

Competitive mechanisms change with ontogeny in coral-dwelling gobies

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Abstract. Recent theory suggests that a mix of lottery and niche processes can facilitate coexistence between competing species, but this has not yet been empirically tested. Previous research has suggested that a competitive lottery for space promotes coexistence between two ecologically similar species, *Gobiodon histrio* and *Gobiodon erythrospilus*. However, not all the assumptions of lottery competition have been tested, and patterns of habitat use by adults suggest niche partitioning. Here, we investigated the hypothesis that the mechanism of competition changes with ontogeny, with a lottery for space operating at settlement and niche partitioning occurring in adults. Patterns of resource use in the field were compared for juveniles and adults of the two species. Pelagic larval duration (PLD) and size-at-settlement was also estimated to determine if size differences at settlement could affect the outcome of competitive interactions among juveniles. Habitat preference and size-based competitive ability were then tested for juveniles and adults in laboratory experiments. Finally, a transplant experiment was performed to test the fitness-associated consequences of niche partitioning among adults and its implications for coexistence of the two species. *G. histrio* had a similar PLD (20.7 ± 2.0 days) to *G. erythrospilus* (18.5 ± 1.9 days), and there was no difference in size-at-settlement between the species. Juveniles of the two species had similar patterns of habitat use and similar competitive abilities, supporting the lottery mechanism at settlement. However, adults differ in their habitat use, supporting the prediction that resource partitioning increases with ontogeny. In laboratory experiments, adults of each species preferred colonies of *Acropora nasuta*. However, *G. histrio* was a superior competitor and prevented *G. erythrospilus* from using *A. nasuta* in >70% of the trials. In the field transplant experiment, *G. erythrospilus* (inferior competitor) suffered less of a fitness loss when occupying the non-preferred coral (*A. spathulata*) compared with *G. histrio*, which could explain its ability to persist when displaced by the superior competitor. These results suggest that the competitive mechanism operating between the two *Gobiodon* species shifts from a lottery for space to niche partitioning through ontogeny, and that these two mechanisms of competitive coexistence are not mutually exclusive.

Key words: competition; coral reefs; *Gobiodon*; Great Barrier Reef; lottery hypothesis; reef fishes; resource partitioning.

INTRODUCTION

Competition is a fundamental ecological process, influencing population size, biomass, species richness, and community structure (Elton 1946, Dayton 1971, Levin 1974, Connell 1983, Tilman 1994). The traditional view of interspecific competition was that one species would dominate, leading either to resource partitioning between the species, or the elimination of the weaker competitor from the habitat (Colwell and Fuentes 1975). While a number of theoretical studies have advanced alternative ideas to account for the coexistence of ecologically similar species in animal communities (Sale 1977, Abrams 1984, Warner and Chesson 1985, Chesson

2000, Hubbell 2001), these hypotheses have not always been adequately tested (Yu and Wilson 2001, Salomon et al. 2010). In fact, a limitation to understanding the role of competition in structuring ecological communities is that theoretical explanations for competitive coexistence have generally advanced more rapidly than empirical investigations, and more field observations and experiments are necessary to test predictions of existing hypotheses (Amarasekare 2003, Shinen and Navarrete 2010, Siepielski and McPeck 2010, Hixon 2011).

Traditional niche-based models of competition propose that competing species coexist through resource partitioning (Colwell and Fuentes 1975, Diamond 1978). These models predict that species are able to coexist in complex environments by partitioning resources, such as food (Hyndes et al. 1997, Pimentel and Joyeux 2010) and shelter (Ross 1986, Schmitt and Holbrook 1999). If a species decreases the range of resource used, thereby

Manuscript received 4 September 2014; revised 14 April 2015; accepted 27 April 2015. Corresponding Editor: M. H. Carr.

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specializing on a narrower range of resources, this could result in reduced levels of competition with other species (Armstrong and McGehee 1980). Consequently, coexistence in a spatially heterogeneous environment is possible by species specialization on different resources (Colwell and Fuentes 1975, Amarasekare 2003). However, competitive abilities may also differ among species, with superior competitors gaining access to preferred resources, whereas inferior competitors are forced to use less favorable resources (Hardin 1960, Violle et al. 2011). As a result, there can be fitness-associated consequences of resource partitioning that favor selection over evolutionary timescales for the ability of inferior competitors to maintain their performance across a range of resources (Lynch and Gabriel 1987, Futuyma and Moreno 1988).

Sale (1977, 1978) proposed an alternative idea, the *lottery hypothesis*, which argues that competing species with identical resource requirements can coexist through chance colonization of vacant space. The lottery hypothesis assumes that space is a limiting resource, that vacant space is recolonized by the first available recruit (analogous to a winning lottery ticket), and that species have similar competitive abilities. The lottery hypothesis was further developed to the *lottery model* by showing that spatial or temporal variation in the relative abundance of recruits is necessary to prevent one species gaining a numerical advantage that could lead to competitive exclusion of other species through time (Chesson and Warner 1981). A lottery for space is potentially ineffective at producing long-term coexistence between species without additional stabilizing mechanisms, such as environmental variation that alternatively favors recruitment rates in the different species (Chesson and Warner 1981). Although there is ample empirical evidence for competitive coexistence by niche partitioning in plant and animal communities, there is much less evidence for competitive coexistence by the lottery mechanism (Robertson 1995, Amarasekare 2003). Therefore, the conditions under which these two competitive mechanisms are likely to be favored have not been resolved for either aquatic (Munday 2004, Salomon et al. 2010, Shinen and Navarrete 2014) or terrestrial systems (Hubbell 2001, Lin et al. 2009, Kalyuzhny et al. 2014).

Interest and debate about lottery models intensified with the development of the neutral model (Hubbell 2001), which proposed that differences between species in ecological communities are irrelevant to the maintenance of biodiversity. The core assumption of the neutral model is that chance variations in demographic (births, deaths, and immigration) and evolutionary rates (speciation and extinction) are responsible for the generation and maintenance of biological diversity (Bell 2000, Hubbell 2001). Recruitment into the population in the neutral model is governed by a simple lottery for space. Competition models have subsequently been classified into those based on: (1) *stabilizing mechanisms*

(known as *niche theory*), such as competitive hierarchies and resource partitioning, which are the most widely accepted mechanisms of species coexistence, and (2) *fitness equivalence* (known as *neutral theory*), where stabilizing mechanisms are absent, species have equivalent fitness, and coexist through demographic stochasticity (Adler et al. 2007, Bode et al. 2012). Neutral models challenge the niche paradigm by proposing that similarities, not differences, explain the high diversity of natural communities. Despite controversy over the neutral model (Whitfield 2002, Mikkelsen 2005) and some studies refuting its assumptions (Adler 2004, Dornelas et al. 2006, Ricklefs and Renner 2012), a lively debate about niche vs. neutral models persists in ecology (Gravel et al. 2011, Connolly et al. 2014).

Theory and experimental tests of competition typically assume that just one competitive mechanism operates between species (Colwell and Fuentes 1975, Amarasekare 2003). However, niche and neutral theory are not mutually exclusive, and both niche and neutral processes could potentially influence the coexistence of competing species (Gravel et al. 2006, Silvertown et al. 2006, Adler et al. 2007). Chesson (2000) proposed that the magnitude of niche-based differences required to stabilize long-term coexistence depends on how similar species are in average fitness. If species have similar average fitness they require only small niche differences to coexist. Neutral mechanisms are the special case where species have equivalent fitness and there are no stabilizing, niche-based processes. Recent theory suggests that niche and neutral theories are the extremes of a continuum and that aspects of both could operate in many communities (Gravel et al. 2006). In this context, niche and lottery processes could operate simultaneously to promote coexistence, or their relative importance could change through time, with similar fitness and a lottery operating in one life stage and differential fitness and niche partitioning operating in another life stage. Ecological and life history changes through ontogeny could affect both fitness consequences of resource use patterns and the potential competitive mechanisms involved. Ontogenetic shifts in habitat (Dahlgren and Eggleston 2000) and food preference (Schmitt and Holbrook 1999, Pereira and Ferreira 2013) could potentially alter the degree of resource overlap between species and their competitive abilities. It is well known that the strength of competitive effects can be stage dependent (Callaway and Walker 1997, Connolly and Moko 2003). However, to our knowledge, no study has empirically demonstrated ontogenetic changes in the competitive mechanisms operating in animal communities.

The coral-associated gobies from the genus *Gobiodon* are some of the most specialized fishes on coral reefs. These fishes associate almost exclusively with corals from the genus *Acropora*, from which they derive multiple resources including shelter, food, and breeding sites (Munday et al. 1997, Hobbs and Munday 2004, Brooker et al. 2010). The close relationship of the gobies

with *Acropora* coral hosts makes them an excellent model group to analyze competitive interactions within reef fish communities. Munday et al. (2001) demonstrated that some coral-dwelling gobies compete for space (*Acropora* coral colonies), and that species coexist by a variety of mechanisms. Most species coexist by niche partitioning, at one or more spatial scales, and interspecific differences in competitive ability result in a competitive hierarchy among species (Munday et al. 2001). However, it appears that some coral-dwelling gobies may coexist by the lottery mechanism. Munday (2004) found that two ecologically similar species (*G. histrio* and *G. erythrospilus*) have similar patterns of habitat use, and that juveniles have similar size-based ability to compete for vacant corals. Removal of one species from coral colonies, resulting in vacant space, caused enhanced recruitment of the other species, demonstrating that habitat space is limited. However, not all the assumptions of the lottery hypotheses were tested. For example, it is not known if the two species recruit to coral habitat at the same size, which could influence their competitive ability. Similarly, it is not known if habitat preferences and competitive abilities remain the same or change through ontogeny. Coexistence of these goby species could involve a mix of both lottery and niche processes if competitive abilities change with ontogeny.

In this study we tested, for the first time, the hypothesis that the competitive process changes from a lottery for space at settlement to niche partitioning in adults. There were four components to evaluating this hypothesis. Firstly, newly settled juveniles were collected to estimate the pelagic larval duration (PLD) and size-at-settlement for each species from otoliths (ear bones). This was to determine if differences in size at settlement could affect the outcome of competitive interactions among juveniles. Secondly, we compared patterns of resource use by the two species to examine potential resource partitioning by either juveniles or adults. To do this we compared the primary biotic and abiotic factors, such as coral species inhabited, size of the coral colonies inhabited, and reef location, that have been found to be important to resource partitioning of gobies in previous studies (Munday 2000, Munday et al. 2001, Hobbs and Munday 2004). Thirdly, habitat preference and size-based competitive abilities were tested for juveniles and adults of both species in laboratory experiments to determine if there was competitive equivalence of a competitive hierarchy. Finally, a transplant experiment was used to determine if individual performance in preferred and non-preferred habitat differed between the two species, which could provide an explanation for the coexistence of the two species based on a niche partitioning model. We hypothesized that coexistence could be achieved if the relative fitness (i.e., growth rate) of the inferior competitor in the non-preferred habitat is greater than that of the superior competitor in that habitat.

MATERIAL AND METHODS

Study location and species

Field surveys and laboratory experiments were conducted in May and September 2012 at Lizard Island in the northern section of the Great Barrier Reef (GBR), Australia (14°38' S, 145°26' E). *Gobiodon histrio* and *Gobiodon erythrospilus* are ecologically similar sister species (Duchene et al. 2013) that overlap broadly in their geographical distribution. At Lizard Island on the GBR they occur in similar abundances and have broadly similar patterns of habitat use (Munday 2004). *G. histrio* and *G. erythrospilus* can be found in neighboring coral colonies, but rarely occupy the same coral colony.

Pelagic larval duration and size at settlement

Munday (2004) showed that juvenile *G. histrio* and *G. erythrospilus* have similar competitive strength when size matched. However, it is unknown if these species actually settle at the same size. Differences in PLD could enable one species to grow larger than the other, leading to a competitive hierarchy at settlement despite similar size-based competitive ability. To estimate size at settlement, sagittal otoliths were removed from 25 juveniles of each species collected from the most commonly inhabited corals, *Acropora nasuta* and *Acropora spathulata*, at Lizard Island. Otoliths were processed using standard methods as described by Epperly et al. (1991) and Secor (1992).

PLD was determined by counting daily growth increments of processed otoliths from the first fine-lined, dark increment to the settlement check mark. The settlement mark was identified by the increment transitions, represented by a zone where the increments are indistinct from one another (Victor 1986, Wilson and McCormick 1999). Otolith radius was measured from the nucleus to the settlement mark and from the nucleus to the otolith edge, along a consistent axis.

Individual fish sizes (standard length, SL) at settlement were then back-calculated using the biological intercept procedure (Campana and Jones 1992), given by $L_a = L_c + (O_a - O_c) (L_c - L_0) (O_c - O_0)^{-1}$, where L_a is the estimated fish length at age a , L_c is fish length (standard length) at capture, O_c is otoliths radius at capture, L_0 and O_0 are the size of the fish and otoliths at the biological intercept, respectively. The biological intercepts of L_0 and O_0 were fixed at 3.0 mm fish length and 0.20 mm otolith radius, respectively. R script was used to perform back calculation. A t test was used to compare mean PLD and size at settlement between the two species.

Habitat use and partitioning

Coral-dwelling gobies can partition habitat either among the coral species they inhabit, or among reefs with different exposure to prevailing wind (Munday 2000, Munday et al. 2001). Therefore, different species may inhabit different coral species on the same reef, or

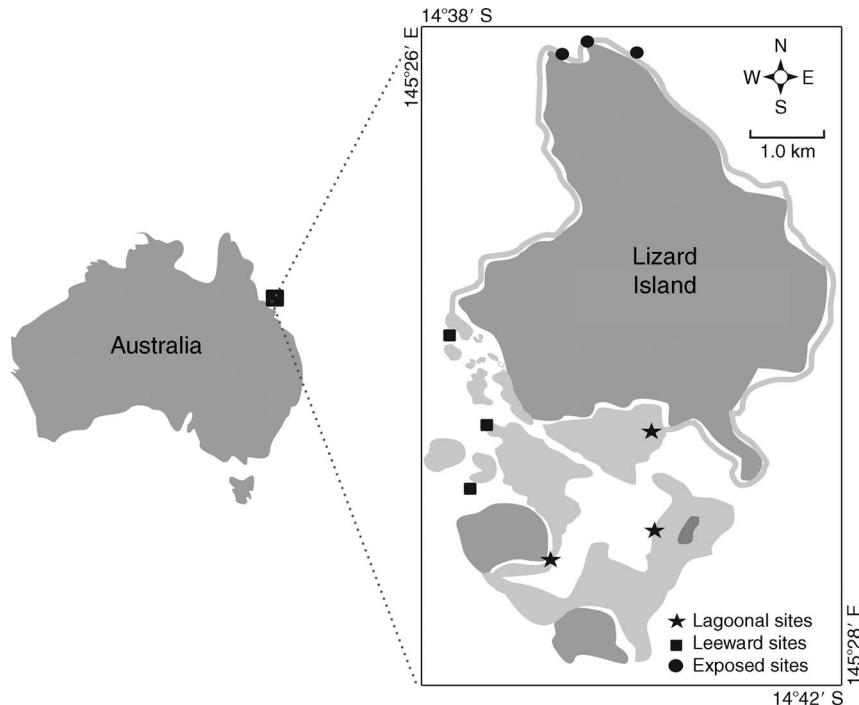


FIG. 1. Map of study area (Lizard Island, northeast Australia) showing the sites surveyed for gobies.

they may inhabit the same coral species, but on different reef types (i.e., exposed vs. sheltered locations). Pattern of habitat use of juveniles and adults was examined in three reef zones, based on their exposure to the prevailing southeasterly trade winds; (1) sheltered lagoon, (2) leeward side of island, and (3) windward side of island. Three replicate sites were selected within each zone (Fig. 1). At each site we recorded habitat use of 50 randomly selected individuals of *G. histrio* and 50 individuals of *G. erythrospilus*. Individuals were recorded by life phase (juveniles and adults) using criteria stipulated by Munday et al. (1997). To examine resource partitioning and correlate this data with ontogeny, a variety of biotic and abiotic factors were recorded. *Acropora* coral colonies were identified to species level according to Wallace (1999) and Veron (2000). Any colonies with doubtful identification were photographed for further identification. Colony size was recorded as the distance across its widest axis, using a tape measure. Coral colonies were categorized as small (0–20 cm), medium (20–40 cm), and large (40–60 cm).

A chi-square test of independence was used to compare the frequency with which *G. histrio* and *G. erythrospilus* used different coral species. Juveniles and adult were analyzed separately. Univariate regression trees (URT) using Tree Plus were then used to explore potential resource partitioning among the habitat variables measured for the two *Gobiodon* species (MathSoft 1998). *Acropora* species inhabited, colony size, prevailing wind exposure, and location were the explanatory variables. URT is well suited for describing

patterns in complex ecological data sets because they separate the variables in a series of binary splits, and continuous and categorical variables can be compared in the same analyses (De'ath and Fabricius 2000).

Habitat preference (laboratory experiments)

Preliminary observations confirmed that *Acropora nasuta* and *A. spathulata* were the two coral species most commonly used by *G. histrio* and *G. erythrospilus* in the field (see also Munday 2004). To determine the preference for these two coral species in the absence of competition, juveniles and adults of each species of *Gobiodon* were given the choice between two coral colonies, one *A. nasuta* and one *A. spathulata*. The protocol used was identical to that used by Munday (2004) for juveniles. Small colonies (15–20 cm diameter) of these two coral species were carefully removed from the reef, transported alive to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). One colony of each coral species (approximately equal size) 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 anesthetizing them with clove oil (Munday and Wilson 1997). A single individual of *G. histrio* or *G. erythrospilus* (ranging from 1.5 to 3.8 cm) was released between 1800 and 1900 hours in the middle of the glass aquarium and their choice of coral recorded between 0600 and 0700 hours the

following morning. 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. A chi-squared test of independence was used to compare the habitat preference of *G. histrio* and *G. erythrospilus*.

Competition experiment

A laboratory experiment was used to test the relative competitive abilities of *G. histrio* and *G. erythrospilus* for preferred habitat. This was performed for both juveniles and adults to determine if there was a shift in competitive ability between life stages. While Munday (2004) has previously reported similar competitive abilities in juveniles, it was important that we repeated this experiment with juveniles at the same time that we tested adult competitive ability. One similar-sized individual of each species was simultaneously placed into a glass aquarium with a colony of *Acropora nasuta* in the middle. The species occupying the coral was recorded after 12 hours. The individual occupying the test coral was considered the superior competitor. *Acropora nasuta* was the coral species used in this experiment because it is the preferred species of coral for both *G. histrio* and *G. erythrospilus* at Lizard Island (Munday et al. 1997, 2001). Coral colonies used in the experiment were carefully removed from the reef, transported to the laboratory, and cleared of all infauna (gobies, crabs, and shrimps). To provide shelter for evicted fish, a similar-sized piece of coral that had been bleached to remove all living tissue was placed at one end of each aquarium.

In order to test whether the origin of individuals (e.g., *Acropora* species they were collected from) affected the competition ability of adults, *G. histrio* and *G. erythrospilus* were collected from *A. nasuta* and *A. spathulata* and held in separate aquaria. Two different combinations were established: (1) Both individuals from *A. nasuta* or (2) *G. histrio* individuals from *A. nasuta* and *G. erythrospilus* from *A. spathulata*. This second combination was chosen because adult *G. erythrospilus* commonly inhabited *A. spathulata* in the field, and this might affect its competitive ability against *G. histrio*, whereas *G. histrio* less frequently inhabited *A. spathulata*. Individuals in each trial were matched for size. Fish were released onto the corals between 1800 and 1900 hours and the outcome recorded at 0700 hours the following morning. A total of 24 trials were performed for juveniles and a total of 24 trials of each combination were performed for adults. A chi-square test of independence was used to compare the frequency of wins in the competition experiment for juveniles and for adults.

Growth experiment

A transplant experiment was performed to test if patterns of habitat use differentially affect individual performance of *G. erythrospilus* and *G. histrio*. Specif-

ically, we predicted that the inferior competitor, *G. erythrospilus*, should experience a relative fitness advantage compared with the superior competitor, *G. histrio*, when occupying a non-preferred habitat, *A. spathulata*. Consequently, *G. erythrospilus* may persist because it suffers less of a decline in fitness-associated traits compared with *G. histrio* when forced to use non-preferred habitat.

We compared the growth rates of *G. erythrospilus* and *G. histrio* on preferred (*A. nasuta*) and non-preferred coral species (*A. spathulata*) over a three-month period between January and April 2014. A total of 50 individuals of both goby species were collected from *A. nasuta* by lightly anesthetizing them with clove oil. 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 et al. 2001). Tagged fishes were held for 24 hours in aquaria to ensure recovery. Fishes were then transported to the reef and released on approximately equal-sized coral colonies of either *A. nasuta* or *A. spathulata*. A total of 25 individuals of each goby species were transplanted to each of the two 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 three months, all the remaining fishes were collected from the marked coral colonies and SL of each tagged fish was measured in the laboratory to determine the increase in size.

A *t* test was used to compare the size of the transplanted gobies at the beginning of the experiment between the two species. Analysis of variance (ANOVA) was then used to compare growth of the two goby species in the two coral species. We predicted that there would be significant interaction between the main factors (goby species and coral species) if the inferior competitor was better able to maintain performance (i.e., growth) in the non-preferred habitat compared with the dominant competitor.

RESULTS

Pelagic larval duration (PLD) and size at settlement analyses

G. erythrospilus had a mean PLD of 18.5 ± 1.9 d (mean \pm SD), and *G. histrio* had a mean PLD of 20.7 ± 2.0 d, which was not significantly different ($t = 10.76$, $df = 1$, $P = 0.1$). Similarly, there was no significant difference in size at settlement estimated for the two species ($t = 6.19$, $df = 1$, $P = 0.7$). *G. erythrospilus* was estimated to settle at 6.66 ± 0.44 mm and *G. histrio* at 6.98 ± 0.49 mm.

Habitat use

Gobiodon histrio and *G. erythrospilus* inhabited a total of 11 *Acropora* species (Fig. 2). Despite this diversity, 62.9% of juveniles and 86.1% of adults occurred in just two main coral species; *Acropora nasuta* and *A.*

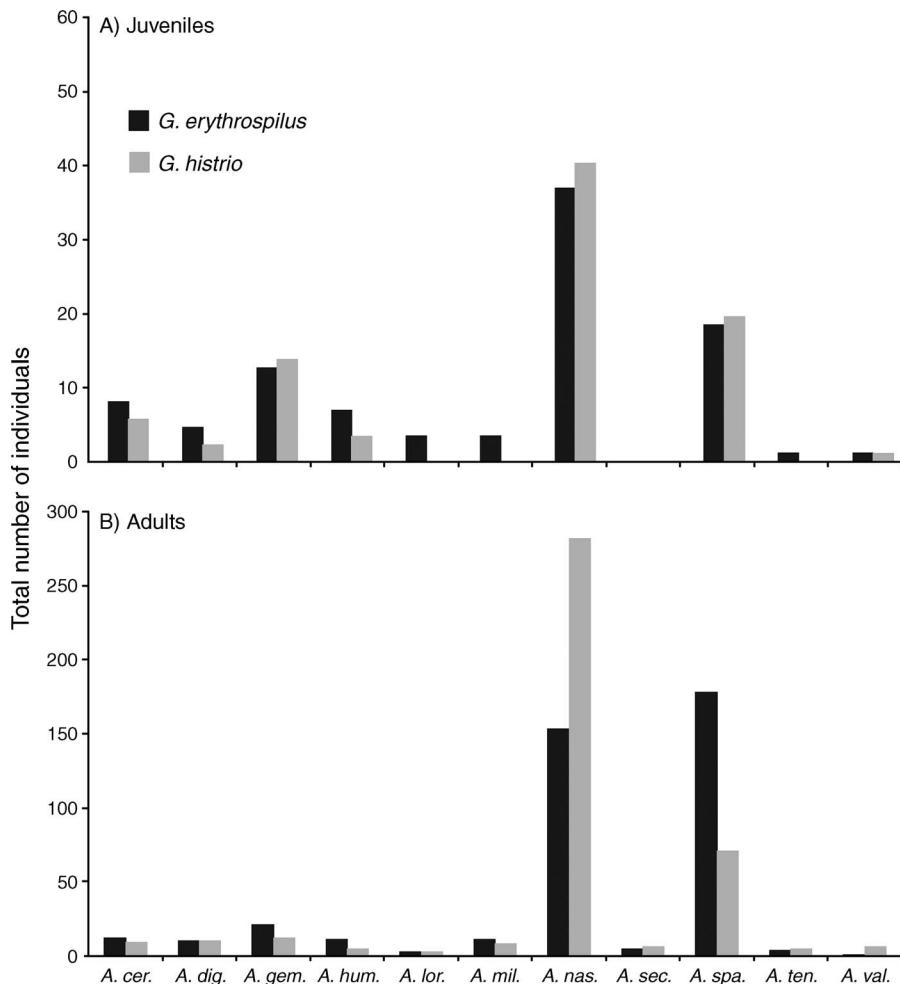


FIG. 2. Habitat use of (A) juveniles and (B) adults of *Gobiodon histrio* and *Gobiodon erythrospilus*. Coral abbreviations: *A. cer.* = *Acropora cerealis*; *A. dig.* = *Acropora digitifera*; *A. gem.* = *Acropora gemmifera*; *A. hum.* = *Acropora humilis*; *A. lor.* = *Acropora loripes*; *A. mil.* = *Acropora millepora*; *A. sec.* = *Acropora secali*; *A. nas.* = *Acropora nasuta*; *A. spa.* = *Acropora spathulata*; *A. ten.* = *Acropora tenuis*; *A. val.* = *Acropora valida*.

spathulata. Juveniles of the two species exhibited nearly identical patterns of habitat use (chi-square = 3.68, df = 10, $P = 0.97$), especially for the two primary coral species (Fig. 2A). However, adults of the two species exhibited significant differences in habitat use (chi-square = 89.21, df = 10, $P = 0.002$) (Fig. 2B). For adults, *G. erythrospilus* was most frequently observed in association with *A. spathulata* (44.1% of observations), whereas *G. histrio* was mostly associated with *A. nasuta* (71.3% of observations) (Fig. 2B).

Univariate regression tree analysis for adults resulted in a seven-leaf tree explaining 35.5% of the total variation (Fig. 3A). Coral species inhabited was the most important variable, explaining >80% of the variation in habitat use between *G. histrio* and *G. erythrospilus* (Fig. 3B). In the first split, *G. erythrospilus* was grouped with *Acropora spathulata*, *A. gemmifera*, and *A. humilis*, whereas *Gobiodon histrio* was associated

with *A. nasuta*, *A. cerealis*, *A. digitifera*, and *A. millepora*. The next split in order of importance was colony size, with *G. erythrospilus* more frequent on large and medium colonies and *G. histrio* more frequent on small colonies (22.5% of the variation). Exposure explained just 6.06% of the variance, indicating that patterns of habitat use by the two species differed little among reefs from different exposure regimes. *G. erythrospilus* tended to be more associated with exposed sites and *G. histrio* exhibited a slight preference for sheltered areas (Fig. 3A, B).

Habitat preference

Despite the difference in *Acropora* use in the field, both *G. histrio* and *G. erythrospilus* exhibited a strong preference for *A. nasuta* in laboratory trials, with no significant difference in habitat preference between the species (chi-square = 0.76, df = 1, $P = 0.66$). *G. histrio*

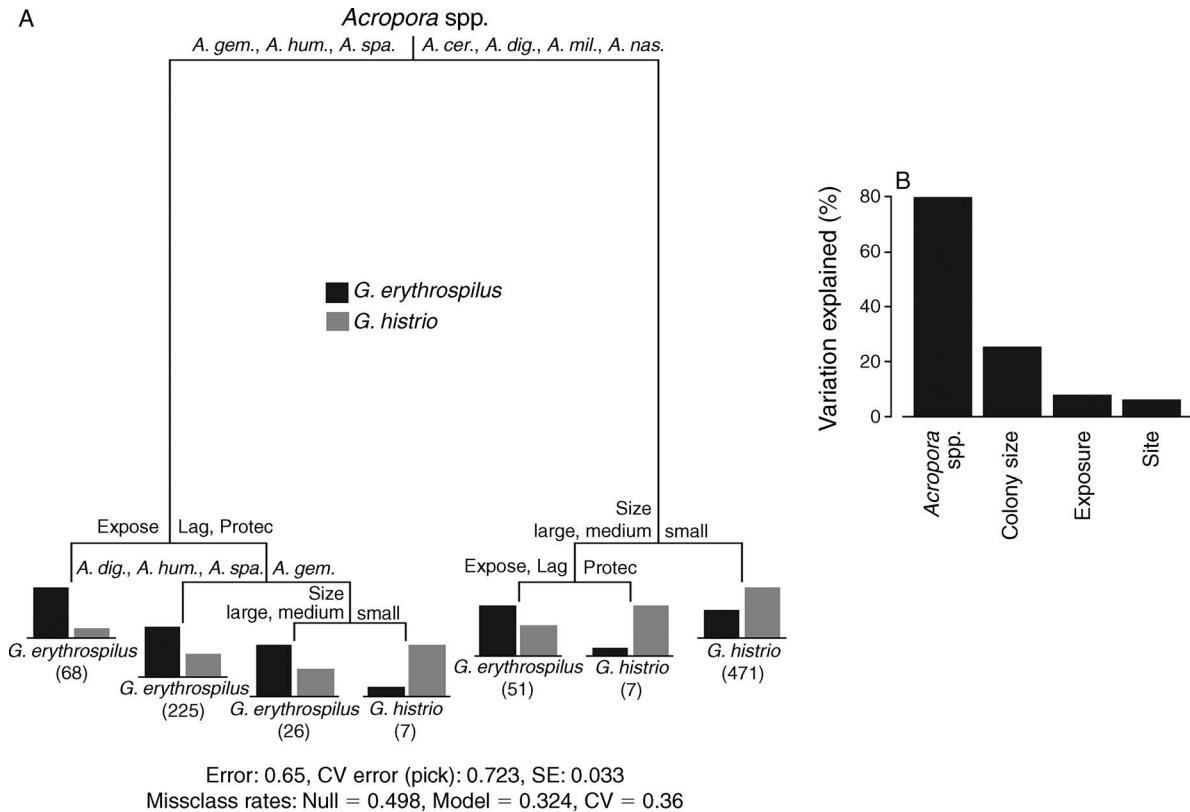


FIG. 3. Univariate regression trees of habitat use by *Gobiodon histrio* and *Gobiodon erythrospilus*. (A) Seven-leaf regression tree showing distribution of *Gobiodon histrio* and *Gobiodon erythrospilus* among the coral species, colony sizes, wind exposure, and locations samples. Each split in the tree indicates the number of recorded gobies in each situation (in parentheses); the length of vertical lines proportionally indicate the percentage of variation explained. (B) The bar graph shows the percentage of variation explained by *Acropora* species inhabited, colony size, prevailing wind exposure, and location. Expose indicates exposed, Lag indicates lagoon, Protec indicates protected sites. See Fig. 2 for full names of corals.

preferred *A. nasuta* in 22 of 24 (91.6%) trials and *G. erythrospilus* in 20 of 24 (83.3%) trials.

Competition experiments

Juvenile *G. erythrospilus* and *G. histrio* exhibited similar ability to compete for preferred coral habitat (*A. nasuta*). In 24 trials, where similar-sized fishes were released simultaneously onto a coral colony, *G. histrio* won 13 and *G. erythrospilus* won 11 trials (chi-square = 1.35, $df = 1$, $P = 0.45$; Fig. 4A). In contrast, for adults, *G. histrio* proved to be the superior competitor compared to *G. erythrospilus*, winning the majority of the trials regardless of the coral of origin (chi-square = 6.03, $df = 2$, $P = 0.001$; Fig. 4B). When both individuals were from *A. nasuta*, *G. histrio* won 16 of 24 trials (chi-square = 5.63, $df = 2$, $P = 0.002$) with 3 draws. Moreover, when *G. histrio* individuals were from *A. nasuta* and *G. erythrospilus* from *A. spathulata*, *G. histrio* won 19 of 24 trials (chi-square = 10.35, $df = 2$, $P = 0.005$) with 3 draws. A draw was characterized in instances that both gobies were recorded associated with the provided *A. nasuta* coral colony.

Growth experiment

The average size of transplanted fishes at the beginning of the experiment was 27.4 mm SL for *G. histrio* and 27.7 mm for *G. erythrospilus*, and there was no difference in the size of the transplanted gobies between the two species ($t = 0.28$, $df = 38$, $P = 0.77$).

There was a significant effect of goby species ($F_1 = 7.25$; $P = 0.01$), coral species ($F_1 = 10.77$; $P = 0.002$) and their interaction ($F_1 = 4.19$; $P = 0.047$), on growth rate of fish transplanted to colonies of *A. nasuta* and *A. spathulata*. Importantly, there was a significant interaction, with the change in growth between the two coral species higher in *G. histrio* compared with *G. erythrospilus* (Fig. 5). *G. histrio* suffered a 37% decline in growth on *A. spathulata* compared with *A. nasuta*, whereas *G. erythrospilus* suffered only a 21% decline in growth on the non-preferred coral.

DISCUSSION

Our results support the conclusion that a competitive lottery between *Gobiodon histrio* and *G. erythrospilus* occurs at settlement. We show that both species settle at

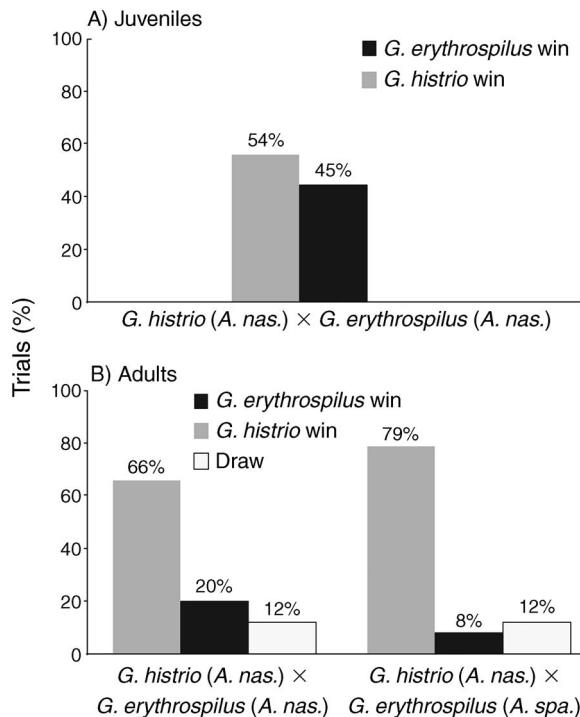


FIG. 4. Outcome of competition experiments for (A) juveniles and (B) adults of *Gobiodon histrio* and *Gobiodon erythrospilus*. For (B) adults, *G. histrio* was collected from *A. nasuta* and *G. erythrospilus* was collected from either *A. nasuta* (left side) or *A. spathulata* (right side). $N = 24$ trials for each combination. *A. nas.* = *Acropora nasuta*; *A. spa.* = *Acropora spathulata*. The numbers above the bars indicate the percentage of trials.

the same size and that juveniles have identical patterns of habitat use. Moreover, a laboratory competition experiment found similar competitive ability between juveniles of the two species, as previously suggested by Munday (2004). Consequently, recruitment to preferred corals is likely to operate on a first come, first served, basis. However, we show that this situation changes later in life. By the adult stage, differences in habitat use have arisen, with *G. histrio* tending to dominate the preferred coral species *A. nasuta*. Competition experiments clearly show that *G. histrio* is the dominant species at this life stage, indicating that differences in habitat use among adults is likely due to competitive displacement. Our results uniquely demonstrate that both niche-partitioning and lottery mechanisms of competitive coexistence could operate between ecologically similar species, and that the relative importance of these processes may change with ontogeny.

Stabilizing and neutral mechanisms of competition are typically viewed as diametrically opposed alternatives. However, recent theory suggests that they are extremes on a continuum that can simultaneously influence species coexistence in natural communities (Chesson 2000, Gravel et al. 2006, Adler et al. 2007).

Using site-attached reef fishes we show, for the first time, that a lottery for living space occurs at settlement, and niche partitioning take place in the adult stage. In the past, these two alternative mechanisms were considered mutually exclusive, and the ensuing debate has been one of the most enduring in the literature on reef fishes through the last few decades (Smith and Tyler 1972, Sale 1977, 1978, Robertson 1995, Forrester 2015). While theoretical and empirical studies have often assumed that the coexistence of two competing species is explained by just one mechanism, there is no a priori reason why this should be true. Attributes that might influence fitness differences between species and their competitive ability, such as growth rates, aggressiveness, and specialization levels can change with ontogeny, as observed for a range of different taxa (Huston and Smith 1987, De Roos et al. 2003, Gagliano et al. 2007, Willson et al. 2010, Pereira and Ferreira 2012). Therefore, it is not surprising that the mechanisms of coexistence may change with development in these reef fishes.

The lottery hypothesis still remains controversial, and there are few studies that fully test all of its assumptions. Results presented here using site-attached reef fishes support an earlier study showing a competitive lottery for space at settlement for two coral-dwelling gobies. Similar to Munday (2004) we found that juveniles of both species exhibited nearly identical size-based ability to compete for preferred habitat. The present study tested and confirmed additional facets of the lottery hypothesis (sensu Sale 1977, 1998); (1) *G. histrio* and *G. erythrospilus* settle at the same size, so there is no potential for a size-based outcome of competitive ability, and (2) there is no niche partitioning between juveniles of the two species. Juveniles of the two species have nearly identical patterns of resource use and inhabit *Acropora* coral species in the same proportion. The

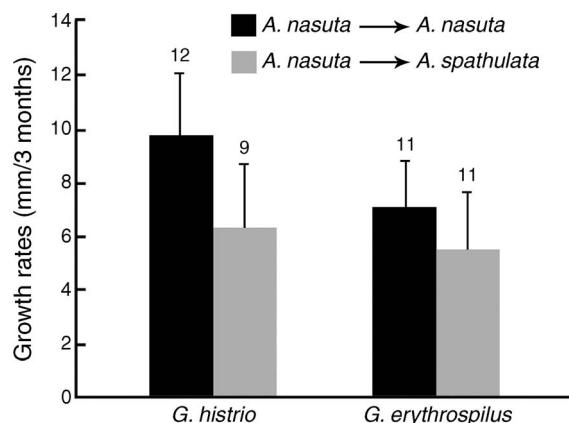


FIG. 5. Growth rates (in millimeters + SE) of *G. histrio* and *G. erythrospilus* transplanted to *A. nasuta* and *A. spathulata* after a three-month transplant experiment on Lizard Island. Numbers above error bars represent the total number of recollected fishes. Numbers of gobies are above the bars.

combination of results suggests that chance alone determines which of the two species occupies a vacant space at settlement. The lottery hypothesis assumes that once space is colonized, there is no displacement through a competitive hierarchy (i.e., there is a strong priority effect). Priority effects are relevant during settlement in reef fish assemblages (Shulman et al. 1983, Geange and Stier 2009), and Munday (2004) showed a priority effect for juveniles of *G. histrio* and *G. erythrospilus*, where the first species to occupy a vacant coral excluded an interspecific intruder of similar body size; further supporting a competitive lottery during early life stages. Different patterns of larval dispersal can also promote coexistence among species with similar competitive abilities (Salomon et al. 2010). However, the two goby species have similar pelagic larval durations, which suggest that significant differences in dispersal abilities are unlikely to be involved in competitive coexistence.

Although the laboratory experiments demonstrated that adults of *G. histrio* and *G. erythrospilus* preferred the same species of coral (*A. nasuta*), they exhibited a different pattern of resource use in the field. *G. histrio* used *A. nasuta* more often than *A. spathulata*. In contrast, *G. erythrospilus* used the less-preferred *Acropora spathulata* more often than *A. nasuta*. In adults, *G. histrio* appears to become the superior competitor, occupying *A. nasuta* at the expense of *G. erythrospilus*, which is displaced onto less-preferred coral habitats. The use of alternative coral species due to limited habitat availability is common for *Gobiodon* spp. (Munday et al. 1997, Dirnwöber and Herler 2007). Habitat partitioning among the two goby species could be explained either by eviction of *G. erythrospilus* from *A. nasuta* colonies by *G. histrio* once competitive strength becomes unbalanced at larger sizes, or biased acquisition of *A. nasuta* colonies by *G. histrio* among juveniles that have settled to small coral colonies and subsequently need to search for larger coral colonies that can support a breeding pair (Hobbs and Munday 2004). At this stage the superior competitor, *G. histrio*, may secure available colonies of *A. nasuta*, whereas *G. erythrospilus* is forced to use more *A. spathulata*. Post-settlement movement is not yet well understood for coral-dwelling gobies, despite the fact that single adults appear to move more than juveniles and breeding pairs (Wall and Herler 2009).

Given the lottery for space at settlement combined with a competitive hierarchy in adults that favors *G. histrio*, the question arises; How does the inferior competitor *Gobiodon erythrospilus* persist? As predicted, *G. erythrospilus* suffered less of a decline in growth by occupying non-preferred habitat, *A. spathulata*, compared with the dominant competitor *G. histrio* in that habitat. Consequently, *G. erythrospilus* appears better able to maintain growth performance in the alternative habitat that it is forced to occupy in greater proportion than *G. histrio* as a result of competition between the two species. Furthermore, *G. erythrospilus* is still able to

maintain some access to the preferred coral, presumably because body size and priority effects prevent *G. histrio* from evicting larger resident *G. erythrospilus* from preferred habitat (Munday et al. 2001). Previous removal experiments of both species at Lizard Island (Munday 2004) found that removal of adult *G. histrio* from *A. nasuta* had a greater effect on recruitment of *G. erythrospilus* than the other way around, which supports the notion that *G. erythrospilus* maintains adequate reproductive capacity despite frequent use of the less-preferred coral. The differences in a fitness-associated trait (growth) detected between adults of the two goby species occupying preferred and non-preferred habitat is consistent with theoretical predictions. *G. histrio* had higher performance than *G. erythrospilus* on the preferred coral, *A. nasuta*, but suffered a greater decline in performance on the alternative habitat. These differences in performance on the two habitats can explain both why *G. histrio* is the dominant competitor for *A. nasuta*, and how the two species coexist through niche partitioning despite the similar preference of *G. erythrospilus* for *A. nasuta*.

Coral colony size also played a minor role in resource partitioning between *G. histrio* and *G. erythrospilus*. *Gobiodon erythrospilus* tends to use large and medium colonies, while *Gobiodon histrio* uses smaller ones. Patterns of habitat use by the two species differed little among reefs from wind exposure regimes, indicating that niche partitioning occurred similarly on all reef types. This suggests that fitness differences between habitats were similar among reef types for the two *Gobiodon* species. If one species was a stronger competitor on a particular reef type, leading to greater use of the preferred coral on those reefs, we would have expected reef type to explain more variance in the data. Nevertheless, minor differences in habitat use in regard to coral colony size and wind exposure could potentially enhance the ability of the inferior adult competitor (*G. erythrospilus*) to persist in the presence of the superior adult competitor (*G. histrio*).

The ontogenetic shift from a lottery for space at settlement to niche partitioning in adults that we observed in the two species of fish studied here is consistent with the continuum model of coexistence explored by Gravel et al. (2006). In that model, individuals recruit into limited space through a lottery, but then exhibit niche differentiation and their probability of surviving to reproduce is a species-specific function of an environmental factor. Here we demonstrate that there is a competitive lottery for space at settlement, there is niche differentiation by adults between coral habitats, and that there is a species-specific fitness-related (growth) function associated with access to different coral habitats. In the continuum model, the coexistence of each species in the community and their relative abundance is determined by the distribution of environmental conditions and the amount of immigration from the metacommunity. This

suggests that variation in the distribution of the coral species occupied by the two goby species, *A. nasuta* and *A. spathulata*, along with regular immigration and connectivity among reefs through the pelagic larval stage is crucial to the coexistence of these two species of fish at a local scale.

In one of the only other studies to empirically test the role of both lottery and niche-based processes in marine organisms, Shinen and Navarrete (2014) examined the processes responsible for the distribution and abundance of barnacles on rocky shorelines in Chile. They concluded that a lottery for space occurs at settlement, and that this largely determines species' distributions within and among sites. Despite some differences in the spatial distribution of two barnacle species on the shore profile (vertical overlap of ~75%, which is similar to the niche partitioning we observed among adult gobies), they found no evidence for differences in competitive ability or fitness trade-offs that could explain distribution patterns. Unlike our study, they did not detect significant differences in vital rates, such as growth, that could account for any slight differences in species distributions. Consequently, the two barnacle species examined in their study appear to be closer to the neutral end of the continuum than the two species of gobies in our study.

Plant communities are another place that a mix of lottery and niche partitioning might be expected. Plants are good candidates for the presence of a lottery for space because of their life histories and mechanisms of dispersal, and indeed, much of the support to date for competitive lotteries comes from plant communities (e.g., Fagerström 1988, Aarssen 1992, Bengtsson et al. 1994, Kubo and Iwasa 1996, Iwata et al. 2007). Fagerström (1988) proposed that no interspecific differences are required for coexistence of plants provided the system is of finite size and spatially heterogeneous (e.g., evident variation in the biotic or abiotic environment, such as humidity and temperature), so variations are at least to some extent asynchronous. Niche partitioning also occurs among plants (Kielland 1994, Mamolos et al. 1995, McKane et al. 2002), and it is known that plants segregate along different environmental niche axes, including gradients of light, soil moisture, and root depth that are likely to facilitate coexistence (Silvertown 2004). Consequently, just as observed for the goby species studied here, it seems that aspects of both neutral and niche models may operate in plant communities (Adler et al. 2007). The life history attributes of perennial plants with a dispersive reproductive phase that will colonize vacant space stochastically (i.e., by lottery) could be potentially compared with reef fishes with a pelagic larval phase, and ontogenetic changes in the mechanisms of competitive coexistence could be also observed in further research on plant communities.

Ecology has progressed from a focus on single ecological processes to a multifactorial perspective of the processes and mechanisms that govern population

dynamics and community structure (Jones 1991, Caley et al. 1996, Hixon et al. 2002, Johnson and Stinchcombe 2007, Wiens et al. 2010). In this context, it is not surprising that the same ecological process might operate in different ways among interacting species. Competition is one of the most important ecological processes in natural communities (Connell 1983, Tilman 1994, Chesson 2000, Amarasekare 2003), yet few empirical studies have tested whether alternative mechanisms of competitive coexistence might co-occur in the same communities. Our results empirically demonstrate ontogenetic changes in the mechanisms of competitive coexistence and suggest that it could be relevant for taxa other than reef fishes. Just as marine ecologists have embraced the idea that multiple ecological processes (predation, competition, dispersal) are responsible for the maintenance of populations and communities (e.g., Jones 1991, Caley et al. 1996, Hixon et al. 2002), our study suggests the need to recognize that a variety of mechanisms within each of these processes may be responsible for the maintenance of biodiversity of coral reefs.

ACKNOWLEDGMENTS

We thank Rohan Brooker, Simone Pennafirme, Matthew Jankowski, Luis Chaves, Wander Godinho and Cecilia Villacorta and the staff at Lizard Island Research Station for assistance with field work. The study was supported by funding from the ARC Centre of Excellence for Coral Reef Studies to P. L. Munday and G. P. Jones. P. H. C. Pereira was supported by a CNPq scholarship.

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