 1975, Cohen et al. 1995). When abundant, *C. maenas* can prevent the establishment of bivalves, snails, urchins, and barnacles through direct predation (Kitching et al. 1959, Muntz et al. 1965, Menge 1983, Jensen & Jensen 1985, Janke 1990). The digging activities of *C. maenas* while foraging can disrupt nematode communities in mud habitats and can interfere with attempts to reestablish native eel grass transplants (Davis et al. 1998, Schratzberger & Warwick 1999).

The arrival of *C. maenas* to the Pacific coast of North America could have severe ecological and economical repercussions on oysters, clams, mussels, and juvenile English sole if the abundance and distribution of this new predator were to increase (Lafferty & Kuris 1996, Jamieson et al. 1998, Grosholz et al. 2000). The mild winters of the Pacific coast allow *C. maenas* to reach sexual maturity within its first year, as opposed to 2 or 3 y for northern Europe and Maine (Behrens Yamada et al. 2005), thus allowing populations to increase rapidly during warm ocean conditions. For example, densities of *C. maenas* in some protected inlets on the west coast of Vancouver Island built up to more than 20 per trap after the mild winters of 2005 and 2006 (Gillespie et al. 2007, Gillespie pers. comm.)

In addition to being an efficient predator on bivalves, *C. maenas* also has the potential to impact negatively smaller individuals of native crabs through competition and predation. After the arrival of *C. maenas*, the abundance of the native shore crab, *Hemigrapsus oregonensis* (Dana 1851), declined on the mudflats of Bodega Harbor, CA (Grosholz et al. 2000). Similar declines in other native species along the west coast of North America could occur after *C. maenas* becomes more abundant. The Dungeness crab, *Cancer magister* (Dana 1852), is of particular concern because it is the most valuable shellfish species (>\$100 million/y) and because its juveniles rear in estuarine mudflats, where they overlap in habitat use with adult green crabs (Behrens Yamada 2001). The exclusion from this nursery habitat by the invading green crab could have a devastating effect on the Dungeness fishery. Laboratory experiments have demonstrated that, when in direct competition, *C. maenas* consistently displaces similar-size *C. magister* from shelters, and wins nocturnal foraging trials for fresh, damaged clams (McDonald et al. 2001). The competition for resources can be further examined by analyzing type and amount of food consumption by each species, in an effort to understand better their respective per capita prey consumption in the ecosystem.

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The consumption rate of hard-shelled prey by crabs is a function of many factors, including water temperature, physiological condition, and hunger level of the crabs, claw size and morphology, as well as behavioral and mechanical defenses of the prey. Stronger claws allow crabs to access shelled prey at a faster rate, hence allowing a higher consumption rate. Behrens Yamada and Boulding (1998) demonstrated that crabs with greater propal height (a proxy for closer muscle mass) and higher mechanical advantage of the claw lever system crush snail shells more quickly than crabs with weaker claws. *C. maenas* possess 2 claws of differing morphology: a slender cutter claw and a larger crusher claw, with mechanical advantages of 0.26 and 0.36, respectively (Warner et al. 1982). The 2 monomorphic claws of *C. magister* are more slender and of lower mechanical advantage (0.26) than the crusher claw of *C. maenas* (Taylor 2001) (Fig. 1). Therefore, based on these differing claw characteristics and the competitive advantage of similar sized *C. maenas* over *C. magister* (McDonald et al. 2001), we hypothesize that *C. maenas* will have a higher average prey consumption rate than *C. magister* of similar size. To test this hypothesis, we initiated the following studies. First, a comparison of claw morphology, closer muscle mass, and mechanical advantage of *C. maenas* and *C. magister* of similar weight. Although the claw characteristics of both species have been described in separate studies (Warner et al. 1982, Taylor 2001), we compare similar-size specimens of both species, collected from the same Oregon estuaries. Second, a comparison of prey consumption rates on the common, thin-shelled bay mussel *Mytilus trossulus*, Gould 1850. Data exist on prey consumption rates by *C. maenas* on various prey species, but so far no study has compared similar-size crabs of the 2 species under the same laboratory conditions. And third, a comparison of the relative ability of the 2 crab species to break harder shelled native oysters (*Ostrea lurida*, Carpenter 1864 = *Ostrea conchaphila*, Carpenter 1857). Palacios and Ferraro (2003) have shown that *C. maenas* prefer *O. lurida* over three other commercial bivalve species. Attempts to reestablish *O. lurida* to its former range could be thwarted if they are more vulnerable to the new predator, *C. maenas*, than to native *Cancer magister*.

MATERIALS AND METHODS

Individuals of *C. maenas* and *C. magister* were collected from the Oregon coast using folding Fukui fish traps (Fukui North America, Eganville, Ontario, Canada) (63 × 46 × 23 cm; 16-mm mesh) with expandable (45-cm) slits. Traps were typically deployed for 24 h using fresh or frozen fish as bait. Only male intermolt crabs of both species with intact claws were selected for our study. Because crabs cease feeding prior to molting, we excluded crabs that did not feed. Crabs were weighed and their carapace widths and claw characteristics measured using digital calipers. Carapace width for *C. maenas* was measured as the distance between the tips of the last spines (tip to tip) and for *C. magister* between the notches behind the last spines (notch to notch), because these are the measurements that are typically reported in the literature. The equation $y = 0.910x + 0.482$ ($R^2 = 0.995$) expresses the relationship between notch-to-notch (y) and point-to-point (x) carapace widths for *C. maenas* (Gillespie et al. 2007).

Claw Comparisons

We compared the claw morphology of 15 similar-size *C. maenas* and *C. magister* (mean ± 95% confidence interval (CI), 168 ± 10 g). After freezing the animals, we severed their claws, examined the dentition of the cutting surfaces, and measured propal height, propal length, propal depth, dactyl length (L2), and the distance from the claw's pivot to the insertion of the closer muscle apodeme (L1; Fig. 2). To compare closer muscle mass between the species directly, we steamed the claws for 5 min then removed and weighed the closer muscles.

Propal height, or the maximum height of the claw, is a proxy for closer muscle mass, and can thus be used to predict claw closing force within a species (Behrens Yamada & Boulding 1998, Taylor 2001). In addition to the 15 crabs we dissected, we also examined the relationship between propal height and the wet weight for a size spectrum of the live crabs we trapped.

Mechanical advantage is a measure of claw leverage, calculated from the ratio of two lever arms (Warner & Jones 1976) (Fig. 2). The first lever arm (L1) is a measure of the distance

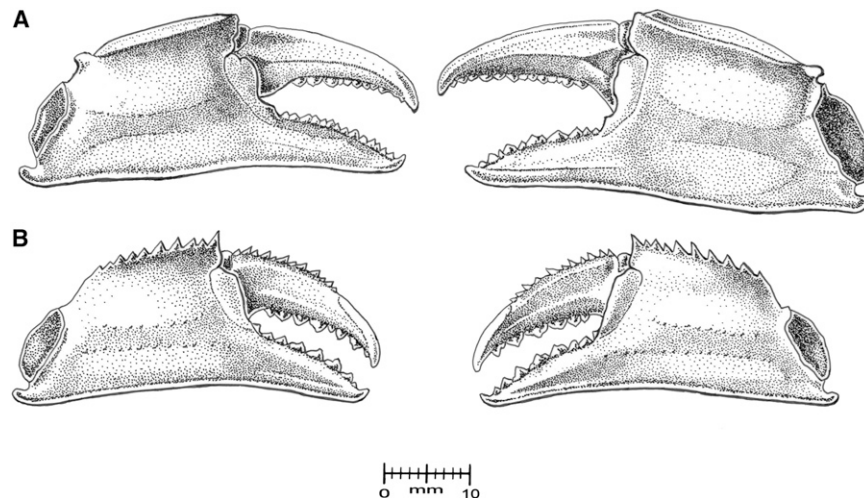


Figure 1. (A, B) Claw comparison of *Carcinus maenas* (A) and *Cancer magister* (B) of similar size (~110 g). Note that for *C. maenas*, the crusher claw (right) is larger than the cutter claw (left).

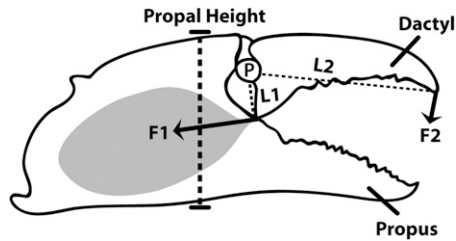


Figure 2. Crab claw showing propus, propal height, dactyl (movable finger), and claw dimensions used to calculate mechanical advantage ($L1/L2$). The shaded region represents the closer apodemes to which the closer muscle is attached. P, dactyl pivot. Adapted from Warner and Jones (1976).

between the claw's pivot (P) and the insertion point of the closer muscle apodeme (F1). The second lever arm (L2) is defined as the distance from the pivot to the tip of the dactyl, or dactyl length. We calculated the mechanical advantage for the cutter and crusher claws of *C. maenas* and for the right and left claws of *C. magister*. The crushing force applied at the tip of the claw's fingers (F2) is a function of the pulling force exerted by the closer muscle at the point of insertion of the closer apodeme (F1), and the mechanical advantage of the claw's lever system (Fig. 2).

Laboratory Feeding Trial on Mussels

To compare the relative consumption rates of *C. maenas* and *C. magister* on thin-shelled mussels, we conducted laboratory feeding trials in free-flowing indoor tanks ($118 \times 40 \times 30$ cm). *C. maenas* (80–92 mm in carapace width; mean weight \pm 95% CI, 163 ± 8 g) and *C. magister* (99–110 mm, mean weight \pm 95% CI, 160 ± 5 g) were collected and individually housed in sealed minnow traps (37×21 cm, 0.5-cm mesh) inside tanks. Temperature remained at $12 \pm 0.5^\circ\text{C}$ and salinity at $33 \pm 0.5\text{‰}$. Because light influences feeding behavior of crabs (Robles 1987), the tanks were covered with black plastic sheets.

Crabs were acclimated to laboratory conditions inside the minnow traps and offered mussels, *M. trossulus*, *ad libitum* for at least 2 wk prior to data collection to standardize hunger levels. Crabs that molted, did not feed, or that crushed shells indiscriminately without eating the meat were rejected. We offered each crab 15 mussels ranging in size from 30–40 mm (average shell thickness, 0.69 mm; average dry tissue weight, 0.22 g). At the end of 24 h, the shells of the eaten mussels were removed, tanks and cages were cleaned, and 15 new mussels were offered. This procedure was repeated for a total of 7 consecutive days.

We calculated the mean number of mussels consumed by each crab over the 7-day experiment and used a 2-sample *t*-test to examine the difference in mean daily consumption rate between *C. maenas* and *C. magister*. The assumptions of normality and homogenous variance were visually evaluated using QQ plots, frequency histograms, and box plots. Transformations failed to normalize the data, but the variances appeared similar, thus we analyzed the untransformed values.

Laboratory Feeding Trial on Native Oysters

Because native oysters, *O. lurida*, are a preferred prey of *C. maenas* (Palacios & Ferraro 2003), we set up feeding trials to determine the relative vulnerability of *O. lurida* to the two crab

species. We used the same procedure as the previous laboratory trials, except that trials lasted 2–3 days and we used crabs of similar claw length (mean dactyl length, 29 mm) rather than weight, thus giving *C. magister* a 1.6 times size advantage (mean live weight, 248 g vs. 151 g). This was done because few *C. magister* less than 110 mm in carapace width could be found. Market-size native oysters 40–50 mm in length (average shell thickness, 1.21 mm; average dry tissue weight, 0.35 g) were fed to 15 crabs of each species. Crabs were initially offered 4 oysters each, but when only one *C. magister* ate only 1 oyster and only 9 *C. maenas* ate 16 oysters in 2 days, we offered each crab 5 oysters and 5 mussels for 3 trials. This was done to allow crabs to obtain some nutrition from mussels while introducing them to oysters. Then for the next 3 trials, crabs were each offered 10 oysters. We noted the number of each prey item consumed by each crab in mixed-prey and oyster-only trials. We averaged the oyster consumption per crab per day for the mixed-prey and oyster-only trials and calculated the 95% CI of the mean. We analyzed untransformed data and tested for significant differences in the mixed-prey consumption rate between the 2 crab species using a 2-sample *t*-test. Differences in mean consumption rate of the oyster-only trials were analyzed using a Welch's 2-sample *t*-test, because these variances were not homogenous.

RESULTS

Claw Comparisons

The claws of *C. maenas* and *C. magister* vary markedly in size, morphology, and muscle mass (Fig. 1, Table 1). The propal heights of the crusher claws of *C. maenas* are significantly greater than the 2 monomorphic claws of *C. magister* for crabs ranging in live weight from 80–220 g (Fig. 3). For example, *C. magister* has to weigh more than twice as much as *C. maenas* for the claws to exhibit similar propal heights. The cutter claws of *C. maenas* are of intermediate size, falling in between the regressions of *C. maenas* crusher claws and the monomorphic claws of *C. magister* (Fig. 3).

Detailed claw analysis of the 2 species shows that the propus and dactyl characteristics of *C. maenas* crusher claws were highest, followed in descending order by *C. maenas* cutter claws, and the right and left claws of *C. magister* (Table 1). Likewise, the mechanical advantage of the claws' lever systems exhibit the same ranking: *C. maenas* crusher claws (mean, 0.368 ± 0.14) were greater than *Carcinus* cutter claws (0.297 ± 0.009) and the right and left claws of *C. magister* (0.255 ± 0.009 ; Table 1). A similar pattern was found for the weight of steamed closer muscle mass (Table 1). The average weight of the closer muscle of the *C. maenas* crusher (3.9 g) was significantly greater than that of the *C. maenas* cutter (2.0 g) and the right (1.7 g) and left (1.5 g) claws of *C. magister* (Table 1).

The occlusal ridges of the cutter claw of *C. maenas* and the claws of *C. magister* consist of single rows of denticles (Fig. 1). The denticle alignment in *C. magister* is such that when the claw is closed, the opposing teeth form a zigzag pattern. This type of morphology is adaptive for cutting, shearing, and shredding of soft prey (Brown et al. 1979). The dentition of the crusher claw of *C. maenas* appears similar in profile, but upon closer examination, it exhibits a ridge of denticles that is very broad near the fulcrum and tapers down to the tip such that the proximal teeth are ~ 3.5 times deeper than the most distal tooth.

TABLE 1.
Comparisons (mean \pm 95% CI) of claw characteristics of similar-sized *Carcinus maenas* and *Cancer magister*.

Claw Characteristics	<i>C. maenas</i>		<i>C. magister</i>		Similarity (=) or Difference (>) between Columns
	A Crusher	B Cutter	C Right	D Left	
Propal length (mm)	57.81 \pm 2.27	53.81 \pm 1.82	47.74 \pm 19.5	47.69 \pm 1.96	A > B > C = D
Propal height (mm)	27.40 \pm 0.78	22.89 \pm 0.85	19.00 \pm 0.64	18.96 \pm 0.80	A > B > C = D
Propal depth (mm)	17.74 \pm 0.63	14.65 \pm 0.53	10.59 \pm 0.43	10.59 \pm 0.40	A > B > C = D
L1 (mm)	10.95 \pm 0.49	8.65 \pm 0.55	6.52 \pm 0.28	6.38 \pm 0.30	A > B > C = D
Dactyl length or L2 (mm)	29.71 \pm 1.04	28.78 \pm 1.28	25.36 \pm 0.93	25.06 \pm 1.07	A = B > C = D
Mechanical Advantage (L1/L2)	0.368 \pm 0.014	0.297 \pm 0.009	0.258 \pm 0.008	0.252 \pm 0.009	A > B > C = D
Closer muscle mass (g)	3.93 \pm 0.47	2.04 \pm 0.29	1.66 \pm 0.25	1.46 \pm 0.23	A > B = C; C = D

This placement of wide proximal molars next to the fulcrum of the claw creates an efficient grinding surface. When the crusher claw closes, it forms a gap between the 2 occlusal surfaces. This gap would aid in the crushing of bulkier, nonplanar objects such as molluscs (Brown et al. 1979).

Laboratory Feeding Trial on Mussels

When similar-size *C. maenas* and *C. magister* were offered thin-shelled mussels, *C. magister* consumed significantly more mussels per day than *C. maenas* of similar weight (Fig. 4). Individual *C. magister* ate 5–9 mussels per day, with an average of 7.22 ± 0.22 mussels per day, whereas *C. maenas* ate from 4–7 mussels per day, with an average of 5.41 ± 0.13 mussels per day ($t = 14.7$, $df = 32$, $P < 0.0001$; Fig. 4). Given an average dry weight of 0.22 g per mussel, the dry biomass consumption rate was 1.6 g and 1.2 g per day, respectively.

Laboratory Feeding Trials on Native Oysters

The number of oysters eaten per crab during the 17 days for both the mixed-prey and oyster-only trials varied greatly, ranging from 0–1.2 oyster per crab per day for *C. maenas* and 0–1.0 oyster per crab per day for *C. magister*. Both species of crabs in the mixed-prey trials consumed the mussels before they attacked the oysters. Of the 5 mussels offered per trial, *C.*

maenas ate an average of 4.9 and *C. magister* ate an average of 4.4. Mussel consumption in these 2–3-day trials represents less than the crabs' daily metabolic requirement, thus crabs were still motivated to feed on oysters. After feeding on mussels, *C. maenas* ate an additional 0.43 oyster and *C. magister* an additional 0.20 oyster per crab per day (Fig. 5). This difference was not statistically significant ($t = 1.99$, $df = 28$, $P = 0.056$). But when only oysters were offered, *C. maenas* ate significantly more oysters per crab per day than *C. magister* (Fig. 5; $t = 2.60$, $df = 26.4$, $P = 0.0149$).

DISCUSSION

For crabs of similar weight, all the metrics suggest that the crusher claw of *C. maenas* is significantly bigger and more powerful than the 2 monomorphic claws of *C. magister*. For example, the propal height and muscle mass for *C. maenas* crusher claws are 1.4 times and 2.6 times as great as those for the claws of *C. magister*. In addition, the crusher claw of *C. maenas* also has a higher mechanical advantage (0.368) than the claws of *C. magister* (0.255). The cutter claws of *C. maenas* are intermediate in size and mechanical advantage (0.297). These mechanical advantage values are similar to those reported by Warner et al. (1982), Taylor (2001), and Mitchell et al. (2003), with the exception of the cutter claw of *C. maenas*. The higher

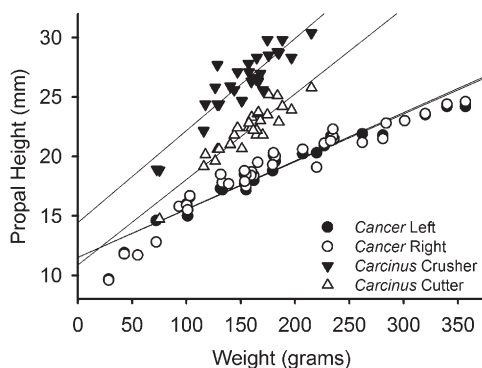


Figure 3. Regressions of claw propal height against live body weight for the crusher and cutter claws of *Carcinus maenas* and the right and left claws of *Cancer magister*.

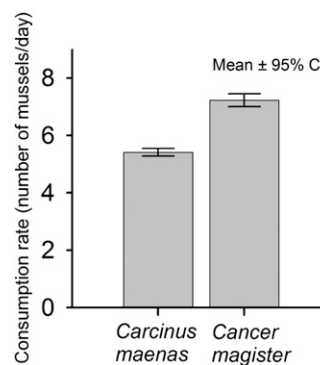


Figure 4. Mean daily consumption rate of mussels (*Mytilus trossulus*) by *Carcinus maenas* and *Cancer magister* of similar mean live weight (161 g). Individual crabs received 15 mussels per day for 7 consecutive days. Error bars represent 95% confidence intervals of the mean.

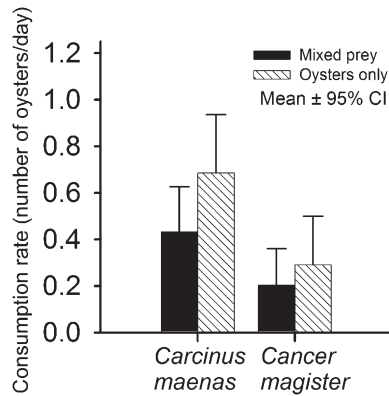


Figure 5. Mean daily consumption rate of native oysters (*Ostrea lurida*) consumed per by *Carcinus maenas* and *Cancer magister* of similar dactyl length (29 mm). Individual crabs received 5 oysters and 5 mussels (mixed prey) for 3 trials and 10 oysters only for 3 trials. Each trial lasted 2–3 days. Error bars represent 95% confidence intervals of the mean.

value that we observed could be linked to the larger size of our crabs. Preston et al. (1996) measured the claw closing forces generated at the tips of both claws of a 50-mm *C. maenas* and found that the crusher claw was twice as strong as the cutter (88 N vs. 44 N).

Biomechanical analyses of decapods crustacean claws have shown that it is mechanically impossible to design a claw that is both fast and strong (Alexander 1968, Warner 1977). Claws that are long relative to their height have high tip velocity per unit distance contracted by the muscle attached to the apodeme, but low mechanical advantage. These types of claws are typically found in crabs that feed on soft, moving prey such as worms, crustaceans, and small molluscs. Strong claws, on the other hand, have greater propal heights and a higher mechanical advantage. Crabs that specialize on hard prey have a mechanical advantage of 0.33 or higher, whereas those with a more generalized diet have a mechanical advantage of less than 0.33 (Behrens Yamada & Boulding 1998). The crusher claw of *C. maenas*, with a mechanical advantage of 0.368, falls into the range of shell-crushing specialists such as *Cancer pagurus* (L, 1758), *Cancer productus*, and *Lophopanopeus bellus* (Stimpson, 1860). The cutter claw of *C. maenas* and both claws of *C. magister* fall into the range of shell-crushing generalists such as *Liocarcinus depurator* (L 1758) and *Hemigrapsus oregonensis* (Behrens Yamada & Boulding 1998, Schenk & Wainright 2001). Because *C. maenas* has both a strong claw with crushing surfaces and a fast claw adapted for cutting, it is possible that this dual tool set might give this species a competitive advantage by being able to exploit a wider range of prey items. For example, the lobster *Homarus americanus* (Milne Edwards, 1837) has been observed to crush molluscs with its crusher claw and to catch fish with its cutter claw (Govind & Blundon 1985).

Because the crushing force applied at the tip of the claw's fingers is a function of the pulling force exerted by the closer muscle and the mechanical advantage of the claw's lever system, we expect that the crusher claw of *C. maenas*, with its larger closer muscle mass and higher mechanical advantage, to be significantly stronger than the cutter claw and the monomorphic claws of *C. magister*. However, having stronger claws did not translate into higher consumption rates when the prey was

thinner shelled mussels. *C. maenas* ate an average of 5.4 mussels, whereas *C. magister* ate 7.2 mussels per day. Lee and Seed (1992) found that it takes 43–68-mm *C. maenas* less than a minute to break 20-mm-long mussels (*Mytilus edulis*, L 1758). Because none of our crabs had any difficulty crushing the thin-shelled mussels, the difference in consumption rate can be linked to the differential metabolic requirements of the 2 species. Adult *C. maenas* typically molt no more than once a year (Behrens Yamada et al. 2005), whereas subadult and young adult *C. magister* are still actively growing. For example, only *C. magister* molted in our feeding trials. Bioenergetic models for both crab species in Willapa Bay, WA, reveal the same trend. Holsman et al. (2003) and McDonald et al. (2006) found that subadult and young adult *C. magister* (40–130 mm) require around 3 kJ/ash-free dry weight/day, whereas adult *C. maenas* require only around 1 kJ.

Although both species of crabs were capable of opening the market-size native oysters, they both preferred smaller, softer shelled mussels. A similar preference for mussels (*M. edulis*) over oysters (*Crassostrea gigas* Thunberg, 1793) was found by Dare et al. (1983) for *C. maenas* in Wales. Juanes (1992) found that crabs generally select smaller and thinner bivalve prey than they are capable of crushing. Although larger prey may provide more meat, smaller prey typically require less handling time and are also less likely to damage claws (Juanes & Hartwick 1990). In the field, more than half the female *C. magister* showed some claw wear, and ~12% exhibited 1 broken claw (Juanes & Hartwick 1990). Risk of claw damage was also a consideration in our study. One *C. magister* developed a chipped dactyl tip after crushing 3 oysters and then stopped feeding even on mussels. It thus appears that *C. magister*, with their smaller and weaker claws, are more reluctant to crush market-size native oysters than *C. maenas* of similar size.

One has to exercise caution when translating our findings to the field. Many factors contribute to the relative per capita prey consumption of various size classes of *C. maenas* and *C. magister*. These not only include claw size and morphology, but also type, abundance, and size composition of the targeted prey; the availability and desirability of alternative prey; crab size and metabolic condition; as well as interactions with conspecifics, competitors, and predators. Both *C. maenas* and *C. magister* are opportunistic omnivores, feeding on a wide variety of prey items throughout their developmental stages, including soft prey such as algae, annelid worms, interstitial crustaceans, nematodes, and carrion as well as hard prey such as barnacles and molluscs (Pauley et al. 1986, Cohen et al. 1995). Although adult *C. maenas* consumed fewer mussels than actively growing *C. magister* of similar size, smaller juveniles of both species would have similar metabolic requirements and potentially could act as ecological equivalents when it comes to per capita impact on small soft-shelled prey species. For example, dramatic declines in small native clams (*Nutricula tantilla*, Gould 1853 and *Nutricula confusa*, Gray 1982) were linked to the arrival *C. maenas* in Bodega Harbor, CA (Grosholz et al. 2000) and also to unusually strong recruitment of young *C. magister* in Coos Bay, OR (Asson-Batres 1986). Thus, either crab species, if abundant enough, can alter community structure. The higher tolerance of *C. maenas* to desiccation would allow this invader to occupy the mid and high intertidal zones, where prey species enjoyed a partial spatial refuge from predation by 5 species of larger adult *Cancer* crabs

(Behrens Yamada & Boulding 1996, Hunt & Behrens Yamada 2003, Jensen et al. 2007; DiBacco, pers. comm.). The presence of an abundant *C. maenas* population could have a devastating impact on many intertidal species. This would be especially true for young native oysters living on gently sloping mud and gravel beaches. We recommend that future studies examine the vulnerability of a wide size spectrum of native oyster and other bivalves to various sizes and species of crab predators in the laboratory and in the field.

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LITERATURE CITED

- Asson-Batres, M. A. 1986. The feeding behavior of the juvenile Dungeness crab, *Cancer magister* Dana, on the bivalve, *Transennella tantilla* (Gould), and a determination of its daily consumption rate. *Calif. Fish Game* 72:144–152.
- Ahyong, S. 2005. Range extension of two invasive crab species in eastern Australia: *Carcinus maenas* (Linnaeus) and *Pyromaia tuberculata* (Lockington). *Mar. Pollut. Bull.* 50:460–462.
- Alexander, R. McN. 1968. Animal mechanics. London: Sedgewick and Jackson. 346 pp.
- Behrens Yamada, S. 2001. Global invader: the European green crab. Oregon Sea Grant. Corvallis: Oregon State University. 123 pp.
- Behrens Yamada, S. & E. G. Boulding. 1996. The role of highly mobile crab predators in the intertidal zonation of their gastropod prey. *J. Exp. Mar. Biol. Ecol.* 204:59–83.
- Behrens Yamada, S. & E. G. Boulding. 1998. Claw morphology, prey size selection and foraging efficiency in generalist and specialist shell-breaking crabs. *J. Exp. Mar. Biol. Ecol.* 220:191–211.
- Behrens Yamada, S., B. R. Dumbauld, A. Kalin, C. E. Hunt, R. Figlar-Barnes & A. Randall. 2005. Growth and persistence of a recent invader in estuaries of the northeastern Pacific. *Biol. Invasions* 7: 309–321.
- Behrens Yamada, S. & G. E. Gillespie. 2008. Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? Fifth International Conference on Marine Bioinvasions. *ICES J. Mar. Sci.* 65:725–729.
- Boulding, E. G. 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.* 76:201–223.
- Brown, S. C., S. R. Cassuto & R. W. Loos. 1979. Biomechanics of chelipeds in some decapods crustaceans. *J. Zool.* 188:143–159.
- Cohen, A. N., J. T. Carlton & M. C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Mar. Biol. (Berl.)* 122:225–237.
- Dare, P. J., G. Davies & E. B. Edwards. 1983. Predation on juvenile Pacific oysters (*Crassostrea gigas* Thunberg) and mussels (*Mytilus edulis* L.) by shore crabs (*Carcinus maenas* L.). Ministry of Agriculture, Fisheries and Food Directorate of Fisheries Research, Fisheries Research Technical Report No. 73, Lowestoft. 19 pp.
- Davis, R. C., F. T. Short & D. M. Burdick. 1998. Quantifying the effect of green crab damage to eelgrass transplants. *Restor. Ecol.* 6:297–302.
- Eriksson, S., S. Evans & B. Tallmark. 1975. On the coexistence of scavengers on shallow sandy bottoms in Gullmar Fjord (Sweden). *Zoon* 3:65–70.
- Gillespie, G. E., A. C. Phillips, D. L. Paltzat & T. W. Therriault. 2007. Status of the European green crab, *Carcinus maenas* in British Columbia—2006. Canadian Technical Report of Fisheries and Aquatic Sciences 2700, Nanaimo, British Columbia, Canada. 39 pp.
- Govind, C. K. & J. A. Blundon. 1985. Form and function of the asymmetric chelae in blue crabs with normal and reversed handedness. *Biol. Bull.* 168:321–331.
- Grosholz, E. D. & G. M. Ruiz. 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. *Mar. Biol.* 122:239–247.
- Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. C. Maron & P. G. Connors. 2000. The implications of a nonindigenous marine predator in a California bay. *Ecology* 81:1206–1224.
- Hidalgo, F. J., P. J. Baron & J. M. Orensanz. 2005. A prediction come true: the green crab invades the Patagonian coast. *Biol. Invasions* 7:547–552.
- Holsman, K. K., D. A. Armstrong, D. A. Beauchamp & J. L. Ruesink. 2003. The necessity for intertidal foraging by estuarine populations of subadult Dungeness crab, *Cancer magister*: evidence from a bioenergetics model. *Estuaries* 26:1155–1173.
- Hunt, C. E. & S. Behrens Yamada. 2003. Biotic resistance experienced by and invasive crustacean in a temperate estuary. *Biol. Invasions* 5: 33–43.
- Jamieson, G. S., E. D. Grosholz, D. A. Armstrong & R. W. Elner. 1998. Potential implications from the introduction of the European green crab, *Carcinus maenas* (Linnaeus), to British Columbia, Canada, and Washington, USA. *J. Nat. Hist.* 32:1587–1598.
- Janke, K. 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). *Helgol. Meeresunters.* 44:219–263.
- Jensen, K. T. & J. N. Jensen. 1985. The importance of some epibenthic predators on the density of juvenile benthic microfauna in the Danish Wadden Sea. *J. Exp. Mar. Biol. Ecol.* 89:157–174.
- Jensen, G. C., P. S. McDonald & D. A. Armstrong. 2007. Biotic resistance to green crab, *Carcinus maenas*, in California bays. *Mar. Biol.* 151:2231–2243.
- Juanes, F. 1992. Why do decapods crustaceans prefer small-sized molluscan prey? *Mar. Ecol. Prog. Ser.* 87:239–249.
- Juanes, F. & E. B. Hartwick. 1990. Prey size selection in Dungeness crabs: the effect of claw damage. *Ecology* 71:744–758.
- Kitching, J. A., J. F. Sloane & F. J. Ebling. 1959. The ecology of Lough Ine VIII. Mussels and their predators. *J. Anim. Ecol.* 28: 331–341.
- Lafferty, K. D. & A. M. Kuris. 1996. Biological control of marine pests. *Ecology* 77:1989–2000.
- Lee, S. Y. & R. Seed. 1992. Ecological implications of cheliped size in crabs: some data from *Carcinus maenas* and *Liocarcinus holsatus*. *Mar. Ecol. Prog. Ser.* 84:151–160.

- LeRoux, P. J., G. M. Branch & M. A. P. Joska. 1990. On the distribution, diet and possible impact of the invasive European shore crab *Carcinus maenas* (L.) along the South African Coast. *South Afr. J. Mar. Sci.* 9:85–93.
- McDonald, P. S., K. K. Holsman, D. A. Beauchamp, B. R. Dumbauld & D. A. Armstrong. 2006. Bioenergetics modeling to investigate habitat use by the non-indigenous crab, *Carcinus maenas*, in Willapa Bay, Washington. *Estuaries Coasts* 29:1132–1149.
- McDonald, S. P., G. C. Jensen & D. A. Armstrong. 2001. The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. *J. Exp. Mar. Biol. Ecol.* 258:30–54.
- Menge, B. A. 1983. Components of predation intensity in the low zone of New England rocky intertidal region. *Oecologia* 58:141–155.
- Menzel, R. W. & S. H. Hopkins. 1955. Crabs as predators of oysters in Louisiana. *Proc. Natl. Shellfish. Assoc.* 46:177–184.
- Mitchell, S. C., S. M. Kennedy, P. J. Williams & M. E. De Mont. 2003. Morphometrics and estimates of force generation by the chelae of a North American population of the invasive green crab, *Carcinus maenas* (L.). *Can. J. Zool.* 81:203–215.
- Muntz, L., F. J. Ebling & J. A. Kitching. 1965. The ecology of Lough Ine XIV. Predatory activity of large crabs. *J. Anim. Ecol.* 34:315–329.
- Palacios, K. C. & S. P. Ferraro. 2003. Green crab (*Carcinus maenas* Linnaeus) consumption on and prey preference among four bivalve prey species. *J. Shellfish Res.* 22:865–871.
- Parsons, J. 1974. Advantages of tray culture of Pacific oysters (*Crassostrea gigas*) in Strangford Lough, N. Ireland. *Aquaculture* 3:221–229.
- Pauley, G. B., D. A. Armstrong & T. W. Heun. 1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest): Dungeness crab. Washington, DC: Fish and Wildlife Service, U.S. Department of the Interior, Coastal Ecology Group. 20 pp.
- Preston, S. J., I. C. Revie, J. F. Orr & D. Roberts. 1996. A comparison of the strength of gastropod shells with forces generated by potential crab predators. *J. Zool.* 238:181–193.
- Quayle, D. B. 1988. Pacific oyster culture in British Columbia. *Can. Bull. Fish. Aquat. Sci.* 218, 241 pp.
- Robles, C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68:1502–1514.
- Say, T. 1817. An account of the crustacea of the United States. *J. Acad. Nat. Sci. Phila.* 1:57–63.
- Schenk, C. & P. C. Wainright. 2001. Dimorphism and the functional basis of claw strength in six brachyuran crabs. *J. Zool. (Lond.)* 255:105–119.
- Schratzberger, M. & R. M. Warwick. 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. *J. Exp. Mar. Biol. Ecol.* 235:255–271.
- Smith, S. E., R. C. Ydenberg & R. W. Elnor. 1999. Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *J. Exp. Mar. Biol. Ecol.* 238:185–197.
- Taylor, G. M. 2001. The evolution of armament strength: evidence for a constraint on the biting performance of claws of durophagous decapods. *Evolution* 55:550–560.
- Wallace, J. C. 1973. Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas*. *Mar. Biol.* 20:277–281.
- Walne, P. R. & G. Davies. 1977. The effect of mesh covers on the survival and growth of *Crassostrea gigas* Thunberg grown on the sea bed. *Aquaculture* 11:313–321.
- Warner, G. F. 1977. The biology of crabs. London: Elek Science. 20 pp.
- Warner, G. F., D. Chapman, N. Hawkey & D. G. Waring. 1982. Structure and function of the chelae and chela closer muscles of the shore crab *Carcinus maenas* (Crustacea: Brachyura). *J. Zool. (Lond.)* 180:57–68.
- Warner, G. F. & A. R. Jones. 1976. Leverage and muscle type in crab chelae (Crustacea: Brachyura). *J. Zool.* 180:57–68.