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THE EFFECT OF SEX, SIZE AND HABITAT ON THE INCIDENCE OF PUNCTURE WOUNDS IN THE CLAWS OF THE PORCELAIN CRAB *PETROLISTHES CINCTIPES* (ANOMURA: PORCELLANIDAE)

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ABSTRACT

Many porcelain crabs have an unusual claw (cheliped) form that is broad, flat and thin. This seemingly flimsy form suggests claws may be used more for display than for feeding or aggressive interactions. However, in the flat-topped porcelain crab *Petrolisthes cinctipes*, one of the most abundant intertidal crustaceans on the Pacific coast of North America, we observed a high proportion of individuals with puncture wounds on their claws. Claws therefore do appear to be used in intra-specific aggression. To examine factors that might influence injury prevalence, samples of *P. cinctipes* were collected from four sites in Barkley Sound, two wave-exposed, and two protected. In addition, laboratory experiments examined the effects of density and crab size on the incidence of puncture wounds. Crabs from wave-exposed, high-density sites and smaller crabs both exhibited significantly higher proportions of puncture wounds. Although not statistically significant, laboratory experiments revealed a trend towards a higher incidence of puncture wounds in high-density groups. Wound frequency did not differ between the sexes, so these injuries are not likely a result of intra- or inter-sexual interactions. Puncture wounds were concentrated on claw fingers (either the dactyl or propus), and along the ventral margin of the manus, both of which are likely to be nearest an opponent during shoving interactions. Overall, these data suggest that the claws of *P. cinctipes* mediate intra-specific competitive interactions that frequently escalate to injury.

INTRODUCTION

Studies of competition in marine ecosystems have established that a variety of resources limit the distribution and population size of most invertebrates. For organisms in the intertidal zone of the Pacific northwest, competition most commonly involves space (Connell, 1961; Paine, 1966; Dayton, 1971; Connolly and Roughgarden, 1999). Although we understand many of the mechanisms used to contest these resources for sessile organisms (Connell, 1961; Dayton, 1971), much less research has been done on mobile invertebrates. For these organisms, the means of competing for resources is less obvious as individuals can escape in space to habitat patches with higher resource levels. It is likely that behavioral interactions between individuals, such as aggression, are responsible for mediating contests for limited resources (Elwood and Glass, 1981; Dowds and Elwood, 1983; Hyatt, 1983; Baeza et al., 2002).

The porcelain crab *Petrolisthes cinctipes* (Randall, 1839) is one of the most ubiquitous intertidal crustaceans on the Pacific coast of North America, ranging from northern British Columbia to California (Hart, 1982). Porcelain crabs aggregate in natural crevices in high densities in the middle to upper intertidal region (up to $\sim$4000 m^{-2}), and therefore constitute a large proportion of the biomass in many intertidal communities (Jensen, 1990). Due to these high densities, access to preferred feeding locations is a limiting resource for *P. cinctipes* (Jensen, 1990). Porcelain crabs are filter feeders (Nicol, 1932; Trager et al., 1992; Trager and Genin, 1993; Achituv and Pedrotti, 1999) and use modified third maxillipeds to sweep the water and collect large particulate matter and oxygen (Nicol, 1932; Wicksten, 1973; Caine, 1975). Whether feeding actively or passively, porcelain crabs require a defined space in which to extend their maxillipeds (Zittin, 1979). As *P. cinctipes* occurs in high densities, both interference competition for space and exploitative competition for food may limit local population size, yet the mechanisms underlying intra-specific competition are poorly characterized.

Porcelain crabs clearly do compete. Both feeding behavior and efficiencies are influenced by water flow (Trager et al., 1992; Trager and Genin, 1993; Achituv and Pedrotti, 1999), and the highly clumped distribution of *Petrolisthes cinctipes* results in reduced growth rates and fecundity of small individuals (carapace width $<$ 4.5 mm), especially under high density conditions (Donahue, 2004). High local population density also directly reduces food availability because the filtering setae of both adults and juveniles have similar spacing (Jensen, 1991). Evidence of competition has also been observed in the laboratory where *P. cinctipes* forms dominance hierarchies (Zittin, 1979), often with a single male controlling access to prime feeding currents and protective shelter (Jensen, 1990). However, the behavioral mechanisms of interference competition remain unclear.

Chelipeds would seem likely to be used during competition, and porcelain crabs do have claws that appear large relative to their body size. However, in most species, these claws are highly flattened and, in contrast to other crabs, do not seem to be very robust. Because of the unusual morphology of these claws, their function has remained unclear. Claws can have several possible functions in mediating

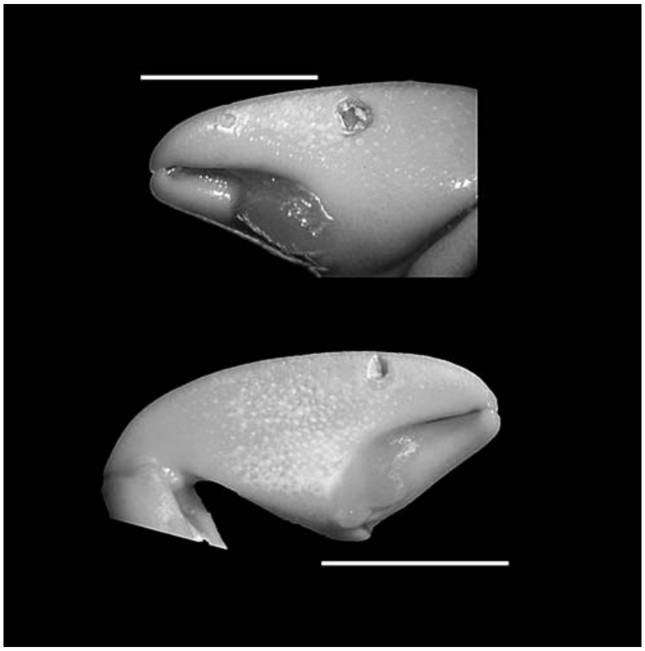

Fig. 1. Examples of puncture wounds on the ventral surfaces of a left (upper) and right (lower) claw of *Petrolisthes cinctipes*. Scale bar is 5 mm.

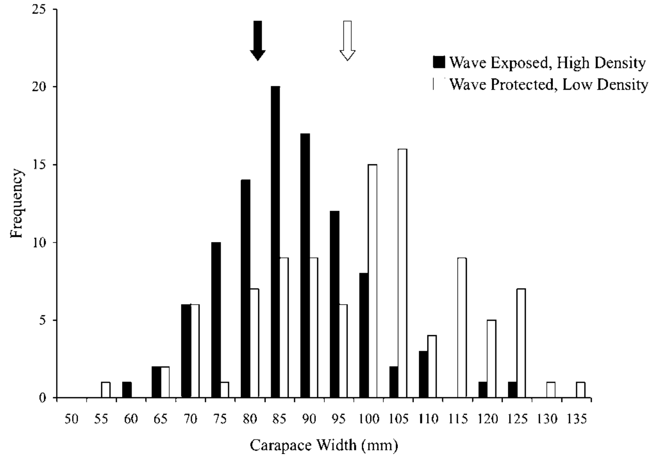

Fig. 2. Frequency histogram of *Petrolisthes cinctipes* carapace width at the wave-exposed and wave-protected field sites. High-density, wave-exposed sites included Cape Beale and Seppings Island, and low-density wave-protected sites included Dixon Island and Grappler Inlet. Arrows indicate the mean carapace width in each habitat type (mean carapace width ± standard deviation: high-density 84.76 ± 11.51 mm; low-density 96.64 ± 16.75 mm; $t = -5.773$, $P < 0.001$).

competitive interactions, including intra-specific agonistic communication (Molenock, 1976), or physically pushing conspecifics away to maintain space in high density habitats (Molenock, 1976; Zittin, 1979; Jensen and Armstrong, 1991). However, preliminary observations of puncture wounds in the claws of this species (Fig. 1; Rypien, unpublished results) suggested that claws might also be used in physical contests during competitive interactions.

To better understand the factors influencing the extent of intra-specific competition in *Petrolisthes cinctipes*, we conducted both field surveys of natural populations and laboratory experiments. Field surveys were used to ascertain which crab sizes were most affected by these aggressive behaviors, and to determine if environmental factors play a role in the incidence of injury. Lab experiments were performed to assess the effects of density, size and sex on the incidence of punctures.

Materials and Methods

Field Survey of Populations in Barkley Sound

Natural levels of puncture wounds were quantified in four populations of *Petrolisthes cinctipes* in Barkley Sound between September 12 and 29, 1999 (Table 1). Two wave-exposed sites were sampled (Cape Beale and Seppings Island), where *P. cinctipes* occurred in high densities beneath beds of the California mussel, *Mytilus californianus*. Two protected-shore sites were also sampled (Dixon Island and Grappler Inlet) where *P. cinctipes* occurred at lower densities under large cobbles. At all four sites, 50 crabs were haphazardly collected ~1 m above MLLW. Crabs were placed in individual bags to avoid artificially increasing the level of puncture wounds during transport. Once in the laboratory, the seawater in each bag was replaced with an anesthetic solution of 7% $MgCl_2$, and after 24 hours the crabs were placed in 70% ethanol.

Table 1. Location of the populations of *Petrolisthes cinctipes* used for field surveys of puncture wounds in Barkley Sound, Vancouver Island, British Columbia, Canada.

Name	Habitat type	North latitude	West longitude
Dixon Island	Wave protected, cobbles	48°51′06″	125°07′20″
Grappler Inlet	Wave protected, cobbles	48°49′91″	125°07′65″
Seppings Island	Wave exposed, mussel bed	48°50′50″	125°12′50″
Cape Beale	Wave exposed, mussel bed	48°47′05″	125°12′54″

Size classes of large (CW > 90 mm), intermediate (CW 80 - 90 mm) and small (CW < 80 mm) were created based on the size distribution of collected crabs (Fig. 2). With the aid of a dissecting microscope, sex, carapace width (CW), and number of puncture wounds was recorded for each individual. The precise position of each puncture, on both the dorsal and ventral sides of the claws, was recorded on a claw drawing (Fig. 3). In addition, wounds were assigned to one of three distinct regions: the dactyl (moving finger of the claw), the propus (fixed finger), or the manus (palm of the claw). Claw wounds due to predators or other environmental factors were not included, and could be easily distinguished by the shape of the injury.

The size distribution of individuals at high-density wave-exposed sites and low-density wave-protected sites was compared using a *t*-test. The presence of puncture wounds in individual crabs was examined as a function of density/wave exposure, sex, and size class using a nominal logistic regression. To compare the incidence of wounds on the different claw surfaces (dorsal versus ventral, right versus left), separate logistic regressions were performed on the punctured individuals, examining the presence of wounds as a function of density/wave exposure, sex, and size class.

Laboratory Experiment: Effect of Density and Relative Size on Injury

To assess the effects of density and size on the incidence of puncture wounds, we performed a laboratory experiment crossing two density treatments by three size-ratio treatments, with each of the six treatments replicated twice. Four randomly chosen treatment combinations were run each week at the Bamfield Marine Sciences Center, and each experiment lasted seven days (08 November to 29 November 1999).

Crabs for the experiments were collected from the south side of Dixon Island (48°51′06″N, 125°07′20″W) and in front of the Bamfield Marine Sciences Center (48°50′06″N, 125°08′20″W). All crabs were individually tagged using numbered Brady wire markers and cyanoacrylate glue, and the following measurements were taken: sex, cyanopace width, number of punctures, and the position of puncture wounds (to allow new punctures to be distinguished from pre-existing punctures). Once crabs were tagged, they were allowed to acclimate to laboratory conditions for 48 hours. After the trials ended, the crabs were isolated, and the position and number of puncture wounds counted and mapped. Crabs were not reused in later trials.

The two density treatments were: high density (50 crabs $tank^{-1}$, ~269 crabs/m^2) and low density (20 crabs $tank^{-1}$, ~ 107 crabs/m^2). Size ratio treatments were created using crabs with CW > 90 mm (large) and < 80 mm (small), and ratios were either equal (1:1 large:small crabs), more large (4:1) or more small (1:4). To simulate natural conditions, each aquarium had a layer of small rocks on the bottom, a large central rock for shelter, and a continuous flow of unfiltered seawater under a 12:12 photoperiod. The crabs were fed once during each trial with ground frozen fish.

To analyze the effects of sex, size ratio treatment, density treatment, and initial wounding status on the increase in individuals with puncture wounds, a logistic regression was performed using a generalized estimating equation, which takes into account correlation between individual crabs within an aquarium (Norton et al., 1996; Kuss, 2002).

Results

Field Survey of Populations in Barkley Sound

The size-frequency distributions differed between wave-exposure regimes: low-density, wave-protected sites had more large crabs and were, on average larger, than the wave-exposed sites (Fig. 2). This difference was highly significant ($t = -5.77$, $P < 0.001$).

No difference was observed in the distribution of puncture wounds between claw surfaces ($\chi^2 = 5.67$, $P = 0.77$) or sides ($\chi^2 = 10.89$, $P = 0.28$), or between sexes ($\chi^2 = 0.20$, $P = 0.65$), and none of the interaction terms were significant (data not shown). Overall, injuries were concentrated on the dactyl and propus, with fewer on the manus (Fig. 3). Those punctures on the manus tended to occur along the ventral margin. The mean number of wounds per individual was 0.87 ± 1.29 at high-density sites, and 0.57 ± 1.41 at low-density sites. The logistic regression revealed a significant effect of density/wave exposure ($\chi^2 = 4.09$, $P = 0.043$) on the presence of puncture wounds, and a nearly significant effect of size class as well ($\chi^2 = 5.42$, $P = 0.066$).

The proportion of punctured individuals was highest in high-density, wave-exposed sites (49.08%), Cape Beale and Seppings Island, and lowest in the wave-protected, low-density sites, Grappler Inlet and Dixon Island (35.40%; Fig. 4). Large crabs exhibited a lower proportion of punctures than small and intermediate sized crabs (29.98% and 48.37% respectively; Fig. 4).

Laboratory Experiment: Effect of Density and Relative Size on Injury

Neither density ($\chi^2 = 0.89$, $P = 0.35$), size ratio treatment ($\chi^2 = 2.18$, $P = 0.34$), nor sex ($\chi^2 = 2.08$, $P = 0.15$) had a significant impact on the proportion of individuals that experienced additional puncture wounds during the course of the laboratory experiment (Fig. 5). Characteristics of individual crabs, such as size class ($\chi^2 = 1.04$, $P = 0.31$), and initial puncture status ($\chi^2 = 0.10$, $P = 0.75$), also had no significant effect on the increase in puncture wounds.

Discussion

The unique claws of *Petrolisthes cinctipes* appear to play a role in aggressive interactions among conspecifics. Field observations revealed a high frequency (~ 40%) of individuals with puncture wounds (Fig. 4), with most crabs having only one injury. Claw injuries may have many effects, including reduction of growth because of injury repair, lower reproductive fitness, reduced ability to obtain or defend shelter, increased susceptibility to disease, and decreased survival (Juanes and Smith, 1995). As preferred feeding habitats are patchy, the escalation of encounters to physical damage would allow more aggressive individuals access to limited food and space resources.

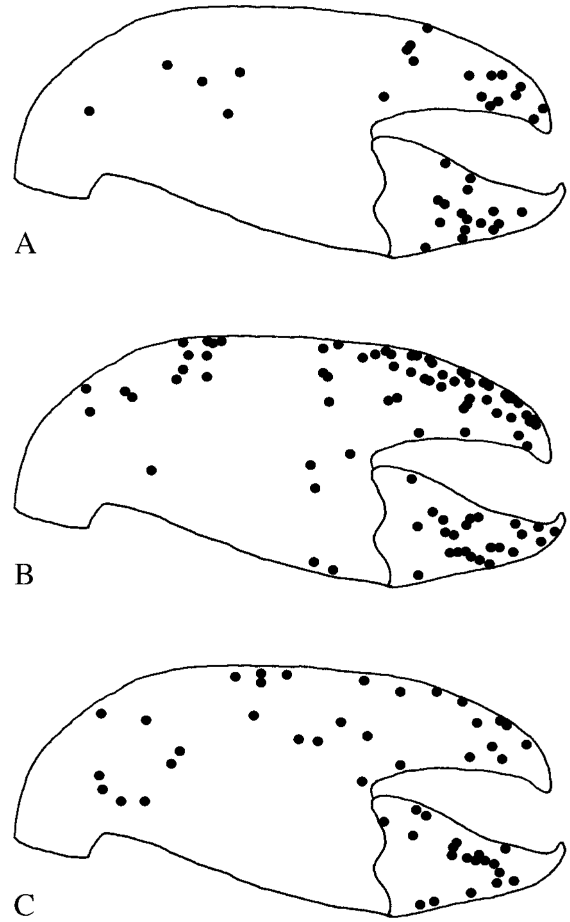

Fig. 3. Puncture wounds mapped onto the dorsal and ventral surfaces of claws of *Petrolisthes cinctipes* pooled for all field sites. Each generalized claw drawing represents all individuals in a given size class. A. Small (carapace width, CW, < 80 mm), B. Intermediate (CW 80 - 90 mm), C. Large (CW > 90 mm).

Sex does not appear to affect the likelihood of being punctured. Puncture wounds occurred equally frequently in both sexes, regardless of size, in field samples and in laboratory experiments. Therefore, the punctures we observed are most likely not a result of intra- or inter-sexual agonistic interactions. However, sex-dependent punctures could be more common during the breeding season, but we did not examine seasonal variation.

Size does appear to play a role: smaller crabs tended to have more puncture wounds, likely due to competitive inferiority (Molenock, 1976; Figs. 3, 4, 5). Laboratory experiments paralleled field observations, but considerable variation among replicates yielded inconclusive results. Taken together, field and laboratory observations indicate that *P. cinctipes* use their unique claws to mediate aggressive encounters, a finding that complements earlier studies showing that claws are used to shove conspecifics during competitive interactions for space (Zittin, 1979; Jensen and

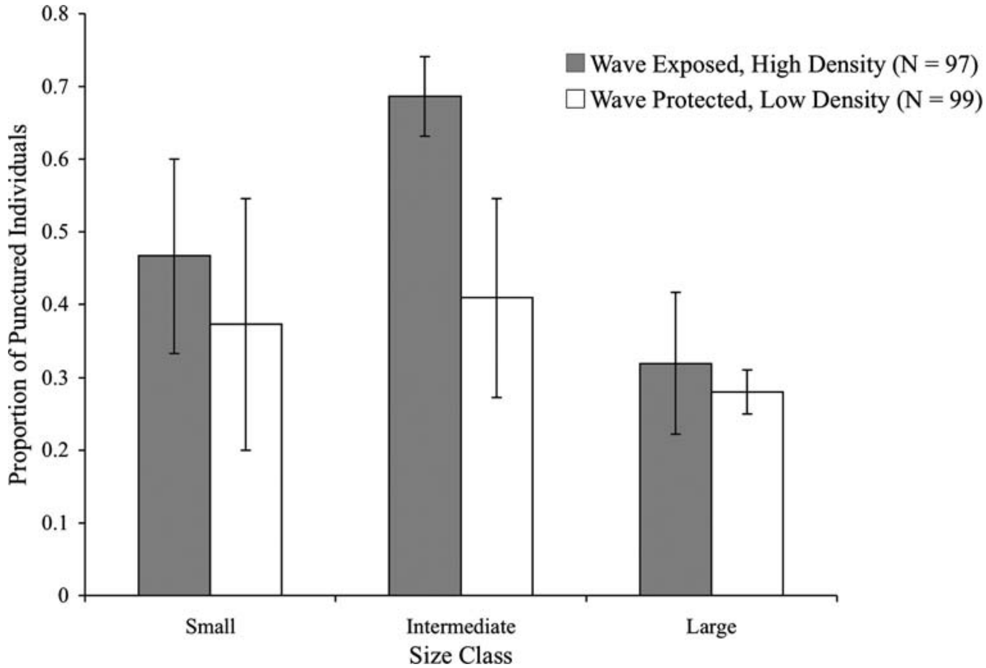

Fig. 4. Proportion of field collected *Petrolisthes cinctipes* with puncture wounds as a function of size class ($P = 0.066$) and collection site ($P = 0.043$), which combine differences in both wave exposure, density and habitat type (± SE). Size classes are based on carapace width (CW): small CW < 80 mm, intermediate CW 80 - 90 mm, and large CW > 90 mm.

Armstrong, 1991), and that these interactions can result in reduced feeding time in smaller crabs (Donahue, 2004).

Location of Claw Punctures

The location of puncture wounds yields some clues about claw use during interactions. Punctures tended to be concentrated in two regions of the claw: the fingers (dactyl and propus) and the ventral margin of the manus (Fig. 3). These regions of the claw would be the most likely to encounter a puncture as they are the ones used during shoving interactions (Zittin, 1979; Jensen and Armstrong, 1991), so punctures here are not too surprising. Also, the low numbers of punctures in the middle of the manus suggests that claws are not interlocked during aggressive interactions, as occurs during aggressive interactions between male fiddler crabs (Hyatt and Salmon, 1977). However, one puzzle remains. Individual *Petrolisthes cinctipes* hold their flattened claws with the plane of dactyl motion nearly parallel to the substratum. If the claws of two interacting crabs are held in this 'horizontal' orientation, it is not clear how one claw can puncture another, because one claw would have to be rotated to a more vertical orientation to deliver a puncture. More careful observations will be required to determine exactly how both the crabs and the claws are oriented when punctures are made. In the future it would also be valuable to incorporate direct observations of aggressive behavior, documenting wound shape, the number of wounds per individual, and other factors that influence the presence of injuries, i.e., molt stage.

Impacts of Density and Relative Size on the Incidence of Claw Injury

The proportion of punctured individuals was significantly higher at the wave-exposed, high-density sites (Cape Beale and Seppings Island) suggesting some role of the physical environment or crab density (Fig. 4). Laboratory experiments also supported this pattern as high density treatments tended towards a larger increase in individuals with puncture wounds, especially in trials with more large individuals (Fig. 5). One explanation for these results is that both exploitative competition for food and interference competition for space lead to aggressive interactions between individuals that result in claw punctures, but direct observations of intra-specific interactions would be necessary to confirm this. Habitats with high population densities are likely have more intense competition, leading to higher levels of injuries. Furthermore, in high density sites crabs have a limited ability to move between habitat patches, as they must climb over the mussel bed where they are exposed to strong waves that are likely to dislodge them (Lau and Martinez, 2003). At wave-protected, low-density sites, individuals live beneath large rocks where they can escape from competitors by moving to different microhabitats (rocks). This difference in the connectedness of habitats at these sites may also contribute to the high frequency of puncture wounds in wave-exposed, high-density habitats (Fig. 4). Alternatively, wave exposure could promote more puncture wounds by causing crabs to grab conspecifics to maintain their position, or to reduce the risk of dislodgment by the waves themselves. These confounding factors can be separated in the laboratory experiments as they examined only the effects of density.

Although it was not statistically significant, there was a strong trend in the field collections towards more punctures in smaller individuals (Fig. 4), which is expected if size influences competitive success. This is a common pattern in crabs, where strength generally increases with crab size, and stronger individuals are more often victorious

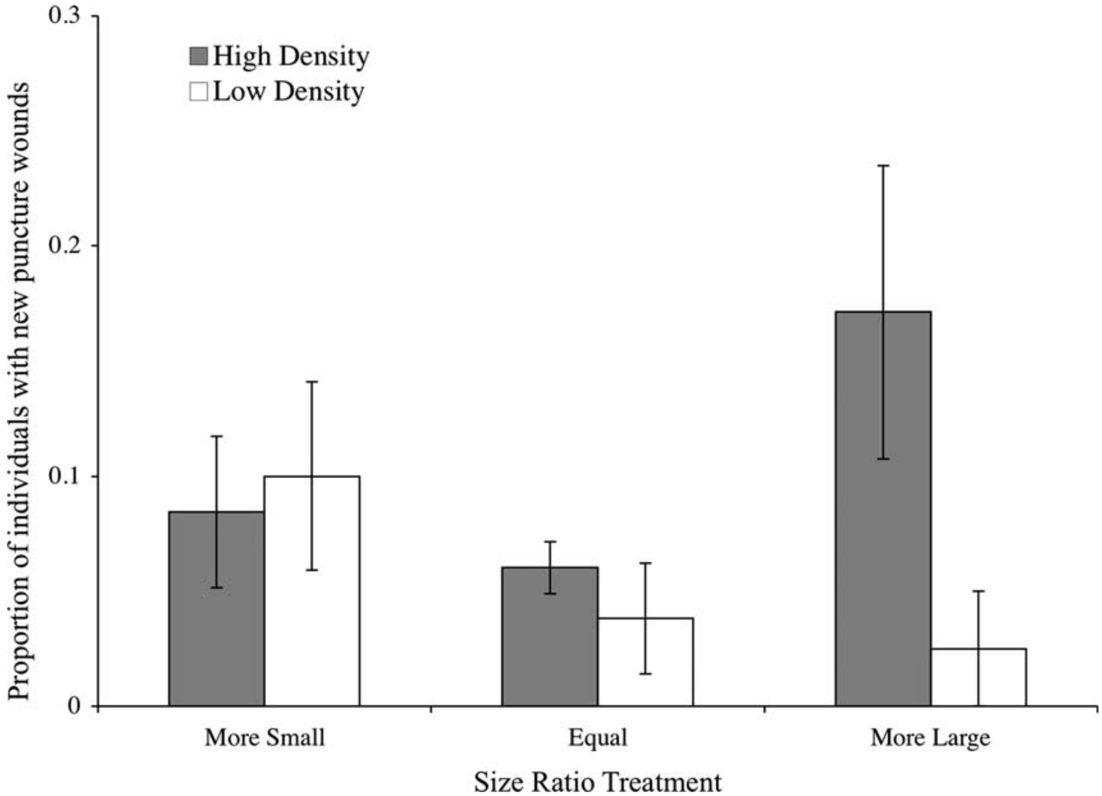

Fig. 5. Proportion of *Petrolisthes cinctipes* that experienced additional puncture wounds following laboratory treatments that manipulated size ratio and density (high density N = 50, low density N = 20) (± SE). From the logistic regression, neither size-ratio treatment ($P = 0.34$) nor density treatment ($P = 0.35$) had a significant effect on the proportion of individuals with new puncture wounds.

(Salmon and Hyatt, 1983; Huntingford et al., 1995). Previous studies of *Petrolisthes cinctipes* demonstrated competitive inferiority of smaller crabs, which had reduced feeding rates and increased cheliped loss in the presence of conspecifics (Donahue, 2004), and more often lost contests for space (Molenock, 1976).

Interactions of Site and Size

There is a significant difference between mean carapace width in sites with different wave exposure and densities (Fig. 2), which provides an alternate explanation for the pattern of injuries observed. For many organisms, competition results in a shift in the size distribution of individuals due to self-thinning (Begon et al., 1986; Fréchette and Lefaivre, 1995). For mobile organisms, this is thought to be either the result of food limitation leading to reduced growth or increased mortality (Begon et al., 1986; Bohlin et al., 1994; Fréchette and Lefaivre, 1995), or competition for space (Grant et al., 1998). Thus, the lower mean carapace width of crabs in high-density habitats may be the result of more intense exploitative and interference competition. As larger individuals are competitive dominants (Salmon and Hyatt, 1983; Jensen, 1990), the higher frequency of puncture wounds in high-density sites may be the outcome of a greater proportion of competitively inferior (smaller) individuals.

Comparing Competition between the Lab and the Field

Field surveys and laboratory experiments showed similar patterns of puncture wounds with regard to density, but not size. In the field surveys, smaller individuals exhibited more injuries (Fig. 4), consistent with smaller crabs being competitively inferior (Molenock, 1976; Salmon and Hyatt, 1983; Huntingford et al., 1995; Donahue, 2004). Laboratory experiments showed no difference in puncture wounds between different size-ratio treatments (Fig. 5). However, the laboratory conditions likely do not mimic natural environments with regard to food availability and population density. As competitive interactions among *Petrolisthes cinctipes* are due to limited food, an excess of food (ground frozen fish added once during each trial) reduced the intensity of competition in the laboratory. This effect is particularly strong for small individuals as they are the most sensitive to agonistic interactions and food limitation (Donahue, 2004). In addition, the densities used in the experiments were several orders of magnitude lower than those observed at wave exposed sites (Jensen, 1990), which also would have resulted in less intense competition and fewer injuries to smaller individuals.

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