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PRIMARY RESEARCH PAPER

Microhabitat use and prey selection of the coral-feeding snail *Drupella cornus* in the northern Red Sea

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Abstract Corallivorous gastropods of the genus *Drupella* are known for population outbreaks throughout the Indo-Pacific region. Despite their potential to destroy wide areas of coral reef, prey preferences have never been analyzed with respect to prey availability, and juvenile ecology and food selectivity remain largely unknown. Here, the influence of water depth, coral abundance, colony shape, prey species, and intraspecific attraction among snails on distribution patterns, prey selection, and microhabitat use of *D. cornus* was studied in the northern Red Sea. Special emphasis was put on ontogenetic differences. The snails were most abundant in the shallowest reef zone (1 m depth). Adults were associated with several substrates and coral growth forms, whereas juveniles were highly cryptic and restricted to live branching corals. The genus *Acropora* was significantly preferred over other acroporid and pocilloporid corals. As revealed by resource selection ratios, *Acropora acuminata* was preferred by juveniles, *A. selago* by adults. In aquarium experiments, intraspecific attraction was high among both life stages. Overall, significant differences in juvenile and adult microhabitat and prey use suggest that juveniles have more specific habitat requirements, and indicate ecological impacts on coral communities different from that of adults. Prey preferences seem to depend on both coral genus and colony shape. *Acropora* corals provide the best combination of food and shelter and therefore determine distribution patterns of *D. cornus*.

Keywords Corallivory · Resource selection · Acroporids · Ontogenetic habitat shift · Intraspecific attraction · Juveniles

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Introduction

Feeding activities of coral predators have detrimental effects on coral survival and reef growth, which vary from relatively minor and patchy damage to fundamental changes in reef state (Turner, 1994a). Whereas most corallivores are considered to have only limited impact on coral health (e.g., Ott & Lewis, 1972; Gochfeld, 2004), the crown-of-thorns starfish *Acanthaster planci* Linnaeus and the muricid gastropod *Drupella* Thiele spp. have the potential to destroy wide areas of coral reefs when occurring at high densities (Moran, 1986; Turner, 1994a).

Many corallivores exhibit significant feeding selectivity and often consume only a small suite of available prey corals (Fujioka & Yamazato, 1983; De'ath & Moran, 1998; Pratchett, 2007; Cole et al., 2008). In addition, many species display high dietary plasticity and are able to include a variety of other, less preferred prey corals in their diet when the preferred corals are not abundant (Cumming & McCorry, 1998; De'ath & Moran, 1998; Berumen et al., 2005; Shafir et al., 2008).

Although prey preferences are often well-documented, the underlying reasons are much less understood. *Drupella* has been considered a "generalist corallivore with no evidence for consistent outright prey specificity" (Turner, 1994a) because the gastropods prey upon a variety of coral genera and species from numerous families. Nevertheless, a review of literature suggests a preference of acroporids (primarily *Acropora* Oken and *Montipora* de Blainville species), and to a lesser degree also pocilloporid and poritid corals. Several authors found a specific prey selection for at least one of the genera or families mentioned above (Fujioka & Yamazato, 1983; Taylor & Reid, 1984; Boucher, 1986; Turner, 1994b; Al-Moghrabi, 1997; McClanahan, 1997; Cumming, 1999; Zuschin et al., 2001; Morton et al., 2002; Shafir et al., 2008; Morton & Blackmore, 2009). Nevertheless, these preferences seem to vary with local differences in coral assemblages and abundance of preferred species (Turner, 1994a; Cumming & McCorry, 1998; Shafir et al., 2008; Morton & Blackmore, 2009).

There is only scarce data on the influence of prey availability on the food selectivity of *Drupella*. Turner (1994b) suggested a certain degree of selectivity for particular coral species and/or growth forms because caespitose/corymbose *Acropora* species were occupied disproportionately more than expected from their availability by *D. cornus* Röding. However, Turner (1994b) did not analyze this selectivity at the species level of corals but only for groups of coral species and/or growth forms. By contrast, McClanahan (1997) proposed that *D. cornus* is strongly associated with the most abundant branching coral species and lacks fidelity for a *particular* branching species. In addition, intraspecific attraction might play a major role in the food selection of *D. cornus* because a tendency to form clusters has been reported from many field observations (Fujioka & Yamazato, 1983; Boucher, 1986; Forde, 1992; Turner, 1994b; Cumming, 1999), but experimental evidence of intraspecific attraction is still lacking.

So far, only very little is known about the ecology and food selection of juvenile *D. cornus* individuals due to their highly cryptic behavior (Forde, 1992; Turner, 1994b). There is evidence that juveniles have different microhabitat and food requirements than adults. For example, they seem to prefer "fine-branching" rather than "open-branching" or "heavy-branching" corals (McClanahan, 1997). It was further suggested that branching growth forms are particularly important in early life stages to provide shelter from predators and waves, and that these associations change with increasing body size (Forde, 1992; McClanahan, 1997).

This study provides deeper insight into the distribution patterns, prey selection and microhabitat use of *D. cornus* in the northern Red Sea with special emphasis on ontogenetic differences. It was hypothesized that (i) distribution of *D. cornus* varies with depth and coral abundance, (ii) the gastropods have preferences for specific coral genera or species regardless of their abundance, (iii) juvenile microhabitat use and prey preferences differ from those of adults and that (iv) intraspecific attraction is high and influences habitat and prey selection of both adult and juvenile *D. cornus*.

Materials and methods

Study area

Field work was conducted from April to June 2007 at Dahab (28°28′N, 34°30′E; Sinai, Egypt), Gulf of Aqaba, northern Red Sea. The location "The Islands" was chosen as the study area. Its name refers to two large reef bodies, which lie somewhat off-shore (about 50 m from the inner reef crest) and extend almost up to the water surface. They protect the inner fringing reef from wave exposure and create sandy patches between the inner reef and the reef bodies. Three sites were distinguished. Site 1 is located at the inner reef slope of the largest sandy patch, and is therefore moderately sheltered. In contrast, site 2 is located south of the off-shore reef bodies and is thus exposed to wind and waves. Site 3 is also exposed to wind and waves due to its location at the outer reef slope of one of the off-shore reef bodies.

Field survey

At each site, belt transects of 5 × 1 m were laid parallel to shore at four different depths: 1, 2, 4, and 7 m. At each site, 3–7 transects were laid at each depth depending on coral abundance to obtain a total of 200 coral colonies (Table 1), which was considered a suitable sample size to calculate resource selection ratios. At greater water depths more transects (up to 7) were laid to obtain this number. Site 2 was dominated by dead corals and gravel at 7 m. Therefore, only one transect was done at this depth. The total sampling included 64 transects covering 320 m^2 of coral reef.

Within transects, five types of substrate (live coral, dead coral, live coral fragments, rock, and gravel) were examined for the presence of *D. cornus* with special emphasis on cryptic individuals. The number and shell length of all individuals were assessed in situ. Shell length was measured to the nearest mm using a sliding calliper. Long forceps were used to access cryptic individuals. Their position on the prey coral (cryptic, colony surface, colony margin, and colony underside) or on the substrate (on rock, in crevices) was examined to study size-dependent differences in microhabitat choice. Here, we define individuals <20 mm shell length as juveniles and those <10 mm shell length as recruits according to Turner (1994b).

All available corals of the genera *Acropora*, *Montipora* (family Acroporidae), *Pocillopora* Lamarck, *Seriatopora* Lamarck and *Stylophora* Schweigger (family Pocilloporidae) within transects were recorded because they were considered to be preferred prey corals (Turner, 1994a). The genus *Galaxea* Oken (family Oculinidae) was also recorded because it is sometimes used by *D. cornus* (Fujioka & Yamazato, 1983; McClanahan, 1994; Al-Moghrabi, 1997; McClanahan, 1997; Cumming, 1999) and occurred several times within transects. *Acropora* colonies, usually the most preferred coral genus of *D. cornus* (Turner, 1994a), were identified to species level to study detailed prey preferences. Identifications of *Acropora* corals were based on Dirnwöber & Herler (2007), who refer to coral skeleton samples determined by Carden Wallace (MTQ, Australia). All other corals were identified at genus level. A list of recorded prey corals is given in Table 2. All colonies with at least half of their outline within the transect and with a minimum diameter of 10 cm were recorded. This size was assumed to be the minimum size for reliable field identification. The maximum diameter of all colonies was measured to the nearest cm.

Intraspecific attraction experiments

Experiments were conducted in October 2008 in Dahab, Egypt, to assess whether intraspecific attraction within life stages exists. Test snails were given the choice between conspecifics and a coral fragment of a frequently used coral species to simulate conditions in the field and to separate attraction by corals from that by conspecifics. Two *Drupella* individuals were tested in each trial by being placed on opposite sides of a round plastic tub (45 cm in diameter for juveniles, 55 cm in diameter for adults). The test individuals were starved for 7–10 days to standardize hunger levels (Brown & Alexander Jr., 1994; Morton et al., 2002). For the experiment, they were given the choice between a coral fragment on

Table 1 Number of transects and recorded coral colonies for all sites and depths

Depth (m)	Site 1		Site 2		Site 3	
	n transects	*n* colonies	*n* transects	*n* colonies	*n* transects	*n* colonies
1	5	239	5	202	3	193
2	6	194	6	200	4	203
4	6	194	7	202	7	209
7	7	199	1	17	7	196

Note that only one transect was done at site 2, 7 m depth, because this area was dominated by dead corals and gravel

Table 2 Habitat preference of *D. cornus* as estimated from resource selection ratios and Bonferroni corrected 95 and 99% confidence intervals

Coral species	Growth form	Resource selection ratios			Occupation (%)	Mean ind. ± SE/ occupied colony
		Total	Juvenile	Adult		
Acropora ssp.	Branching and plates	**	**	**	15.1	
A. acuminata	Corymbose	*	*	NS	22.8	4.6 ± 1.00
A. digitifera	Digitate to corymbose	NS	NS	NS	14.6	5.5 ± 1.98
A. eurystoma	Caespitose-corymbose	NS	NS	NS	14.7	4.8 ± 1.46
A. gemmifera	Digitate	NS	NS	NS	15.3	2.6 ± 0.53
A. hyacinthus	Plate to corymbose	NS	NS	NS	27.8	1.8 ± 0.15
A. loripes	Corymbose	NS	NS	NS	5.6	4.2 ± 1.90
A. samoensis	Digitate to corymbose	NS	NS	NS	16.7	3.1 ± 1.13
A. secale	Caespitose-corymbose	NS	NS	NS	9.8	5.5 ± 1.33
A. selago	Corymbose	*	NS	*	18.9	5.6 ± 1.62
A. squarrosa	Corymbose	U	U	U	0.0	
A. subulata	Table/plate	NS	U	NS	43.8	12.4 ± 2.98
A. variolosa	Caespitose-arborescent	NS	NS	NS	9.1	2.6 ± 0.87
Galaxea spp.	Encrusting	U	U	U	0.0	
Montipora spp.	Encrusting	–	U	–	1.2	
Pocillopora spp.	Branching	–	–	–	1.9	2.1 ± 0.67
Seriatopora spp.	Branching	U	U	U	0.0	
Stylophora spp.	Branching	–	–	–	0.9	
n colonies		2,249	2,249	2,249		
n occupied		188	96	120		

Growth form, occupation rates (in % of available colonies) and mean group size (±SE per occupied colony) are given for all coral taxa. * Preferred at $P \leq 0.05$, ** preferred at $P \leq 0.01$, – = used significantly less than expected from its availability (avoided, $P < 0.05$), NS = used according to availability ($P > 0.05$), U = unused

the left side and five conspecifics on the right side of the tub. The conspecifics were kept together in a fine fishing net fixed to the wall of the tub. The aerator was placed in the middle of the tub to be at similar distance to both snails. The two test snails could move freely overnight. After 12 h, the position of each snail was recorded. Four trials with six replicates each were conducted for each setup (see below), so that 48 individuals were tested within each setup. In all replicates of one trial, coral fragments from the same coral colony were used to be able to pool results for statistical analysis. Corals were maintained in fresh seawater with aeration for several hours to acclimate before they were used.

Setup 1—attraction among juveniles

The provided coral species was *Acropora selago* Studer, which was used according to its availability by juvenile snails in the field. Test individuals as well as all conspecifics were juveniles.

Setup 2—attraction among adults

Test individuals as well as all conspecifics were adult snails. The provided coral species was *A. subulata Dana* because it was used according to its availability by adults in the field.

Statistical analyses

Field survey

The effect of site and depth on the abundance of *D. cornus* was analyzed using Kruskal–Wallis tests. Tukey–Kramer-post-hoc tests were used in case of significant differences. Chi-squared tests were used to compare juvenile and adult abundance, prey preferences, and position within microhabitats. Mann–Whitney *U*-test and Chi-square statistics were used to determine differences in mean group size between juveniles and adults. Linear regression was calculated to determine the relationship between coral colony size and the number of occupying *D. cornus*.

The distribution and abundance of coral species used as prey by *D. cornus* are likely to influence the distribution and abundance of the predator. Therefore, similarity of coral species distribution for sites and depths was analyzed using analysis of similarity ANOSIM (Clarke & Warwick, 1994) based on the Bray–Curtis similarity coefficient (Bray & Curtis, 1957). More important than the significance level are the pair-wise *R*-values, which give an absolute measure of separation for all groups. *R*-values range from 0 (indistinguishable) to 1 (all compositional dissimilarities between groups are larger than any dissimilarity among samples within groups). *R*-values >0.75 are interpreted as “well-separated groups”, *R*-values > 0.5 as “overlapping but clearly different groups”, *R*-values >0.25 as “strongly overlapping groups,” and *R*-values <0.25 as “barely separable groups” (Clarke & Gorley, 2001).

In order to investigate potential prey preferences of *D. cornus* with respect to prey availability, resource selection ratios (Manly et al., 1993) were calculated to determine which coral species were used significantly more or less than expected from their availability in the field. Selection ratios (ω_i) were estimated using the formula:

$$\omega_i = o_i / a_i$$

where o_i is the proportion of occupied colonies of coral species i among occupied colonies of all species, and a_i is the proportion of available colonies of coral species i among available colonies of all species. Bonferroni corrected 95 and 99% confidence intervals were estimated using the formula:

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

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 *D. cornus*. 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 (not significantly used less or more frequently than expected), 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 (“avoided”), and a confidence interval >1 indicated that the habitat was used significantly more than expected (“preferred”). Instead of total abundance data, only the presence or absence of *D. cornus* in a given colony was used for analyses, as recommended by Thomas & Taylor (1990) to ensure independence of habitat observations. Resource selection ratios were calculated not only for the total of all *D. cornus* individuals but also separately for juvenile and adult snails.

Intraspecific attraction experiments

Experiments were analyzed using one-sample chi-square statistics (observed versus expected number of individuals). The analysis included all individuals found within a perimeter of 5 cm of either coral or conspecifics. The latter also included test snails that have approached each other closer than 5 cm instead of their conspecifics in the net. Results from all trials within one setup were pooled for chi-square statistics.

Analyses were performed using Statistica version 6.0. Primer version 6.1.6 was used for ANOSIM (Clarke & Warwick, 1994) and PAST version 1.69 (Hammer et al., 2001) for chi-square statistics.

Results

Abundance and distribution of *D. cornus*

The 320 m^2 (64 transects) of coral reef investigated yielded 2,249 coral colonies identified and examined for the presence of *D. cornus*. A total of 941 snails were mainly found on live corals and rock, respectively. This yields an average density of 2.9 (±0.5 SE) individuals m^{-2} for the location “The Islands”. Variation among and within sites and depth was high, with local mean densities ranging from 0.7 (±0.4 SE) individuals m^{-2} at site 3, 7 m depth, up to 13.4 (±2.0 SE) individuals m^{-2} at site 3, 1 m depth.

There were no significant differences in snail density among sites ($H = 0.08$, df $= 2$, $P = 0.96$), but density declined significantly with depth ($H = 23.53$, df $= 3$, $P < 0.001$; Fig. 1a). Mean density at 1 m depth for all sites was 7.3 (±1.4 SE), but only 0.8 (±0.3 SE) individuals m^{-2} at 7 m. Although abundance generally declined with depth, significant differences between juvenile and adult *D. cornus* were detected ($\chi^2 = 81.71$, df $= 3$, $P < 0.001$). Whereas adult abundance decreased steadily, juveniles had a second peak at 4 m depth (Fig. 1a).

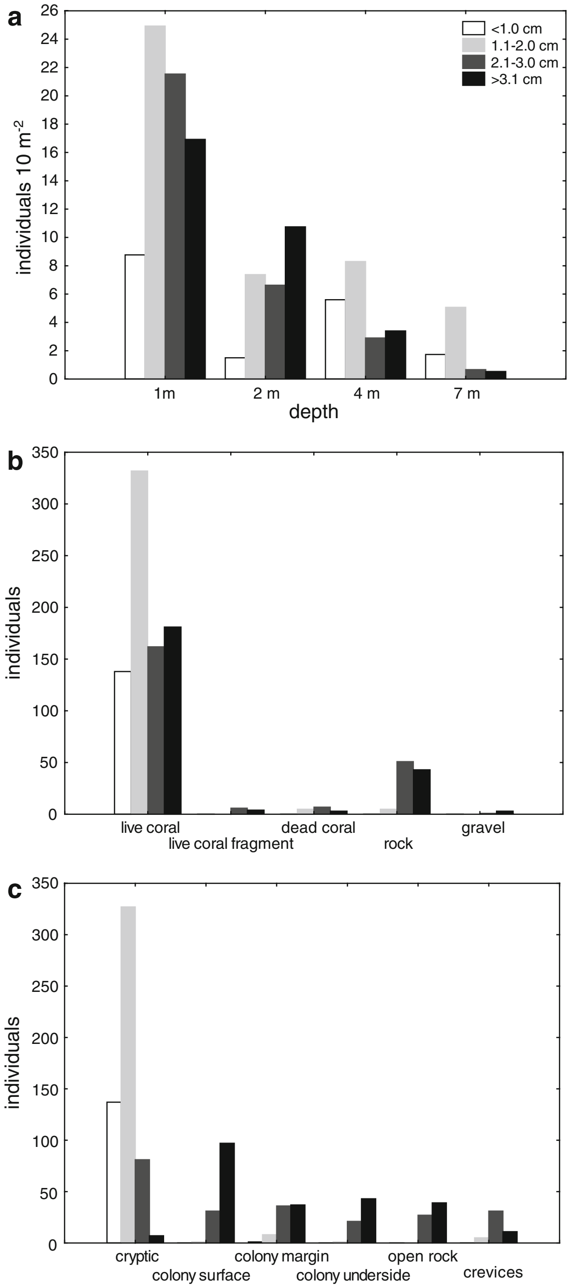

Fig. 1 Distribution patterns of four major size classes (shell length) of *Drupella cornus* in the Gulf of Aqaba, northern Red Sea. **a** Variation in density with depth. **b** and **c** Abundance within different microhabitats and positions on substrate, respectively

Although both juvenile and adult snails preferred live corals as microhabitat (Fig. 1b), there were significant differences in microhabitat use between the two groups ($\chi^2 = 111.96$, df $= 2$, $P < 0.001$). Nearly all juvenile snails (98%) were found on live corals and only 1% on dead corals and on rock, respectively. In contrast, only 74.4% of all adult snails were observed on live corals, followed by 20.4% on rock and 5.2% on dead corals, live coral fragments and gravel.

Position on substrate differed significantly between juvenile and adult snails ($\chi^2 = 587.14$, df $= 5$, $P < 0.001$). Nearly all juveniles (96.7%) were hidden between coral branches (cryptic) and only few (1.9%) occupied colony margins (Fig. 1c). Only one individual was found beneath a colony and one on a colony surface. In contrast, adults were spread much more evenly over all positions. The highest percentage (27.8%) was on the colony surface, the lowest (9.1%) in crevices.

Prey selection of *D. cornus*

A total of 216 colonies were occupied by *D. cornus*. Juveniles were found on 98 colonies whereas adults were found on 138 colonies. Nineteen colonies from eight coral species were occupied by both juvenile and adult snails: *A. acuminata* Verill (8 colonies), *A. secale* Studer (4), *A. selago* (2), *A. gemmifera* Brook (2), *A. eurystoma* Klunzinger, *A. samoensis* Brook, and *Pocillopora* sp. (1 each).

The mean number of individuals per occupied colony was 4.3 (±0.4 SE) for all individuals taken together. Mean group size was significantly different ($U = 4793.5$, $z = 2.32$, $P < 0.02$) between juveniles with 4.8 (±0.7 SE) individuals per occupied colony and adults with 2.8 (±0.3 SE; Fig. 2a). Mean group size was also calculated for individual coral species, and ranged from 1.8 individuals (±0.2 SE) per occupied colony in *A. hyacinthus* Dana to 12.4 (±3.0 SE) in *A. subulata* (Table 2). When calculated separately for juveniles and adults across all species,

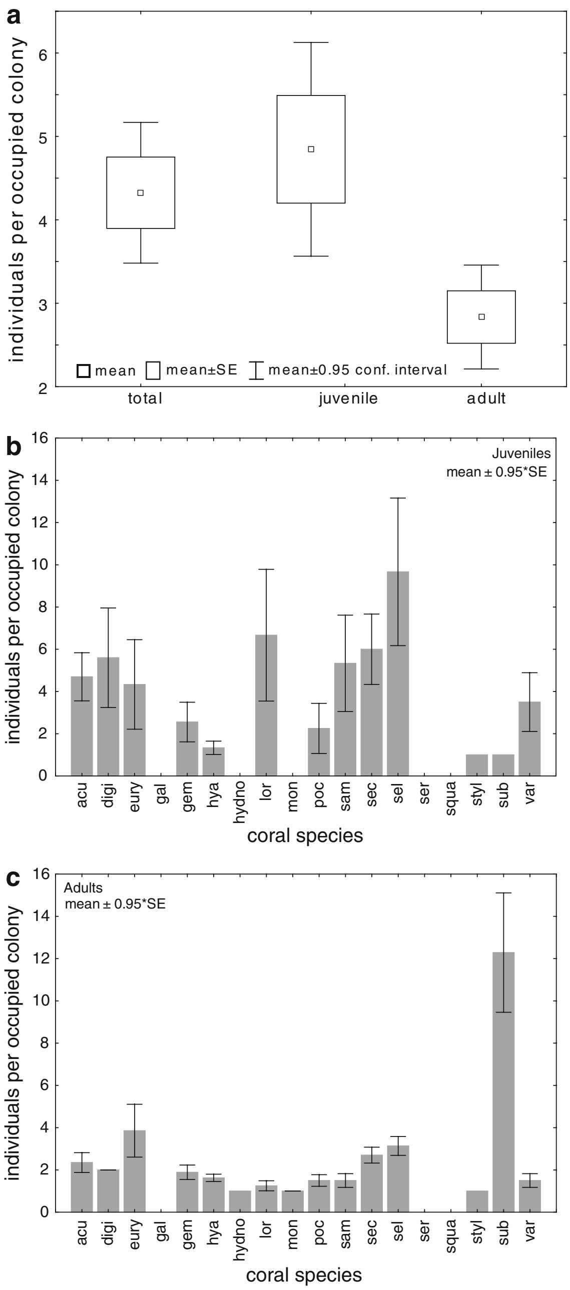

Fig. 2 **a** Mean (±SE) number of individuals per occupied colony for all *D. cornus*, and for juveniles and adults, respectively. Mean (±0.95 SE) group size of **b** juveniles and **c** adults is also given for all recorded coral taxa. acu = *Acropora acuminata*, digi = *A. digitifera*, eury = *A. eurystoma*, gal = *Galaxea* spp., gem = *A. gemmifera*, hya = *A. hyacinthus*, hydno = *Hydnophora* sp., lor = *A. loripes*, mon = *Montipora* spp., poc = *Pocillopora* spp., sam = *A. samoensis*, sec = *A. secale*, sel = *A. selago*, ser = *Seriatopora* spp., squa = *A. squarrosa*, styl = *Stylophora* spp., sub = *A. subulata*, var = *A. variolosa*

significant differences were detected ($\chi^2 = 21.49$, df = 12, $P < 0.04$; Fig. 2b, c) with higher variation in juveniles. A significant positive correlation between coral colony size and individual numbers of *D. cornus* ($r = 0.266$, $P < 0.001$) was found for all snails and for adults ($r = 0.432$, $P < 0.001$), but not for juveniles ($r = 0.047$, $P = 0.648$).

All sites had similar occupation rates (percent occupied colonies of available colonies), whereas occupation varied considerably with depth, ranging from 2.7% occupied colonies at 7 m up to 14.2% at 1 m. For all acroporids and pocilloporids, 9.6% of all available colonies were occupied by *D. cornus*. With 15.2%, the genus *Acropora* had the highest occupation rate. Within this genus, the highest occupations were in *A. subulata* (43.8%), *A. hyacinthus* (27.8%), and *A. acuminata* (22.8%) (Table 2).

Prey coral species of *D. cornus* were distributed similarly across all sites (global $R = 0.14$), but not across all depths. Species distribution between 1 and 4 m depth did overlap, but was clearly different ($R = 0.69$); the difference was even more pronounced between 1 and 7 m ($R = 0.77$).

Resource selection ratios showed that, on genus level, *Acropora* was preferred ($P < 0.01$) by all snails (Table 2). The other genera were either avoided (*Montipora* by adults, *Pocillopora* and *Stylophora*) or remained unused (*Galaxea* and *Seriatopora*; *Montipora* by juveniles). Within the genus *Acropora*, *A. acuminata* and *A. selago* were significantly preferred ($P < 0.05$), with juveniles showing a preference only for *A. acuminata* ($P < 0.01$), and adults only for *A. selago* ($P < 0.05$). Most other species were used according to their availability except for the tabular *A. subulata*, which was not used by juveniles. *Acropora squarrosa* Ehrenberg remained unused, but occurred only three times in all transects.

Only 19 out of 941 individuals were not associated with *Acropora* corals. The occupied *Pocillopora* and *Stylophora* colonies were identified to species level. Two individuals were found on *P. damicornis* Linnaeus, five individuals on *P. verrucosa* Ellis & Solander and two individuals on *S. pistillata* Esper. All other snails were found on *Montipora* spp. except for a single adult snail, which was observed feeding upon *Hydnophora microconos* Lamarck (family Merulinidae).

Recruits ($n = 136$) were found on eight *Acropora* species (*A. acuminata*, *A. secale*, *A. variolosa*

Table 3 Significance of intraspecific attraction experiments between juvenile ($n = 48$) and adult ($n = 48$) snails of *Drupella cornus*

Setup	Choice	n^{O}	n^{E}	χ^2	*P*-level	*n* snails	% Snails that made a choice
Juvenile versus juvenile	Coral	9	17	7.529	0.006	48	70.8
	Snails	25	17				
Adult versus adult	Coral	4	12.5	11.560	0.001	48	52.1
	Snails	21	12.5				

n^O number observed, n^E number expected

Klunzinger, *A. eurystoma*, *A. selago*, *A. hyacinthus*, *A. digitifera* Dana, *A. loripes* Brook, and *A. samoensis*; arranged by decreasing number of individuals per species) as well as on *Pocillopora* spp. Both *A. secale* and *A. acuminata* had the highest recruit occupation.

Intraspecific attraction experiments

There was a significant intraspecific attraction among both juveniles and adults ($P < 0.01$; Table 3). Adult snails often aggregated with their test partners rather than with the conspecifics provided in the net, whereas juveniles most often chose the conspecifics in the net. The percentage of individuals that made a choice was much greater in juveniles than in adults. Only two (juvenile) snails out of 96 fed upon the provided coral although all test individuals had been starved for 7–10 days.

Discussion

This study revealed significant differences in prey selection and microhabitat use between different life stages of the corallivorous gastropod *Drupella cornus* in the Gulf of Aqaba, northern Red Sea. Juveniles were found to be restricted to cryptic microhabitats within live branching *Acropora* corals, whereas adults used a broad range of microhabitats and prey corals. Significant accumulation was found among juveniles and adults in the field and intraspecific attraction was confirmed by laboratory experiments.

Abundance and distribution of *D. cornus*

The mean density of 2.9 individuals m^{-2} in Dahab, Egypt, appears to be much higher than reported previously from other areas of the Red Sea—except for the population outbreaks along the Sinai coast of the northern Gulf of Aqaba (Al-Moghrabi, 1997; Antonius & Riegl, 1997, 1998; Shafir et al., 2008). Mean densities from other areas range from 0.8 and 0.3 individuals m^{-2} in Safaga and Aqaba (Zuschin et al., 2001; Zuschin and Stachowitsch, 2007), respectively, to 1.3 individuals m^{-2} at Sanganeb Atoll off Port Sudan (Schuhmacher, 1992).

Although different sampling protocols make comparisons between studies difficult, a review of literature from the past four decades suggests that population densities of *D. cornus* are increasing gradually, since the last 20 years. The gastropods were probably uncommon on Red Sea coral reefs before the 1990s because early studies on the molluscan fauna of the Red Sea rarely mentioned *D. cornus* (Mergner & Schuhmacher, 1974; Mastaller, 1978, 1979; Taylor & Reid, 1984). Distinct population increases were observed in the early 1990s (Schuhmacher, 1992; Schuhmacher et al., 1995), and the first population outbreaks were recorded soon after (Al-Moghrabi, 1997; Antonius & Riegl, 1997, 1998). More recent investigations (Zuschin et al., 2001; Zuschin & Stachowitsch, 2007; Shafir et al., 2008) and the present study also provide evidence that population densities have increased.

Highest *D. cornus* densities were found along the reef edge and declined significantly with depth. This preference for shallow reef parts has often been reported (Schuhmacher, 1992; Turner, 1994a; Al-Moghrabi, 1997) although the gastropods occur down to at least 20 m depth, but at a much lower density (Al-Moghrabi, 1997; Zuschin & Stachowitsch, 2007). This distribution pattern is probably influenced by the zonation of coral assemblages, which significantly varied with depth in this study (compare also Riegl & Velimirov, 1994) but not between sites. This indicates that snail distribution correlates with coral community composition, i.e., they prefer certain assemblages over others.

Specifically, the high abundance of *Acropora* (preferred habitat and prey) at shallow depth as well as variation of *Acropora* assemblages with depth (Wallace, 1999; Dirnwöber & Herler, 2007) may determine the observed pattern. Decrease in abundance or disappearance of preferred *Acropora* species with depth might result in a concentration of snails in shallow reef parts. For example, *A. acuminata* and *A. selago*, which were used more often than expected from their availability, were most abundant at 1 m depth and decreased considerably with depth. However, there are reports that *Acropora* abundance does not always explain the distribution pattern of *D. cornus* (Turner, 1994a; Al-Moghrabi, 1997).

The snail's attraction to freshly damaged corals (Forde, 1992; Morton et al., 2002) might also contribute to higher abundance at shallow depth because shallow corals are more prone to natural and anthropogenic destruction. Many coral fragments and mechanically damaged corals were found along the reef edge, and were occupied at a high rate.

Microhabitat use

Live corals were the preferred microhabitat of both juvenile, and adult *D. cornus* but many of the adult snails were also found on rock, dead corals, and between gravel (see also Taylor & Reid, 1984; Al-Moghrabi, 1997; Cumming, 1999) whereas juveniles were nearly exclusively associated with live corals. Nearly all juveniles occupied highly cryptic positions at the base of coral branches, whereas adults were found at various positions including the surface, margin, and underside of colonies or rock crevices. This indicates that juveniles may have a higher need for protection from predators and/or waves, and are therefore restricted to cryptic microhabitats. Adults, by contrast, seem to be able to use also less protective microhabitats. Their thick, algae-overgrown shells and cryptic coloration, which are not present in juveniles, probably make them less prone to predation (Forde, 1992). They may, thus, be also more mobile, so that they were more frequently encountered in habitats other than live corals.

Further evidence for this assumption comes from the differences in juvenile and adult prey selection. In contrast to adults, juveniles were almost exclusively associated with tightly branching *Acropora* species and did neither feed upon plate-like *A. subulata* nor on encrusting *Montipora*. This suggests that colony shape plays an important role in juvenile prey selection because it determines the degree of protection offered by a specific coral. Tightly branching species providing the highest possible protection may therefore fulfill crucial juvenile habitat requirements. The few studies that included juveniles observed similar associations of juveniles with "fine-branching" rather than "open- or heavy-branching" corals (McClanahan, 1997) and with either digitate or caespitose/corymbose growth forms of *Acropora* (Forde, 1992; Johnson et al., 1993; Cumming, 1999), respectively.

There is also evidence that patterns in epifaunal communities of *Acropora* corals on the Great Barrier Reef are determined more importantly by colony morphology than environmental regime or specific prey species (Vytopil & Willis, 2001). It is, however, likely that also a number of other factors characterizing microhabitat quality—such as interbranch space, nutritional value, or degree of physical defense—may influence microhabitat and prey selection of juvenile *D. cornus*.

Such ontogenetic shifts from structurally complex microhabitats to more open ones are also known from several other marine invertebrate species, such as mussels, snails, nudibranchs, isopods, crabs, lobsters, sea stars, and urchins (Gosselin, 1997 and references therein). This indicates that shelter requirements often play a major role in determining microhabitat use during early juvenile life.

Prey selection and intraspecific attraction

This study is the first to calculate resource selection ratios (RSR) for a *Drupella* species and revealed that *Acropora* is significantly preferred over all other acroporid and pocilloporid coral genera, which were either used significantly less than expected from their availability (*Pocillopora*, *Stylophora*, and *Montipora* by adults) or remained unused (*Seriatopora* and *Montipora* by juveniles). Moreover, only a minority were not associated with *Acropora* corals. Acroporidae and Pocilloporidae both have the highest protein and energy content compared to other coral families, such as the Faviidae and Poritidae (Keesing, 1990). Branching and tabular *Acropora* colonies were also found to have the greatest complexity, thereby providing greater surface area and more tissue to feed upon than other colony shapes (Keesing, 1990). Thus, *Acropora* corals may offer the best combination of protection and food for *D. cornus*. Prey preferences are therefore likely to depend on both coral genus and colony shape, which has also been shown for *Acanthaster planci* (De'ath & Moran, 1998).

It is important to note, though, that the snails are also known for their dietary plasticity. Although a preference for *Acropora* has been reported in many studies, they are able to adapt their diet to different local coral communities (Turner, 1994a). In Hawaii, for example, *D. cornus* is confined to *Pocillopora* spp. and *Porites compressa* Dana because the genus *Acropora* is absent (Robertson, 1970). In Kenya, the gastropods were most often associated with branching and massive *Porites* (McClanahan, 1994, 1997). In Hong Kong, where branching corals are not available, *D. rugosa* Born feeds primarily on massive and encrusting corals despite its preference for acroporids (Cumming & McCorry, 1998; Morton et al., 2002). *D. cornus* also displays dietary plasticity across small temporal scales because it is able to switch to less preferred prey in areas where preferred corals have become scarce due to coral bleaching (Zuschin & Oliver, 2003) or extensive coral predation (Forde, 1992; Shafir et al., 2008).

In the northern Red Sea, most *Acropora* species were used according to their availability except for *A. acuminata* and *A. selago* (both preferred), and *A. subulata,* which was unused by juveniles. *Acropora squarrosa* remained unused but occurred only three times within all transects. On species level, however, RSR have to be interpreted carefully depending on whether emphasis is put on (1) the identification of prey preferences or (2) the ecological consequences of coral occupation by *D. cornus*. When focusing on potential prey preferences, presence/absence of *D. cornus* per colony instead of abundance of individuals per occupied colony has to be used for analysis to ensure independency of habitat or prey observations (Thomas & Taylor, 1990). This is, in particular, important for species such as *Drupella* spp., which have a tendency to aggregate because otherwise intraspecific attraction effects might confound potential prey preferences (Thomas & Taylor, 1990).

In contrast, when ecological consequences of coral occupation instead of prey preferences are emphasized, RSR underestimate coral occupation due to the exclusion of the intensity of resource use, i.e., the number of individuals found per colony. Mean group size was 4.3 individuals per occupied colony and intraspecific attraction was found to be significant among both juveniles and adults. It is therefore likely that predation by *D. cornus* also considerably affects coral species that were used only according to their availabilities. For example, plate-like *A. subulata* had the highest occupation rate of all *Acropora* species with 44% of all colonies occupied and the greatest group size with a mean of 12 individuals per occupied colony. Still, RSR only detected usage according to its availability (by adults).

Intraspecific attraction experiments revealed significant attraction within both juveniles and adults. Conspecifics were significantly preferred over the provided coral (species used according to its availability in the field) by all life stages, although test snails had been starved for at least 7 days. This indicates that prey selection of *D. cornus* is not only influenced by preferences for specific coral species only but also by the presence of conspecifics, no matter whether they are feeding or not. A tendency for *Drupella* species to form clusters has been reported from many field observations (e.g., Fujioka & Yamazato, 1983; Forde, 1992; Turner, 1994b) and several reasons for this behavior have been mentioned. Group foraging can decrease predation risk, improve foraging efficiency and chances of locating food, and provide opportunities to steal food (e.g., Brown & Alexander Jr., 1994 and references therein). In *D. cornus*, facilitated prey location might be an important advantage of group foraging. The attractive effect of feeding muricids has been reported in literature (Morton et al., 2002) and might be of particular importance on reefs with low coral cover. Later arriving snails might also benefit from open tissue wounds as the snails in general seem to avoid crawling on live coral tissue, and are often observed feeding at the interface between live polyps and areas of dead corallites (Fujioka & Yamazato, 1983; Antonius & Riegl, 1997; Cumming & McCorry, 1998; Cumming, 1999).

Ecological consequences of coral occupation

The different ecology of juveniles and adults results in differential ecological impacts on coral communities and coral-associated fauna, especially on the microhabitat level. Juveniles mainly affect the inner base of coral colonies where obligate coral associates, such as small crabs, shrimp, and gobies dwell. This microhabitat provides shelter, food, and breeding ground to the epifaunal organisms (Glynn et al., 1985; Patton, 1994; Munday, 2000; Vytopil & Willis, 2001). It is therefore likely that intruders feeding upon the coral will have severe effects on epifaunal fitness and abundance. For example, mucus release by stressed (bleached) *Pocillopora* corals decreased significantly, so that crustacean symbionts were deprived of a considerable proportion of their food and displayed higher mortality and migration rates (Glynn et al., 1985). Abilities to migrate to healthy colonies can be restricted in obligate coral associates (Feary, 2007; Wall & Herler, 2009). On a larger scale, increased partial mortality and decreased coral abundance at a reef cause severe population declines in crustacean coral symbionts (Glynn et al., 1985) and obligate coral-dwelling fishes (Munday, 2004; Feary, 2007; Schiemer et al., 2008).

Adult snails, by contrast, affect all colony parts more or less equally. They fed in smaller groups than juveniles but tended to occupy more colonies. However, as they are probably less prone to predation and move more frequently, they might not necessarily consume whole colonies at normal densities. It was often observed that colonies occupied by adults had only small feeding marks, whereas those occupied by juveniles showed significant partial mortality caused by recent feeding activities. Corals occupied by adults would then suffer tissue loss in the short term, but would potentially be able to recover. Under this scenario, adult *D. cornus* might be ecologically less harmful to coral communities and their associates than juveniles because their feeding activities are less concentrated on single colonies. Exceptions may be the few large tabulate *Acropora* species that support large feeding groups of snails.

Conclusion

Feeding activities of corallivores have been considered, so far, to threaten coral communities only at high abundance, then providing a source of reef degradation and habitat loss. In addition, high coral mortality caused by predator outbreaks can initiate rapid bioerosion and accelerate reef decline (Glynn, 2001). Nevertheless, even at normal population densities, it can be assumed that the continuing removal of coral tissue has sublethal effects on coral communities and their epifauna, such as reduced growth, reproduction, and capacity to cope with additional stress (e.g., Cole et al., 2008). *Acropora* communities and their associated fauna will be affected, in particular, not only because they are the preferred prey of *Drupella* spp., *Acanthaster planci* (De'ath & Moran, 1998), and most coral-feeding butterflyfishes (Cole et al., 2008) but also as they are particularly sensitive to environmental stress (McClanahan et al., 2005). Thus, it can be expected that predation pressure of selectively feeding corallivorous invertebrates contributes to the effect of several other environmental stress factors causing coral community shifts.

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