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Feeding strategies in a territorial corallivorous butterflyfish
with respect to coral identity, size and occupation by coral
gobies.

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Abstract

Corallivory is an equivalent to terrestrial plant-herbivory and therefore important for the successful functioning of marine ecosystems. Nonetheless, the role of coral feeding butterflyfishes has long been underestimated. In this study the food preferences of an obligate corallivorous butterflyfish *Chaetodon austriacus* were determined on a fringing reef near Dahab, in the Gulf of Aqaba, northern Red Sea. The main prey corals of *Chaetodon austriacus* were *Acropora*, *Stylophora* and *Pocillopora*. Ivlev's electivity index revealed that only *Acropora selago* and *Pocillopora* were consumed more than they were available whereas *Stylophora* was consumed according to its availability. The density of *Acropora selago* was found to be an important determinant for territory size in *Chaetodon austriacus* as high density of this coral species lead to smaller territories along with higher feeding rates of the fish. Thus, it can be assumed that *Acropora selago* is a high quality prey coral for *Chaetodon austriacus*. Predation on the coral colony level was investigated by tagging corals and collecting data on the frequency of visits and the bites taken per visit and fish. Predation frequency was very high on large colonies but predation intensity, as it is size-related, decreased with colony size. Furthermore, larger colonies were preferred over medium and especially over small-sized coral colonies.

The hypothesis that mutualistic gobies of the genus *Gobiodon* are able to defend their host colony from high predation by butterflyfishes could be confirmed and the size in which this effect is present could be determined. Colonies of *A. selago* with occupation of *Gobiodon* sp.3 in a size range of 250-500 cm² received significantly less bites and visits per hour and less time was spent feeding on occupied colonies than on unoccupied. Predation intensity was highest in small and medium-sized colonies as it is size-related. Due to ongoing climate change along with frequent bleaching events, future acroporid coral communities are expected to consist mainly of juvenile small or medium-sized colonies. Thus, the effect of resource defense of mutualistic gobies will become even more crucial, as they can direct predation of butterflyfish towards unoccupied coral colonies.

Introduction

Corallivory has long been studied in invertebrates and fishes with its resulting effect on corals being looked at in the last decades (Rotjan and Lewis 2008). Altogether 114 vertebrates (osteichthyan fishes) and 51 invertebrates are known to feed on living coral tissue, either obligatory or facultative (Robertson 1970), and with different modes of feeding (Rotjan and Lewis 2008). The mucus-feeders are the most harmless of all corallivorous species, as mucus is produced and released by corals constantly over the day, whereas browsers remove living coral tissue but do not harm the underlying calcium-carbonate skeleton (Hiatt and Strasburg 1960). Another two feeding types are given in parrotfishes. One of these two feeding types are the scrapers, which scrape off living coral tissue from the coral surface along with small amounts of carbonate skeleton. The other type are the most destructive ones in terms of coral damage, the excavators. Excavators not only consume the living coral tissue but also great parts of the skeleton, for example, by biting off entire coral branches (Bellwood and Choat 1990).

Among corallivorous fishes, the butterflyfishes (Chaetodontidae) belong to the most prominent coral feeders, as more than 50 % of this family feeds at least partially on scleractinian corals (Cox 1986; Pratchett 2005). They are also very common in tropical reefs. Previously, corallivory of butterflyfishes has been considered to play a minor role in coral communities (Robertson 1970; Harmelin-Vivien and Bouchon-Navaro 1983; Hixon and Carr 1997); yet Cole et al. (2011) estimated the amount of coral tissue removed by a single adult butterflyfish to be 2 to 3 g per day. Since this amount of removed tissue is large, it has been hypothesized that corals may suffer from chronic predation due to frequent predation events. This “grazing” behavior of butterflyfishes can be compared to plant herbivory in terrestrial ecosystems, where repeated partial consumption of plant individuals leads to less reproduction (Leavitt and Robertson 2006; Hladun and Adler 2009). Additionally effects are growth reduction and lower ability to store energy (Midoko-Iponga et al. 2005; Maron and Crone 2006; Rotjan and Lewis 2008).

Many butterflyfishes are known to defend territories against intraspecific or sometimes also interspecific competitors (Hourigan 1989; Roberts and Ormond 1992; Wrathall et al. 1992). These territories range in size between 90 and 300 m² and can be maintained for at least 8 years in some butterflyfish species (Reese 1981). Since the food resources within the territories are limited, a balance between coral consumption and growth must be given to maintain a stable territory. It is thus assumed that butterflyfishes avoid overgrazing on corals

by defending larger territories, which leads to less predation intensity on colonies within the territory (Gochfeld 1997). Another way to prevent massive grazing is selective feeding on large corals, as the impact of feeding on large colonies is less than for small colonies (Cole and Pratchett 2011). Resource partitioning between conspecifics or different butterflyfish species might also be a mechanism to avoid overgrazing. Apart from that corals themselves may have evolved mechanisms to avoid excessive predation. For example, corals can increase the number of nematocysts after heavy predation (Gochfeld 2004). It was also hypothesized that corals can store energy-rich components within the skeleton which would lead to less energy-rich coral tissue available for predation, leading to less interest to prey upon those corals (Tricas 1989a).

Mutualistic coral inhabitants which defend their host coral could also contribute to the reduction of predation pressure on corals. Mutualistic relationships between corals and their inhabitants have already been proven. For example, resident Trapeziidae (Crustacea: Brachyura) actively drive away the crown-of-thorns star fish (*Acanthaster planci*) when attacking their host coral (Weber and Woodhead 1970; Glynn 1976; Pratchett 2001). A very common inhabitant of acroporid corals are gobies of the genus *Gobiodon*. These fishes possess a toxic skin mucus instead of scales (Hashimoto et al. 1974; Lassig 1981). A recently published study about *Gobiodon* and its host coral revealed a very interesting relationship, whereby *Gobiodon* removed a toxic seaweed after it had received a signal from its host coral (Dixson and Hay 2012). The toxicity of *Gobiodon* was shown to fulfill several duties such as to protect the goby of ecto-parasites (Munday et al. 2003) or to serve as protection against predators if *Gobiodon* is forced to leave its host corals to find a more adequate coral (Schubert et al. 2003). The toxin of *Gobiodon* might act also as a repellent against butterflyfishes (Lassig 1981). Although in this experiment the concentration of the toxin was much higher than it would occur under natural conditions. Dirnwoeber and Herler (2012) demonstrated that the ichthyotoxin from *Gobiodon* species possesses the power to repel *C. austriacus* even when highly diluted (1:200,000). Additionally, it was shown that gobies also actively defend their host colony upon encounters with butterflyfishes (Dirnwoeber and Herler 2012).

Although corallivory may represent an important factor for reef-building processes, only 18 out of 111 coral genera are reported to be consumed by coral-feeders. Upon them *Acropora*, *Pocillopora*, *Montipora* and *Porites* are the most commonly grazed genera. *Acropora* is a widespread genus in the Indo-Pacific region and belongs, due to its fast growth rates, to the most important reef building corals. This genus has a broad range of growth forms and is found throughout all reef zones. Despite of its great variability and occurrence,

some species of *Acropora* are more consumed, such as *A. hyacinthus* or *A. cytherea* on the Great Barrier Reef (Irons 1989; Berumen et al. 2005; Pratchett 2005, 2007; Cole and Pratchett 2011; Cole et al. 2012). Cole et al. (2012) found that 61-68 % of the total consumption of coral tissue was directed towards the tabular acroporid corals *A. hyacinthus* and *A. cytherea*. In the northern Red Sea, *A. selago* represents the main acroporid food source for the most common corallivorous butterflyfish *Chaetodon austriacus* (Niedermueller et al. 2009).

Chaetodon austriacus, the exquisite butterflyfish, is endemic to the Red Sea (Randall 1983). This butterflyfish is monogamous and defends, as many other reef-associated fish, a territory against intraspecific competitors (Fricke 1986). *Chaetodon austriacus* is obligate corallivorous and feeds almost exclusively on scleractinian corals (Neudecker 1979; Randall 1983). In the Gulf of Aqaba, *Acropora* represents its main food source followed by *Pocillopora*, *Porites* and *Stylophora* (Alwany et al. 2003; Niedermueller et al. 2009).

In many climate change scenarios it has been predicted that due to rising water temperatures along with the acidification of the oceans (Hoegh-Guldberg et al. 2007; Anthony et al. 2008; Veron et al. 2009), corals might be disabled to calcify in the habitual speed (Kleypas et al. 2006). In addition, the increasing temperature of the ocean will lead to higher frequency of bleaching events, which results in higher mortality of *Acropora*, since this genus is very susceptible to such disturbances (McClanahan et al. 2008). In future, the acroporid coral community is therefore expected to consist predominantly of small-sized colonies (Hoegh-Guldberg et al. 2007). As the availability of large prey corals will decrease significantly, the predation of corallivorous butterflyfishes will be directed towards small colonies, which might increase coral mortality if corals are already stressed by bleaching or direct anthropogenic disturbances (Cole et al. 2011).

Corals occupied by *Gobiodon histrio* were generally avoided by butterflyfish compared to unoccupied corals as shown in Niedermueller et al. (2009). Experiments increased the evidence that gobies may have an effect on coral predation (Dirnwoeber and Herler 2012). Therefore it can be hypothesized that these gobies are able to defend their host corals against *C. austriacus*. Hence, the aims of the present study were to assess whether an effect of resource defense is present in the field and whether it is colony-size dependent. Additionally, the general feeding selectivity of *C. austriacus* regarding colony size and the predation rate on colony level were determine. Furthermore, a video experiment was conducted to compare the natural feeding rates on colony level with maximum bite rates under experimentally reduced coral availability. The study focused on two species of *Gobiodon*, *G. histrio* and *G. sp.3* living in *Acropora gemmifera* and *A. digitifera*, and in

Acropora selago, respectively (Dirnwoeber and Herler 2007). In addition to free-ranging field observations, corals in different size classes and different occupation states were tagged in 10 territories of *C. austriacus* in a fringing reef in the northern Red Sea.

Material and Methods

Study site and data acquisition

The study was conducted between May and June 2012 at a fringing reef near Dahab (28°28'N, 34°30'E) in the Gulf of Aqaba, northern Red Sea, Egypt. This reef was chosen because fishes in this area are used to swimmers and snorkelers and coral community structure is very homogeneous. Ten territories of *Chaetodon austriacus* pairs were observed at the reef flat between 4 to 8 hours using snorkeling equipment. Territories were selected with regard to obvious territorial behavior of *C. austriacus* pairs. Before feeding behavior recordings, each pair of *C. austriacus* was observed for 4 h and all visited coral colonies of *A. selago* (the main host coral of *Gobiodon* sp.3 (sensu Herler and Hilgers 2005)), *A. digitifera* and *A. gemmifera* (the main host corals of *Gobiodon histrio* in this reef) were tagged. Additional corals were tagged to obtain a more balanced sample within the coral size class and with respect to occupation state. Tags consisted of white waterproof PE foil labeled with permanent marker and fixed to nearby structures (dead corals). The tagged colonies were then measured (maximal width, S1 and maximal length, S2) to estimate the planar projected area by calculating an ellipse ($S1/2 * S2/2 * \pi$). In addition, the occupation status of colonies by *Gobiodon*, including identity, individual number and life cycle stage (juvenile or adult) were noted. The occupation status of colonies was controlled again after finishing the observations. Tagged colonies occupied by species other than *Gobiodon histrio* or *Gobiodon* sp. 3 were not considered (Herler and Hilgers 2005). The size of each territory was measured by marking the territory borders (indicated by the maximum home range of butterflyfishes) with buoys and GPS and approximating an ellipse by measuring maximal width and length in Google Earth, to which the coordinates had been transferred. Coral density in each territory was estimated from counts of potential food corals of *C. austriacus* within representative belt transects (10 x 2.5 m). Two replicate transect were laid parallel to each other at the sides of the territory, as pairs of *C. austriacus* tend to feed mostly along the borders of their territory (Righton 1997; Righton et al. 1998). Corals were identified to genus level, except for *Acropora*, which was identified to species level.

Tab. 1 Number of colonies in the three size classes: 1: < 250cm²; 2: 250-500cm², 3: > 500 cm² (0 unoccupied and 1, occupied corals).

	<250		250-500		>500		
	0	1	0	1	0	1	total
<i>A. selago</i>	36	26	35	62	16	58	233
<i>A. gemmifera</i>	18	10	30	11	12	7	88
<i>A. digitifera</i>	14	29	5	21	0	8	77

Behavioral field observation

Behavioral data collection started the day after plot preparation. Butterflyfishes were observed for two to four intervals of 30 minutes each before and after midday. As *Chaetodon austriacus* remained mostly inactive during low-tides (personal observation), the observation time between the plots varied accordingly. During observations, each bite taken by the butterflyfish was documented on a slate. In addition, the duration of a visit at marked colonies was documented by taking pictures with a time stamp using a head-mounted GoPro® camera at both the beginning and the end of the visit. Observation patterns were the following: 1, 2, 1, 2 before midday and 2, 1, 2, 1 after midday, with each number representing one individual fish of the pair. Individuals could be easily distinguished by differences in their body coloration patterns, allowing for repeated observations of the same specimen.

Video experiment for experimental change of feeding patterns

To estimate changes in feeding rates and behavior under strongly reduced coral availability, a video analysis of feeding on preferred food corals (*A. selago*) of caged butterflyfishes was carried out. An *in situ* caging video experiment was simultaneously conducted in the same area by Markus Dirnwoeber. This experiment was established to investigate coral growth of *A. selago* under high butterflyfish predation. Sixteen healthy corals with an average planar projected area of 470cm² and without any visible injuries such as breakages were carefully transplanted to PVC plates for buoyant weighing (Herler and Dirnwoeber 2011). To allow recovery from recent corallivory and transplantation, the corals were protected with cages for 11 days. Before the start and throughout the whole experiment all infauna was removed (gobies by shaking them out at air, a non-invasive method to avoid the application of clove

oil, which negatively influences coral growth (Boyer et al. 2009) and crabs by using small sticks). Two cages, containing 8 transplanted corals each, were each equipped with two reef-surveillance cameras that recorded all colonies in bird's eye view (Dirnwoeber et al. 2012). In each cage, 2 to 7 adult *Chaetodon austriacus* were kept and their feeding activity was recorded for a total period of 26 days. Recording times lasted from about 9am to 5pm. The videos were analyzed by counting all visible bites along with the duration of each visit within intervals of 5 minutes per hour. If not all bites of a butterflyfish could be observed directly, because it was partly feeding below a colony, the assumed number of all bites for this visit was calculated (visible bites / time visible * total visit duration). If a butterflyfish was feeding below a coral throughout the visit, the average bite rate of all fish on this day was multiplied with the visit duration to approximate the number of bites. Altogether, 344 periods of 5 minutes were analyzed for both cages.

Statistical analyses

As territorial defense was assumed to be absent in juvenile gobies due to high migration in this life cycle stage, colonies occupied by juvenile *Gobiodon* and “unoccupied” corals were combined in the group unoccupied (occupation status 0), whereas single adults and breeding pairs were pooled in the group occupied (1). Three different coral size classes were established: Size class 1: < 250; class 2: 250-500 and class 3: > 500cm² projected planar area (Tab. 1). The size class 3 sample was unbalanced (only few unoccupied corals) due to the fact that under natural conditions large coral colonies have very high occupation rates.

The Chi-squared test was used to determine differences in homogeneity of total coral abundance between the plots and the individuality in food selection between pairs of butterflyfishes, using data from tagged and untagged corals. Differences in diurnal feeding activity were tested with a Kruskal-Wallis test and Mann-Whitney tests (with Bonferroni correction of p-values). Food electivity of Ivlev (1961) was calculated for all available prey corals of *C. austriacus*. Ivlev's electivity index is calculated by: $Ei = (ri - pi)(ri + pi)^{-1}$, whereby Ei is the electivity index of a certain food type i , ri is the proportion of food type in the diet and pi is the proportion of food type i in the environment. Possible values range between +1 and -1, in which a positive value indicates preference, a negative value indicates avoidance and 0 indicates neither. To calculate predation frequency and intensity as well as the predation frequency with respect to occupation by coral gobies, only data of tagged coral colonies were used. Pairwise comparisons using the Mann-Whitney U-test were performed to find significant differences between bite rates in different size classes of corals with respect to

goby occupation. Pearson's correlation was used to define the correlation between territory size and density of preferred prey corals, as well as for the correlation between predation frequency/intensity and colony size. Additionally to the Pearson correlation, Spearman correlation was used to define the correlation between *Acropora selago* and *A. gemmifera* in terms of colony density per 100 m². Differences in bites per hour between the two cages in the video experiment were tested using the Mann-Whitney U-test. Statistics were carried out for both the field observation and the video-supported experiment using Past 2.1 (Hammer et al. 2001) and IBM SPSS Statistics 20.

Results

Diurnal feeding activity

Altogether 9870 individual observations on the feeding activity of *Chaetodon austriacus* were recorded. *C. austriacus* fed constantly throughout the day, although highest feeding rates were observed between 2 and 4pm (Fig. 1). Nevertheless, no significant differences between any of the 5 day time periods in bites per hour per individual were found. Similarly, no significant differences were found between all *C. austriacus* specimens with respect to the number of bites per visit, in visits per hour, in bites per hour or between morning (8am – 12pm) and afternoon (12pm – 18pm). The bites per hour per fish ranged between 212 and 756 with an average of 494 ± 107 bites per hour.

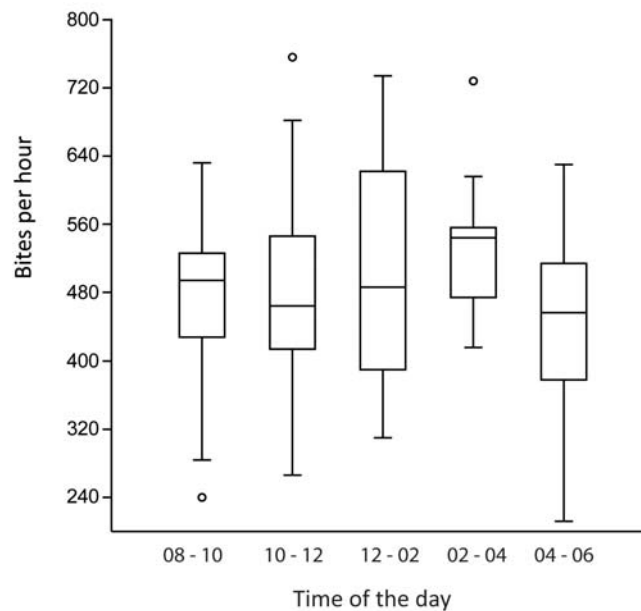


Fig. 1 Feeding rates of 20 individuals of *Chaetodon austriacus* throughout the day. Values are median (horizontal line), upper and lower quartiles (boxes), ranges excluding outliers (whiskers) and outliers (dots; > 1.5 times the box height from the box).

The territories had an average size of $166 \pm 67\text{m}^2$ and ranged between 98 and 294m^2 . Table 2 shows the coral abundance and the main feeding parameters of butterflyfishes in the 10 territories. Pairwise comparison between the territories with respect to homogeneity of the coral community was performed, whereby 8 out of 45 tests differed significantly ($0.006 < p < 0.033$, $14.8 < \text{Chi}^2 < 25.4$).

Tab. 2 Description of number of colonies per plot and the bites per visit as well as the visits per hour, bites per h and bites per h per colony for 4 different scleractinian genera (Sty: *Stylophora*; Poc: *Pocillopora*; Por: *Porites*; Acro: unidentified *Acropora* corals) and 10 species of *Acropora* (sel: *A. selago*; gem: *A. gemmifera*; val: *A. valida*; dig: *A. digitifera*; eur: *A. eurytoma*; sec: *A. secale*; acu: *A. acuminata*; sam: *A. samoensis*; var: *A. variolosa*) and non-identified corals (ind: indetermined). Note that bites per hour, visits per hour and bites per hour per colony refer to one individual of *C. austriacus*. To obtain information about the total predation on the corals within a territory, these values must be doubled. Values are means $\pm$ SE and, in parentheses, ranges.

coral	colonies/100 m ²		Bites/visit		Visits/h		Bites/h		Bites/h/colony	
Sty	192.3 $\pm$ 14.8	(167-228)	3.2 $\pm$ 0.1	(1-43)	53.5 $\pm$ 0.3	(8-178)	171.1 $\pm$ 14.2	(14-686)	6.3 $\pm$ 0.2	(0-11)
Poc	84.0 $\pm$ 2.2	(47-125)	3.7 $\pm$ 0.1	(1-759)	31.6 $\pm$ 0.1	(2-32)	125.3 $\pm$ 8.7	(4-362)	7.2 $\pm$ 0.4	(0-29)
sel	76.0 $\pm$ 4.9	(47-100)	2 $\pm$ 0.2	(1-26)	48 $\pm$ 0.4	(10-120)	98.2 $\pm$ 5.6	(12-256)	5.4 $\pm$ 0.3	(0-18)
gem	71.8 $\pm$ 7.7	(27-115)	2 $\pm$ 0.1	(1-15)	20.5 $\pm$ 0.6	(0-78)	41 $\pm$ 0.1	(0-160)	2.6 $\pm$ 0.2	(0-11)
Por	56.5 $\pm$ 8.1	(37-138)	2.8 $\pm$ 0.1	(1-38)	12 $\pm$ 0.7	(0-68)	37.3 $\pm$ 3	(0-140)	4.1 $\pm$ 0.1	(0-8)
val	40.3 $\pm$ 5.6	(15-70)	1.7 $\pm$ 0.1	(1-6)	4.7 $\pm$ 2.8	(0-4)	7.7 $\pm$ 1	(0-44)	3.9 $\pm$ 0.2	(0-12)
acro	22.3 $\pm$ 4.8	(0-53)	1.9 $\pm$ 0.1	(1-9)	6.1 $\pm$ 0.5	(0-24)	8.2 $\pm$ 0.9	(0-40)	2.4 $\pm$ 0.2	(0-10)
ind	21.0 $\pm$ 3.8	(0-50)	2.1 $\pm$ 0.1	(1-18)	7 $\pm$ 0.3	(0-32)	7.4 $\pm$ 0.7	(0-82)	2.1 $\pm$ 0.2	(0-7)
dig	17.5 $\pm$ 2.2	(5-30)	1.7 $\pm$ 0.1	(1-15)	4 $\pm$ 0.4	(0-18)	7.1 $\pm$ 0.9	(0-42)	3 $\pm$ 0.3	(0-18)
eur	14.3 $\pm$ 1.8	(0-25)	2.4 $\pm$ 0.2	(1-22)	3.5 $\pm$ 0	(0-28)	8 $\pm$ 1.8	(0-88)	2.6 $\pm$ 0.3	(0-14)
sec	13.5 $\pm$ 4.1	(0-50)	2.2 $\pm$ 0.2	(1-7)	1.2 $\pm$ 0.9	(0-8)	3.6 $\pm$ 0.7	(0-32)	1.8 $\pm$ 0.3	(0-18)
acu	11.0 $\pm$ 2.1	(0-25)	1.6 $\pm$ 0.1	(1-8)	2.8 $\pm$ 0.4	(0-18)	6 $\pm$ 1	(0-46)	0.5 $\pm$ 0.1	(0-6)
sam	10.3 $\pm$ 1.9	(0-20)	1.9 $\pm$ 0.1	(1-11)	3 $\pm$ 1.9	(0-16)	6.3 $\pm$ 0.8	(0-38)	1.7 $\pm$ 0.2	(0-10)
var	2.8 $\pm$ 1.2	(0-10)	1.8 $\pm$ 0.2	(1-6)	0.3 $\pm$ 3.3	(0-4)	1.2 $\pm$ 0.4	(0-28)	3.8 $\pm$ 0.2	(0-12)

The highest density as well as the highest number of visits (53.5 ± 0.3) and bites (171.1 ± 14.2) per hour were found in corals of the genus *Stylophora*. Corals of the genus *Pocillopora* received the highest bites per visit (3.7 ± 0.1) and the highest bites per hour per colony (7.2 ± 0.4).

Interestingly, territory size in *Chaetodon austriacus* was partially explained by the abundance of *Acropora selago* and *A. gemmifera*. A significant ($p < 0.05$) correlation of 77% between territory size and abundance of *A. selago* as well as 71% ($p < 0.05$) for *A. gemmifera* was detected. When coral density per 100m² of all ten plots is plotted against territory size, abundances of *A. selago* and *A. gemmifera* colonies decreased significantly with increasing territory size (Fig. 2). A correlation between the abundance of *A. selago* and *A. gemmifera* revealed a significant positive correlation ($p < 0.05$) between the two coral species. This indicates that both corals do co-occur. In contrast, the density of *Pocillopora* tended to increase with increasing territory size, whereas territory size was unaffected by the density of

Stylophora (Fig. 2); no significant relationship was found for these coral genera or other food corals of *C. austriacus*.

Interestingly, the mean number of bites per hour decreased significantly ($p < 0.01$) with increasing territory size, as shown in figure 3.

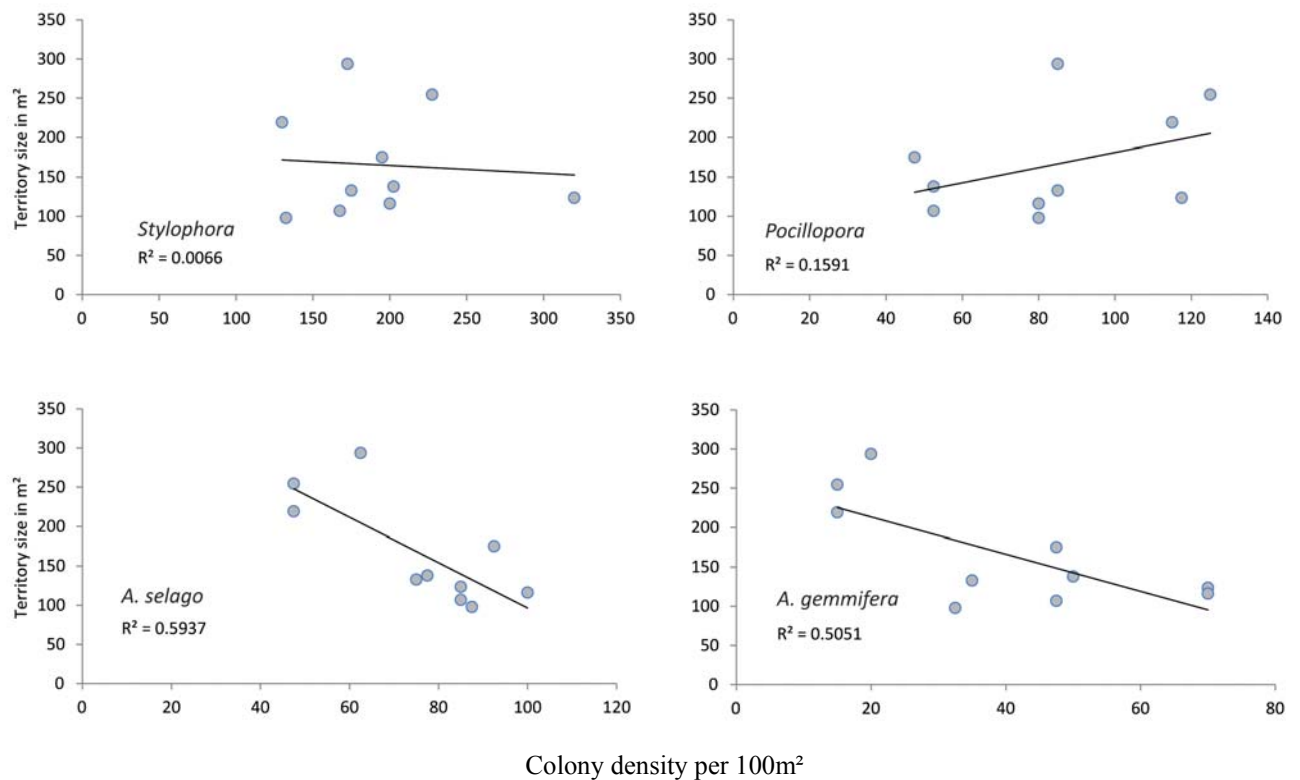


Fig. 2 Colony density per 100 m² of *Stylophora*, *Pocillopora*, *A. selago* and *A. gemmifera* related to territory size in m² of the ten plots.

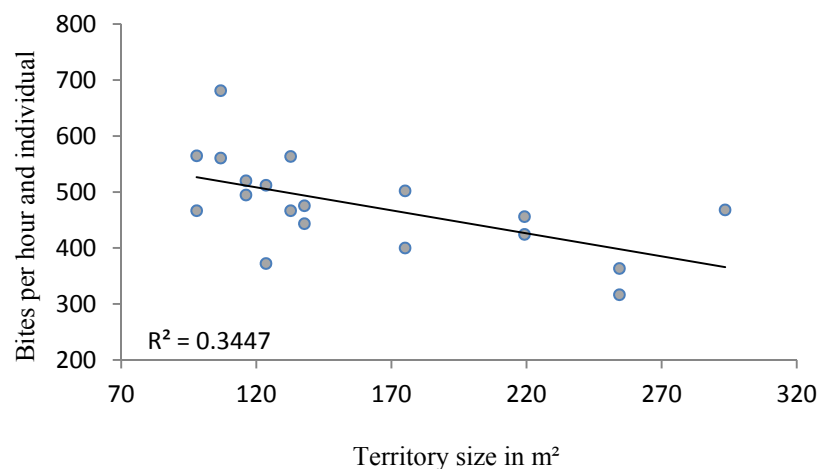


Fig. 3 Mean bites per hour on all corals related to territory size in m². Values are average bites per hour and individual of 19 individuals plotted against the size of 10 territories of *Chaetodon austriacus*.

Individuality in the food selection of butterflyfishes

In only two out of the 10 territories, the pair of butterflyfish exhibited significantly different food preferences ($13.5 < \chi^2 < 14.4$; $0.018 < p < 0.024$). In one of the two territories, one individual fed twice as much on *Stylophora* than its partner (30.5 vs. 15%), while the partner fed twice as much on *Acropora selago* (30.3 vs. 14%) and *A. gemmifera* (11 vs. 6%). In the second territory, one individual preferred *Pocillopora*, it fed five times more on this coral (18 vs. 3%), whereas the other one showed a higher preference for *Acropora* corals (50 vs. 41%) and *Porites* (10 vs. 5%). Some kind of food partitioning could be seen in the other territories, but these pairs did not reveal significant differences ($0.17 < p < 0.98$).

Food preferences

Stylophora represented the most common (30.3% of all coral taxa) food source in *Chaetodon austriacus* territories (Fig. 4a), followed by *Pocillopora* (14%) and *Acropora selago* (12%). Those three taxa are also preferred according to the Ivlev's electivity index (Fig. 4b). *Acropora* represents 34.6 % (Fig. 4c) of the total consumption, in which *A. selago* accounts for 55% and *A. gemmifera* for 27%. Other *Acropora* species, such as *A. valida*, *A. variolosa*, *A. secale* or *A. eurystoma* seemed to be avoided, as they were far less consumed than they were available (Fig. 4b). The average time for re-visiting a coral colony was calculated and revealed that in an average territory, a certain colony of *A. selago* was visited every 2 h 27 min followed by *Pocillopora* with 4 h and 37 min. Considering all feeding parameters (Table 2) it can be seen that *Stylophora*, *Pocillopora* and *A. selago* clearly represent the main diet of *C. austriacus*. Only in three territories the food consumption (relative proportional frequencies of corals used) of *C. austriacus* specimens differed significantly from the available food spectrum ($13.5 < \chi^2 < 22.5$, $0.001 < p < 0.018$).

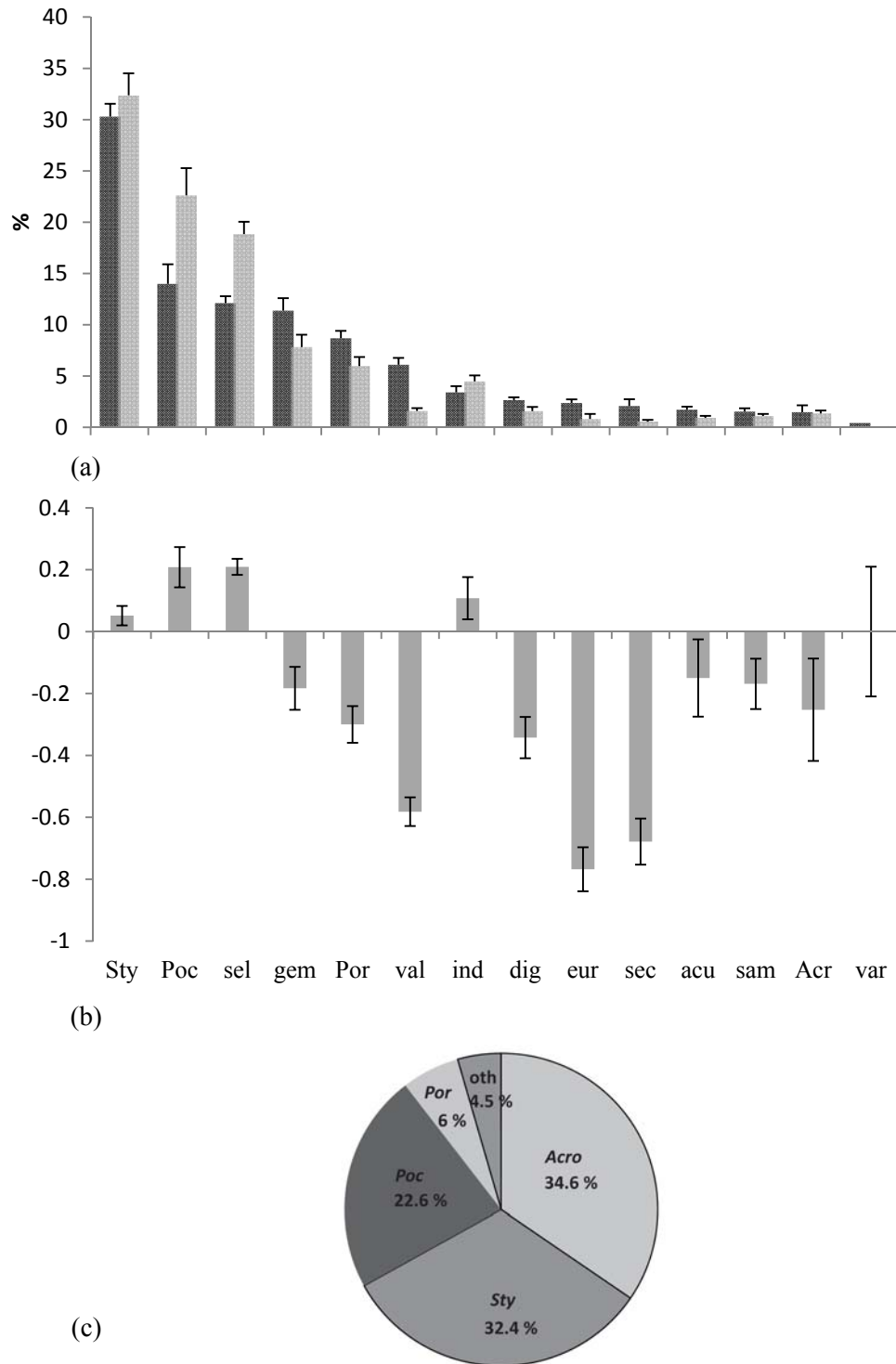


Fig. 4 (a) Frequency (relative percentages) of corals available in the territories (■) and of bites on corals selected (▒) by *Chaetodon austriacus* in the Gulf of Aqaba, northern Red Sea. Values are mean $\pm$ SE of proportion of total corals available and consumed. (b) Ivlev's electivity index for consumed corals. Values are mean $\pm$ SE. (c) Relative proportions of coral taxa consumed by *C. austriacus*. Acro: sum of all identified and unidentified *Acropora* corals. For other coral abbreviations see Table 2.

Predation frequency and intensity

Predation frequency was estimated by calculating the bites per hour of tagged colonies. A highly significant correlation of 41% ($p < 0.001$) was found between colony size and bites per hour received in *Acropora selago*, whereas in *A. gemmifera* no significant correlation was found. Due to extremely low feeding rates on *A. digitifera*, no size-related correlations were detectable.

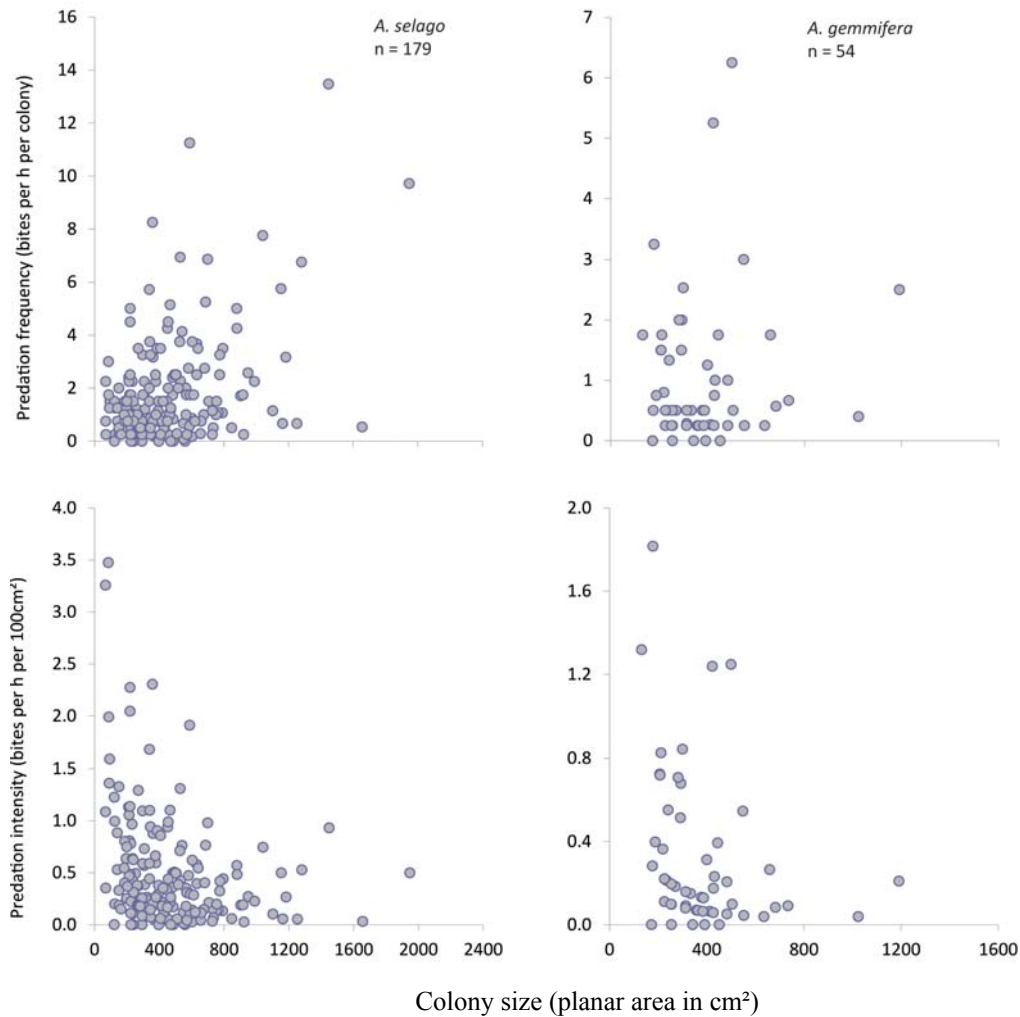


Fig. 5 Predation frequency (bites per hour per colony) and predation intensity (bites per hour per 100cm² planar projected colony size). Note the different scales in y- and x-axes between graphs.

A highly significant negative correlation ($p < 0.001$) was found between colony size and predation intensity in *Acropora selago* and in *A. gemmifera* ($p < 0.05$). As can be seen in figure 5, small colonies had higher predation intensities than larger colonies. The highest predation intensity with 3.5 bites per hour per 100cm² was observed on an *A. selago* colony with only 87cm² planar area, whereas the largest colony with 1947cm² received only 0.5 bites

per hour per 100cm². Similarly, in *A. gemmifera* one small colony with 179cm² received 1.8 bites per hour, whereas the largest colony with 1192cm² received 0.2 bites per hour per 100cm². Average predation intensity of consumed colonies in *A. selago* was 0.86 ± 0.1 in size class 1 (< 250cm²), 0.45 ± 0.05 in size class 2 (250-500cm²) and 0.35 ± 0.04 (SE) in size class 3 (> 500cm²). Average predation intensity in *A. gemmifera* was 0.68 ± 0.1 in size class 1, 0.27 ± 0.05 in size class 2 and 0.27 ± 0.01 in size class 3. The Ivlev electivity index calculated for the tagged corals (*A. selago*, *A. gemmifera*, *A. digitifera*) with respect to colony size showed that colonies in size class 1 and 2 were generally avoided (-0.18 and -0.13, respectively), while corals in size class 3 were generally favored (+0.21).

Predation frequency with respect to occupation by coral gobies

A difference in the bite rate between unoccupied *Acropora selago* and colonies occupied by gobies was found in size class 2 (Fig. 6). Occupied corals in this size class received significantly less bites ($p < 0.05$) and visits ($p < 0.05$) per h than any other size class regardless of occupation state. Also the visit duration per hour differed significantly between occupied and unoccupied corals in size class 2 ($p < 0.05$). Nevertheless, the lower number of visits per hour in occupied colonies of size class 2 was crucial for the lower predation rate on these colonies. In *A. gemmifera* and *A. digitifera* combined, the bites per hour were also less in unoccupied corals of size class 2, but this difference was not statistically significant. In all three coral species, occupied colonies in size class 2 had a lower visit duration. Visit duration increased with colony size. This indicates that regardless of the occupation state of colonies, *Chaetodon austriacus* spent more time feeding on larger colonies than on smaller colonies. In *A. selago*, 41% of corals in size class 3 received more than 2 bites per h, in size class 2, 20% and in class 1 only 15%. In average, corals in size class 3 were visited 1.06 times per h, whereas corals in size class 2 and 1 received only half of the visits per h with values of 0.55 and 0.56, respectively.

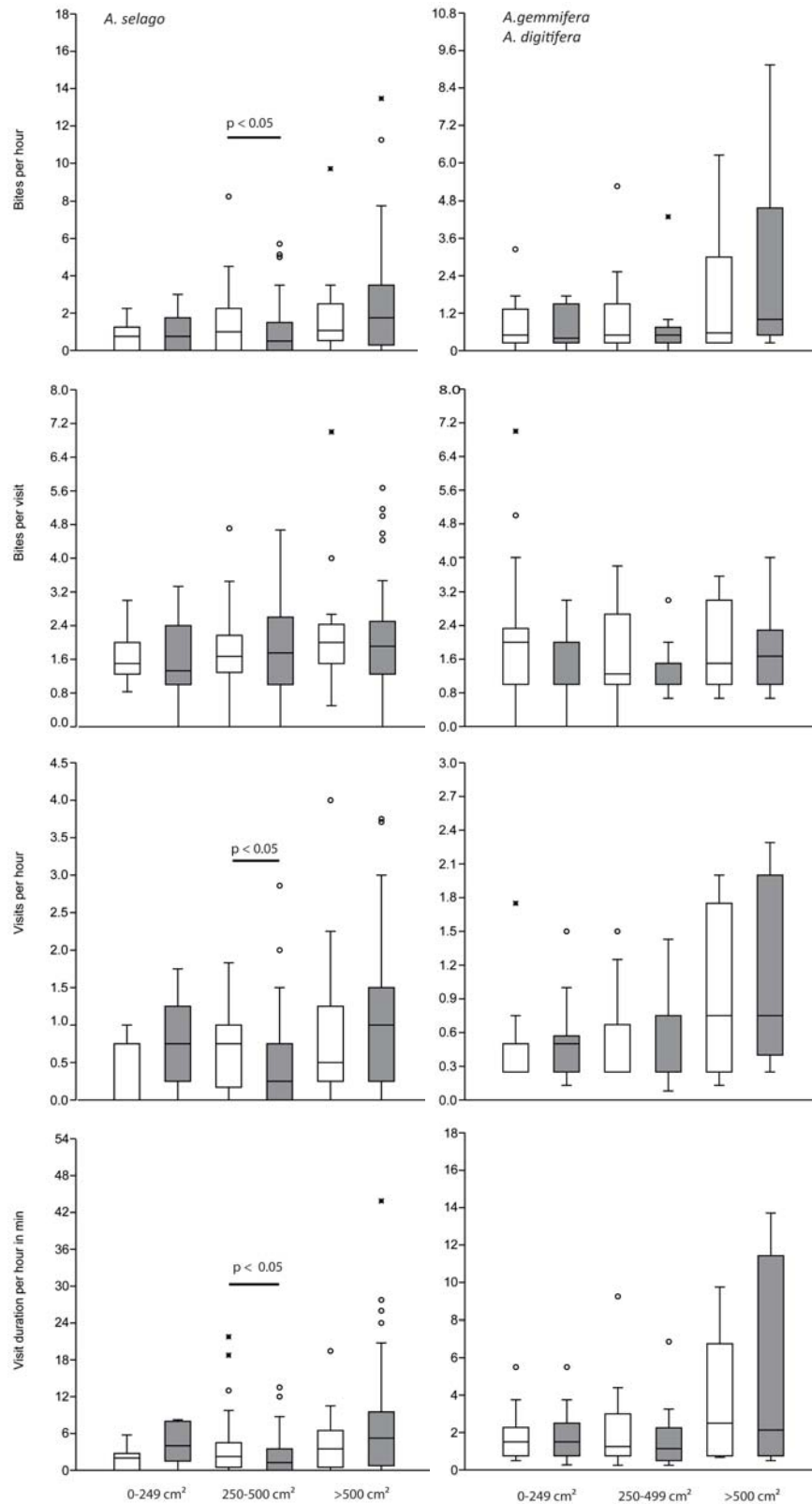


Fig. 6 Bites and visits per h and visit duration per h in minutes of all *Chaetodon austriacus* on 87 unoccupied (□) and 146 occupied (■) tagged colonies of *A. selago* (occupied by *G. sp.3*) and of 79 unoccupied and 86 occupied tagged colonies of *A. gemmifera* and *A. digitifera* (occupied by *G. histrio*) across three size classes (planar projected area). Boxplots show median (horizontal line), upper and lower quartiles (boxes), ranges excluding outliers (whiskers) and outliers (dots and stars). Horizontal lines represent significant differences (Mann Whitney-U test) between plots with significance levels indicated. Note the different scales in the y-axes between left and right column.

On tagged colonies the maximum bite rate was 13.5 bites per hour on *A. selago*, 6.3 on *A. gemmifera* and 9.1 on *A. digitifera*, suggesting a maximum number of annual bites per fish on the given species of 58,984 (*A. selago*), 29,565 (*A. gemmifera*) and 40,045 (*A. digitifera*).

Experimental change of feeding patterns

The largest differences in feeding rates between the two cages were in the first week after the experiment had started (Fig. 7). In the first 2 days, the number of bites was very low in both cages, but especially in cage 2. After adding new fish to the cage, the number of bites per hour increased. In cage 1, the highest feeding rate per hour per fish occurred within the third week of the experiment with an average of 369 bites per hour per fish and a maximum of 508. In cage 2, the highest feeding rate could be detected during the second week with a mean of 319 bites per hour per fish. The Mann-Whitney U-test revealed that the feeding motivation varied significantly ($p < 0.01$) between the two cages.

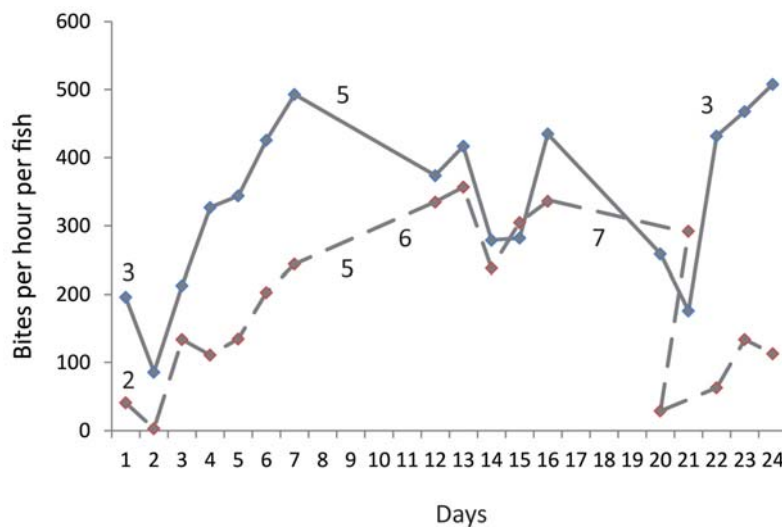


Fig. 7 Bites per hour per individual of *Chaetodon austriacus* in cage 1 (continuous line) and 2 (dotted line) throughout the duration of the experiment. Values above or below the lines indicate the number of fish present in the cage at the given period of time.

Discussion

Feeding patterns and individuality in food selection of butterflyfish

In the northern Red Sea, the corallivorous butterflyfish *Chaetodon austriacus* showed variation in feeding activity throughout the day. The highest feeding rates were observed in the early afternoon. This diurnal variation in the feeding rates was most likely associated with the varying nutritive content of prey corals. Several studies showed that the quality of nutrients of algae and corals is highest at midday (Crossland et al. 1980; Crossland 1987; Zoufal and Taborsky 1991). For example, coral mucus leaching of *Acropora acuminata* and *A. variabilis* is higher during early to mid-afternoon (2 to 4pm) and it has also higher carbon content at this time of the day (Crossland et al. 1980; 1987). Exactly at this time *C. austriacus* showed higher feeding rates than at any other time of the day. Although no mucus was found in stomach contents of *C. austriacus*, other butterflyfishes such as the polyp-feeding sibling species *C. trifascialis* also fed on coral mucus (Irons 1989). Mucus might also be ingested partially by *C. austriacus* while feeding on polyps. *C. trifascialis* exhibited the same diurnal variations as observed for *C. austriacus*, with highest feeding rates in the early afternoon at Hawaii (Irons 1989) and the Great Barrier Reef (Gregson et al. 2008).

Several explanations for the food specialization in butterflyfishes have been discussed in the past years. *Pocillopora meandrina* was found to have a higher caloric density than *Porites* in Hawaii (Tricas 1989a). The mucus of *Acropora* was also found to have higher carbon content in the Caribbean and Indo-Pacific (Coles and Strathmann 1973; Benson and Muscatine 1974; Benson et al. 1978). These findings could explain the high percentage of *Acropora* (34.6%) and *Pocillopora* (22.6%) in the food spectrum of *Chaetodon austriacus*. As mentioned before, *A. selago* accounted for 55% of total consumption within *Acropora*. *A. hyacinthus* is the most favored acroporid species in the Great Barrier Reef for several butterflyfishes (Cole et al. 2011). Interestingly, both corals evert their polyps also during daytime. Supposedly, more coral tissue can be removed by a single bite and therefore energy uptake can be maximized. However, the nutritive content of *Pocillopora verrucosa* and *Stylophora pistillata* is lower in the Red Sea (Harland et al. 1993). It was therefore hypothesized that the lower nutrition level of the main prey corals (*Stylophora* and *Pocillopora*) of *C. austriacus* might be compensated by higher feeding rates (Alwany et al. 2003). At the Great Barrier Reef, obligate corallivorous butterflyfishes had in average 620 bites per hour (Gregson et al. 2008). In Hawaii, the feeding rate of *C. multicinctus* ranged between 575 and 700 bites per hour (Hourigan 1987; Tricas 1989b; Gochfeld 2004). In this

study, the average bite rate was 494 bites per hour, which is lower than the average estimated for obligate corallivorous butterflyfishes at the Great Barrier Reef and Hawaii. Therefore, the lower nutritive levels of corals in the Red Sea are compensated by higher predation on high quality prey corals such as *A. selago* rather than by higher general feeding rates.

In addition to the nutritive content of prey corals, the prey specialization of *Chaetodon austriacus* might have other reasons as well, such as the size of contact surface that is available for the fish (Tricas 1989b), the variation in size and number of nematocysts of the coral (Tricas 1989a; Gochfeld 2004) or other defense mechanisms such as mutualistic relationships between corals and their inhabitants (Weber and Woodhead 1970; Glynn 1976; Lassig 1981; Niedermueller et al. 2009; Dirnwoeber and Herler 2012). Another supplemental explanation for prey specialization could be interspecific competition among butterflyfishes as they can reach high densities in reefs (Pratchett 2005). Apart from *C. austriacus* two other obligate corallivorous butterflyfishes, *C. melannotus* (Schneider 1801) and *C. trifascialis* (Reese 1981), occur in the Gulf of Aqaba (Froese and Pauly 2008). In addition to scleractinian corals, *C. melannotus* also feeds on octocorallia (Bouchon-Navaro 1986; Alino et al. 1992), whereas *C. trifascialis* is specialized on *Acropora* (*A. valida*, *A. cytherea*) and *Pocillopora* (Harmelin-Vivien 1989; Irons 1989; Sano 1989; Alwany et al. 2003; Pratchett 2005; Samways 2005). In contrast, *C. austriacus* is more generalistic in prey selection and showed also high predation on *Stylophora* in this study. Thus, it seems that there is a small though measureable partitioning of prey corals between the three species. In contrast, on the Great Barrier Reef many different species are occurring within the same area despite of dietary overlap of up to 73% (Pratchett 2005). Coral feeding butterflyfish in Hawaii had also a dietary overlap of > 70% (Cox 1994). This might be explained either by the fact that coral prey is not limited within these areas or temporary specialization in butterflyfishes is given (Anderson et al. 2012). Similarly, spatial specialization could also be an explanation. This study was conducted on the reef flat where *C. austriacus* was common and *C. trifascialis* was infrequent, while the latter is common at the reef edge (personal observation). In addition to the interspecific specialization the present study showed a partitioning of food sources between pairs of *C. austriacus* and even between the individuals. Although only two pairs in this study differed significantly in prey selection, all pairs showed variation in the proportion of consumed prey corals. Dominant partners seemed to exclude their partners from favored prey corals. This observation is also important when considering total predation rate on coral colony level. However, *Acropora* and *Pocillopora* have been reported to be the main food source for many different species of Chaetodontidae and it seems that this food preference

remains relatively stable across large geographical distances (Irons 1989; Alwany et al. 2003; Pratchett 2005; Pratchett and Berumen 2008).

Several studies proposed the maximum area defendable to be the main determinant of territory size (Sutton 1985). In this study, a clear relationship between territory size and the abundance of potential prey corals of *Acropora selago* and *A. gemmifera* was found, whereas there was no such significant correlation with other main food corals. Considering the fact that *A. gemmifera* was rather avoided and a correlation showed that both *A. gemmifera* and *A. selago* co-occur, *A. selago* should be considered as the main territory-size determinant. Furthermore, the general feeding rates decreased significantly with increasing territory size. Fricke (1986) suggested that excessive aggression against territory neighbors may be diminished by advertising their presence to the neighbors. According to this theory, *C. austriacus* was observed to circuit the territory by feeding along the borders of the territory, which might be interpreted as passive territory patrolling over the day (Fricke 1986). The fish spent a great time on foraging for prey corals during patrolling their territory. If territory size is very large because of low density of acroporid prey corals, they have to swim longer distances to reach the next coral of interest. Furthermore less time can be spent on feeding and less time can be spent on searching exclusively for preferred prey corals. This in turn would lead to a higher proportion of other food corals within the food spectrum of *C. austriacus*, such as *Stylophora*, which is not preferred but is consumed because of its ubiquitous presence on the reef flat. Summing up, the density of *A. selago* obviously belongs to the main determinants of territory size in *C. austriacus*, where a high density of *A. selago* colonies leads to smaller territories, higher feeding rates and higher proportion of this coral species in the food spectrum.

Predation frequency and intensity

Previous studies estimated the amount of coral tissue removed to be evenly distributed across a reef (Harmelin-Vivien and Bouchon-Navaro 1981; Harmelin-Vivien and Bouchon-Navaro 1983). However, as described above, *Chaetodon austriacus* preferentially targets certain coral species and therefore, actual predation rates for such corals are much higher than assumed. Although our data showed that larger coral colonies were preferred over smaller colonies, the distribution of bites between the size classes of tagged colonies differed slightly from findings of Cole and Pratchett (2011). In their study less than 1% of all bites observed were directed towards colonies smaller than 200cm² planar projected area. In the present study 9% of bites taken during an average interval on all tagged colonies were directed towards small colonies

(< 200cm²). Hence, corals below 200cm² planar projected area were consumed more often than in previous studies. Coral colony size was the most important factor for predation as indicated by the Ivlev's electivity index. Despite of higher predation intensity and higher predation frequency than previously thought, corals in size class 1 and 2 were generally avoided, while corals in size class 3 were favored. Coral colony size affected also the amount of bites taken per visit. In *A. selago* for example, the average number of bites per visit in size class 3 was 21% higher than in size class 1 and 9% higher than in size class 2.

The bites per visit conducted by *Chaetodon austriacus* varied between coral genera and ranged between 1.6 and 3.7 bites per visit. This might be explained by different strategies of predation response in corals. It has been demonstrated that butterflyfishes select prey corals by chemical and visual cues (Alino et al. 1992). In accordance with optimal foraging strategies (Schoener 1971), butterflyfishes preferentially target colonies with fully extended polyps (Gochfeld 2004). Coral colonies can thereby avoid multiple grazing by retraction of polyps. Polyp retraction patterns differ between the coral genera *Acropora*, *Pocillopora*, *Stylophora* and *Porites* (Horridge 1957). In *Acropora*, the first stimulus already results in several signal waves (4 to 6) leading to polyp retraction and spreading out over the colony. One stimulus is sufficient to cause simultaneous retraction of many hundred polyps. Following stimuli lead to similar shocks and a coral with 50cm² of diameter would have all polyps withdrawn after the third to fourth stimulus. As the fish also needs some time focusing on single polyps prior to ingestion, on small colonies less bites can be made before complete polyp retraction occurred than on larger colonies. In contrast, the retraction area in *Pocillopora* and *Stylophora* does not increase with subsequent stimuli and polyp retraction only occurs within 2 to 3cm² of the stimulus. Consequently, optimum foraging on such colonies allows taking multiple bites as a function of size rather than time. In accordance with this, the average number of bites per visit on *Stylophora* colonies was more than 1 bite higher than in *A. selago* (3.2 vs. 2) and almost 2 bites higher in *Pocillopora* (3.7 vs. 2). Although optimum foraging strategies in response to polyp withdrawal explained why larger colonies received more bites per visit and were generally preferred over smaller ones, there were also considerable exceptions with up to 26 bites per visit in *A. selago*, indicating that polyp withdrawal patterns do not solely explain the number of bites per visit.

Predation frequency with respect to occupation by coral gobies

Coral-dwelling gobies of the genus *Gobiodon* prefer larger colonies as 79% of all large tagged colonies were occupied. One of the main research questions was, whether predation rates of inhabited colonies differed from uninhabited corals. It was observed that both *Gobiodon histrio* and *G. sp.3* decreased predation rates among host colonies and that this resource defense is colony-size dependent. Although predation rates generally increased with colony size, observed predation rates on occupied colonies in size class 2 were even lower than predation rates on smaller-sized colonies, which highlights that occupied colonies with a size of 250-500 cm² were less attractive for *Chaetodon austriacus* than all other colonies, while colonies over 500cm² were most attractive regardless of occupation by gobies. Therefore, the deterrent effect of *Gobiodon* found in lab experiments (Dirnwoeber and Herler 2012), was also present in the field under natural conditions. However, this effect was lost with increasing colony size, as it is obviously difficult for *Gobiodon* to defend very large colonies against a highly motile predator. In large colonies the possibility for even a goby breeding pair to be in the same area where butterflyfish predation is taking place is relatively low and the deterrent effect of aggression and/or goby skin toxins might only be given within a small effective area. Predation rates on occupied colonies in size class 1 were generally lower than those on unoccupied colonies, however, this difference was not statistically significant. This lack of significance might be explained by the fact that only few colonies in that size class were inhabited by breeding pairs and were mainly occupied by single adults.

It has been demonstrated that single adults, settling in small corals have higher migration rates compared to both juveniles and breeding pairs (Wall and Herler 2008). Hence, single adults of *Gobiodon* might not invest into resource defense and rather use small colonies as intermediate stops in search for larger breeding colonies. Moreover, *C. austriacus* preferred feeding on the stalk of colonies rather than on the upper surface area (personal observation). Interestingly, *C. austriacus* showed this behavior mainly on occupied colonies. It can be assumed that *C. austriacus* individually recognizes the colonies in its territory and is aware of occupation states, which indicates considerable cognitive capacities. In the video experiment, butterflyfishes fed first on the stalk and after a few days started feeding mostly on the top of the colonies. Future studies need to assess out whether this behavior is an artefact of experimental conditions (feeding activity directed towards remaining polyps after already long continuous feeding on these colonies), an opportunistic behavior related to preferences

for stalk tissue or indeed the consequence of cognitive capacities in recognizing that colonies were unoccupied.

Experimental change of feeding patterns

The feeding rates of fish varied greatly in the video experiment both with time and between the two experimental cages. This might be due to the artificial environment, the new situation and/or that territorial individuals were kept together. In cage 2, it seemed that the fish did not adapt to the new environment, as feeding rates per fish were about half (in the most active period) than that in the field. The video experiment provided a possibility to see how *Chaetodon austriacus* would adjust its feeding rates if food coral availability was greatly reduced. If the bites per hour and individual are compared to the natural feeding rates, the fish in the cages had about a third lower feeding rate than in the field (336 vs. 494 bites per hour), even though only 8 corals were offered. In a previous lab experiment, bites per hour and individual were only one tenth of natural bite rates (Dirnwoeber and Herler 2012). In this lab experiment only 2 colonies were offered (one goby-occupied, one unoccupied). Therefore it seems that *C. austriacus* significantly reduces its feeding rate when coral availability is very low, to prevent over-grazing on colony level, but when a higher number of colonies is offered, predation frequency on individual colonies is strongly increased and experimental overall bite rate may almost match those in the field. Although it has to be mentioned that the duration of the lab experiment was short (24 to 48h for each fish), the fish could easily reduce their feeding rate since they were not starving for a long time. Such a low feeding motivation could also be seen in the field experiment during the first week. Due to the fact that after a short period of time the fish in the field experiment fed at almost normal rates indicates that under natural conditions it is very unlikely that feeding rates may be reduced at lower coral abundance. Therefore, massive over-grazing could occur if coral abundance is strongly reduced and territory size could not be extended due to intensified aggressive behavior of neighbor territory owners.

Conclusion

In future climate scenarios, corals will suffer higher mortality rates due to frequent coral bleaching events. Therefore, abundance of older and larger *Acropora* colonies is expected to decrease. Consequently, average colony size will become lower (McClanahan et al. 2008) and predation pressure as well as predation intensity on medium and small-sized colonies might

further increase and the occupation of colonies with gobies will very likely positively affect colony fitness, while unoccupied colonies will suffer from considerable higher predation rates than observed today.

Zusammenfassung

In Riffökosystemen stellt die Korallivorie das Äquivalent zur terrestrischen Herbivorie dar und ist somit ein wichtiger Bestandteil in einem Korallenriff. Dennoch wurde die Beweidung von Korallen durch Falterfische lange Zeit als ökologisch unbedeutend angesehen. In dieser Studie wurden deshalb die Nahrungspräferenzen von *Chaetodon austriacus*, einem obligat korallivoren Falterfisch, in einem Saumriff in der Nähe von Dahab, Golf von Aqaba, im nördlichen Roten Meer untersucht. Diese Falterfischart lebt in monogamen Pärchen und verteidigt Territorien gegenüber anderen Individuen seiner Art. Die wichtigste Nahrung sind Korallen der Gattungen *Acropora*, *Stylophora* und *Pocillopora*, wobei nur eine Korallenart innerhalb von *Acropora*, nämlich *Acropora selago* und die Gattung *Pocillopora* wirklich präferiert wurden. *Stylophora* wurde hingegen nur entsprechend ihrer Verfügbarkeit gefressen. Es wurde auch ein signifikanter Zusammenhang zwischen Dichte von *Acropora selago* und der Territoriengröße von *Chaetodon austriacus* gefunden. Eine hohe Dichte an *Acropora selago* führte dabei einerseits zu einem kleineren Territorium von *Chaetodon austriacus* und andererseits auch zu einer höheren allgemeinen Fressrate der Falterfische. Diese Korallenart scheint somit eine qualitativ sehr hochwertige Futterkoralle zu sein.

Um herauszufinden wie stark einzelne Futterkorallen wirklich beweidet werden, wurden Kolonien von *Acropora selago*, *A. gemmifera* und *A. digitifera* markiert und in Freilandbeobachtungen die Anzahl und die Bisse pro Stunde und Falterfisch sowie die Besuchszeit bestimmt. Dabei konnte herausgefunden werden, dass die Fraßrate mit der Größe der Korallenkolonie zunahm, während die Intensität der Prädation (flächenbezogene Fraßrate) mit der Koloniegöße abnahm. Es zeigte sich ebenfalls, dass größere Kolonien generell bevorzugt wurden. Um festzustellen ob mutualistische Korallenbewohner wie Grundeln der Gattung *Gobiodon* in der Lage sind ihre Wirtskorallen gegen Falterfische zu verteidigen, wurde in den markierten Korallen auch der Besiedelungszustand bestimmt. Es zeigte sich dass in bewohnten Kolonien mittlerer Größe (250 bis 500 cm² Oberfläche), weniger Bisse und Besuche pro Stunde und auch kürzere Besuchszeiten stattfanden, als an unbewohnten Kolonien. Dieser Effekt der Ressourcenverteidigung von *Gobiodon* wird zukünftig für Riffe

von großer Bedeutung sein. Aufgrund der ständig voranschreitenden Erderwärmung werden zukünftige Korallengemeinschaften vermehrt aus kleinen bis mittelgroßen Korallen bestehen, da die Häufigkeit von Korallenbleiche zunehmen wird. In diesen stark gestressten Riffen wird eine Besiedelung von *Gobiodon* für die Nahrungskorallen von *Chaetodon austriacus* sehr wichtig werden, da die Prädation auf die nun von *Chaetodon austriacus* stärker beweideten mittelgroßen Kolonien auf unbesiedelte Kolonien gelenkt werden kann.

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