Climate-driven coral reorganization influences aggressive behaviour in juvenile coral-reef fishes

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Abstract

Globally, habitat degradation is altering the abundance and diversity of species in a variety of ecosystems. This study aimed to determine how habitat degradation, in terms of changing coral composition under climate change, affected abundance, species richness and aggressive behaviour of juveniles of three damselfishes (*Pomacentrus moluccensis, P. amboinensis* and *Dischistodus perspicillatus,* with decreasing reliance on coral). Patch reefs were constructed to simulate present-day reefs that are vulnerable to climate-induced coral bleaching versus reefs with more bleaching-robust coral taxa, thereby simulating the likely future of coral reefs under a warming climate. Fish communities were allowed to establish naturally on the reefs during the summer recruitment period. Results showed that climate-robust reefs had lower total species richness of coral-reef fishes than climate-vulnerable reefs, but total fish abundance was not significantly different between reef types (both across all species and life-history stages). The nature of aggressive interactions, measured as the number of aggressive chases, varied according to coral composition: on climate-robust reefs, juveniles used the substratum less often to avoid aggression from competitors, and interspecific aggression became relatively more frequent than intraspecific aggression for juveniles of the coral-obligate *P. moluccensis.* This study highlights the importance of coral composition as a determinant of behaviour and diversity of coral-reef fishes.

Keywords: *Benthic composition, habitat degradation, intraspecific and interspecific aggression, species richness, community dynamics*

Introduction

The species composition of communities is changing in a wide variety of ecosystems worldwide (Dornelas et al. 2014), and many of these changes are likely attributable to habitat degradation. For example, habitat degradation has caused many endemic species in biodiversity hotspots to become extinct or threatened with extinction (Brooks et al. 2002). Habitat degradation can influence organisms directly, for example through impaired performance under adverse conditions. Alternatively, indirect effects can occur when changes in the quality and/or quantity of resources result in changes in the intensity of competition and predation, in the demographic rates of species, like fecundity, or in the behaviour of individuals (Fahrig 2003; Fischer and Lindenmayer 2007). To date, studies examining habitat degradation have been largely observational, describing how communities have changed (Fahrig 2003; Dornelas et al. 2014), while empirical studies examining the mechanisms responsible for these changes are limited. High-diversity coral-reef ecosystems are vulnerable to climate change and habitat degradation (Hughes et al. 2003; Wilson et al. 2006; Graham et al. 2015). Globally, coral cover and structural complexity are declining (Gardner et al. 2003; Bellwood et al. 2004; Alvarez-Filip et al. 2009), due to a variety of stressors, including storm dislodgement, declining water quality, and coral bleaching induced by high seawater temperatures (Bellwood et al. 2004; De'ath et al. 2012). For instance, coral cover in the Indian Ocean declined on average by 46% following the 1998 global mass-bleaching event (Hoegh-Guldberg 2004). Coral taxa show clearly defined differential susceptibility to stressors (Hughes and Connell 1999), like coral bleaching (Marshall and Baird 2000; Loya et al. 2001) and storm-related mortality (Madin et al. 2014). The frequency and severity of climate-induced coral bleaching is expected to increase over the coming decades due to increases in ocean temperatures (Hoegh-Guldberg 1999). As a result, coral communities are expected to display long-term shifts from currently abundant and bleaching-vulnerable coral taxa to more bleaching-robust taxa (Marshall and Baird 2000; Hughes et al. 2003; Graham et al. 2014), with associated losses in coral cover and structural complexity.

Shifts in coral-species composition are expected to cause associated changes in coral-reef fish communities, in terms of abundance, diversity and species composition of fishes. Mechanisms driving the effects of coral-reef degradation on reef-fish communities potentially include changes in recruitment of juvenile fishes (Feary et al. 2007; Coker et al. 2012a), emigration of fish from degraded to healthy habitats (Coker et al. 2012b), direct fish mortality due to habitat degradation, and indirect mortality through increased predation and/or competition as the availability of suitable or optimal habitat decreases (Pratchett et al. 2008). Loss of live-coral cover has strong and immediate, yet selective, negative effects on fish that directly depend on live coral for food and shelter (e.g., reviewed by Wilson et al. 2006; Pratchett et al. 2008; Pratchett et al. 2011). Loss of structural complexity can also cause general declines in fish abundance and diversity (reviewed by Pratchett et al. 2008). Many fishes that do not depend on live-coral cover specifically, still depend on topographic structural complexity provided by corals, as complexity is thought to moderate the interactions between individuals (Graham and Nash 2013). However, it is largely unknown how the changes in coral composition anticipated in the future will affect the abundance and interactions between coral-reef fishes.

Aggressive behaviour is commonly observed in coral-reef fishes (e.g., Myrberg and Thresher 1974; Bay et al. 2001; McCormick and Weaver 2012) and direct interactions among individuals, like interference competition and territoriality, are often mediated by aggressive behaviour (Peiman and Robinson 2010). Coral-reef fish often use aggression to secure resources (e.g., Myrberg and Thresher 1974; McCormick and Weaver 2012), including food (Jones 1986), territories (Myrberg and Thresher 1974) and refuge from competitors and predators (Shulman 1984). For example, juveniles and small fish, which are especially vulnerable to predation, aggressively interact for feeding locations close to the reef, where both food and refuge from predation are available (McCormick 2009). Aggression can affect an individual's fitness by influencing resource intake, growth, survival, and reproductive success (Peiman and Robinson 2010), and the ratio of intraspecific to interspecific aggression indicates whether the negative effects of aggression primarily influence conspecific or heterospecific individuals.

Loss of structural complexity can potentially increase aggression, by increasing the frequency with which individuals encounter each other, and/or because there are fewer resources available, which leads to enhanced aggression to obtain resources (Schoener 1987; Barley and Coleman 2010). Indeed, a decrease in the availability of refuges led to more intense aggression in temperate reef fish (Basquill and Grant 1998) and freshwater fish (Baird et al. 2006; Barley and Coleman 2010). Loss of coral health increased the intensity of intra- and interspecific aggression in juvenile coral-reef fishes (McCormick 2012), with smaller and competitively inferior individuals being pushed further from refuges, exposing them to higher predation-induced mortality (McCormick 2009,2012). Further research is required to assess whether and how intra- and interspecific aggression is likely to change on future coral reefs given predicted changes in coral community composition and associated declines in structural complexity and live-coral cover.

In this study, coral composition was manipulated on patch reefs in a coral-reef lagoon to mimic climate-change impacts, and differences in abundance and diversity, and aggressive behaviour, of juvenile coral-reef fishes were monitored. Juveniles of three reef-fish 'focal' species were investigated (*Pomacentrus moluccensis, P. amboinensis and Dischistodus perspicillatus*, representing species with decreasing order of reliance on live coral). Specifically, we assessed if differences in coral composition lead to (1) a decrease in total fish abundance and diversity (pooled across all species and life-history stages), and a decrease in focal juvenile fish abundance, and (2) an increase in the intensity, and changes in the nature of, aggressive interactions instigated by juvenile coral-reef fish. These results provide insight into how habitat degradation is likely to affect fish abundance and behaviour.

Materials and methods

Experimental design and study site

To examine how changes in coral composition under climate change affected abundance and diversity of coral-reef fishes, and the incidence of aggressive behaviour within and between juvenile reef-fish species, patch reefs were constructed in October 2013 at Lizard Island, northern Great Barrier Reef (GBR), Australia (14°41'S, 145°27'E). Sixteen patches were constructed with two distinct treatments: (1) 'climate-vulnerable' patch reefs (n=8), which consisted of six coral species that are currently abundant and relatively sensitive to coral bleaching, and (2) 'climate-robust' patch reefs (n=8), which consisted of six coral species that have moderate or low susceptibility to coral bleaching, simulating what coral assemblages may consist of in the future (Table 1). The coral species for these assemblages were chosen based on their bleaching vulnerability according to recent studies that have recorded the response of coral taxa and coral community-composition after large-scale natural bleaching events (Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2007). For the present study, all chosen coral species were also naturally abundant at the study location.

Patch reefs were constructed using live corals on a rubble base, on a shallow sand flat in the lagoon at Lizard Island, in water between 2.5 and 5 m deep. The percentage cover of live coral was measured using line-intercept transects, in which a transect line was placed over each patch reef, and subsequent coral cover calculated as the ratio between the length of the transect covering live coral, compared to the total length of the transect. Structural complexity was defined as the physical three-dimensional structure of the patch reef, and was expressed as a rugosity index, displaying the ratio between the linear distance covered when the chain was pulled taught, compared to the distance when the chain was draped over the contours of the reefs (Graham and Nash 2013), meaning a higher rugosity ratio indicated higher structural complexity. Because coral composition, coral cover, and structural complexity co-vary in nature, we did not attempt to separate these three variables in our study. Hence, manipulating coral composition meant that coral cover and structural complexity were significantly higher on climate-vulnerable than on climate-robust patch reefs (coral cover, log10(x+1)-transformed data: t-Test, $t_{2,14}$=-6.08, $p<0.0001$; structural complexity, log10(x+1)-transformed data: Welch Modified two-sample t-Test, $t_{2,12.31}$=-3.33, $p<0.01$). On average, coral cover was 53.5% (SE ±1.46) on climate-vulnerable reefs, compared to 31.3% (SE ±3.4) on climate-robust reefs. All patch reefs showed moderate structural complexity, but this was higher (mean 2.04 SE ±0.05) on climate-vulnerable reefs compared with climate-robust reefs (mean 1.73 SE ±0.08). This difference meant there was a substantially lower availability of refuges for fishes on climate-robust reefs. Treatment was randomly allocated to the patch reefs. Patch reefs were on average 1.5 m in diameter, and separated by at least 15 m of sand from other patches and natural reefs. Patches were constructed immediately before the main part of the fish recruitment season, which takes place on the GBR between November and January (e.g., Kerrigan 1996). Data for the present study were collected at the end of the main recruitment season, in January - February 2014. Juveniles living on the patch reefs were assumed to have naturally recruited during previous months, as juvenile movement between separated patches of reef tends to be minimal (Doherty 1982; Almany and Webster 2006).

Focal species

Preliminary surveys conducted in early December 2013 indicated that 18-40 fish species were present on the patch reefs, with a total abundance of 46-213 fish per patch reef. Focal species for the present study were selected based on their abundance on these reefs, and also on whether they interacted aggressively, and differed in their dependence on live-coral habitat. This project focused on aggressive interactions instigated by juveniles, because aggressive behaviour is common between juveniles (e.g., McCormick 2012), and juveniles have a critical role in replenishing adult populations. Three focal species were selected: (1) *Pomacentrus moluccensis,* (2) *Pomacentrus amboinensis* and (3) *Dischistodus perspicillatus. P. moluccensis* is an obligate coral-dweller, *P. amboinensis* is a coral associate and *D. perspicillatus* is a non-coral associate (Randall et al. 1997; Coker et al. 2014). *P. moluccensis* and *P. amboinensis* are both planktivores that feed in the water column, preferentially settle onto live, healthy coral (McCormick et al. 2010) and compete for shelter at settlement (McCormick and Weaver 2012). Within two months after settlement, these two species occupy distinct microhabitats: *P. moluccensis* occupies live coral at the top of the reef, while *P. amboinensis* occupies the base of the reef (McCormick and Weaver 2012). *D. perspicillatus* is associated with sand and rubble, feeds on algae and detritus (Randall et al. 1997) and aggressively defends its territory from adult conspecifics and heterospecifics (Randall et al. 1997; Bay et al. 2001). *P. moluccensis* reaches a maximum adult length of 7.5 cm, *P. amboinensis* 11 cm, and *D. perspicillatus* 20 cm (Randall et al. 1997). Juveniles of *P. amboinensis* on the patch reefs were found to be between 1.5 - 6 cm, *P. moluccensis* 1.5 - 6.5 cm, and *D. perspicillatus* 1.5 - 7 cm (see Electronic Supplementary Material). The few individuals larger than these size thresholds were assumed to have migrated to the reef patches from nearby reefs, and were excluded from analysis. Preliminary surveys indicated that adults of the focal species used the habitat distinctly different from juveniles (see

Electronic Supplementary Material), and that aggressive interactions between adults and juvenile conspecifics were rare.

Initial fish abundance and diversity and focal juvenile abundance through time

To examine how changes in coral composition affected total fish diversity and abundance, the abundance and size of all fish (all species and life-history stages) was sampled by visual census on SCUBA on all patches on 28/29 January 2014. Differences in total fish abundance and diversity between patch reef treatments were analysed using t-tests on log10(x+1)-transformed data. To examine changes in abundance through time of focal juveniles, and whether these changes were consistent between treatments, the abundance and size of focal species were sampled on each patch reef every 4-5 days for 20 days (at t=0, t=4, t=10, t=15, t=20 days). Variation in initial abundance through time for juveniles of the focal species was tested using a linear mixed effects model, with dependent variable log10(abundance+1), with reef included as a random factor to account for repeated measures of reefs, and independent variables time, treatment and species.

Intensity and nature of aggressive interactions

Video observations were used to examine how changes in coral composition affected the intensity and nature of aggressive interactions. Go Pro Hero 3 cameras were mounted on a small concrete block that was positioned approximately 20 cm above the sand and 50 cm away from patch reefs. The cameras were deployed on the side of the patch where most juvenile focal species were present. Video observations were made in the morning while fish were actively feeding. At the beginning of each video, a measuring stick of one meter was placed at several positions on the reefs to serve as a scale bar to enable later estimation of fish size from the videos, enabling juveniles to be distinguished from adults. Video recording was continuous for at least 50 minutes per patch and was replicated two times per patch reef, on 7-8 February 2014, and again on 17-18 February 2014, with video recordings of four reef patches per treatment per day.

During subsequent video analysis, the number and characteristics of aggressive chases were analysed. Aggressive chases were characterised as rapid movement in the direction of another fish accompanied by flaring of the fins, and could be easily distinguished from general swimming activities on the videos. For each video, a random ten minute fragment was viewed, at least ten minutes into the recording period and 20 minutes from the end, to minimize effects of diver presence. From each video segment the following variables were recorded for each aggressive chase: fish species of the chaser and chased fish, and if the chased fish used the substratum (coral or rubble) to find refuge from or divert the chaser. Refuges were used by both the chaser and the chased fish during aggressive interactions, but could also be used to hide from nearby predators. However, because predator-associated refuge use was rare in our data (it was only observed once), and this was not the direct focus of this paper, this specific behaviour was excluded from analysis. The nature and intensity of aggressive interactions of juvenile focal fish on reefs with differing coral composition was characterised with the following variables: (1) total number of chases instigated by a juvenile focal species (regardless of species identity of the chased fish), (2) total number of chases instigated by a juvenile focal species, standardised for total fish abundance (across all species and life-history stages), (3) intraspecific:interspecific ratio of aggressive chases, (4) use of substratum (coral or rubble) by a chased juvenile focal species to find refuge from or divert the chaser.

The number of chases was used as a proxy for the intensity of aggression. Where fish go when they are chasing or being chased has potential implications for mortality, because fish that do not use the substratum during aggressive chases are potentially more vulnerable to predation, especially when they are less vigilant while chasing or being chased (Carr et al. 2002). In addition, predation rates tend to be higher on bleached and dead coral (rubble) compared to live coral, as fish are generally more visible against the pale/white background of dead coral (Coker et al. 2009). Hence, a loss of live-coral cover, structural complexity and refuges may indirectly increase predation rates. Reefs where abundance of a focal species was zero were excluded from analysis of aggressive interactions instigated by that particular species. Differences between treatments in the total number of chases, and number of chases standardised by total fish abundance were analysed using two linear mixed effects models, with dependent variables respectively log10(x+1) number of chases and standardised number of chases, independent variables treatment and species, and reef included as a random effect. There was quite high variation in the amount of aggressive chases between replicate samples of each reef. In addition, the intensity of intraspecific compared with interspecific aggression was expressed as a ratio (intraspecific:interspecific). This ratio and the use of substratum during aggression on climate-vulnerable and climate-robust reefs were expressed as relative frequencies and analysed using Pearson's Chi-squared tests on untransformed data.

Results

Effect of coral composition on fish abundance and richness

Total fish abundance (across all species and life-history stages) was not significantly different between climate-vulnerable and climate-robust reefs (Fig. 1a) ($t_{2,14}$=-2.07, p=0.057). Similar overall abundances of fishes on the climate-robust versus climate-vulnerable reefs were also related to the fact that some species were equally abundant on both reef types (e.g., *P. amboinensis*), some species decreased in abundance on climate-robust reefs (e.g., *Apogon doederleini*) and other species increased in abundance (e.g., *Apogon cyanosoma*). Residual variation in fish abundance was not correlated with the variation in structural complexity or coral cover between reefs within treatments. Total fish species richness (across all species and life-history stages) was significantly higher on climate-vulnerable reefs ($t_{2,14}$=-3.31, p<0.01), which had, on average, 1.6 times more species than climate-robust reefs (Fig. 1b). These results indicate that reefs with climate-vulnerable coral species, and therefore high coral cover and high topographic complexity, support more fish species per unit area, but approximately equivalent (and variable) fish abundances.

The abundance of juveniles of all focal species was largely consistent across the sampling period, regardless of coral composition (i.e., no ‘time’ effect, Table 2). However, coral composition had species-specific effects on juvenile fish abundance: *P. moluccensis* was 7.5 times more abundant on climate-vulnerable reefs, while the abundance of *P. amboinensis* and *D. perspicillatus* were approximately equal between treatments (species*treatment interaction, Table 2; Fig. 2).

Effect of coral composition on aggressive interactions

On climate-vulnerable reefs, the total number of chases instigated by juveniles of the three focal species was not statistically significant different between climate-vulnerable and climate-robust reefs (Table 3).. *P. amboinensis* instigated a significantly higher number of total chases than *P. moluccensis* and *D. perspicillatus* (Fig. 3a; Table 3). When the number of aggressive chases was standardised for total fish abundance on each patch reef, differences between treatments were reduced and remained non-significant (Fig. 3b; Table 4).

The ratio between intra- and interspecific aggressive chases ('who chases who') significantly differed among the focal species and coral-composition (Fig. 4). Chases instigated by juvenile *P. moluccensis* were mainly interspecific, and the proportion of interspecific chases compared to intraspecific chases was significantly higher on climate-robust compared with climate-vulnerable reefs (χ^2=5.22, df=1, p<0.05) (Fig. 4). However, the intraspecific:interspecific ratio was approximately equal across treatments for *P. amboinensis* (χ^2=1.56, df=1, p=0.21) and *D. perspicillatus* (χ^2=0.36, df=1, p=0.55) (Fig. 4).

On climate-robust and climate-vulnerable reefs, there were differences in substratum use to find refuge from chasers for all three focus species, and the focal species also showed differential use of the substratum among each other(*P. moluccensis*: χ^2=12.84, df=2, p<0.01; *P. amboinensis*: χ^2=152.89, df=2, p<0.0001; *D. perspicillatus:* χ^2=7.97, df=2, p<0.05) (Fig. 5). The proportion of chases in which the chased fish sought refuge from aggression in live coral was ~2 – 3 fold higher on climate-vulnerable reefs for all species (Fig. 5). The proportion in which rubble was used in aggressive chases was higher on climate-robust than on climate-vulnerable reefs for *P. amboinensis* (Fig. 5), whereas the opposite trend was observed for *D. perspicillatus*. In contrast, chased *P. moluccensis* were not observed to use rubble on climate-vulnerable reefs, and only in a very small proportion of the cases on climate-robust reefs (Fig. 5).

Discussion

The coral species compositions of climate-vulnerable and climate-robust patch reefs used in this study reflect a plausible future composition of coral species under ocean warming scenarios. This is the first study actively manipulating coral composition to mimic climate-impacts that examines the abundance of, and interactions between, juvenile coral-reef fishes. Results showed that climate-robust reefs support a lower total species richness of reef fishes compared to climate-vulnerable reefs, but have similar overall abundances, likely because responses to coral-composition are species-specific. Between coral compositions, there were differences in the nature of aggressive interactions, in terms of who chases who and where fish go when they are being chased: the intra:interspecific ratio of aggression was lower for the obligate coral-dwelling fish (*P. moluccensis*), and juvenile fish used the substratum less often to avoid aggression from competitors on climate-robust reefs. However, the overall intensity of aggression did not differ between climate-vulnerable and climate-robust reefs, congruent with the consistent total fish abundance across both coral compositions.

Coral composition expected under climate-change supported lower total species richness than on present-day reefs. This finding is congruent with other studies that have found negative effects of habitat degradation on species richness, both in coral-reef fishes (as reviewed by Pratchett et al. 2011), and in other taxa, including invertebrates (Dean and Connell 1987), birds (MacArthur and MacArthur 1961; Karr and Roth 1971) and insects (Lawton 1983). However, total abundance of coral-reef fishes (across all species and life-history stages) was consistent across coral compositions. Loss of live-coral cover seems to have selective effects on coral-reef fishes, based on their dependence on live coral for food and refuges (as reviewed by Wilson et al. 2006; Pratchett et al. 2008; Pratchett et al. 2011). Hence, the absence of an effect of coral composition (and related lower coral cover and structural complexity) on total fish abundance may be because some species can increase in abundance following coral loss while others decrease. However, to resolve the effects of changing coral composition on the relative abundances of reef fishes in general, future studies are required that manipulate coral composition and monitor the community composition of coral-reef fish over a longer time period.

Coral composition affected the ratio of intraspecific to interspecific aggression ('who chases who'). On climate-robust reefs, the relative importance of interspecific interactions was higher than on climate-vulnerable reefs for juveniles of the obligate coral-dweller *P. moluccensis*, while overall aggression was independent of reef type. The high interspecific aggression on climate-robust reefs instigated by *P. moluccensis* may have been an effect of the lower abundance of this species on these reefs compared to the climate-vulnerable reefs. Although it was beyond the scope of this study, the ratio of intraspecific to interspecific aggression may ultimately have important implications for fish community composition, because it indicates whether the negative effects of aggressive interactions will tend to exclude conspecifics or heterospecifics from reef patches. To understand the relative impacts of intra- versus interspecific aggression on individuals and populations, longer term studies are required, monitoring recruitment, growth and survival of tagged individuals. Also, future studies are required to determine whether and how local abundances of particular species and their competitors mediate the levels of intraspecific and interspecific competition, and how such patterns depend on resource availability.

This is the first study to demonstrate that coral-reef fish use the substratum differently, in terms of where they go to avoid aggressive interactions under different coral compositions. On climate-robust reefs, juvenile reef fish seem to partly compensate for a lower availability of coral by using rubble more frequently than on climate-vulnerable reefs. However, the number of 'unsheltered' chases was also higher on climate-robust reefs, likely as a result of the lower structural complexity on these reefs. On future reefs, this lower frequency of shelter-use could lead to higher predation-related mortality rates. Small-bodied fishes, like the juveniles examined in this study, are highly susceptible to predation, and often depend on specific microhabitats to evade predators (Hixon and Beets 1993; Beukers and Jones 1997), making them especially vulnerable to habitat degradation and changes in coral composition. Although no changes in fish abundance were observed over time during the course of this study, the limited availability of refuges on climate-robust reefs may result in higher predation mortality in the longer term compared to reefs with present-day coral composition (Beukers and Jones 1997; Almany 2004b; Graham et al. 2007), in particular, if fish are less vigilant to predators while chasing or being chased (Carr et al. 2002).

Contrary to expectations, the overall intensity of aggressive interactions was approximately equal on climate-vulnerable and climate-robust reefs.. This indicates that aggression may be more strongly related to fish abundance compared with coral composition and other habitat limitations. To date, no studies have examined the effect of coral composition on aggression dynamics in fishes, but some studies have been conducted on the effect of declining habitat complexity (Basquill and Grant 1998; Baird et al. 2006; Barley and Coleman 2010) and coral health (McCormick 2012) on aggression. In contrast to our results, declining habitat complexity has been associated with an increase in the rate of aggression (Basquill and Grant 1998; Baird et al. 2006), the total time spent interacting with competitors and chasing competitors (Baird et al. 2006; Barley and Coleman 2010), number of bites directed at subordinate fish (Barley and Coleman 2010) and monopolization of food (Basquill and Grant 1998) for temperate reef fish and freshwater fish. Also, as coral health declined, the intensity of aggression of a coral-reef fish toward a competing species increased (McCormick 2012). The abundance of fish on the patch reefs used in this study was much higher than observed in previous studies on (artificial) temperate reefs (Basquill and Grant 1998), on small patch coral-reefs (McCormick 2012) and in freshwater systems (Baird et al. 2006; Barley and Coleman 2010), where sometimes only two individuals per trial were used. As the costs of aggression are known to outweigh the benefits when abundance of competitors is high (Grant 1993), the absence of an effect of coral composition and subsequent differences in habitat complexity on the intensity of aggression in the present study might be driven by the relatively high abundance of fish across treatments.

While this study increases our understanding of behavioural interactions between individuals in coral-reef fishes under climate-induced changes in coral composition, the study also has several limitations. First, unambiguously assigning causality in this study is complicated: coral composition, coral cover and habitat complexity all varied between climate-vulnerable and climate-robust reefs. This was a deliberate choice of the study design, as these variables are confounded in nature. Quantifying the relative importance of complexity versus coral composition on reef fish competition would require further studies using an experimental set up of coral reefs with the same complexity but different coral species composition. Second, there was quite high variation (error bars 12-48% of the mean number of chases) in the total number of aggressive interactions between reefs within treatments. Video analysis was used in this study because aggressive interactions are numerous on these reefs and occur too quickly to be observed accurately on SCUBA. More frequent sampling would help to resolve the drivers of changes in fish behaviour as coral community composition changes. Third, aggressive interactions among individuals can have important effects on outcomes other than abundance, as has for example been shown for feeding rates, growth rates, weight and body condition (Jones 1987; Höjesjö et al. 2004; McCormick and Lönnstedt 2013). As body size and fecundity are closely related in most coral-reef fishes (Kuwamura et al. 1994; Hobbs and Munday 2004), longer term studies monitoring growth and adult fecundity will be useful to determine longer-term effects of aggressive behaviour on vulnerable and robust reefs on community composition of reef fishes. Fourth, the presence and abundance of adult fishes can have major effects on the recruitment, behaviour and abundance of fishes (Almany 2004a,b; Lecchini et al. 2005). Hence, future studies examining the effect of coral composition under climate-change on recruitment, priority effects and post-recruitment survival and behaviour will give a more comprehensive understanding of how habitat change affects coral-reef fishes.

This study highlights the importance of coral composition for coral-reef fishes in terms of species richness and interactions between fishes. This is the first study to show that specific differences in coral composition that are independent of coral health, and are mimicking present-day coral composition and coral composition predicted under climate change, are linked to species-specific differences in the ratio of intra:interspecific aggression, and where fishes go in the substratum when they are being chased. Predictions of how community composition of reef fishes will change as a result of climate change depends on understanding what mechanisms are driving the effects of climate-induced changes in coral composition on reef fish communities. To contribute to addressing this knowledge gap, the present study has shown that changes in coral composition affected the nature and intensity of aggression in juvenile reef fishes.

Acknowledgements: We thank Tessa Hempson, Aaron MacNeil, and Karen Chong-Seng for assistance with building the patch reefs, and for census data of fish on the patch reefs collected in early December 2013 and late January 2014. The authors also thank Grace Frank, Alex Vail, Kirsty Nash and staff of Lizard Island Research Station for assistance during fieldwork, and two anonymous reviewers whose comments helped to clarify the interpretation of our results. Funding for this project was provided by the Australian Research Council and James Cook University.

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Figure legends

Fig. 1 (**a**) Total fish abundance, across all species and life-history stages, expressed as average number of fish per patch reef, and (**b**) species richness, pooled across all fish species and life-history stages, expressed as average number of fish species per patch reef, both including all species of reef-fish and life-history stages, on climate-vulnerable and climate-robust reef patches. * indicates a significant difference between treatments at p=0.05 or lower; error bars indicate standard errors.

Fig. 2 Average abundance of juvenile *Pomacentrus moluccensis, P. amboinensis* and *Dischistodus perspicillatus* on climate-robust and climate-vulnerable reefs. Values are the number of juvenile focal species per patch reef. * indicates a significant difference between treatments at p=0.05 or lower.

Fig. 3 (**a**) Average total number of chases, and (**b**) average number of chases standardised for total fish abundance, instigated by a juvenile focal species, on climate-robust and climate-vulnerable reefs. Values indicate number of aggressive chases per ten minute video fragment per patch reef.

Fig. 4 Relative frequency of intraspecific and interspecific aggressive chases instigated by juveniles of the three focal species, on climate-robust and climate-vulnerable reefs. * indicates a significant difference between treatments for that particular species at p=0.05.

Fig. 5 Relative frequency with which chased individuals of the focal species use the substratum to seek refuge from, or divert juvenile focal chasers on climate-robust and climate-vulnerable reefs. * indicates a significant difference between treatments for that particular species at p=0.05 or lower.