Journal of Experimental Marine Biology and Ecology 448 (2013) 85–92

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Strong intraspecific competition and habitat selectivity influence abundance of a coral-dwelling damselfish

Lisa Boström-Einarsson *, Mary C. Bonin, Philip L. Munday, Geoffrey P. Jones

School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia
ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

ARTICLE INFO

Article history:
Received 7 November 2012
Received in revised form 10 June 2013
Accepted 25 June 2013
Available online xxxx

Keywords:
Agonistic interactions
Behaviour
Competition
Crowding
Density-dependent mortality
Habitat degradation

ABSTRACT

Coral reef ecosystems are experiencing a global decline in coral cover, with direct effects on reef fishes. A decline in habitat may lead to crowding of live coral specialists into remnant habitat patches, intensifying intraspecific competition. Increased local densities of conspecifics are known to negatively affect key demographic processes, but the magnitude of density effects and the role of crowding in response to habitat loss are poorly understood. In this study we examined habitat use and relationships between habitat availability and population density in a coral-dwelling damselfish — *Chrysiptera parasema*. First, we conducted habitat use and availability surveys to establish the level of habitat selectivity. We then investigated the evidence for crowding due to habitat loss by comparing densities within juvenile aggregations on natural reefs with high and low cover of the preferred habitat. Finally, we used a manipulative patch-reef experiment to measure the potential effects of crowding on mortality of juvenile *C. parasema*. Surveys revealed that 97% of juvenile *C. parasema* were associated with *Acropora* corals. Furthermore, *C. parasema* densities were closely related to the cover of bottlebrush *Acropora*, the preferred growth form. Contrary to predictions, there was no evidence of crowding on natural reefs with low coral cover, but rather, reefs with abundant *Acropora* cover supported larger aggregations with double the density of juveniles. We hypothesized that low densities of *C. parasema* on natural reefs with low coral cover could be explained by intense intraspecific competition. Experimental manipulations showed that juvenile mortality was density-dependent, with mortality 20% higher on high-density experimental patch-reefs compared to low-density reefs. Behavioural observations on the patch-reefs revealed that the frequency of agonistic interactions and distance to shelter were both unrelated to conspecific densities, highlighting the need for further research into mechanisms underpinning density dependent mortality. These results suggest that intraspecific competition may play an important role in reducing reef fish abundance as a consequence of habitat loss. Given that coral reef systems are currently under threat, with a global decline in coral cover, this study adds to the growing body of knowledge of how disturbances to habitat may affect reef fish communities.

1. Introduction

Intraspecific competition for critical resources is an important mechanism of demographic density-dependence and may lead to higher mortality, reduced growth or lower fecundity with increasing density (Connell, 1983; Diamond, 1978; Schoener, 1983). However, population density and demographic rates can also directly vary in response to changes in the availability of resources, making density-dependent processes difficult to detect (so called 'cryptic density-dependence' sensu Shima et al., 2008). It is therefore critical to evaluate mechanisms of density-dependence in conjunction with the direct effects of limiting resources on population demography.

Many critical resources are provided by the physical habitat a species inhabits, and habitat loss has been implicated as the chief cause of species loss (Fischer and Lindenmayer, 2007). Direct loss of habitat is often concomitant with the fragmentation and reconfiguration of the landscape (Caley et al., 2001; Fahrig, 1997). This breaking apart of continuous habitat into smaller patches often results in a temporary increase in densities, dubbed the 'crowding effect' (Debinski and Holt, 2000) as individuals crowd into remnant patches of suitable habitat. Habitat degradation has been shown to exacerbate intraspecific competition across a range of ecological systems and organisms, (Caley et al., 2001; Coker et al., 2012; Eggleston et al., 2005; Ford et al., 2001; Luiselli, 2006; Stella et al., 2011) although few studies have directly linked this to the crowding effect (but see: Foster and Gaines, 1991; Schmiegelow and Machtans, 1997; Bender and Fahrig, 2005). The potentially complex relationships between competition

* Corresponding author at: School of Marine and Tropical Biology, James Cook University, Townsville, QLD 4811, Australia. Tel.: +61 402379935.
E-mail addresses: lisa.bostromeinarsson@my.jcu.edu.au (L. Boström-Einarsson), mary.bonin@jcu.edu.au (M.C. Bonin), philip.munday@jcu.edu.au (P.L. Munday), geoffrey.jones@jcu.edu.au (G.P. Jones).

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http://dx.doi.org/10.1016/j.jembe.2013.06.017

and habitat availability must be unravelled in order to understand how habitat loss threatens the persistence of natural populations.

Although density-dependent processes have been extensively studied in coral reef fishes, their role in population regulation has historically been controversial (see reviews by Sale, 1980; Doherty and Williams, 1988; Doherty, 1991; Jones, 1991; Hixon and Webster, 2002; Hixon et al., 2012). A lack of evidence for density-dependence in early studies of adult populations led to the theory that community structure is a dynamic response to stochastic recruitment into a space-limited environment (*lottery-hypothesis*) (Sale, 1974, 1977, 1978, 1979). Later it was argued that recruitment is generally too low for significant density-dependence, and populations fluctuate in response to recruitment variability (*recruitment limitation-hypothesis*) (Doherty and Fowler, 1994; Victor, 1983). Nevertheless, considerable evidence for density-dependence has accumulated over several decades of research (see reviews by Jones, 1991; Hixon and Webster, 2002; Jones and McCormick, 2002; Hixon et al., 2012). The historical debate has evolved into a more pluralistic view that both density-dependence and independence can operate on the same demographic parameters and that both are important in limiting populations.

Negative density-dependent effects have been documented for all vital demographic rates in coral reef fish populations, including effects on growth (Booth, 1995; Jones, 1991), fecundity (Hixon and Jones, 2005; Winemiller and Rose, 1992) and mortality (Beukers and Jones, 1998; Bonin et al., 2009; Forrester, 1990; Forrester et al., 2006; Hixon and Webster, 2002; Jones, 1987a; Samhouri et al., 2009; Schmitt and Holbrook, 1999; Shima, 2001). Unexpectedly, there have also been a number of studies finding inverse or positive density-dependence, where survival or fitness increases in the presence of higher densities of conspecifics (Booth, 1995; Sandin and Pacala, 2005; White, 2011). This has been attributed to behavioural mechanisms, such as increased vigilance in larger groups associated with patches of shelter.

Detection of density dependence largely depends on the spatial and temporal scales investigated, which has led to contrasting outcomes, sometimes in the same study system and with the same species (e.g. Caselle, 1999; Sandin and Pacala, 2005). Due to this, our understanding of the conditions under which density-dependent processes operate in reef fish populations is an unresolved issue, yet it has increasing importance for the management and conservation of fish populations as the quality of reef habitats continues to decline worldwide (Hixon and Webster, 2002; Jones et al., 2004; Pratchett et al., 2008; White, 2011; Wilson et al., 2006).

The available evidence suggests that intraspecific competition is likely to be a particularly important source of density-dependence in coral reef fishes, with a number of experimental studies demonstrating negative effects of conspecific density on growth rates (Buchheim and Hixon, 1992; Hixon and Jones, 2005; Jones, 1987b, 1988; Thompson, 2005) and mortality (e.g. Almany, 2003; Hixon and Jones, 2005; Holbrook and Schmitt, 2002; Johnson, 2008; Samhouri et al., 2009; Webster, 2003, 2004). Given that overlap in resource use is often greater between individuals of the same species than between species, the strength of intraspecific competition is often assumed greater than interspecific competition (Chesson, 2000). Consequently, growth effects due to intraspecific competitors generally appear to be greater than those of interspecific competitors (Forrester et al., 2006; Jones, 1991).

Although predation is usually the agent of mortality (Hixon and Jones, 2005), intraspecific competition for shelter space from predators may often be the ultimate cause of density-dependent mortality (Buchheim and Hixon, 1992; Hixon and Beets, 1993; Hixon and Webster, 2002; Jones and McCormick, 2002). Engaging in competitive interactions inevitably carries a metabolic cost, with less energy available for other activities such as growth and reproduction (e.g. Booth, 1995; Munday, 2001). Reduced growth can affect the demography of a population in two ways. Firstly, given that fecundity and age of mortality in reef fishes is often size based, smaller fish will contribute less to population growth (Jones and McCormick, 2002). Secondly, smaller fish are more vulnerable to predation from predators with a large range of gape sizes (Steele and Forrester, 2002; Werner and Gilliam, 1984). They are likely to remain in vulnerable size classes for longer if they are subjected to high levels of competition. Where such factors operate, competition is likely to be an important source of density-dependent mortality for coral reef fishes (Sogard, 1997).

For species of reef fish that are specialised on live coral there is often a strong correlation between their abundance and the availability of preferred coral habitats (Ault and Johnson, 1998; Bell and Galzin, 1984; Jones et al., 2004; Munday et al., 1997; Pratchett et al., 2006; Wilson et al., 2006). Declining coral cover has been shown to lead to dramatic declines in the abundance of coral-dwelling reef fishes (Halford et al., 2004; Jones and Syms, 1998; Jones et al., 2004; Munday, 2004; Wilson et al., 2006), but the biological interactions and demographic mechanisms responsible for these declines are not well understood. Coral loss and increasing fragmentation are likely to initially lead to crowding in surviving coral fragments, potentially increasing the intensity of intraspecific competition (McCormick et al., 2010). Although increased densities have been documented to negatively affect key demographic processes, we know relatively little about crowding of conspecifics in response to habitat change and any mechanisms underpinning crowding responses in coral reef systems.

The overall aim of this study was to examine the roles of intraspecific competition and the availability of preferred habitat in the demography of a coral reef fish species. The study focuses on *Chrysiptera parasema* (Fowler 1918), a coral-dwelling damselfish (Pomacentridae) and builds on previous work using damselfish as a model group for experimentally evaluating competitive interactions in coral reef fishes (Bonin et al., 2009, 2011; Hixon and Jones, 2005; Jones, 1987a,b, 1988; Limbourn et al., 2007). The study links a descriptive study of natural aggregation densities on a range of densities to an experimental study of intraspecific competition, providing a holistic view of responses to habitat change amongst coral reef associated damselfishes. The specific goals were to: (1) identify the preferred coral habitat occupied by *C. parasema* and describe the relationship between fish density and the availability of preferred corals. (2) Compare the densities within juvenile aggregations with the percent cover of their preferred live coral habitat on natural reefs at the study site to test if declining coral cover leads to permanent crowding within remaining patches of live coral. (3) Undertake a manipulative experiment to test for effects of intraspecific competition on mortality within *C. parasema* groups. The experiment was coupled with behavioural observations to identify potential mechanisms that underpinned the results from the manipulative experiment.

2. Methods

2.1. Conspecific densities and habitat associations

C. parasema is a live-coral dwelling planktivorous damselfish (max. size ~5 cm), which frequently occurs in large adult aggregations. More tightly clustered juvenile groups occur within these aggregations. Aggregations tend to be clustered over distinct coral morphologies, with little movement between preferred habitat patches. Patterns of habitat use, availability and densities within aggregations were quantified on eight nearshore platform reefs with resident populations of *C. parasema*. Reefs were located in the Kilu–Tamare section of Kimbe Bay, Papua New Guinea (5°25′S, 150°05′E). Kimbe Bay is located within the Coral Triangle, the centre of diversity for scleractinian corals, in particular members of the genus *Acropora* (Wallace, 1999). Reefs were all located < 1 km from shore and were separated from each other by a minimum of 200 m of deep water (depths exceeding 50 m), and were considered independent of each

other. Reef sites were obliquely exposed to wave action and were characterised by gentle slopes from the reef crest (depth ~2 m) towards a sandy bottom (~30 m). Reef sites were haphazardly selected with a range of coral cover (35–65% hard coral cover, 1–24% *Acropora* cover). The similar characteristics between reefs in terms of slope and exposure suggest that any differences in community composition of corals are likely to be a result of previous habitat degradation and disturbances in the past. On each reef a 500 m^2 quadrat (10 × 50 m) was established on the reef slope, with the depth within the quadrat ranging from 6 to 12 m. The large size of the quadrat was designed to capture continuous patches of preferred habitat, and the aggregations of *C. parasema* that inhabit them.

Recruitment of reef fishes within Kimbe Bay is continuous throughout the year, with a steady supply of fish larvae entering reefs around each new moon. Since *C. parasema* juveniles form distinct high-density aggregations within the more diffuse adult aggregation, and many density dependent processes are likely to be particularly strong in the early post-recruitment stage, the focus of this study was recently recruited (~within approximately 3 weeks) juveniles. All *C. parasema* juveniles (<20 mm) were counted within the quadrat area to estimate population density. In order to determine aggregation densities, juvenile *C. parasema* aggregations were observed for approximately 1 min to determine outer boundaries of the aggregation. To estimate the habitat patch area used by each aggregation, the height (defined as the longest diameter of the area), and width (at the midpoint perpendicular to the height axis) of each aggregation habitat were measured to the nearest centimetre. The area of the patch of habitat supporting an aggregation was calculated as width × height. Two types of juvenile density were calculated; the overall density in the quadrat (individuals per 500 m^2) and an aggregation density (individuals per patch). These densities were expressed as individuals per m^2 for ease of comparison with experimental densities.

Habitat use of *C. parasema* juveniles was quantified by recording the coral type directly under each individual. Corals were identified to genus level, and growth forms described for *Acropora* and *Porites* genera (using coral morphologies outlined in Jackson, 1979; Wallace, 1999). To estimate the availability of different habitat types, 50 m transect tapes were laid at 6, 9, and 12 m within each quadrat. Benthic composition was then quantified using a point intercept method in which each 50 m transect tape was marked with 100 random points and the habitat type directly under each point was recorded. Percent coverage of each category was calculated for each depth and then pooled across depths to provide estimates of percent cover that were representative of the 500 m^2 survey area.

Microhabitat selectivity by juvenile *C. parasema* was analysed using resource selection ratios (Manly, 2002;). Selection ratios ($\hat{w}_I = o_i/\pi_i$) were calculated for 15 categories of microhabitat, where o_i is the proportion of recruits recorded in category i, and π_i is the proportion of microhabitat i available in the quadrat. Microhabitat data was then pooled across the range of sites and depths surveyed, to provide an overall estimate of habitat use. A Bonferroni corrected 95% confidence interval was calculated around each selection ratio, using the formula $z_{\alpha/2I}\sqrt{\{o_i(o_i-1)/(u_+\pi_i^2)\}}$, where $\alpha = 0.05$, I = number of microhabitat categories and u_+ = total number of recruits recorded (Manly, 2002). Confidence intervals containing the value 1 indicate that a microhabitat is used in proportion to its availability, while intervals which span values greater or less than 1 indicate that a microhabitat is used more or less, respectively, than expected by its availability in the study area.

Linear regression was used to examine the relationship between the density of juvenile *C. parasema* (per 500 m^2 survey area) and the percent cover of live coral habitat within the sampling area. As results from previous studies suggest that *C. parasema* prefer *Acropora* microhabitats (Bonin et al., 2009; Srinivasan, 2003), the pooled percent cover of all *Acropora* spp. was used in this analysis. Densities within aggregations were calculated as number of individuals per square metre of aggregation area. Another linear regression then examined the relationship between the density of *C. parasema* within aggregations and percent cover of *Acropora*. Densities within aggregations were log-transformed to better meet the assumptions of General Linear Models, but are presented in figures untransformed for ease of interpretation. Two reefs with low percentage *Acropora* did not sustain any aggregations of juveniles, and were therefore excluded from the regression analysis, but included in figures for comparison. Using these two analyses it was possible to determine whether *C. parasema* densities are associated with the cover of live coral and if declining coral cover causes crowding within remaining coral patches.

2.2. Experimental density manipulation

An experiment in which densities were manipulated was carried out to test for effects of intraspecific competition on mortality in juvenile *C. parasema*. An array of 15 identical patch-reefs was constructed on a large sandy area near the natural reefs where density and habitat associations had been observed. Experimental patch-reefs were constructed approximately 100 m away from the shore and were separated from each other by 15 m and from natural reefs by at least 20 m. Each reef consisted of a coral-rubble base topped with live 0.5 m^2 of *Acropora longicyathus* (bottlebrush growth form). In Kimbe Bay, bottlebrush *Acropora* forms extensive fields of continuous coral, however juvenile *C. parasema* form tight aggregations that use only a relatively small proportion of available habitat (average size, from this study, = 0.23 m^2 of habitat per juvenile aggregation). At the time of stocking the experimental reefs, juveniles at the lower end of stocking densities would not be limited for space, however space would increasingly become limited with increasing numbers. Juvenile *C. parasema* (13–20 mm) were collected from nearby reefs using diluted clove oil (Munday and Wilson, 1997) and hand nets.

The manipulation of juvenile densities followed a regression design with initial densities on patch-reefs (n = 15) ranging from 20 to 120 *C. parasema* per m^2. This approach allows the detection of a functional relationship between survival and conspecific densities across a range of naturally occurring densities (Forrester, 1995). There was no significant difference in total length (TL) between reefs of a random sample of 5 individuals measured from each reef (ANOVA $F_{(11,48)} = 1.7$, $p = 0.09$). Juveniles were allowed to recover for approximately 24 h from collection and handling and then released on patch-reefs. Individuals placed on reefs represented a random and novel collection of individuals with no reference to aggregation membership prior to collection. Any resident predators were removed from the reefs before stocking. An observer remained near the reef for approximately 10 min following release of juveniles to keep transient predators from exploiting the newly transplanted *C. parasema*'s unfamiliarity to the new habitat. Additional juvenile *C. parasema* were supplemented in the first few days to maintain density treatments until they stabilised. Reefs were then monitored every two days for the first three weeks of the experiment period to detect and remove any new *C. parasema* recruits, distinguished by their size and bright colouration. A total of only 5 new recruits were recorded at the patch reefs, and recruitment is therefore concluded to have a negligible effect on the outcome of the experiment. The experiment ran for 60 days between May and August 2011. At the conclusion of the experiment (day 60) reefs were monitored and all remaining fish were recaptured and counted. Three reefs suffered catastrophic loss of structure and coral cover (through anchor damage and sinkholes) reducing the total number of reefs to 12.

Nearby natural reefs (which lacked populations of *C. parasema*) were searched approximately twice weekly for any *C. parasema* that had emigrated from the patch-reefs, but none were found, suggesting

that any emigration from the patch-reefs resulted in mortality. Losses from the patch-reefs have consequently been classed as mortality. In order to investigate the effects of intraspecific competition on juvenile survival, the mortality of *C. parasema* on each patch reef was plotted against initial stocking density and analysed using linear regression. Densities on 0.5 m^2 patch-reefs are expressed as individuals per m^2 for ease of comparison between observational and experimental data.

Predators observed around the patch-reefs were counted to determine whether they aggregate around high-density patches. Six separate counts of predators observed at each patch reef were conducted over the two-month experimental period. Counts were conducted between 8 am and 12 pm and therefore represent a measure of non-cryptic diurnal predators. Crepuscular and nocturnal predators were not included in the counts. Predators were identified to genus level and grouped into two size classes; large (>100 mm) and small predators (<100 mm). Large predators included roving species such as *Caranx* spp. (Carangidae) and *Lethrinus* spp. (Lethrinidae), while the smaller size class was dominated by juvenile *Lutjanus* spp. (Lutjanidae). Linear regression was used to evaluate whether there was a relationship between numbers of small and large predators present on patch-reefs (dependent variable) and the density of *C. parasema* on the patch-reefs (independent variable).

2.3. Behavioural observations

To evaluate potential mechanisms causing density-dependent effects observed in the manipulative experiment, behavioural observations of juvenile *C. parasema* were undertaken at the end of the experiment; agonistic interactions and distance from shelter were recorded by an observer situated 2 m from the reef. Fish were allowed to become accustomed to the presence of the observer for 1 min before behaviours were scored. Agonistic interactions (defined as a nip or chase) were recorded during a six-minute period following the acclimation period. Distance to shelter was then estimated for three haphazardly selected individuals on each reef. Since outcomes of competitive interactions are often size based, focal individuals were chosen to include the size range of juveniles on each reef (i.e. small, intermediate, and large individuals on each reef). Distance to nearest shelter (defined as coral structure) was recorded every 15 s during 1 min giving a mean distance to shelter for each fish. The same observer conducted all surveys to avoid observer bias, and frequently calibrated distance measures by estimating the distance between two fixed points and comparing with measured distance. Behavioural data (agonistic interactions and distance to shelter) were plotted against the density of conspecifics on the day of observation to examine potential mechanisms leading to density-dependent mortality. This density was used (instead of initial stocking density) under the assumption that behaviours are affected by current densities and not by "ghosts of competition past" (Connell, 1980).

Assumptions of normality, linearity and homogeneity of residuals were evaluated using residual plots for all regression analyses. No violations of assumptions were found and data is presented untransformed.

3. Results

3.1. Conspecific densities and habitat associations

A total of 1387 juvenile *C. parasema* within 71 aggregations were observed across the eight reefs surveyed. Juvenile *C. parasema* were almost exclusively (97.7% of observations) associated with live coral from the genus *Acropora* (Fig. 1). Furthermore, nearly all individuals (92.2%) were associated with the bottlebrush growth form. *C. parasema* juveniles were observed inhabiting bottlebrush *Acropora* significantly more often than expected based on the availability of that microhabitat, while branching *Porites* and other hard corals were avoided (Fig. 1).

Densities of juvenile *C. parasema* exhibited a close linear relationship with percent cover of *Acropora* corals ($R^2 = 0.92$, $F_{(1,6)} = 66.67$, $p < 0.001$) at the reef scale (Fig. 2). Reefs with approximately 20% *Acropora* cover ($n = 2$) supported almost five times higher overall densities of *C. parasema* juveniles than reefs with approximately 10% *Acropora* cover ($n = 6$).

Densities within juvenile aggregations ($n = 71$) on these reefs spanned 16–555 juveniles per m^2. Contrary to the prediction that crowding might occur on reefs with low coral cover, densities of juvenile *C. parasema* within aggregations did not increase as coral cover declined at the reef scale. Instead, aggregation densities were higher on reefs with a high percent *Acropora* cover (Fig. 3) and were positively related with percent *Acropora* cover ($R^2 = 0.10$, $F_{(1,69)} = 7.8$, $p = 0.007$). There was a high degree of variability in the density of aggregations between reefs, with the amount of variability increasing with increasing *Acropora* cover. Nevertheless, the mean density of *C. parasema* within aggregations on the reef with highest *Acropora* cover (24.2%) was approximately double that of the site with the lowest *Acropora* cover (3.1%) that still supported aggregations of juveniles.

3.2. Experimental density manipulation

Density-dependent mortality was observed amongst juvenile *C. parasema* on the experimental patch-reefs, with mortality increasing linearly with stocking density (Fig. 4) ($R^2 = 0.45$, $F_{(1,10)} = 8.1$, $p = 0.02$). Reefs with 100–120 juveniles per m^2 suffered up to 50% mortality while reefs stocked with less than 40 conspecifics per m^2 had approximately 30% mortality. Each patch-reef was visited by an average of 0.86 ± 0.2(SE) large and 10.96 ± 2.4(SE) small predators. There was no significant relationship between either large ($R^2 = 0.06$, $F_{(1,10)} = 0.67$, $p = 0.43$) or small ($R^2 = 2.6^{-5}$, $F_{(1,10)} = 2.6^{-4}$, $p = 0.99$) predators and the density of *C. parasema*, indicating that predator abundance was unaffected by the number of individuals on each patch-reef.

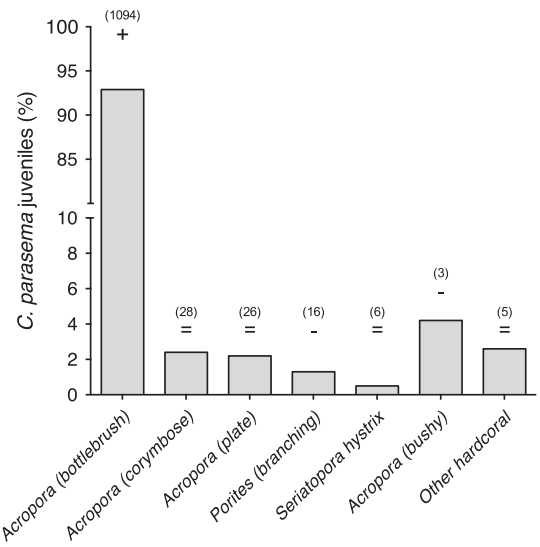

Fig. 1. Percentage of *C. parasema* juveniles in each of 15 microhabitat categories (arranged with increasing availability along the x-axis). A (+) indicates a microhabitat used more frequently than expected by its availability, (−) indicates a microhabitat used less frequently than expected by its availability, (=) indicates a habitat used in proportion to its availability. Numbers above bars indicate the total number of juveniles recorded in that microhabitat. Microhabitat present in surveys but not used by *C. parasema* juveniles includes *Acropora* (staghorn and digitate), other hard coral (massive, foliose and encrusting growth morphologies), sponges/softcorals, algae (macro, turf, coralline), bare rock, sand, rubble and dead coral. Note break and different scale in the y-axis.

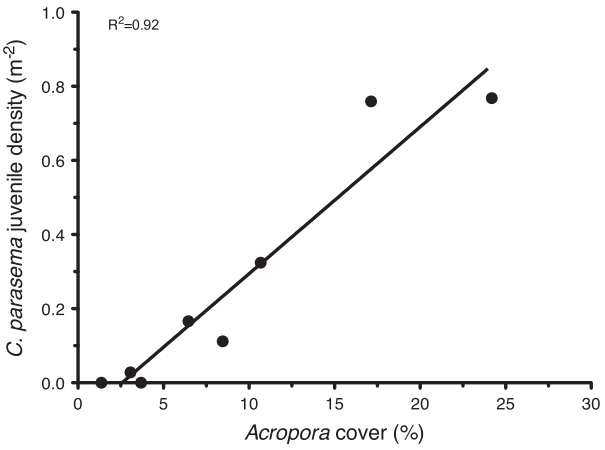

Fig. 2. Relationship between the density of *C. parasema* juveniles (per m^2) in 500 m^2 quadrats and the availability of preferred coral habitat (*Acropora* spp.) on 8 survey reefs in Kimbe Bay, Papua New Guinea.

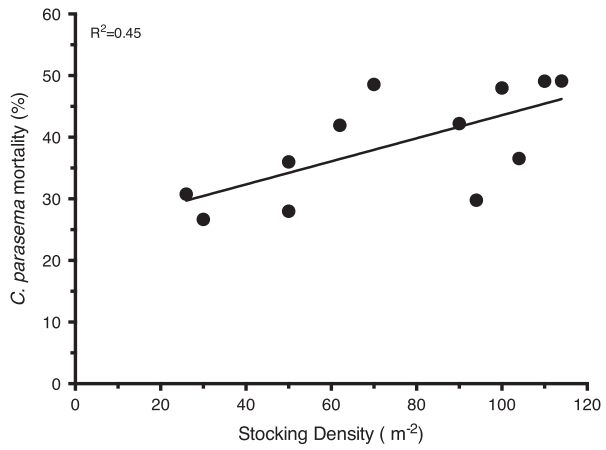

Fig. 4. The relationship between the mortality of *C. parasema* after 60 days and the stocking density of juveniles per patch reef (expressed per m^2 for ease of comparison).

3.3. Behavioural observations

Agonistic interactions were uncommon amongst *C. parasema* juveniles, with the average individual experiencing one agonistic interaction approximately every 10 min. Furthermore, per capita agonistic interactions were not associated with the density of conspecifics (Fig. 5). Similarly, there was no relationship between the density of individuals on reefs and the average distance to shelter (Fig. 6). *C. parasema* juveniles remained close to shelter at all times, with 80% remaining within 5 cm from coral structures.

4. Discussion

In this study the density of *C. parasema* exhibited a strong relationship with the availability of preferred habitat. However, there was no evidence for increased crowding within individual aggregations on reefs with low coral cover. In fact, it was reefs with abundant *Acropora* cover that supported larger and more densely packed aggregations of juvenile *C. parasema*. The density manipulation clearly showed that intraspecific competition causes density-dependent mortality in *C. parasema*. Consequently, intraspecific competition on remnant preferred habitat patches is one mechanism that could clearly explain the lower densities observed on reefs with little suitable habitat. While crowding may occur initially, we argue that competition for shelter and increased mortality may rapidly reduce numbers as habitat declines.

This study supports an increasing body of evidence that density-dependent mortality is a factor regulating coral reef fish populations (Forrester, 1995; Hixon and Jones, 2005; Samhouri et al., 2009; Shima, 2001). When subjected to increasing densities of conspecifics, intraspecific competition over habitat caused negative density-dependent mortality in *C. parasema*. There was no evidence for inverse density-dependence, such as described in other gregarious species (Booth, 1995; Sandin and Pacala, 2005). White et al. (2010) have argued that density-dependent mortality at a patch-reef scale is likely to be observed in non-social, non-aggregating species driven by competition over shelter space. The authors argue however that socially aggregating species benefit from predation risk dilution, and should therefore be inversely (positively) density-dependent at the patch-reef scale, while negatively density-dependent at larger spatial scales. Despite the fact that our study was investigated at a patch-reef scale, using socially aggregating species, no positive effects of density were observed. Our results mirror those of a recent temperate reef fish study, where potential positive and negative effects of increasing conspecific densities were teased apart. Similar to this study it was demonstrated that competition over food and shelter overshadowed benefits of group living (Ford and Swearer, 2013).

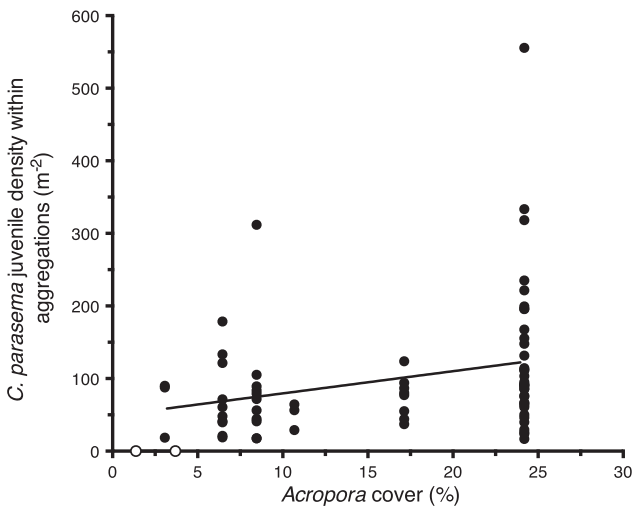

Fig. 3. The relationship between density of *C. parasema* (per m^2) within aggregations and availability of preferred coral habitat (*Acropora* spp.) on eight survey reefs in Kimbe Bay, Papua New Guinea. Black symbols include the six reefs that sustained juvenile aggregations, while white symbols represent two reefs lacking *C. parasema* juveniles. These two reefs have not been included in the analysis, but are presented here for clarity.

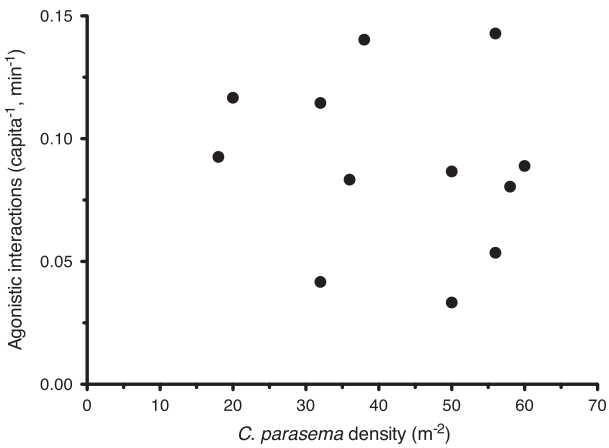

Fig. 5. The number of agonistic interactions (per capita, min^{-1}) of *C. parasema* versus conspecific density (expressed per m^2 for ease of comparison).

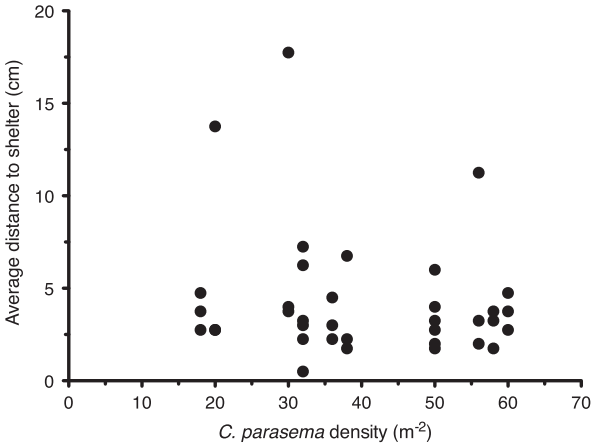

Fig. 6. The average distance to shelter of *C. parasema* focal individuals versus the density of conspecifics (expressed per m^2). N = 36.

In contrast to our results, strong negative effects of density on survival were not evident amongst juvenile *C. parasema* in a previous study. Instead, Bonin et al. (2009) described a slight, albeit not statistically significant, positive influence of increased density of conspecifics. Their study used similarly sized patch reefs but markedly lower treatment densities (i.e. 8–32 individuals/m^2) compared to the present study. It may be that effects of conspecific density are non-linear. At very low densities, populations suffer from the loss of cooperative interactions and facilitation from conspecifics (Courchamp et al., 1999). As densities start increasing (up to 32 individuals/m^2), so does the potential benefits of aggregating behaviour in juvenile *C. parasema* (e.g. Bonin et al., 2009). Finally, with further increases in densities described in this study (up to 120 individuals/m^2) the negative effects of intraspecific competition over resources ultimately result in density dependent mortality patterns. Populations displaying this type of bimodal relationship between survival and density are exhibiting the "Allee effect" (Allee and Bowen, 1932). Given the global decline in coral cover and subsequent loss of reef-associated fishes, the presence of Allee effects in populations has important implications to conservation efforts.

Although competition may be the underlying cause, predation is often the agent of density-dependent mortality in reef fishes (Hixon, 1991; Hixon and Jones, 2005). We found no evidence that transient predators were aggregating around high-density patch-reefs in our experiment, a key mechanism that can cause density-dependent mortality. Instead, predators were observed visiting patch-reefs independently of the density of fish, thus reducing the per capita risk of predation in our study species.

It should be noted, however; that these predator counts represent a subset of the total predator community likely to be visiting the reefs, since nocturnal/crepuscular predators as well as any transient predators that avoid scuba divers are not included in the estimates.

Behavioural traits such as aggression or distance from shelter could influence vulnerability to predators and also potentially explain the density-dependent mortality observed for *C. parasema*. Conspecific density has been shown to affect behaviours such as aggression rates (Forrester et al., 2006), feeding rates (Connell, 2002), foraging positions (Whiteman and Cote, 2004) and habitat use (Laurel et al., 2004) in other reef fishes. Increased aggression with density has often been proposed as a mechanism underlying density-dependent mortality in reef fishes because it may reduce predator vigilance (e.g. Carr et al., 2002). However, in this study we found no evidence for increased aggression at higher densities, despite strong density-dependent mortality. Moreover, juvenile *C. parasema* remained in close proximity to shelter (i.e. within 5 cm) regardless of conspecific density, which indicates that higher conspecific densities on a habitat patch do not push individuals further from shelter during normal daily activities. Although one of the most common causes of density-dependent mortality is competition for shelter space (Chesson, 2000; White et al., 2010) possible alternative mechanisms include exploitative competition for food (e.g. Booth, 1995; Munday, 2001; Steele and Forrester, 2002) or increased disease and parasitism in high density populations (Finley and Forrester, 2003; Forrester and Finley, 2006). Our findings suggest that increased aggression and access to shelter space were unlikely to be the underlying mechanisms, and further research is needed to elucidate alternative ways in which increased conspecific density could lead to decreased juvenile survivorship.

Densities within natural aggregations may be the most appropriate scale for assessing the local competitive conditions experienced by juvenile *C. parasema*. Intuitively, a coral-dwelling species would be particularly vulnerable to changes in the availability of its preferred habitat (Pratchett et al., 2008; Wilson et al., 2008). Within aggregations, densities may increase following habitat degradation as individuals crowd into the remaining suitable habitat (McCormick et al., 2010). This type of crowding following habitat degradation has been described in many terrestrial communities (Debinski and Holt, 2000). The 'crowding effect' is usually transient and densities subsequently drop down to a level sustainable in the remaining habitat (Grez et al., 2004), indicating that a new carrying capacity has been set. In a recent marine example, Coker et al. (2012) found that the damselfish *Dascyllus aruanus* would vacate dead coral colonies and attempt to relocate to nearby healthy habitat. In cases where adjacent live coral colonies were inhabited by a conspecific, only the dominant competitor would be allowed to remain, usurping the subordinate individual.

In this study, our initial hypothesis was that habitat degradation would cause crowding in aggregations. It follows that densities within aggregations would decrease with increasing availability of habitat. However, the results from this study indicate the inverse relationship for *C. parasema*; with five times higher densities at the reef with highest cover of *Acropora*, compared to the reef with lowest densities that still maintained juveniles. The low densities on small remnant habitat patches could be a result of two non-mutually exclusive mechanisms. Firstly, the distribution of *C. parasema* from this study may reflect the outcome of past competitive interactions, brought on by an initial transient crowding. This temporary crowding mediated by competitive interactions has been described in terrestrial systems (Debinski and Holt, 2000; Grez et al., 2004) and represents an adjustment of the carrying capacity of the environment. Secondly the higher densities of juvenile *C. parasema* in areas of higher coral cover may be driven by selective recruitment or post-recruitment persistence. In our study, the increasing variability of densities within aggregations with increasing availability of preferred habitat supports the hypothesis of an adjusted carrying capacity. On reefs where juveniles are not limited by habitat availability, we would expect a range of densities to occur due to natural variability in recruitment and survival. On degraded reefs, however; we would expect variability to decrease as densities are capped by limited habitat availability. Finally, in this study, two reefs with some of the lowest percent *Acropora* cover did not support any juvenile *C. parasema*, which further support the profound effect of limited habitat availability on juvenile abundance and density. Although the particular resource accessed by *C. parasema* from live coral habitat remains unknown, it is evident that the loss of critical habitat is likely to have devastating effects to the persistence of this species.

Observations of habitat use revealed that juvenile *C. parasema* are highly reliant on corals from the genus *Acropora*, in particular the structurally complex bottlebrush growth form. Over 90% of juveniles surveyed were found on bottlebrush *Acropora*, indicating a strong preference for this type of complex habitat in the early post-settlement phase. The results are in concordance with previous studies of *C. parasema*, where similar patterns of habitat use have been described. Srinivasan (2003) found 99.5% of *C. parasema* recruits

settling on *Acropora* corals, while Bonin et al (2009) showed that 72% of recruits use corymbose or bottlebrush growth forms of *Acropora*.

The abundance of *C. parasema* would clearly be susceptible to a decline in *Acropora* habitat, due to their strong preference to this microhabitat type (Bonin, 2012). Given that *C. parasema* are unlikely to migrate long distances in search of new habitat, and in light of the density-dependent mortality observed in the patch reef experiment, it is likely that a transient 'crowding effect' is followed by a decline in *C. parasema* abundance regulated by intraspecific competition. This is further reflected in a recent experiment investigating the effects of habitat loss and fragmentation on *C. parasema* by Bonin et al. (2011). When comparing reefs with 75% habitat loss, fragmented reefs resulted in significantly higher survivorship than reefs with remaining habitat intact. This was attributed to a reduction in competitive interactions in fragmented habitat (Bonin et al., 2011).

In conclusion, our results have demonstrated a strong association between *C. parasema* and a single growth form of coral. Reefs with high availability of preferred live coral supported the highest densities of juveniles, while degraded reefs supported markedly smaller aggregations. Intraspecific competition within coral patches and consequent density-dependent mortality may contribute to this pattern. The high degree of specialisation and intense competition over the resources this habitat provides, indicate that *C. parasema* will be highly vulnerable to habitat loss. While juveniles do not appear to persist in crowded conditions at low coral cover, the behavioural mechanisms reducing numbers at low coral cover require further investigation. Given that intraspecific competition causes density-dependent mortality, it is likely that any crowding in natural reefs following habitat degradation will be stabilised through competitive interactions, down to a level sustainable by the available habitat (i.e. a new carrying capacity). This study adds to the growing body of knowledge of how density dependent processes affect the demography and persistence of species in times of rapid global decline in coral cover.

Acknowledgements

We are grateful to E. Gerard, M. Giru and J. Atherton for their assistance in the field, as well as to Mahonia Na Dari Research and Conservation Centre and Walindi Plantation Resort for logistical support for the duration of the project. Comments from two anonymous reviewers greatly improved the manuscript. This project was funded by the Australian Research Council through the Centre of Excellence for Coral Reef Studies, and the School of Marine and Tropical Biology, James Cook University. **[RH]**

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