Coral colony size and structure as determinants of habitat use and fitness of coral-dwelling fishes

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ABSTRACT: Competition for space affects patterns of habitat use and individual performance of coral-dwelling fishes; however, the physical attributes of corals that influence habitat preferences are uncertain. In this study, we investigated the influence of coral colony size and branching structure of 2 coral species, *Acropora nasuta* and *Acropora spathulata*, on habitat use and growth rate of 2 coral gobies, *Gobiodon histrio* and *G. erythrospilus.* First, we examined 2 key aspects of coral colony structure (interbranch depth and interbranch width) that may influence habitat preferences. We then used laboratory and field-based experiments to test the effects of coral species, coral colony size and branching structure on habitat preference and growth rates of *G. histrio* and *G. erythrospilus.* The preferred coral species, *A. nasuta*, had smaller interbranch width than *A. spathulata*. A binary-choice laboratory experiment demonstrated that both goby species preferred coral colonies with smaller interbranch width, except when they had the opportunity to occupy *A. nasuta* over *A. spathulata*. A field transplant experiment showed that both goby species grew faster on larger coral colonies and in colonies with smaller interbranch width. *G. erythrospilus* grew faster than *G. histrio* on *A. spathulata*, indicating that it suffers less fitness loss when occupying this alternative habitat. Our results show that coral physical attributes are important factors driving habitat preference of coral-dwelling gobies; however, there must also be additional factors that influence their habitat use. Declining average coral size and reduced habitat complexity on coral reefs could have significant impacts on the performance of fishes, affecting ecological processes such as competition.

KEY WORDS: Habitat complexity · Competition · Growth rate · Goby · *Gobiodon* spp. · *Acropora* spp.

INTRODUCTION

Habitat characteristics have a profound influence on the distribution, abundance and diversity of animals associated with complex habitats, such as rainforests (McIntyre 1995) and coral reefs (Friedlander & Parrish 1998, Jones & Syms 1998). Habitat quality, patch size, location and structural complexity can all be important predictors of species diversity and influence ecological interactions among resident species (Crowder & Cooper 1982, Grabowski 2004, Kovalenko et al. 2012, Fabricius et al. 2014). Species are expected to select habitat types that benefit individ-

ual fitness and may compete for access to these habitats (Adler & Gordon 2003, Wakefield et al. 2014). However, competitive interactions are often asymmetric, such that superior competitors gain greater access to preferred habitats and inferior competitors are forced to use suboptimal habitat, regardless of their natural preference, with consequences for growth, survival and reproduction (Gibb 2011, Carrington 2014, Bonin et al. 2015).

Coral reefs are well known for their astonishing diversity of fishes (Sale 1977). A range of habitat-associated variables such as coral cover, coral diversity and structural complexity can influence the com-

munity structure and population dynamics of reef fish (Messmer et al. 2011, Coker et al. 2012, Komyakova et al. 2013). Habitat characteristics may be especially important for species that have a close association with live coral habitat, influencing recruitment, survival, group size and individual growth (e.g. Kuwamura et al. 1994, Holbrook & Schmitt 2003, Thompson et al. 2007, Schiemer et al. 2009, Noonan et al. 2012). The complex architecture of coral colonies created by their branching structure constitutes the living space for many small reef fishes (Coker et al. 2014). Coral species differ greatly in their structural complexity and this may influence the diversity and abundance of coral-associated fishes (Messmer et al. 2011). Furthermore, many coral species exhibit substantial intraspecific morphological variation (Veron & Pichon 1976, Vytopil & Willis 2001, Schiemer et al. 2009), which may influence the quality of shelter they provide for fish (Untersteggaber et al. 2014). Variation in habitat quality and structural complexity can influence ecological interactions among reef fishes, such as competition and predation (Beukers & Jones 1997, Almany 2004, Harborne et al. 2011). Consequently, variation in coral colony physical characteristics is likely to play an important role in determining the population dynamics of coral-associated fishes.

Gobies in the genus *Gobiodon* are obligate coral-dwelling fishes that live among the branches of *Acropora* coral colonies. Some goby species are highly specialized, inhabiting just 1 or 2 species of *Acropora*, whereas other species are more generalist and will use a variety of *Acropora* species (Munday et al. 1997, Dirnwöber & Herler 2007). Coral-dwelling gobies compete for access to preferred coral colonies (Munday et al. 2001, Hobbs & Munday 2004, Pereira et al. 2015) and utilization of different coral species has significant effects on individual performance (Munday 2001, Caley & Munday 2003). However, the physical attributes of coral colonies (e.g. coral size and branching structure) that drive habitat preferences and competition for different *Acropora* species are unknown. If coral colony structure influences the risk of predation, we expect that coral species with greater interbranch depth (ID) and smaller interbranch width (IW) will be preferred as they will provide more protection against predators. Interbranch spacing could also influence foraging efficiency through an interaction between predation risk and ease of access to food resources. Consequently, we expect that growth and survival rates of coral-dwelling gobies will be associated with coral interbranch spacing. Coral-dwelling gobies also prefer

larger coral colonies (Hobbs & Munday 2004, Schiemer et al. 2009), possibly because they enhance growth and survival. Several studies have explored the relationship between coral colony structure and the body shape of coral-dwelling gobies (Untersteggaber et al. 2014, Wehrberger & Herler 2014), but the inter-relationships among coral colony structure, habitat preferences, and the individual performance of coral-dwelling gobies has not yet been tested.

Gobiodon histrio and *G. erythrospilus* are ecologically similar goby species that compete for access to their preferred habitat, *Acropora nasuta* (Munday 2004, Pereira et al. 2015). Previous studies have shown that both niche-partitioning and lottery mechanisms of competition influence habitat use and abundance of these 2 goby species, and that the relative importance of these competitive mechanisms changes with ontogeny (Pereira et al. 2015). Furthermore, the 2 species have similar patterns of habitat use when *A. nasuta* is abundant, but the subordinate competitor, *G. erythrospilus*, is forced to use disproportionately more of an alternative coral host, *A. spathulata*, when *A. nasuta* is scarce (Pereira et al. unpubl.). While competitive interactions between these 2 goby species have been studied in detail, the characteristics of coral colonies that drive habitat preferences and differences in individual performance for fish inhabiting the 2 coral species remain unknown. Coral interbranch space appears to have influenced the evolution of body shapes among *Gobiodon* species (Wehrberger & Herler 2014); therefore, the physical attributes of coral colonies are likely to be determinants of habitat use and fitness of these coral-dwelling fishes.

This study aimed to better understand the physical characteristics of coral colonies that drive habitat preference and competition in coral-dwelling gobies. First, we compared key aspects of coral colony branching structure (ID and IW) between *A. nasuta* and *A. spathulata*. We then used binary-choice laboratory experiments to test the preference of *G. histrio* and *G. erythrospilus* for *A. nasuta* and *A. spathulata* colonies with either wide or narrow branching structure. Finally, we transplanted gobies to colonies of *A. nasuta* and *A. spathulata* in the field and correlated growth rates with coral species, coral colony size and branching structure. We predicted higher growth rates of both goby species when inhabiting the preferred habitat (*A. nasuta*) compared with the alternative habitat (*A. spathulata*), and also an increase in growth rate with increasing coral colony size and increasing structural complexity. Furthermore, for

individuals inhabiting the alternative habitat, we expect a greater cost to growth rate for the superior competitor (*G. histrio*) compared with the subordinate competitor (*G. erythrospilus*).

MATERIALS AND METHODS

Study location

Field surveys and a transplant experiment were conducted in October 2013 and January 2014 on reefs at Lizard Island in the northern Great Barrier Reef, Australia (14° 38′ S, 145°′ 26′ E).

Coral interbranch space

Coral interbranch depth (ID) and interbranch width (IW) are key parameters associated with the body shape of coral-dwelling gobies and have been implicated in the differences in growth rates of goby species. ID and IW were measured in a total of 50 colonies of *Acropora nasuta* and 50 colonies of *A. spathulata*. Only colonies inhabited by 1 or more *Gobiodon histrio* or *G. erythrospilus* were measured. To control for a possible correlation between coral colony size and interbranch space, the size of coral colonies was standardized between 20 and 30 cm at their longest axis. The relationship between coral colony size and interbranch space for *A. nasuta* and *A. spathulata* was later tested using coral colonies in the field transplant experiment (see 'Field transplant experiment' below). An underwater calliper was used to precisely measure ID and IW with a total of 10 measurements of each variable taken at haphazard locations on each coral colony. The average of the 10 measurements was calculated for each coral colony.

A *t*-test was used to compare mean ID and IW between similar sized colonies of the 2 coral species. ANCOVA was then applied to coral data collected during the field transplant experiment to test if coral colony size, within and among species, influences the IW of *A. nasuta* and *A. spathulata*. This analysis tested for homogeneity of regression slopes of IW on coral colony size for the 2 coral species, and for a significant relationship between IW and coral colony size.

Coral complexity binary-choice experiment

A binary-choice experiment was used to test the preference of *G. histrio* and *G. erythrospilus* for colonies of different IW. Colonies (15–20 cm diameter) of *A. nasuta* and *A. spathulata* were carefully removed from the reef, transported alive to the laboratory, and cleared of all infauna (gobies, crabs and shrimps). Colonies were visually characterized as having a wide or narrow IW. Subsequently, at the end of the experiment, the volume and IW of each colony was measured. The water-displacement method (Herler & Dirnwöber 2011) was used to estimate the total volume, and average IW was calculated by the mean of 10 measurements of IW per coral colony.

Four different combinations of coral species and IW were used to test the preference of *G. histrio* and *G. erythrospilus* for colonies of each coral species and with either wide or narrow IW: (1) *A. nasuta* with wide IW vs. *A. nasuta* with narrow IW, (2) *A. spathulata* with wide IW vs. *A. spathulata* with narrow IW, (3) *A. spathulata* with wide IW vs. *A. nasuta* with narrow IW and (4) *A. nasuta* with wide IW vs. *A. spathulata* with narrow IW. One colony of each coral species (approximately equal volume) was placed at opposite ends of a glass aquarium (50 × 30 × 30 cm). The position of each coral species on either the left or right side of each aquarium was changed regularly during the experiment and coral colonies were replaced if their condition visibly deteriorated. Gobies were collected from the field by lightly anaesthetizing them with clove oil (Munday & Wilson 1997). A single individual of *G. histrio* or *G. erythrospilus* (ranging from 1.5 to 3.8 cm) was released between 18:00 and 19:00 h in the middle of the glass aquarium and their choice of *A. nasuta* or *A. spathulata* recorded between 06:00 and 07:00 h the following morning (Munday et al. 2001, Pereira et al. 2015). Initial trials indicated that individual fish were unlikely to move between coral colonies after 12 h. Habitat preference was tested for 24 individuals of each species in each of the 4 coral combinations.

A chi-squared goodness of fit test was used to test for non-random habitat preference for *G. histrio* and *G. erythrospilus* in each of the 4 combinations.

Field transplant experiment

A transplant experiment was used to test if growth rates of *G. histrio* and *G. erythrospilus* were influenced by coral colony size and IW. Specifically, we predicted that growth of the 2 goby species would be positively correlated with coral size and negatively correlated with IW. In other words, we predicted that both species of goby would grow faster

in larger coral colonies with narrower IW. Further, we predicted that growth of the subordinate competitor, *G. erythrospilus*, would be higher compared with the superior competitor, *G. histrio*, when occupying an alternative habitat, *A. spathulata*, and that IW and coral colony size could directly influence this relationship.

Growth rates of *G. erythrospilus* and *G. histrio* on the preferred (*A. nasuta*) and alternative (*A. spathulata*) coral species were determined in a 3 mo period between January and April 2014. A total of 25 individuals of each goby species were collected from *A. nasuta* by lightly anaesthetizing them with clove oil. Only juvenile gobies (<2.0 cm standard length [SL]) were used during the transplant experiment in order to achieve a good growth potential. Collected fishes were transported to the laboratory, measured (SL to 0.1 mm) and individually marked with a small fluorescent-elastomer tag injected into the dorsal musculature (Munday 2001). Tagged fishes were held for 24 h in aquaria to ensure recovery. Fishes were then transported to the reef and released on coral colonies of *A. nasuta* and *A. spathulata*. A total of 25 individuals of each goby species were transplanted to each of the 2 coral species. Coral colonies were tagged for subsequent identification and any resident fishes present were removed before a goby was released onto a coral colony. After 3 mo, all the remaining fishes were collected from marked coral colonies and the SL of each tagged fish was measured in the laboratory to determine the increase in size. The size and IW of each coral colony were measured as described in 'Materials and methods: Coral interbranch space'.

Chi-squared analysis was used to compare survivorship of both goby species between the 2 species of coral and also the survival of the 2 goby species independent of the coral they were transplanted to.

Linear mixed effects (LME) models were used to compare the growth of both goby species in both coral species (*A. nasuta* and *A. spathulata*), while accounting for IW and coral colony size. In the LME model, the fixed effects were goby species and coral species and the random effects were coral colony size and IW. Individual goby growth was the dependant variable. Interactions between fixed and random effects and the growth rates of *G. erythrospilus* and *G. histrio* were also tested. If the effects of coral colony size and IW on goby growth differed between coral species, we expected to find a significant interaction between IW and coral species, and also coral colony size and coral species. LME was performed in R using the package nLme.

RESULTS

Coral interbranch space

Acropora nasuta had a mean ID of 81.37 ± 14.01 mm and *A. spathulata* had a mean ID of 72.53 ± 15.12 mm, which was not significantly different ($t = 10.76$, df = 1, p = 0.1). However, there was a significant difference in IW between the 2 coral species ($t = 6.19$, df = 1, p = 0.001). *A. nasuta* had a mean IW of 16.078 ± 4.12 mm and *A. spathulata* had a mean IW of 23.84 ± 4.82 mm (Fig. 1). There was no correlation between IW and coral colony size for either *A. nasuta* ($R^2 = 0.01$; p = 0.3) or *A. spathulata* ($R^2 = 0.09$; p = 0.2). Furthermore, there was no difference in the relationship between coral colony size and IW for the 2 coral species, as indicated by the homogeneity of slopes ($F_{1, 29} = 3.63$, p = 0.5) (Fig. 2).

Coral complexity binary-choice experiment

Both goby species exhibited a strong preference for coral colonies with narrow IW, both for *A. nasuta* (*Gobiodon histrio*: $\chi^2 = 5.93$, df = 1, p = 0.001; *G. erythrospilus*: $\chi^2 = 6.03$, df = 1, p = 0.001) and *A. spathulata* (*G. histrio*: $\chi^2 = 5.59$, df = 1, p = 0.001; *G. erythrospilus*: $\chi^2 = 5.59$, df = 1, p = 0.001) (Fig. 3A,B). Both goby species also exhibited a strong preference for *A. nasuta* when given the choice of *A. spathulata* with wide IW or *A. nasuta* with narrow IW (*G. histrio*: $\chi^2 = 4.13$, df = 1, p = 0.001; *G. erythrospilus*: $\chi^2 = 3.56$, df = 1, p = 0.001) (Fig. 3C). However, they did not
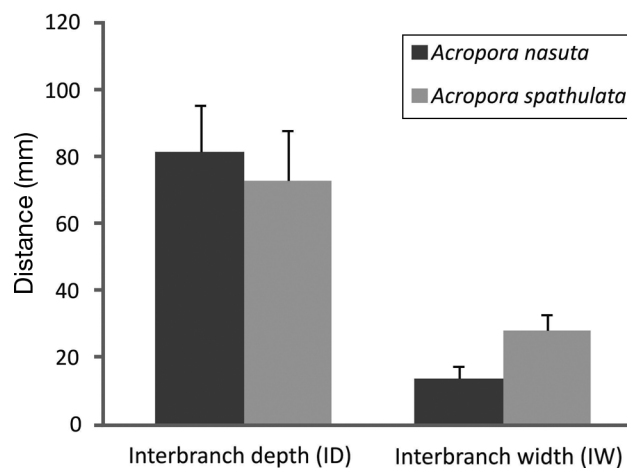

Fig. 1. Interbranch space of *Acropora nasuta* and *A. spathulata* coral colonies. N = 50 for each coral species. Error bars: + SD

prefer the coral colony with narrow IW in the reverse combination. Both goby species preferred coral colonies of *A. nasuta* with wide IW over a colony of *A. spathulata* with narrow IW (*G. histrio*: χ^2 = 3.72, df = 1, p = 0.001; *G. erythrospilus*: χ^2 = 2.91, df = 1, p = 0.001) (Fig. 3D).
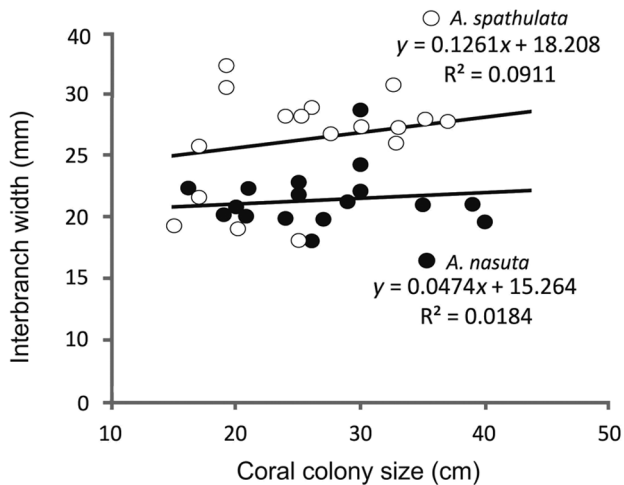

Fig. 2. Relationship between interbranch width and coral colony size of *Acropora spathulata* and *A. nasuta* using corals from the transplant experiment. N = 17 for each coral species

Field transplant experiment

The average size of transplanted fishes at the beginning of the experiment was 17.4 mm SL for *G. histrio* and 17.7 mm for *G. erythrospilus*, and there was no difference in the size of the transplanted gobies between the 2 species (*t* = 0.28, df = 48, p = 0.77).

There was no difference in survivorship of *G. histrio* transplanted to *A. nasuta* (44%) and *A. spathulata* (36%) (χ^2 = 0.86, df = 1, p = 0.86). Similarly, there was no difference in survivorship of *G. erythrospilus* transplanted to *A. nasuta* (48%) and *A. spathulata* (44%) (χ^2 = 0.14, df = 1, p = 0.70). Overall, no significant different was observed in the survivorship of the 2 goby species in the experiment (χ^2 = 8.14, df = 1, p = 0.93).

LME revealed a significant effect of coral species on growth of fish transplanted to colonies of *A. nasuta* and *A. spathulata* (Table 1). Additionally, there were significant interactions between IW and coral species, and colony size and coral species, on the growth of gobies (Table 1). In general, both *G. histrio* and *G. erythrospilus* grew faster on larger coral colonies with smaller IW (Figs. 4 & 5). There was a negative relationship between IW and growth of *G. erythrospilus* and *G. histrio*; however, the effect
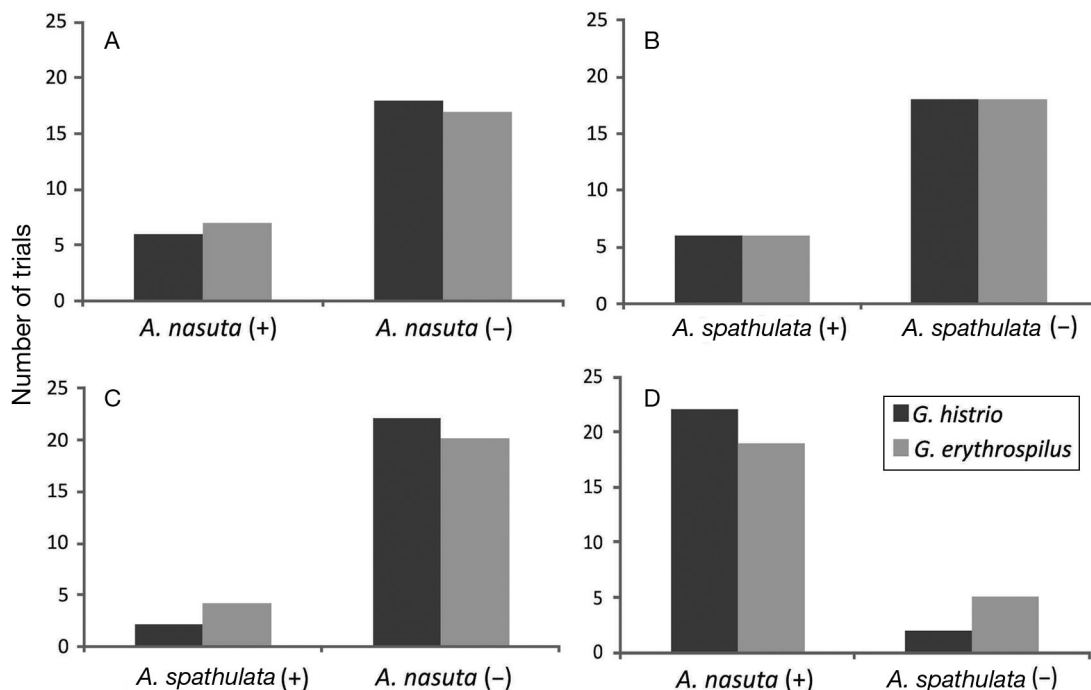

Fig. 3. Preference of *Gobiodon histrio* and *G. erythrospilus* for colonies of *Acropora nasuta* and *A. spathulata* with either a wide (+) or narrow (−) interbranch width in the binary-choice experiment: (A) *A. nasuta* (+) or (−), (B) *A. spathulata* (+) or (−), (C) *A. spathulata* (+) or *A. nasuta* (−), (D) *A. nasuta* (+) or *A. spathulata* (−). N = 24 for each goby species in each combination

was stronger for fish inhabiting *A. spathulata* coral colonies compared to *A. nasuta* (Fig. 4). Gobies grew faster on larger coral colonies, but there was an interaction with coral species (Fig. 5).

Table 1. Linear mixed effects model comparing growth rates of *Gobiodon erythrospilus* and *G. histrio* transplanted from *Acropora nasuta* to *A. nasuta* or *A. spathulata* with covariance of interbranch width (IW) and coral size

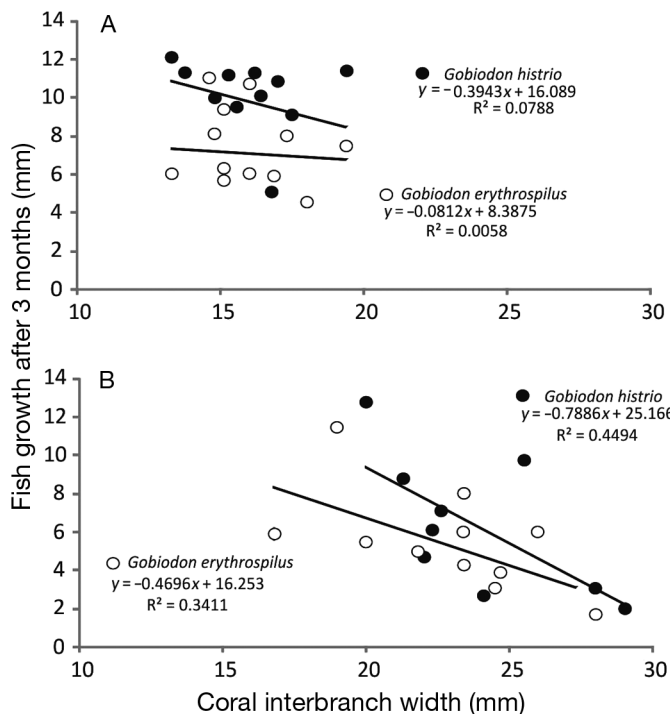|	Value	SE	df	*t*	p
Intercept	16.6840	11.3210	28	1.47	0.15
Goby spp.	−1.7136	5.0544	28	−1.34	0.73
Coral spp.	−8.5414	4.9010	28	−0.47	0.03
Colony size	−0.2011	0.4234	28	−1.74	0.63
IW	−0.9400	0.6980	28	−0.33	0.18
IW × Colony size	0.0265	0.0255	28	1.03	0.30
IW × Coral spp.	0.7581	0.2816	28	2.69	0.01
IW × Goby spp.	−0.1110	0.2788	28	−0.39	0.06
Colony size × Coral spp.	−0.2992	0.1861	28	−1.60	0.02
Colony size × Goby spp.	0.2666	0.1216	28	2.19	0.06
Coral spp. × Goby spp.	−4.5829	2.0556	28	−2.22	0.07

Fig. 4. Relationship between coral interbranch width and growth (SL) of gobies *Gobiodon histrio* and *G. erythrospilus* transplanted from colonies of *Acropora nasuta* to colonies of (A) *A. nasuta* and (B) *A. spathulata*. N = 11 *G. histrio* and 12 *G. erythrospilus* for (A), and N = 9 *G. histrio* and 11 *G. erythrospilus* for (B)
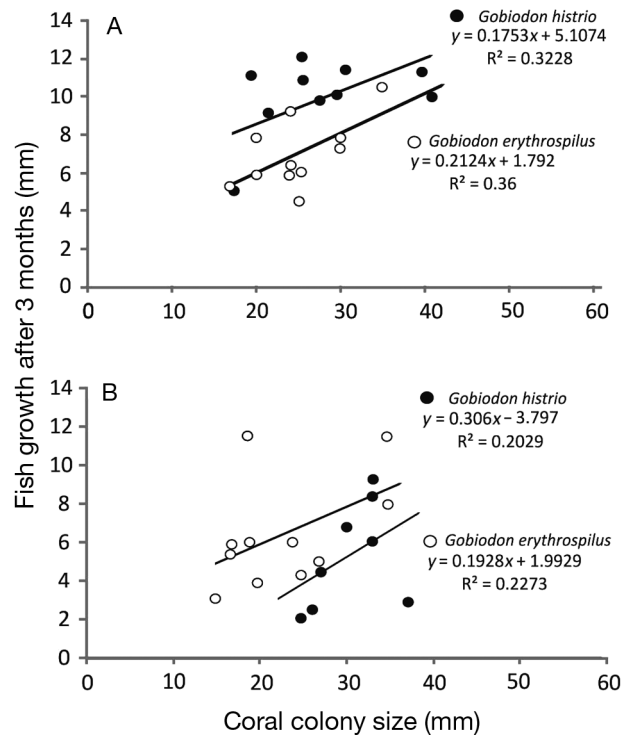

Fig. 5. Relationship between coral colony size and growth of gobies *Gobiodon histrio* and *G. erythrospilus* transplanted from colonies of *Acropora nasuta* to colonies of (A) *Acropora nasuta* and (B) *A. spathulata*. N = 10 *G. histrio* and 11 *G. erythrospilus* for (A), and N = 8 *G. histrio* and 11 *G. erythrospilus* for (B)

While interactions between goby growth and (1) IW and goby species, (2) colony size and goby species, and (3) coral species and goby species were not statistically significant (p = 0.06−0.07; Table 1), there were important trends to highlight. Most notably, *G. histrio* tended to grow faster on *A. nasuta* compared to *G. erythrospilus*, whereas *G. erythrospilus* maintained similar growth on both coral species (Figs. 4 & 5).

DISCUSSION

Our results empirically demonstrate that coral colony size and branching structure directly influence habitat use and growth of coral-dwelling fishes. When considering coral colonies with the same habitat volume, both goby species preferred corals with smaller IW, supporting the hypothesis that coral complexity is an important component of habitat selection for these fishes. However, gobies still preferred *Acropora nasuta* over *A. spathulata* when they had the opportunity to occupy it, suggesting that there

must also be other factors (e.g. coral nutritional quality) that determine the preference of one coral species over another. Additionally, a field transplant experiment demonstrated a negative correlation between coral IW and growth for gobies transplanted from *A. nasuta* to *A. spathulata*, which can explain the preference of gobies for coral colonies with narrow interbranch space. Furthermore, there was a positive correlation between coral colony size and growth rates of *Gobiodon histrio* and *G. erythrospilus*, with both species growing faster on larger coral colonies. Yet, goby growth was also influenced by interactions between IW, coral colony size and coral species, indicating that the effects the physical characteristics of coral colonies have on goby growth rates differed between coral species.

Habitat patch size is often a good predictor of abundance and species richness in natural communities (Gaston & Blackburn 1996, Robles & Ciudad 2012, Leal et al. 2015). On coral reefs, it also seems that habitat patch size could influence the fitness-associated traits (e.g. growth and survival) of reef fishes (Noonan et al. 2012). During the present study, we found that gobies grew faster in larger coral colonies. Coral-dwelling gobies usually tend to exclude other fishes from their coral habitat and defend corals from corallivorous predators (Dirnwöber & Herler 2013). Just one breeding pair normally occupies each coral colony; therefore, it is likely that larger coral colonies could require more time and energy to defend, but overall are probably optimal habitats because they provide larger feeding areas. The concept of economic defensibility (Brown 1964) is widely used to explain territorial behaviour in reef fishes (Mumby & Wabnitz 2002). It predicts the development of territorial behaviour if the benefits derived from exclusivity of access to a particular resource are greater than the cost of defending it. Therefore, it is likely that the growth benefits that gobies attain from access to larger coral colonies outweigh any additional cost of defence. A similar trend was observed for damselfishes occupying fire-coral on Brazilian reefs, where regardless of an increase in *Stegastes fuscus* aggressive behaviour, larger *Millepora* spp. coral colonies were still preferred (Leal et al. 2015).

Habitat complexity can influence the distribution and abundance of coral reef fishes on a variety of spatial scales (Friedlander et al. 2003, Coker et al. 2013, Komyakova et al. 2013). Specifically, for coral-dwelling fishes, attributes of coral colony branching structure are likely to be important variables in determining individual fitness. For example, Wehrberger & Herler (2014) showed that coral architecture influences the size, shape and growth of coral-associated fishes. We found that *G. histrio* and *G. erythrospilus* both exhibited a preference toward and grew faster on coral colonies with narrow IW. Factors such as protection for predators and superior nesting sites seem to be the most important variables driving habitat preference of coral-associated fishes. For example, Holbrook & Schmitt (2002) showed that juvenile coral specialists are more likely to be eaten by predators that were closer to their own body size than larger ones; therefore, even subtle differences in branching structure could influence predation rates on coral-dwelling gobies.

As observed in previous studies (Pereira et al. 2015), we found that *G. histrio* and *G. erythrospilus* preferred colonies of *A. nasuta* over *A. spathulata*. IW differed among the 2 coral species, and growth rates of the gobies was directly correlated with IW, suggesting that coral branching structure is possibly one of the most important factors influencing goby habitat preference and subsequent fitness. However, both goby species still exhibited a strong preference for *A. nasuta* when it had a wider IW than *A. spathulata*. This indicates that factors other than IW must influence habitat selection by coral-dwelling gobies. *A. nasuta* is the preferred habitat for a number of *Gobiodon* species, including the 2 species studied here (Munday 2001, Pereira et al. 2015), and must provide additional resources above and beyond suitable habitat structure. The additional benefits of inhabiting *A. nasuta* are unknown, but could be associated with nutrition or breeding sites. Coral-dwelling gobies attain part of their nutritional resources from their host corals (Brooker et al. 2010), and *A. nasuta* might have a higher nutritional status. Future studies could examine lipids levels in coral tissue to test this hypothesis. Alternatively, regardless of differences in branching structure, *A. nasuta* colonies might offer superior locations for nesting due to other aspects of coral morphology.

Interactions between IW and coral species, and also colony size and coral species, influenced goby growth in the field experiment. These interactions demonstrate that a complex set of coral colony physical characteristics define optimal habitat for coral-dwelling fishes. Goby growth was lowest on *A. spathulata* colonies with wide IW (i.e. less complex habitats) and highest on *A. nasuta* colonies with narrow IW. Colony size also interacted significantly with coral species. *G. histrio* and *G. erythrospilus* inhabiting larger *A. nasuta* coral colonies exhibited higher growth rates compared to gobies living on *A. spathulata*. Additionally, as a general trend, both species

demonstrated significantly higher growth rates on *A. nasuta* compared with *A. spathulata*. The interactions observed in our field-based experiment highlight the fact that combinations of different coral physical attributes influence the growth of coral-dwelling fishes, but these relationships are not identical for fish occupying different coral species. The diet of coral-dwelling gobies is composed of a mix of macrofauna, zooplankton invertebrates and coral tissue (Riedlecker & Herler 2008, Brooker et al. 2010). Therefore, variations in the abundance and diversity of coral-associated invertebrates due to changes in coral complexity (Vytopil & Willis 2001, Stella et al. 2014), and also ontogenetic changes in the nutritional quality of *Acropora* species per se (Pratchett 2007), are likely to influence the performance of coral-dwelling gobies. If the availability of food resources is unequal on different coral species with different size and branching structure, this could potentially explain the interaction between IW and coral species, and also colony size and coral species, on goby growth.

Preferred habitat is a limited resource for coral-dwelling gobies (Munday et al. 2001), with up to 98.0% of all colonies of *A. nasuta* occupied (Hobbs & Munday 2004). Our results indicate that both *G. histrio* and *G. erythrospilus* are likely to prefer larger and structurally complex *A. nasuta* coral colonies. However, these habitat preferences are altered by competition between species. Coral-dwelling gobies coexist by a range of mechanisms, including niche partitioning and lotteries (Munday et al. 2001, Pereira et al. 2015). Even though innate preferences exist, it seems that larger individuals of *G. histrio* are the superior competitors and thus have greater access to preferred habitat. As a result, *G. erythrospilus* is often forced to use the alternative habitat, *A. spathulata*. The ability of *G. erythrospilus* to maintain its performance on *A. spathulata* coral colonies appears to be critical in enabling it to coexist with *G. histrio* (Pereira et al. 2015). Our transplant experiment demonstrated that *G. erythrospilus* suffered much less of a fitness loss when occupying the non-preferred coral, compared with *G. histrio*, which could explain its ability to persist when displaced by the superior competitor.

The role of habitat identity and structure on species performance and fitness has been extensively analysed in a broad range of ecosystems such as tropical rainforests, savannas and rivers (Crowder & Cooper 1982, Wellborn 2002, Gibson et al. 2004). Similar to our results from coral reef gobies, species performance was positively associated with habitat complexity in tropical seagrass beds (Stoner & Lewis 1985) and kelp forests (Bodkin 1988). Habitat identity and complexity in marine ecosystems are likely to influence individual performance due to an increase in resource availability and/or protection from predators. Our findings support the hypothesis that higher food resources could sustain superior growth rates, and appropriate habitat complexity allows individuals to reduce energy demands associated with avoiding predators.

Coral reef habitat is being degraded by the combined effects of storms, crown-of-thorns starfish outbreaks, coral bleaching and diseases (Gardner et al. 2003, Alvarez-Filip et al. 2009, De'ath et al. 2012). Loss of habitat structure has a major effect on reef fish communities. For example, loss of reef structural complexity by cyclones has a larger impact on reef fish communities than an outbreak of the coral-eating sea star *Acanthaster* spp., which cause widespread coral mortality, but leave the physical structure of the reef intact in the short term (Adam et al. 2014). Likewise, the average size of coral colonies is declining due to the increasing frequency of disturbances that cause partial or whole colony mortality (Baird & Marshall 2002, Nugues & Roberts 2003, McClanahan et al. 2008). Our results suggest that a decrease in the average size and structural complexity of coral colonies, caused by ongoing disturbances, may affect patterns of habitat use and subsequent fitness of coral-associated fishes. Furthermore, a decrease in coral architectural complexity may affect recruitment and competition within reef fish communities. Competition could be increased as the availability of large and complex coral colonies diminishes, with consequences for the populations of fishes that depend on coral habitat for their survival.

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