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Spatial distribution of the upside-down jellyfish *Cassiopea* sp. within fringing coral reef environments of the Northern Red Sea – implications for its life cycle

Wolfgang Niggl[1*] and Christian Wild[1]

[1]Coral Reef Ecology Group (CORE), GeoBio-Center & Department of Earth and Environmental Science, Ludwig-Maximilians Universität, Richard-Wagner-Str. 10, 80333 München, Germany

e-mail: w.niggl@lrz.uni-muenchen.de

Phone: +49-89-21806633

Fax: +49-89-2180-6601

Abstract. The zooxanthellate mangrove jellyfish *Cassiopea* sp. represents a prominent invasive species and a potential bioindicator for nutrient monitoring in coral reefs. However, information about its spatial distribution in combination with abundance, habitat specificity and life cycle elements is barely available. This study therefore presents the results of field surveys conducted within four different benthic habitat types (coral reef, seagrass meadow, reef-sand transition and sand flat) in the Northern Red Sea. *Cassiopea* sp. exhibited a highly patchy distribution within the entire study area with mean abundance of 1.6 ± 0.3 animals m^{-2} and benthic coverage of 3.2 %. Within coral reef habitats maximum abundance of up to 31 animals m^{-2} and benthic coverage of up to 20 % were detected. Additionally, this study revealed that 65 % of all observed *Cassiopea* specimens were associated with the commensalistic crustacean mysid *Idiomysis tsurnamali*. *Cassiopea* abundance and size as well as association patterns with mysids differed between most of the surveyed habitats. In summary, the findings of the present study (i) characterize *Cassiopea* as one the key organisms in investigated benthic habitats, (ii) indicate active habitat selection by the jellyfish and (iii) may hint to an unexplored life cycle of *Cassiopea* with central role of seagrass meadows providing cues for larval settlement and metamorphosis in the absence of mangroves.

Keywords: Cassiopea, abundance, coral reef, benthic habitat, Idiomysis tsurnamali, life cycle

Introduction

Cassiopea sp., commonly referred to as mangrove or upside-down jellyfish, represents a study organism within several scientific disciplines. Interorganismic interaction - typically an ecological topic- such as the jellyfish’s symbiotic relationship with dinoflagellates or the commensalistic relationship with the crustacean mysid *Idiomysis tsunrnamali* (Bacescu 1973), has been addressed by marine scientists from various fields (e. g. Bacescu 1973; Hofmann and Kremer 1981; Thornhill et al. 2006). The lifecycle of the scyphozoan *Cassiopea* is classically metagenetic and therefore alters between a medusoid and polypal stage, with an intermediate larval stage (e. g. Bigelow 1900; Gohar & Eisawy

1960b; Smith 1936). Many studies have focused on factors influencing the development of *Cassiopea*, dealing with endogenous (Thieme and Hofmann 2003a; Thieme and Hofmann 2003b) or exogenous (e. g. Bischoff et al. 1991; Curtis and Cowden 1971; Fleck and Fitt 1999; Fitt and Costley 1998; Hofmann et al. 1978) cues for larval settlement and metamorphosis, as well as factors influencing strobilation (e. g. Fitt 1984; Hofmann & Kremer 1981; Ludwig 1969; Rahat and Adar 1980). Additionally the upside-down jellyfish has drawn attention as a possible bioindicator species for low nutrient environments. In this context, Todd et al. (2006) demonstrated the potential of *Cassiopea* sp. as a susceptible indicator species for environmental phosphates.

However, information about its spatial distribution in combination with abundance is barely available. Holland et al. (2004) described *Cassiopea* as globally distributed, occurring in shallow, tropical inshore marine waters on sandy mudflats. Reports on remarkably high *Cassiopea* abundances, e .g. in the Caribbean and the Red Sea, were first summarized by Mayer (1910). However, quantitative data is only provided by Collado Vides et al. (1988) for the Nichupte lagoon system off the Mexican Caribbean coast and by Mergner & Schumacher (1981) for a 25 m² seafloor patch in the Northern Red Sea. Recently, a *Cassiopea* sp. was reported to increase its spatial distribution by invading into e.g. Hawaiian and Mediterranean waters (Çevik et al. 2006; Holland et al. 2004; Özgür and Öztürk 2008; Panucci-Papadopoulou et al. 2005). As invasive species are a principle threat to biodiversity and responsible for enormous economic losses (Bolton and Graham 2006), and especially jellyfish are known for their direct negative effect on human enterprises (Purcell et al. 2007), alterations in distribution and abundance of *Cassiopea* sp. require monitoring.

The present study therefore aims to provide data on abundance, habitat selection and life cylce elements like size classes and the commensalism with *Idiomysis tsurnamali* for *Cassiopea* in Northern Red sea fringing reef environments. It thereby aims to contribute to understand the ecology of the jellyfish and to deliver a dataset for further monitoring. For this purpose, a study area in the Northern Gulf of Aqaba, Jordan, comprising several different benthic habitat types, was surveyed using two transect techniques and subsequent digital image as well as statistical analyses.

Material and Methods

Description of study site

The study was conducted in May 2008 in the northern Gulf of Aqaba at the marine reserve of the Marine Science Station (MSS), Aqaba, Jordan (29° 27′ N, 34° 58′ E). All surveys took place at water depths of 5 to 20 m in a study area located directly North of the MSS jetty, ranging from 50 m North and 50 m South relative to the coordinates 29° 27′ x″ N, 34° 58′ E (Fig. 1). Because surveys for the present study took only place during one season, and jellyfish blooms may occur seasonally (Mills 2001), also supporting semi-quantitative data from other investigations during other seasons and years, but at identical study site was collected. These data are summarized in Table 1 and confirm that the observations displayed in the present study are not atypical.

Benthic composition

Benthic composition of the study area was determined using 50 m line point intercept (LPI) transects (modified after English et al. 1994) with recording intervals of 1 m. These transects were conducted at 5.0 m, 7.5 m, 10.0 m, 12.5 m, 15.0 m and 20.0 m water depth each to the north and the south of the MSS jetty. Sediment type and seafloor coverage by benthic fauna and flora was recorded to get an overview of occurring benthic habitats in the study area. LPI transects revealed four distinct, main habitats: a, the *reef* habitat which describes the patchy reef northern of the MSS; b, the *sand flat* consisting predominantly of silicate sands (Wild et al. 2005); c, the *transition zone* which is located between the reef habitat and the sand flat and d, the *seagrass meadow*. These four habitats were examined for habitat-specific *Cassiopea* abundance and size dimensions as well as association with mysids (see below). Results of Holland et al. (2004) indicate that the species investigated by the present study was likely *Cassiopea andromeda*. However, as no molecular analysis was performed and determination of species affiliation based on morphology is rather vague within the genus *Cassiopea* (Holland et al. 2004), in the following the generic notation *Cassiopea* sp. was used.

Cassiopea sp. abundance

In order to determine average abundance of *Cassiopea* sp. (specimen m^{-2}) within each benthic habitat type, multiple single quadrate surveys were conducted. Thereby, a quadrate of 1 m side length was randomly placed on the seafloor at 13 m water depth. Subsequently, the quadrate was flipped over towards a more shallow area and again the number of abundant *Cassiopea* sp. recorded. This was repeated until a water depth of 7 m was reached. With this preset methodology, subjective placement on obviously high abundance spots was avoided. This procedure was carried out on all four distinguished main habitats except the *seagrass meadow,* where due to its spatial extensions (upper limit at 10 m water depth) the survey was conducted between 16 m and 10 m water depths. The abundance of *Cassiopea* sp. in all 14 to 23 resulting replicate quadrates was recorded, and a photograph taken from directly above using a Panasonic TZ5 (9.1 megapixel) digital camera with underwater housing. There was no correlation ($p = 0.44$; Spearman rank-order correlation) between *Cassiopea* abundance and water depth so that the slightly deeper benthic habitat *seagrass meadow* could be compared to the other habitats.

Cassiopea sp. abundance was related to the *entire study area* by multiplication of habitat-specific mean abundance and proportional seafloor coverage of each habitat.

Maximum abundance of *Cassiopea* sp. in each habitat was quantified by placing quadrates specifically at spots with high *Cassiopea* sp. abundance. This procedure was repeated within each of the four habitat types at least 10 times and maximum abundances were recorded from these subjective assessments.

Cassiopea sp. benthic coverage

Benthic coverage of *Cassiopea* sp. as well as the proportion of unoccupied sand flats in the four habitats were analysed using the image processing software ImageJ on digital photographs of the single quadrate surveys (see above) using the quadrate side length of 1 m as a scale. Maximum benthic coverage at each habitat was analysed accordingly using the pictures from maximum abundance determination (see above). Benthic coverage of *Cassiopea* sp. in the *entire study area* was calculated from the data obtained by LPI transects.

Cassiopea **sp. size and association with** ***Idiomysis tsurnamali***

Cassiopea sp. specimens at all four habitats were also parallel surveyed concerning jellyfish diameter and association with *Idiomysis tsurnamali*. Specimens (n = 22 to 36 per habitat) were randomly selected and their oral surface diameters were measured using a ruler (accuracy: ± 0.1 cm). All specimens were also examined for the occurrence of associated *Idiomysis tsurnamali* (Fig. 2a), and the swarm size of the mysids was estimated using the categories described in Table 2.

Statistical analysis

In order to investigate habitat-specific differences in jellyfish diameter, one-way ANOVAs followed by a LSD post-hoc test were carried out. One-Way ANOVA was chosen as the parameter “jellyfish diameter” was independent within and between samples. In contrast, due to the “end to end” placement, quadrates of the habitat surveys and resulting data for *Cassiopea* abundance and benthic coverage were not independent. Hence, these parameters were tested for habitat-specific differences using Mann-Whitney U tests. All categorical data (e .g. mysids size categories) was converted into discrete data and tested using Mann-Whitney U tests. Correlations were tested using the Spearman rank-order correlation.

Results

Benthic composition

Sand flats, consisting of predominantly silicates sands, dominated the study area, comprising 60.2 %. However, patchy reef structures (19.0 %), areas with high seagrass cover (10.5 %), and the transition zone (5.3 %) between reef and sand flats also contributed to the benthic composition in the study area. Artificial constructions, terrigenous stones and carbonate sand flats each accounted for less then 3 % of the study area.

Cassiopea **sp. abundance**

Cassiopea sp. exhibited a patchy distribution (Fig. 2b) between and within different benthic habitats, as indicated by the high standard deviations (Table 2). Nevertheless, there were significant (Table 3) differences concerning *Cassiopea* sp. abundances between the four habitats, ranging from less than one jellyfish m^{-2} in the *seagrass meadow* to almost eight jellyfish m^{-2} in the *transition zone* (Table 2). Maximum abundance occurred in the *reef,* exhibiting more than six fold higher abundances than the *seagrass meadow*.
Within the *entire study area, Cassiopea* sp. exhibited a mean abundance of 1.6 ± 0.3 with a range from 0 to 22 animals m^{-2} (n = 71).

Cassiopea **sp. benthic coverage**

Results obtained from image processing revealed significant differences (Table 3) in benthic coverage by *Cassiopea* sp. between the four main habitats, ranging from less than 1 % in the *seagrass meadow* to more than 7 % at the *transition* *zone* (Table 2). Maximum benthic coverage was reached in the *reef* habitat, with *Cassiopea* sp. covering up to 20.1 % of the seafloor.

The *seagrass meadow* exhibited lowest proportion of unoccupied bare sand flats (Table 2).

Cassiopea sp. benthic coverage in the *entire study area* was 3.2 % as revealed by line point intercept transect work. There was a strong bias between transects to the north (6 %) and transects to the south (0.4 %).

Cassiopea sp. size and association with *Idiomysis tsurnamali*

Additionally to habitat-specific differences in abundance and benthic coverage, significant habitat-specific differences in jellyfish mean diameter were found. Mean diameter was lowest at the *seagrass meadow* and highest at the *sand flat* (Table 2). The percentage of *Cassiopea sp.* associated with *Idiomysis tsurnamali* also differed significantly (Table 3) between the habitats, with the highest percentage of associations at the *transition zone* and lowest jellyfish-mysids association at the *seagrass meadow* (Table 2).

Furthermore, a correlation between jellyfish diameter and association with mysids was found ($p < 0.001$), with smaller *Cassiopea* sp. specimens exhibiting associations to *Idiomysis tsurnamali* less frequently.

Cassiopea sp. located at the reef exhibited significantly different swarm sizes of *Idiomysis tsurnamali* compared to those at the transition zone and the sand flat (Table 2 & 3). *Cassiopea* sp. swarm sizes were largest within the transition zone. *Idiomysis tsurnamali* swarm sizes were found to positively correlate with *Cassiopea* sp. diameter ($p < 0.01$). No habitat-specific differences could be found concerning size classes of *Idiomysis tsurnamali* specimens themselves.

Discussion

The findings of the present study characterize *Cassiopea* to be one of the key organisms within the benthic community in investigated coral reef-associated environments of the Northern Red Sea, exhibiting abundance and benthic coverage comparable to soft corals. On smaller scales *Cassiopea* can even act as the dominant benthic organism due to its patchy distribution which further results in habitat-specific differences concerning *Cassiopea* abundance, size and association patterns to *Idiomysis tsurnamali*.

These findings complement previous studies (e.g. Collado Vides et al. 1988; Holland et al. 2004; Mergner and Schumacher 1981) by describing high *Cassiopea* abundance in coral reef ecosystems for the first time and indicating active habitat selection potentially controlled by the availability of suitable substrates, inorganic nutrients and prey.

Cassiopea sp. abundance and benthic coverage

There are only two previous studies in which mean *Cassiopea* abundance and benthic coverage was quantified. In a fringing reef adjacent to the area investigated in the present study Mergner and Schumacher (1981) observed two *Cassiopea* sp. specimens in a 25 m² survey area resulting in an abundance of 0.08 animals m^{-2} and a benthic coverage of 0.03 %. This is much lower than the values observed in the present study. Although the study of Mergner and Schumacher (1981) was conducted during the winter half-year and jellyfish abundances are known to rapidly fluctuate (Pitt et al. 2005), differences to present study likely can not be ascribed to seasonal changes. Observations during other investigations at the study site (Table 1) indicate a constantly high *Cassiopea* abundance throughout all seasons over the last 7 years. This is further confirmed by the study of Fitt and Costeley (1998), in which no seasonal changes in *Cassiopea* medusae population were found.

The higher medusae abundance and benthic coverage described in the present study may therefore indicate an increase in *Cassiopea* abundance over the last decades. A second explanation for lower abundances reported by Mergner and Schumacher (1981) may be the patchy distribution *Cassiopea* exhibited (Fig. 2). Mergner and Schumacher only investigated a small section of 25 m², thereby potentially omitting patches with high jellyfish abundances.

The patchy distribution of *Cassiopea* is further reflected by the significant differences in jellyfish abundance and benthic coverage between the four investigated main habitats (*reef*, *transition zone*, *sand flat*, *seagrass meadow*). Limited availability of bare sediment likely caused the lowest *Cassiopea* abundances in the *seagrass meadow*, which is supported by the findings of Collado Vides et al. (1988). Availability of prey, e. g. copepods or crustacean larvae, which *Cassiopea* was shown to feed on (Gohar and Eisawy 1960a), may also influence *Cassiopea* abundance and likely differs between the four habitats. In addition, *Cassiopea* was shown to actively extract and take up inorganic nutrients from the sediment (Jantzen et al., unpublished). Sites with higher input of organic matter, which is rapidly recycled to regenerated nutrients in permeable reef sands (Wild et al. 2004a, Wild et al. 2004b, Wild et al. 2005) may therefore be favoured by *Cassiopea* specimens. The direct vicinity to reef corals could lead to a high supply of organic matter to the adjacent sediments (Wild et al. 2005) and potentially explain the highest *Cassiopea* abundances within coral reef associated habitats (Table 2).

Maximum observed *Cassiopea* abundance of up to 31 animals m^{-2} is similar to that observed by Collado Vides et al. (1988), who reported a very high mean abundance of 42 medusae m^{-2} in Bojórquez lagoon (Mexican Caribbean). For coral reef ecosystems the high abundances observed in present study are described for the first time.

The average benthic cover by *Cassiopea* sp. of 3.2 % in the study area was lower than described for hermatypic corals (Bouchon-Navaro and Bouchon 1989; Khalaf and Kochzius 2002; Mergner and Schumacher 1974) and benthic algae (Haas et al., unpublished), but similar compared to soft corals (Khalaf and Kochzius 2002), thereby characterising *Cassiopea* as one of the key representatives of the benthic community. On smaller scales, *Cassiopea* can even act as the dominant benthic organism in coral-reef associated habitats.

Implications for *Cassiopea* life cycles

It is generally reported that *Cassiopea* is associated with mangrove dominated habitats (Holland et al. 2004). In this context, Fleck and Fitt (1999) demonstrated in a laboratory study that degrading mangrove leaves provide a natural cue for *Cassiopea* sp. larval settlement and metamorphosis, whereas settlement on the seagrass *Thalassia testudinum* only marginally occurred. These findings were supported by *in situ* observations, which showed that *Cassiopea* sp. polyps frequently occur on mangrove leaves, but rarely on any other substratum (Fitt 1991, Fitt and Costley 1998). However, in the present study, high abundances of *Cassiopea* sp. were found more than 150 km North from the closest mangrove ecosystem (Nabeq, Egypt). As the main current in the Gulf of Aqaba runs from

North to South (Berman et al. 2000), it is unlikely that observed high abundances of the almost stationary jellyfish *Cassiopea* are solely maintained by migration. Therefore, the *seagrass meadow* (*Thalassia testudinum*) is suggested to have provided natural cues, e.g. degrading organic material, for larval settlement and metamorphosis sufficient to sustain high abundances. This is further supported by the occurrence of very small medusae of about 1.5 cm in bell diameter and an estimated age of about six weeks (R. Kaiser, personal communication) and the lowest mean diameters of all four habitats in the *seagrass meadow*.

When medusae grow, bare substrate becomes limited in the *seagrass meadow*, which may force the jellyfish to leave. This may deliver an explanation for lowest numbers of medusae in the *seagrass meadow* despite the provision of natural cues. Highest mean *Cassiopea* diameter at the *sand flat*, the habitat with the highest percentage of unoccupied substrate, supports this assumption.

Cassiopea* association with *Idiomysis tsurnamali

More than 60 % of all jellyfish exhibited an association to mysids, whereby a positive correlation between jellyfish diameter, the presence of mysids and the mysids swarm size was found. An explanation may be that larger sized *Cassiopea* offer more refuge to the mysids, which withdraw between the tentacles in case of danger (W. Niggl, personal observation). In addition, *Cassiopea* sp. was found to release organic matter (Ducklow and Mitchell 1979) which is consumed and mineralized by the mysids (Niggl et al. unpublished). As organic matter release by *Cassiopea* sp. positively correlates with surface area, larger *Cassiopea* specimens may be able to provide larger mysid swarms with food.

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Figure Legend

Figure 1: Map of the Gulf of Aqaba (top left). Aerial image (property of Aqaba Special Economic Zone Authority) of the Marine Science Station (MSS) in Aqaba with the study area indicated by transparent ellipses (top right). Benthic composition of the study area revealed by line point intercept transects (bottom). No transect derived data was recorded in areas indicated by transparent icons. Red ellipses indicate distinguished main habitats (RF = reef, TZ = transition zone, SF = sand flat, SM = seagrass meadow).

Figure 2: a, *Cassiopea* sp. exhibiting a swarm of *Idiomysis tsurnamali*. b, High abundance of *Cassiopea* sp. in the *reef* habitat.

Tables

Table 1: Summary about previous and successive observations of high *Cassiopea* abundances (> 5 animals m^{-2}) in benthic habitats identical to those investigated in present study during spring 2008.

Table 2: *Cassiopea* sp. abundance, benthic coverage, diameter and association with *Idiomysis tsurnamali* in the respective benthic habitat. Swarm size categories describe abundance of mysids per jellyfish (0 = no mysids, 1 = 0 – 4 mysids, 2 = 5 – 9 mysids, 3 = more than 10 mysids).

Table 3: Statistical analyses of habitat-specific *Cassiopea* abundance, benthic coverage and association with mysids. Given are p values for hypothesis for no differences between high abundance habitats (TZ = transition zone, SM = seagrass meadow, SF = sand flat, RF = reef) concerning listed parameters. *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$

Table 1:

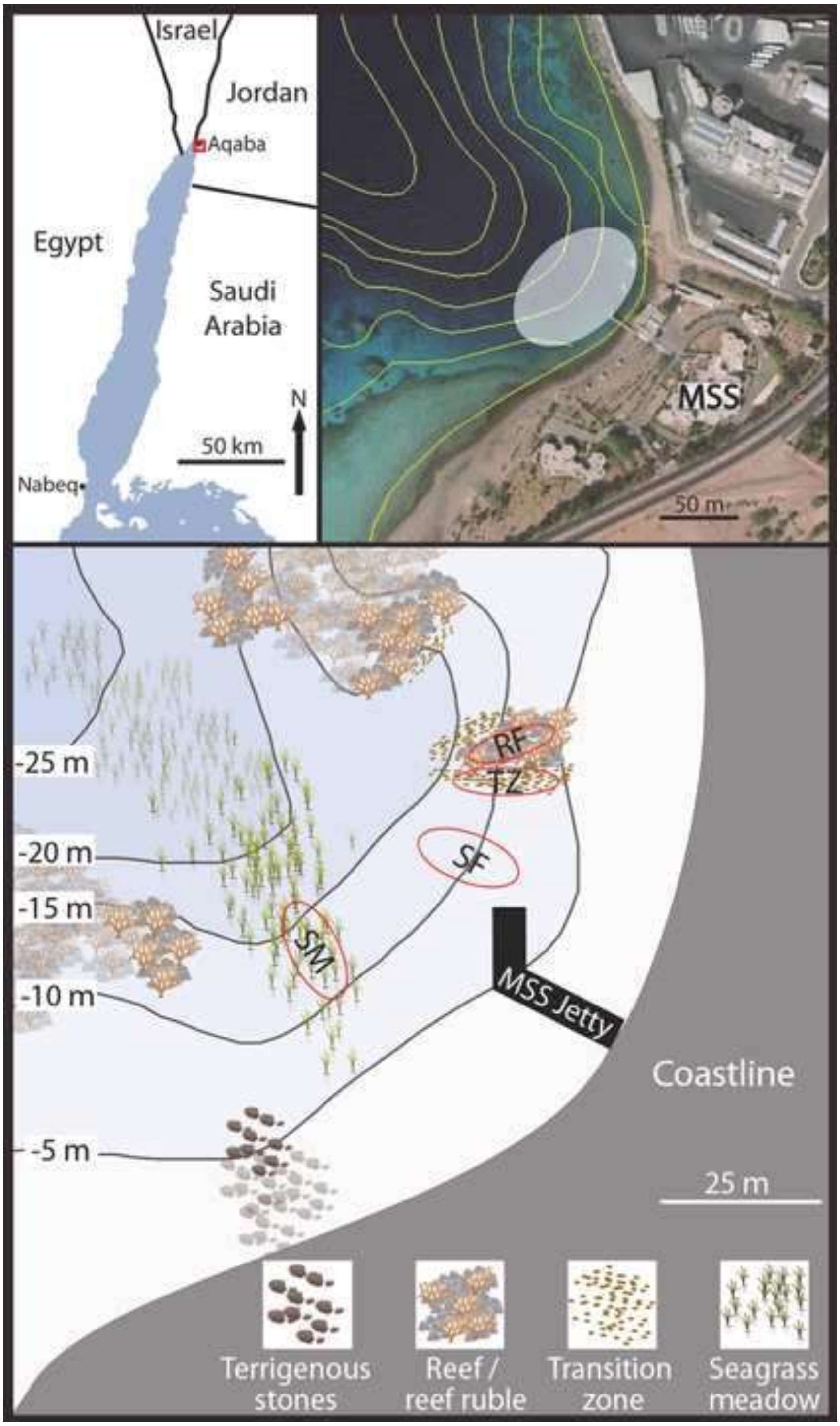
Year	**Season**	**Observer**
2002	Spring	E.M. Zetsche
2004	Spring Summer Autumn	C. Jantzen C. Jantzen/ C. Wild M. Naumann
2005	Winter	M. Naumann
2006	Autumn	C. Jantzen/ C. Wild
2007	Summer Autumn	C. Wild C. Jantzen
2008	Winter Summer	C. Wild/ W. Niggl/ A. Haas L. Kamphausen

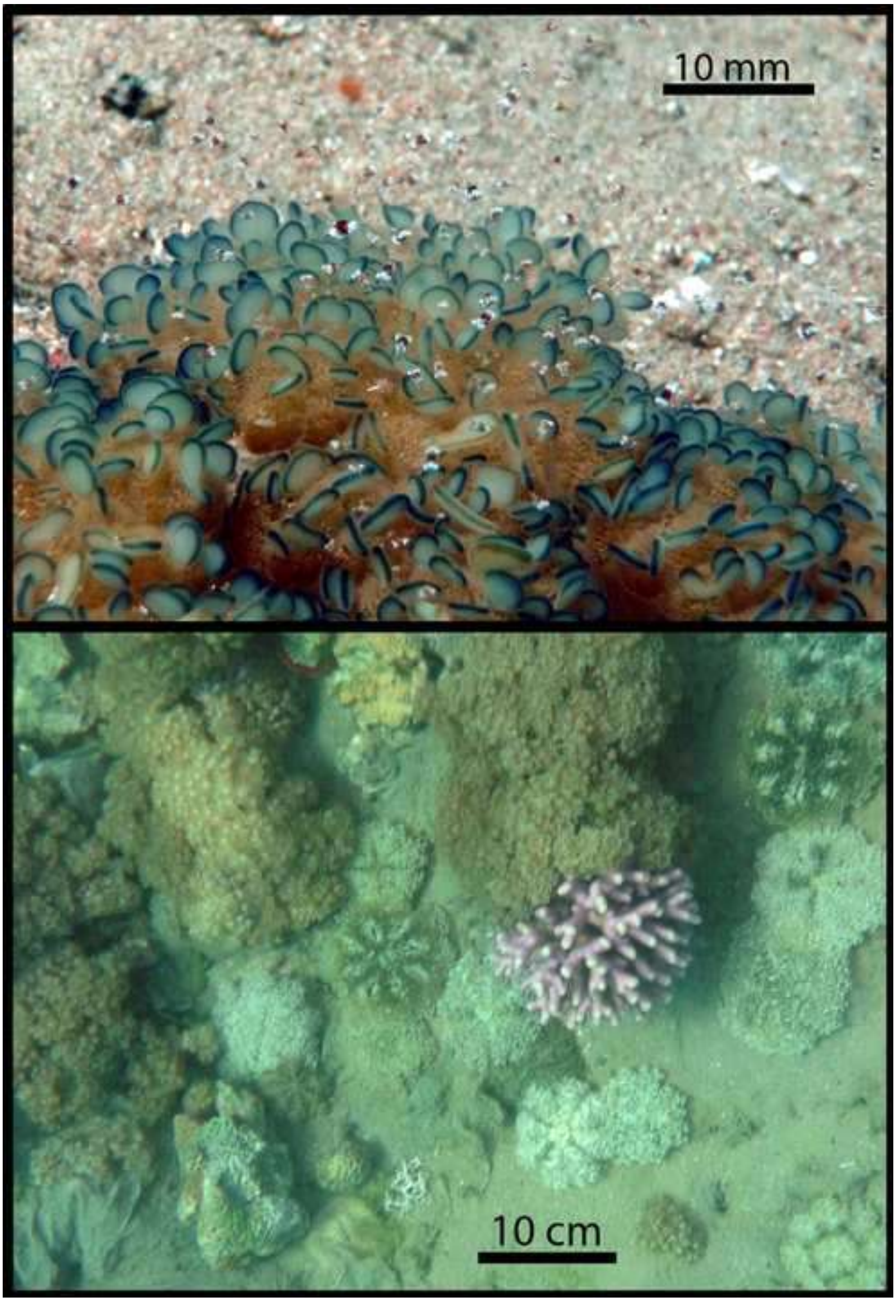
Table 2:

Site	**Mean abundance (animals m^{-2})**	**Maximum abundance (animals m^{-2})**	**Mean diameter (cm)**	**Mean benthic coverage (%)**	**Unoccupied, bare sand flats (%)**	**as**
Reef	1.6 ± 2.2	31	10.3 ± 2.3	1.0 ± 1.1	24 ± 19	
Transition zone	7.9 ± 6.7	27	13.1 ± 2.7	7.5 ± 5.8	84 ± 11	
Seagrass meadow	0.4 ± 0.8	5	8.3 ± 3.2	0.1 ± 0.3	8 ± 9	
Sand flat	1.3 ± 1.4	14	13.5 ± 2.4	1.6 ± 1.8	95 ± 4	

Table 3:

	Mean abundance			**Benthic coverage**			**Mean diameter**			***Cassiopea* - mysids association**			**Mysids swarm size**		
	TZ	SM	SF	TZ	SM	SF	TZ	SM	SF	TZ	SM	SF	TZ	SM	SF
RF	***	0.08	0.96	***	*	0.39	***	**	***	0.21	***	0.08	**	0.23	*
TZ		***	***		***	***		***	0.56		***	**		0.93	0.7
SM			0.07			*			***			**			0.8


Israel
Jordan
Aqaba
Egypt
Saudi Arabia
N
50 km
Nabeq
MSS
50 m
-25 m
-20 m
-15 m
-10 m
-5 m
RF
TZ
SF
SM
MSS Jetty
Coastline
25 m
Terrigenous stones
Reef / reef ruble
Transition zone
Seagrass meadow


10 mm
10 cm