Diversity, habitats and size-frequency distribution of the gastropod genus *Conus* at Dahab in the Gulf of Aqaba, Northern Red Sea

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(Received 23 August 2015; accepted 19 March 2016; first published online 9 May 2016)

Topographically complex subtidal reefs of the Indo-West Pacific region are characterised by a high species richness of cone snails of the genus *Conus* (up to 36 on some reefs) but low population densities (≤1 individual/m²), whereas *Conus* assemblages on reef flats usually support fewer species (5-9) and high population densities (up to 5.2 individuals/m²). Subtidal sand areas are known to be least species-rich (1-6 species). Although the diversity of this predatory gastropod genus has been described previously from different areas of the Indo-Pacific, little ecological information is available on *Conus* in the Northern Red Sea. Therefore, data from five habitat types were obtained along 73 line-transects (245 m²), which yielded ecological data for a total of 175 individuals of 9 species. In accordance with former findings, our results demonstrate that the reef flat was the habitat with the highest observed population densities (6.15 individuals/m²) but low species diversity (\(H' = 0.9\); 5 species); subtidal reefs, in contrast, were characterised by low densities (0.13 individuals/m²) and a relatively high species diversity (\(H' = 1.5\); 6 species). This suggests that *Conus* diversity and species richness in the Northern Red Sea around Dahab is lower than in other parts of the Indo-West Pacific region. Furthermore, hard- and soft substrata were dominated by different *Conus* species in accordance to the distribution of favourable microhabitat patches, the degree of physical stress and the availability of refuges and prey organisms. The fact that these *Conus* were predominantly small-bodied vermivores (size range: 6-85 mm; mean shell size: 15 mm; SD = 9 mm) suggests that this size class possesses an advantage over molluscivores and piscivores. Except for subtidal reefs, which showed a highly variable species composition, the studied habitat types around Dahab were characterised by distinct assemblages of *Conus*.

**Keywords:** Northern Red Sea; Southern Gulf of Aqaba; *Conus*; size-frequency distribution; species diversity; habitat occupation

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feeding ecology of the particular species (see e.g. Kohn, 1959; Kohn et al., 1972; Kohn et al., 1999). Three groups of Conus species can be distinguished according to their feeding mode (Kohn, 1959): vermivores, the largest group of Conus species, prey on polychaetes of different families, whereas molluscivores and piscivores prefer mollusks and fishes, respectively.

The geographic distribution of the family Conidae stretches across tropical waters worldwide, with only a few species occurring at latitudes beyond 40° North and South (Kohn & Perron, 1994; Beesley, Ross, & Wells, 1998). Biogeographical patterns of Conus are diverse, with some species having a rather broad range of distribution and others being endemic to certain areas (Röckel, Korn, & Kohn, 1995; Monteiro, Tenorio, & Poppe, 2004). The highest diversity of Conus is present in the Indo-Pacific region, which contains the largest number of extant species in many groups (Kohn, 1967; Kohn & Nybakken, 1975; Röckel et al., 1995). On coral reefs of the tropical Indo-West-Pacific, high Conus population density and low diversity characterise reef flats, whereas low population density and high diversity characterise subtidal reefs, and Conus populations on extensive stretches of subtidal sand are the least diverse (Kohn, 1968). Surveys on Micronesian and Australian coral reefs revealed that microhabitat type and availability of refuges could be important factors for Conus diversity and abundance (Kohn & Leviten, 1976; Leviten & Kohn, 1980; Kohn, 1983). Although details on the ecology and species diversity of Conus from different areas of the Indo-Pacific are known (Kohn, 1967, 1968, 1983, 2015; Kohn & Nybakken, 1975; Kohn & Leviten, 1976; Leviten & Kohn, 1980; Kohn & Perron, 1994; Vallejo, 2005), little ecological information is available on Conus in the Northern Red Sea: Several studies mostly listed the species present (Kohn, 1964; Fishelson, 1971; Fainzilber, Mienis, & Heller, 1992), and studies on the distribution pattern of conids on hard substrata did not distinguish between species (Zuschin et al., 2001; Zuschin & Stachowitsch, 2007).

The objective of the present study is to assess and compare species diversity, habitat occupation and size-frequency distribution of Conus in different shallow marine habitats and to obtain information on the importance of substrate type and habitat complexity for the abundance of this diverse genus in the Gulf of Aqaba.

Material and Methods

Habitat types and sampling stations. Diversity, abundance and size-frequency distribution of predatory Conus assemblages were studied in several habitat types (hard and soft substrata) at Dahab in the southern Gulf of Aqaba (28°30’N 34°30’E): subtidal coral reefs, reef flat, subtidal sand, intertidal sand and seagrass meadows (Supplementary Table S1). The habitat types distinguished are similar to the classification of Conus habitat types of Kohn (1967). Subtidal coral reefs along the Dahab coast are exclusively of the fringing type, which form belts along the shelving shoreline and show a typical zonation (Fishelson, 1973). Reef slopes, coral carpets and coral patches border the reef flats around Dahab, such as in many other areas of the Red Sea (Reiss & Hottinger, 1984; Piller & Pervesler, 1989). Alternating microhabitats such as coral boulders, rock, sand substratum and coral rubble provide daytime refuges for many conids and establish the reef’s heterogeneous character (Kohn, 1967). Extensive areas of sand, where species of Conus can burrow during the day, are common in shallow bays or lagoons, sometimes covered by seagrass; these sandy areas are often associated with patchy reefs or bordering the reef flats and reef slopes.

The reef flat studied was an approximately 20-30 m wide, table-shaped bench at “The Islands” (28°28’N, 34°30’E; Supplementary Table S1). Although of simple topography, the flat provides numerous sand-filled depressions and crevices, and large portions of the reef flat are covered with algal turf serving, which provides shelter for many marine taxa such as gastropods of the genus Conus (Kohn, 1968, Leviten & Kohn, 1980). The whole flat is covered by water even during low tide (mid water level 0.5-1m). Subtidal reefs were sampled at four locations...
(Supplementary Table S1): “The Lighthouse” (28°29’N, 34°31’E; reef slope and coral patches), “The Islands” (28°28’N, 34°30’E; reef slope and coral patches), “Moray Garden” (28°26’N, 34°27’E; coral carpet) and “Abu Helal” (28°32’N, 34°31’E; coral carpet). All stations displayed a similar structure and topography dominated by coral associations of Porites, Acropora and Millepora. They were characterised by an approximately 20–30 m wide reef flat, an initially steep reef slope descending to 20-40 m, followed by either extensive coral carpets or sand-dominated patch reefs.

Subtidal sand stretches were sampled at three locations: "Coral Garden" (28°33’N, 34°31’E), “Golden Blocks” (28°26’N, 34°27’E) and “Moray Garden” (28°26’N, 34°27’E) (Supplementary Table S1). These areas were extensive at all sampling locations, alternating with coral patches, boulders and seagrass. Sandy seagrass meadows were studied at “Mashraba” (28°29’N, 34°31’E), “Bannerfish Bay” (28°29’N, 34°31’E) and “The Lighthouse” (28°29’N, 34°31’E), where they were found to be most abundant in depths ranging from 3-18m. The intertidal was surveyed at a lagoon (Supplementary Table S1; 28°28’N, 34°30’E), protected behind fringing reefs and of low relief. Here, a large tidal flat is developed, popular for recreational activities (Zuschin & Ebner, 2015).

**Sampling design.** Specimens were collected at different depths in the range of 0 to 15 m using SCUBA and snorkelling (Supplementary Table S1, S2). Line transects in combination with the quadrat method were laid parallel to shore at each location and habitat type. On hard substrata, a 20 m transect line was used with a 1 m² quadrat placed at intervals of 5 m, yielding a sampled area of 5 m² for each transect. Within each quadrat along transects, all Conus were collected. For soft substrata, a 10 m transect line was used with a 0.25 m² quadrat placed every 2.5 m (1.25 m²/transect). The starting point for each transect was chosen by haphazardly throwing a quadrat from a few metres above the substratum. Quadrats from subtidal sand transects were excavated with a shovel to a depth of approximately 7 cm and sieved with 2 mm mesh size in order to include endobenthic individuals. In order to evaluate whether certain Conus species have preferences in terms of microhabitat utilization, microhabitat types (according to Kohn, 1983) were recorded for every specimen collected on subtidal reefs and the reef flat. Individuals were collected for identification, and size was measured with callipers to the nearest millimetre. Abundances were recorded for transects and habitats. Whenever necessary, encrustations were removed for species identification, which was based on Rusmore-Villaume (2008) and Röckel et al. (1995).

Ecological information was obtained for a total of 175 individuals of 9 species from 73 transects, covering an area of 245 m². Unidentifiable specimens (i.e., bleached colour patterns) were grouped together and accounted for ~3% (n = 5) of the total assemblage. This group was excluded from species-related statistics.

**Data analysis.** Diversity was measured with the Shannon-Wiener index H’ (Shannon 1948). The data set was tested using analysis of similarities (ANOSIM, Clarke & Warwick, 1994) in order to identify differences among Conus habitats. The data was prepared by generating a similarity matrix from transect data using the Bray-Curtis coefficient of similarity (Bray & Curtis, 1957). The matrix was standardised by total (i.e., percentages were used) and square root transformed to downweight high abundances of some species. R values ≥ 0.5 indicate clearly different groups, whereas values < 0.25 indicate minimal separation (Clarke & Gorley, 2001). This parameter was used as a comparative measure for the degree of separation of habitat types. To visually represent the similarities between the transects, non-metric multidimensional scaling (nMDS, Kruskal, 1964) was performed based on the Bray-Curtis similarity matrix. Size-frequency distributions were summarised for each habitat. Normality tests were performed using the Chi-square test and the Shapiro-Wilk test. Statistical differences between two groups were tested using the Student’s t test or the Mann-Whitney U test. Kruskal-Wallis one-way analyses of variance on ranks were conducted to compare the effect of habitat type and species on Conus shell length (ANOVA). In order to deal with unequal sample sizes, Dunn post hoc multiple comparison procedures were performed (Dunn, 1961). Statistical significance was measured at the 95% confidence level. Statistical analyses were conducted using the software packages Sigmaplot 13.0 (Systat Inc., San José, USA), PRIMER 6 (Clarke & Warwick, 1994) and Past (Paleontological Statistics; Hammer, Harper, & Ryan, 2001).
Figure 1. Size-frequency distribution of all conids. Small-sized species are numerically most abundant.

Results

Species composition and abundance. The quantitatively most important species in this study were the vermivorous Conus parvatus, C. taeniatus and C. tessulatus (Figures 1, 2; Supplementary Figure S1). Together, these species accounted for 80% of the assemblage.

The ubiquitous C. parvatus occurred in all habitats except in seagrass meadows and was most abundant on reef flats and subtidal reefs (Figure 2). C. taeniatus most frequently occupied different microhabitats on subtidal reef flats, preferentially algae on reef limestone (Supplementary Figure S2). In contrast, C. tessulatus was the dominant species on soft substratum, where specimens occurred primarily buried in the sand. Other vermivorous species recorded in this study were C. miliaris Hwass in Bruguière, 1792, which was most frequently found on the reef flat, and C. flavidus Lamarck, 1810, which occupied both hard and soft substrata. C. arenatus Hwass in Bruguière, 1792 and C. maldivus Hwass in Bruguière, 1792 were both found on sand substrata and on dead coral. Specimens of C. textile could be reported only from a seagrass meadow. Among hard substrata, the reef flat was the habitat with the highest observed population densities (approximately 6 individuals/m², ranging from 2.8 to 13.2; Table 1; Supplementary Table S2). Species diversity, however, was low (H’ = 0.9, Table 1). At this topographically simpler habitat type, 120 individuals of five species were recorded, comprising approximately 68% of the entire collection. The most abundant species were C. parvatus, C. taeniatus and C. flavidus. Subtidal reefs around Dahab were characterised by low Conus densities (<1 individual/m²; Table 1; Supplementary Table S2) and a moderate species diversity (H’ = 1.5; Table 1). A total of six species constituted the assemblage of this habitat type, and C. parvatus (Figures 1, 2) was dominant. Subtidal sand was the soft substrata habitat with the highest population densities (approximately 2 individuals/m²; Table 1; Supplementary Table S2) and ranked second among all substrate types. Species diversity was relatively low (H’ = 0.9; Table 1). Four species occurred in the extensive subtidal areas of sand, dominated by C. tessulatus (Figure 2). Sandy seagrass meadows showed low population densities (<1 individual/m²; H’ = 1; Table 1) and were
Table 1. Abundance, density and species diversity of Conus at Dahab. $H'$= Shannon-Wiener Index.

| Habitat type        | Sampled area [m²] | No. of species | No. of individuals | Density [no./m²] | $H'$ |
|---------------------|-------------------|----------------|-------------------|-----------------|-----|
| Reef flat           | 20                | 5              | 120               | 6.15            | 0.9 |
| Subtidal reef       | 180               | 6              | 15                | 0.13            | 1.5 |
| Subtidal sand       | 11.25             | 4              | 24                | 2.11            | 0.9 |
| Seagrass meadow     | 22.5              | 3              | 7                 | 0.31            | 1.0 |
| Intertidal sand     | 11.25             | 2              | 4                 | 0.35            | 0.6 |

Table 2. Results of analyses of similarity (ANOSIM) evaluating variation in the composition of Conus assemblages in different habitat types. R-values >0.5 indicate clearly separable groups (bold values). The last column gives the number of permuted statistics which are $\geq$ observed R.

| Living Conidae       | $R$ statistic | Sign. level % | Actual permut. | No. permuted $\geq$ observed R |
|----------------------|---------------|---------------|----------------|-------------------------------|
| Subtidal reef, reef flat | -0.248         | 99.2          | 999            | 991                           |
| Subtidal reef, subtidal sand | 0.317          | 0.3           | 999            | 2                             |
| Subtidal reef, seagrass meadow | 0.083          | 15.6          | 999            | 155                           |
| Subtidal reef, intertidal sand | 0.150          | 8.8           | 91             | 8                             |
| Reef flat, subtidal sand | **0.955**      | 0.3           | 330            | 1                             |
| Reef flat, seagrass meadow | 0.256          | 8.7           | 126            | 11                            |
| Reef flat, intertidal sand | **1.000**      | 6.7           | 15             | 1                             |
| Subtidal sand, seagrass meadow | **0.703**      | 0.1           | 792            | 1                             |
| Subtidal sand, intertidal sand | -0.179         | 77.8          | 36             | 28                            |
| Seagrass meadow, intertidal sand | **0.636**      | 4.8           | 21             | 1                             |

dominated by *C. parvatus* and the sand-associated *C. arenatus*. This substrate type was also occupied by a third species, *C. textile*. The intertidal sand area was the least diverse habitat type ($H'$ = 0.6; Table 1), with only two species, *C. tessulatus* and *C. maldiveus* (Figure 2). Based on the species composition of the assemblage, most habitat types were well distinguishable.

The nMDS and ANOSIM analyses of 27 transects showed two distinct clusters corresponding to two substrate types, reef flat and sand substratum (Figure 3, Table 2). The differences in species composition among these groups were statistically significant ($R = 0.95; p = 0.03$). Accordingly, nMDS axis 1 in Figure 3 displayed a substrate gradient from soft (right) to hard substrata (left).

The reef flat constituted a relatively homogeneous habitat clearly delineated from subtidal and intertidal sand, but with minor overlap with seagrass meadows (Table 2).

**Microhabitat use.** Microhabitat occupation data were assessed for all specimens in all habitats and the results are summarised in Supplementary Figure S2. More than 60% of all specimens occurred on soft substrata: a layer of sand bound by filamentous algae on the reef flat (n = 59), sub- and intertidal sand patches, or extensive sand areas (n=42) as
Figure 2. Size-frequency distributions for the 9 *Conus* species. A. Reef flat; B. Subtidal reef; C. Seagrass meadow and Intertidal sand; D. Subtidal sand. Cross-hatched pattern in C represents intertidal sand. Note numerical dominance of the smallest size classes. For legend see Figure 1.

well as sandy seagrass (n=7) were frequently occupied. The most utilised hard substrata were macro-algae on reef limestone (n=30) and limestone usually covered with a very thin layer of sand (n=16; Supplementary Figure S2).

*Conus parvatus*, *C. taeniatus* and *C. tessulatus* were the dominant species. The majority of *C. parvatus* (n=48) inhabited algal-bound sand on limestone, whereas *C. taeniatus* was predominantly found on or underneath algae on limestone. On subtidal reefs, however, dominant *C. parvatus* mostly occupied bare rock or small rock cracks. Although less abundant on other substrates, these species showed a broad range of micro-habitat utilization compared to other species and thus seemed to be less specialised. Specimens of *C. tessulatus*, *C. arenatus*, *C. maldivus* and *C. flavidus* almost exclusively occupied sandy substrate.

Although unusual for many gastropods, including *Conus*, some individuals (*C. flavidus*, *C. tessulatus*, *C. parvatus*) were found to occupy living coral. We observed this unexpected behaviour (active avoidance of stinging nematocysts) more than once, mostly involving small individuals (mainly *C. parvatus*).

**Size-frequency distribution.** The size range of the total assemblage was 6-85 mm (mean size 15±9 mm; Figure 1) and the size-frequency distribution was distinctly right skewed (i.e., small individuals dominate). Analyses of variance showed that *Conus* shell
size significantly varied among habitats and species \((p<0.001;\) Supplementary Tables S4, S5). Post hoc comparisons indicate that sand substrate (mean 14.3±9.8 mm) and reef flat (12.6±5.1 mm) accommodated the smallest conids \((p\leq0.009;\) Table 3; Supplementary Table S6, S7) and that the species *C. parvatus* (mean 11.2±1.9 mm) and *C. tessulatus* (16.5±14 mm) were both significantly smaller than *C. maldivus* (34.2±6.8 mm) and *C. flavidus* (26.8±4.5 mm; Supplementary Table S8). Furthermore, *C. tessulatus* and *C. arenatus* were smallest on subtidal sand, whereas *C. parvatus* was smallest on the reef flat (Supplementary Table S9, S10). *Conus flavidus* and *C. taeniatus* did not significantly differ in size between habitats \((U\) test: \(p = 0.944\) and \(p = 0.58;\) Supplementary Table S10). Other species were not statistically tested due to their small sample sizes.

**Discussion**

**Species diversity and abundance**

Distribution patterns and species richness of *Conus* are often influenced by topography and substrate type (Kohn, 1967, 1983). Prior studies from the Indo-West Pacific region (e.g., Kohn, 1959, 1967, 1980, 1983, 1990, 2001; Leviten & Kohn, 1980) have
Table 3. Average shell lengths of Conus per habitat.

| Habitat type       | Sample size (n) | Mean shell length [mm] |
|--------------------|-----------------|------------------------|
| Subtidal reef      | 20              | 17.9 ± 7.1             |
| Reef flat          | 120             | 12.6 ± 5.1             |
| Subtidal sand      | 24              | 14.3 ± 9.8             |
| Seagrass meadow    | 7               | 31.4 ± 21.9            |
| Intertidal sand    | 4               | 42.3 ± 13.6            |

demonstrated that topographically complex subtidal reefs support the highest number of species, although abundance there is usually low. Intertidal reef flats are of intermediate diversity and high abundance, whereas extensive subtidal sand areas are least diverse and have low abundance. The present study partially supports the earlier findings: Subtidal reefs displayed the highest species richness and the lowest population densities in the sampling area ($H' = 1.5; n = 15; < 1 \text{ individual/m}^2$). However, the species richness of reef flat and subtidal sand assemblages was identical, and density varied by a factor of nearly three (Table 1).

Only a few species that are known from the region were not sampled in the present study: C. sanguinolentus Quoy & Gaimard, 1834 and C. coronatus Gmelin, 1791 are small vermivorous species, usually found under boulders or in crevices on reef flats. C. quercinus Lightfoot, 1786, C. vexillum sumatrensis Hwass in Bruguière, 1792 and C. aulicus Linnaeus, 1758 are rare in the northern Red Sea and would be expected on subtidal reefs and reef flats. One reason for undersampling of these rare species might be the numerous possibilities for specimens to hide in topographically complex subtidal reefs with varying microhabitats. Small individuals in rock fissures, for instance, can easily be overlooked, potentially yielding a reduced species diversity. Nevertheless, subtidal reefs are generally known to support the lowest number of specimens (e.g. Kohn, 1967, 1968, 1983; Kohn & Leviten, 1976). This is because living coral harbours the lowest prey densities, and Conus probably avoids contact with the coral’s nematocysts (Kohn, 1967, 1983). The reef flat, a topographically simpler habitat type, supported the largest densities. Favourable conditions might include the high proportion of algal-bound sand, which tends to stabilise the substrate and thus provides a refuge for small individuals from strong water movement at high tide (Kohn, 1959; Kohn & Leviten, 1976). Crevices, sand patches and rubble-filled depressions are also known to function as refuges, supporting higher species abundance in an otherwise harsh environment. The structurally uniform subtidal sand areas around Dahab were characterised by intermediate population densities of a few dominating species. The results suggest that these most abundant species are well adapted to burrowing into the substrate and utilizing it as both a refuge and hunting ground. Seagrass meadows supported low Conus population densities, similar to those previously investigated by Kohn (1980); there is evidence that ecological mechanisms similar to those in subtidal sand areas limit Conus abundance in this habitat type (Kohn, 1980). The intertidal sand area showed a species composition related to subtidal sand areas, although Conus abundance differed and was the lowest recorded. One hypothesis is that desiccation at low tide is a limiting factor in this habitat.
Species distribution and microhabitat utilisation

Vermivorous species. Vermivorous species were the most abundant feeding type in shallow marine habitats around Dahab. These species are highly specialised, preying on distinct groups of polychaetes. Many of them have adapted a unique hunting technique in order to prey on tube-dwelling polychaetes common to subtidal reef and reef flat habitats. There, a sufficient number of different polychaete species burrow into reef limestone and corals. Both *C. flavidus* and *C. parvatus* mainly feed on tube-dwelling polychaetes that live on the underside of coral rock or on coral rubble. They are known to be more abundant on subtidal reefs interspersed with sufficient amounts of sand patches (Kohn, 1959; Röckel et al., 1995). Other vermivorous species (e.g., *C. tessulatus*, *C. arenatus*, *C. maldivus*) predominately prey on sand-dwelling polychaetes and thus prefer extensive sand stretches in which they can burrow (Fishelson, 1971; Kohn & Nybakken, 1975; Kohn 1968; Reichelt & Kohn, 1985; Röckel et al., 1995; Kohn 2001). Kohn (1959) also reported *C. rattus* as a common species on reef flats in Hawaii. The only specimen of this species recorded from the present study, though, was an empty shell collected from subtidal sand.

Molluscivorous and piscivorous species. The only two molluscivorous and piscivorous species, *C. textile* and *C. nigropunctatus* (synonymised under *C. catus* Hwass in Bru-guière, 1792 form nigropunctatus by Röckel et al., 1995), found around Dahab were previously reported by other studies in the same habitat types (e.g. Kohn, 1959). *C. textile*, as a predator of epifaunal grazers and other *Conus* species, was found on seagrass meadows and rarely on subtidal reefs. *C. nigropunctatus*, in turn, typically inhabited reef flats but was also present in small numbers on sand bottom or rubble of subtidal reefs (Kohn, 1959, 1960; Kohn & Nybakken, 1975; Kohn 1968; Reichelt & Kohn, 1985; Fishelson, 1971; Röckel et al., 1995). On reef flats, *C. nigropunctatus* is usually the only entirely piscivorous species. These results suggest that prey resources for molluscivores and piscivores are scarce, especially in topographically simpler habitat types. One explanation is that large, highly specialised species such as *C. textile* prey on larger organisms than do vermivores, and this larger food resource is usually less abundant (Leviten, 1976; Kohn, 1980).

Species composition of habitat types

Ordination of *Conus* abundance, as well as the frequency distribution of *Conus*, indicate that most of the habitat types showed characteristic species assemblages (Table 2; Figures 2, 3). Differences in species composition among habitat types can be explained by the different physical and environmental conditions of the distinct habitat types. The reef flat, with its generally harsh conditions, is subject to strong wave action, water movement, high salinity and irradiation. A dense layer of algal-bound sand is crucial to provide *Conus* with a burrowing medium suitable as a refuge against predation, water movement and desiccation. This, however, requires enough algae capable of binding sand. Kohn (1959) stated that the usually lower abundance of sandy areas on reef flats compared to subtidal reefs can limit the density of certain sand-dwelling *Conus* species. In addition, species such as the vermivorous *C. flavidus* are so specialized on sand-dwelling polychaetes that the absence of sand patches limits their abundance. The present study, however, showed that *C. flavidus* was most abundant on reef flats, where individuals commonly occupied algal-bound sand on reef limestone. This discrepancy can likely be explained by differences in the density of the algal mat and the amount of sandy areas between the reef flats studied by Kohn (1959) and in the present study.
Subtidal and intertidal sand showed similar compositions and their species diversities were the lowest recorded. Extensive areas of pure sand characterised both habitat types, although the intertidal was especially exposed to desiccation and predation. These generally harsh conditions might act as limiting factors for *Conus* abundance in this habitat type.

Seagrass meadows seemed to be habitats of an intermediate type, with features similar to those of other soft substrata, and thus supported similar species. This might explain the differences among assemblages of seagrass meadows and other soft substrata shown in the nMDS plot (Figure 3).

Subtidal reefs showed the largest within-habitat differences in terms of species composition because they comprised very different microhabitats. One hypothesis is that this was generally due to the heterogeneity of this habitat type, where coral blocks, alternating with sand patches and rock of varying portions, established numerous microhabitats for *Conus*. Alternatively, soft substrata may in general support species with a higher degree of specialization in terms of food and microhabitat. Resource partitioning has also been suggested by Kohn (1968, 1980), Kohn and Nybakken (1975), and Leviten and Kohn (1980).

**Size-frequency distribution**

The size-frequency distribution of the total assemblage peaked between 9 and 15 mm shell length (Figure 1), indicating a strong numerical predominance of small-bodied species. Reef flat and subtidal sand assemblages harboured the smallest specimens, which is best evident in the abundance of *C. parvatus* and *C. tessulatus*. This is also consistent with findings from previous studies conducted by Kohn (1968) and Leviten & Kohn (1980). Both studies show that the generally strong water movement associated with tidal flats and a lack of refuges in this topographically simpler habitat type might be factors influencing *Conus* body size. This might also hold true for subtidal sand, where refuges are mostly absent, except that specimens can burrow into the substrate. The topographically more complex subtidal reef habitat, in contrast, provides shelter from predators and is much less exposed to water movement. Furthermore, we hypothesise that prey organisms of larger, mostly molluscivorous and piscivorous *Conus* species are more abundant on the subtidal reef, where food supply and the quantity of refuges are larger.

**Acknowledgements**

We thank the Red Sea Environmental Centre and Sinai Divers Backpackers in Dahab for help with logistics and field assistance, Mag. F. Scharhauser for fruitful discussions, H. Breitenfellner for the photographs, Michael Stachowitsch for comments and Alan J. Kohn for a careful review of the manuscript.

**Disclosure Statement**

No potential conflicts of interest are reported by the authors.

**Supplementary Material**

The tables and figures are given as a Supplementary Annex, which is available via the “Supplementary” tab on the article’s online page (http://dx.doi.org/10.1080/09397140.2016.1182781).
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