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Does consumer injury modify invasion impact?

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Abstract Predicting the impacts of an invasive species solely by its abundance is common, yet it ignores other potentially important moderating factors. One such factor is injury. Severe injury can lead to mortality, which can directly reduce the abundance of the invader. However, more moderate, sublethal injury can also temper the impact of invasive species. Therefore, to predict impacts, it may be useful to examine not only abundance, but also moderating factors (e.g., injury) and predictors of these factors (e.g., density, size). We documented the density, injury (i.e., limb loss), and size of two conspicuous invaders, the European green crab (*Carcinus maenas*) and the Asian shore crab (*Hemigrapsus sanguineus*), at thirty sites from Shinnecock County Park, New York to Lubec, Maine. In addition, we used a field experiment to determine how injury influenced the consumption rate of mussels (*Mytilus edulis*) by each crab species.

31.6% of all *C. maenas* (1,493/4,721) and 30.7% of *H. sanguineus* (2,003/6,523) were missing appendage(s). Of the crabs injured, 38.4% (573/1,493) and 30.5% (611/2,003) were missing cheliped(s) for *C. maenas* and *H. sanguineus*, respectively. In our experiments, cheliped loss reduced consumption of both species on *M. edulis*. Injured *C. maenas* consumed 21% fewer mussels than uninjured crabs. Injury completely eliminated mussel consumption by *H. sanguineus*. Previous studies have highlighted the detrimental impacts of these two invaders on native bivalve prey. While the loss of a single cheliped can greatly reduce or even eliminate the ability of *C. maenas* and *H. sanguineus* to consume *M. edulis*, our results suggest that injury has a relatively minor role in reducing overall population-level impacts on prey such as mussels. However, injury on an individual-level can play a role in moderating the consumptive impacts of these invaders.

Keywords Aggression · *Carcinus maenas* · Competition · *Hemigrapsus sanguineus* · Impact · Injury · *Mytilus edulis* · Trait-mediated effect

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Introduction

Although predicting the impact of an invader is a central focus in invasion biology, currently there are few approaches (Parker et al. 1999). The impact of

invasive consumers, for example, is often predicted solely by their abundance and diet. This type of approach has been extensively used to predict the impacts of both terrestrial (Medd et al. 1985; Bobbink and Willems 1987; Alvarez and Cushman 2002; Hester et al. 2006; Whittle et al. 2007) and aquatic invasive species (Crivelli 1983; Ricciardi et al. 1995; Grosholz et al. 2000; Chumchal et al. 2005; Driver et al. 2005; Finnoff et al. 2005).

While abundance and diet are logically related to impact of an invasive consumer, other factors could also be related and may moderate the effects of abundance. Particularly, it is reasonable that as abundance (or density) increases, inter- or intra-specific interactions also increase (Griffen and Williamson 2008), and if they are aggressive, potentially cause injury to individuals. Injury in turn, has the potential to moderate both ecological and economic impacts by reducing per capita consumption rates of an invader. Further, invasion biologists might expect that injury rates relate to other attributes such as sex and size of organisms, which could likewise affect consumption. Thus, moderating factors such as injury rates could potentially be used to help predict the impacts of invasive species, particularly if invasion biologists can identify correlations between injury and environmental drivers across sites within an invaded region. If predictors of injury exist and if injury reduces the impact of an invader, then incorporating injury may facilitate better predictions of invader impacts than those derived solely from species abundance and diet. We examined this by gathering large datasets on injury that allowed us to assess how injury varies with different factors such as sex, size, and latitude.

The above arguments, if applicable to invasive species at all, will most likely apply to taxa where frequent aggressive interactions facilitate injury, and where invasion is common. Crustaceans are a highly invasive taxa in general that frequently have large impacts in invaded regions (Smith et al. 1999; Galil and Clark in press). We examined the influence of injury on the impacts of two invasive marine crustaceans on the east coast of North America.

Two conspicuous and abundant marine invaders to North America with potentially large impacts are the European green crab (Carcinus maenas) and the Asian shore crab (Hemigrapsus sanguineus). Currently, C. maenas can be found on the east coast from Virginia to Prince Edward Island and has recently been detected as far north as Newfoundland and Magdalen Islands, Canada (Klassen and Locke 2007; USGS 2009). On the west coast, its introduced range is from California, USA to British Columbia, Canada (GCC 2002; Carlton and Cohen 2003; USGS 2009). Additionally, C. maenas is found on sections of all non-polar continents (Carlton and Cohen 2003), and often has large impacts by feeding on economically important species, such as blue mussels (Mytilus edulis) and other shellfish species (Ropes 1968; Grosholz and Ruiz 1996; Griffen and Delaney 2007). For example, C. maenas has severely damaged the soft-shell clam industry in New England and the Maritime Provinces of Canada (Smith and Chin 1951; Glude 1955; Moulton and Gustafson 1956; Ropes 1968; Miron et al. 2005). Much more recently, H. sanguineus also colonized the east coast of North America, but has not been as well studied. H. sanguineus was first detected in New Jersey in 1988, then spread north and south to create a distribution that already spans almost 10 degrees of latitude (Williams and McDermott 1990; Lohrer and Whitlatch 2002; USGS 2009) and is still currently expanding north in Maine (Delaney et al. 2008). During its expansion, H. sanguineus has largely replaced C. maenas in the rocky intertidal zone of southern New England (Lohrer and Whitlatch 2002; Griffen and Delaney 2007). This replacement appears to have resulted from aggressive interactions between adult H. sanguineus and juvenile C. maenas (Lohrer and Whitlatch 2002). These interactions, coupled with other factors (e.g., invasion history, temperature), cause densities of these species to vary greatly with latitude.

Latitude has been shown to be an important predictor of many aspects of an ecosystem and its biota. Examples of such gradients include latitudinal trends in biodiversity (Stevens 1989; Rohde 1992; Gaston 2000) as well as abundance and distribution of organisms (Fretwell 1972; Stevens 1989; Rosenzweig 1995; Griffen and Delaney 2007). In addition, temperature, which varies greatly with latitude, can affect not only the distribution and density of a species (Helmuth et al. 2002, Stephenson et al. 2009), it can also regulate the activity rates, such as feeding rates and aggression of species (Ropes 1968; Hill 1980; Taniguchi and Nakano 2000). We have previously demonstrated a strong inverse gradient in the density of C. maenas and

H. sanguineus with latitude (Griffen and Delaney 2007). Given the importance of latitude (and confounding factors such as temperature and availability of habitat) as a predictor of ecological patterns and the wide range of latitudes invaded by these crabs, a latitudinal gradient in injury may exist. If latitudinal trends in injury do occur, these may modify the impacts of these invaders across sites. Therefore while relative abundance and density are most important, latitude could be an important predictor of injury and we will examine whether a relationship exists between latitude and the frequency of injury for these invasive species along the coast of New England and New York.

We used a broad regional survey coupled with a field experiment to examine injury and its effects on *C. maenas* and *H. sanguineus*. First, we observed the injury status of more than 11,000 crabs across 30 sites on the coast of New England and New York to assess the frequency of injury and to determine whether conspecific and heterospecific density and size are correlated with injury. Also we used a field experiment to quantify the extent to which the loss of a single cheliped (the most common form of injury for these two species, McVean 1976; Abello et al. 1994; Davis et al. 2005) reduces foraging efficiency. We then use these results to infer the effect of injury, its importance relative to other impact-moderating factors, and the regions where the impacts of these two invaders should be moderated most by injury.

Methods

Natural levels of crab injury

We quantified the density, injury, and size of *C. maenas* and *H. sanguineus* at 30 sites from Shinnecock County Park, New York (40.842N, −72.499W) to Lubec, Maine (44.815N, −66.950W) from late June to late August, 2006 (Table 1; Fig. 1). We chose sites with suitable habitat for both species, such as rocks that were big enough not to be turned over by waves but could be turned over by 1–2 people and also dominant canopy forming macrophyte species (i.e., *Ascophyllum nodosum* and *Fucus vesiculosus*). Sampling of sites at different latitudes was interspersed throughout the sampling period to

avoid confounding seasonal changes with latitudinal changes. To determine the average density of each introduced species at a site, we sampled 16 randomly placed 1 m^2 quadrats in the mid and low intertidal zone (i.e., from 0.5 m below to 3.5 m above mean lower low water line). Crabs collected from within these quadrats were also used for assessment of limb loss. If time permitted during the sampling day for that site, additional sampling was conducted outside the quadrats but within the study area in an attempt to increase sample size for the injury analysis rather than determine density. We searched, rock by rock, in an exhaustive manner to collect crabs from all size classes. For each crab, we recorded its carapace width (CW), sex, and if any appendages were missing. Following the protocol of Davis et al. (2005), regenerating limbs were considered intact. This provided a conservative estimate of injury and avoids having to differentiate between healthy limbs compared to limbs that are fully intact but slightly smaller since not fully regenerated. We performed two separate analyses on these data—an individual-level analysis to examine patterns of limb loss between individual crabs, and a regional-scale analysis to examine patterns of limb loss across sites.

We examined whether injury status (yes/no) varied with sex or with CW using a stepwise mixed model logistic ANCOVA with sex as a fixed factor, CW as a covariate, and site as a blocking (random) factor to control for variation between sites. We performed this analysis for each species separately (4,721 *C. maenas* and 6,523 *H. sanguineus*). We performed our regional-scale analysis using multiple regressions separately for each species at each site (Table 1). Given variation in density of each species from north to south (Lohrer and Whitlatch 2002; Griffen and Delaney 2007), we were unable to collect the same number of crabs at each site. We therefore used sample size of the focal crab species at each site as a weighting factor in the regression. We used the percent of crabs injured at a site as the response variable and latitude, average size of conspecifics and heterospecifics, and density of conspecifics and heterospecifics as predictor variables. For the analysis of *C. maenas*, we could not include average size of *H. sanguineus* because *H. sanguineus* was not present at many of the sites where *C. maenas* is established. Also, the average size of *C. maenas* was log-transformed to improve linearity.

Table 1 The latitude ("lat") and longitude ("lon") of 30 sites from Shinnecock County Park, New York to Lubec, Maine with the density (crabs/m^2), percent of crabs that were missing appendage(s) ("% injury"), the percent of individuals missing cheliped(s) ("% missing cheliped[s]"), mean size (mm), and sample size of *Carcinus maenas* and *Hemigrapsus sanguineus*

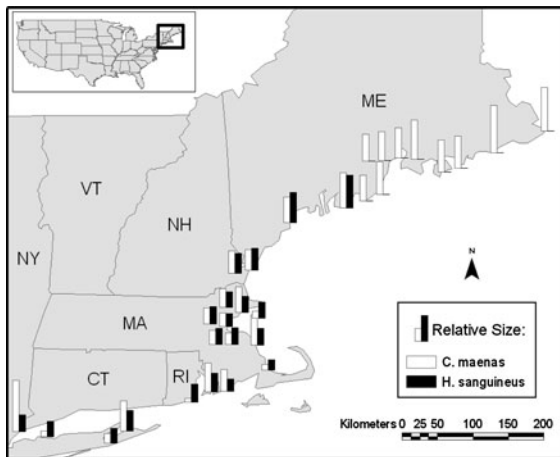| Lat	Lon	Density of C. maenas	% Injury of C. maenas	% Missing cheliped(s) C. maenas	Mean size of C. maenas	# Of C. maenas collected	Density of H. sanguineus	% Injury of H. sanguineus	% Missing cheliped(s) H. sanguineus	Mean size of H. sanguineus	# Of H. sanguineus collected
40.842	−72.499	0.9	20.0	20.0	9.3	15	12.6	32.4	8.8	14.3	339
40.927	−73.311	5.3	14.1	8.2	5.2	85	20.0	23.8	5.6	14.6	320
40.966	−73.668	0.3	80.0	60.0	48.5	5	79.5	37.3	10.1	15.9	635
41.003	−72.298	0.1	25.0	25.0	28.1	4	6.5	43.6	13.8	19.2	218
41.364	−71.481	0.1	0.0	0.0	3.8	2	52.5	30.5	7.4	16.9	840
41.493	−71.039	0.9	55.6	22.2	27.7	18	14.6	45.6	13.3	17.6	316
41.505	−71.022	0.6	40.0	10.0	20.5	10	28.2	22.0	6.0	11.3	451
41.773	−70.500	2.8	4.5	2.3	5.4	44	18.9	15.2	6.3	10.0	303
42.092	−70.642	1.0	18.8	12.5	28.7	16	28.3	30.5	8.2	15.7	453
42.269	−70.848	2.3	22.2	11.1	7.1	36	25.1	26.4	7.9	15.3	713
42.280	−70.955	4.5	26.5	14.4	15.1	181	1.3	32.9	11.3	16.7	231
42.322	−70.930	2.8	35.7	10.4	13.4	154	2.8	29.7	12.2	15.4	327
42.326	−70.964	6.8	31.1	9.0	11.1	177	5.2	31.0	9.7	16.0	352
42.331	−70.955	6.4	36.3	18.6	12.6	102	14.2	26.9	9.7	12.1	227
42.420	−70.906	1.9	39.8	16.1	17.4	118	2.2	38.2	14.1	14.1	170
42.505	−70.832	2.6	43.3	20.7	24.6	261	6.9	32.5	12.0	15.2	249
43.002	−70.743	6.9	27.2	12.1	21.3	206	4.4	35.9	11.7	18.9	145
43.042	−70.715	7.9	26.6	7.8	19.4	218	0.7	31.0	14.2	20.8	226
43.648	−70.226	2.7	36.7	15.9	24.2	245	0.0	33.3	0.0	28.3	6
43.836	−69.507	1.9	39.1	14.6	33.5	253	0.1	50.0	50.0	31.0	2
43.926	−69.258	5.0	34.8	10.8	24.4	342	0				
44.093	−69.045	3.1	39.2	17.3	30.6	260	0				
44.292	−68.237	2.4	25.2	10.5	29.9	238	0				
44.338	−68.053	4.3	24.2	6.1	30.5	244	0				
44.425	−68.999	0.8	29.5	7.6	25.6	278	0				
44.439	−68.932	3.5	22.4	9.3	26.9	366	0				
44.455	−68.879	1.1	35.2	14.0	37.0	321	0				
44.470	−68.810	1.5	36.1	14.3	28.4	252	0				
44.535	−67.593	1.4	27.4	8.5	44.6	212	0				
44.815	−66.950	0.4	37.9	5.2	41.1	58	0				

Fig. 1 The average size of *C. maenas* (*white bars*) and *H. sanguineus* (*black bars*) at sites from Shinnecock County Park, NY to Lubec, ME. The survey was conducted in 2006. The size of the bar is proportional to the average carapace width of that species at that site

Changes in mussel consumption with crab injury

In 2006, we conducted a field experiment at Odiorne Point State Park, New Hampshire (43.038N, −70.716W), which is approximately mid-way point of our large-scale survey, to examine how injury influenced mussel consumption by *C. maenas* and *H. sanguineus*. A full description of the site is given in Griffen et al. (2008). Following methods described in Griffen and Delaney (2007), we placed individual *C. maenas* (CW = 52.7 ± 8.4 mm) or *H. sanguineus* (CW = 23.6 ± 2.2 mm) into field enclosures (0.5 × 0.6 × 0.3 m), which are constructed of lobster wire mesh lined with 0.25 cm plastic mesh, and filled with denuded small boulders. Crabs were either uninjured (i.e., no limbs missing) or injured (i.e., by removal of the right cheliped 24 h before the experiment began) (n = 4). The loss of a cheliped is the most common form of injury for both *C. maenas* (McVean 1976; Abello et al. 1994) and *H. sanguineus* (Davis et al. 2005). We scattered 300 mussels into each cage 24 h before introducing crabs to allow sufficient time for byssal thread attachment. We used mussel sizes that reflected the preference of each crab species (14–17 mm shell length for cages with *C. maenas*, and 7–10 mm shell length for cages with *H. sanguineus*) (Elner and Hughes 1978; DeGraaf and Tyrrell 2004). Crabs were allowed to forage for 3 days, after which the contents of each

cage were removed and the number of mussels surviving was assessed. We determined mean daily mussel consumption as mussel mortality divided by 3 for each cage. We compared mean daily mussel consumption by injured and uninjured crabs for each species separately using one-sided *t*-tests.

Relative influence of injury on invasive crab impacts

We used the large-scale survey data and field experiment to determine the extent to which injury should influence population consumption rates in each of our sampling areas. To do this we calculated approximate population consumption rate as the density of crabs at a site, multiplied by the mean consumption rate of uninjured crabs observed in our field experiment. We then repeated this calculation, but this time incorporated the influence of injury (i.e., crabs missing cheliped[s]) on consumption rates as determined by our field experiment. We then used the ratio of total crab impact with and without accounting for injury to determine the percent reduction in mussel consumption projected to result from injury. This simple calculation makes the simplifying assumptions that all crabs are the same size, that all sites have the same density and size distribution of mussel prey, and that crab density does not influence consumption rates. Each of these assumptions is clearly false; however, this simplification allows us to make rough comparisons of the influence of injury on population consumption rates across sites.

For *C. maenas*, we then removed these simplifying assumptions in order to determine the importance of injury to the consumptive impacts of individual focal crabs, relative to other contributing factors, such as the ratio of crab size to prey size, the density of mussel prey, and the density of competing crabs. We did this using a model developed by Griffen (2009) for calculating the functional response of individual *C. maenas* that accounts for all of these factors. To do this, we calculated the consumption rate of a single foraging *C. maenas* using equations given in Griffen (2009). These equations give the functional response of individual crabs (equation 7 from Griffen 2009, which is a Holling's type III functional response equation) as modified by search efficiency that is a function of predator density (equation 2 from Griffen 2009) and by handling time that is a function of

predator density, prey size, and predator size (equation 6 from Griffen 2009). For our calculations using these equations we initially assume a 53 mm carapace width crab (i.e., the mean size from the field experiment) that foraged during night-time high tide (~ 0.25 of the day) alone on a density of 300 mussels m^{-2} (same as field experiment) that were each 15 mm shell length. These mussel densities are much higher than average densities at our field site, so we also conducted model calculations with much lower, more natural densities (using 40 mussels m^{-2} as a baseline). We then used these same equations to determine the percent change in calculated consumption rate that occurred if we increased or decreased by 50% the size of the crab, the size of mussel prey, the density of mussel prey, and the density of competing crabs. We then compared each of these percent changes in calculated consumption rates to the decrease in consumption rate obtained for injured *C. maenas*, relative to uninjured *C. maenas*, in our field experiment. We did not make a similar individual-level calculation and comparison for *H. sanguineus* because our field experiment indicated that cheliped loss was 100% effective at eliminating mussel consumption by *H. sanguineus* (see "Results").

Results

Natural levels of crab injury

Overall, 31.6% of all *C. maenas* (1,493/4,721) and 30.7% of *H. sanguineus* (2,003/6,523) were missing appendage(s). Of the crabs injured, 38.4% (573/1,493) and 30.5% (611/2,003) were missing cheliped(s) for *C. maenas* and *H. sanguineus*, respectively. We found that for *C. maenas*, the loss of the left or right cheliped was the most common form of injury and for *H. sanguineus* chelipeds were commonly missing but not with the highest frequency. We found that crab injury was influenced by both individual- and regional-level factors. At the individual-level, the frequency of injury for *C. maenas* increased with its size ($F_{1,4607} = 53.46$, $P < 0.001$), and differed between sites ($F_{29,4607} = 4.23$, $P < 0.001$), and the interaction term (size × site, $F_{29,4607} = 2.01$, $P = 0.001$) was also significant. Injury did not differ significantly by sex for *C. maenas* ($F_{1,4607} = 0.08$, $P = 0.77$). For *H. sanguineus* the frequency of injury

increased with crab size ($F_{1,6445} = 418.57$, $P < 0.001$), differed between sites ($F_{19,6445} = 4.13$, $P < 0.001$), and differed between males and females ($F_{1,6445} = 10.09$, $P = 0.001$). There was also a significant interaction term between crab size and sex for *H. sanguineus* ($F_{1,6445} = 7.24$, $P = 0.007$).

At the regional-scale, for *C. maenas*, the overall regression was significant ($F_{4,25} = 4.18$, $P = 0.010$, $R^2 = 0.305$) and injury increased with the average size of *C. maenas* at a site ($t_{1,25} = 3.28$, $P = 0.003$, Fig. 2) and decreased with latitude ($t_{1,25} = -3.27$, $P = 0.003$), but was not influenced by density of conspecifics ($t_{1,25} = -1.28$, $P = 0.214$) or *H. sanguineus* ($t_{1,25} = -0.86$, $P = 0.397$). For *H. sanguineus* (overall regression: $F_{5,14} = 9.85$, $P < 0.001$, $R^2 = 0.699$), injury increased with the average size of *C. maenas* ($t_{1,14} = 3.50$, $P = 0.004$, Fig. 3a) and conspecifics ($t_{1,14} = 5.02$, $P < 0.001$, Fig. 3b) and was inversely related to conspecific density ($t_{1,14} = -2.22$, $P = 0.044$). *H. sanguineus* injury was not influenced by *C. maenas* density ($t_{1,14} = -1.38$, $P = 0.190$) or latitude ($t_{1,14} = -1.35$, $P = 0.198$). Injury of both species was highly variable across sites, ranging from 0 to 80% and 15.2–50% percent for *C. maenas* and *H. sanguineus*, respectively (Table 1).

Changes in mussel consumption with crab injury

Our field experiment demonstrated that the loss of the cheliped reduced mussel consumption by both crab species, although to different extents. Injured *C. maenas* consumed 21% fewer mussels than uninjured crabs (one-sided *t*-test, $t = 1.87$, $df = 6$, $P = 0.056$, Fig. 4), decreasing from 29.3 to 23.1 mussels per day. Uninjured *H. sanguineus* consumed
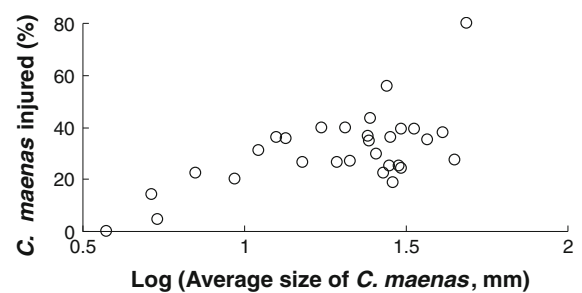
Fig. 2 Percent of *Carcinus maenas* at each site that were injured (missing any appendage) versus the mean log-transformed carapace width
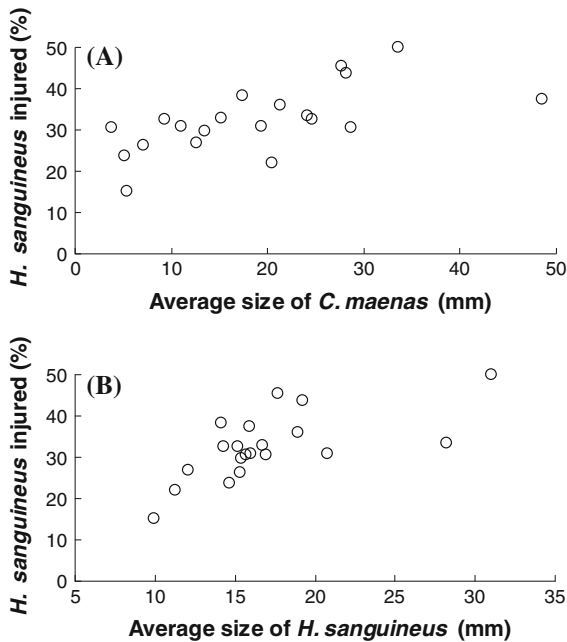
Fig. 3 Percent of *Hemigrapsus sanguineus* injured at each site (missing any appendage) versus mean size of *C. maenas* (**a**) and of *H. sanguineus* (**b**)
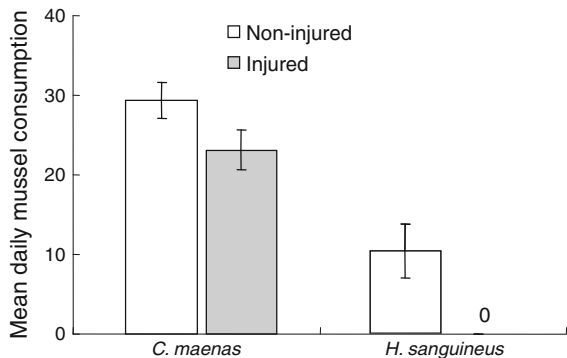

Fig. 4 Effect of injury (loss of single cheliped) on mussel consumption by *C. maenas* and *H. sanguineus*. Values are means ± SE (n = 4 replicates)

on average 10.3 mussels per day, while injured *H. sanguineus* did not consume any mussels (one-sided *t*-test, t = 1.94, df = 6, P = 0.010, Fig. 4).

Relative influence of injury on invasive crab impact

The estimated reduction in consumption rate of mussels across sites varied considerably depending on the proportion of crabs at each site that were missing chelipeds, and ranged from 0 to 60% for

C. maenas, and 0 to 50% for *H. sanguineus* (Table 1). At the individual level, effects of injury differ considerably for the two crabs. As reported in the preceding section, for *C. maenas*, injury reduced consumption by 21%. The relative importance of this reduction compared to other factors depended on the density of mussels examined. When mussel densities reflecting those in our experimental cages were used (300 mussels m^{-2}), our model calculations suggested that injury-induced changes in mussel consumption were modest compared to the changes that would occur with a 50% change in crab size or mussel prey size, but were large compared to changes in mussel prey density or competing crab density (Table 2). When lower (more natural) prey densities were examined (40 mussels m^{-2} as baseline), reducing mussel prey density by 50% also had larger impacts than injury (Table 2). For *H. sanguineus*, our experiment demonstrated a total elimination of mussel consumption when crabs, which were missing a single cheliped, were given 3 days to forage on small mussels (see previous section). Thus, at the individual

Table 2 Model-estimated changes in consumption rate for individual *C. maenas* that result from 50% changes to the size of crab, the size of mussel prey, the density of mussel prey, the density of competing crabs, or the presence of crab injury

Calculation	Consumption rate (% change) assuming 300 mussels m^{-2}	Consumption rate (% change) assuming 40 mussels m^2
Control	30.0 (0%)	21.3 (0%)
50% Larger predator	99.6 (232%)	42.2 (98%)
50% Smaller predator	3.8 (−87%)	3.6 (−83%)
50% More prey	30.1 (0%)	25.5 (20%)
50% Fewer prey	29.4 (−2%)	11.3 (−47%)
50% Larger prey	9.6 (−68%)	8.5 (−60%)
50% Smaller prey	190.0 (533%)	52.9 (148%)
50% More predators	28.9 (−4%)	18.2 (−14%)
50% Fewer predators	31.2 (4%)	25.7 (20%)
Injury	23.7 (−21%)	16.8 (−21%)

Calculations were made using equations 2, 6, and 7 of the model presented in Griffen (2009). The left hand column indicates the change in model calculations, relative to control calculations shown in the top row. The second column provides the calculated number of mussels consumed over 24 h assuming 300 mussels m^{-2}, with the percent change in consumption rate as a result of model modification, relative to the control calculation, given in parentheses. The third column gives analogous results, but assuming 40 mussels m^{-2}

level, the loss of a single cheliped is at least as important as any other factor that may influence consumption rates of *H. sanguineus*.

Discussion

Factors affecting crab injury

Factors leading to high frequency of injury in these invasive species and in other crustaceans are unclear. Some argue that intraspecific interactions are highly ritualized and therefore rarely lead to limb loss (Hiatt 1948; Jachowski 1974; Sinclair 1977; Hyatt and Salmon 1978; Juanes and Smith 1995), while others argue that intraspecific aggression is among the most important factors for injury (McVean 1976; Shirley and Shirley 1988; Smith and Hines 1991; Davis et al. 2005). Aggression can have strong moderating impacts on predation rates independent of the effects of injury (Mansour and Lipcius 1991; Mistri 2003; Griffen 2006; Griffen and Delaney 2007). An extreme form of aggression, cannibalism, is also common within these species (Moksnes 2004), but is also more prevalent among *C. maenas* than *H. sanguineus* (Griffen and Byers 2009).

Contrary to our expectations, we found that crab density was not significantly related to injury for *C. maenas* and that *H. sanguineus* injury was negatively correlated with conspecific density. This result may potentially be explained by one or more of the following reasons. First, intraspecific aggression may not frequently result in injury. Second, an implicit assumption of the expected relationship between injury and crab density is that intraspecific aggression increases with density and sublethal injury is the most likely outcome of aggressive interactions. However, injury-related mortality (e.g., cannibalism) is also a likely outcome. If injury is relatively uncommon as compared to cannibalism or other aggression-related mortality, then we may not in fact expect a strong relationship between crab density and injury. Third, our intertidal samples obtained at low tide might poorly reflect interacting *C. maenas* densities, as this species inhabits intertidal and subtidal zones and engages in tidal migratory behavior (Hunter and Naylor 1993). Fourth, other factors, such as sublethal attacks from competitors and predators may also be responsible for a substantial portion of the observed crab injury (Dumas and Witman 1993; Torchin et al. 2001; de Rivera et al. 2005; Jensen et al. 2007), which could obscure any relationship between injury and crab density. Rome and Ellis (2004) have found that the gut content of gulls, such as great black-backed gulls (*Larus marinus*) and herring gulls (*L. argentatus*), contain limbs of crabs with no associated carapace, though sublethal bird predation may be more important for the larger and more conspicuous native crabs of New England than for *C. maenas* and *H. sanguineus* (Lohrer 2001; Rome and Ellis 2004; Ellis et al. 2007). Fish can also inflict limb loss on crabs, and limbs without the accompanying carapace have been documented in the guts of the common mummichog (*Fundulus heteroclitus*) and the striped killifish (*F. majalis*) (Brousseau et al. 2008). Finally, local conditions, which we did not record (e.g., water temperature) could also be important in understanding the incidence of injury. Thus, the lack of an expected relationship between injury and conspecific density may be attributable to one or more of the above factors. We therefore have less confidence in our finding that density is an unimportant factor for crab injury.

The relationship between injury and crab size was much clearer, and previous studies have also found a positive relationship between size and injury (McVean 1976; Mathews et al. 1999; Davis et al. 2005). This relationship could occur for various reasons. For example, attacks may more frequently result in mortality rather than injury for smaller crabs. Also, this pattern may be attributed to simple accumulation of injury with age as longer inter-molt intervals in older crabs (Bauchau 1961) provides longer periods for injury to occur with a reduced ability to regenerate the limb(s). In addition, older crabs lose the ability to regenerate limbs altogether after terminal anecdysis (Carlisle 1957). Yet, we also found that injury of *H. sanguineus* was positively related to the average size of *C. maenas* across sites. This suggests that injury is also therefore related to interspecific aggression. Increasing frequency of injury with crab size may therefore result from a combination of multiple mechanisms that require further investigation to disentangle.

Effect of injury on feeding rates and management implications

While the causal effect of limb loss is hard to identify, we did document that injury is common and

varies between sites. We also demonstrated that injury reduces the ability of injured crabs to consume an economically and ecologically important native species. Also based on the results of this study, we are able to predict areas where injury may be expected to have a stronger influence on the impacts by these invasive species. For *C. maenas*, injury rates increased with its size and decreased with latitude. Therefore injury should have the greatest moderating effect on impact in southern sites that are composed of larger individuals (Table 1; Fig. 1). We found that injury of *H. sanguineus* increased with its individual size and with the average size of conspecifics and *C. maenas*, but declined with the density of conspecifics. This corresponds to conditions commonly found in the northern part of *H. sanguineus'* range (Table 1; Fig. 1), suggesting that injury should more likely reduce the impact of *H. sanguineus* in northern than in southern areas. Despite the prevalence of injury, these overall trends in its occurrence, and the fact that injury may elicit considerable foraging costs for individual crabs (particularly for *H. sanguineus*), our back-of-the-envelope calculations suggest that injury only has a minor influence on the population-level impacts of these invaders. Since we only quantified the impact from the loss of a single limb, our estimates of reduction in impacts are admittedly conservative. Also effects of injury on mussel consumption likely interact with other important factors, such as the size of crab and size of mussel prey, and further reduce the impact of invasive species. However, even accounting for these interactions, it is unlikely that injury has a substantial influence on the intensity of invasion impact, but this conclusion requires additional investigation for other species and environments.

In conclusion, we have shown that injury is common among two widespread invasive predators throughout the Northwest Atlantic. Our results show that even the loss of a single cheliped can substantially reduce or even eliminate mussel consumption by individual crabs. These organisms, when injured, likely shift to more palatable prey that is less economically important (e.g., macrophytes). However, these individual-level effects are relatively small compared to the effects of size and density of prey and of competing crabs. Thus, once these individual-level effects are extrapolated to the population level, they have a somewhat minor influence

on the overall consumption rates of these invaders. Nevertheless, while the effect of injury was modest, by not considering injury and other moderating factors, we reduce our ability to accurately predict the ecological and economical impacts of invasive species.

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