



## Cannibalism and inter-specific predation in early stages of intertidal crab species that compete for refuges



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### ABSTRACT

Most benthic species with dispersive life stages suffer high mortality rates in hours to days following settlement. Predation exerted by other species and predation by self (cannibalism) are commonly the chief sources of post-settlement mortality and can profoundly influence population dynamics and adult spatial distribution. In Chile, two predatory crab species (*Acanthocyclus gayi* and *Acanthocyclus hassleri*) coexist in the intertidal zone. Both settle preferentially in mussel beds, but adults show remarkable spatial segregation, apparently as a result of asymmetric competition for refuges. Although early recruits of *A. gayi* are an order of magnitude more abundant than *A. hassleri*, late juveniles are similarly abundant. Recruits of *A. gayi* are probably subjected to higher mortality before competition for refuges intensifies. Here, through laboratory experiments, we quantified the strength of intra and inter-cohort cannibalism and inter-specific predation as probable sources of differential post-settlement mortality. Intra-cohort cannibalism (among recruits of same size) accounted for the mortality of up to 30% of recruits in both species, with no evidence of density-dependent effects on mortality. Rates of cannibalism between juveniles and recruits (inter-cohorts) were also similar between the two species. Both species exhibit type III functional responses of juvenile predators with a tendency to consume heavily upon the most abundant recruits (*A. gayi* in the field), which could potentially provide *A. hassleri* recruits with a “virtual refuge” from the inter-cohort predation in the field. The combination of these different sources of mortality might contribute to the large reduction in abundance of *A. gayi* recruits by the time they reach juvenile stages. Our results illustrate the complexity of mechanisms that can underlay patterns of distribution and relative abundances among competitors through different life stages, especially among coexisting species in which attacking peers can provide higher rewards later in development than just the energy obtained from other food.

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### 1. Introduction

For aquatic species with planktonic larvae, the period that follows settlement is one of the most critical of their life history. After the physiologically-demanding metamorphosis, individuals are exposed to a suite of ‘novel’ sources of stress that typically produce high mortality rates (Caley et al., 1996; Keough and Downes, 1982), often obscuring the link between the abundance of recruits and adults (Gosselin and Qian, 1996; Shanks, 2009). Predation is one of the chief processes causing mortality of early stages and forcing recently settled individual to use refuges, cryptic colorations, or change patterns of behavior and foraging to reduce the risk of being consumed. In many cases, the new settlers face important predation risks not only by individuals of other, usually larger sized species, but also by individuals of same species (intra-specific predation or cannibalism). Indeed, the co-occurrence of high densities

of recruits and juveniles, as a consequence of gregarious settlement, or the shared use of the same structurally complex habitat as refuges (Moksnes, 2004), can generate favorable conditions for the emergence of cannibalism, which usually occurs between cohorts of settlers of different size/age (Fernández, 1999; Fernández et al., 1993; Moksnes, 2004; Moksnes et al., 1997).

Cannibalism can be a successful strategy to gain exclusive use of resources, generally increasing the likelihood of survival of the predator (Polis, 1980, 1981). It is an important factor affecting year class strength and recruitment success among invertebrate species, causing differential survival of successive cohorts (reviewed by Fox, 1975; Gosselin and Qian, 1997; Hunt and Scheibling, 1997; Polis, 1981; Rodriguez et al., 1993). It frequently takes place when resources are in short supply (Polis et al., 1989), and particularly when coexisting predators and prey differ widely in body size either as adults or through ontogeny (Claessen et al., 2000; Diehl, 1993; Fernández, 1999; Fox, 1975; Polis, 1981).

The occurrence of intra-cohort cannibalism appears to be much less widespread in nature, probably because attacking a similar sized victim entails high energy costs, and a high risk, as ‘predator’ and ‘prey’ are expected to be equally matched in strength (Schausberger, 2003). However, given the spatio-temporal overlap of individuals of the same

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cohort, as compared to individuals of different sizes, “intra-cohort interactions” can potentially be as important or more than inter-cohort cannibalism and influence individual growth and survival rates before individuals reach the size needed to successfully recruit to later life stages (Huss et al., 2010).

Due to their potential to be a major factor modulating population dynamics and distribution, it is critically important to evaluate whether predatory intra- and inter-specific interactions occurring soon after settlement can be sufficiently high to control the abundance of later life history stages. Indeed, such knowledge has deep implications on broader questions about recruitment variability, evolution and in the case of commercial species, the sustainability of invertebrate fisheries (Hastings and Costantino, 1991; Moksnes, 2004; Sogard, 1997). Furthermore, a better understanding of the nature of predation/cannibalism may contribute to our knowledge about how competing species coexist, since both mechanisms can contribute to decrease the population size and generate more exclusive access to resources for a particular group of individuals (Polis, 1981). However, few studies have simultaneously evaluated the importance of intra- and inter-cohort cannibalism among species that share habitat and food resources.

Here, we conducted laboratory experiments to quantify the strength of intra- and inter-cohort cannibalism and, at the same time, assess the role of cannibalism versus inter-specific predation as sources of differential mortality in early stages of predatory crab species that share prey and compete for refuges when they reach juvenile stage. The species, *Acanthocyclus gayi* (Milne Edwards et Lucas, 1844) and *A. hassleri* (Rathbun, 1898), are morphologically similar, overlap amply in their patterns of activity and foraging behaviors, and coexist in the rocky intertidal zone along the central coast of Chile (Navarrete and Castilla, 1988; Sotomayor and Zamorano, 1985; Wieters et al., 2009). Their preference for the same type of refuges (Wieters et al., 2009), i.e. galleries under mussel beds of *Perumytilus purpuratus* (Castilla et al., 1989), generates aggressive encounters in the dispute for such refuges once individuals reach late juvenile stages (> 1 cm carapace width). Short-term field experiments (Navarrete and Castilla, 1990) demonstrated that late juveniles and adult crabs engage in agonistic interactions to defend refuges. Thus, active competition for refuges has been proposed as the chief explanation for the remarkable local spatial segregation between late juveniles and adults of the two species, where *A. hassleri* competitively exclude *A. gayi* from mussel bed galleries and restrict them to crevices and other alternative habitat. Interestingly, recruits of both species are primarily found in the mussel beds (Navarrete et al., 2008), which appear to be the preferred settlement habitat for both species (Januario and Navarrete in preparation). Although *A. gayi* recruits are about an order of magnitude more abundant than those of *A. hassleri* (Navarrete et al., 2008), such difference in abundance is no longer observed among late juveniles. It appears that *A. gayi* suffers higher mortality rate after settlement and even before competition for refuges intensifies.

The combined effect of an extensive recruitment season (Navarrete et al., 2008) and similar preferences for nursery habitat (Januario and Navarrete in preparation), associated with an aggressive territorial behavior (Navarrete and Castilla, 1990), favors encounters among individuals, creating the conditions for the emergence of predation/cannibalism within and between juvenile cohorts. It must be noted that despite the existence of agonistic interactions, and the widespread occurrence of cannibalism among many crustacean decapod species (among others: Fernández, 1999; Fernández et al., 1993; Kneib et al., 1999; Lovrich and Sainte-Marie, 1997; Luppi et al., 2001; Marshall et al., 2005; Moksnes, 2004; Ventura et al., 2008), predation between late juveniles and adults of *Acanthocyclus* has rarely been observed in the laboratory (Navarrete and Castilla, 1990) and never in the field. Thus, if cannibalism and predation does occur in these species, it must be largely restricted to early life stages.

Here, through laboratory experiments we quantified intra and inter-cohort cannibalism rates as well as predation between early

juveniles and recruits of *A. gayi* and *A. hassleri*. We evaluated whether these different sources of post-settlement mortality can play a role in the large difference in abundance observed once *A. gayi* recent recruits reach late juvenile stages, i.e. before the onset of competition for refuges.

## 2. Material and methods

### 2.1. Field sampling

We estimated recruit and juvenile crab density in the intertidal zone near ECIM (Estación Costera de Investigaciones Marinas), at Las Cruces, central Chile where beds of the mussel *P. purpuratus* dominate the mid intertidal zone (Broitman et al., 2001). Since recruits of the species are observed year round at most sites of central Chile, but with peaks in spring (mostly *A. gayi*) and late summer (both species, Navarrete et al., 2008), we conducted field surveys between spring 2008 and late summer 2009. Additional individuals were collected year-round to provide predators and prey for the experiments. Previous studies have shown that most recruits of the two species are found in mussel beds, with no apparent segregation between early stages (Navarrete and Castilla, 1990; Navarrete et al., 2008). Samples were obtained by removing all mussels in 10 × 10 cm quadrats (n = 23), haphazardly placed along 10 to 20 m long horizontal transects at mid tidal heights of 3 rocky platforms separated by about 100 m. We used a small quadrat size to reduce the impact of destructive sampling on the mussel bed habitat. The samples were taken to the laboratory where individual crabs were carefully removed under a stereomicroscope, identified to species (according to Navarrete et al., 2008), measured to the nearest 0.01 mm with an ocular micrometer and placed in plastic vials partially filled with seawater, which was replaced daily. The main characters to identify recruits <45 d old is the presence of hairs in the rough carapace and in the chelae of *A. gayi* recruits and the absence of these in the smooth, more oval-shape carapace and in the chelae of *A. hassleri* recruit. Older individuals start to exhibit the distinctive pigmentation in walking legs and chelae, and early juveniles also have the differences in rostrum that characterize juveniles and adults (Navarrete et al., 2008). Before experiments, the smallest individuals (<4 mm CW) were reared with recently hatched *Artemia nauplii*. Larger individuals were fed with fresh mussels. Observations of individuals reared at laboratory conditions show that individuals <4 mm CW correspond to the first 2 to 3 juvenile stages.

### 2.2. General procedure

In all experiments, recently molted individuals were discarded to ensure the same susceptibility to predation among prey. Individuals with missing limbs were excluded, and all individuals were used only once. This conservative procedure might under-estimate the rates of cannibalism and predation observed in the field. To simulate a natural refuge, each arena was provided with an adult mussel (26.69 ± 1.03 mm length), which was big enough to avoid being eaten by crabs and thus were not considered an alternative prey. The experimental arenas (plastic trays 10 cm in diameter) were placed in large, outdoor aquaria under a roof and in this manner were exposed to ambient light and temperature conditions. We controlled the rise and drop of water into the aquaria every 6 h throughout the experiments to simulate the natural semi-diurnal tidal cycle. The small size of recruits precluded any type of direct observations without interfering with their behavior during the experiments, so we could not follow individuals. At the end of 48 h, the number of dead individuals was counted.

#### 2.2.1. Intra-cohort cannibalism

To quantify and compare rates of intra-cohort cannibalism in recruits of *A. gayi* and *A. hassleri*, we considered similarly sized individuals collected in the field as coming from the same cohort. For *A. gayi*,

recruits were  $3.43 \pm 0.08$  mm of carapace width (CW), while *A. hassleri* recruits were  $3.28 \pm 0.12$  mm CW. To examine whether cannibalism was density-dependent, we used three different densities: low = 5, intermediate = 10 and high = 14 ind./10 cm<sup>2</sup> (n = 4, 3, 5 replicates, respectively), which encompass the range of densities observed in field surveys for *A. gayi* (see Section 3.1). To ensure that starvation prior to experiments did not affect results, recently hatched *A. nauplii* and small portions of fresh mussels were provided as food ad libitum until the beginning of the experiments.

We assumed that natural mortality during the brief period of time of the experiments was nearly null and density-independent (invariant across density treatments), so all mortality was attributed to intra-cohort cannibalism. We calculated a *proportional mortality rate* as the “number of dead recruits/initial number of recruits” over a given period of time, which is a measure of the average intensity of intra-cohort cannibalism at a given initial density of individuals (Luppi et al., 2001; Moksnes et al., 1997).

Proportional mortality rates were then compared between species and recruit densities using a two-way ANOVA, considering recruit density (3 levels) and crab species as fixed factors.

### 2.2.2. Inter-size cannibalism

To quantify the rates of inter-cohort cannibalism between juveniles and recruits of each species, we carried out two experiments considering either *A. gayi* juveniles ( $7.66 \pm 0.37$  mm CW) or *A. hassleri* juveniles ( $9.66 \pm 0.20$  mm CW) as predators, which were replicated 8 and 5 times, respectively. The level of replication varied according to availability of recruits at the time of experiments. Conspecific recruits ( $2.42 \pm 0.11$  mm CW and  $3.30 \pm 0.14$  mm CW for *A. gayi* and *A. hassleri*, respectively) were considered prey. In each trial, one juvenile predator was exposed to either low (5 ind./10 cm<sup>2</sup>) or high (14 ind./10 cm<sup>2</sup>) recruit density. To standardize hunger levels, the juvenile crab predators were starved for 72 h before the beginning of each trial, but recruits were fed ad libitum as in the previous experiment. In all cases the juvenile predator was alive at the end of the trials.

Following the procedure used in previous studies (Fernández et al., 1993; Luppi et al., 2001; Moksnes et al., 1997), the inter-cohort cannibalism rate was obtained as: number of dead recruits/initial number of recruits over time. Since there is one juvenile predator per arena, this value represents a per capita predation rate. But in these experiments we cannot unequivocally attribute recruit mortality to predation by the larger juvenile as some cannibalism among same sized individuals might have also occurred. Therefore, assuming that the levels of intra-cohort cannibalism are not affected by the presence of the larger juvenile, we corrected the total proportional mortality rate observed in each replicate, by subtracting the mean mortality due to intra-cohort cannibalism at each level of recruit density (low: 5 ind./10 cm<sup>2</sup> and high: 14 ind./10 cm<sup>2</sup>).

The “corrected” inter-cohort cannibalism was compared between each recruit density and species of predator with a two-way ANOVA, considering species and recruit densities as fixed factors. We also compared mortality rates due to intra-cohort cannibalism against those exclusively due to inter-cohort cannibalism (“corrected”), between crab species, and between recruit densities (only low and high recruit densities, 5 and 14 ind./10 cm<sup>2</sup>, respectively) with a three-way ANOVA, considering all factors as fixed. For all these analysis, data were arcsin square root transformed to meet variance homogeneity assumption of ANOVA (Sokal and Rohlf, 1995).

### 2.2.3. Inter-specific predation between recruits and juveniles

To quantify rates of predation of juveniles consuming recruits of the other species, we carried out two independent experiments. We first considered *A. hassleri* juveniles as predators and later *A. gayi* juveniles as predators. Juvenile predators were  $7.58 \pm 0.30$  mm (CW), while prey were  $2.82 \pm 0.04$  mm CW, which roughly correspond to first and second instars (“recruits”). Experiments followed Holling’s (1959a, 1959b)

methodology to characterize the functional response of individual predators. In this manner, a single predator was positioned in an arena (plastic trays 10 cm in diameter) with a fixed density of 4 individuals of the ‘alternate’ prey (*A. hassleri*), and varying densities (2, 4, 8, 12, or 16 individuals) of the ‘target’ prey species (*A. gayi*). The densities used in treatments corresponded to the lowest, mean, and maximum number of recruit of *A. gayi*/10 cm<sup>2</sup> observed in the field (see Section 3.1). The design with a target and an alternative prey optimizes the evaluation of prey switching for generalist predators and, in this case, followed the naturally higher variation in *A. gayi* density observed in the field. A total of 4 replicates of each prey density combination were used for juveniles of *A. hassleri* and 5 replicates for experiments with juveniles of *A. gayi*.

To standardize hunger levels, predators were starved for 72 h before the beginning of each trial. Prey recruits were provided with food until the beginning of each trial. At the end of 48 h the number of surviving individuals was recorded. Killed prey recruits were not replaced during the experiment, as suggested by Jalali et al. (2010). Although such procedure could potentially influence predators selection as preferred prey were consumed, it proved impossible to identify the small recruits that were consumed without manipulation and considerable interference with crabs’ behavior. We therefore do not present a specific test for prey selectivity; however, we provide a general evaluation of selection by comparing proportions of prey offered and consumed (see below). The number of prey killed under each density condition and each replicate at the end of the 48 h was used to estimate parameters of the general functional response equation (Michaelis–Menten–Holling):

$$N_a = \frac{K \times N^b}{X^b + N^b}, \quad (1)$$

where  $N_a$  = number of prey eaten,  $K$  = maximum feeding rate (satiation),  $N$  = initial prey density,  $X$  = prey density at which  $N_a = K/2$  (sensu Holling, 1959b).

The exponent “b” in Eq. (1) is the parameter associated with the form of the functional response curve. When  $b = 0$  the response is type I, when  $b = 1$  the response is type II or saturating, and when  $b > 1$  this corresponds to type III functional responses. Estimates of these parameters were obtained using nonlinear least-squares fitting implemented in the “nls package” in R software. The best model was chosen according to Bayesian information criterion (BICw).

Mortality rates (number of prey consumed by each predator/initial number of prey offered) were compared between predator species and levels of prey density with a two way ANOVA, considering prey density and predator species as fixed factors.

Prey switching was evaluated by comparing the ratio of prey consumed at the end of the experiment with a linear model of no-switching (equal selection), in which the expected prey ratio in the diet is equal to the prey ratio offered at the beginning of each experiment (Murdoch, 1969). A disproportional consumption of one prey across all prey ratios offered indicates persistent selection for one species, and a disproportionate consumption of a different prey at opposite ends indicates switching by predators. We calculated the mean and standard error for each ratio of consumed prey to help determine how strong the switching trend was.

## 3. Results

### 3.1. Characterization of field abundance

Recruits of *A. gayi* were almost 9 times more abundant ( $5.16 \pm 0.85$  ind./10 cm<sup>2</sup>) (mean  $\pm$  error) than recruits of *A. hassleri* ( $0.57 \pm 0.15$  ind./10 cm<sup>2</sup>) (Fig. 1 A, B, notice different scales). For juveniles ( $\geq 4.0$  mm CW), the difference between species was small and reversed, with a slight predominance of *A. hassleri* ( $0.92 \pm 0.17$  ind./10 cm<sup>2</sup>) over *A. gayi* ( $0.57 \pm 0.25$  ind./10 cm<sup>2</sup>).

Most recruits of *A. gayi* (>79%) were smaller than 2.5 mm CW, with a modal size at 1.5 mm CW (Fig. 1C), while size frequency distribution of *A. hassleri* was more homogeneous, with a modal size around 3.5 mm CW (Fig. 1D). Mean recruit sizes of *A. hassleri* were significantly larger than those of *A. gayi* ( $t = 2.47$ ; d.f. = 209;  $p = 0.0222$ ) and the same pattern was observed in sizes of juveniles ( $t = 2.72$ ; d.f. = 57;  $p = 0.0098$ ).

### 3.2. Intra-size cannibalism

Dead individuals at the end of the 48 h long experiments represented 20–25% of the total number of recruits of the two crab species in the experimental arenas. We usually found remains of dead individuals (e.g. half of the carapace, legs) that indicated aggressive encounters and only few (<2%) were found dead with little damage (loss of appendages but complete carapace). Most of the survivors were active, and only few of them had missing limbs.

Mortality suffered by recruits due to other recruits did not increase uniformly with increasing recruit density (Fig. 2A). For *A. gayi* mortality rate decreased slightly at the highest density used in the experiments, while for *A. hassleri* it increased slightly at intermediate and high densities, but differences among the three density-treatments were not statistically significant ( $F_{[2; 18]} = 0.88$ ;  $p = 0.4317$ ). Moreover, no overall statistical difference between the two species was found ( $F_{[1; 18]} = 0.04$ ;  $p = 0.8496$ ), independently of the density treatment (no interaction  $F_{[2; 18]} = 0.46$ ;  $p = 0.6372$ ).

### 3.3. Inter-size cannibalism

The pattern of body damage in dead animals of the inter-cohort cannibalism experiment was different to that observed in intra-cohort

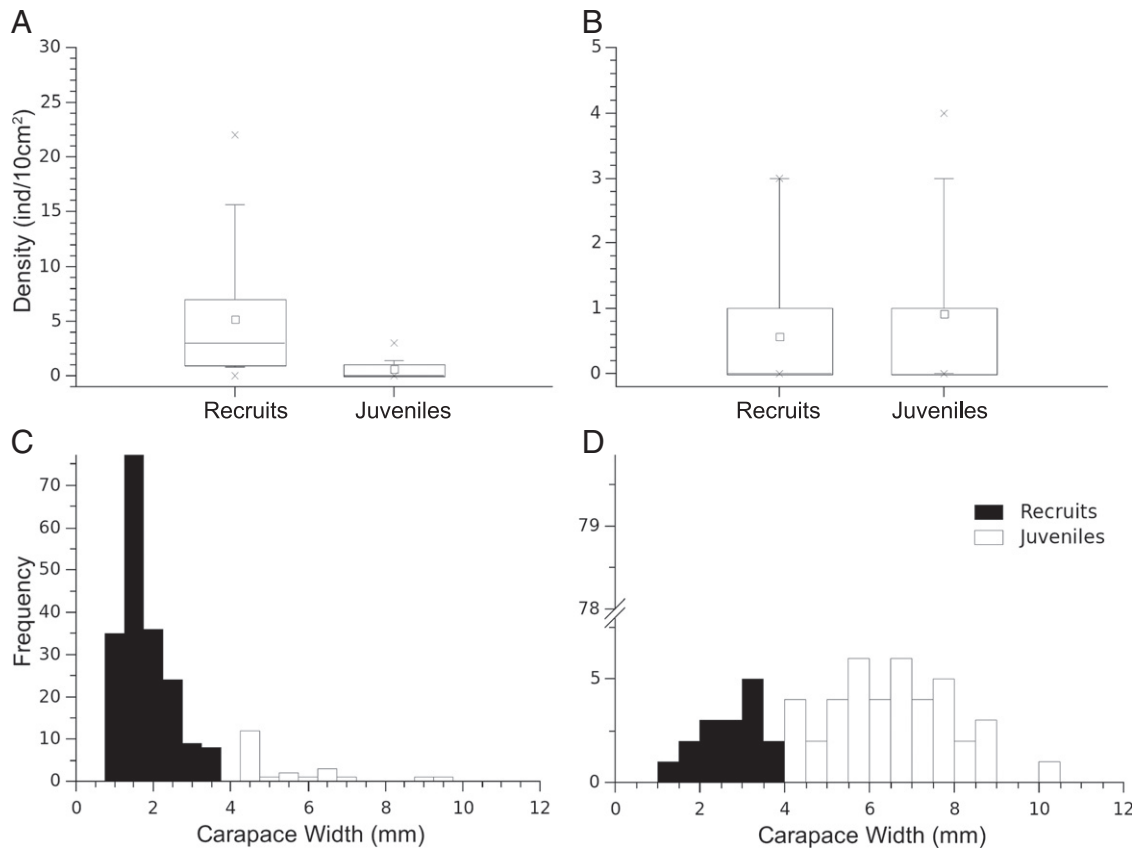
cannibalism experiments. In the former, most remains were with all appendages but with a diagonal hole across the usually empty carapace, probably done by the larger cheliped of the juvenile conspecific predator. Only dead individuals with signs of being eaten were considered in the analysis.

Rates of inter-cohort cannibalism reached over 25% in both crab species at low density of recruits (Fig. 2B). At the highest density, mortality of *A. gayi* recruits decreased to 17%, while it remained at 30% among *A. hassleri* recruits. After correcting by the intra-cohort cannibalism, the pattern of inter-cohort cannibalism was more similar between the two species at low and high recruit densities (Fig. 2C). These corrected mortality rates showed a decreasing trend at increasing recruit density, but the trend was not statistically significant ( $F_{[1; 21]} = 0.08$ ;  $p = 0.7823$ ) for any of the species ( $F_{[1; 21]} = 0.08$ ;  $p = 0.7829$ ) and with no interaction between these factors ( $F_{[1; 21]} = 0.02$ ;  $p = 0.9634$ ).

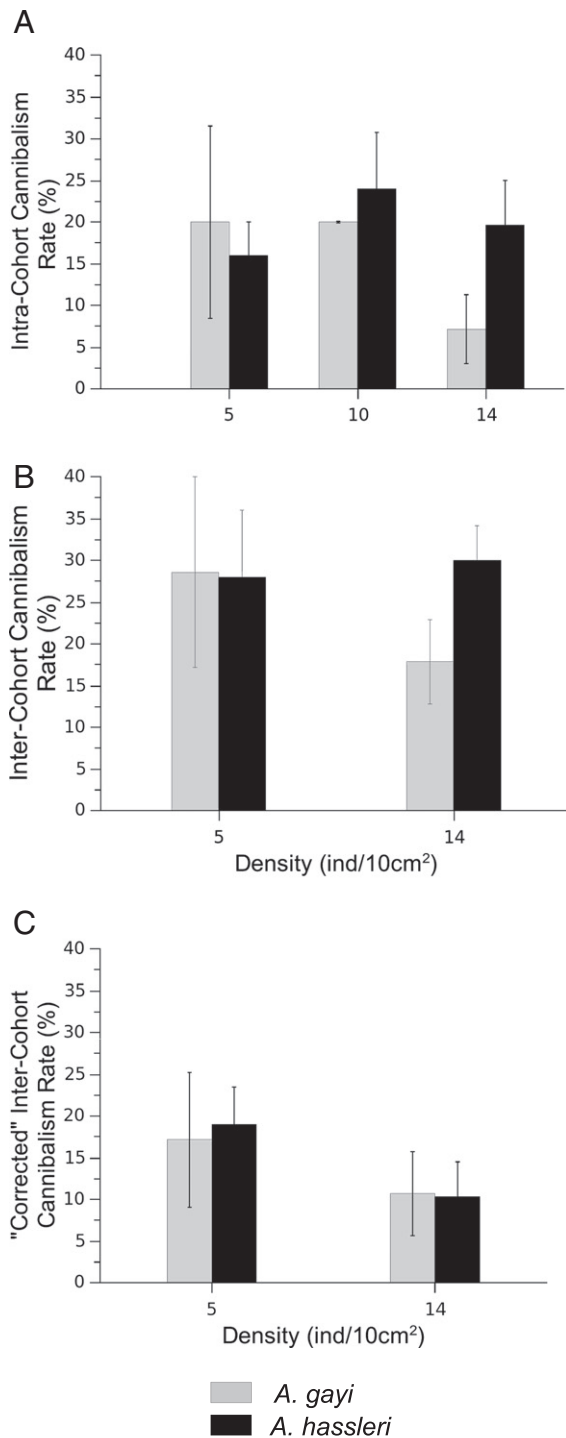
Mortality due to intra-cohort cannibalism was generally similar to that imposed by juveniles on conspecific recruits (inter-cohort cannibalism) for both crab species and at low and high densities of recruits (Fig. 3A for *A. gayi* and B for *A. hassleri*). No statistically significant differences were observed between the species, between intra- and inter-cohort cannibalism, or recruit densities or their interactions (Table 1).

### 3.4. Inter-specific predation between recruits and juveniles

When consuming recruits of the other species, juvenile crabs of both species presented a typical type III functional response (Fig. 4, Table 2). Per capita predation rates increased in accelerated fashion at low levels of prey densities. As prey density increased further, predation rates decelerated and at the highest recruit densities, per capita consumption showed signs of saturation (Fig. 4A, B). Table 3 shows the estimated



**Fig. 1.** A, B: Box plot for the density (ind./10 cm<sup>2</sup>) of recruits and juveniles. The central box represents the values from the lower to upper quartile (25th and 75th percentile). The middle line represents the median. A line extends from the minimum to the maximum value. C, D: Size (carapace width) frequency distribution of recruits and juveniles in the field. Individuals <4.0 mm CW were considered recruits.



**Fig. 2.** A: Mean intra-cohort cannibalism rate (%) ( $\pm$ SE) at low, intermediate and high densities of recruits. B, C: Mean per capita inter-cohort cannibalism ( $\pm$ SE) at low and high densities of recruits: "raw" cannibalism rate and "corrected" by the intra-cohort cannibalism rate (see Section 2.2.2), respectively.

parameters describing the functional response of juveniles of the two species. Per capita mortality rates suffered by recruits increased at low prey density, but later declined as prey density increased farther (Fig. 4C, D), which is also a characteristic of an S-shape functional response. The overall mortality of the "target prey" (*A. gayi* recruits) varied significantly with density ( $F = 3.19$ ; d.f. = 4, 32;  $p = 0.0259$ ), but was similar between the juvenile predator species ( $F = 0.59$ ; d.f. = 1, 32;  $p = 0.4469$ ), with no interaction between these factors ( $F = 0.70$ ; d.f. = 4, 32;  $p = 0.5955$ ).

The *A. gayi* juveniles consumed mostly of *A. hassleri* recruits when they were in higher proportion than their own, but quickly switched to consuming mostly conspecific recruits when they were offered in equal or higher proportion than *A. hassleri* recruits (Fig. 5A). The trend was consistent through most prey ratios offered, except at the highest prey ratio when large variability among replicates made it indistinguishable from the null model of no preference (Fig. 5A). In the case of *A. hassleri*, prey switching was not as clear, although at the extremes of the prey offer the juveniles disproportionately consumed the most abundant prey (Fig. 5B). At intermediate ratios of recruit species, *A. hassleri* juveniles consumed either in proportion to the offer or mostly their own recruits (Fig. 5B).

#### 4. Discussion

Our results provide experimental evidence that cannibalism both within and between cohorts of yearly juvenile stages, as well as inter-specific predation between recruits and juveniles can be important sources of mortality for recruits of *A. gayi* and *A. hassleri*. Rates of intra-cohort and inter-cohort cannibalism were similar between species and, over the range of densities used in experiments, we did not detect density-dependence. Considering the difference in magnitude of recruitment and the natural abundance of recruits and juveniles in the field, we expect higher total mortality due to intra-cohort cannibalism in *A. gayi* recruits, and higher total mortality of recruits due to predation by juveniles in the case of *A. hassleri*. When feeding simultaneously on recruits of the two species, juveniles presented similar type III functional responses, although prey switching was clearer in *A. gayi*. The trend to consume heavily the most abundant recruit species, *A. gayi* under natural conditions, could provide *A. hassleri* recruits with a "virtual refuge" in low density (Berryman and Hawkins, 2006) from inter-cohort cannibalism and predation. The association of these different sources of mortality might ultimately contribute to the large reduction in abundance of *A. gayi* recruits by the time they reach juvenile stages. We discuss how these sources of mortality could ultimately contribute to patterns of abundance between the two species.

##### 4.1. Intra-cohort cannibalism

Most published accounts on decapod crustaceans have documented low rates of cannibalism among similarly sized individuals (Fernández, 1999; Fernández et al., 1993; Moksnes, 2004). Our results contrast sharply, showing that in *Acanthocyclus* species, intra-cohort cannibalism can account for the mortality of up to 30% of recruits within 48 h. Attacking a similarly sized enemy is more risky than attacking a smaller prey (Claessen et al., 2000), and this has been the main explanation as to why, for many species, intra-cohort cannibalism has not been examined or has been shown to be of lesser importance. In most cases in which some intra-cohort cannibalism was recorded (*Cancer magister*, Fernández et al., 1993; *Chasmagnathus granulata* and *Cyrtograpsus angulatus*, Luppi et al., 2001), attacks occurred on recently molted individuals. Indeed, during and immediately after ecdysis, individuals are more vulnerable to attacks as they are less mobile and soft shelled (Marshall et al., 2005; Polis, 1981). In our study, individuals that molted immediately before the beginning of the experiments were discarded and no *exuvia* was observed during the brief duration of the experiments. Although we probably mixed individuals more and less vulnerable in the same arena, the high rates of mortality recorded in only 48 h and after recruits had been fed ad libitum, make us believe that intra-size cannibalism is a common phenomenon under natural conditions. Moreover, eliminating recently molted individuals from experiments, i.e. the most vulnerable stage until hardening of the carapace, probably under-estimates the true rates of cannibalism and predation suffered by recruits.

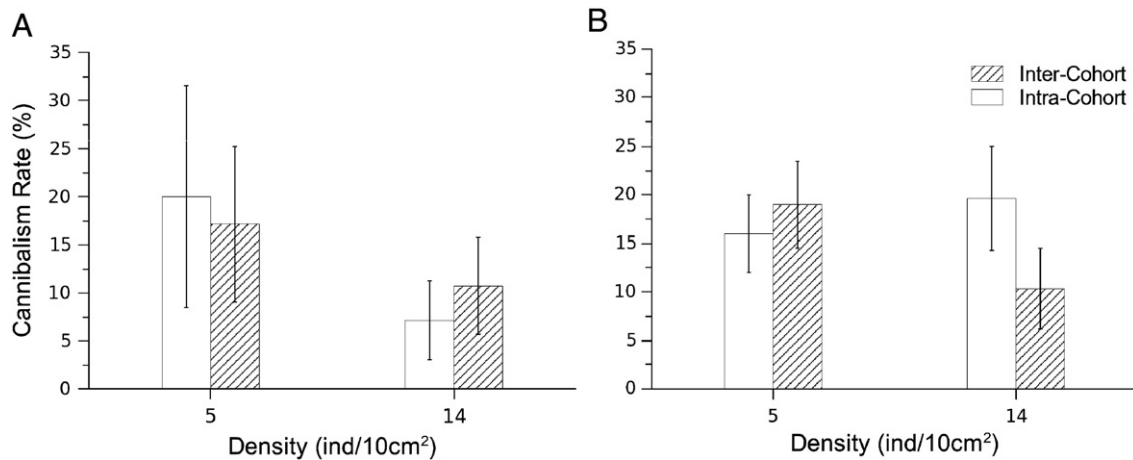


Fig. 3. A, B: Mean intra and inter-cohort cannibalism rate ( $\pm$  SE) at low and high densities of recruits of *A. gayi* and *A. hassleri*, respectively.

In the field, the presence of a different type of prey (not presented in our experiments) can potentially reduce the rates of intra-cohort cannibalism that we observed under laboratory conditions. But abundance of these small preys might be highly variable, hard to capture and scarce during the days following settlement. Under these circumstances, other conspecific recruits could be a 'convenient' food item readily available throughout the recruitment season. Moreover, observed high rates of mortality among recruits that had been fed ad libitum before the beginning of the experiments make us believe that intra-size cannibalism is a common phenomenon in this study system. Further studies are needed to determine how intra-cohort cannibalism varies with the presence of other prey.

Interestingly, the total mortality rate due to intra-cohort cannibalism did not increase with recruit density. Indeed, our results run counter the assumed positive effect of crowding on cannibalistic behavior (FitzGerald, 1992; Fox, 1975; Polis, 1981; Schausberger, 2003) and suggest that in *Acanthocyclus* crabs there is an increased risk of performing a cannibalistic attack with increasing recruit density. The experimental densities were well within the mean and range of recruit densities commonly observed for *A. gayi* in the field and, therefore, the level of cannibalism in experiments might represent well the maximum rates in the natural environment, when other preys are scarce. But experimental densities were above the density we ever recorded for *A. hassleri* (see also Navarrete and Castilla, 1990). Experimental estimates of cannibalism could thus over-estimate the realized levels of intra-cohort cannibalism for this species. Experiments at lower densities than the ones used here are thus necessary to better determine whether cannibalistic behavior is density-induced or fixed in the population. Unfortunately, low densities require evaluation over a much longer period of time (e.g. Moksnes, 2004), which increase the possibility of experimental artifacts (e.g. increased starvation, molting individuals).

Table 1

Three-way ANOVA comparing mortality rates due to intra-cohort cannibalism and due exclusively to inter-cohort cannibalism ("corrected") between species and recruit density (only low and high recruit densities, 5 and 14 ind./10 cm<sup>2</sup>, respectively).

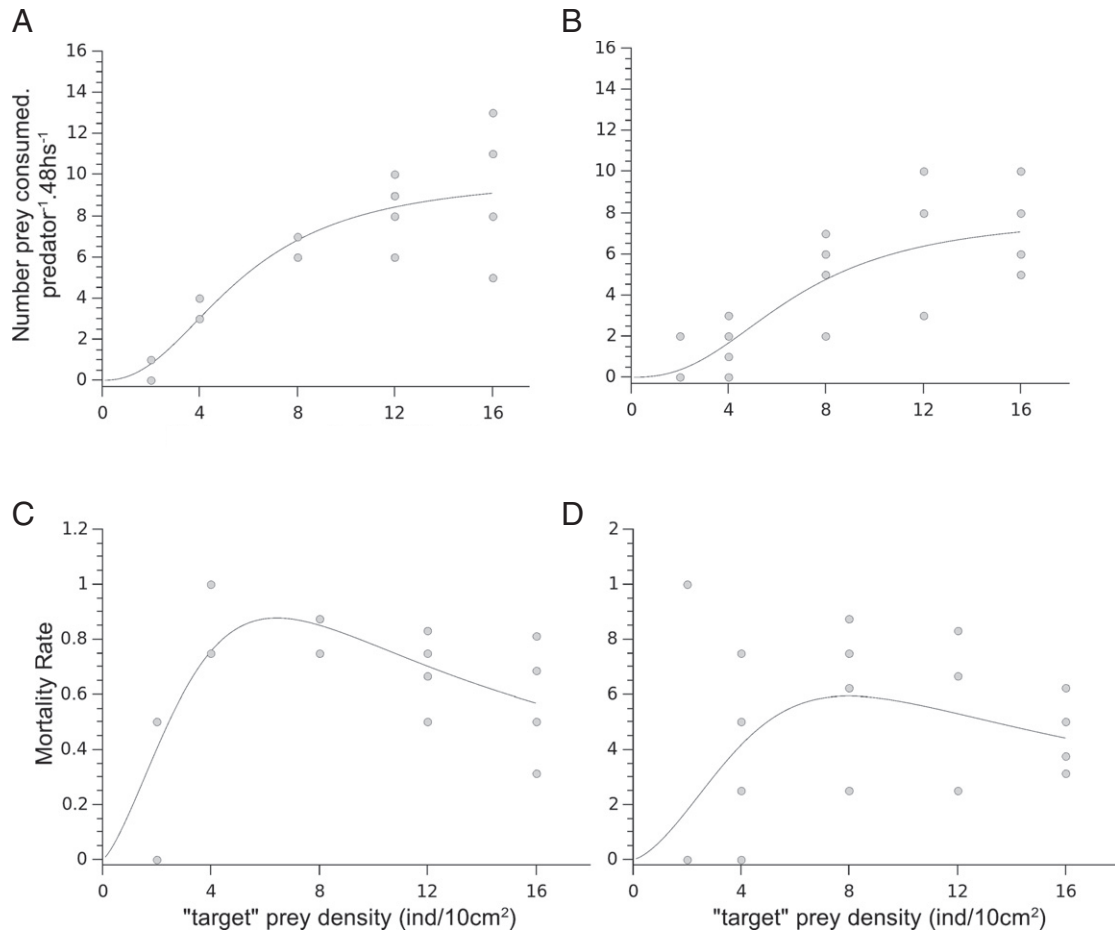
Source	d.f.	F	P
Species (S)	1	0.08	0.78
Type of cannibalism (T)	1	0.04	0.85
Density (D)	1	0.08	0.78
S $\times$ T	1	0.52	0.48
S $\times$ D	1	0.01	0.96
T $\times$ D	1	0.11	0.74
S $\times$ T $\times$ D	1	0.36	0.55
Residuals	33		

#### 4.2. Inter-cohort cannibalism

Rates of inter-cohort cannibalism were similarly high for the two species. This type of cannibalism is common among crustacean species probably because aggressive behavior directed against substantially smaller individuals carries lower risk of injury for the larger predator (Kneib et al., 1999). Characteristics of the settlement process, such as larval settlement extended throughout the year, similar habitat selection by larvae and juveniles, result in high densities of juveniles of different size classes within a restricted area, and might explain the commonness of cannibalistic interactions in this group of organism (Moksnes, 2004). Furthermore, the potential for long distance dispersal by the planktonic larvae decreases the probability of eliminating a genetically close peer via cannibalism (Polis, 1981). Slight differences between species in the time at which peak recruitment is observed (mostly spring time, but also late summer in *A. gayi* and mostly late summer in *A. hassleri*), as shown by long-term averages of monthly recruitment across several sites by Navarrete et al. (2008), might reduce somewhat encounter rates among settlers. But it is uncertain whether such differences would persist over time scales of settlement events and whether they would be sufficient to significantly reduce inter-cohort cannibalism for species that settle year round.

As observed with intra-cohort cannibalism, there was no evidence that rates of inter-cohort cannibalism intensified with increasing recruit density, even after subtracting the effect of intra-cohort cannibalism. However, most studies with decapod species have shown that cannibalistic behavior can be triggered by an increase in recruit density during recruitment season (Fernández, 1999; Moksnes, 2004). In our case, correcting rates of inter-cohort cannibalism by the expected mortality suffered from predators of similar size led to slightly lower cannibalism at higher recruit density, again suggesting that over the range of experimental densities cannibalism is not stimulated by density.

We corrected rates of inter-cohort cannibalism by subtracting the mean intra-cohort cannibalism at each level of prey density. This procedure makes the assumption that intra-cohort cannibalism behavior remains unaltered by the presence of a larger juvenile conspecific; an assumption that needs further evaluation. But not making this correction, in the face of demonstrated high levels of intra-cohort cannibalism, would lead to a clear over-estimation of inter-cohort predation. Our corrected rates rendered mortality values comparable to intra-cohort cannibalism and very similar between crab species. However, considering the difference in magnitude of recruitment and the size structure of recruits and juveniles that can be observed year-round in the field (personal observation), we might expect higher total mortality due to intra-cohort cannibalism in *A. gayi* recruits, and higher mortality exerted by their own juveniles in *A. hassleri* recruits.



**Fig. 4.** Functional response of juvenile predators. A, B: Mean number of prey eaten per predator per 48 h. The fitted curve is from the general functional response model:  $N_a = (9.94 \times N2.31) / (5.722.31 + N2.31)$  for *A. gayi* and  $N_a = (7.89 \times N2.5) / (6.782.5 + N2.5)$  for *A. hassleri* predators, respectively. C, D: Mortality rate of prey for *A. gayi* and *A. hassleri* predators, respectively.

In systems like the *Acanthocyclus* species studied here, in which related-competitors closely coexist, cannibalism might be part of the 'normal' foraging behavior of the species. Then, making the first move to attack a conspecific might be advantageous because it reduces the risk of becoming a victim (Michaud, 2003). Under this scenario, hunger is no longer a prerequisite for eliciting an attack, because it is an opportunity to eliminate a potential competitor/predator (Wise, 2006), especially for an abundant species such as *A. gayi*. If this was true, then, the earlier the aggressive behavior is expressed, the more likely the individual will survive during this critical period (few days and weeks after settlement). Interestingly and in contrast to many other decapod species, cannibalism and inter-specific predation are nearly absent in juvenile and adults of these species (Navarrete and Castilla, 1990; Wieters et al., 2009, personal observations). Further studies are needed

to determine when cannibalistic behavior changes through ontogeny and whether such strategy is favored by selection in the context of inter-specific competition.

#### 4.3. Predation on recruits by juveniles

A type III functional response provided the best fit to experimental data for juvenile predators of both species feeding on recruits. This type of sigmoid functional response means that juveniles may increase their per capita predation rates in response to higher densities of recruits during the settlement season, resulting in density-dependent predation (Moksnes, 2004). High levels of mortality due to predation during the early juvenile stage have been suggested as the main factor controlling abundance of several crustaceans, such as cancer crabs (Eggleston and Armstrong, 1995; Fernández et al., 1993; Pardo et al., 2007), shore crab (Moksnes et al., 1998), mud crabs (Kurihara et al., 1988), lobsters (Palma et al., 1999; Smith and Herrkind, 1992) and

**Table 2**

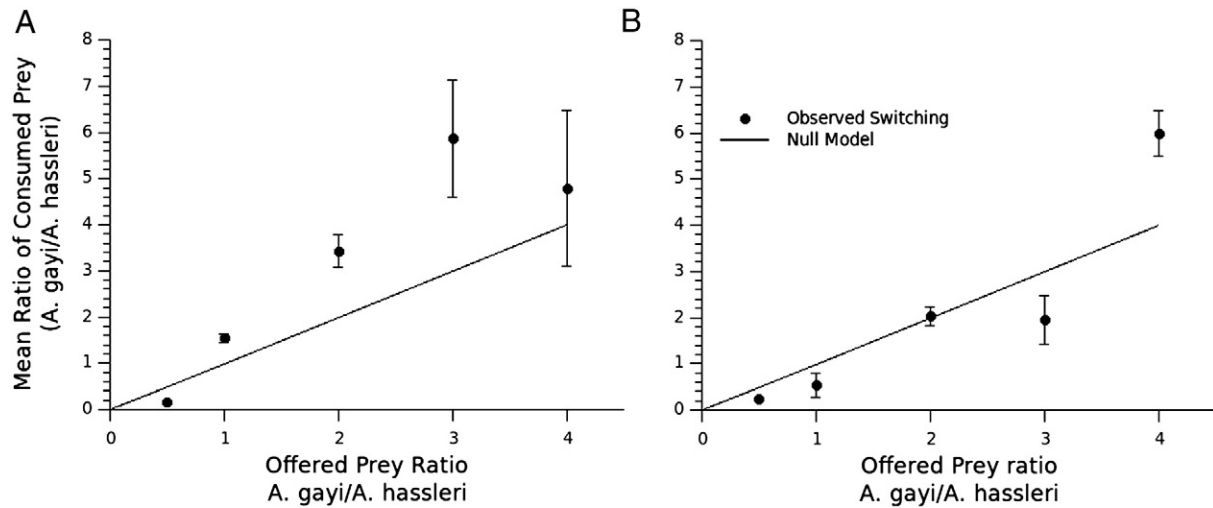
Results of non-linear curve fitting of the Holling functional response model for juvenile crab predators feeding on recruits. The Bayesian information criterion (BICw) values for each of the three functional response model fitted to the data are presented for *Acanthocyclus gayi* and *A. hassleri*.

Functional response models	BICw	
	<i>A. gayi</i>	<i>A. hassleri</i>
$N_a = aN$	0.03	0.02304
$N_a = \frac{K \times N}{X + N}$	0.1252	0.2642
$N_a = \frac{K^b \times N}{X^b + N}$	0.8449	0.5054

**Table 3**

Parameters that describe the functional response model for *Acanthocyclus gayi* and *A. hassleri* juvenile predators ( $\pm$  SE).

Model parameters		
	<i>A. gayi</i>	<i>A. hassleri</i>
K	9.936 $\pm$ 1.68	1.889 $\pm$ 2.53
X	5.717 $\pm$ 1.32	6.776 $\pm$ 1.55
b	2.312 $\pm$ 0.83	2.498 $\pm$ 2.65



**Fig. 5.** Prey selection of *A. gayi*, *A.* and *A. hassleri* juvenile predators, B. Mean ratio ( $\pm$  standard error) of recruits (*A. gayi/A. hassleri*) consumed at the end of the experiment ( $\bullet$ ) and linear model of no-switching (equal selection) (—).

shrimps (Posey and Hines, 1991). Our results suggest that juveniles of both *Acanthocyclus* species have the potential to reduce the density of recruits after settlement. In fact, in our experiments of inter-specific predation with crab recruits as the sole prey, *A. gayi* juveniles consumed up to 80% of recruits and *A. hassleri* juveniles up to 60%.

Another characteristic of a predator with type III functional response is the prey switching behavior, in which the consumption of the most abundant prey stabilizes the predator–prey system (Murdoch, 1969; Oaten and Murdoch, 1975). Juveniles of *A. gayi* consumed mostly recruits of *A. hassleri* when those were more abundant than conspecific recruits, but quickly switched to consume their conspecific recruits when their abundance was similar or higher than that of heterospecific recruits. In the case of *A. hassleri*, switching behavior was less clear because at intermediate prey ratios, *A. hassleri* juveniles consumed prey species either in the same proportion offered or consumed mostly conspecific recruits. At the extreme prey ratios, however, *A. hassleri* juveniles did consume disproportionately more whichever recruit species was most abundant. Since *A. hassleri* recruitment is several times lower than that of *A. gayi* (Navarrete et al., 2008, this study), and the arrival of *A. gayi* larvae from the plankton is persistently high, especially throughout the settlement season, *A. hassleri* recruits might enjoy a relative “density refuge” (Berryman and Hawkins, 2006) from predation during the first life stages. Thus, taken together, our results suggest that the different sources of mortality might be stronger on *A. gayi* and ultimately contribute to the large reduction in abundance of this species by the time they reach juvenile stages.

The experimental conditions used in our experiment, i.e. the use of artificial arenas with large mussel, where individuals have no chance to escape, could certainly intensify the frequency/occurrence of aggressive interactions. However, recruit individuals are always found in close contact under natural conditions (personal observations made in  $5 \times 5$  cm plots) and it is unlikely that they can escape an attack by peers. We provided a “natural” refuge within the experimental arenas (large mussel) and recruits were observed underneath, so it is unlikely that lack of refuge elicited the cannibalistic behavior. As indicated above, alternative prey can also reduce predation/cannibalism in the field. Unfortunately, we know little about feeding preferences of recruits in the field, although small mussels, as well as amphipods, polychaetes and small limpets can be consumed by juveniles in the field. In our trials, recruits were fed before experiments and the duration of the trials was only 48 h. Therefore, it is unlikely that alternative prey would prevent attacks. Although predation/cannibalism are not the only sources of mortality of *Acanthocyclus* recruits, our results suggest that the combination of

intra- and inter-cohort cannibalism and predation of recruits by juveniles can potentially impose high post-settlement mortality, especially over the most abundant recruits.

Our results illustrate the complexity of mechanisms that can underlay patterns of distribution and relative abundances among competitors through different life stages, especially among coexisting species in which attacking peers can provide higher rewards later in development than just the energy obtained from other food. By quantifying rates of predation among the first cohorts of intertidal crabs we were able to evaluate the potential of predatory interactions to produce high mortality and limit effective recruitment to the adult population. Similar studies in other biological systems, where closely-related species coexist, are necessary to evaluate the generality of our results and improve our knowledge about the role of the different types of predation to establish and modify patterns of abundance and distribution in the field.

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## References

- Berryman, A.A., Hawkins, B.A., 2006. The refuge as an integrating concept in ecology and evolution. *Oikos* 115, 192–196.
- Broitman, B.R., Navarrete, S.A., Smith, F., Gaines, S.D., 2001. Geographic variation of southeastern Pacific intertidal communities. *Mar. Ecol. Prog. Ser.* 224, 21–34.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the Local Dynamics of Open Marine Populations. *Annu. Rev. Ecol. Syst.* 27, 477–500.
- Castilla, J.C., Luxoro, C., Navarrete, S.A., 1989. Galleries of the crabs *Acanthocyclus* under intertidal mussel beds: their effects on the use of primary substratum. *Rev. Chil. Hist. Nat.* 62, 199–204.
- Claessen, D., de Roos, A.M., Persson, L., 2000. Dwarfs and giants: cannibalism and competition in size-structured populations. *Am. Nat.* 155, 219–237.
- Diehl, S., 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68, 151–157.
- Eggleston, D.B., Armstrong, D.A., 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. *Ecol. Monogr.* 65, 193–216.
- Fernández, M., 1999. Cannibalism in Dungeness crab *Cancer magister*: effects of predator–prey size ratio, density, and habitat type. *Mar. Ecol. Prog. Ser.* 182, 221–230.



- Fernandez, M., Armstrong, D., Iribarne, O., 1993. First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. *Can. J. Fish. Aquat. Sci.* 50, 2100–2105.
- FitzGerald, G.J., 1992. Filial cannibalism in fishes: why do parents eat their offspring. *Trends Ecol. Evol.* 7, 7–10.
- Fox, L.R., 1975. Cannibalism in natural populations. *Annu. Rev. Ecol. Syst.* 6, 87–106.
- Gosselin, L.A., Qian, P.Y., 1996. Early post-settlement mortality of an intertidal barnacle: a critical period for survival. *Mar. Ecol. Prog. Ser.* 135, 69–75.
- Gosselin, L.A., Qian, P., 1997. Juvenile mortality in benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 146, 265–282.
- Hastings, A., Costantino, R.F., 1991. Oscillations in population numbers: age-dependent cannibalism. *J. Anim. Ecol.* 471–482.
- Holling, C.S., 1959a. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. *Can. Entomol.* 91, 293–320.
- Holling, C.S., 1959b. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* 91, 385–398.
- Hunt, H.L., Scheibling, R.E., 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 155, 269–301.
- Huss, M., van Kooten, T., Persson, L., 2010. Intra-cohort cannibalism and size bimodality: a balance between hatching synchrony and resource feedbacks. *Oikos* 119, 2000–2011.
- Jalali, M., Tirry, L., De Clercq, P., 2010. Effect of temperature on the functional response of *Adalia bipunctata* to *Myzus persicae*. *BioControl* 55, 261–269.
- Januario, S.M., Navarrete, S.A., 2013. Habitat selection during settlement in two intertidal predatory crabs that compete for refuges: implications for coexistence (in preparation).
- Keough, M.J., Downes, B.J., 1982. Recruitment of marine invertebrates: the role of active larval choices and early mortality. *Oecologia* 54, 348–352.
- Kneib, R.T., Lee, S.Y., Kneib, J.P., 1999. Adult-juvenile interactions in the crabs *Sesarma (Perisesarma) bidens* and *S. (Holometopus) dehaani* (Decapoda: Grapsidae) from intertidal mangrove habitats in Hong Kong. *J. Exp. Mar. Biol. Ecol.* 234, 255–273.
- Kurihara, Y., Sekimoto, K., Miyata, M., 1988. Wandering behavior of the mud-crab *Helice tridens* related to evasion of cannibalism. *Mar. Ecol. Prog. Ser.* 49, 41–50.
- Lovrich, G.A., Sainte-Marie, B., 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. *J. Exp. Mar. Biol. Ecol.* 211, 225–245.
- Luppi, T.A., Spivak, E.D., Anger, K., 2001. Experimental studies on predation and cannibalism of the settlers of *Chasmagnathus granulata* and *Cyrtograpsus angulatus* (Brachyura: Grapsidae). *J. Exp. Mar. Biol. Ecol.* 265, 29–48.
- Marshall, S., Warburton, K., Paterson, B., Mann, D., 2005. Cannibalism in juvenile blue-swimmer crabs *Portunus pelagicus* (Linnaeus, 1766): effects of body size, moult stage and refuge availability. *Appl. Anim. Behav. Sci.* 90, 65–82.
- Michaud, J.A., 2003. Comparative study of larval cannibalism in three species of ladybird. *Ecol. Entomol.* 28, 92–101.
- Moksnes, P.O., 2004. Self-regulating mechanisms in cannibalistic populations of juvenile shore crabs *Carcinus maenas*. *Ecology* 85, 1343–1354.
- Moksnes, P.O., Lipcius, R.N., Pihl, L., van Montfrans, J., 1997. Cannibal-prey dynamics in young juveniles and postlarvae of the blue crab. *J. Exp. Mar. Biol. Ecol.* 215, 157–187.
- Moksnes, P.O., Pihl, L., van Montfrans, J., 1998. Predation on postlarvae and juveniles of the shore crab *Carcinus maenas*: importance of shelter, size and cannibalism. *Mar. Ecol. Prog. Ser.* 166, 211–225.
- Murdoch, W.W., 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39, 335–354.
- Navarrete, S.A., Castilla, J.C., 1988. Foraging activities of Chilean intertidal crabs *Acanthocyclus gayi* Milne-Edwards et Lucas and *Acanthocyclus hassleri* Rathbun. *J. Exp. Mar. Biol. Ecol.* 118, 115–136.
- Navarrete, S.A., Castilla, J.C., 1990. Resource partitioning between intertidal predatory crabs – interference and refuge utilization. *J. Exp. Mar. Biol. Ecol.* 143, 101–129.
- Navarrete, S.A., Parragué, M., Wieters, E.A., 2008. Local and meso-scale patterns of recruitment and abundance of two intertidal crab species that compete for refuges. *Mar. Biol.* 155, 223–232.
- Oaten, A., Murdoch, W.W., 1975. Switching, functional response and stability in predator-prey systems. *Am. Nat.* 109 (967), 299–318.
- Palma, A.T., Steneck, R.S., Wilson, C.J., 1999. Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* 241, 107–136.
- Pardo, L.M., Palma, A.T., Prieto, C., Sepulveda, P., Valdivia, I., Ojeda, F.P., 2007. Processes regulating early post-settlement habitat use in a subtidal assemblage of brachyuran decapods. *J. Exp. Mar. Biol. Ecol.* 344, 10–22.
- Polis, G.A., 1980. The effect of cannibalism on the demography and activity of a natural population of desert scorpions. *Behav. Ecol. Sociobiol.* 7, 25–35.
- Polis, G.A., 1981. The evolution and dynamics of intraspecific predation. *Annu. Rev. Ecol. Syst.* 12, 225–251.
- Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annu. Rev. Ecol. Syst.* 20, 297–330.
- Posey, M.H., Hines, A.H., 1991. Complex predator-prey interactions within an estuarine benthic community. *Ecology* 72, 2155–2169.
- Rodríguez, S.R., Ojeda, F.P., Inestrosa, N.C., 1993. Settlement of benthic marine invertebrates. *Mar. Ecol. Prog. Ser.* 97, 193–207.
- Schausberger, P., 2003. Cannibalism among phytoseiid mites: a review. *Exp. Appl. Acarol.* 29, 173–191.
- Shanks, A.L., 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216, 373.
- Smith, K.N., Herrkind, W.F., 1992. Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *J. Exp. Mar. Biol. Ecol.* 157, 3–18.
- Sogard, S.M., 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull. Mar. Sci.* 60, 1129–1157.
- Sokal, R.R., Rohlf, F.J., 1995. *Biometry: The Principles and Practice of Statistic in Biological Research* (3 de.). W. H. Freeman and Company, New York (887 pp.).
- Sotomayor, J.F., Zamorano, J.H., 1985. Hábitos alimentarios de *Acanthocyclus gayi* Milne Edwards y *A. hassleri* Rathbun 1898 (Decapoda-Ateleyclidae), en el intermareal rocoso de Mehuin, Chile. *Medio Ambiente (Chile)* 7, 135–142.
- Ventura, R., Silva, U.A.T., Perbiche-Neves, G., Ostrensky, A., Boeger, W.A., Pie, M.R., 2008. Larval cannibalism rates in the mangrove crab *Ucides cordatus* (Decapoda: Ocypodidae) under laboratory conditions. *Aquac. Res.* 39, 263–267.
- Wieters, E.A., Salles, E., Januario, S.M., Navarrete, S.A., 2009. Refuge utilization and preferences between competing intertidal crab species. *J. Exp. Mar. Biol. Ecol.* 374, 37–44.
- Wise, D.H., 2006. Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Annu. Rev. Entomol.* 51, 441–465.