Postsettlement movement patterns and homing in a coral-associated fish

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Coral reefs are highly productive and complex ecosystems that support a huge functional and species diversity, but they are currently facing a series of natural and anthropogenic disturbances such as coral bleaching (Hoegh-Guldberg 1999; McClanahan 2000, 2004), outbreaks of crown-of-thorns sea star \textit{Acanthaster planci}, overfishing, pollution, and coastal development (Hughes 1994; Hughes et al. 2003; Wilkinson 2004). The synergistic effect of combined natural and anthropogenic stresses on coral reefs constrains their resilience. The result is a worldwide decline in the abundance and diversity of corals and habitat structure (Pandolfi et al. 2003; Wilkinson 2004). Habitat loss and degradation, including the partial mortality of stressed reefs, especially affects specialized reef fish that heavily depend on live corals (Jones et al. 2004; Munday et al. 2006). The consequences may vary with life stage (Feary, Almany, McCormick, and Jones 2007) and degree of habitat specialization (Feary 2007; Feary, Almany, Jones, et al. 2007). The ability to migrate to better habitats may reduce the effect of habitat degradation (Wilson et al. 2006), but this ability may be lower in specialists (Feary 2007).

Movement is a common process in terrestrial and aquatic organisms. Such changes in location and/or habitat can involve a wide range of spatial and temporal scales (Dingle and Drake 2007). Ecological causes such as seasonal environmental changes or the need to exploit different resources can cause entire populations to migrate. However, behavioral traits always define individual movements (Dingle and Drake 2007). Such traits may be ontogenetic, for example, when habitats become unsuitable due to growth (Vytopil and Willis 2001), triggering individual movement behavior. Coral reef fishes may directly settle into their adult habitats or modify initial settlement patterns by movement (Jones 1991; Lecchini and Galzin 2005). At different postsettlement life stages, they can thus have distinct habitat preferences. Postsettlement movement is an important process to redefine habitat choice (McCormick 1995; Lewis 1997; McCormick and Makey 1997; Pittman and McAlpine 2001). Later in life, the movement of most reef fishes is restricted to a defined area that provides all they require for their normal activity. The validity of the home range concept in fishes is supported by the observation of homing behavior and strong site fidelity (Marnane et al. 2001; Thorrold et al. 2001; Kolm et al. 2005). Such behavior and fidelity were detected even for species living in homogeneous environments (Burrows et al. 2004). These studies highlight that fishes have a good knowledge about their physical environment. However, the role of postsettlement movement in structuring communities of highly specialized reef fish is not well understood. This calls for considering behavioral interactions and life history strategies—in addition to ecological factors—to fully comprehend distribution patterns (Levin et al. 2000).

The present investigation focuses on postsettlement movement, homing ability as well as partner and habitat recognition in fish tightly associated with live corals, such as gobies of the genus \textit{Gobiodon}. Seven species of \textit{Gobiodon} occur in the Gulf of Aqaba, northern Red Sea (Herler and Hilgers 2005). \textit{Gobiodon histrio} was chosen as a study species because of its home-coral fidelity and high abundance in shallow water reefs of the Gulf of Aqaba. This habitat-specialized reef fish occupies the interbranch spaces of certain \textit{Acropora} spp., where it preferably establishes breeding pairs (Dirnwo¨ber and Herler 2007). This microhabitat provides shelter, food, and breeding ground (Patton 1994; Nakashima et al. 1996; Munday et al. 2001). At the Great Barrier Reef (GBR), \textit{G. histrio} appears to be more specialized than in the northern Red Sea. It inhabits fewer \textit{Acropora} species (Hobbs and Munday 2004; Dirnwo¨ber and...
Herler 2007) at the GBR, even though this region has a higher Acropora diversity. In both regions, however, the social system is similar and each coral colony is typically occupied by one breeding pair; only very rarely do juveniles share colonies with adult fishes (Munday et al. 1998; Dirnöwer and Herler 2007). The comparison of habitat selection by juvenile and adult individuals reveals a slight discrepancy in inhabited Acropora species and, hence, a transition from juvenile to adult habitat must take place (Hobbs and Munday 2004; Dirnöwer and Herler 2007). Adult individuals show extreme habitat fidelity. This is supported by its hypoxia tolerance and air-breathing ability: the fishes can remain in their corals even when exposed to air during spring tide ebbs (Nilsson et al. 2004).

The mating system of G. histrio typically comprises single-pair formation in coral colonies (Munday et al. 1998; Munday and Molony 2002). Pairs probably remain within a single coral colony throughout their adult life (Feary 2007). Furthermore, G. histrio individuals can adjust their growth rate to their partner’s size (Munday, Cardoni, and Syms 2006) to increase their reproductive success (Kuwamura et al. 1993). The ability of bidirectional sex change is also widespread among coral-dwelling fishes, including G. histrio (Munday et al. 1998). This, combined with cooperative growth, benefits coral-dwelling species by minimizing movement and thus the risk of predation (Munday, Cardoni, and Syms 2006). All these characteristics of G. histrio can be interpreted as adaptations for avoiding movement between corals. Although movement of G. histrio has not been quantified, it appears to be infrequent (Munday et al. 2001; Feary 2007). Feary (2007) showed that G. histrio is able to move from experimentally degraded to healthy coral colonies but that emigration success from a degraded colony decreases substantially when the distance to the next available coral exceeds 100 cm. Nonetheless, sexually mature individuals from a breeding pair will have to move if their partner is lost or their host coral becomes degraded. This study examines the patterns and frequency of postsettlement movement in G. histrio to shed light on the sensitivity of specialists to host coral or partner loss at different life and social stages.

We hypothesize that

1. Juveniles and single adult individuals show higher movement frequencies due to intraspecific competition for optimal corals and the need of finding breeding corals and/or a mate, whereas fishes in established breeding pairs avoid movement and show a high habitat and partner fidelity and

2. Habitat fidelity will exceed partner fidelity when the driving force for movement is the search for an optimal coral rather than for a specific partner (mate choice flexibility is enhanced by bidirectional sex change [Munday, Buston, et al. 2006] and cooperative growth [Munday, Cardoni, and Syms 2006]).

MATERIALS AND METHODS

Study location and species

The study was carried out from April to June 2007 in Dahab (28°30’N, 34°31’E), Gulf of Aqaba, northern Red Sea, Egypt. To investigate goby movement patterns between corals, we chose an area north of the Napoleon Reef flat (hereafter referred to as Napoleon Reef) due to high abundance of G. histrio, good accessibility, and a long and horizontal extension (~200 m) of the reef flat. Tides in this area are semidiurnal, and water depth here fluctuates at spring tide from 0.2 to 1.2 m and at neap tide from 0.4 to 0.9 m. During the investigation period, no coral colonies were air exposed. Gobiodon histrio is a suitable study species because of its large size and its individual color pattern, which enables specimen identification via photos (Figure 1): short-term studies require no individual marking.

Sampling method

All field investigations were done by visual census using SCUBA and an underwater torch to identify fishes. To reidentify individual G. histrio during the homing experiment, narcotized specimens were digitally photographed underwater in lateral view. We used photo ID instead of tagging because the prominent markings of G. histrio are appropriate for this identification method, and it significantly reduces underwater handling time. Moreover, it does not affect the specimens except for the short time of narcotization while the photograph is taken. Because color patterns did not change over our short-term trials (up to 1 week; Figure 1), reidentification was 100% successful. Fishes were anesthetized using clove oil (10 ml in 100 ml 95% ethanol and diluted with 200 ml seawater). Clove oil is efficient even in low concentration and yields long but good recovery—a characteristic necessary for field experiments (Munday and Wilson 1997; Ackerman and Bellwood 2002). After documenting movement patterns between corals under natural conditions, a combination of manipulative field and laboratory experiments were conducted.

Figure 1

Photo ID method used in homing and aquarium experiments. The lineup shows the 4 specimens of Gobiodon histrio before and after displacement, right and left column, respectively. Time between pictures (a) and (b) is 48 h and between (c) and (d) 7 days (grid dimension: 10 × 10 mm).
Movement patterns

Data were collected in 4 plots of approximately 10 m² (3.2 × 3.2 m) at the Napoleon Reef flat. The study site was selected in a representative area of the reef, ensuring that the 4 plots exhibited a similar Acropora assemblage. This assumption was tested using the G test (homogeneity test) comparing the frequency distribution of Acropora corals between plots (\(G = 35.25\), degrees of freedom [df] = 30, \(P = 0.11\)).

The plots were traced out, and all Acropora colonies with >50% of their surface area within the plot were marked by tags fixed to the substrate nearby the colony and identified to species level. Only colonies >10 cm in diameter were considered (the minimum size colonized by Gobiodon [Dirnwo¨ber and Herler 2007; Schiemer 2007]). This minimum colony size also ensured correct coral species identification. The difficulties in monitoring patterns of postsettlement movement in coral-dwelling fishes lie in tagging a large number of small fishes to recognize them individually. Hence, to avoid the impact of anesthetization, we surveyed population size in several size classes to determine net changes (Jones 1991; Lewis 1997). Marked colonies were carefully surveyed for the presence of G. histrio. Munday et al. (1998) showed that individuals reached maturity at a total length (TL) of 25 mm. Therefore, individuals up to 25 mm TL were recorded as juveniles, beyond this as single adults (>25 mm TL) or breeding pairs. Juvenile individuals <10 mm TL were not included in this study because they cannot be reliably detected and are easily confused with juveniles of Gobiodon riviculatus during visual surveys. The presence of any other species of Gobiodon in the colonies was also recorded. Acropora hyacinthus and Acropora selago colonies were excluded from surveys because they were never occupied by G. histrio (Dirnwo¨ber and Herler 2007; Herler J, unpublished data). We resurveyed the occupation status of each colony in the 4 plots after 2, 7, and 14 days. The movement frequency in each plot was defined by comparing the occupation status of each colony and calculating the proportion of change for all time intervals. The occupation status was surveyed on 4 observation days within 2 weeks, yielding a total of 5 different time intervals (2, 5, 7 [twice], 9, and 14 days).

Manipulations were subsequently carried out to test whether increased habitat or partner availability changes movement rates. Accordingly, in 1 plot, all breeding pairs were removed, whereas in 2 of the 3 other plots only 1 partner of each breeding pair was removed to increase the availability of suitable habitat and of potential breeding partners, respectively. We assumed that the movement rate of single adults would decrease over time when more suitable coral colonies become available and that experimentally established single adults would increase their movement frequency compared with their previous breeding pair state for the search of a new mate. The fourth plot was not manipulated and treated as a control. Removal involved well-directed anesthetization of fishes with clove oil. Removed and fully recovered fishes (gill respiration and swimming movements observed) were released approximately 100 m away from plots into unoccupied Acropora colonies. In manipulation and control plots, the occupation status of each colony was examined immediately after manipulation to record the status quo and after 2, 7, and 14 days.

Homing experiment

In the field, we tested the maximum distance for successful homing of individual fish. For this purpose, we marked coral colonies inhabited by a breeding pair (TL ≥ 30 mm). Both fishes were anesthetized, photographed, and held separately in 50-ml plastic tubes (with perforated cover) for recovery. After that, fully recovered fishes were released. Whereas one individual was repositioned into the same coral colony, the other was displaced for 0.5, 2.25, or 4 m across the reef. The displaced fishes were released close to structures that provided refuge so that they could hide from predators and acclimatize to the new situation. For each distance, a minimum of 12 individuals was tested. Two days later, marked colonies were resurveyed to check for successful homing by the same procedure as before: both fish were anesthetized and photographed, but this time both were released back into the coral colony. Individuals were recognized by their individual color pattern from photos (Figure 1). Colony size as a potential correlate for successful homing was not considered because preliminary observations in the investigation area revealed no difference between the size of coral colonies inhabited by single adults (334 ± 547 cm²; mean ± standard deviation [SD]) and by breeding pairs (406 ± 204 cm²; mean ± SD; \(n = 188\), t-test: \(P = 0.083\)). Colonies to which partners had not returned after 2 days were resurveyed 5 days later (1 week total time).

We conducted a preliminary experiment to determine whether functional females (dichromes and males [determined by the characteristic development of their genital papillae]) perform similarly or whether separate experiments for each sex are necessary. Here, 18 female and 18 male individuals were displaced 2.25 m. No difference was detected between the female and male homing ability: the number of returning males (9 of 18) did not significantly differ from the females (10 of 18) (\(G_{adj} = 0.105\), df = 1, \(P = 0.75\)).

Home-coral and partner fidelity experiments

We tested the ability of G. histrio individuals to recognize their home-coral and breeding pair partner in aquaria. To determine home-coral recognition, one G. histrio individual was given the choice of 3 colonies. One of the colonies represented the original home coral. After 24 h of isolation from its home coral, one individual from a breeding pair derived from this coral was tested. A second experiment was undertaken to examine whether functional males can recognize their female breeding pair partner. The 3 colonies (none of them represented the original home coral) in the experimental setup were inhabited by a female G. histrio, one of which was the original partner of the tested male. The breeding pairs used in this experiment were separated in the morning (between 0700 and 0800 h) prior to the experiments. Standard length of fishes used in this experiment varied between 30 and 42 mm. Care was taken to use similarly sized alternative female partners because the average size difference of the 10 natural breeding pairs used in the trials was very small (mean ± standard error [SE] = 6.0 ± 1.3%). The average size difference between each male and the 3 corresponding females used in the trials (including their original partner) was 8.4 ± 1.1%.

To eliminate possible habitat preferences, only Acropora digitifera, the preferred microhabitat of G. histrio breeding pairs (Dirnwo¨ber and Herler 2007), was employed in all experiments, and all tested pairs also derived from this coral species. Coral colonies of approximately the same size (15–20 cm maximum diameter) were carefully removed from the reef. In the field, they were cleared of all infauna (gobies, crabs, and shrimps), immediately transported to the laboratory, placed in round aquaria (80 cm ø, 35 cm height, ~180 l volume), and acclimatized for 24 h. Water quality was maintained by a flow-through system of filtered and aerated sea water, with a daily exchange for fresh sea water. To ensure similar distance to each colony, the corals were arranged in an equilateral triangle. For both home-coral and partner recognition experiment, an acclimatization tube (10 cm diameter) was located in the center of the triangle. New breeding
pairs were collected every 1–2 days from the field with clove oil, fully recovered immediately after capture, and held in separate aquaria with fresh and aerated sea water. The tested fish were positioned in the acclimatization tube for 45 min before they were released. This tube extended from the bottom to above the water level and was provided with small holes around its circumference to ensure water exchange (Munday 2001). All aquarium experiments were started between 1900 and 2000 h; the first choice was noted, and the final outcome was recorded the following day between 0700 and 0800 h.

Data analysis

The G test was used to test homogeneity and goodness of fit of data. This test was applied to determine differences before and after manipulation in the percent change of juveniles, single adults, and breeding pairs. Home-coral and partner recognition experiments were analyzed by the G test to a one-way classification of frequencies to test for goodness of fit. For these experiments, we assumed the same chance of choosing any of the 3 colonies and accordingly expected that one-third of the tested individuals will choose the right one and two-thirds will choose the wrong coral (home coral: n = 12; random expectation = 4 vs. 8, df = 1; partner: n = 10, random expectation = 3.33 vs. 6.67, df = 1). Williams’ correction was applied by dividing the calculated G value by the factor \( F = 1 + (a^2 - 1)/6n \), in which a is the number of categories, n is the total number of observed frequencies, and v is the df \((a - 1)\). One-way analysis of variance (ANOVA) was used to investigate differences between the percent change within and among categories (juveniles, single adults, breeding pairs) for several observation periods. A Duncan post hoc test was applied to test which means are significantly different, within and among categories (juveniles, single adults, breeding pairs). Home-coral and partner manipulation. Analyses were carried out using SPSS 11.5 and Microsoft Excel 2003 for Windows.

RESULTS

Coral assemblages, colony, and fish density

A total of 162 Acropora colonies were repeatedly visually censused for the presence of G. histrio to examine movement patterns in the 4 investigation plots. North of Napoleon Reef, 10 species of Acropora were found. They differed in abundance: Acropora gemmifera (34%) followed by Acropora samoensis (16%), A. selago (13%), and Acropora loripes (12%) were the most abundant species. In contrast, Acropora acuminata (1.2%) and Acropora eurytoma (1.2%) represented a minor fraction in the sampling area. The number of coral colonies between plots varied from 32 to 50 (mean \( \pm SE = 40.5 \pm 3.8 \)); of these, between 17 and 29 (20.8 \( \pm 2.8 \)) were inhabited at least once during the first 2-week observation period (Table 1).

Fish population density during the 2-week period before manipulation was 31 \( \pm 2 \) (mean \( \pm SE \)) individuals per 10 m\(^2\). Juveniles showed the highest variation in abundance of individuals per 10 m\(^2\), ranging from 8 to 15.5 (10.9 \( \pm 1.0 \)). The number of individuals encountered in all 4 plots together varied slightly during the 2 weeks and increased from 117 to 135, but this was not significant \( (r^2 = 0.907, t = 3.04, df = 2, P = 0.095) \). Numbers (mean \( \pm SE \) over the 2 weeks) of juveniles increased from 43 to 50 (43.5 \( \pm 2.5 \)) and of breeding pairs from 25 to 32 (29.3 \( \pm 1.5 \)) but decreased from 24 to 21 in single adults (23.8 \( \pm 1.3 \)). Variation in the number of adult individuals is negligible compared with overall individual numbers. The variation in the number of fish in the control plot reveals that the overall individual number was about 25 fishes during the full 4-week observation period.

Social structure in G. histrio

The examination of social groups of G. histrio at the Napoleon Reef flat revealed that 26% and 34% of all occupied colonies were inhabited by single adults or breeding pairs, respectively. In approximately 10% of the colonies, juveniles and adults were found together, and only 3% of all occupied colonies had more than 2 adults (ranging from 3 to 5 adult individuals, the maximum observed only once; Figure 2).

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<th>Acropora spp. assemblages of the 4 investigation plots at Napoleon Reef, Gulf of Aqaba, northern Red Sea</th>
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Figure 2

Social structure of Gobiodon histrio within coral colonies (n = 71) at the Napoleon Reef flat, Gulf of Aqaba, northern Red Sea. Values are mean proportions \( \pm SE \) from the 4 investigation plots.
Movement pattern

Under natural conditions, each life stage category (juveniles, single adults, and breeding pairs) showed an upward trend for net changes of position with time. Breeding pair movement was low and did not change with time (correlation values $r^2 = 0.024, n = 24, P = 0.47$; Figure 3). The percentage of moving juveniles and single adults showed a slight increase with time, but this was significant only for juveniles ($r^2 = 0.18, n = 24, P = 0.04$; Figure 3). Breeding pair and single adult movement rate (percent change of occupation; Figure 3) were significantly different for each observation period (ANOVA Duncan test: level of significance $P < 0.05$—single adults and breeding pairs represent two homogeneous subgroups). No significant difference was found between several data points within each category (ANOVA within categories: juvenile individuals $P = 0.40$, single adults $P = 0.27$, breeding pairs $P = 0.89$; Duncan post hoc test of all data for each category grouped together).

Because correlations between movement frequency and time were weak and not significant (except for juveniles), movement data from all observation periods were pooled (Figure 4). The relative percentage of position changes among breeding pairs (mean ± SE = 14.0 ± 2.6) was lowest followed by 31.8 ± 3.3% changes among juvenile individuals and 47.5 ± 5.0% of single adults (all results are significantly different from each other; Mann–Whitney $U$-test—juvenile vs. single adult: $U = 139.5, P = 0.002$, single adult vs. breeding pair: $U = 28, P = 0.000$, juvenile vs. breeding pair: $U = 117.5, P = 0.000$). This means that, on average, every second single adult changed its position during the observation period. After we monitored movement patterns under natural conditions (observation period 1), 3 of the 4 plots were manipulated (observation period 2). No significant differences were found between the 2 observation periods in the control (plot 1) for single adults and breeding pairs ($G = 0.46, P = 0.95, G = 1.78, P = 0.62, df = 3$, respectively), whereas juveniles differed significantly in their movement ($G = 9.2, P = 0.026$). Analysis of the manipulation plots revealed no significant difference between movement patterns before and after manipulation, except for single adult movement, which slightly decreased ($G = 13.33, P = 0.004, df = 3$) in the plot where all breeding pairs were removed (Figure 5). Within the 2 plots in which one partner from a breeding pair was removed, the occupation states of those colonies ($n = 13$) became unstable. Out of 39 possible changes in occupation (13 colonies, 3 successive observations on days 2, 7, and 14), only 3 changes (7.7%) were observed among breeding pairs before manipulation, whereas 13 changes (33.3%) occurred among the single adults after partner removal. Subsequently, only 6 of the 13 experimental single adults associated at least once with a new partner during the entire postmanipulation period (14 days) and only 3 maintained a new partnership until the end of this period.

![Figure 3](https://example.com/f3.png)

**Figure 3**

Movement between corals for juveniles, single adults, and breeding pairs of *Gobiodon histrio* plotted against increasing observation intervals (time between 2 observations). All intervals were measured in the 2 weeks before plot manipulation. Data points are means (±SE) of percent of position changes of 4 investigation plots, and numbers indicate mean individuals over all observation intervals.

![Figure 4](https://example.com/f4.png)

**Figure 4**

Frequency of change in position for juveniles, single adults, and breeding pairs of *Gobiodon histrio*. Box plots show median, first and third quartiles, 10th and 90th percentiles (T-bars), and 5th and 95th percentiles (dots).

![Figure 5](https://example.com/f5.png)

**Figure 5**

Comparison of movement patterns before and after manipulation as well as for the control plot. Light gray bars represent the percent of change under natural conditions and dark gray bars show the changes after manipulation ($n = 48$ for all light gray bars, $n = 6$ for dark gray bars in control and breeding pair removal, $n = 12$ for the dark gray bars in the partner removal). Box plots show median, first and third quartiles, 10th and 90th percentiles (T-bars), and 5th and 95th percentiles (dots).
Homing and fidelity experiments

The success of homing significantly decreased \((r^2 = 1.0, t = 12.998, df = 1, P = 0.049)\) between minimum and maximum displacement distance. After 2 days, all individuals had returned from a distance of 0.5 m, but the value decreased strongly with distance (Figure 6a). Colonies to which the partner had not returned after 48 h were resurveyed after 5 more days (i.e., total of 1 week) but revealed only a negligible number of additional successful returns for the 2.25-m distance and none for 4 m (Figure 6b). We also analyzed whether homing success depended on coral species. Displacement colonies comprised Acropora samoensis, Acropora gemmifera, Acropora secale, and Acropora digitifera, and no difference in homing success was found between any species \((G = 2.75, df = 3, P = 0.43)\).

Because we observed a homing behavior in G. histrio, we designed aquarium experiments to test which effect is stronger—partner or home-coral fidelity. The experiments revealed high home-coral fidelity (75% of all tested individuals recognized their original home coral) but also considerable partner fidelity (60% recognition), although the latter was not statistically significant (random expectation for both experiments: one-third [right] vs. two-thirds [wrong]; home coral: \(n = 12, G_{adj} = 8.563, df = 1, P = 0.004\) and partner: \(n = 10, G_{adj} = 2.848, df = 1, P = 0.076\); Figure 6c).

DISCUSSION

Our investigations in the Gulf of Aqaba, northern Red Sea, revealed different natural movement frequencies for juveniles, single adults, and breeding pairs of the coral-associated goby G. histrio. Single adults show the highest mobility, whereas individuals from breeding pairs infrequently change corals. As supported by this study, the more generalized habitat choice of this species in the northern Red Sea (vs. western Pacific populations; Dirnwo¨ber and Herler 2007) results from a high number of single adults with unstable habitat choice. These fishes switch between corals frequently because they search for optimal breeding habitats and/or mates.

Microhabitat analysis in the Gulf of Aqaba for G. histrio revealed that it only accepts 2 species of corals as breeding habitat and that habitat choice of juveniles and single adults deviates from that of breeding pairs (Dirnwo¨ber and Herler 2007). Accordingly, the reproductive fitness and abundance of G. histrio are limited by the availability of specific breeding habitats. Although direct settlement into optimal breeding corals should promote fitness (Ohman et al. 1998), a trade-off between competitive ability and use of alternative habitat forces juvenile and single adult individuals into suboptimal corals (Itzkowitz 1977). Moreover, the observed social structure of a low proportion of adult/juvenile associations indicates no queuing for breeding opportunity within the same colony by juveniles and also points to intraspecific aggression and competition for mating partners and breeding ground (Thompson et al. 2007). Intraspecific and intrasexual aggression in coral-associated gobies occurs during territorial or resource defense (Whiteman and Côté 2003; Hobbs and Munday 2004; Wong et al. 2008) and can also explain the high home-coral and partner fidelity as well as homing behavior. Accordingly, there is a potential trade-off between predation risk and homing to return to the previously established, optimal breeding conditions.

The movement frequency of fish calculated based on net changes of coral occupation can be caused not only by movement (immigration and emigration from coral colonies) but also by change of absolute fish abundance through recruitment or mortality (Jones 1991; Buston 2003). However, recruitment cannot account for the calculated movement rate of

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in the present study because first settlers (<10 mm body length) were not considered in our survey. Because the number of individuals in our investigation plots increased with time, we also assume that predation on adults that were not yet part of new partnerships at the beginning of our investigation plots increased in number. This indicates rather a biased visual survey by detecting more juveniles with increasing observation time of juvenile fish. In contrast, the decrease in the absolute numbers of single adults may be explained by breeding pair formation because the number of the latter increased over the same period. A low mortality rate for juveniles may explain our findings that predation or other causes of mortality did not significantly contribute to net changes. Predation is very unlikely because, especially, juveniles, which are considered to suffer the greatest risk of predation, increased in number. This indicates that predation did not significantly contribute to net changes. Predation is very unlikely because, especially, juveniles, which are considered to suffer the greatest risk of predation, increased in number. This indicates that predation did not significantly contribute to net changes.

The movement frequency for breeding pairs was very low. Removing one partner from a breeding pair, however, changed the home range of these fish. Previous breeding pair partners increased their movement frequency to a level of a natural single adult, although during the 2 weeks after manipulation we did not observe newly established, stable partnerships. Nakashima et al. (1995) carried out mate removal experiments in the field with Paragobiodon echieneuctus. After 7 weeks, 10 out of 12 fish have mated with new partners, and pair formation occurred within a 5-m range. The 2-week period in the present study may have been too short to detect an increase in remating with new partners. Such successful remating with the original partner after 1 week, as observed in a few individuals during our homing experiment, was possible because of the lag in new partnership establishment. Both partner and home-coral fidelity support a monogamous behavior in G. histrio, as also indicated by other biological features such as bidirectional sex change and cooperative growth (Munday et al. 1998). Individual partner recognition and the low movement rates of breeding pairs also suggest stable partnerships, independent of regional social structure. A coevolution of different mating systems with mate guarding, parental care, and complex spawning behavior is expected to account for the inflexibility even if ecological conditions change in a manner that would favor another mating system (Hernaman and Munday 2007). The many single individuals and their high frequency of changes indicate a search for high-quality habitat, in which they can establish a breeding pair, as the driving force for the observed movement patterns. In general, habitat quality strongly affects fitness, and selection pressure thus generates strategies for optimal breeding habitat choice (Martin 1993) and its defense. The frequency of optimal breeding corals influences the social structure of G. histrio populations, leading to different single adult/breeding pair ratios in different regions. In the western Pacific, this species shows much fewer single adults than breeding pairs (Munday et al. 1998); in the northern Red Sea, the ratio was 0.7:1. The Napoleon Reef site has a low proportion of optimal breeding corals for G. histrio (Dirnwöber and Herler 2007), potentially explaining the high proportion of single adults. This high number of single adults increases the total abundance to a much higher value than observed in the western Pacific. This may be due to the lack of heterospecific competitors of a similar competitive rank than G. histrio in the northern Red Sea (Dirnwöber and Herler 2007).

The homing experiment showed that fishes are able to return to their home coral, even over a distance of several meters. Homing behavior is known from many marine fish including some coral reef species (Marnane 2000), and evidence, this ability exists in coral-associated fishes. In cichlids, Hert (1992) assumed that the costs for establishing new territory are higher than returning to an existing territory. Because finding a high-quality habitat and suitable mate clearly causes high costs for G. histrio, homing to an established, stable condition is preferred over searching for a new breeding coral and mate. Gobiodon histrio could either directly return to its partner and/or its home coral or indirectly by chance by being expelled from other colonies by conspecifics. Although we did not control for the latter, these explanations need not be mutually exclusive. The extent to which expulsion from other corals by conspecifics is a driving force requires further experiments with a competitor-free environment. Our photo IDs (e.g., Figure 1b) revealed fin damage in several returning individuals that may stem from encounters with conspecifics or other species. The aquarium experiments demonstrated that G. histrio has a high home-coral and partner recognition ability.

The usual home range of these fishes is small and only contains the size of their home coral. Kramer and Chapman (1999) found a logarithmic relationship between body size and home range for coral reef fish species. According to their equation, G. histrio (maximum TL ~55 mm) would maintain a home range of only 0.34 m, which is very close to the average size of most home corals. Successful homing rapidly decreased with distance but occurred even after 4-m displacement. This was obviously supported by the low distance (average of about 20 cm) between coral colonies in the investigation area. Feary (2007) showed that G. histrio could hardly move between colonies in a distance of more than 1 m. This suggests that reefs with low coral coverage do not support high movement rates and one would expect a low number of moving single adults and a higher rate of breeding pair establishment, which was confirmed by Schiemer et al. (2008). Successful homing over a distance in which several coral colonies had to be passed indicates that they very much depend on their original home coral. Optimal breeding corals, for which single adults have been searching, provide them with all necessary resources, such as food, shelter, and mate (Dingle and Drake 2007) and there might not exist a continuous need to look beyond once a breeding pair is established. Such individual behavior is important for explaining the movement pattern of entire populations or species, and the single adult movement observed herein should be designated as ranging rather than migration (Dingle and Drake 2007).

Munday (2004) and Feary (2007) investigated the susceptibility of coral-dwelling fishes to habitat degradation and loss. They found a decline in abundance, but with greater losses for specialist than generalist species. Gobiodon histrio, although very abundant in the northern Red Sea, is specialized in terms of breeding habitats. If only breeding pairs were considered, the level of specialization would increase because in this social state G. histrio shows high habitat fidelity to very particular corals and very little movement between colonies. Hypoxia tolerance, homing behavior, as well as habitat and partner recognition reveal high site fidelity of G. histrio. This species has a strong dependence and association with a particular
coral, even at the colony level. Our study shows that a general-
istic coral-associated fish (when viewed from the population
level) is actually highly specialized in its choice of breeding
habitat and mate (when viewed from the individual level).
Such high partner and home-coral fidelity, coupled with low
flexibility in the choice of breeding corals, increase the vul-
nerness to habitat degradation, especially when breeding
couples are established. In the northern Red Sea, breeding pairs
of coral-associated gobies additionally avoid colonies with
high partial mortality (Schiemer et al. 2008). Further studies
and specific manipulative experiments are necessary to dis-
cover the sensory cues that guide fish to their corals and mates
and to reveal the characteristics of optimal breeding corals.
This input will better underline the consequences of habitat
loss on the reproductive fitness of coral-associated fishes.

FUNDING

University of Vienna (Research grants: brief scientific stays
abroad and research scholarship) (to M.W.); Austrian Program
for Advanced Research and Technology grant (No. 11031) of
the Austrian Academy of Sciences (to J.H.).

We are grateful to Moustafa Fouda (Egyptian Environmental
Affairs Agency) and Ayman Mabrouk (Nabq Managed Resource
Protected Area) for granting research permission. Jorg Ott supervised the
Master’s thesis of Marlene Wall. Andy Tischler and Hans Lange (Diveln
Dahab and Dahab Association for Environmental Development) sup-
ported with diving and laboratory facilities. Jürgen Herler is grateful to
Helge Hilgers for providing work space. David Feary provided valu-
able comments on the manuscript and Michael Stachowitsch added
linguistic corrections.

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