

Geographic divergence in the relationship between *Paragobiodon echinocephalus* and its obligate coral host

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The redhead goby *Paragobiodon echinocephalus* lives exclusively within the branching coral *Stylophora pistillata*. While in the Great Barrier Reef fish occupation rate of large coral is higher than that of small coral, an opposite pattern exists in the northern Red Sea. It is suggested that this pattern is caused by a limitation on the adult body size of fish in the northern Red Sea.

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Understanding the relationship between organisms and their environment is a fundamental aspect of ecology. The study of this relationship, however, is complicated when the response of an organism to its environment varies spatially along environmental gradients (Prinzing *et al.*, 2002; Krasnov *et al.*, 2005; Murphy & Lovett-Doust, 2007). The cause of this variation can be biological, such as the existence of predators or competitors, or abiotic, such as temperature or water chemistry. The ‘niche variation hypothesis’ states that species would be less variable in morphological characteristics when occupying a narrow niche than when occupying a wider niche (Van Valen, 1965). Accordingly, specialized species, restricted to a certain habitat, may be less likely to exhibit geographical variation in the way they utilize their habitat as compared to generalist species. Nonetheless, the ‘niche variation hypothesis’ remains equivocal (Soule & Stewart, 1970; Meiri *et al.*, 2005).

Coral-dwelling fishes rely on their coral habitat for shelter from predation and for a breeding site (Kuwamura *et al.*, 1993; Munday *et al.*, 1997). Coral size plays a pivotal role in many of the life-history variables of coral-dwelling fishes, including adult size and abundance (Kuwamura *et al.*, 1994), mating system (Fricke, 1980; Wong *et al.*, 2005) and reproductive success (Kuwamura *et al.*,

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1996). The redhead goby *Paragobiodon echinocephalus* (Rüppell, 1830) lives exclusively among the branches of the branching coral *Stylophora pistillata* and is therefore extremely specialized in its habitat requirements (Kuwamura *et al.*, 1994; Herler & Hilgers, 2005). In a study from the Japanese island of Okinawa, Kuwamura *et al.* (1994) have shown that the maximum size and the number of resident fish increases linearly with the size of the host coral. In the present study, the relationship between *P. echinocephalus* and its host coral is compared in two distinct biogeographical regions to examine whether an extreme specialist species varies its habitat requirements across a wide distribution range.

The study was conducted at two geographically separated regions: (1) the Inter-University Institute for Marine Science (IUI) on the Israeli coast of the Gulf of Aqaba, which is an extension of the northern Red Sea (NRS) and (2) Heron Island Research Station, located on the Great Barrier Reef (GBR). Five sites were surveyed in the NRS and three in the GBR. At each site, several 50 × 1 m belt transects were placed. The number of transects within a site varied (two to 20), such that sites with low coral cover were sampled more intensively to achieve a reasonable sample size (*i.e.* at least 12 corals). In addition, several more coral heads were selected haphazardly at each site to increase sample size. Most analyses, apart from coral occupancy rate within a site, were performed on all corals within the region combined. Therefore, transects and sites describe the way coral heads were surveyed, but do not factor into the analyses. All *S. pistillata* coral with a diameter >5 cm (Kuwamura *et al.*, 1994) found within the belt transect were examined. Coral diameter was calculated as the geometric mean of the length, width and height (Loya, 1976).

The number and size of *P. echinocephalus* in each coral was recorded. In addition, presence of potential predators, such as dottybacks from the genus *Pseudochromis*, was recorded. Visual observation was aided by a torch. Such visual estimations may underestimate the true number of individuals. To examine whether a bias exists in the visual surveys fish were anaesthetized in 10 corals using clove oil (Munday & Wilson, 1997) following visual census. In all corals examined, the number of fish estimated visually was identical to the number of fish actually present, as revealed by anaesthetization (ranging between one and three). Fish total lengths (L_T) were estimated to the nearest 5 mm by comparing them underwater to a ruler. A regression of estimated L_T and real L_T , measured after anaesthetization, revealed a slope that was not significantly different from 1 and an intercept not significantly different from 0 (slope ± 95% CI = 1.13 ± 0.35 and intercept ± 95% of CI = -0.23 ± 0.68; $n = 12$). Therefore, estimated length is a reliable measure.

The average number of individuals within an occupied coral colony did not differ between the NRS (mean ± s.e. 1.41 ± 0.05) and the GBR (1.59 ± 0.01) (Kruskal–Wallis, d.f. = 1, $P > 0.05$). Unlike Kuwamura *et al.* (1994), more than two individuals were seldom found within a coral. Overall coral occupancy rate within a site did not differ significantly between the regions (0.31 ± 0.02 in the GBR compared to 0.22 ± 0.04 in the NRS; Kruskal–Wallis, d.f. = 1, $P > 0.05$), although sample size was noticeably small ($n = 8$).

To examine whether coral size had similar effects on *P. echinocephalus* occurrence between regions, a logistic regression was performed, with coral diameter

and region (NRS v. GBR) as a continuous predictor and a categorical predictor, respectively. A significant interaction indicates differences between regions in the fish–coral relationship. The full model was highly significant (logistic regression, $n = 541$, $P < 0.001$), as well as the interaction term between region and coral diameter ($P < 0.001$). Moreover, the regression slope coefficients describing the effect of coral diameter showed opposite signs (slope = -0.126 for the NRS and slope = 0.25 for the GBR). Therefore, while in the NRS *P. echinocephalus* occupancy rate decreased with coral size, the opposite trend existed in the GBR (Fig. 1). To confirm that this was a general phenomenon, another data set (unpubl. data) was analysed in which surveys were carried out at six locations in each region (located at least 20 km apart, covering an extent of 275 km in the GBR and 182 km in the NRS). Only *S. pistillata* with a diameter >200 mm were included in this survey. Indeed, a similar pattern of a lower occupancy rates in large coral in the NRS as compared to the GBR was found (3%, $n = 118$ in the NRS v. 43%, $n = 37$ in the GBR; Fisher exact test, $P < 0.001$).

The positive relationship between occupancy rate and coral size found in the GBR is consistent with a previous study in Okinawa that found a linear relationship between *P. echinocephalus* abundance and coral size (Kuwamura *et al.*, 1994). The negative relationship found in the NRS may be explained, to some extent, by the presence of young fish that prefer small corals (Kuwamura *et al.*,

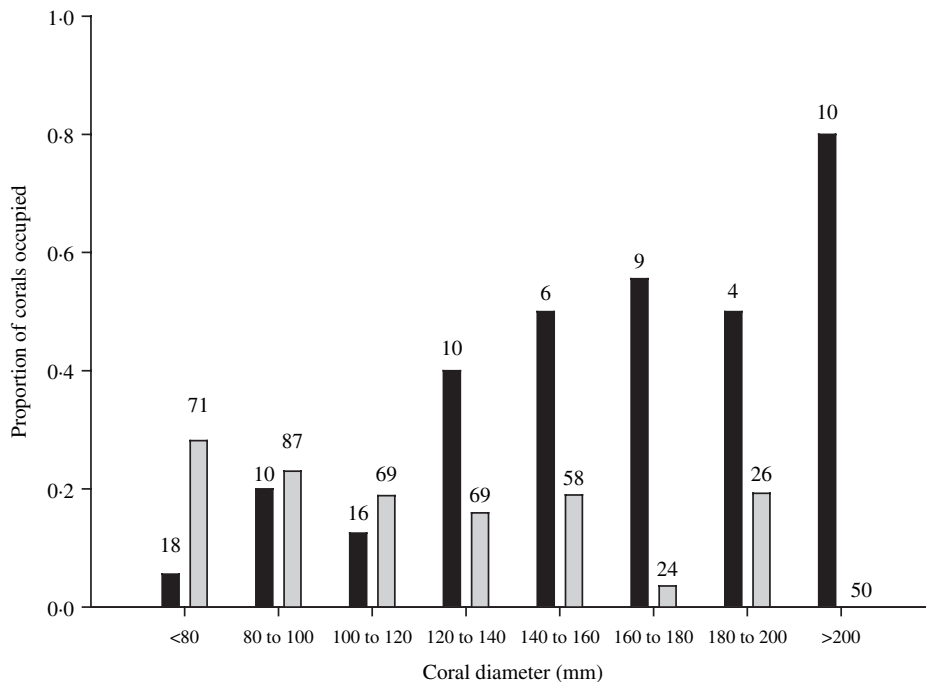


FIG. 1. The proportion of corals occupied by *Paragobiodon echinocephalus* in the different regions [northern Red Sea (□) and Great Barrier Reef (■)] at various categories of coral diameter. The numbers indicate sample sizes.

1994). The pattern excluding young fish is likely to be unimodal, as suggested by Herler & Hilgers (2005). Nevertheless, the decrease in the occupation rate of *P. echinocephalus* in large corals in the NRS is still markedly different than the positive relationship with coral size found in the GBR (e.g. 0% occupancy in corals with a diameter >200 mm in the NRS compared to 80% in the GBR; Fig. 1).

Geographical variation in life-history variables has been documented for several coral reef fishes (Meekan *et al.*, 2001; Kritzer, 2002; Williams *et al.*, 2003; Robertson *et al.*, 2005). Geographical variation in habitat use, however, is less well documented. A large proportion of the geographical variation in the abundance of coral-dwelling gobies can be explained by the availability of suitable habitat, although residual geographical variation still exists for certain species (Munday, 2002). Abundance of the obligate coral-dwelling damselfish *Dascyllus aruanus* (L., 1758) was also determined by the availability of habitat across large geographical distances (Holbrook *et al.*, 2000). This study suggests that considerable variation in a species' response to a particular habitat may be possible also for extremely specialized species. It also emphasizes the complexities associated with ecological generalizations, as studies conducted in different regions reveal distinct patterns.

Several mechanisms can explain such a divergent relationship between regions. The underlying habitat preference may be modified by different post-recruitment processes in each region. Some species of dottybacks *Pseudochromis* spp. are voracious predators of small fishes (Beukers & Jones, 1998) and may also eat *P. echinocephalus* (pers. obs.). The percentage of corals containing *Pseudochromis* spp. was much greater in the NRS (12%, $n = 458$) than in the GBR (0%, $n = 83$ for the corals sampled, although *Pseudochromis* spp. were seen within corals during occasional observations). Moreover, *Pseudochromis olivaceus* (Rüppell, 1835), a common Red Sea species, is found mainly in large *S. pistillata* (logistic regression, $n = 458$, $P < 0.001$). In large corals (diameter >180 mm), similar occurrence rates of *P. echinocephalus* in corals with and without *P. olivaceus* were found (Fisher exact test, $P > 0.05$). It should be noted that *P. olivaceus* is faithful to its home coral head, staying a mean \pm s.e. $96 \pm 2\%$, of their time within a single coral (unpubl. data). Therefore, there is no evidence that predation by *P. olivaceus* causes the decrease in the occupancy rate of *P. echinocephalus* in large corals in the NRS. Nevertheless, the possibility that other post-recruitment processes cause the difference between the regions cannot be excluded.

Potentially, underlying habitat preference in both regions may be similar with a preference for medium-sized corals. In sites with high occupancy rates, however, competition for host corals may force individuals to the supposedly less suitable large corals (Fretwell & Lucas, 1969). If this hypothesis is true, occupancy rates of small and large corals might be expected to be positively correlated. No correlation between fish occupation rate in a site for small and large corals was found (Spearman's rank correlation, $r = -0.11$, $P > 0.05$), and therefore, this hypothesis is not supported. Differences in coral architecture between the NRS and the GBR might also cause separate habitat preferences in each region. As coral growth form and shape appear to be similar between the regions, however, this seems to be an unlikely explanation.

The relationship between *P. echinocephalus* size (the L_T of the largest individual in the coral) and coral diameter was compared between the two regions (Fig. 2). The full model was found to be significant (separate slopes ANCOVA, $F_{3,113}$, $P < 0.001$). Although fish were significantly larger in the GBR compared to the NRS ($P < 0.01$) and fish size significantly increased with coral diameter ($P < 0.001$), the two variables did not interact ($P > 0.05$). The non-significant interaction term suggests that fish size responds similarly to coral size in the two regions examined. Nevertheless, when examining the data it becomes clear that no fish in the NRS, from any size, appeared to live in corals >200 mm (Fig. 2). This helps explain why mean L_T was found to be larger in the GBR compared to the NRS. A close association between the size of the host coral and the size of the *P. echinocephalus* individuals which occupy it was also found by Kuwamura *et al.* (1994). In addition, the reproductive success of *P. echinocephalus* is closely associated with its size (Kuwamura *et al.*, 1993). Therefore, absence of gobies from large corals in the NRS seems to be maladaptive and may result from some independent constraint on size, causing under-exploitation of large host corals in this region. The possible contribution of the small size of adult *P. echinocephalus* in the NRS to the fish–coral relationship was already noticed by Herler & Hilgers (2005), who found specimens from the NRS to be smaller than those reported by Kuwamura *et al.* (1993). Possibly, conditions in this region prevent *P. echinocephalus* from reaching larger sizes, causing the locally smaller individuals to select smaller host corals. Experimental manipulations

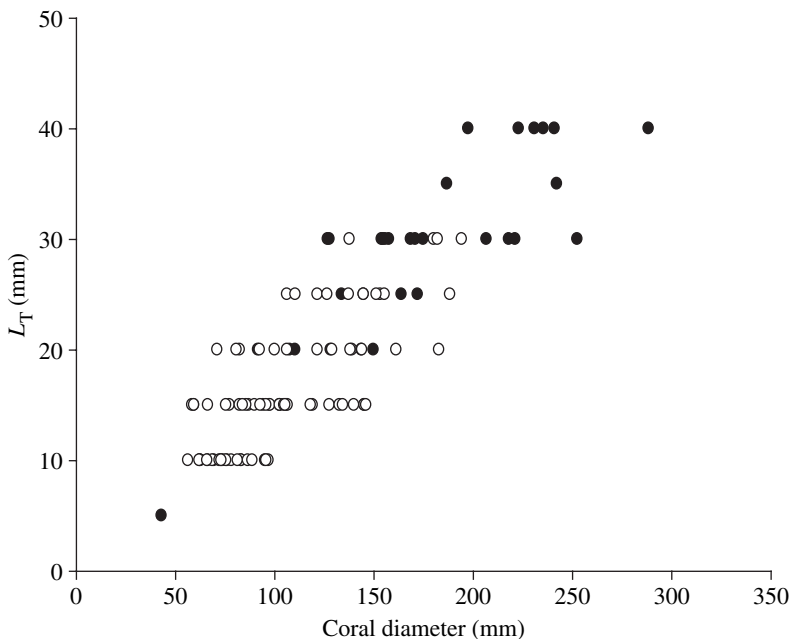


FIG. 2. The total length (L_T) of the largest individual *Paragobiodon echinocephalus* occupying a coral and coral diameter for the two regions examined [northern Red Sea (○) and Great Barrier Reef (●)].

are necessary to demonstrate unambiguously that the under-exploitation of large coral in the NRS is due to constraints on maximal adult size.

It has been shown above that the association between the fish *P. echinocephalus* and its coral host differs in the NRS as compared to other Pacific sites (at least the GBR and South Japan). The data support the hypothesis that this difference is caused by dissimilarity in maximal adult body size and not by an alteration of habitat preference *per se*. Although geographical variation in fish body size is not uncommon (Meekan *et al.*, 2001; Corriero *et al.*, 2005; Robertson *et al.*, 2005), there is no report, as far as is known, of smaller body size of other reef fishes in the NRS compared to other regions. Since body size is strongly correlated with reproductive successes in this species (Kuwamura *et al.*, 1993) such a limitation on adult size may have adverse effects on long-term population viability of *P. echinocephalus* in the NRS.

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