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Habitat morphology constrains the depth distribution and growth rate of a coral-associated reef fish

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ABSTRACT: The distribution of coral reef fishes is often closely linked to the availability of preferred habitats. However, even in specialized gobies associated with a single coral species, their distribution does not always match that of the coral host. The coral goby *Paragobiodon xanthosoma* is primarily restricted to shallow water (<20 m), while its coral host *Seriatopora hystrix* extends to depths >30 m. Here, we use observational and experimental approaches to test whether depth-associated changes in morphology and partial mortality of the coral decrease habitat quality. Quantitative surveys from the surface to 30 m found pronounced changes in colony morphology over depth. *S. hystrix* colonies most likely to be occupied by *P. xanthosoma* were those with shallow-water characteristics, especially lower partial mortality and a more complex branching structure. In a binary choice experiment, *P. xanthosoma* individuals preferentially selected colonies from shallow water (5 m) over deep water (30 m) and with high complexity over low complexity when colonies were collected from a standardized depth (15 m). Finally, a transplant experiment examined the effect of depth-associated changes in the coral habitat on patterns of growth of *P. xanthosoma*. When the depth of placement was standardized, the growth of *P. xanthosoma* was 8-fold lower on colonies collected from deep water (30 m) compared to colonies from shallower water (5 and 15 m). Together, these patterns suggest that depth-related changes in the morphology of the coral host are responsible for driving patterns of distribution over depth in their associated reef fish.

KEY WORDS: Depth · Habitat preference · Transplant experiment · Coral morphology · *Paragobiodon* · *Seriatopora*

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INTRODUCTION

It is widely acknowledged that the characteristics of an organisms' habitat are major drivers of patterns in their distribution and demographic structure (Bell & Galzin 1984, Wiens 1989, Bean et al. 2014). The distribution and abundance of many species are influenced by the presence and availability of preferred habitat (Freemark & Merriam 1986, Rahbek 1997, Skroblin & Legge 2012). However, habitats vary in quality as well as quantity, and the specific habitat features that are critical to species survival are not always known. The nature of habitat can vary along physical gradients such as altitude (Rahbek 1997), latitude (Serreze et al. 2000) and exposure (Lawton 1982), which can affect habitat quality by

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limiting the availability of critical resources such as food and shelter (Martin 1988, Skroblin & Legge 2012). In turn, variation in habitat quality can influence key demographic processes, including recruitment, growth and survival (Gibson 1994, Edwards & Estes 2006), and individuals may exhibit strong habitat selection for the highest quality components of the habitat (Minias 2014). Consequently, variation in habitat quality may be equally important in limiting species distributions as the overall availability of habitat.

On coral reefs, the population dynamics and distribution of coral-associated reef fish are known to be strongly influenced by the availability of habitat-forming scleractinian corals (Kuwamura et al. 1994, Tolimieri 1995, Holbrook & Schmitt 2002, Pratchett et al. 2008). The abundance of coral-associated fishes is often broadly correlated with the cover of preferred coral species (Munday 2002, Brokovich et al. 2008, Messmer et al. 2011). However, variation in coral characteristics such as colony size (Thompson et al. 2007), health (Schiemer et al. 2009) or branching structure (Kane et al. 2009) can each influence patterns of occurrence and habitat use in associated reef fish. Differences in colony health (Noonan et al. 2012), complexity (Hixon & Beets 1993, Almany 2004b) and coral type (Munday 2001, Holbrook & Schmitt 2002) can also affect post-recruitment processes such as growth and survival. Consequently, there is a strong selective pressure for recruiting individuals to settle on colonies of higher quality (Tolimieri 1995, Holbrook et al. 2000, Almany 2004a, Feary et al. 2007). Variation in habitat quality may explain why the distribution of some specialized reef fishes does not match that of their host coral species. However, while the effect of coral habitat quality on reef fish populations is well established, few studies have connected these patterns to the physical processes that drive changes in the characteristics of live coral.

Depth is one of the strongest physical gradients that influences the morphological characteristics of coral species, thus potentially affecting their suitability as habitat (Brokovich et al. 2008). Scleractinian corals show a high degree of plasticity in both morphological and physiological traits over depth (Falkowski & Dubinski 1981, Bruno & Edmunds 1997), often attributed to declining light availability (Jerlov 1968, Falkowski & Raven 2007) and other factors including sedimentation, hydrodynamic energy and temperature (Lesser et al. 2009). In low light conditions, coral colonies are characteristically wider and more open 2-dimensional forms that maximize the surface area exposed to light and minimize intra-colony shading (Vermeij & Bak 2002, Anthony & Hoegh-Guldberg 2003, Frike & Schuhmacher 1983). For branching species, branches become thinner and more horizontally arranged at greater depth (Mass et al. 2007, Nir et al. 2011), while spherical species shift to flatter, wider forms (Bak & Meesters 1998, Muko et al. 2000). The size distribution and overall health of coral colonies also varies over depth, with differences in size (Falkowski & Dubinski 1981) as well as degree of partial mortality (Bak & Meesters 1998). These changes in morphology also correspond to physiological changes over depth, with deep corals exhibiting reduced growth and metabolic rates coupled with an increase in photosynthetic efficiency (Dustan 1975, Anthony & Hoegh-Guldberg 2003, Mass et al. 2007, Cooper et al. 2011). Although variation in the morphology of corals over depth is now increasingly understood, the effects of these changing habitat characteristics on the distribution and fitness of coral-associated reef fish remain unclear.

There are pronounced differences in the distribution and abundance of reef fish species over depth (Jones 1991, Williams 1991, Freidlander & Parish 1998, Jankowski et al. 2015, Macdonald et al. 2016), and these patterns have been associated with trends in species recruitment and habitat selection (Gutierres 1998, Bay et al. 2001, Srinivasan 2003). Depth-related patterns of recruitment have also been associated with variation in the growth and survival of reef fishes (Wellington 1992, Srinivasan 2003). While the effect of these demographic processes in structuring the depth distribution of species has received some attention, the degree to which changes in habitat quality drive these patterns is unknown. Changes in coral characteristics such as colony size, condition and branching complexity all affect reef fish dynamics over a horizontal gradient (Graham et al. 2006, Thompson et al. 2007, Noonan et al. 2012), and these same characteristics also exhibit significant variation over depth (Falkowski & Dubinski 1981, Bak & Meesters 1998, Nir et al. 2011). It is likely, therefore, that these changing habitat characteristics are a key factor driving the pronounced shift in reef fish community structure over depth.

Species with highly specialized habitat requirements are likely to be particularly responsive to changing habitat characteristics and quality (Wilson et al. 2008). The coral-dwelling goby *Paragobiodon xanthosoma* is one of the most habitat-specialized fishes on coral reefs, inhabiting a single species of coral, the needle coral *Seriatopora hystrix* (Lassig 1976). Accordingly, the abundance and population structure of *P. xanthosoma* is strongly influenced by changes in the habitat quality of *S. hystrix* (Thompson et al. 2007, Wong 2010). *S. hystrix* has a broad depth distribution, commonly occurring to 60 m, and exhibits a high degree of variation in morphological and physiological characteristics over this depth range (Bongaerts et al. 2011, Nir et al. 2011). In contrast, *P. xanthosoma* occurs only in relatively shallow water <25 m and is most abundant at depths of 5 to 15 m (Smallhorn-West et al. 2017). The proportion of *S. hystrix* colonies occupied by *P. xanthosoma* also declines with increasing depth due to reduced growth and survival of *P. xanthosoma* in deeper water (Smallhorn-West et al. 2017). The combination of well-defined morphological plasticity in the coral host, *S. hystrix,* and restriction to shallow water by *P. xanthosoma* provides an ideal opportunity to investigate the relationship between the individual performance of a coral-associated reef fish and changes in the quality of its coral host over depth.

Here, we examine the effects of changing habitat characteristics over depth on the habitat use, preference and individual performance of *P. xanthosoma*. Quantitative surveys were undertaken to investigate morphological changes in *S. hystrix* over depth and to determine the relationship between these changes and patterns of habitat use by *P. xanthosoma*. Following this, a binary choice experiment examined the preference of *P. xanthosoma* for its coral habitat (*S. hystrix*) collected from deep (30 m) or shallow location (5 m) and for 'deep' or 'shallow' morphologies collected from a mid-depth location. Finally, a transplant experiment was conducted to isolate the effect of changes in the coral habitat over depth on the individual performance of *P. xanthosoma*. Specifically, this experiment examined whether patterns of growth differed in individuals transplanted to coral colonies of different morphologies collected from different depths, but transplanted to the same mid-depth strata.

MATERIALS AND METHODS

Study site and species

This study was conducted in Kimbe Bay (5° 30′ S, 150° 05′ E), Papua New Guinea (Fig. 1). Quantitative surveys of depth-related changes in coral morphology were conducted on small fringing reefs, known locally as Matane Walindi and Rosemary's Reef. The choice and transplant experiments were performed at Madaro reef, adjacent to the Mahonia Na Dari Research and Conservation Centre. Both *Seriatopora hystrix* and *Paragobiodon xanthosoma* commonly occur on these 3 reefs, which have abundant coral growth from the surface to depths >60 m.

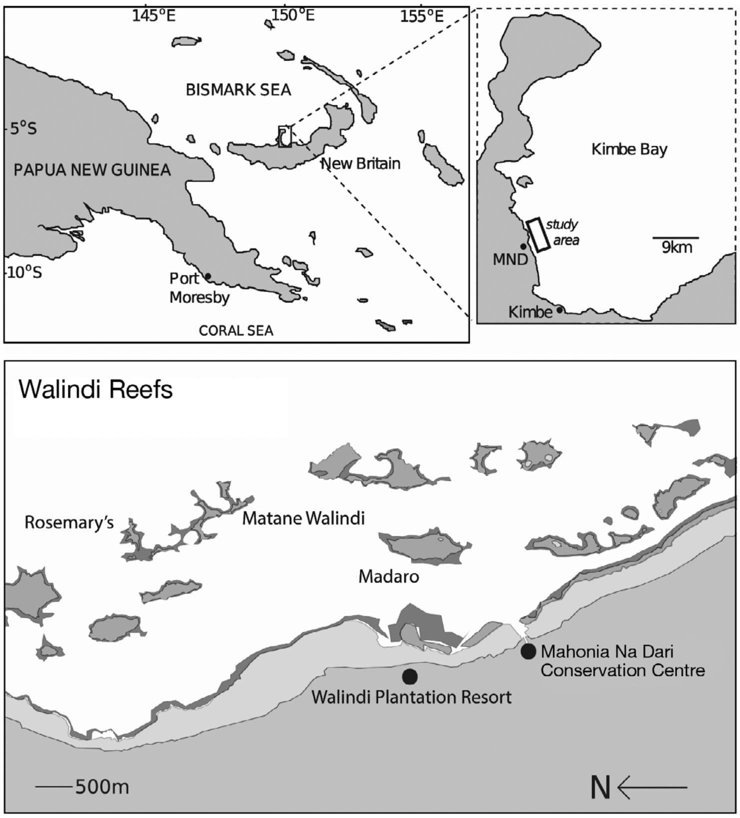

Fig. 1. Location of Kimbe Bay, Papua New Guinea, as well as the reefs studied

Quantitative surveys of coral morphology

Changes in the morphological characteristics of *S. hystrix* over depth were assessed using a combination of visual surveys and image analysis. The presence of *P. xanthosoma* was also recorded in all colonies to determine the association between their occurrence and the morphological characteristics of *S. hystrix*. The visual surveys consisted of eight 25 × 2 m belt transects conducted at 5 m intervals between 30 m and the surface (total of 56 transects). On each transect, data was collected on the size, height and percentage of partial mortality for each colony of *S. hystrix*. Colony size was estimated as the mean value between the colonies' greatest diameter and a perpendicular central diameter (Edmunds 2005). Colony height was estimated as the height of the colony from its base to its highest point. Colony height was compared to the mean colony size to calculate a height ratio (height: size) describing the flatness of the colony, where a lower ratio indicates a flatter colony. Coral partial mortality was visually estimated as the proportional area of deceased tissue per colony to the nearest 10%.

To assess changes in the branching structure of *S. hystrix* over depth, top-view and side-view high-resolution images were taken with a digital SLR camera of 15 coral colonies at each depth from the surface to 30 m at 5 m intervals (total of 105 coral colonies). Corals were selected along a transect tape running parallel to the depth contour using random points on the tape and the closest colony to each point.

Three metrics of colony branching structure were then quantified using the program ImageJ: colony complexity, mean branching angle and mean branch thickness. Colony complexity was estimated by counting the number of branch tips within a 25 cm^2 area at the centre of each colony image (Noonan et al. 2012), where a higher number of branch tips per quadrat indicates a more complex coral colony. To determine the mean branching angle, 10 branches were selected using a random number generator and a quadrat overlaid on the side-view image of each colony. The angle of each branch from the horizontal (−90° to +90°) was measured from its tip to its first bifurcation. To quantify mean branch thickness, 5 branches of each colony were randomly selected (as previously described) and their thickness measured 1 cm from each tip. The mean value of within-colony replicates was then calculated to give a single value per colony for each branching metric.

Multivariate analyses were used to examine changes in the morphological traits of *S. hystrix* among depths using the software PRIMER v6. Differences in the mean values of each morphological trait at each depth were compared using a Bray-Curtis similarity matrix. The similarity in morphological traits among depths was examined using non-metric multidimensional scaling (nMDS), while cluster analysis of group averages was used to identify groups. In addition, 1-way ANOVAs were performed for each metric to examine differences in individual colony traits over depth. Data were log transformed to meet the assumptions of normality and homogeneity of variance. A logistic regression was performed to examine the association between whole coral-colony characteristics (size, height and partial mortality) and the presence of *P. xanthosoma* in a coral colony. A second logistic regression was used to examine the relationship between more detailed changes in colony structure (complexity, branch angle and branch thickness) and the presence of *P. xanthosoma* in a coral colony.

Habitat preferences based on branch-morphology: pair-wise choice experiments

Two binary choice experiments were conducted to test whether adults preferred coral colonies collected from shallow or deep water and colonies with shallow- or deep-water characteristics (i.e. complexity) collected from a standardized depth. In the first experiment (depth preference), *S. hystrix* colonies were collected from the same shallow (3 to 6 m) and deep (27 to 30 m) sites as the surveys (N = 10 colonies from each depth). Adult *P. xanthosoma* were given the choice of coral colonies collected from deep or shallow locations, but presented at an intermediate depth (13 to 17 m). In the second experiment (complexity preference), adults were given a choice of coral colonies from a mid-depth that had low or high structural complexity. Coral colonies were classified as either low or high complexity based on the number of branch tips that occurred in a 25 cm^2 quadrat in the centre of the colony. Based on patterns observed in the surveys, a cut-off point of >50 branch tips and <30 branch tips were used for colonies of high and low complexity, respectively. Ten colonies of high complexity and 10 colonies of low complexity were collected from the intermediate depth range, and all colonies were selected to minimize differences in non-treatment characteristics (i.e. size, shape and health). Following collection, the colonies were left for a period of 72 h to acclimatize to their new environment, and none showed signs of stress.

Preference trials for the 2 experiments followed the same methodology. Coral colonies were placed on sandy substratum at least 5 m from any other reef habitat that may interfere with habitat selection. Colonies were placed so that they were touching in order to allow the fish to move freely between both corals and sample each habitat with minimal disturbance. The location of each treatment (left or right) was also randomly allocated to minimise lateralisation bias. *P. xanthosoma* were collected from the nearby reef using clove oil at a depth of 13 to 17 m. Individuals were given 1 h to recover following capture. In each trial, an individual *P. xanthosoma* was placed under a small hand net on the sandy substratum in front of 1 randomly selected *S. hystrix* colony from each treatment. The fish was then provided a period of 1 min to acclimate before the net was gently removed. The immediate habitat choice for each fish was recorded, as well as the choice after 10 min and 24 h. The latter was scored as the individual's final choice because previous studies have shown that the habitat choice of *P. xanthosoma* remains stable after 24 h (Wong et al. 2007). Following each set of trials (N = 10), all coral colonies were randomly re-paired and then the preference trials were repeated with new fish. The trials were repeated 3 times for a total of 30 depth-preference and 30 complexity-preference trials.

To determine whether *P. xanthosoma* exhibited a significant preference between corals of differing depth and complexity, a chi-squared goodness-of-fit test between observed and predicted values was used to test whether the number of colonies chosen differed significantly from 1:1 (deep vs. shallow N = 26; high vs. low N = 28). Replicates in which individuals were no longer present after a 24 h period were discarded (N = 4 for the depth-preference experiment and N = 2 for the complexity-preference experiment).

Influence of coral habitat quality on goby growth

A transplant experiment was conducted to test whether differences in the quality of the coral host occur between depths (Fig. 2). Colonies of *S. hystrix* collected from deep (27 to 30 m) and shallow (3 to 5 m) water were transplanted to a standardized mid depth (13 to 17 m), and 1 *P. xanthosoma* individual was transplanted onto each colony (N = 15 for each treatment). All fish and coral colonies were separate to those used in the choice trials. In addition, 3 control treatments were created consisting of coral colonies transplanted to the shallow, mid and deep sites, using colonies collected from the same depths (shallow-control, mid-control and deep-control; N = 15 for each treatment). While high mortality rates in coral colonies transplanted over large depth gradients (Bongaerts et al. 2011) meant that a fully reciprocal experimental design was not possible, our design enabled the effect of changing coral habitat on the performance of *P. xanthosoma* to be isolated from other factors that might covary over depth.

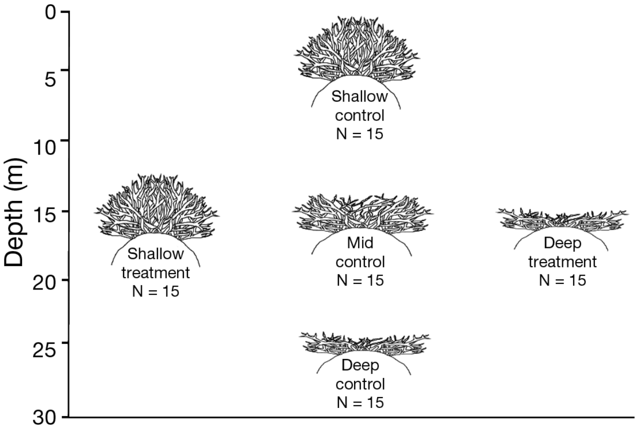

Fig. 2. Transplant experiment, with *Seriatopora hystrix* treatment colonies from shallow and deep water transplanted to a standardized mid depth, in addition to 3 control groups consisting of colonies placed at the depths from which they were collected. All *Paragobiodon xanthosoma* were collected from the shallow site

Seventy-five coral colonies were collected from Matane Walindi and Rosemary's Reef using chisels and buckets and placed in a sandy sloping lagoon on Madaro reef extending 80 m across and down to a maximum depth of 30 m. To ensure colonies were secure, they were attached to concrete blocks using fishing line. Colonies were placed a minimum of 5 m apart and 15 m from wild *S. hystrix* colonies. Negligible movement has been shown to occur in settled *P. xanthosoma* between colonies >1 m apart (Wong et al. 2007).

In total, 75 sub-adult *P. xanthosoma* were then collected from 13 to 17 m using clove oil and hand nets. Individuals were transported back to the laboratory where they were tagged with individual colour combinations of fluorescent elastomer into the dorsal musculature. Each individual was photographed and the standard length measured to the nearest 0.01 mm using the program ImageJ. Following a recovery period of 3 h, individuals were transported using SCUBA back to the reef in small plastic bags filled with seawater, released onto the *S. hystrix* patch reefs and, after a period of 21 d, recaptured and remeasured. There was no significant difference in the size of fish (mean ± SE standard length: 11.1 ± 0.02 mm, ANOVA: $F_{(4,75)} = 0.83$, $p = 0.53$) or coral colonies (mean width: 17.1 ± 0.02 cm, ANOVA: $F_{(4,75)} = 1.681$, $p = 0.16$) between treatments.

RESULTS

Quantitative surveys of coral morphology

There were pronounced differences in the morphological characteristics of *Seriatopora hystrix* over depth in all 6 metrics examined (Fig. 3). Overlaid clusters using a resemblance level of 90% revealed

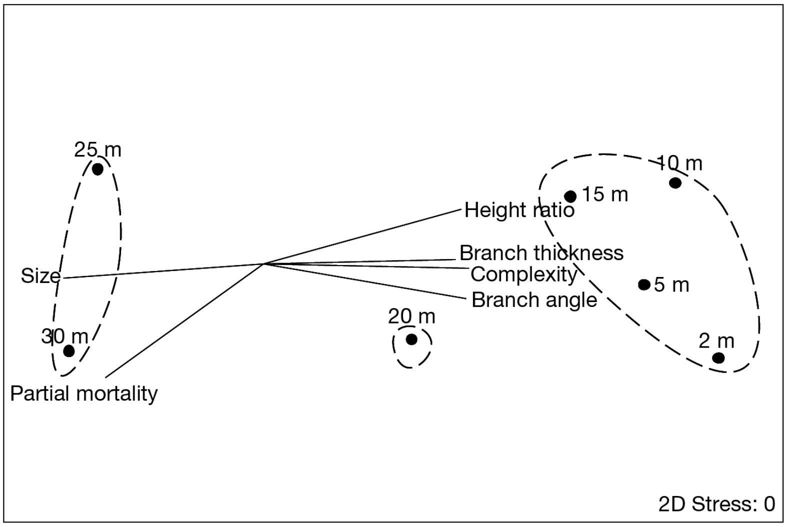

Fig. 3. nMDS performed on morphological colony attributes of *Seriatopora hystrix*. Points represent the mean values for each metric. Groupings are based on cluster analysis with a resemblance level of 90%

that coral from 2 to 15 m and from 25 to 30 m grouped together, while colonies from 20 m displayed an intermediate position. There were also significant differences between depths across all 6 of the metrics examined (Table 1). Colony width increased with depth from a mean (±SE) width of 9.7 ± 0.2 cm at 2 m to 19.7 ± 0.3 cm at 30 m. The height ratio of colonies decreased with depth, with colonies becoming flatter for any given width in deeper water (mean height ratio: 0.54 ± 0.01:1 at 2 m and 0.39 ± 0.05:1 at 30 m). Branching structure also varied over depth, with deeper colonies becoming less complex (mean number of branch tips: 51.6 ± 0.9 at 2 m and 26.4 ± 0.4 at 30 m), having thinner branches (mean branch width: 3.6 ± 0.02 mm at 2 m and 2.1 ± 0.02 mm 30 m) and a lower angle of branch growth (mean angle: 43 ± 1.2° at 2 m and 8 ± 0.7° at 30 m). Colony health also declined with depth, evidenced by higher levels of partial mortality in colonies from deeper water (mean partial mortality: 12 ± 0.04% at 2 m and 18 ± 0.46% at 30 m).

Logistic regression analysis on colony size, height and health revealed that colony size and health were useful in predicting the occupation of *S. hystrix* by *Paragobiodon xanthosoma* (χ^2 = 137.25, df = 3, p = 0.001; Table 2) and that colony size was the most important whole-colony characteristic associated with occupation. Similarly, the logistic regression examining colony structure showed that characteristics of both colony complexity and branch thickness were significant predictors of occupation by *P. xanthosoma* (χ^2 = 46.27, df = 3, p = 0.001), but that branching angle was not a useful indicator of occupancy.

Habitat preferences based on branch morphology: pair-wise choice experiments

P. xanthosoma exhibited a strong preference for shallow over deep coral colonies (24 h: χ^2 = 22.15, df = 1, p = 0.001; Fig. 4A). After 10 min, only 3.8% of individuals occupied a deep colony, and after 24 h, no individuals were observed on deep colonies. Individuals were also repeatedly observed to swim directly through the deep colonies to settle on the shallow colonies.

Table 1. Results of 1-way ANOVA ($p < 0.05$ for all) for each colony metric examined over depth. Data were log(x) transformed to meet the assumptions of normality and homogeneity of variance

	df	*F*
Whole colony characteristics		
Size	6, 1263	23.02
Height	6, 919	9.73
Partial mortality	6, 2248	6.815
Colony structure		
Complexity	6, 99	13.65
Branch thickness	6, 99	41.24
Branch angle	6, 99	9.587

Table 2. Logistic regressions examining the relationship between changes in *Seriatopora hystrix* morphology and occupation of corals by *Paragobiodon xanthosoma*. Estimates were used to define whether the effect of coral morphology was positive or negative. ns: not significant

	β	df	Wald χ^2	p	Odds ratio	95% CI	Effect
Whole colony characteristics							
Size	0.143	1	0.69	<0.05	1.15	1.12–1.19	Positive
Height	0.625	1	14.06	0.117	1.87	0.85–4.09	ns
Partial mortality	−0.024	1	4.13	<0.05	0.98	0.97–0.99	Negative
Colony structure							
Complexity	0.038	1	4.13	<0.05	1.04	1.01–1.07	Positive
Branch thickness	1.932	1	14.06	<0.05	6.90	2.52–18.95	Positive
Branch angle	0.011	1	0.69	0.404	1.01	0.98–1.04	ns

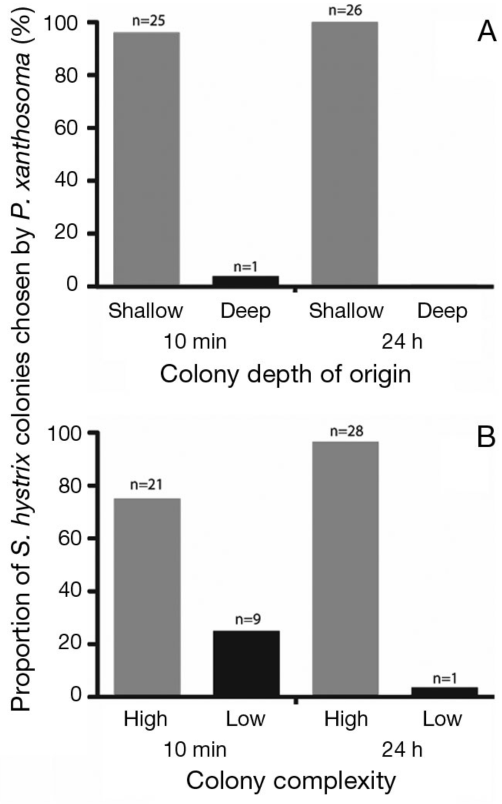

Fig. 4. Choice trials between *Seriatopora hystrix* colonies (A) collected from shallow and deep water (N = 26) and (B) of high and low complexity (N = 28)

P. xanthosoma also displayed a strong preference for corals of high complexity over low collected from the same mid-depth locations (24 h: $\chi^2 = 24.14$, df = 1, $p = 0.001$; Fig. 4B). After 10 min, >75 % of individuals occupied high complexity (>50 branch tips per 5 cm^2) colonies, and after 24 h, 96.4 % of individuals occupied high complexity corals.

Influence of coral habitat quality on goby growth

Growth of *P. xanthosoma* individuals was significantly reduced on colonies originating from deep water (deep-treatment and deep-control), regardless of the depths at which the colonies were placed (Fig. 5, Table 3). In contrast, individuals transplanted onto colonies originating from shallow or mid depths (shallow-treatment, shallow-control and mid-control) exhibited higher growth regardless of the depths at which these colonies were placed. There was no significant difference between the growth of either the deep-treatment and deep-control colonies or among the shallow-treatment, shallow-control and mid-control colonies.

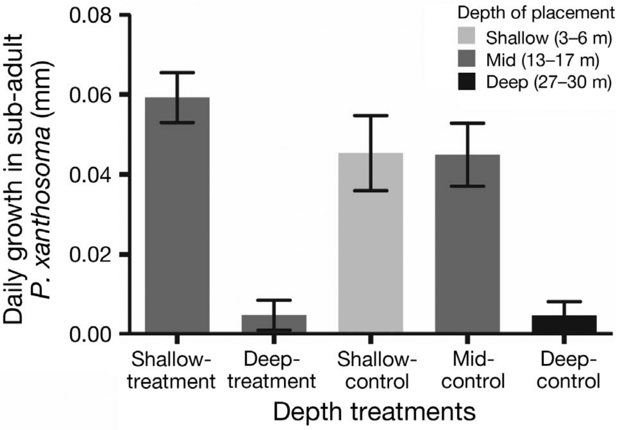

Fig. 5. Mean (±SE) daily growth of *Paragobiodon xanthosoma* transplanted to patch reefs of *Seriatopora hystrix* between depth treatments (N = 60)

Table 3. Results of ANCOVA comparing growth of *Paragobiodon xanthosoma* between depth treatments. Initial size is the covariate. Interaction terms were pooled in the higher-level effects. Data were log(x + 1) transformed to achieve homogeneity of variances

	MS	df	*F*	p
Depth treatment	0.0011	4	12.11	<0.05
Initial length	0.00091	1	9.29	<0.05
Error	0.005	54		

DISCUSSION

This study supports the hypothesis that host coral morphology is a major determinant of the depth distribution and population structure of *Paragobiodon xanthosoma.* Shallow-water colonies of *Seriatopora hystrix* were characterized by high structural complexity, a vertical branch angle, thick branches and a higher height ratio, smaller size and lower degree of partial mortality than deep-water colonies. These morphological features varied significantly over depth and influenced patterns of habitat use in *P. xanthosoma*, which were more likely to occupy colonies with shallow-water characteristics. The preference of *P. xanthosoma* for shallow-water colonies, as well as those with 'shallow' morphologies, further suggests that changes in coral morphology are likely driving the depth distribution of *P. xanthosoma*. Finally, pronounced differences in the growth of *P. xanthosoma* were explained by depth-related changes in coral habitat, suggesting that individual performance may be associated with patterns of morphological variation and condition in the coral host. It is therefore likely that habitat preferences, associated with a demographic response to changes in habitat quality among depths, are a key factor structuring the depth distribution of this species.

Our results show that the morphology of *S. hystrix*, like many other coral species, varies considerably with depth. Changes in the height ratio and branching structure of the coral habitat, e.g. complexity, branch angle and branch thickness, all correspond to differences in the light regime between deep water and shallow water environments (Bak & Meesters 1998, Falkowski & Raven 2007, Mass et al. 2007). The shift to flatter, less complex colony morphologies at depth in *S. hystrix* is consistent with previous studies examining these patterns of change over depth or between high- and low-light environments in various species of coral (Fricke & Schuhmacher 1983, Vermeij & Bak 2002, Anthony & Hoegh-Guldberg 2003). In addition to variation in morphological characteristics, *S. hystrix* colonies also showed an increase in partial mortality over depth. This increase in partial mortality in deep *S. hystrix* colonies could be connected to the overall increase in colony size at depth because larger coral colonies tend to have proportionally higher partial mortality (Bak & Meesters 1998). However, coral health is also associated with changes in environmental conditions such as sedimentation (Fabricius et al. 2005) and temperature extremes (Hughes et al. 2003), which also vary over depth (Kahng et al. 2010). While temperature stress is reduced at depth, other stressors such as sedimentation can increase in deeper locations and may additionally reduce coral health in deeper water (Bejarano et al. 2014, Appeldoorn et al. 2016). The depth-associated decline in colony health may therefore be due to a combination of changes in environmental conditions and an increase in colony size.

The increase in mean colony width of *S. hystrix* over depth contrasts with the findings of previous morphological studies and may reflect differences in sampling techniques or patterns of recruitment and survival. In the Red Sea, Nir et al. (2011) showed no differences in the size distribution of *S. hystrix* over depth; however, their study only documented colonies that were large enough to collect 5 cm fragments. In contrast, the present study recorded the size of every visible colony and therefore presents a more complete description of the size distribution of this species. The increased mean width of colonies at depth could be the result of either larger adult colonies or a lower abundance of smaller colonies in deep locations, both of which were observed. This would suggest that patterns of recruitment and juvenile survival could be depth-dependent, with fewer recruits settling in deeper water but higher or consistent rates of survival once colonies become established. This hypothesis is supported by previous studies demonstrating reduced rates of recruitment (Mundy & Babcock 1998, Carlon 2002) but consistent rates of survival (Bak & Engel 1979) in similar coral species over the similar depth ranges.

Changes in the characteristics of *S. hystrix* associated with depth strongly influenced patterns of habitat use by its associated reef fish *P. xanthosoma.* Colonies of *S. hystrix* in shallow water exhibited characteristics likely associated with greater habitat quality, namely low partial mortality, high morphological complexity and wider branches compared to colonies in deep water. Accordingly, occupancy of coral colonies by *P. xanthosoma* is far greater in shallow than deep water (Smallhorn-West et al. 2017). The higher rate of occupancy in colonies with reduced partial mortality supports previous studies demonstrating that coral health drives changes in group size (Noonan et al. 2012), habitat use (Schiemer et al. 2009) and levels of recruitment (Feary et al. 2007) in coral-associated reef fish. Similarly, high colony complexity and branch thickness are related to increased survival (Noonan et al. 2012) and occupancy (Unterteggaber et al. 2014) in coral-associated associated reef fish due to the importance of habitat structure in providing shelter from predation (Eggleston & Lipcius 1992, Hixon & Beets 1993). The positive relationship between habitat size and occupancy by *P. xanthosoma* is consistent with the findings of previous studies (Thompson et al. 2007, Wong 2011). However, these relationships do not explain the high abundance of *P. xanthosoma* in shallow colonies, where mean colony size is smaller. This suggests that while colony size exhibits a strong correlation with habitat use, changes in other aspects of the quality of the coral host over depth may be sufficient to outweigh the benefits provided by larger coral colonies.

The preference of *P. xanthosoma* for shallow- over deep-water coral colonies further suggests that the quality of their coral habitat declines with depth. Numerous studies have demonstrated that reef fish will preferentially select environments in which individual performance is maximized (Munday 2001, Srinivasan 2003, Noonan et al. 2012), suggesting shallow-water coral colonies offer superior habitat compared to colonies from deeper water. While these results do not distinguish the mechanisms by which coral quality changes, the strong preference for high-complexity coral habitat over low suggests that depth-driven changes in the branching structure of *S. hystrix* may be an important determinant of habitat use in this species.

Habitat complexity is a well-established driver of trends in species distributions across multiple scales (Roberts & Ormond 1987, Almany 2004a,b, Graham et al. 2006, Noonan et al. 2012). Most notably, the increased habitat complexity provides greater shelter from predation, thereby affecting survival (Eggleston & Lipcius 1992, Hixon & Beets 1993, Graham et al. 2006). Similarly, changes in habitat complexity can also affect patterns of growth (Connell & Jones 1991, Munday 2001, Höjesjö et al. 2004). Variation in these demographic processes provides a strong selection pressure for both adults and recruits to select high-quality habitats that will maximize individual performance (Almany 2004a, Noonan et al. 2012). The change in coral colony complexity over depth, in conjunction with the preference and increased habitat use in high-complexity, 'shallow' morphologies, suggests these differences may be responsible for structuring the depth distribution of *P. xanthosoma.*

While the surveys and preference trials established correlations between habitat quality and use by *P. xanthosoma* over depth, the direct causal relationship between these factors was examined using the transplant experiment, which isolated changes in habitat quality over depth as a driver of individual performance in *P. xanthosoma.* The 8-fold lower growth in *P. xanthosoma* individuals transplanted onto deep-water coral colonies demonstrates that there are substantial costs to individual performance specifically associated with characteristics of the deep-water coral habitat. This further supports the hypothesis that there is a substantial decline in the quality of their coral host over depth and that the fitness costs associated with this declining quality are important in explaining differences in habitat use and the depth distribution of *P. xanthosoma*. This study adds to an increasing body of knowledge outlining how differences in habitat quality (e.g. coral health and branching structure) influence the preference and individual performance of coral-associated reef fish (Munday 2001, Feary et al. 2007, Bonin et al. 2009, Kane et al. 2009, Noonan et al. 2012).

Although the experiments conducted here demonstrate that there are significant consequences to individual performance for fish settling onto deep-water *S. hystrix* colonies, the reason for the decreased growth rate are uncertain. In reef fish, patterns of growth are often associated with food availability (Jones 1986, Boisclair & Leggett 1989, Jones & McCormick 2002). Gut content analysis of *P. xanthosoma* suggests that they may feed on coral tissue (Lassig 1976) and therefore changes in their coral habitat over depth could also result in differences in its nutritional value or palatability for this species. Furthermore, deep and shallow populations of *S. hystrix* can be genetically distinct and may even represent cryptic species (Bongaerts et al. 2011, van Oppen et al. 2011), which could further drive differences between shallow- and deep-water colonies. The maximum size of fish has also been shown to increase in larger colonies (Thompson et al. 2007). Given the ability of this species to regulate its growth based on the surrounding environment, it is likely that other aspects of habitat quality, including complexity and branching structure, may also regulate their growth. Because none of the above factors are mutually exclusive, all may play a role in explaining the observed differences in the growth of *P. xanthosoma* between coral habitat from different depths.

Overall, these results support the conclusion that depth-driven changes in the structure of *S. hystrix* influence the depth distribution of *P. xanthosoma*. Differences in the morphological characteristics and partial mortality of the coral habitat were observed over depth, and these differences were shown to influence patterns of habitat use in *P. xanthosoma*. A preference for colonies with characteristics from shallow locations suggests that specific changes in coral morphology and partial mortality may be driving their distribution. Finally, the reduced growth of individuals on deep colonies provides the demographic mechanism by which these patterns may be enforced. The present findings highlight that the availability of suitable habitat can be based on differences in habitat quality, not solely abundance. Heterogeneity in habitat quality along environmental gradients such as depth therefore need to be considered in order to better understand the effects of changing environmental conditions on the distribution and demography of species. Future studies should investigate the specific nature of changes in habitat quality over environmental gradients, which would allow more accurate predictions of how species distributions may respond to changes in the environment.

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