

Microhabitat specialisation and ecological consequences for coral gobies of the genus *Gobiodon* in the Gulf of Aqaba, northern Red Sea

Markus Dirnwöber¹, Jürgen Herler^{2,*}

¹Department of Marine Biology, and ²Department of Theoretical Biology, Morphology Section, Faculty of Life Sciences, University of Vienna, Althanstrasse 14, 1090 Vienna, Austria

ABSTRACT: The microhabitat selection and distribution of 6 coral-associated species of *Gobiodon* were examined in the Gulf of Aqaba, northern Red Sea, including 3 recently discovered species. A total of 1626 fishes were counted visually using 10 × 1 m belt transects in 1731 colonies of 13 species of *Acropora*. Niche segregation was observed at the level of coral species. *Gobiodon* sp. 2 was the most specialised, occupying only *A. hyacinthus*; *Gobiodon* sp. 1 was most generalised (occupying 3 species of *Acropora* more frequently than expected). *G. reticulatus* was a zone specialist that preferred deeper water regions. Less specialised species were able to use substitute host corals, which enabled them to maintain extraordinarily high abundance. *G. histrio*, for example, preferred the rare *A. digitifera*, but was common in the very abundant *A. acuminata*, although proportionally fewer breeding pairs were established in the latter. When compared to the western Pacific, *G. histrio* showed a more generalised behaviour in the northern Red Sea, and different coral species served as host corals; the latter also holds true for the even more generalised *G. rivulatus*. Hence, species of *Gobiodon* appear to alter host-use and degree of specialisation on a global scale.

KEY WORDS: *Gobiodon* spp. · *Acropora* spp. · Gobiidae · Habitat associations · Abundance · Reef fish · Coral reefs · Red Sea

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Microhabitat specialisation is common among small coral reef fishes such as pomacentrid, apogonid, pseudochromid, or gobiid species and is often found at the level of coral species (Munday et al. 1997, Gardiner & Jones 2005). These fishes are therefore highly dependent upon the cover, diversity and complexity of the respective habitat, and natural or anthropogenic impacts will affect their populations (Jones & Syms 1998, Jones et al. 2004, Graham et al. 2006). The degree of microhabitat specialisation is likely to be an important factor influencing the abundance and geographic distribution of species (Brown 1984, Brown et al. 1995, Jones et al. 2002, Munday 2002). Most studies of these relationships, however, have been carried out at a few Indo-Pacific sites (Munday 2002, Gardiner &

Jones 2005), and little is known about how this dependence on habitat structure varies in different geographic regions. Coral diversity and abundance strongly influence associated reef fishes, especially when there is strong interspecific competition for limited habitats. Competition among coral reef fishes with similar ecological demands may reduce the abundance and change the patterns of microhabitat choice of especially inferior competitors (Robertson 1996, Munday et al. 2001), while habitat availability may alter these patterns even in superior competitors (Munday 2002).

The Red Sea is an appropriate region to study such geographical differences, because, although it belongs to the western Pacific/Indian Ocean reef province, it is largely isolated, has a unique fauna and also high degrees of endemism among many reef organisms

*Corresponding author. Email: juergen.herler@univie.ac.at

(Head 1987). It is characterised by well-developed coral reefs, but a reduced biodiversity of hermatypic corals compared to the eastern Indian or western Pacific Ocean (Veron 2000). A key question that can be posed is: How does the level of reef fish specialisation or dependence upon coral differ in a region of reduced coral diversity? Suitable reef fishes to examine this question need to: (1) exhibit specific microhabitat selection that can be easily investigated and quantified and (2) have a wide distribution area to allow comparable studies at the species level on a global scale. Such requirements are fulfilled by a series of coral-associated gobiid fishes.

Coral-dwelling gobies belong to the most specialised reef fishes and are good study models because they show distinct microhabitat choices at the level of coral species. Due to their small body size and the high structural variation among hard corals, these fishes can potentially occupy a broad range of microhabitats (Munday et al. 1997). Coral-associated species belong to the genera *Gobiodon*, *Paragobiodon*, *Bryaninops*, or *Pleurosicya* (Herler 2007). Although these fishes are difficult to study, detailed ecological studies on their habitat preferences hold the key to understanding the population dynamics, distribution and evolution of small reef fishes with strong habitat fidelity (Kuwamura et al. 1994, Munday et al. 1997, 2001), especially for species associated with living hosts. The degree of habitat specialisation among *Gobiodon* spp. was revealed by Munday et al. (1997), who showed that species distribution is disproportional among the various *Acropora* spp. at the Great Barrier Reef (GBR). This makes them optimally suited to study variation of patterns of distribution and abundance.

Most studies on the ecology of *Gobiodon* spp. focused on the tropical Indo-West Pacific region rather than on the Red Sea, which is the north-western boundary of their distribution. *Acropora* is represented in the Red Sea by about 40 species (Wallace 1999), and *Acropora* diversity at single reefs can drop down to <15 species (J. Herler & M. Dirnwöber pers. obs.). In contrast, local diversity of potential host corals of the genus *Acropora* was much higher on western Pacific reefs, e.g. at Lizard Island (GBR, Australia) (Munday et al. 1997). Similarly, reef fish diversity is lower in the Red Sea (Bellwood & Wainwright 2002). Among *Gobiodon* spp., only 4 species were known from the Red Sea prior to our studies: *G. citrinus* (Rüppell, 1838), *G. histrio* (Valenciennes, 1837), *G. rivulatus* (Rüppell, 1830) and *G. reticulatus* Playfair, 1867. Three additional species were recently discovered as new records for the Red Sea and are probably even new to science, but of questionable taxonomic status (Herler & Hilgers 2005).

The abundance of *Gobiodon* spp. is usually limited by host coral abundance (Munday 2000), and intensive

competition is the norm, especially for those coral species used by >1 *Gobiodon* spp. (Munday et al. 2001, Hobbs & Munday 2004). Occupation rates of approximately 80% have been reported among certain species of *Acropora* (Munday et al. 1998), while highly preferred *Acropora* spp. — like *A. nasuta* — reach occupation rates of almost 100%, especially among the larger colony size classes (Hobbs & Munday 2004). These high occupation rates limit the opportunities for juveniles and inferior competitors to settle. Munday et al. (2001) demonstrated that species can coexist by diverse mechanisms. The various adaptations that structure this coral-dwelling community will depend on the number and species of *Gobiodon* inhabiting a region and the availability and diversity of suitable coral colonies. At geographical scales, e.g. between the GBR and Papua New Guinea (PNG), habitat use by certain *Gobiodon* spp. differed. Other species, such as *G. histrio*, for example, exhibited a very conservative pattern of habitat use on such a scale (Munday et al. 1997, Munday 2002).

The present study investigates the local diversity, abundance and microhabitat selection of *Gobiodon* spp. with respect to the availability of potential host corals in the northern Red Sea. We also examine whether habitat choice patterns are retained at larger geographic levels depending on the presence of host corals. We provide the first data on microhabitat selection and niche segregation of a guild of coral-gobies in the Red Sea. This, in turn, allows insights into changes in the ecology of certain species on a global spatial scale, when we compare our results with previously published data (Munday et al. 1997, Munday 2002). We tested the following hypotheses for small reef fishes: (1) species of a guild of habitat-specialised fishes differ in their microhabitat choice (host coral selection), as assumed by Munday et al. (1997); (2) the degree of specialisation differs among coral-associated conspecifics (Munday et al. 1997) and explains local abundance of species (Brown et al. 1995); (3) a lower coral diversity results in a less diverse community of obligate coral-associated fishes and higher specialisation (narrower spatial niche) of species; and (4) the degree of specialisation and specific host preferences may be altered over large geographical distance on, e.g., a 'global scale'.

MATERIALS AND METHODS

Study area. The study was conducted between March and June 2004 at Dahab (28° 28' N, 34° 30' E), in the Gulf of Aqaba, northern Red Sea, Egypt (Fig. 1). To investigate the habitat preferences among the different species of *Gobiodon*, 2 study sites about 1 km apart

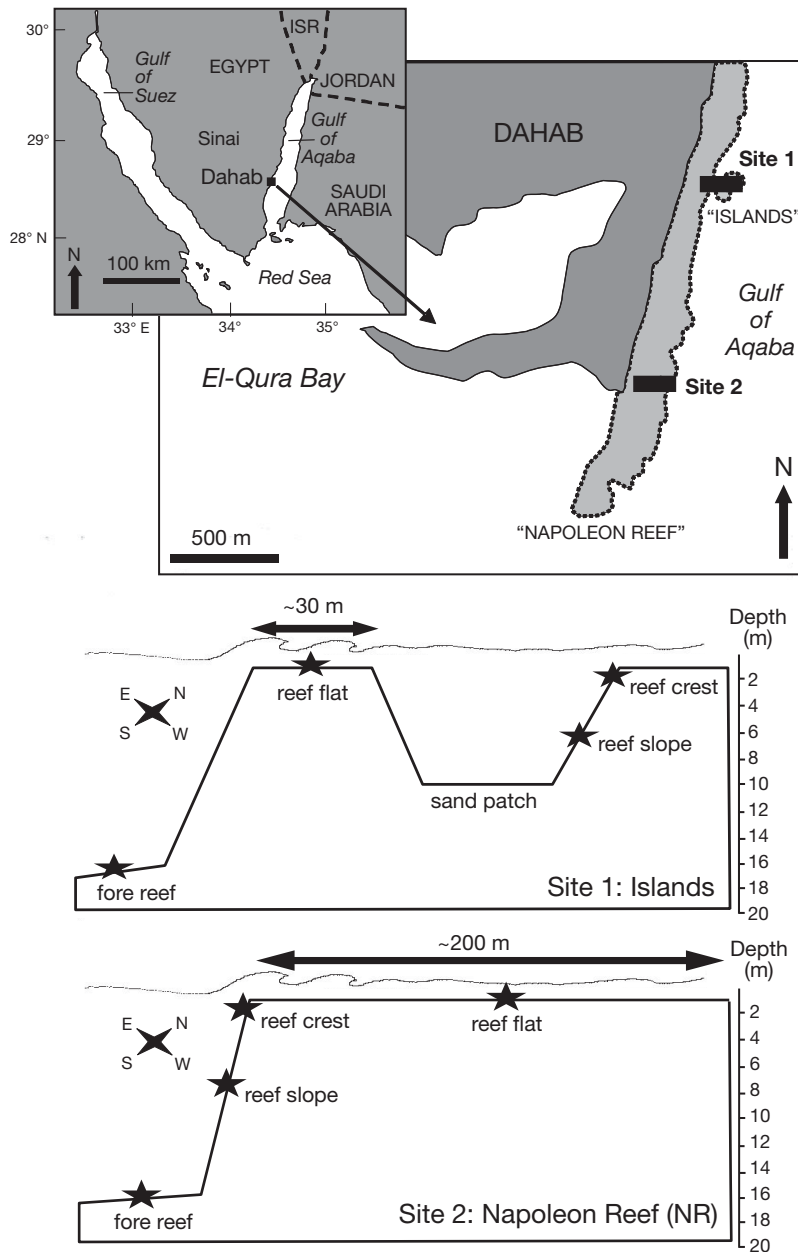


Fig. 1. Sampling sites in the vicinity of Dahab, Sinai. Inset shows Gulf of Aqaba, northern Red Sea, and the Sinai Peninsula, Egypt. The dotted line indicates the course of the reef crest and of the offshore islands. The 2 investigation sites are marked by black rectangles (upper panel). Transect positions are indicated by black stars for each site (lower panels)

were chosen (Fig. 1). The first site is known as 'Islands'; the second site was approximately 500 m north of the 'Napoleon Reef', at the outermost part of the promontory (Fig. 1) and will be referred to as 'NR' in the following. Both study sites had similar exposure to prevailing winds, but the inshore fringing reef of Site 1 is protected by 2 large offshore reef bodies (the 'Islands'), which reach up to the water surface; the reef flat of the

inshore fringing reef is strongly eroded, with little live coral coverage. Therefore, the adjacent, wave-exposed patch reefs—offering high coral cover—were used as the reef flat zone. The reef crest and slope at Site 1, however, were less wave-exposed due to the offshore reefs. At Site 2 (NR), reef zones were more continuous, and large areas of the reef flat were less exposed due to its long horizontal extension and the dissipation of wave energy at the reef edge.

Data sampling. To determine *Gobiodon* spp. coral preferences, all species of *Acropora* were censused regardless of growth form. At each site, 5 belt transects of 10×1 m were established in the centre of the reef flat, along the reef crest (between 1 and 3 m depth) and in the lower half of the reef slope (average depth about 8 m). Ten transects were laid at the reef slope of Site 2 to guarantee a sufficient amount of colonies for analyses, because this reef zone had an extremely low abundance of *Acropora* spp. Transects were laid roughly parallel to the coast line, and the position of each transect was haphazardly selected. Each *Acropora* colony with a minimum diameter of 10 cm (necessary for reliable field identification at species level) and located more than half within the belt transects was considered. Maximum diameters were measured to the nearest 5 cm. Colonies were carefully censused for the presence of *Gobiodon* spp. using an underwater torch; the identity and number of fish were recorded. Fish size was estimated *in situ* using a series of artificial fish templates representing 5 mm size classes (<15 to >40 mm total length). The fore reef zone of the Islands site was additionally sampled for information on deeper-living *Gobiodon* spp. SCUBA-diving constraints and the low and patchy coverage of *Acropora* spp. within the Islands fore reef required an alternate sampling design here: data were gained through random swims between 15 and 17 m depth. Every *Acropora* colony was examined as stated above, until 200 colonies had been sampled. Overall coral abundance here was subsequently estimated by counting colonies within 5 randomly laid 10 m^2 belt transects.

Coral and fish species studied. Preliminary identifications of *Acropora* spp. followed Wallace (1999) and Veron (2000). Representative samples of coral colonies of every species of *Acropora* were sent to Dr. Carden Wallace (Museum of Tropical Queensland, Townsville, Australia) for confirmation of coral identities. Samples were taken in accordance with national and international laws (NSC/EEAA and CITES-permissions from Egypt and Australia). Thirteen species of *Acropora* were identified during this study (Table 1).

Six species of *Gobiodon* inhabiting *Acropora* spp. were selected for this study: *G. histrio* (his), *G. reticulatus* (ret), *G. rivulatus* (riv), and 3 undescribed species—*Gobiodon* sp. 1 (sp1), *Gobiodon* sp. 2 (sp2) and *Gobiodon* sp. 3 (sp3). For detailed descriptions of the 3 latter species see Herler & Hilgers (2005). Although *G. citrinus* is present in the Gulf of Aqaba (Herler & Hilgers 2005), this species did not occur at the selected sites. *Gobiodon* spp. could be easily identified *in situ* based on their distinctive colour patterns. *G. rivulatus* exhibits 2 colour morphs—a light and a dark form—which have already been observed in the western Pacific (Munday et al. 1999). Both forms occurred in the Gulf of Aqaba (Herler & Hilgers 2005) and were considered separately, as the taxonomy of this species is not yet resolved. Minimum body size for adult fish was estimated for each species after juveniles were distinguished from adult males and females by their characteristically developed genital papilla. The thresholds for total length were 25 mm for *G. histrio* and *Gobiodon* sp. 3, 20 mm for *G. reticulatus*, *G. rivulatus* and *Gobiodon* sp. 1, and 15 mm for *Gobiodon* sp. 2.

Table 1. *Acropora* spp. Species of *Acropora* corals investigated for microhabitat choice of *Gobiodon* spp. in the Gulf of Aqaba, northern Red Sea, including the total number (n) and relative percentage (%) of examined colonies and the abbreviations used in further tables and graphs

Coral	n	%	Abbrev.
<i>A. acuminata</i> (Verrill, 1864)	424	24	acu
<i>A. loripes</i> (Brook, 1892)	234	14	lor
<i>A. gemmifera</i> (Brook, 1892)	190	11	gem
<i>A. hyacinthus</i> (Dana, 1846)	185	11	hya
<i>A. secale</i> (Studer, 1878)	162	9	sec
<i>A. variolosa</i> (Klunzinger, 1879)	115	7	var
<i>A. samoensis</i> (Brook, 1891)	109	6	sam
<i>A. selago</i> (Studer, 1878)	90	5	sel
<i>A. eurystoma</i> (Klunzinger, 1879)	84	5	eur
<i>A. digitifera</i> (Dana, 1846)	51	3	dig
<i>A. humilis</i> (Dana, 1846)	47	3	hum
<i>A. squarrosa</i> (Ehrenberg, 1834)	34	2	squ
<i>A. subulata</i> (Dana, 1846)	6	0	sub
Total	1731	100	

Statistical analyses. Chi-squared homogeneity tests were used to compare the *Acropora* spp. assemblage between the reef zones of both study sites. Analyses of habitat associations were conducted following Munday et al. (1997) and Munday (2000). Chi-squared goodness-of-fit tests were used to compare juvenile and adult patterns of habitat use for each species of *Gobiodon*, except for the dark colour morph of *G. rivulatus*, where juveniles were extremely rare. Chi-squared goodness-of-fit tests were also used to determine if any *Gobiodon* spp. used coral species disproportionately to their availability. Where *Gobiodon* spp. used corals disproportionately to their abundance, resource selection ratios (Manly et al. 1993) were used to determine which particular coral species was used significantly more or less frequently than expected. All species of *Acropora* with an abundance exceeding 10 colonies were used for statistical analyses (i.e. all coral species except *A. subulata*).

Selection ratios (ω_i) were estimated using the formula:

$$\omega_i = o_i / a_i \quad (1)$$

where o_i is the proportion of *Acropora* sp. *i* colonies occupied by a *Gobiodon* species of all *Acropora* spp. colonies occupied by this goby, and a_i is the proportion of available *Acropora* sp. *i* colonies of all available *Acropora* spp. colonies. Bonferroni-corrected 95 and 99% confidence intervals were estimated for each selection ratio using the formula:

$$Z_{\alpha/2k} \sqrt{[o_i(1-o_i)/(u_+ a_i^2)]} \quad (2)$$

where $Z_{\alpha/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $\alpha/2k$, α equals 0.05 or 0.01, k is the total number of coral species and u_+ is the total number of coral colonies of all species occupied by that species of *Gobiodon*. Definitions of o_i and a_i are given above. If the 95 or 99% confidence interval of the selection ratio encompassed 1, the use of the coral species was considered to be proportional to its availability, whereas it was considered disproportionate to its availability if the confidence interval did not encompass 1 (Manly et al. 1993). A confidence interval <1 indicated that the habitat was used significantly less than expected, and a confidence interval >1 indicated that the habitat was used significantly more than expected. Instead of total abundance data, only the presence or absence of each *Gobiodon* spp. per colony was used for analyses, as recommended by Thomas & Tyler (1990) in order to ensure independence of habitat observations. The degree of host specialisation was estimated calculating a Shannon-Wiener index (H') for gobiid species with respect to the corals they occupied:

$$H' = \sum_{i=1}^{i=n} (\ln P_i \times P_i) \quad (3)$$

where P_i is the proportional use of coral species i by a species of *Gobiodon* and n is the number of coral species used.

RESULTS

Habitat associations among corals and between reef zones

General distribution

The total abundance of the 13 species of *Acropora* varied considerably (Table 1), and coral assemblages (Fig. 2) at the 2 sites were different at corresponding reef zones (reef flat: $\chi^2 = 282.5$, $df = 11$, $p < 0.001$; reef crest: $\chi^2 = 53.5$, $df = 9$, $p < 0.001$; reef slope: $\chi^2 = 64.6$, $df = 6$, $p < 0.001$). Among the 1731 coral colonies, 1626 gobies were observed (Table 1, Fig. 3). The number of coral species used by each species of *Gobiodon* varied, from 5 used by the most specialised species, *Gobiodon* sp. 2 (Fig. 3), to 12 used by the most generalistic species, *Gobiodon* sp. 1 (Fig. 3). Although the habitat use of juveniles differed statistically from that of adults in all species (Table 2), juveniles and adults of a particular gobiid were most often found inhabiting the same

coral species, but in different proportions (Fig. 3). Thus, the gross pattern was the same for juveniles and adults. The juvenile/adult pattern of habitat use differing most was exhibited by *Gobiodon* sp. 3 (Fig. 3). All *Gobiodon* spp. were distributed unequally over all *Acropora* spp. occupied (Table 2). Specialisation indices (Shannon-Wiener) varied considerably, and highly specialised species (e.g. *Gobiodon* sp. 2) were usually less abundant than generalised species (e.g. *G. histrio*, *G. rivulatus*, *Gobiodon* sp. 1). However, *G. reticulatus* and *Gobiodon* sp. 3 did not follow this trend closely.

Host corals

Resource selection ratios were calculated for each species with juveniles and adults combined (Table 3). Confidence intervals of 95 and 99% around proportions of habitats used indicated that all species of *Gobiodon* inhabited at least 1 coral species more frequently than expected (i.e. host coral), occurred significantly less frequently than expected in a range of coral species, and inhabited a number of other species in accordance with their availability (Table 3). *G. histrio* inhabited *Acropora acuminata* and *A. digitifera* more frequently than expected. *G. reticulatus* most frequently inhabited *A. loripes*, *A. samoensis* and *A. squarrosa*. The 2 forms of *G. rivulatus* had 2 identical host corals (*A. acuminata* and *A. secale*), but with opposite levels of significance. *Gobiodon* sp. 1 had 3 host coral species: *A. gemmifera*, *A. samoensis* and *A. secale*. *Gobiodon* sp. 2 was most specialised and most frequently inhabited *A. hyacinthus*. *Gobiodon* sp. 3 inhabited *A. selago* more frequently than expected.

Reef zones

All *Gobiodon* spp. showed their maximum abundance on the reef crest, except for *G. reticulatus* (fore reef; Fig. 4). Within that deeper zone, the diversity and abundance of *Acropora* spp. is comparatively low and no other *Gobiodon* spp. were found except for a few *Gobiodon* sp. 1 and *G. rivulatus*. A separate analysis of the fore reef zone revealed that *G. reticulatus* inhabits all abundant corals there in accordance with their availability, without favouring certain coral species.

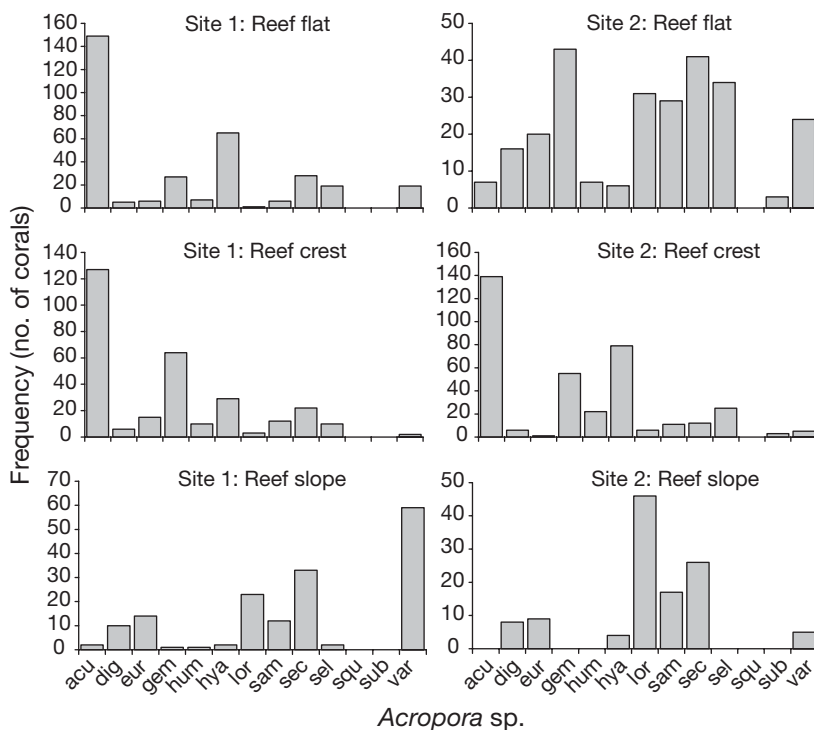


Fig. 2. *Acropora* spp. Frequency distributions across 3 reef zones at 2 investigation sites (Site 1: Islands, Site 2: Napoleon Reef; see Fig. 1) in the Gulf of Aqaba, northern Red Sea. Note that the number of *Acropora* corals at the reef slope of Site 2 comes from twice as many transects as performed in all other zones. For *Acropora* spp. abbreviations, see Table 1

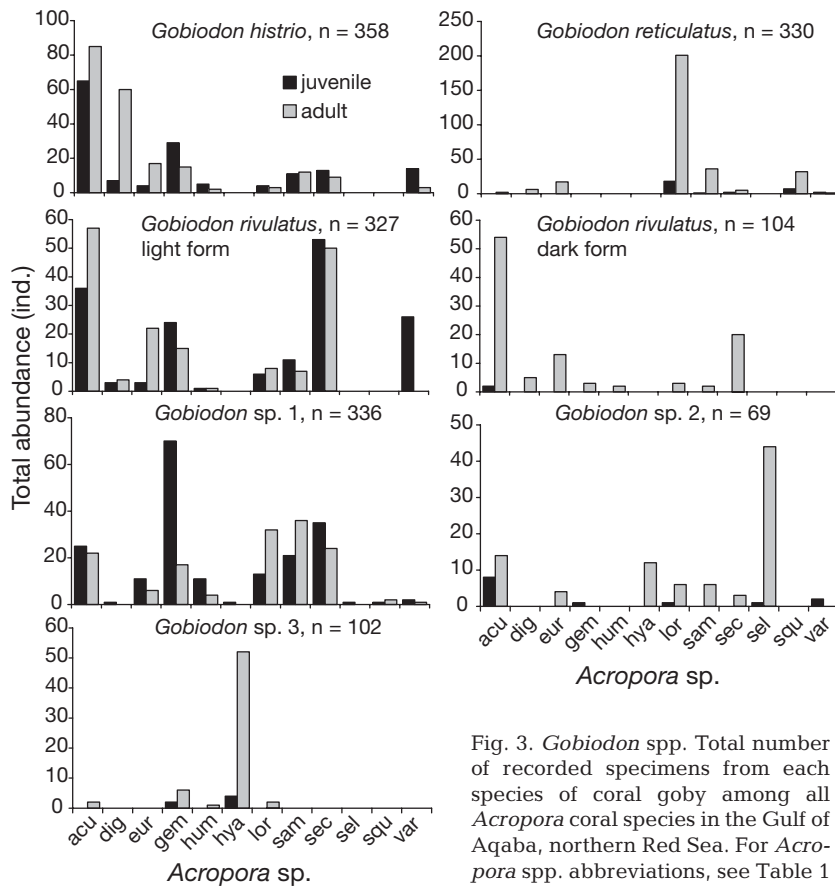


Fig. 3. *Gobiodon* spp. Total number of recorded specimens from each species of coral goby among all *Acropora* coral species in the Gulf of Aqaba, northern Red Sea. For *Acropora* spp. abbreviations, see Table 1

Relation between abundance of *Gobiodon* and *Acropora* host corals

Gobiodon histrio inhabited the reef flat and the reef crest, with only a few individuals on the reef slope (Fig. 4). It was most abundant in more sheltered and shallow reef zones, i.e. the reef crest at Islands and the reef flat at NR (Fig. 5a,b). Although its host coral *Acropora digitifera* was rare at the shallow zones, *G. histrio*

abundance was not affected: this goby occupied about 90% of the available *A. digitifera* colonies. The few individuals on the reef slope were found in this coral (yet with only 50% occupancy of the available *A. digitifera* colonies). It used *A. acuminata* as an additional host coral. Even in shallow and sheltered reef zones like the reef flat at NR, where the abundance of both host corals was very low, *G. histrio* maintained high abundance through inhabiting a range of other coral species according to their availability. The proportion of adult breeding pairs varied within the 2 host-coral species: approximately 70% of all occupied *A. digitifera* versus about 30% of all occupied *A. acuminata* colonies.

Gobiodon reticulatus inhabited almost only the deeper and, hence, calmer reef zones (reef slope and fore reef) and was completely absent in turbulent water regardless of the distribution of its host corals (Fig. 5c,d). Only the sheltered reef flat at NR yielded a few individuals in the host coral *Acropora loripes*.

The light form of *Gobiodon rivulatus* was more strongly associated with the abundance of 2 of its host corals (*Acropora secale* and *A. eurystoma*) than with the third (*A. acuminata*) (Fig. 5e,f). Peak abundance was recorded on the reef slope at the Islands, although *A. acuminata* was absent. At NR, the maximum abundance shifted to the reef crest zone in accordance with *A. acuminata* abundance; the significant preference for this coral mainly reflects the results from this zone. The dark colour morph of *G. rivulatus* was more closely associated with *A. acuminata* than with *A. secale* abundance.

Table 2. *Gobiodon* spp. Chi-squared goodness-of-fit tests for 6 species of coral gobies (light and dark morphs of *G. rivulatus* are treated separately) from the Gulf of Aqaba, northern Red Sea (for testing differences between juvenile and adult habitat choice and whether species are distributed unequally over all available *Acropora* corals); specialisation indices (Shannon-Wiener H' : the lower the index, the higher the specialisation); and total number (n) of individuals. Calculations are made for juveniles and adults combined from all 4 reef zones

	Juvenile vs. adult habitat			Distribution over <i>Acropora</i>			H'	n
	χ^2	df	p	χ^2	df	p		
<i>G. histrio</i>	91.7	8	<0.001	932	8	<0.001	1.75	358
<i>G. reticulatus</i>	24.9	4	<0.001	4189	7	<0.001	1.15	330
<i>G. rivulatus</i> (light)	109.1	8	<0.001	624	8	<0.001	1.78	327
<i>G. rivulatus</i> (dark)	–	–	–	1258	7	<0.001	1.41	104
<i>Gobiodon</i> sp. 1	54.5	8	<0.001	1858	11	<0.001	1.93	336
<i>Gobiodon</i> sp. 2	49.7	5	<0.001	2471	4	<0.001	0.79	69
<i>Gobiodon</i> sp. 3	227.9	8	<0.001	1606	8	<0.001	1.71	102

Table 3. *Gobiodon* spp. Significance of habitat use by 6 species (light [riv] and dark [riv-d] morphs of *G. rivulatus* are treated separately) of coral gobies (juveniles and adults combined) in the Gulf of Aqaba using resource selection ratios and Bonferroni corrected 95 and 99% confidence intervals. U: habitat unused; NS: not significant ($\alpha = 0.05$); *: habitat used significantly more than expected with $p \leq 0.05$; **: habitat used significantly more than expected with $p \leq 0.01$; -: habitat used significantly less than expected ($\alpha = 0.05$). For abbreviations see 'Materials and methods' (gobies) and Table 1 (corals), respectively

Corals	Coral gobies						
	his	ret	riv	riv-d	sp1	sp2	sp3
acu	**	-	*	**	-	-	NS
dig	**	NS	NS	NS	-	U	U
eur	NS	NS	NS	NS	NS	U	NS
gem	NS	U	NS	-	**	NS	-
hum	NS	U	-	NS	NS	NS	U
hya	U	U	U	U	-	**	NS
lor	-	**	-	-	NS	-	NS
sam	NS	*	NS	-	**	U	NS
sec	-	-	**	*	**	U	-
sel	U	U	U	U	-	U	**
squ	U	**	U	U	NS	U	U
var	NS	-	NS	U	-	U	-

In contrast to the light form, it was therefore most abundant in shallow-water reef zones and was found only occasionally on the reef slope (Figs. 4 & 5g,h).

Gobiodon sp. 1 was closely associated with the abundance of its 3 host corals *Acropora gemmifera*, *A. samoensis* and *A. secale*—and with the reef crest zone at both study sites (Fig. 5i,j). Only at the calm reef flat at NR was the abundance lower than expected from habitat availability.

Gobiodon sp. 2 was closely associated with the abundance of its host coral *Acropora hyacinthus* (Fig. 5k,l). This coral typically inhabited turbulent and shallow reef zones and was therefore mainly distributed at the reef flat and the reef crest of the Islands site and at the reef crest of NR. Although its abundance was relatively low, the maxima of fish and host coral coincided. No individuals were found on the reef slope despite the presence of a few *A. hyacinthus* colonies.

Gobiodon sp. 3 was not strongly associated with the abundance of *Acropora selago* (Fig. 5m,n), the coral species it inhabited most frequently: while the host coral was typically most abundant at the reef flat, the fish preferred the reef crest at both study sites. However, at exposed reef zones, associations were close.

Overlaps in habitat use and interspecific associations

Together, all species of *Gobiodon* used a broad range of *Acropora* spp. as host corals (Table 3) and were found inhabiting all common species of *Acropora* (Fig. 3). Of the 12 corals analysed, 9 were used as hosts by the 6 gobiid species. The broad host-coral use meant overlaps of gobiid habitats (Table 3). One niche overlap occurred in *A. secale* between *G. rivulatus* (including the dark form) and *Gobiodon* sp. 1. The other 2 overlaps concerned *A. acuminata*, which was used by *G. histrio* and by both forms of *G. rivulatus*, and *A. samoensis*, which was used by *G. reticulatus* and by *Gobiodon* sp. 1 (Table 3). No habitat overlaps were observed for *Gobiodon* sp. 2 or *Gobiodon* sp. 3, which used only 1 coral more frequently than expected. The microhabitat choices of the light and the dark form of *G. rivulatus* were not regarded as overlaps in habitat use.

Rarely was >1 species of *Gobiodon* found within a single coral colony. If

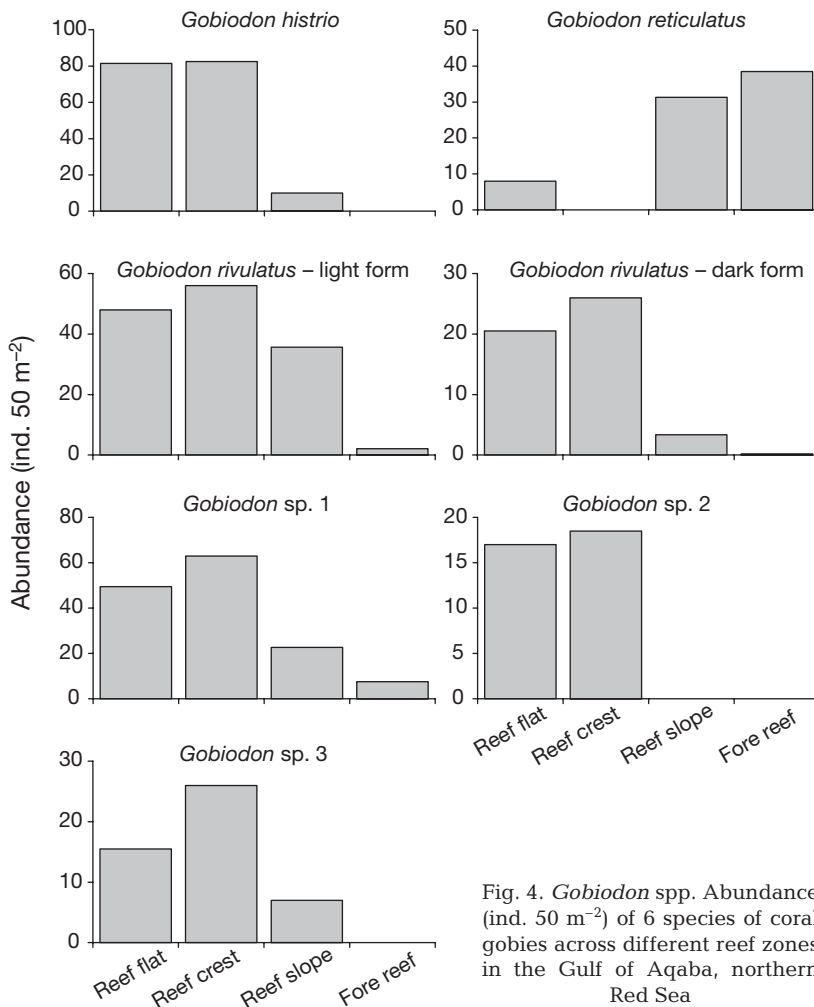


Fig. 4. *Gobiodon* spp. Abundance (ind. 50 m⁻²) of 6 species of coral gobies across different reef zones in the Gulf of Aqaba, northern Red Sea

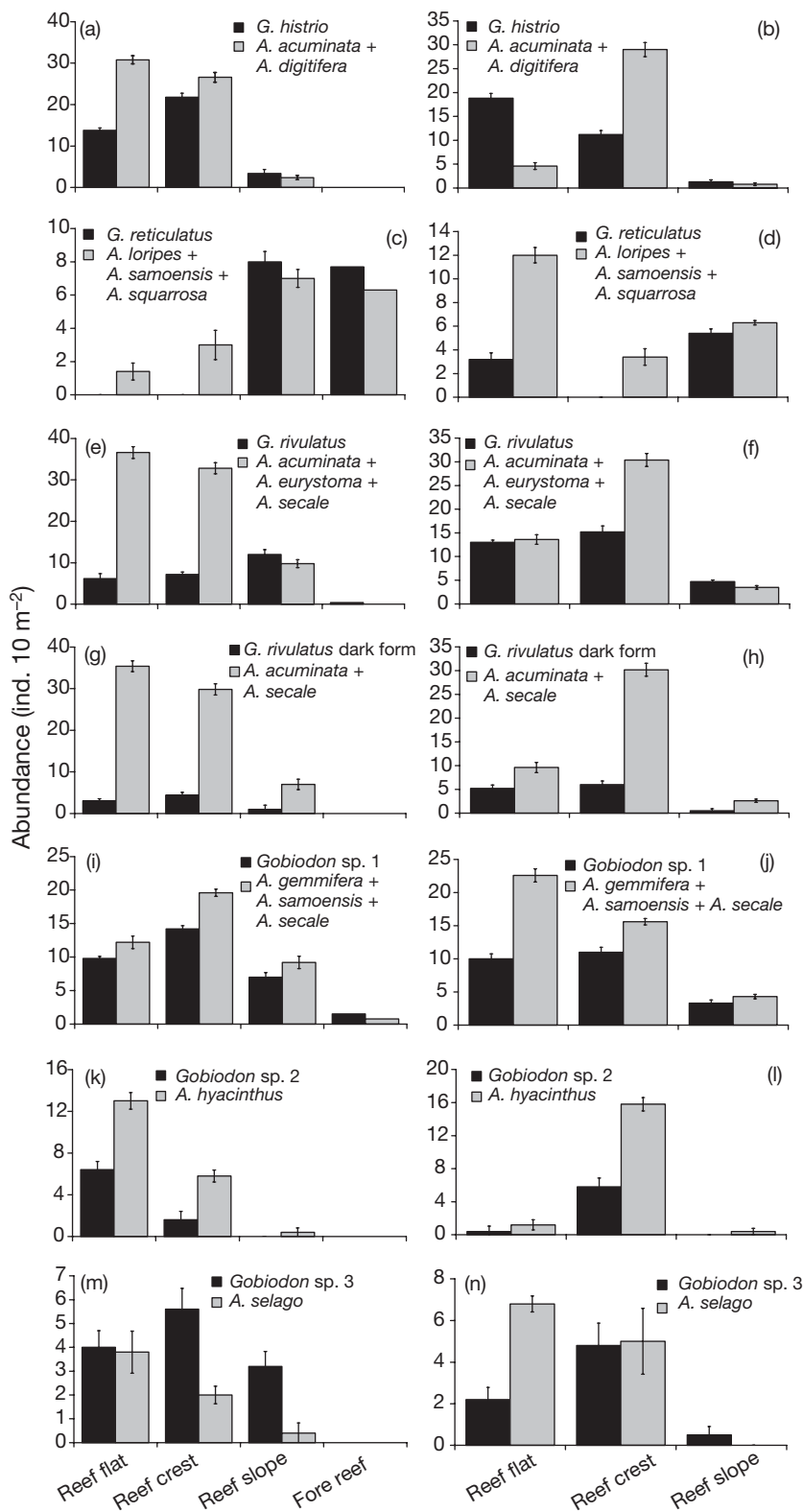


Fig. 5. *Gobiodon* spp. (a to n). Mean abundance (\pm SE) per 10 m² of coral gobiid species and their most frequently inhabited *Acropora* coral species across reef zones in the Gulf of Aqaba, northern Red Sea. Left panels: Site 1 (Islands); right panels: Site 2 (NR)

associations of the dark and light forms of *G. rivulatus* are not considered as interspecific associations, such associations were only observed in 3% of all colonies. Only these cases are described in the following: it was most often observed that 2 single individuals from 2 different species shared a colony (in 40% of the cases), while associations of 2 adult breeding pairs were uncommon (10%). In *G. histrio* and *Gobiodon* sp. 1, mostly juveniles (>70%) were associated with other species, while, in *G. reticulatus* and *Gobiodon* sp. 3, adults dominated interspecific associations (>80%). *G. rivulatus* was by far most frequently observed in associations (>80%). *G. rivulatus* was by far most frequently observed in associations, and slightly more adults participated. Except for the most specialised species (*Gobiodon* sp. 2), all species were observed in interspecific associations (Fig. 6). In all cases, 1 partner was always either *G. rivulatus* or *Gobiodon* sp. 1, and, in about half of all cases, those 2 species were found together (Fig. 6). In only 4 of all censused colonies (= 0.2%) were 3 different fish species observed. Among the coral species involved in interspecific fish associations, *Acropora secale* and *A. acuminata* dominated by far.

DISCUSSION

Observations of *Gobiodon* spp. habitat specialisations in the Gulf of Aqaba (northern Red Sea) revealed only 6 common species of this genus, reflecting a less diverse host-coral spectrum, when compared to the western Pacific (Munday et al. 1997). Most species differed in the host corals they used. Except for 1 *Acropora* species, all were inhabited by at least 1 *Gobiodon* species, and about 75% of all coral species were used as host corals, which is a much more intensive use of the available spectrum than was observed in the western Pacific by Munday et al. (1997). All species of *Gobiodon* occupied a range of *Acropora* spp., but used 1 to 3 species more frequently than expected, indicating specialisation at the level of coral species. The levels of

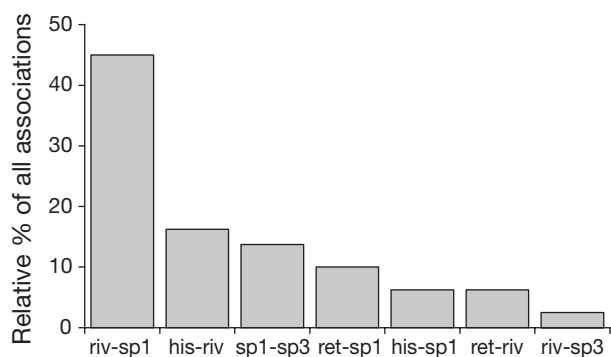


Fig. 6. *Gobiodon* spp. Frequency of interspecific associations of coral gobies found in colonies of different species of *Acropora* corals in the Gulf of Aqaba, northern Red Sea. For abbreviations of goby species, see 'Materials and methods'

specialisation and abundance varied considerably between species, and the data here support the hypothesis that specialists are less abundant than the more generalist species (Brown 1984, Brown et al. 1995). This is even indicated by the global abundance variation of a single species: the more generalistic behaviour of *G. histrio* in the Gulf of Aqaba is associated with a much higher abundance than in the western Pacific. Very similar abundance and specialisation values were found for *G. rivulatus* in both regions.

The spatial patterns of *Gobiodon* spp. abundances across reef zones were generally associated with the abundances of their most frequently inhabited coral species. Nevertheless, the distribution of some gobiids, like *Gobiodon* sp. 3, also reflected preferences for certain exposure regimes or reef zones, independent of host-coral availability. *G. histrio*, for example, was limited to shallow reef zones, and within these zones it was most abundant in less-exposed reef zones. There was a significant decline of *Gobiodon* spp. richness and abundance between the upper reef slope and the fore reef area, reflecting the very low diversity of *Acropora* spp. in the latter. One exception was *G. reticulatus*, which was most frequent in the fore reef. It extended down to a depth of 33 m, and its maximum depth might be limited only by the depth limit of suitable *Acropora* spp. Compared to other *Gobiodon* spp., which clearly avoid competition by utilising different microhabitats, *G. reticulatus* shows bathymetric segregation towards an almost competitor-free reef zone. There was an inverse relation between coral abundance and occupation rates of corals, and the contribution of *G. reticulatus* to the latter varied with depth: on the reef slope, the overall occupation rate of *Acropora* spp. colonies was 67%, but *G. reticulatus* contributed only 20% to this, whereas in the fore reef zone the overall occupation rate was 84% and the contribution of *G. reticulatus* was 68%. Since *G. reticulatus* inhabited

all abundant coral species proportionately, its population size is limited by the total abundance of colonies rather than by that of any particular coral. The high occupation rates in the fore reef yielded relatively high abundance, underlining the advantage of occupying an almost competitor-free environment.

The use of alternative microhabitats due to limited habitat availability may be a common phenomenon in both juveniles and adults. Host corals of the various *Gobiodon* spp. were usually dominated by breeding pairs (up to 70% in *Gobiodon* sp. 2 and *Gobiodon* sp. 3), with the exception of *G. rivulatus*. In species with >1 host coral, like *G. histrio*, most breeding pairs preferred 1 particular coral species. This indicates that only host corals harbouring a high percentage of breeding pairs are a primary habitat of superior competitors, in which interspecific competition plays a major role. In high-density populations, individuals may initially have to settle in suboptimal habitats (Itzkowitz 1977) and then move to better territories when they become available; this adjustment is accompanied by increased reproductive performance (Itzkowitz 1991).

Dominance hierarchies among *Gobiodon* spp. are largely driven by body size (Munday et al. 2001), and similar size-based dominance hierarchies have been observed in a number of site-attached reef fish species (Webster & Hixon 2000). In the northern Red Sea, the most specialised species (*Gobiodon* sp. 2) was also the smallest species, ultimately making it a subordinate competitor with a small spatial niche. Its host coral was rarely used by other species. Its small body size may force it to occupy a suboptimal habitat, where negative effects on growth, survival and reproductive output become more likely (Huey 1991). However, the costs of using alternative habitats differ for competing species (Munday 2001). This would lead to a trade-off between competitive ability and fitness in alternative habitats, providing a mechanism for coexistence (Rosenzweig & Abramsky 1997). *Gobiodon* sp. 2 is a habitat specialist, implying that its host coral *Acropora hyacinthus* (in which this goby has the lowest fitness-related costs) is a rather suboptimal habitat for most *Gobiodon* spp. Caley & Munday (2003) observed that growth trades off with habitat specialisation among *Gobiodon* spp., and specialists avoid corals with high fitness-related costs. *A. hyacinthus* seems unsuitable for most other gobiid fishes and does not support large species, as is reflected in the very small size of *Gobiodon* sp. 2.

Although interspecific competition was largely avoided by selecting different hosts in the Gulf of Aqaba, certain overlaps in coral use occurred among *Gobiodon* spp. All cases of niche overlap involved only 2 of the 4 species *G. histrio*, *G. rivulatus*, *G. reticulatus* and *Gobiodon* sp. 1. Species that overlap in resources may

not necessarily compete (Munday et al. 2001), and interspecific competition for shared host corals was variously avoided in the present study: (1) preference for an unsaturated microhabitat (coral species) that is not limited (i.e. *Acropora acuminata*, shared by *G. histrio* and *G. rivulatus*), (2) bathymetric segregation (in *A. samoensis*, shared by *Gobiodon* sp. 1 and *G. reticulatus*) and (3) tolerance (in *A. secale*, shared by *Gobiodon* sp. 1 and *G. rivulatus*, which commonly co-habited this coral).

The present study of *Gobiodon* spp. in the Red Sea allows us to compare microhabitat selection patterns on a global scale, at least for the widely distributed species noted in Table 4. Microhabitat choice of *G. histrio* and *G. rivulatus* (light and dark forms), for example, has also been investigated at the GBR (Munday et al. 1997) and in PNG (Munday 2000). These comparisons illustrate that microhabitat choice can vary among geographically distant regions and that modifications depend on factors like regional coral assemblages, availability of preferred host corals, and the competitive ability of a species within changing guilds. *G. histrio* is a superior competitor among *Gobiodon* spp. fishes (Munday et al. 2001), and its habitat preferences will not be significantly influenced by competitive interactions. When compared to the western Pacific, host corals were different in the Gulf of Aqaba (Table 4). Furthermore, there was less specialisation but much higher abundance observed in the Gulf of Aqaba, which is consistent with the observations of Brown et al. (1995), who proposed an inverse relationship between specialisation and abundance. The much higher abundance in the Gulf of Aqaba may also reflect the absence of competing species of a similar rank in the competitive hierarchy. In *G. rivulatus*, host coral species were also different in both regions, but specialisation and abundance were very similar (Table 4). *G. rivulatus* exhibits generalistic behaviour in all regions. Such generalisation best explains why hosts may differ between geographic locations that have significantly different *Acropora* spp. communities and different *Gobiodon* spp. guilds, affecting interspecific interactions. *G. rivulatus* occupied different corals at different sites and zones to achieve maximum abundance, even within 1 location in the northern Red Sea. This indicates the ability to shift to other corals if the preferred hosts become rare. Similar observations were made at the GBR, where *G. rivulatus* was abundant on the reef slope, despite the absence of its preferred host (Munday et al. 1997). Finally, the suitability

Table 4. *Gobiodon* spp. Comparison of *G. rivulatus* (light and dark morphs combined) and *G. histrio* from the Gulf of Aqaba (northern Red Sea) and the western Pacific region concerning their host coral species (occupied significantly more often than expected as revealed by resource selection ratios, see also Table 3), degree of habitat specialisation (expressed as the Shannon-Wiener index H') and abundance (values are ranges of means from 3 different reef zones [flat, crest and slope], and, in parentheses, the overall mean). Data for the Gulf of Aqaba are from the present study; data for the western Pacific are from Munday et al. (1997) and Munday (2004). Abundance values for the western Pacific are estimated from Munday et al. (1997, their Fig. 4)

	<i>G. histrio</i>		<i>G. rivulatus</i>	
	Gulf of Aqaba	Western Pacific	Gulf of Aqaba	Western Pacific
Host corals	<i>A. digitifera</i> , <i>A. acuminata</i>	<i>A. nasuta</i>	<i>A. secale</i> , <i>A. acuminata</i>	<i>A. gemmifera</i>
Specialisation (H')	1.75	1.34	1.75	1.80
Abundance (ind. 10 m ⁻²)	1.3–21.8 (10.2)	2.3–6.1 (3.6)	5.2–21.2 (11.9)	7.0–15.0 (10.5)

of a given microhabitat can be context specific, such as when a fish inhabits a particular microhabitat only when it occurs in a particular reef area (e.g. Elliott et al. 1995). Accordingly, broad habitat choice patterns within a guild remained even at a global scale, although changes in the host-coral spectrum occurred and superior competitors became more generalised when fishes adapted to the Red Sea environment. Future research (including molecular genetics) will reveal more about the actual relationship between Red Sea and Indo-West Pacific populations.

Acknowledgements. We are grateful to M. Fouda (NCS/EEAA) and A. Mabrouk (Nabq Managed Resource Protection Area) for research permits. M.D. is indebted to J. Ott (University of Vienna) for supervising this master thesis and for providing work space. Many thanks to C. Wallace and R. Winterbottom for taxonomic help with fishes and corals. P. Munday offered essential comments on an earlier draft of the manuscript, and M. Stachowitsch added linguistic corrections. Two anonymous reviewers provided very constructive criticism. A. Tischer (DAED) supported us through logistical help and provided diving and laboratory facilities. This research was funded by grants from the International Office, Vienna (M.D.), the Emil Boral foundation, Switzerland (2004) and the Austrian Academy of Sciences (APART: Austrian Programme of Advanced Research and Technology, 2005/2006) (J.H.).

LITERATURE CITED

- Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, London, p 5–32
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Brown JH, Mehlman DW, Stevens GC (1995) Spatial variation in abundance. *Ecology* 76:2028–2043

- Caley MJ, Munday PL (2003) Growth trades off with habitat specialization. *Proc R Soc Lond B* 270:175–177
- Elliott JK, Elliott JM, Mariscal RN (1995) Host selection, location, and association behaviors of anemonefishes in field settlement experiments. *Mar Biol* 122:377–389
- Gardiner NM, Jones GP (2005) Habitat specialization and overlap in a guild of coral reef cardinalfish (Apogonidae). *Mar Ecol Prog Ser* 305:163–175
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *Proc Natl Acad Sci USA* 103:8425–8429
- Head SM (1987) Introduction. In: Edwards AJ, Head SM (eds) Key environments: Red Sea. Pergamon Press, Oxford, p 1–21
- Herler J (2007) Microhabitats and ecomorphology of coral- and coral rock-associated gobiid fish (Teleostei: Gobiidae) in the northern Red Sea. *Mar Ecol-Evol Persp* (in press)
- Herler J, Hilgers H (2005) A synopsis of coral and coral-rock associated gobies (Pisces: Gobiidae) in the Gulf of Aqaba, northern Red Sea. *Aqua J Ichthyol Aquat Biol* 10:103–132
- Hobbs JPA, Munday PL (2004) Intraspecific competition controls spatial distribution and social organisation of the coral-dwelling goby *Gobiodon histrio*. *Mar Ecol Prog Ser* 278:253–259
- Huey RB (1991) Physiological consequences of habitat selection. *Am Nat* 137:91–115
- Itzkowitz M (1977) Spatial organisation of the Jamaican damselfish community. *J Exp Mar Biol Ecol* 28:217–241
- Itzkowitz M (1991) Habitat selection and subsequent reproductive success in the beaugregory damselfish. *Environ Biol Fish* 30:287–293
- Jones GP, Syms C (1998) Disturbance, habitat structure and the ecology of fishes on coral reefs. *Aust J Ecol* 23:287–297
- Jones GP, Caley MJ, Munday PL (2002) Rarity in coral reef fish communities. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, London, p 81–101
- Jones GP, McCormick MI, Sirinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. *Proc Natl Acad Sci USA* 101:8251–8253
- Kuwamura T, Yogo Y, Nakashima Y (1994) Population dynamics of goby *Paragobiodon echinocephalus* and host coral *Stylophora pistillata*. *Mar Ecol Prog Ser* 103:17–23
- Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London
- Munday PL (2000) Interactions between habitat use and patterns of abundance in coral-dwelling fishes of the genus *Gobiodon*. *Environ Biol Fish* 58:355–369
- Munday PL (2001) Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia* 128: 585–593
- Munday PL (2002) Does habitat availability determine geographical-scale abundances of coral-dwelling fishes? *Coral Reefs* 21:105–116
- Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs. *Global Change Biol* 10:1642–1647
- Munday PL, Jones GP, Caley MJ (1997) Habitat specialization and the distribution and abundance of coral-dwelling gobies. *Mar Ecol Prog Ser* 152:227–239
- Munday PL, Caley MJ, Jones GP (1998) Bi-directional sex change in a coral-dwelling goby. *Behav Ecol Sociobiol* 43: 371–377
- Munday PL, Harold AS, Winterbottom R (1999) Guide to coral-dwelling gobies, genus *Gobiodon* (Gobiidae), from Papua New Guinea and the Great Barrier Reef. *Rev Fr Aquariol Herpetol* 26:53–58
- Munday PL, Jones GP, Caley MJ (2001) Interspecific competition and coexistence in a guild of coral-dwelling fishes. *Ecology* 82:2177–2189
- Robertson DR (1996) Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77:885–899
- Rosenzweig ML, Abramsky Z (1997) Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evol Ecol* 11:733–756
- Thomas DL, Taylor EJ (1990) Study designs and tests for comparing resource use and availability. *J Wildl Manage* 54: 322–330
- Veron JEN (2000) Corals of the world, Vol 1. Australian Institute of Marine Science, Townsville
- Wallace CC (1999) Staghorn corals of the world: a revision of the genus *Acropora*. CSIRO Publishing, Collingwood
- Webster MS, Hixon MA (2000) Mechanisms and individual consequences of intraspecific competition in a coral reef fish. *Mar Ecol Prog Ser* 196:187–194

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: June 6, 2006; Accepted: December 19, 2006
Proofs received from author(s): July 2, 2007