Habitat degradation modifies the strength of interspecific competition in coral dwelling damselfishes

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Abstract. Habitat degradation is predicted to exacerbate competition for critical resources; however, the relationship between habitat quality and competition is poorly understood. In this study, we used a manipulative experiment to test the effects of habitat degradation on competition between two planktivorous, coral-dwelling damselfishes, *Chrysiptera parasema* and *Dascyllus melanurus*. Experimental reefs were constructed with either healthy (100% live) or degraded (10% live) *Acropora longicyathus* coral, stocked with varying densities of these two fish species, and monitored for two months. On healthy habitat, the mortality of *C. parasema* was density dependent, and increased substantially in the presence of the dominant interspecific competitor *D. melanurus*. In contrast, on reefs where habitat was degraded, *C. parasema* mortality was highly variable, density independent, and was no longer influenced by the presence of dominant competitor *D. melanurus*. Behavioral observations revealed that agonistic interactions for both species increased with density on degraded habitat, but not on healthy habitat. In addition, on degraded reefs, both species displayed a reduced association with reef habitat and ventured further away from shelter with increasing densities of the dominant competitor *D. melanurus*. These results suggest that reduced habitat quality can have such a profound effect on reef fishes, that it eliminates density-dependent mortality and competitive dominance hierarchies, thereby substantially altering the mechanisms that structure reef fish communities.

Key words: agonistic behavior; Chrysiptera parasema; *coral reef fishes; damselfish;* Dascyllus melanurus; *density dependence; habitat degradation; habitat loss; interspecific competition; intraspecific competition.*

Introduction

Competition is the interaction among individuals of the same or different species for finite resources and is a fundamental process shaping many ecological communities (Connell 1978). As a primary mechanism of density dependence, competition can regulate populations and influence community structure by governing the demographic parameters (e.g., mortality, growth, and fecundity) that ultimately determine the abundance of each species in a community (Cappuccino 1995). Complex heterogeneous habitats (e.g., tropical rainforests, coral reefs) support remarkably diverse ecological communities, presumably, because they offer such an abundance of resources that even species with similar resource requirements can successfully compete. The degradation and loss of natural habitats alters resource quality and availability, and numerous studies have documented dramatic shifts in species abundance and diversity as a consequence (e.g., Ford et al. 2001, Scott et al. 2006, Wilson et al. 2006). Although competition over changing resources is likely to play an important role in

causing these shifts, our understanding of how habitat degradation influences the outcomes of intra- and interspecific competition is limited.

Habitat degradation could potentially affect competition in a number of different ways. A higher degree of resource limitation in degraded habitats could intensify the effects of both intra- and interspecific competition, and, in the case of interspecific competition, it could result in the dominant species completely excluding the subordinate (Griffis and Jaeger 1998, Orrock and Watling 2010). Alternatively, some theoretical models suggest that habitat change has the potential to reverse competitive hierarchies and allow formerly subordinate species to dominate in degraded habitats, particularly if the subordinate species is less sensitive to changing habitat conditions or is better able to exploit them (Tilman et al. 1994). Finally, habitat change could also create new rivalries if it forces species that are usually resource-partitioned and not directly competing in healthy habitats to have higher resource overlap in degraded environments (Auer and Martin 2013). Ecologists are increasingly faced with the challenge of mitigating species loss and preserving species interactions in a rapidly changing world. Understanding when habitat degradation is likely to intensify, reverse, or create new competitive outcomes will provide insight

into how communities are likely to respond to habitat change.

Coral reef habitats are composed of a complex mosaic of live corals that support rich communities of fish. After many decades of debate (reviewed by Jones 1991, Hixon and Webster 2002), a substantial body of research now suggests competition for space can influence the structure of reef fish communities (e.g., Robertson 1996, Munday et al. 2001, Holbrook and Schmitt 2002, Forrester et al. 2006). Reef habitats provide critical shelter from predators and, therefore, competition for refuges is considered an important mechanism in regulating fish communities and populations (Hixon and Jones 2005, White et al. 2010). Experimental manipulations of the densities of competitors and/or their refuges have demonstrated that mortality is density dependent when shelter spaces become limited (e.g., Forrester 1995, Samhouri et al. 2009). In one of these studies, video monitoring revealed that interference competition among juvenile damselfishes for prime sheltering sites resulted in increased predator-induced mortality at high competitor densities (Holbrook and Schmitt 2002). Competitively dominant species can increase the mortality rates of subordinate species or limit the abundance and distribution of subordinate species by restricting their access to mutually preferred habitats (Robertson 1996, Munday 2001). A number of studies have also found close links between the abundance of coral-dwelling fishes and the availability of their preferred corals (Munday et al. 1997, Holbrook et al. 2000), which suggests that suitable habitats can be a limited resource for coral-dwelling fishes even on relatively healthy reefs.

Coral reefs are increasingly affected by habitat loss and degradation as a result of compounding threats, including climate-induced coral bleaching, crown-of-thorns starfish outbreaks, coral disease, and poor water quality (Gardner et al. 2003, Bruno and Selig 2007, De'ath et al. 2012). These drivers of coral mortality reduce the cover of live corals, and also lead to eventual reductions in the structural complexity of reef habitats. While it is clear that both declines in live coral cover and reduced habitat complexity can cause substantial reductions in fish abundance (Graham et al. 2006, Wilson et al. 2006, Pratchett et al. 2008), little is known about the demographic mechanisms driving these changes. However, given that many coral reef fish species rely on live corals for recruitment habitat (Jones et al. 2004), the effects of habitat degradation on the settlement and post-settlement survival of reef fishes may be particularly important in driving community-wide changes in abundance. Declining coral cover can reduce the abundance and diversity of fishes that settle in coral reef habitats (Booth and Beretta 2002, Feary et al. 2007) and increase post-settlement mortality rates (Osenberg et al. 2006, Bonin et al. 2009b, 2011). Agonistic interactions can make it difficult for individuals living in degraded habitat patches to relocate to

healthy habitats (Coker et al. 2012) and may increase predator-induced mortality (McCormick 2012). Further research on the interaction between competition and habitat degradation is integral to understanding the processes that regulate and structure reef fish communities in degraded environments.

In this study, we explore, for the first time, how habitat degradation influences the outcome of both intra- and interspecific competition for shelter among juvenile coral reef fish. The study species, *Chrysiptera parasema* and *Dascyllus melanurus*, occupy a similar ecological niche and rely on live coral habitat that is highly vulnerable to degradation (see Plate 1). Both species are planktivorous and occupy similar coral microhabitats as juveniles (Bonin 2012). They are gregarious throughout their lives and tend to live in high density aggregations during their juvenile stage. At our study site in Kimbe Bay, Papua New Guinea, the two species co-occur on inshore reefs and frequently use patches of live branching coral surrounded by sand. A previous experiment with these species indicated that *D. melanurus* is the dominant competitor in healthy live coral habitat, and can significantly increase the mortality of juvenile *C. parasema* when they inhabit the same habitat patch (Bonin et al. 2009a).

Here, we employ a manipulative field experiment to quantify the mortality of juvenile *C. parasema* and *D. melanurus* across a range of intra- and interspecific competitor densities in both healthy and degraded coral habitats. This allows us to assess the extent to which competitor density regulates juvenile mortality for both species; and test if habitat degradation influences the outcome and regulatory function of competition within and among species or alters their competitive hierarchy. In addition, we quantify three aspects of behavior across a range of densities (i.e., aggression, distance to shelter, and frequency of association with live coral) that could provide mechanistic insight into the mortality patterns observed.

METHODS

Experimental design

The experiment was conducted between May and July 2011 in the Kilu-Tamare region of Kimbe Bay, Papua New Guinea (150°05′ E, 5°25′ S). Coral reefs in Kimbe Bay are characterized by an exceptionally high diversity of fish and corals, although the region has experienced several episodes of coral mortality and subsequent reef fish declines in recent years (Jones et al. 2004). An array of experimental reefs was constructed on a large sandy area, approximately 100 m from shore. Each of the 48 experimental reefs was isolated from others in the array by 15 m and was constructed with a coral-rubble base that was topped with 0.5 m² of either all healthy or a mixture of healthy and dead colonies of the branching coral *Acropora longicyathus*. This coral species is used by juveniles of both damselfish species in Kimbe Bay, with *C. parasema* selectively using this coral and *D. melanurus*
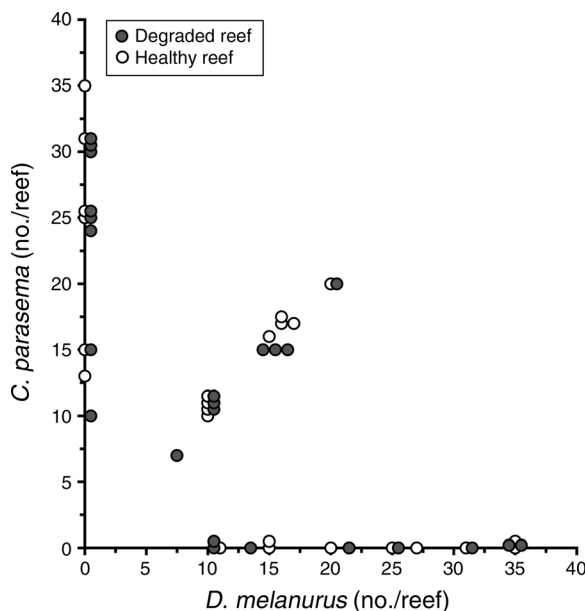
Fig. 1. Stocking numbers of *Chrysiptera parasema* and *Dascyllus melanurus* at the start of the experiment. Note that to avoid complete overlap in the figure, degraded reefs have been shifted 0.5 units along the *x*-axis, while replicate reefs have been sequentially shifted 0.5 units along the *y*-axis. Total number of reefs was 48; *C. parasema* intraspecific and healthy (six experimental reefs), *C. parasema* intraspecific and degraded (eight), *D. melanurus* intraspecific and healthy (nine), *D. melanurus* intraspecific and degraded (eight), interspecific and healthy (nine), interspecific and degraded (eight). Healthy treatments were topped with 100% live bottlebrush *Acropora*, while degraded treatments were topped with 10% live and 90% dead bottlebrush *Acropora*.

using it in proportion to its availability (Bonin 2012). This habitat is also highly susceptible to mortality from coral bleaching (Marshall and Baird 2000, Bonin 2012) and predation by crown-of-thorns starfish (De'ath and Moran 1998, Pratchett et al. 2009). Healthy treatments consisted of 100% live coral, whereas degraded treatments consisted of 10% live and 90% dead coral. The dead coral portion of degraded reefs was constructed with recently dead coral colonies, so that the degraded treatments were initially similar in structure to healthy treatments, and mimicked a disturbance event that caused live coral mortality but little initial structural habitat damage (e.g., coral bleaching, crown-of-thorns starfish outbreaks, or coral disease). A healthy bottlebrush *Acropora*, presumably, offers shelter space at two scales; between individual branchlets on colony branches, and between branches themselves. However, during the two-month experiment, the branchlets of dead coral became overgrown with algae and covered with sediment, resulting in a gradual reduction in structural complexity and a decline in shelter space on degraded reefs. This experiment, therefore, tests the effects of a reduction in habitat quality in the form of an immediate 90% loss of live coral followed by a gradual reduction in

habitat structure. This is in contrast to several previous experiments examining the effects of habitat degradation on coral reef fishes that have reduced both live coral cover and habitat structure simultaneously (Syms and Jones 2000, Bonin et al. 2011), thereby testing the effect of complete habitat loss from acute impacts, such as tropical storms. By manipulating both the numbers of fish on reefs, as well as the habitat quality, we are manipulating access to resources provided by the habitat to fish living on these reefs. On healthy reefs, it is likely that it is space that is the limited resource. While we may not know what specific aspect of this space is of primary importance to the juvenile fish living among the live coral branches, the second part of our experiment (degraded reefs) allows us to test whether it is some aspect of live coral in particular that is limiting.

Juvenile *C. parasema* and *D. melanurus* (13–20 mm total length approximately two to three weeks post-settlement) were collected using clove oil anesthetic and hand nets, and translocated to the experimental reefs. Prior to stocking, damselfish were measured and tagged subcutaneously with florescent elastomer so that all fish on each reef had a mark unique to that reef. An observer remained near each reef for approximately 10 minutes following the release of juveniles in order to discourage attacks by transient predators while they acclimated to the new habitat. Experimental reefs were stocked with juvenile damselfish using an experimental design in which the densities of the two competitors were manipulated across a range of naturally occurring densities (Boström-Einarsson et al. 2013). The initial densities of damselfish stocked on the experimental reefs ranged from 10 to 40 fish per 0.5 m^2 reef (i.e., 20–80 individuals/m^2) and each density level included competition treatments with each species in isolation as well as a combination of both species in equal numbers (Fig. 1). Competitor density treatments were crossed with two habitat treatments (healthy or degraded) and were randomly allocated across the experimental reefs to avoid systematic bias of treatment effects across any existing environmental gradients. Several of the habitat treatments were replicated at a particular density level (see Fig. 1), although replication of each density–competitor–habitat combination was not strictly necessary due to the regression-based approach to analysis. This experimental design has several advantages that make it more suitable than an additive design for addressing the objectives of our study. First, because competition effects are measured across a range of densities, conclusions regarding the effect of competition are not limited to a particular density treatment. Moreover, including competition treatments with each species in isolation and also together at each density level allows reciprocal competitive effects to be measured (i.e., both the effect of *C. parasema* on *D. melanurus* and the effect of *D. melanurus* on *C. parasema*) and facilitates the comparison of intra- vs. interspecific effects on mortality. Note that densities of

the two species were stocked in equal numbers on interspecific reefs, and were not varied independently of each other (Fig. 1).

Once treatments were established, the reefs were monitored closely for the first three to four days to monitor the potential movement of juveniles between experimental reefs or emigration to nearby natural reefs using elastomer tags on the stocked damselfish. Although minimal movement was observed, when it did occur, we removed or replaced juvenile *C. parasema* and *D. melanurus* as necessary to ensure that density and competitor treatments were successfully established. After this initial acclimation period, the experiment began and reefs were left to run undisturbed for the next 60 days, at which point, they were revisited to monitor the mortality of the two focal species. We considered it unlikely that acclimated fish would later begin to move between reefs separated by 15 m of open sand. Given that tagged migrants were never found on surrounding reefs we attributed losses at the end of the study to mortality from predators rather than emigration.

Mortality

The effects of habitat degradation and the densities of intra- and interspecific competitors on the mortality of each species were evaluated using multiple logistic regressions. This analysis is ideal for modeling proportional mortality data because it is a type of binomial data (i.e., *x* out of *y* fish survived), and is preferable over a linear modeling approach using arcsine-transformed proportions (Warton and Hui 2011). The logistic regressions modeled the proportional mortality on each replicate experimental reef as a function of habitat quality (categorical), intraspecific competitor density (continuous), and interspecific competitor density (continuous), and the response variable was weighted by the number of individuals used to calculate proportional mortality on each reef. Akaike's information criterion (AIC) were used to select a model that provided the best fit to our data using the fewest possible predictor variables and the fit of that selected model to our data was then evaluated using a likelihood ratio test. In addition, the significance of each term in the reduced model was evaluated using the Wald χ^2 test. The predictor variables intraspecific competitor density and interspecific competitor density would provide tests of density-dependent mortality induced by intra- or interspecific competitors respectively. A significant interaction between intra- and interspecific competitor density would indicate that the effect of density on mortality differs depending on whether conspecific or interspecific competitors are present on the reefs. A significant three-way interaction between habitat quality, intraspecific competitor density, and interspecific competitor density would indicate that the effects of the densities of both conspecifics and interspecific competitors differ between healthy and degraded reefs. Regression coefficients (β) provided an indication of relative effect size for each

term in our model; however, in logistic regression, the value of the slope relates to the effect of the predictor variable on the log odds of mortality (not the probability of mortality). In order to estimate how the probability of mortality differed between treatments, we calculated mortality at the mean competitor density levels used in the experiment (i.e., 24 individuals in intraspecific treatments and 12 individuals of each species in interspecific treatments [Jaccard 2001]). This allowed us to directly compare the probability of mortality at a particular density level between intra- and interspecific competition treatments on both healthy and degraded reefs.

Finally, to determine whether predators aggregated around high-density experimental reefs, repeated surveys of predator abundance were conducted during approximately two weeks following each reef establishment (6.6 ± 0.25 survey times [mean ± SE]). Because the surveys were conducted between 08:00 and 11:00, these counts represent a measure of non-cryptic diurnal predators only. Predators were identified to genus level and grouped into two size classes, large (>100 mm) and small predators (<100 mm), and an average number sighted on each reef was calculated. Large predators included transient species such as *Caranx* spp. (Carangidae) and *Lethrinus* spp. (Lethrinidae), while the smaller size class was dominated by juvenile *Lutjanus* spp. (Lutjanidae). Linear regressions were used to evaluate whether there was a relationship between numbers of small or large predators present near experimental reefs (dependent variable) and the total density of prey on the reefs (i.e., the combined density of all juvenile *C. parasema* and *D. melanurus*; independent variable).

Behavioral observations

Given that density-dependent behavior may increase an individual's vulnerability to predation, behavioral observation can provide insight into mechanisms underlying density-dependent mortality. At the end of the experiment (60 days) we measured three different aspects of behavior that could explain mortality patterns across the experimental reefs. Given that interactions between species are most likely strongest shortly after the start of the experiment, these measures represent a conservative estimate of behaviors that may have been influencing our study species for the duration of the experiment. First, we explored how competitor density and habitat quality influenced the number of agonistic interactions on experimental reefs. A stationary observer situated 2 m from each reef conducted the observations and fish were allowed to adjust to the presence of the observer for at least one minute before behavior was quantified. The observer then recorded the total number of agonistic interactions (defined as a nip or chase) during a 6-minute observation period for each experimental reef, noting the aggressor and recipient species in each interaction. Such aggression is indicative of
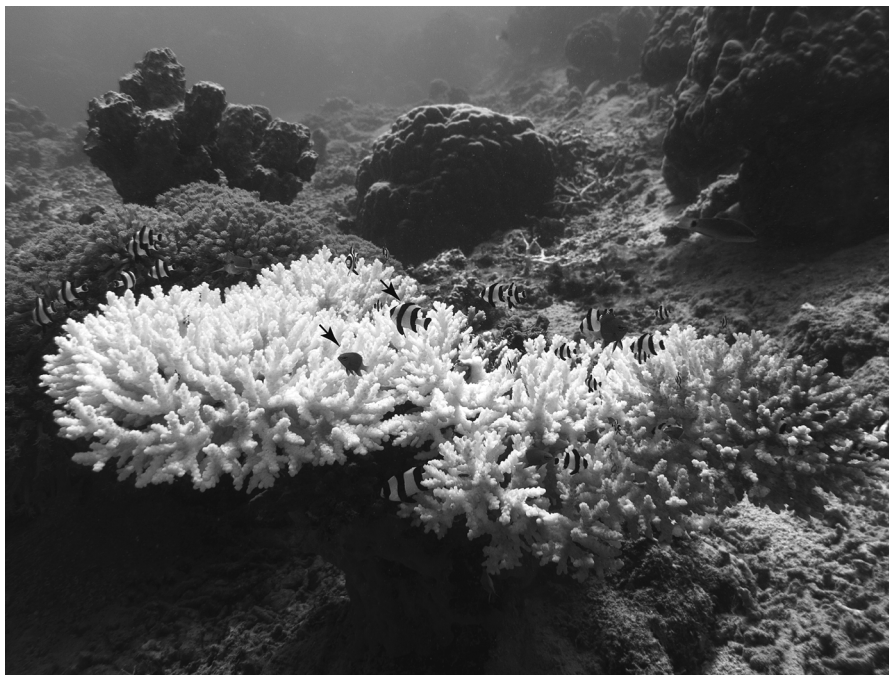
PLATE 1.   *Chrysiptera parasema* (indicated by arrow) and *Dascyllus melanurus* (indicated by arrow, black and white stripes) commonly co-occur on several growth morphologies of *Acropora* corals. Coral colonies of this common genus are prone to disturbances and are often the first to bleach and be consumed by crown-of-thorns starfish, *Acanthaster planci*. Both study species are pictured here on a partially bleached corymbose *Acropora* colony. Photo credit: L. Boström-Einarsson.

interference competition, which can increase predation risk by limiting the recipient's access to shelter and/or reducing their predator vigilance (Carr et al. 2002). Agonistic interactions per minute were divided by the number of fish on the reef (i.e., transformed to a per capita rate) to standardize for the different total densities among reefs. We then used multiple linear regressions to explore the effects of competitor density and habitat quality on the per capita rate of agonistic interactions for each damselfish species. We were unable to evaluate the effects of increasing interspecific competitor density on rates of aggression because there were few interspecific reefs that still had both species present in sufficient numbers at the end of the study. Therefore only intraspecific reefs were included in this analysis. The regression modeled per capita intraspecific aggression as a function of habitat quality (categorical) and intraspecific competitor density at the time of observation (continuous); and AIC criterion were used to select the combination of predictor variables that best fit the data. In addition, on the few reefs where both species were present in sufficient numbers to assess relative rates of aggression ($n = 14$ reefs), the per capita agonistic interactions per minute per reef (response variable) were compared across four interaction types (initiator–receiver, between and among the two species). Per capita calculations were based on the number of individuals present on each reef, using both the number of individuals of the initiator species as well as the

receiver species, resulting in two separate response variables. Given that there were no significant differences between the two types of per capita calculations (ANOVA $F_{1, 107} = 0.135$, $P = 0.71$), post-hoc comparisons between interactions were conducted on each response variable type separately.

The second aspect of behavior we quantified was distance to shelter, since dominant competitors may occupy optimal positions in a group that provide best predator avoidance and escape, thereby forcing subordinates to occupy more risky peripheral positions (Webster 2004, Tsurim et al. 2010). Average distance to shelter was estimated for three haphazardly selected individuals of each species on each reef (*C. parasema*, $n = 71$ individuals; *D. melanurus*, $n = 104$ individuals). For each focal individual, the distance away from shelter was estimated to the nearest centimeter every 15 s for one minute and an overall mean for each individual was calculated. Shelter was defined as any coral habitat on the reef, whether alive or dead, and distance measures were routinely calibrated by estimating the distance between fixed points on experimental reefs and then verifying through exact measurement. The average distance to shelter of focal individuals (pooled across the two species) was then modeled as a function of habitat quality (categorical), *C. parasema* density at the time of observation (continuous), *D. melanurus* density at the time of observation (continuous), the focal species (categorical), and reef competition type (inter- or

TABLE 1. Logistic regression of mortality for (a) *Chrysiptera parasema* and (b) *Dascyllus melanurus* on experimental patch reefs.

Factors	a) Mortality of *C. parasema*					b) Mortality of *D. melanurus*				
	β	SE β	χ^2	df	P	β	SE β	χ^2	df	P
Constant	−1.66	0.43			<0.001	−1.77	0.155			<0.001
Conspecific density	0.047	0.01	9.8	1	0.002					
Interspecific competitor density	0.114	0.02	30	1	<0.001					
Habitat quality	2.001	0.24	67	1	<0.001	0.94	0.202	21.7	1	<0.001
Conspecific density × Interspecific Density × Habitat quality	−0.01	0.001	18	1	<0.001					
Likelihood ratio test (full model)			85.4	4	<0.001			21.7	1	<0.001

Notes: Reefs were stocked with either 100% live coral (healthy treatment) or 10% live (degraded treatment), while the experimental design included reefs with interspecific competitors present or absent across a range of densities. The Wald χ^2 test evaluates the importance of each term in the model, while the likelihood ratio test evaluates the fit of the whole model against a simple null model. β is the regression coefficient.

intraspecific) using multiple linear regression and AIC to select the best fit model.

Finally, focal animal observations were conducted for both species on the degraded reefs in order to assess the frequency of association with the live and dead coral portions of the degraded reefs. If the damselfishes associated with the live coral more frequently than expected despite its lower availability, it would suggest that live coral provides higher quality shelter compared to dead coral for these two damselfish species. A total of four focal individuals were observed on each reef, split evenly between species on reefs with both species present. In order to determine which type of coral the damselfish used most frequently as habitat, each focal individual was observed for a period of two minutes and its habitat association was tallied every five seconds as either associating with live coral, associating with dead coral, or not habitat associated (*C. parasema*, n = 225 observations; *D. melanurus*, n = 675 observations). An individual fish was determined to be associating with the habitat when it was observed <5 cm from the habitat type and not actively feeding. This data was used to assign each individual to one of two habitat association categories, primarily associating with live coral or primarily associating with dead coral. Chi-square tests with Yates corrections were then used to compare the observed habitat association frequencies of each species with those expected if the damselfish associated with the two habitat types on the degraded reefs in proportion to their availability (i.e., 10% live coral, 90% dead coral). Association frequencies were also compared between the two species to determine if they utilized the habitat on degraded reefs in a similar way.

RESULTS

Calculation of AIC for every possible combination of main effects and interaction terms revealed that *C. parasema* proportional mortality was best modeled as a function of habitat quality, intraspecific competitor density, interspecific competitor density, and their three-way interaction. The highly significant three-way interaction indicated that the density-dependent effects of competitors on mortality varied depending on both competitor identity and habitat quality (Table 1a) and prevented us from examining the main effects in isolation. Although the effect size (β) of the three-way interaction was quite small, the significant Wald χ^2 test (Table 1a) suggests it is important in modeling *C. parasema* mortality. Moreover, visual inspection of the data also supported the conclusion of the logistic regression analysis; the effects of both intra- and interspecific competitor density were clearly not consistent across habitat types.

On healthy reefs, *C. parasema* mortality increased with increasing densities of both intra- and interspecific competitors (i.e., was density dependent), although overall levels of mortality were much higher on reefs with competitor *D. melanurus* compared to reefs with conspecifics only (Fig. 2a). In contrast, there was no difference in mortality levels on degraded reefs with or without interspecific competitor *D. melanurus* (Table 1a, Fig. 2b). Instead, mortality of *C. parasema* was highly variable (0–100% mortality observed) and density independent across all the degraded reefs. The main effect of habitat alone predicted that overall probability of *C. parasema* mortality tended to increase more than threefold (from 0.16 to 0.58) between healthy and degraded reefs. Caution should be exercised when examining the main effect of habitat; however, as the significant interaction term indicates, this effect is not consistent across treatments (i.e., intra- and interspecific competitor densities).

The effect of interspecific competitors was stronger than that of intraspecific competitors on healthy habitats. The logistic model predicted that the probability of *C. parasema* mortality could be markedly higher on reefs with interspecific competitors. For example, at a fixed density of 24 individuals the probability of mortality was 0.57 on reefs with 12 conspecifics and 12 *D. melanurus* and 0.36 on reefs with 24 conspecifics (65% increase; Appendix A: Fig. A1). Moreover, there was a steeper slope in the density-dependent relationship between interspecific competitor density and *C. parasema* mortality (β = 0.114) compared to the slope of conspecific density and *C. parasema* mortality (β = 0.047; Table 1, Fig. 2a). This suggests that not only were
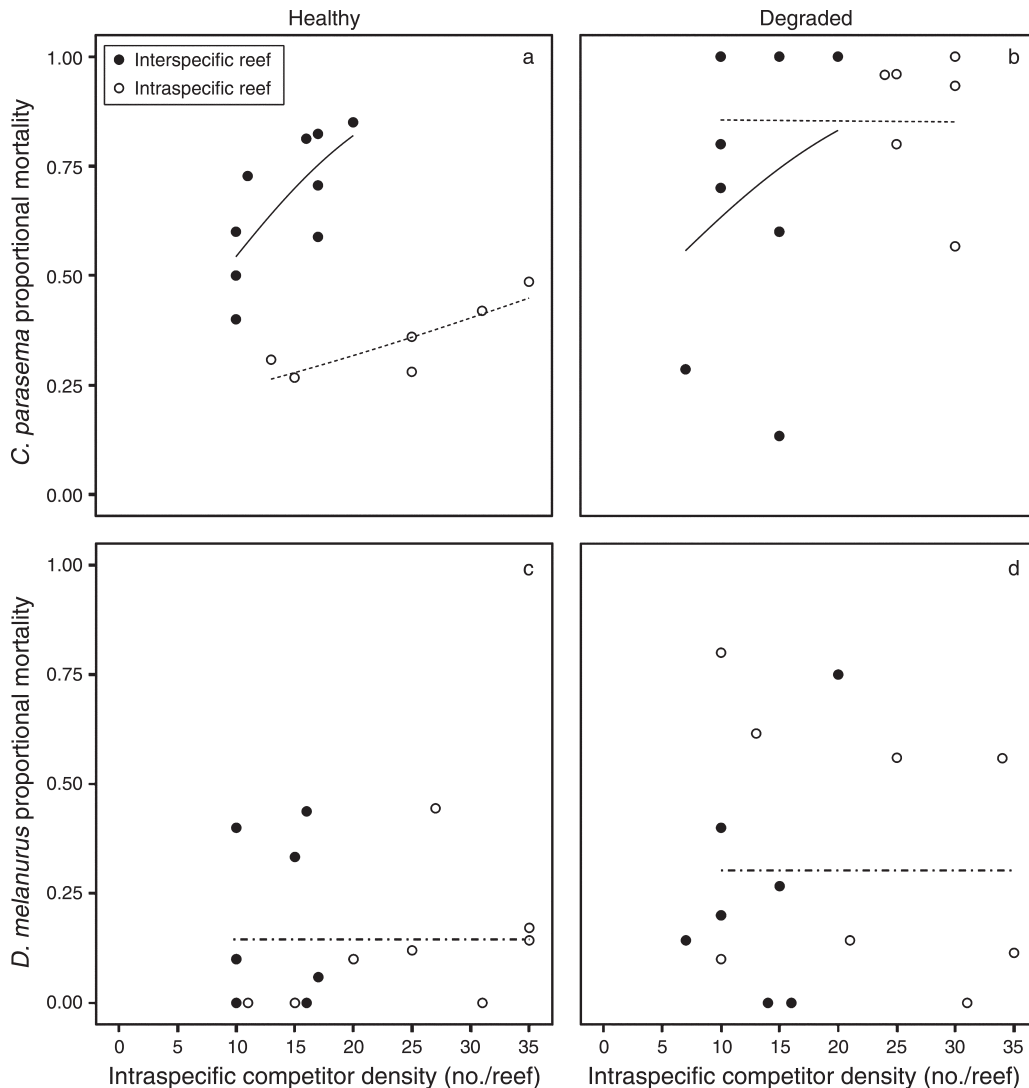
FIG. 2.   Proportional mortality of (a, b) *C. parasema* on experimental reefs across varying densities of intraspecific (dashed lines) and interspecific competitors (solid lines) on two types of habitat, healthy (100% live coral) or degraded (10% live coral). Each data point represents one experimental reef and lines indicate the fitted logistic model (*C. parasema* mortality ~ intraspecific competitor density + interspecific competitor density + habitat + [intraspecific competitor density × interspecific competitor density × habitat]). Proportional mortality of (c, d) *D. melanurus* on healthy and degraded treatments (dot-dash line; *D. melanurus* mortality ~ habitat). Note that mortality is plotted against conspecific density (Fig. 2a–c). Given that interspecific reefs were stocked with near equal numbers of both species, the corresponding figure for interspecific competitor density can be accessed in Appendix A: Fig. A2.

overall mortality levels higher on reefs with interspecific competitors present, increasing densities of *D. melanurus* also had a stronger effect on per capita mortality rates of *C. parasema*. The mortality of juvenile *D. melanurus* was best modeled as a function of habitat quality alone (Table 1b). The probability of mortality was twice as high on degraded reefs compared to the healthy reefs (0.14 and 0.30 respectively), indicated by a logistic regression coefficient of 0.939 (β; Table 1b, Fig. A3). In contrast to the clear density dependence observed for *C. parasema*, the mortality of juvenile *D. melanurus* did not increase with increasing densities of either intra- or

interspecific competitors on healthy or degraded reefs (Fig. 2c, d).

A total of 3974 small and 298 large predators were observed on the experimental reefs, and each reef had an average of 12.6 ± 1.2 (mean $\pm$ SE) small and 1.1 ± 0.1 large predators. There was no significant relationship between the total number of damselfish present on each reef and the abundance of predators in either size class (small $R^2 = 0.004$, $F_{1,46} = 0.19$, $P = 0.67$; large $R^2 = 0.01$, $F_{1,46} = 0.49$, $P = 0.49$).

For both *C. parasema* and *D. melanurus*, rates of aggression among conspecifics increased significantly

TABLE 2. Multiple linear regressions of intraspecific agonistic interactions and distance to shelter of (a) *C. parasema*, (b) *D. melanurus*, and (c) focal individuals of both species.

Factor	SS	MS	F	df	P
a) Agonistic interactions of *C. parasema*					
Conspecific density	0.004	0.004	4.503	1	0.072
Habitat quality	0.001	0.001	1.300	1	0.292
Conspecific density × habitat quality	0.005	0.005	5.699	1	0.048
Error	0.007	0.001		7	
b) Agonistic interactions of *D. melanurus*					
Conspecific density	0.014	0.014	4.532	1	0.049
Habitat quality	0.019	0.019	5.941	1	0.027
Conspecific density × habitat quality	0.037	0.037	11.64	1	<0.01
Error	0.050	0.003		16	
c) Distance to shelter					
C. parasema density	59.82	59.82	2.0844	1	0.154
D. melanurus density	357.34	357.34	12.4508	1	<0.001
Habitat quality	308.28	308.28	10.7414	1	0.002
Focal species	245.04	245.04	8.5379	1	0.005
Error	1578.5	28.7		55	
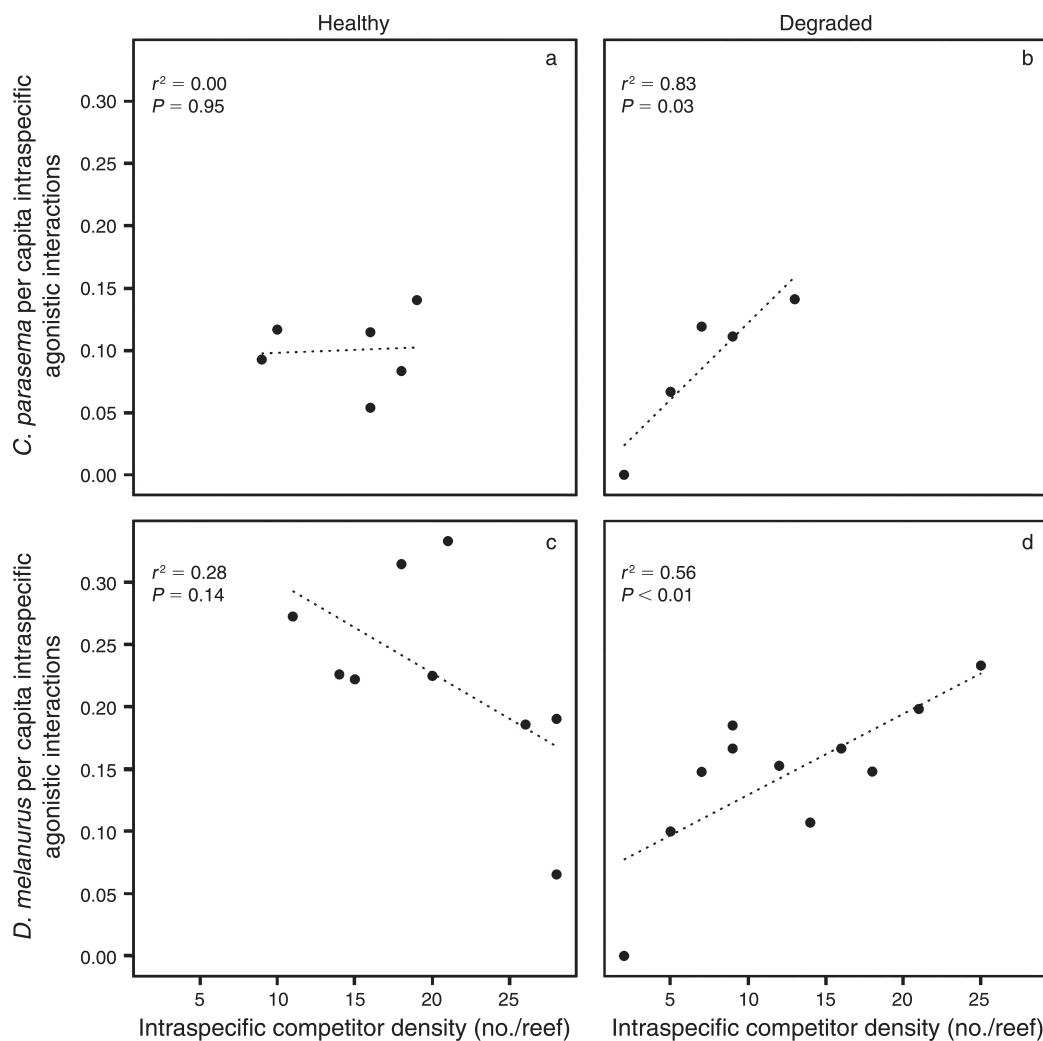
FIG. 3. Intraspecific agonistic interactions per experimental patch reef for (a, b) *C. parasema* and (c, d) *D. melanurus*. Agonistic interactions were defined as a nip or chase. Each data point in figures represent one experimental patch reef; dashed lines indicate linear regression model fit.

with increasing conspecific density on degraded reefs, but were density independent on healthy reefs (Table 2a, b, Fig. 3a–d). On the reefs with both species present, *D. melanurus* initiated significantly more agonistic interactions (per capita) overall (i.e., both directed at con- and heterospecifics) than *C. parasema* (*D. melanurus* had a total of 154 individuals and 153 agonistic interactions, *C. parasema* had a total of 75 individuals and 17 agonistic interactions; ANOVA $F_{1,54} = 44.66$, $P < 0.001$). Moreover, *D. melanurus* instigated significantly more agonistic interactions per capita towards *C. parasema* than *C. parasema* reciprocated (Appendix B: Fig. B1), suggesting that *D. melanurus* is the dominant interspecific competitor in this pairing.

Distance to shelter was best modeled as a function of *C. parasema* density, *D. melanurus* density, and focal species. Given that distance to shelter of both species was pooled to comply with assumptions of homogeneity and normality of variances, the results must be interpreted for both species jointly. There was a significant effect of habitat quality on the average distance to shelter, with damselfishes remaining closer to the habitat on healthy reefs compared to degraded reefs (Table 2c, Fig. B2). There were also interspecific differences in habitat association, with *D. melanurus* straying further from shelter on average compared to *C. parasema* (Table 2c). Given that the factor for reef type (intra- and interspecific) did not explain sufficient variation (based on AIC) to warrant inclusion in the model, there are no overall differences between intra- and interspecific reefs. Finally, the damselfish on degraded reefs also moved farther away from shelter as densities of the dominant competitor *D. melanurus* increased, whereas there was no effect of increasing densities of *C. parasema* on average distance to shelter (Table 2c, Fig. B2).

On degraded reefs, both *C. parasema* and *D. melanurus* associated with the 10% live coral on the reef more frequently than would be expected based on its availability (*C. parasema* $\chi^2 = 20.7$, df = 1, $P = 0.001$; *D. melanurus* $\chi^2 = 10.9$, df = 1, $P < 0.001$).

DISCUSSION

Our study confirms that habitat degradation can dramatically alter the outcomes of competitive interactions within and among species of coral reef fishes. The field experiment showed that on healthy reefs, mortality of *C. parasema* increased as the density of both intra- and interspecific competitors increased, with the presence of the interspecific competitor *D. melanurus* having a stronger negative effect than increasing densities of conspecifics. In contrast, the effects of intra- and interspecific competition on *C. parasema* were completely disrupted by habitat degradation. On degraded reefs, there was no evidence of density dependence in either the intra- or interspecific competition treatments and mortality levels were similar on reefs regardless of *D. melanurus* presence. Hence, habitat

degradation appears to have eliminated a key process regulating population densities on healthy reefs.

Intraspecific density-dependent mortality has been well documented in animals (Sauer and Boyce 1983, Skogland 1983, Ekman 1984, Stiling 1988, Whitfield 2003), and plants (Lambers et al. 2002, Bell et al. 2006). While many of these studies do not identify the specific resource causing population regulation to occur, in our study, it is quite likely that access to shelter sites provided by living coral colonies is the limiting factor. In reef fishes, density-dependent mortality due to competition over refuge space has primarily been observed within a species, either among juveniles (Holbrook and Schmitt 2002, Boström-Einarsson et al. 2013), among adults (Forrester 1995, Forrester and Steele 2004) or between juveniles and adults of the same species (Schmitt and Holbrook 1999, Webster 2004, Samhouri et al. 2009).

Although there are numerous studies describing a negative effect of one animal species on the mortality of another (Connell 1983, Schoener 1983, Denno et al. 1995), few studies have demonstrated that this effect increases with increasing densities of competitors (i.e., is density dependent). Notable exceptions include studies with birds (Merilä and Wiggins 1995), intertidal gastropods (Underwood 1978), cnidarians (Kastendiek 1982), and ungulates (Sinclair 1985). In reef fishes, there is one example of adults of one species increasing the mortality of recruits of another species (Carr et al. 2002). Our study is one of the few ecological studies demonstrating density-dependent mortality due to interspecific competition, and, to our knowledge, the first to demonstrate this concept in juvenile reef fishes. These findings support the notion that early post-recruitment processes can shape and regulate future adult reef fish populations, and that interspecific competition is an important regulatory process in ecological communities.

The results from this study do not conform to the general expectation that intraspecific competition should be a stronger regulating force than interspecific competition (Forrester et al. 2006). This is expected because overlap in ecological niche within species is likely to be greater than between species, causing more intense competition over finite resources (Chesson 2000). In our study system, *C. parasema* population was regulated by the presence of *D. melanurus*, with drastically increased mortality in the presence of the interspecific competitor, while *D. melanurus* populations showed no evidence of density-dependent mortality. Given that *C. parasema* is highly specialized on vulnerable coral habitat, and competition over limited resources is a key regulatory process, it seems likely that *C. parasema* would be affected by a decline in available habitat.

Degradation of habitat may influence intra- and interspecific competition in a number of ways. First, a reduction in the availability of resources may intensify competition causing dominant species to completely

exclude subordinate species (Griffis and Jaeger 1998, Orrock and Watling 2010). Second, habitat degradation may induce competition among species for remnant habitats (Auer and Martin 2013, Pelegrin et al. 2013). Finally, it may reverse preexisting competitive hierarchies (Tilman 1994). Our study was the first to test these interactive effects for coral reef fishes. We did not detect competitive reversal or complete exclusion of subordinate species. Instead, the competitive dominance of *D. melanurus* over *C. parasema* is effectively lost on degraded reefs. Competitive interactions are a key process in not only limiting the size of populations, but also in regulating the allocation of space in ecological systems. Given that space is likely to be at a premium following habitat degradation, the loss of this regulatory process can have significant consequences to ecological processes within these systems.

Our results support the accumulating evidence that live coral habitat plays an important role in structuring reef fish communities. A 90% reduction in live coral resulted in threefold higher mortality of *C. parasema*, and approximately twofold higher mortality of *D. melanurus*. Habitat degradation had a large, density independent, negative effect on the survival of juveniles of both damselfish species. This is consistent with previous studies, where habitat degradation has led to a loss of coral reef associated fishes, both mensuratively (Jones et al. 2004, Munday 2004, Wilson et al. 2008, Bonin et al. 2009*b*) and through manipulative experiments (Caley et al. 2001, Coker et al. 2009, Bonin et al. 2011). In our study, loss of habitat quality caused both species to be less associated with shelter and introduced strong density dependence in both agonistic interactions and distance to shelter. On degraded reefs, both species associated more with the 10% live coral portion than would be expected based on its availability, suggesting they no longer perceive the dead coral structure as suitable habitat.

Density-dependent mortality for *C. parasema* on healthy reefs suggests competition over shelter space, while the large impact of habitat degradation on both mortality and behavior indicates that it is some aspect of live coral habitat in particular that is a crucial resource. Given that mortality was density independent while behavior was density dependent on degraded reefs, it begs the question of how to reconcile these disparate results? There are several possible explanations. Firstly, the trade-off between the costs and benefits of engaging in aggressive interactions may be altered by habitat degradation. On healthy reefs, there may be sufficient space to shelter all individuals within live coral branches; however, certain areas carry a higher risk of predation (e.g., on the periphery of the colony; Holbrook and Schmitt 2002). Avoidance behavior by altering spatial distributions may result in increased vulnerability to predators, as subordinate individuals occupy higher risk areas (Webster 2004). This type of conflict avoidance could produce density-dependent mortality with density-

independent aggressive interactions. On degraded reefs, however, the cost of not securing the limited shelter spaces in live coral may become sufficiently high to warrant the need for aggressive interactions. Second, it is possible that mortality was indeed density dependent at different densities than those tested here; however, the marked increase and variability in mortality due to habitat degradation masked the detection of any linear effects (Overholtzer-McLeod 2004). Finally, it is possible that habitat degradation has affected the carrying capacity by forcing population densities below this threshold level where they are limited by density-dependent processes (White et al. 2010), or the loss of resources provided by a healthy habitat may have lowered the carrying capacity itself to a point below densities stocked in the experiment.

We acknowledge that the data presented here reflect a snapshot in time of the effects of habitat degradation on the competitive relationships within and between *C. parasema* and *D. melanurus*. Given that the detection of density-dependent relationships will often differ depending on the time sampled (White et al. 2010), the patterns described may be of a temporary nature. In terrestrial systems, habitat degradation has been shown to result in a temporary crowding effect that is mediated by intense intra- and interspecific competition, followed by a drop in abundance down to densities that can be sustained by the environment (Tilman et al. 1994, Grez et al. 2004). A recent study has suggested that *C. parasema* mortality may conform to this pattern following habitat degradation (Boström-Einarsson et al. 2013). Whichever scenario is true, for *C. parasema* the combination of being a relatively weak interspecific competitor for habitat, whilst being highly specialized to vulnerable habitat does not bode well for the persistence of this species in the face of future habitat degradation events.

Given that coral reef ecosystems are particularly vulnerable to disturbances, and that live coral habitats are in global decline, it is important to evaluate how this will impact reef fish communities. We demonstrate that the impact of reduced habitat quality is so profound that it eliminates density-dependent mortality and modifies the behavior of reef fishes. The loss of this regulatory mechanism may increase the likelihood of local extinctions as populations are reduced to low numbers. Together, these findings suggest that habitat degradation has the potential to substantially alter key demographic rates that regulate and shape reef fish communities.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/13-1345.1.sm