MASTERARBEIT

Titel der Masterarbeit

„Diversity, habitats & size-frequency distribution of the gastropod genus *Conus* at Dahab (Gulf of Aqaba, Northern Red Sea)“

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angestrebter akademischer Grad

Master of Science (MSc)

Wien, 2015

Studienkennzahl lt. Studienblatt:	A 066 833
Studienrichtung lt. Studienblatt:	Master Ökologie
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ABSTRACT

The venomous gastropod genus *Conus,* one of the most diverse marine genera, is widely distributed throughout coastal marine environments of the tropics and is particularly diverse in the Indo-West Pacific region. Previous ecological assessments have demonstrated that topographically complex subtidal coral reefs support the highest number of *Conus* species with the lowest population densities, intertidal reef flats are of intermediate diversity and high abundance, and extensive subtidal sand areas are the least diverse habitat types. However, no study has so far particularly addressed *Conus* distribution patterns in the Northern Red Sea. Therefore, I provide a first ecological assessment of the genus *Conus* along a fringing reef coastline in the Southern Sinai (Dahab, Egypt), analyzing sampling quadrats from a total of 73 line-transects in five ecologically distinct habitats with water depths ranging from 0 to 15 m. Ecological information was obtained for a total of 258 individuals of 14 species (9 living and 12 dead). 175 living and 83 dead individuals were collected for identification and size measurement with calipers. The three most abundant species *C. parvatus* Walls, 1979, *C. taeniatus* Hwass in Bruguière, 1792 and *C. tessulatus* Born, 1779*,* predominantly feeding on polychaetes, accounted for 80 % of the total living assemblage. Hard substrata were dominated by *C. parvatus* whereas soft substrata supported a high abundance of *C. tessulatus*, suggesting that hard and soft substrata are generally dominated by different *Conus* species according to their feeding ecology and the availability of refuges. Results demonstrated that the distribution of *Conus* on subtidal reefs around Dahab strongly overlapped with other habitat types from the region. Subtidal reefs are considered to be the most heterogeneous habitat type, where coral blocks alternating with sand patches and rock of varying portions establish numerous microhabitats which can be exploited by *Conus*. Contrastingly, the other habitats showed a more characteristic species composition, whereby subtidal and intertidal sand characterized by large, uniform areas of soft substratum with similar ecological properties were almost identical in species composition. The average shell length of *Conus* was 15 ± 9 mm in the living and 17 ± 14 mm in the dead assemblage with a general size range of 6 - 85 mm. Furthermore, except for the intertidal, living and dead assemblages of the individual habitats showed high similarities and peaked between 9 and 15 mm of size, indicating that postmortem processes may not be influential for the distribution of *Conus* around Dahab. Living and dead specimens from subtidal sand and the reef flat averagely consisted of smaller individuals than those of other habitats suggesting that these topographically simpler habitat types do not provide adequate refuges for larger specimens. The most dominant and smallest shells (*C. parvatus*, *C. taeniatus* and *C. miliaris*), were the ones most frequently occupied by hermit crabs, preferentially on the reef flat where the abundance of empty *Conus* shells was high. Results indicate that hermit crab distribution is influenced by favorable environmental conditions and the availability of empty gastropod shells such as *Conus* as a resource and that this supply is well utilized due to their general rarity.

ZUSAMMENFASSUNG

Die giftige Gastropoden-Gattung *Conus*, als eine der diversesten marinen Gattungen, ist in den Küstenlebensräumen der Tropen weit verbreitet und besonders artenreich im Indo-West Pazifik. Vorangegangene ökologische Erhebungen haben gezeigt, dass topographisch komplexe subtidale Korallenriffe die höchste *Conus* Diversität jedoch die geringste Populationsdichte aufweisen. Das intertidale Riffdach weist intermediate Diversität und hohe Abundanz auf und extensive subtidale Sandflächen sind jene Habitate mit der niedrigsten Diversität. Bis dato wurden jedoch in keiner Studie die Verteilungsmuster der Gattung *Conus* im nördlichen roten Meer untersucht, weshalb hier der erste ökologische Zensus dieser Art entlang einer Saumriffküste im Süd-Sinai (Ägypten) erhoben wurde. Die Probennahme erfolgte mittels Quadraten entlang von 73 Transekten in fünf unterschiedlichen Habitat Typen in Tiefenstufen von 0 bis 15 m. Ökologische Daten wurden für 258 Individuen aus 14 Arten erfasst (9 lebende, 12 tote). 175 lebende und 83 tote Individuen wurden bestimmt und mittels Schiebelehre vermessen. Die drei häufigsten Arten *C. parvatus*, Walls, 1979, *C. taeniatus* Hwass in Bruguière, 1792 und *C. tessulatus* Born, 1779, die sich hauptsächlich von Polychaeten ernähren, machten 80 % der Lebendvergesellschaftung aus. Hartsubstrate wurden von *C. parvatus* dominiert, wohingegen *C. tessulatus* in Weichsubstraten eine hohe Abundanz aufwies. Dies lässt darauf schließen, dass Hart- und Weichsubstrate von unterschiedlichen *Conus* Arten dominiert werden, entsprechend der Ökologie ihrer Ernährung und der Verfügbarkeit von Refugien. Die aktuelle Studie hat gezeigt, dass die Artenzusammensetzung in subtidalen Korallenriffen um Dahab sehr heterogen ist und die dort gesammelten Arten auch in den anderen Lebensräumen vorkommen. Man kann daher annehmen, dass diese Tatsache von der generellen Heterogenität dieses Habitattypes herrührt, da dort Korallenblöcke abwechselnd mit Sandflächen und Fels variablen Anteils vorkommen und dadurch eine Reihe von Mikrohabitaten für *Conus* schaffen wie es in keinem anderen Lebensraum der Fall ist. Im Gegensatz dazu, zeigten die anderen Lebensräume klare Abgrenzungen in ihrer Artenzusammensetzung, speziell die reinen Sandhabitate, die sich durch ähnliche ökologische Eigenschaften auszeichneten, zeigten starke Ähnlichkeit untereinander jedoch starke Abgrenzung zu den anderen Lebensräumen. Weiters wiesen auch Lebend- und Totvergesellschaftung der einzelnen Lebensräume untereinander keine Unterschiede auf, mit Ausnahme des Intertidals. Bei einem Größenbereich von 6 - 85 mm betrug die mittlere Schalengröße der Lebendvergesellschaftung 15 ± 9 mm, die der Totvergesellschaftung 17 ± 14 mm. Die häufigste Größenklasse war jene von 9 bis 15 mm. Diese Ähnlichkeiten zwischen Lebend- und Totvergesellschaftungen lassen annehmen, dass postmortem Prozesse keinen oder nur geringen Einfluss auf das Verteilungsmuster von *Conus* ausüben. Generell waren jene Individuen des Riffdaches und der subtidalen Sandflächen am kleinsten, was auf ein Fehlen von geeigneten Refugien hindeuten könnte. Die dominantesten und zugleich kleinsten Arten (*C. parvatus, C. taeniatus* und *C. tessulatus*) wurden am häufigsten von Einsiedlerkrebsen, vorzugsweise am Riffdach besiedelt, wo auch die Abundanz von leeren *Conus* Schalen hoch war. Dies deutet darauf hin, dass die Verteilung der Einsiedlerkrebse von den Umweltfaktoren und der Verfügbarkeit leerer Gastropoden-Schalen wie *Conus* beeinflusst wird und diese Ressource aufgrund ihres limitierten Vorkommens optimal ausgenutzt wird.

INTRODUCTION

The predatory gastropod genus *Conus* (Linnaeus 1758) constitutes the monotypic family Conidae (Fleming 1822) and is one of the most species-rich marine genera with currently 761 recognized species with predominately tropical distribution (Kohn 1990). The gastropod superfamily Conoidea includes the widely distributed families Conidae, Terrebridae and Turridae. The Conoidea form part of the order Neogastropoda in the sub-class Prosobranchia of the class Gastropoda of the phylum Mollusca (Röckel et al. 1995). This diverse superfamily, also known as Toxoglossa shares one feature common to all species: the venom apparatus, used to rapidly capture prey (Kohn 1959; Taylor et al. 1993). *Conus* immobilizes prey by injecting a neurotoxic venom through a harpoon-like radula tooth (up to six in some molluscivorous species), which can vary in shape, depending on the feeding ecology of the particular species (Kohn 1998; Kohn et al. 1999; Duda et al. 2001). Three groups of *Conus* species can be distinguished according to their feeding mode (Kohn 1959): Vermivors, as the largest group of *Conus* species, prey on polychaetes of different families, whereas molluscivors and piscivors 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 1994; Beesley et al. 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 et al. 1995; Monteiro et al. 2004). The highest diversity of *Conus* is present in the Indo Pacific region, which is known to contain the largest number of extant species in many groups (Röckel et al. 1995). A recent study gives reasonable evidence to suggest that at least 10 % of the *Conus* species worldwide are under threat, with some endemic species even being critically endangered (Peters et al. 2013).

On coral reefs of the tropical Indo-West Pacific, high *Conus* population density and low diversity characterize reef flats, whereas low population density and high diversity characterize subtital 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 an important factor for *Conus* diversity and abundance (Kohn and Leviten 1976; Leviten and 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, 1994; Kohn & Nybakken 1975; Kohn & Leviten 1976; Leviten & Kohn 1980; Kohn & Perron 1994; Vallejo 2005), little ecological information is available on the distribution patterns of *Conus* in the Northern Red Sea (Kohn 1964; Fishelson 1971; Fainzilber et al. 1992; Zuschin et al. 2000, 2001).Therefore, the goal of the present work was to study the distribution patterns of *Conus* in different shallow marine habitats around

Dahab (Northern Red Sea) and to obtain information on the importance of substrate type and habitat complexity for the abundance of this diverse genus.

STUDY AREA

The Gulf of Aqaba

The Gulf of Aqaba is a narrow subtropical marine water body with a width of 14-26 km extends over 170 km from the Israeli and Jordanian coast in the North to the Strait of Tiran in the South (Klinker et al. 1978; Fig. 1). As part of the African rift valley the Gulf is descending to over 1,800 m depth and forms a unique topography consisting of various types of shore. The arid desert climate characterized by low rainfall averages (22-25mm/year) and predominantly northern and northeastern winds, results in high evaporation and high salinities, ranging between 40 and 41.5 ‰ (Friedmann 1968; Usiel 1968; Loya 2004). These climatic, oceanographic and geological conditions together with the Gulf's oligotrophic character have shaped the Red Sea's rich marine flora and fauna with its high endemism ratio (Sheppard et al. 1992).

Habitat types

Distribution patterns of predatory *Conus* assemblages were studied in several habitat types (hard and soft substrata): subtidal reef, reef flat, subtidal sand, intertidal sand and seagrass meadow (Tab. 1). Coral reefs along the Dahab coast are exclusively of the fringing type which form belts along the shelving shoreline and show the typical zonation into reef flat, reef crest and reef slope (Fishelson 1973). Habitat types distinguished here are similar to the classification of *Conus* habitat types of Kohn (1967).

1. *Reef flats.* This emerged shoreward habitat type consisting of coral rock bottom is highly affected by tidal fluctuations, wave action and variations of temperature and salinity. These factors limit coral growth but support other organisms such as encrusting and filamentous algae. Although of simple topography, reef flats provide numerous crevices and algal mats serving as shelter for many marine taxa such as gastropods of the genus *Conus* (Kohn 1968, Leviten & Kohn 1980).
2. *Subtidal coral reefs.* Reef slopes, coral carpets and coral patches border the reef flats around Dahab, such as in many other areas of the Red Sea (Reiss and Hottinger 1984; Piller and Pervesler 1989). They are of a more complex topography and dominated by coral associations of *Porites, Acropora* and *Millepora*. Subtidal reefs consist of several microhabitats

- living and dead coral heads, coral rock, sand and coral rubble – which provide important daytime shelter for many conids (Kohn 1967). Reef slopes across the sampling area start at the outer edge of the fringing reef and were characterized by high coral coverage in the upper 10 m where light intensity and water mixing are highest. The reef slope plunges down steeply to depths of 30 – 50 m or flattens out into a relatively shallow sand bottom. Coral carpets are defined as low-relief coral communities and are common around Dahab down to 30 – 40 m. Coral patches are subtidal coral reefs, patchy in their spatial distribution and are isolated across soft substrata from other subtidal reefs or coral patches. In the sampling area, coral patches occurred commonly at depths ranging from 3 – 40 m.

3. *Subtidal sand.* This habitat type is characterized by extensive areas of sand where species of *Conus* can burrow during the day. These areas are common in shallow bays or lagoons and often border the reef flats and reef slopes around Dahab. They are known to be the habitat type with the lowest *Conus* diversity (Kohn 1967).
4. *Seagrass meadows.* This habitat type usually ranges from 2 – 18 m depth around Dahab, exhibited extensive areas of sand covered by seagrass of the species *Halophila stipulacea*.
5. *Intertidal sand.* Characterized by vast stretches of sand, this habitat type is distinguished from subtidal sand only by the fact that it partially falls dry in a semidiurnal manner.

MATERIAL & METHODS

Sampling stations

Table 1 gives an overview of the habitat types and sampling stations. The reef flat studied was an approximately 20 - 30 m wide table-shaped bench at 'The Islands' (28°28.593' N 034°30.391' E), with a relatively high algal coverage shoreward and declining in a seaward direction where coral abundance increases. Sand-filled depressions and rock cracks are common and large portions of the reef flat are covered with algal-bound sand or a thin layer of sand. The whole flat is covered by water even during low tide (mid water level 0.5 – 1m).

Subtidal reefs were sampled at four different locations (Tab. 1, 2): 'The Lighthouse' (28° 29.944' N 34° 31.182' E; reef slope and coral patches), 'The Islands' (28°28.655' N 034°30.731' E; reef slope and coral patches), 'Moray Garden' (28°26.262' N 034°27.534' E; coral carpet) and 'Abu Helal' (28°32.542' N 034°30.998' E; coral carpet). All stations displayed a similar structure and topography and were characterized 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 patchy reefs.

Subtidal sand was sampled at three locations: 'Coral Garden' (28°33.294' N 34°31.257' E), 'Golden Blocks' (28°26.342' N 34°27.812' E) and 'Moray Garden' (28°26.262' N 34°27.534' E). These were shallow sand stretches adjacent to the reef table.

Sandy seagrass meadows were studied at 'Mashraba' (28° 29.712' N 34° 31.021' E), 'Bannerfish Bay' (28° 29.934' N 34° 31.125' E) and 'The Lighthouse' (28° 29.944' N 34° 31.182' E).

The intertidal was surveyed at the Kite lagoon in Dahab (Fig. 1;28° 28.593' N 34° 30.391' E). The Kite lagoon can be characterized by its protected location behind fringing reefs and its low relief which let develop a large tidal flat, popular for recreational activities (Zuschin et al. 2015).

Sampling design

Specimens were collected at different depths in the range of 0 to 15 m using SCUBA and snorkelling (Tab. 1, 2). Line transects in combination with the quadrat method were performed parallel to shore at each location and habitat type. On hard substrata, a 20 m transect line was used with a 1 m^2 quadrat placed at intervals of 5 m resulting in a sampled area of 5 m^2 for each transect (Fig. 2). Due to the time and labor-intensive sampling method for soft substrata, a 10 m transect line was used with a 0.25 m^2 quadrat placed every 2.5 m (1.25 m^2 per transect). The starting point for each transect was chosen by haphazardly throwing a quadrat from a few meters above the substratum. Quadrats from subtidal sand transects were sieved (Ø 2 mm) in order to include endobenthic individuals. Different microhabitats are known to be utilized by different *Conus* species (Kohn 1967, Kohn 1968, Leviten & Kohn 1980, Kohn 1983, Kohn 2001). In order to evaluate whether certain 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. Living and dead individuals (empty shells and those inhabited by hermit crabs) were collected for identification and size measurement with calipers. Abundances of living and dead species were recorded for all habitats. Easily identifiable individual or especially large specimens were not collected but measured and identified *in situ*. *Conus* identification was based on Rusmore-Villaume (2008), Röckel et al. (1995) and on a well sorted collection present at the Red Sea Environmental Centre (RSEC) in Dahab. All specimens were released after identification and size measurement.

Data analysis

The data set was tested using analysis of similarities (ANOSIM, Clarke and Warwick 1994) in order to identify differences among *Conus* habitats for living and dead assemblages. Preparation of the data was performed by generating a similarity matrix from transect data using the Bray-Curtis coefficient of similarity (Bray and Curtis 1957). Samples with no occurrence of *Conus* were excluded from the analysis (37 transects) and the matrix was standardized by total (i.e., percentages were used) and square root transformed to downweight high abundances of some species. The one-way ANOSIM generates pairwise *R* values between 0 (no differences between transects) and 1 (perfect separation). The *R* statistic itself is a useful comparative measure of the degree of separation of sites, and its value is at least as important as its statistical significance which can be argued to be low if only few replicates in each group occur (Clarke and Gorley 2001). As stated in Clarke and Gorley (2001) *R* values ≥ 0.5 indicate clearly different groups whereas values < 0.25 indicate hardly any separation.

For a visual representation of the similarities between the 34 transects, non-metric multidimensional scaling (nMDS, Kruskal 1964) was performed based on the Bray Curtis similarity matrix. ANOSIM, nMDS, diversity index (Shannon-Wiener 1949: $H' = -\Sigma$ (pi) (log pi)) and species accumulation curves (species observed; 999 permutations) were conducted using the software package PRIMER 6 (Clarke and Warwick 1994). Species abundance distribution (living and dead assemblage) was summarized by histograms for each habitat using the software package Past (Paleontological Statistics; Hammer et al. 2001). Normality tests were performed using the Chi-square test (Yates 1934) and the Shapiro-Wilk test (Shapiro & Wilk 1965). Statistical differences between two or more samples were tested using the Student´s *t* test (Student 1908), the Mann-Whitney *U* test (Mann & Whitney 1947) and the Kruskal Wallis test (Kruskal & Wallis 1952).

RESULTS

Species composition & abundance

Ecological information was obtained for a total of 258 individuals of 14 species (9 living and 12 dead) from 73 transects, covering an area of 245 m^2. 175 living and 83 dead individuals were collected (Fig. 3A). Unidentifiable specimens (e.g. heavily encrusted shells) were grouped together and accounted for 7 % (N = 19) of the total assemblage. This group was excluded from species-related statistics. Half of the recorded species were represented by only one or two specimens.

The quantitatively most important species in this study were the vermivorous *Conus parvatus*, *Conus taeniatus* and *Conus tessulatus* (Tab. 3; Fig. 3 B, C; Supplementary Fig. 1, 2). Together, these species accounted for 80% of the living and 59% of the dead assemblage. The ubiquitous *C. parvatus* occurred in all habitats except in seagrass meadows and was most abundant on reef flats and subtidal reefs (Fig. 4 A-D). *Conus taeniatus* most frequently occupied different microhabitats on subtidal reef flats, preferentially algae on reef limestone (Fig. 5). In contrast, *C. tessulatus* was the dominant species on soft substratum where specimens were primarily buried in the sand. Other vermivorous species recorded in this study were *Conus miliaris* Hwass in Bruguière, 1792 most frequently found on the reef flat and *Conus flavidus* Lamarck, 1810 which occupied both hard- and soft substrata but is generally known to be more abundant on subtidal reefs interspersed with sufficient amounts of sand patches (Fig. 6)*. Conus arenatus* Hwass in Bruguière, 1792 and *Conus maldivus* Hwass in Bruguière, 1792 found on sand substrata and on dead coral, are both known to be associated with sand substratum and prey on polychaetes of different species whereas *Conus rattus* Hwass in Bruguière, 1792 is predominantly reported from subtidal reefs where specimens occasionally are found on dead coral covered with algae (Kohn 1959; Röckel et al. 1995). The latter species could only be found dead, buried in sand. The molluscivorous species *Conus pennaceus* Born, 1778 rarely occurs on reef flats but rather where sandy areas are large enough to provide substrate for burrowing during daytime. However, the only specimen found was an empty shell from the reef flat. *Conus textile* Da Motta, 1982 preys on *Conus* and other mollusks, generally prefers sand substratum and is considered rare on subtidal reefs. Specimens in this study could only be reported alive from a seagrass meadow and dead from subtidal sand. *Conus nussatella* Linnaeus, 1758*, Conus geographus* Linnaeus, 1758 and *Conus striatus* Linnaeus, 1758 are reported to be molluscivorous and where only represented by dead specimens (subtidal reef and reef flat). They are generally found in close vicinity to subtidal reefs buried in sand under coral rock or in rubble (Röckel et al. 1995; Kohn 1959).

Species accumulation curves approached, but did not reach asymptote in the habitat types suggesting that the sampling effort - although high - was unsufficient to cover the whole diversity per habitat, especially on the reef flat (Fig. 7).

Among the hard substrata, the reef flat was the habitat with the highest observed population densities of living and dead conids (~ 4 individuals/m^2, ranging from 1.8 to 13.2; Tab. 2). Species diversity was rather low (H' = 1.1, Tab. 4). At this topographically simpler habitat type, 120 living and 53 dead individuals of nine species were recorded, comprising approximately 60% of the entire collection. The dead assemblage on the reef flat consisted of more species than the living assemblage (eight/five – Tab. 4). The most abundant species were *C. parvatus, C. taeniatus* and *C. flavidus*.

Subtidal reefs around Dahab were characterized by low *Conus* densities (< 1 individual/m^2; Tab. 2) and a moderate species diversity (H' = 1.8, Tab. 4). From a total of nine species collected in this habitat type, six constituted the living assemblage and four the dead assemblage, both dominated by *C. parvatus* (Fig. 4, Tab. 4). The great majority of specimens from shallow subtidal reefs around Dahab occurred at 5 m depth (N = 16; see Fig. 8A) with the station 'Lighthouse' being most prominent (*N* = 9; Tab. 5). Due to the small sampling sizes for 10 and 15 m depth, no conclusions can be drawn as to whether certain species prefer particular depth ranges.

Subtidal sand was the soft substrata habitat with the highest population densities of living and dead conids (~ 2 individuals/m^2, highest densities at the station 'Golden Blocks'; Tab. 2) and ranked second among all substrate types. Species diversity was relatively low (H' = 1.3, Tab. 4). Six species occurred in the extensive subtidal areas of sand, four of which constituted the living and five the dead assemblage (Tab. 4). Here, the living assemblage was dominated by *C. tessulatus,* whereas *C. parvatus* and *C. tessulatus* were dominant among the dead assemblage (Fig. 4).

Sandy Seagrass meadows showed low population densities of living and dead conids (<1 individual/m^2; H' = 1, Tab. 4) and were dominated by *C. parvatus* and the sand-associated *C. arenatus*. This substrate type was occupied by three species, all of which occurred in the living assemblage but only two were also found in the dead assemblage.

The intertidal sand area was the least diverse habitat type (H' = 0.5, Tab. 4) with only two species, *C. tessulatus* and *C. maldivus;* only the former occurred in the living and the dead assemblage (Tab. 4, Fig. 4).

Based on the species composition of living and dead assemblages, most habitat types were well distinguishable (Tab. 6, 7, 8, Fig. 9). The reef flat constituted a relatively homogenous habitat clearly delineated from subtidal- and intertidal sand, but was rather similar to the species composition of seagrass meadows (Tab. 6, 7). Sub- and intertidal sand habitats formed a distinct cluster and did not show similarities in species composition with seagrass meadows. In sharp contrast, subtidal reefs were the most heterogeneous habitat type with a species composition overlapping with the fauna of adjacent habitats. The dead assemblage (Fig. 9B) showed nearly the same differences between habitat types, although with slight variations (Tab. 7).

Comparison of live and death assemblages did not show clear separation indicating a rather similar species composition within the habitats except for the intertidal (global R = 0.141; Tab. 8, Fig. 9C).

Microhabitat utilization

Microhabitat utilization was studied for reef flats (Fig. 5) and subtidal reefs (Fig. 6). The most frequently occupied substrate types on reef flats were limestone covered by a thin layer of sand bound by filamentous algae and macro-algae on reef limestone. These substrates were predominantly occupied by *C. parvatus* and *C. taeniatus,* the most abundant species found on the reef flat (Fig. 4). The majority of *C. parvatus* ($N = 50$) occupied algal-bound sand on limestone, whereas *C. taeniatus* was predominantly found on or underneath algae on limestone. *Conus flavidus* and *C. miliaris* were low in abundance and primarily occupied algal-bound sand on limestone. In addition, *C. parvatus, C. taeniatus* and *C. miliaris* were the most abundant species among the dead assemblage on reef flats (Fig. 4).

More than 90% of all *Conus* specimens occurred on hard substrata; here, living coral heads and bare rock were occupied most frequently (Fig. 6). The most abundant species *C. parvatus,* mostly occupied bare rock or small rock cracks (Fig. 6).

Size-frequency distribution

The size-frequency distribution of both, living and dead assemblage peaked between 9 and 15 mm of size (Fig. 3). The average shell length was 15 ± 9 mm in the living and 17 ± 14 mm in the dead assemblage (size range 6 - 85 mm) and this size difference is statistically significant (U-test: $p = 0.04$). From all the species only *C. taeniatus* showed a significant difference in size between its living and dead assemblage (U-test: $p < 0.002$). Living and dead *Conus* populations of subtidal sand and reef flat consisted of smaller individuals than those of other habitats (U test: $p < 0.02$). No correlation between shell length and sampling depth could be found. In addition, no significant differences in shell length of living *Conus* could be found between habitats of sampling stations (Tab. 4). Moreover, shell lengths of living and dead specimens did not vary significantly among different microhabitat types of the reef flat ($p > 0.5$).

In this habitat however, specimens occupying different substrate types did not show significant variations in size (Kruskal-Wallis test: $p > 0.4$).

Individuals of the same species showed generally little variance in size between habitats (Tab. 9). Comparison of shell lengths of the numerically most important species (*C. parvatus, C. taeniatus* and *C. tessulatus*) for all habitat types revealed that specimens of *C. parvatus* were significantly smaller on the reef flat than in any other habitat (U-test: $p < 0.02$). This, however, holds only true for the living assemblage, whereas dead assemblages showed no significant differences in size between habitats (mainly due to either very small sample sizes or large variation among sample sizes). *Conus taeniatus* did not differ in size between habitats whereas *C. tessulatus* was significantly smaller on subtidal sand than on the intertidal sandy beach of Dahab´s lagoon (U-test: $p < 0.02$).

Hermit crab-inhabited shells

In total, 83 dead shells were found, of which 51 were hermit crab-inhabited and 32 were empty (Tab. 4, 6; Fig 10). The quantitatively most important species occupied by hermit crabs were *C. parvatus* (N = 19), *C. taeniatus* (N = 10) and *C. miliaris* (N = 7). The remaining four species (*C. flavidus, C. striatus, C. tessulatus, C. nussatella*) were represented by only one or two individuals. The average size of hermit crab-inhabited shells was 17 ± 14 mm, compared to 18 ± 15 mm for empty shells, but the size frequency distribution of dead empty shells and hermit crab-inhabited shells is not significantly different (Fig. 10). The great majority of dead specimens was found on the reef flat and almost all of those (88%; six species) were hermit crab inhabited. There, algae-covered limestone was the most frequently occupied microhabitat type (52%), followed by sand-covered limestone (21%) and algal-bound sand on limestone (17%). Sand patches were only occupied by 9% of the hermit-inhabited shells on the reef flat. The remaining 12 % which were occupied by hermit crabs were found on subtidal reefs, subtidal sand and seagrass.

DISCUSSION

Species diversity and abundance

As a general rule, 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 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, and extensive subtidal sand areas are least diverse. This is partially supported by the findings of the present study: Subtidal reefs displayed the highest species richness and the lowest population densities in the sampling area (H' = 1.5; n = 15; < 1 individual/m^2) but reef flat and subtidal sand assemblages were fairly similar in species richness and population density (Tab. 3, Fig. 4).

These minor differences between the habitats could be attributable to an unsufficient sampling effort. The number of recorded species in all species accumulation curves (Fig. 6) did not reach asymptote, suggesting that the samples were not saturated. This holds particularly true for subtidal reefs, where the rather steep slope of the species accumulation curve indicates that at least a small fraction of the species diversity remains to be discovered. This could in particular be *Conus sanguinolentus* Quoy & Gaimard, 1834, a small vermivorous species, which is usually found under coral boulders or in crevices on reef flats. Additionally, although rare in the Northern Red Sea, *C. quercinus* Lightfoot, 1786, *C. vexillum sumatrensis* Hwass in Bruguière, 1792 and *C. aulicus* Linnaeus, 1758 would have especially matched the subtidal reef and reef flat assemblage. One reason for undersampling 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 which might lead to a reduced species diversity observed. Nevertheless, subtidal reefs are generally known to support the lowest number of specimens (e.g. Kohn 1967, 1968, 1983; Kohn & Leviten 1976) due to the fact that living coral harbors the lowest prey densities. Moreover, it is thought that *Conus* avoids contact with the coral's nematocysts (Kohn 1967).

The reef flat, as topographically simpler habitat type, supported the largest number of specimens. Favorable conditions might include the high proportion of algal-bound sand, which tends to stabilize 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, and thus support high species abundance in an otherwise harsh environment. It can also be taken into account that the sampled reef flat, in contrast to those studied by Kohn et al. (e.g. 1967; Leviten & Kohn 1983), was never exposed to air at low tide and thus lacked an important stress factor which might play a role in *Conus* abundance on reef flats.

The structurally uniform subtidal sand areas around Dahab were characterized by intermediate population densities of few dominating species. The results thus suggest that these most abundant species have well adapted to burrowing into the substrate and utilizing it as both, refuge and nutrient source.

Seagrass meadows supported low *Conus* population densities, similar to those previously investigated by Kohn (1980) and there is evidence that similar ecological mechanisms as in subtidal sand areas limit *Conus* abundance in this habitat type.

The intertidal sand area showed a species composition related to subtidal sand areas although *Conus* abundance differed and was the lowest recorded. It can be hypothesized that desiccation at low tide is a limiting factor in this habitat.

Species distribution & microhabitat utilization

Vermivorous species

Vermivorous species were the most abundant in shallow marine habitats around Dahab. These species, known to prey on various groups of polychaetes, are considered to be highly specialized. 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. In order to access this food source, the radula tooth of many vermivorous species has a special shape and is not held by the proboscis after injection (Kohn 1959) but rather remains in the prey while the proboscis quickly retracts. Both, *C. flavidus* and *C. parvatus* mainly feed on tube-dwelling polychaetes that live on the underside of coral rock or on coral rubble. Other vermivorous species predominantly prey on sand-dwelling polychaetes and thus prefer extensive sand stretches in which they can burrow (e.g. *C. tessulatus*). 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. Results from the present study conclude, that many vermivorous species are associated with either hard substrata (e.g. *C. parvatus)* or soft substrata (e.g. *C. tessulatus)* according to their feeding behavior and that distribution of these species depends on the availability of refuges and prey organisms, respectively.

Molluscivorous and piscivorous species

The only two living molluscivorous and piscivorous species *(C. textile* and *C. nigropunctatus)* found around Dahab were previously reported from other studies in the same habitat types (e.g. Kohn 1959). *Conus textile,* as a predator of epifaunal grazers and other *Conus* species on seagrass meadows and rarely on subtidal reefs and *Conus nigropunctatus* typically on reef flats but also in small numbers on sand bottom or rubble of subtidal reefs. On reef flats, *C. nigropunctatus* is usually the only entirely piscivorous species. These results suggest that food supply for molluscivors and piscivors is generally lower than for vermivors especially in topographically simpler habitat types such as subtidal sand and can therefore be considered lower in abundance than that of vermivors.

Species composition of habitat types

Ordination of *Conus* abundance as well as frequency distribution of *Conus* indicate that most of the habitat types showed a characteristic species assemblage (Tab. 6, 7; Fig. 4, 9). Differences in species composition among habitat types can be explained by the varying physical and environmental conditions of the distinct habitat types. The reef flat, with its generally harsh conditions is subject to heavy wave action, water movement, high salinity and irradiation. A varyingly dense layer of algal-bound sand is crucial to provide *Conus* with a burrowing medium suitable as 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 such as *C. pennaceus* and that other species, such as the vermivorous *C. flavidus*, are so specialized on sand-dwelling polychaetes that the absence of sand patches limits their abundance. In contrast to this, the results of the present study showed that *C. flavidus* was most abundant on reef flats where individuals commonly occupied algal-bound sand on reef limestone. The only individual of *C. pennaceus*, although dead, was also found on the reef flat. These differences can be explained by a varying density of the algal mat and the amount of sandy areas between the reef flats studied by Kohn (1959) and the one at Dahab.

Subtidal and intertidal sand showed a similar species composition and their species diversities were the lowest recorded. This indicates that the two habitat types are rather uniform and that they only differ in their physical conditions. Extensive areas of pure sand characterize both habitat types, although the intertidal is especially exposed to desiccation and predation. These generally harsh conditions might act as limiting factor for *Conus* abundance in this habitat type.

Seagrass meadows seem to be habitats of an intermediate type with similar features to those of other soft substrata, and thus support similar species. However, there are some species reported to especially prey on fishes in seagrass meadows such as *C. textile*. This explains the differences in living as well as dead assemblages of the nMDS ordination between seagrass meadows and other soft substrata.

Subtidal reefs, as heterogeneous habitat types, show the largest within-habitat differences in terms of species composition due to the fact that they comprise of different microhabitats. It can be hypothesized, that this is generally due to the heterogeneity of this habitat type where coral blocks alternating with sand patches and rock of varying portions establish numerous microhabitats for *Conus.* It can be hypothesized though, that soft substrata in general support species with a higher degree of specialization in terms of food and microhabitat. Resource partitioning has also been suggested from Kohn (1968, 1980), Kohn & Nybakken (1975), and Leviten & Kohn (1980) and has to be further investigated in future studies.

Moreover, living and dead *Conus* assemblages inhabiting different habitat types were different in species composition, whereby rare species represented by only a single specimen (singletons) were negligible in quantitative terms. On the one hand, these specimens in the dead assemblage could have originated from other habitat types and transported to its location via water movement, hermit crabs or predators. On the other hand, it can be argued that these singletons represent very rare species which, in fact, are unlikely to be observed alive and therefore are part of the species community.

Size frequency distribution

The size-frequency distribution of both, living and dead assemblages peaked between 9 and 15 mm of shell length (Fig. 3), indicating that post-mortem processes such as transportation and redistribution of empty shells into surrounding habitats by water movement or hermit crabs may not be influential on *Conus* distribution patterns of different habitat types around Dahab. The living assemblages of the reef flat and subtidal sand consisted of the smallest specimens, which can be best seen in the abundance of *C. parvatus* and *C. tessulatus*. This is also consistent with findings from previous studies carried out by Kohn (1968) and Leviten & Kohn (1980). They both stated, that the generally strong water movement associated with tidal benches and a lack of refuges in this topographically simpler habitat type might be factors influencing the body size of *Conus*. This might hold true also for subtidal sand, where refuges are virtually not present, only in a way that specimens can burrow into the substrate. The topographically more complex subtidal reef habitat in contrast, provides shelter from predators and is to a much lesser extent exposed to water movement. Furthermore, it can be hypothesized, that prey organisms of larger, mostly molluscivorous and piscivorous *Conus* species are more abundant on the subtidal reef where food supply and quantity of refuges is usually larger.

Hermit crab occupation

Hermit crabs are known to have preferences for particular shells in terms of size, shape of the aperture and thickness and some species have even specialized on inhabiting long, narrow apertures such as those of *Conus* (Briffa & Mowles 2007; Vermeij 1978). Although several studies reported that hermit crabs rarely use empty *Conus* shells, the availability of particular size ranges for hermit crabs is likely to be determining for selection (Reese 1968, 1969; Mitchell 1975; Reddy & Biseswar 1993).

As the present results showed, size-frequency distribution of the dead and the hermit crab-inhabited assemblage correlated in shape and peaked between 9 and 15 mm of shell length. Consequently, the most dominant and smallest shells (*C. parvatus*, *C. taeniatus* and *C. miliaris*), were the ones most frequently occupied by hermit crabs, preferentially on the reef flat where the abundance of empty *Conus* shells was high. These results indicate that hermit crab distribution is influenced by the availability of empty gastropod shells such as *Conus* as a resource and that this supply is well utilized due to their general rarity (Provenzano 1960; Childress 1972; Vance 1972; Spight 1977; Elwood et al. 1979; Garcia et al. 2001). Conversely, it should be pointed out that empty shells from the subtidal were not utilized to the same extent, suggesting that conditions there were less favorable for hermit crabs than on the reef flat, where nutrient- and microhabitat availability is better. It can therefore be concluded that favorable environmental conditions and the available size range of each shell species determine the colonization of empty *Conus* shells by hermit crabs.

CONCLUSION

The results of this study showed that *Conus* diversity in the Northern Red Sea around Dahab is lower than in other parts of the Indo-West Pacific region. This is not surprising, taking into account the high latitude of the sampling area and the fact that *Conus* diversity decreases gradually away from the tropics. From a total of 14 species collected, five were exclusively found dead and only once, indicating that a considerable fraction of the total assemblage is rare in all sampled habitat types around Dahab. Furthermore, the results of the present study suggest that hard- and soft substrata support different *Conus* species. Possible factors for these variations in habitat use might be: the distribution of favorable microhabitat patches, the degree of physical stress and the availability of refuges and prey organisms. Subtidal coral reefs around Dahab, however, were not distinguishable from any other habitat in terms of species composition. The heterogeneity of this habitat type with different microhabitats forms an environment suitable for different *Conus* species and thus supports the biodiversity of *Conus* such as already known from subtidal reefs of the Indo-West Pacific. The three most abundant species *C. parvatus*, *C. taeniatus* and *C. tessulatus* were vermivors and accounted for 80 % of the living assemblage with *C. parvatus* dominating hard substrata and *C. tessulatus* supporting a high abundance on soft substrata. These findings suggest that hard- and soft substrata are generally dominated by different *Conus* species according to their feeding ecology and availability of refuges and that small vermivors must possess a clear advantage over molluscivors and piscivors. The size frequency distributions of the living, dead and hermit crab-occupied assemblage is of similar shape and peaked between 9 and 15 mm of shell length. It can therefore be concluded that this similarity indicates a rather negligible impact of postmortem processes on the distribution of *Conus* around Dahab and that hermit crabs which most frequently occupied the dominant *Conus* species on reef flats, tend to fully utilize their limiting resources.

ACKNOWLEDGEMENTS

I thank my supervisor Univ. Prof. Mag. Dr. Martin Zuschin for professional support and constructive criticism during the progress of this work. I would like to express my special appreciation to S. Raus for aiding with field work and F. Scharhauser for critical input and fruitful discussions. I would also like to thank H. Breitenfellner for professionally photographing my *Conus* collection and for his technical input. In addition, a thank you also to the Red Sea Environmental Center and Sinai Divers Backpackers in Dahab especially to MSc N. Milton and T. Furler for sharing their knowledge with me and supplying me with compressed air. My family and closest friends deserve the greatest thanks and respect for being my all-time back-up light.

Figure 1. Map of Gulf of Aqaba and the area around Dahab showing positions of all sampling stations at which samples were taken. For GPS coordinates see text. (Maps: Google Earth).

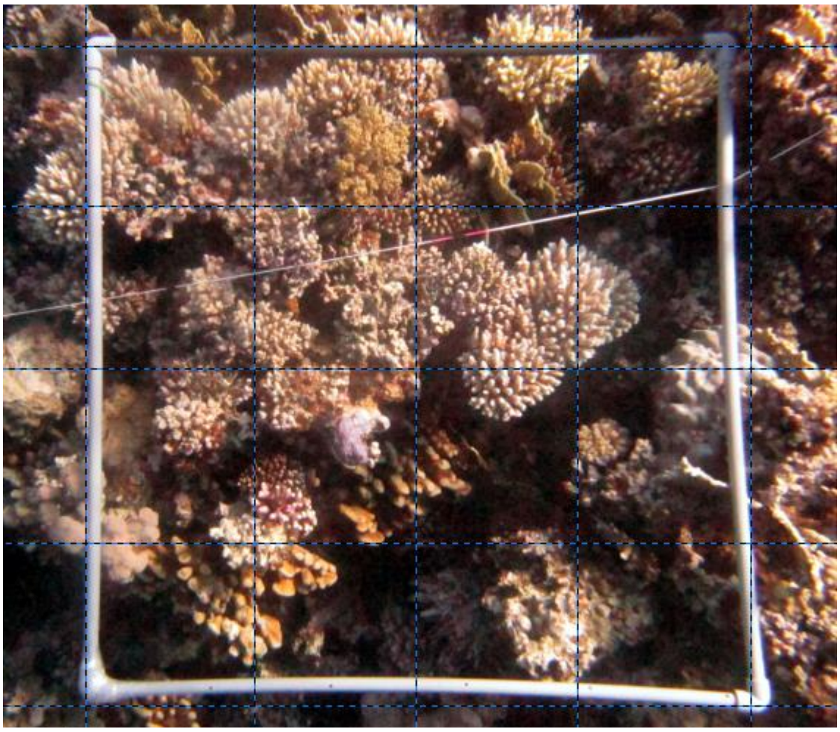


Figure 2. 1 m x 1 m sampling quadrat at a marked point on a line transect.

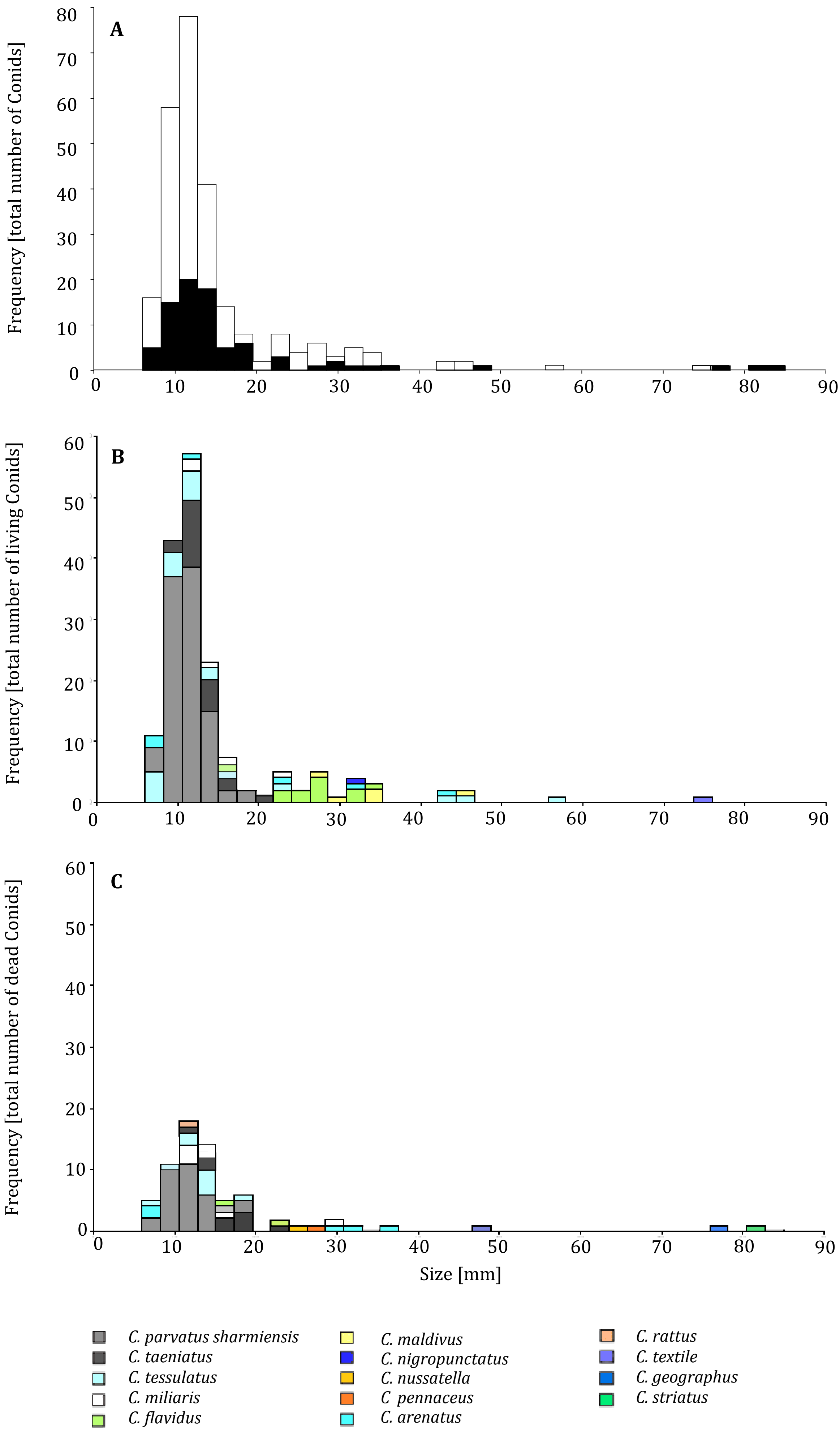


Figure 3. Size frequency distributions for the total number of Conids (A) with □ total assemblage ■ dead assemblage, total number of living Conids (B) and total number of dead Conids (C).

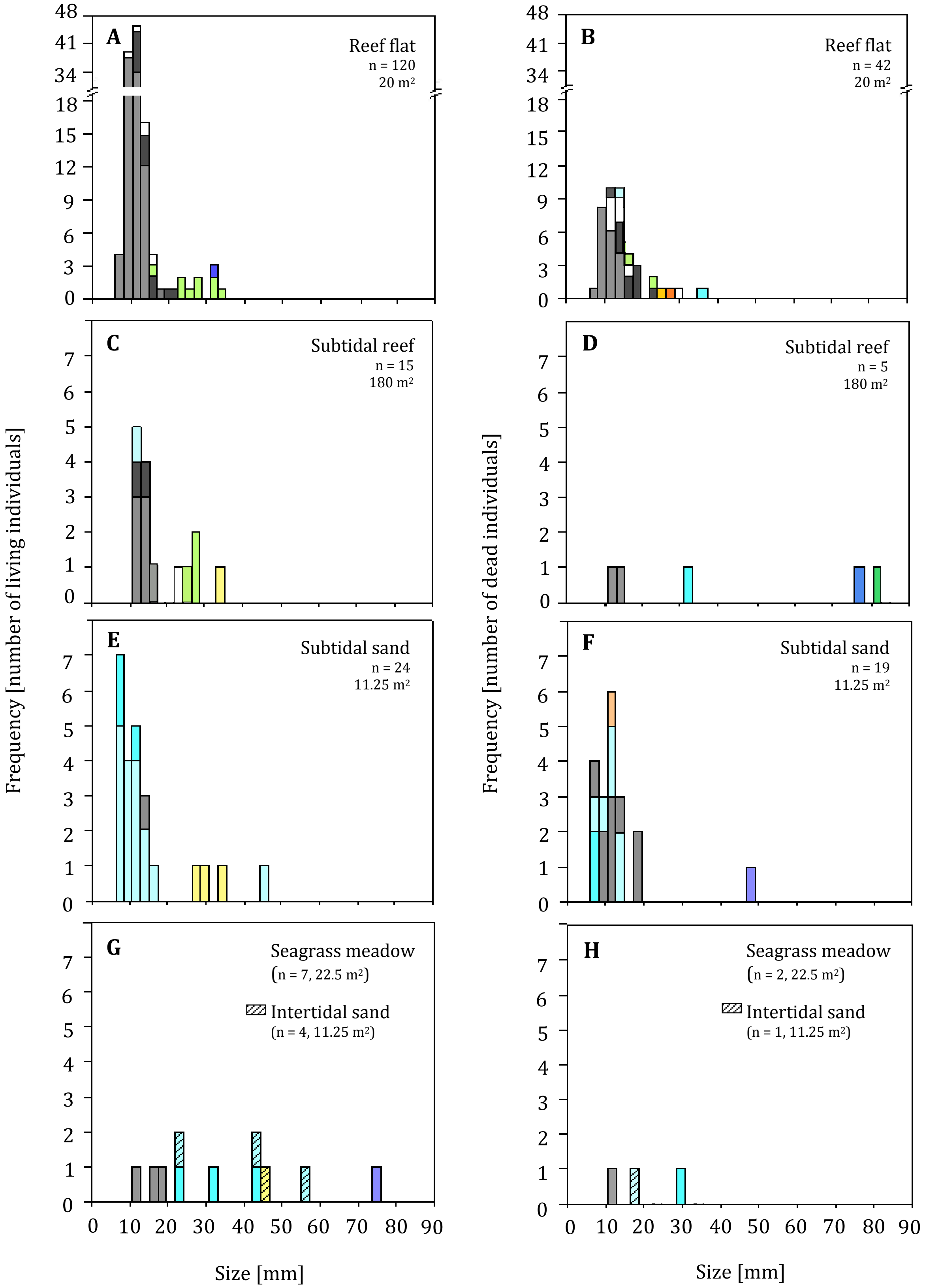
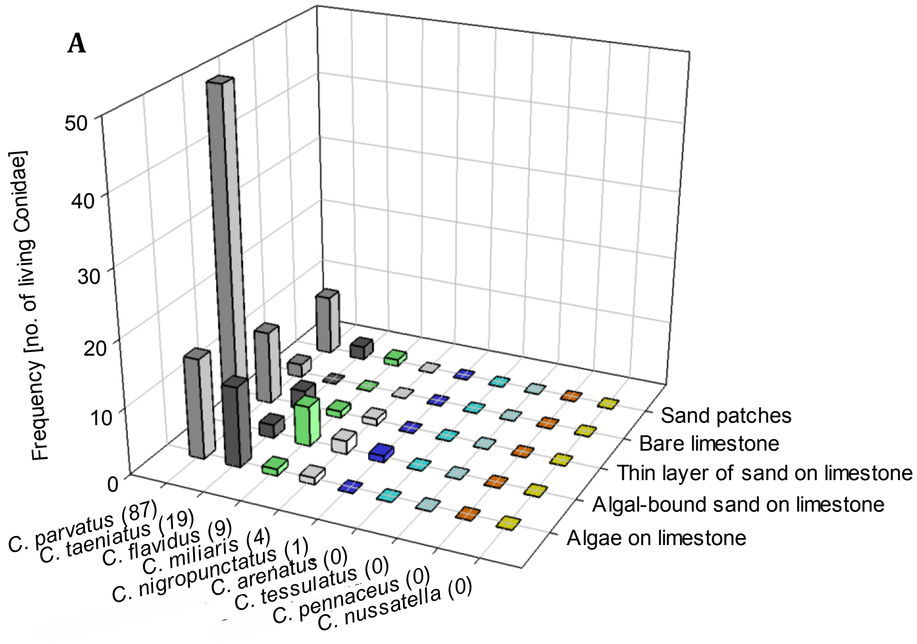


Figure 4. Size frequency distributions for the 14 *Conus* species per habitat. Sizes plotted for living (A-G) and dead (B-H) individuals. Reef flats (A-B), subtidal coral reefs (C-D), subtidal sand (E-F), seagrass meadows and intertidal sand (G-H). Cross-hatched patterns in G and H represent intertidal sand. Note the numerical dominance of the smallest size classes. For legend see Fig. 3.



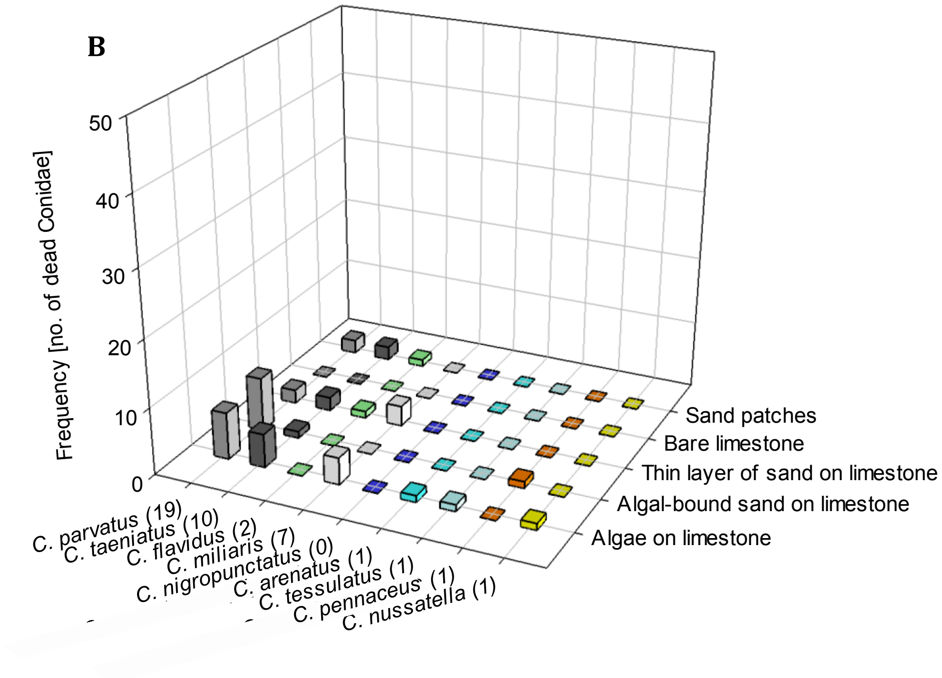
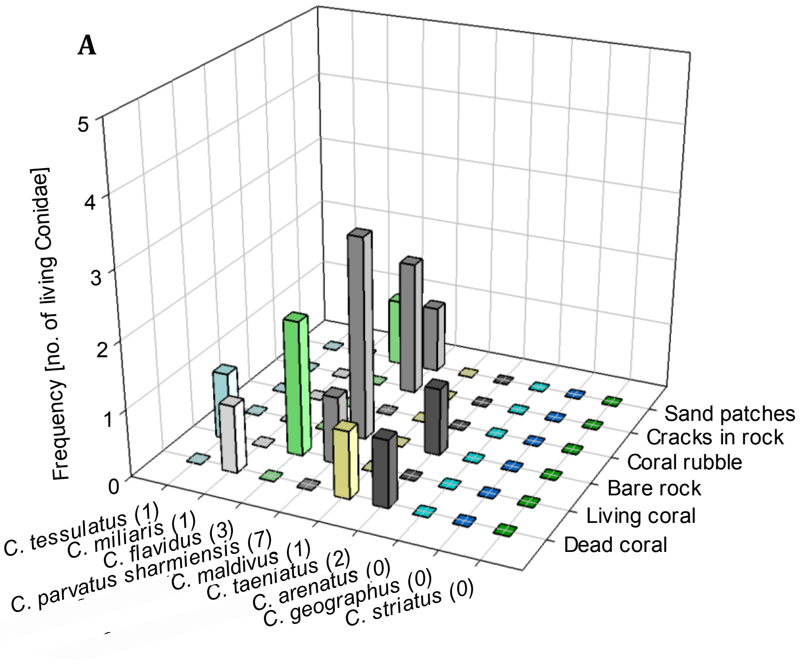


Figure 5. Microhabitat occupation on the reef flat of the location 'The Islands'. Vertical columns indicate the number of living (A) and dead (B) individuals per species found on different substrates of the reef flat. Numbers in brackets denote sample sizes.



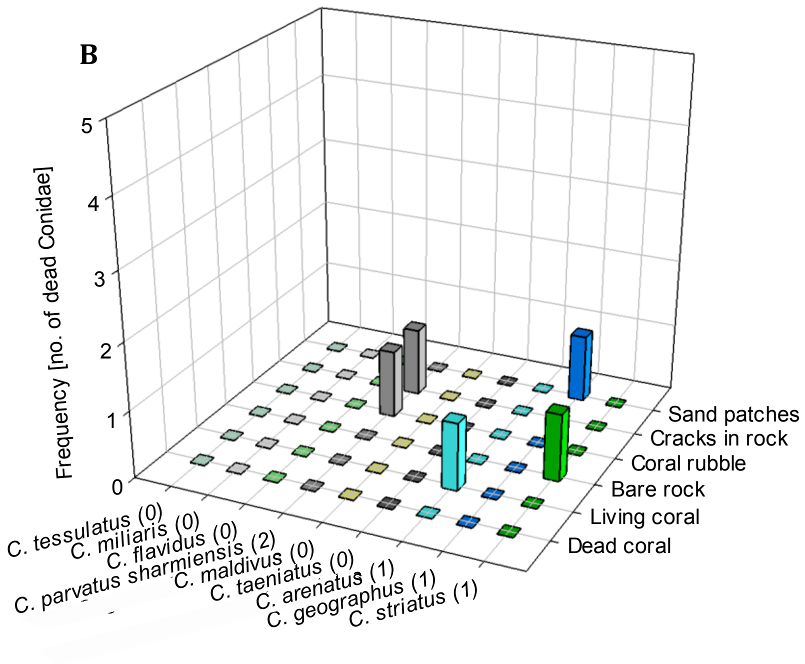


Figure 6. Microhabitat occupation on subtidal reefs. Vertical columns indicate the number of living (A) and dead (B) individuals of each species occurring on each microhabitat type at the four sampling stations listed in Table 2. Numbers in brackets denote sample sizes.

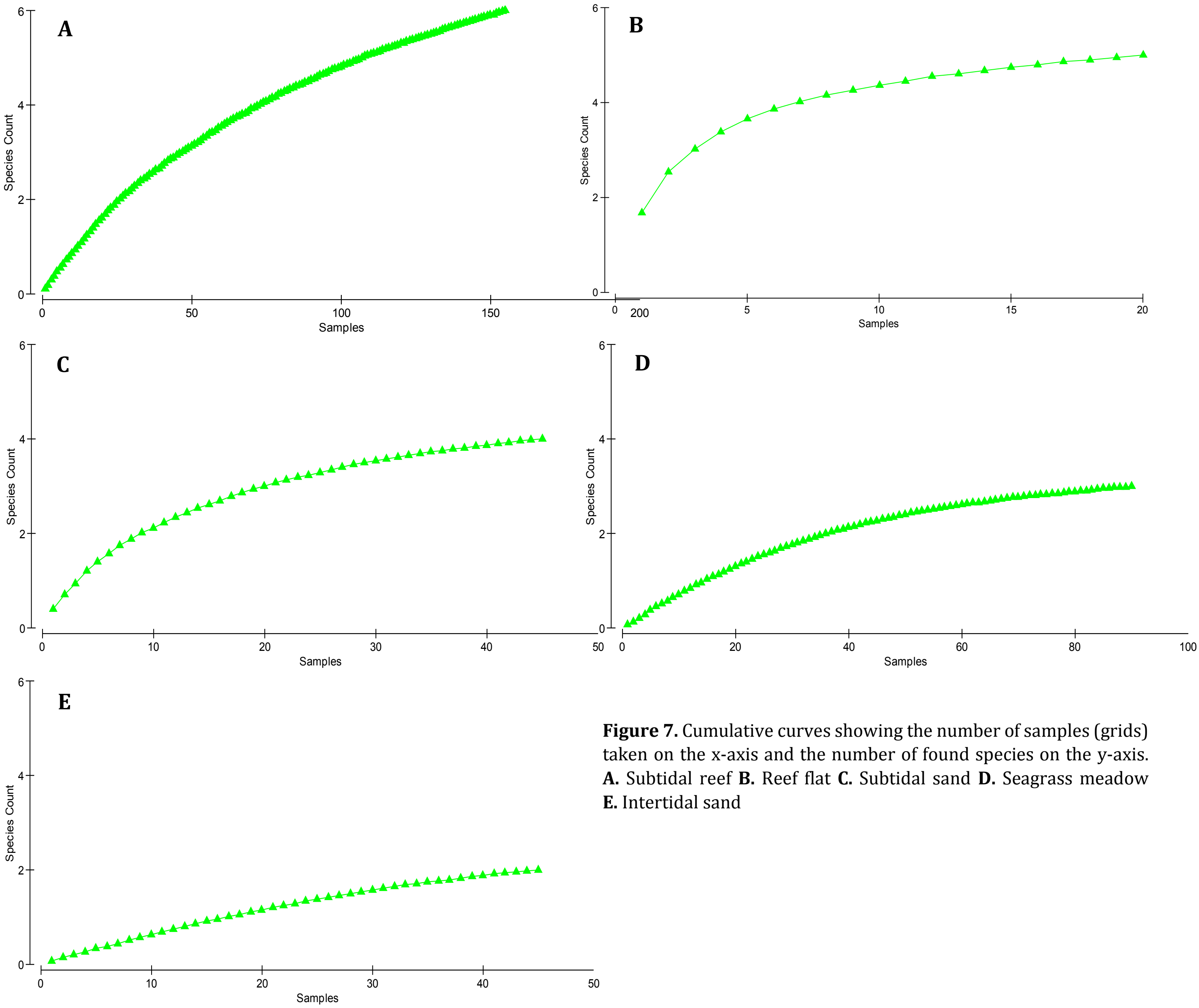
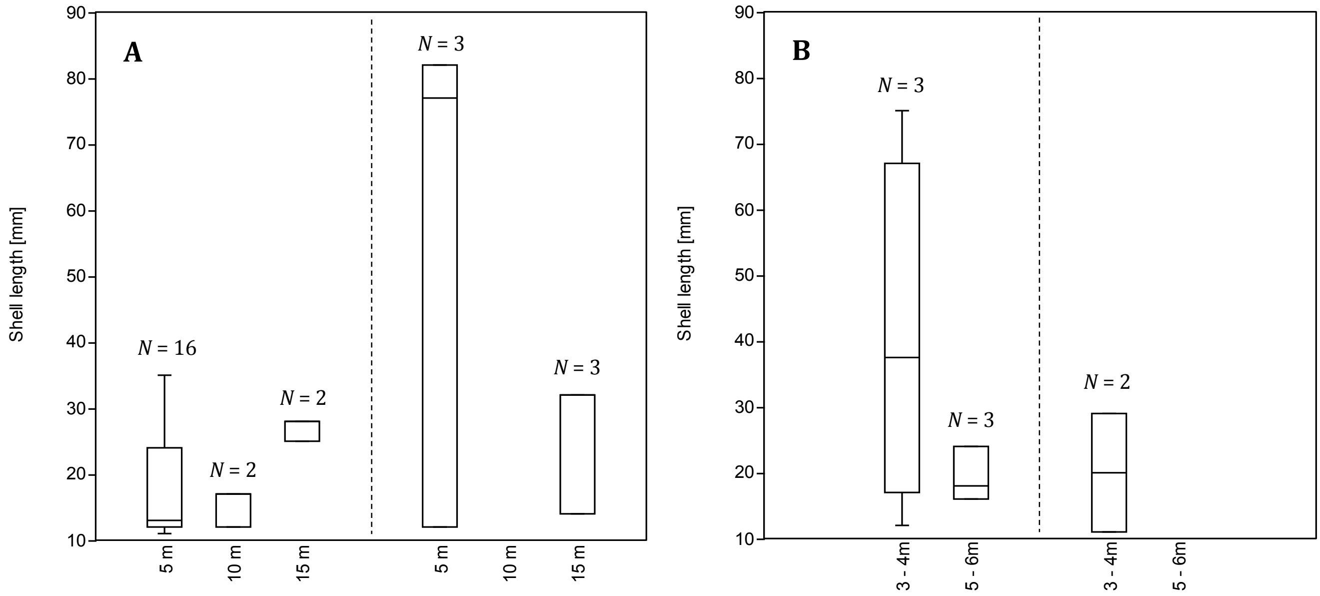


Figure 7. Cumulative curves showing the number of samples (grids) taken on the x-axis and the number of found species on the y-axis. **A.** Subtidal reef **B.** Reef flat **C.** Subtidal sand **D.** Seagrass meadow **E.** Intertidal sand



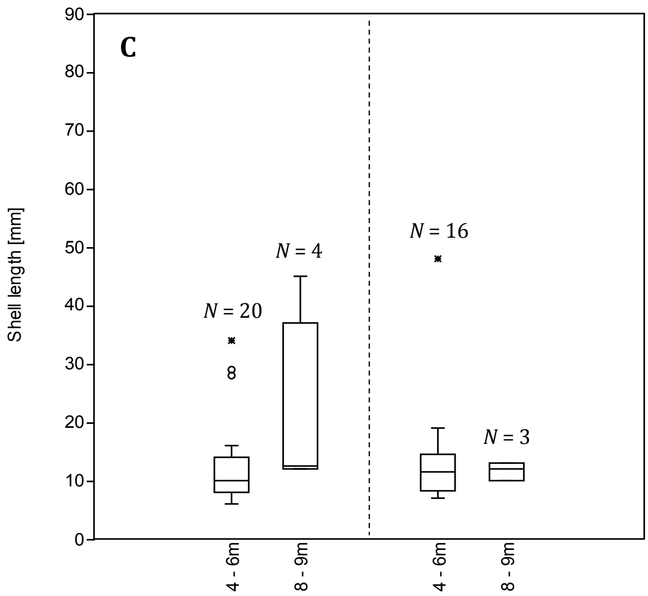


Figure 8. Comparison of shell lengths at different depths for three different habitat types. Living assemblages shown to the left of the dashed line, dead assemblages shown on the right. **A.** Subtidal reefs. **B.** Seagrass meadows. **C.** Subtidal Sand. Mild outliers (square) are defined as values greater than the upper quartile + 1.5x the interquartile range but smaller than the upper quartile + 3x the interquartile range, extreme outliers (asterisk) lie beyond that upper limit. Unidentifiable specimens are included.

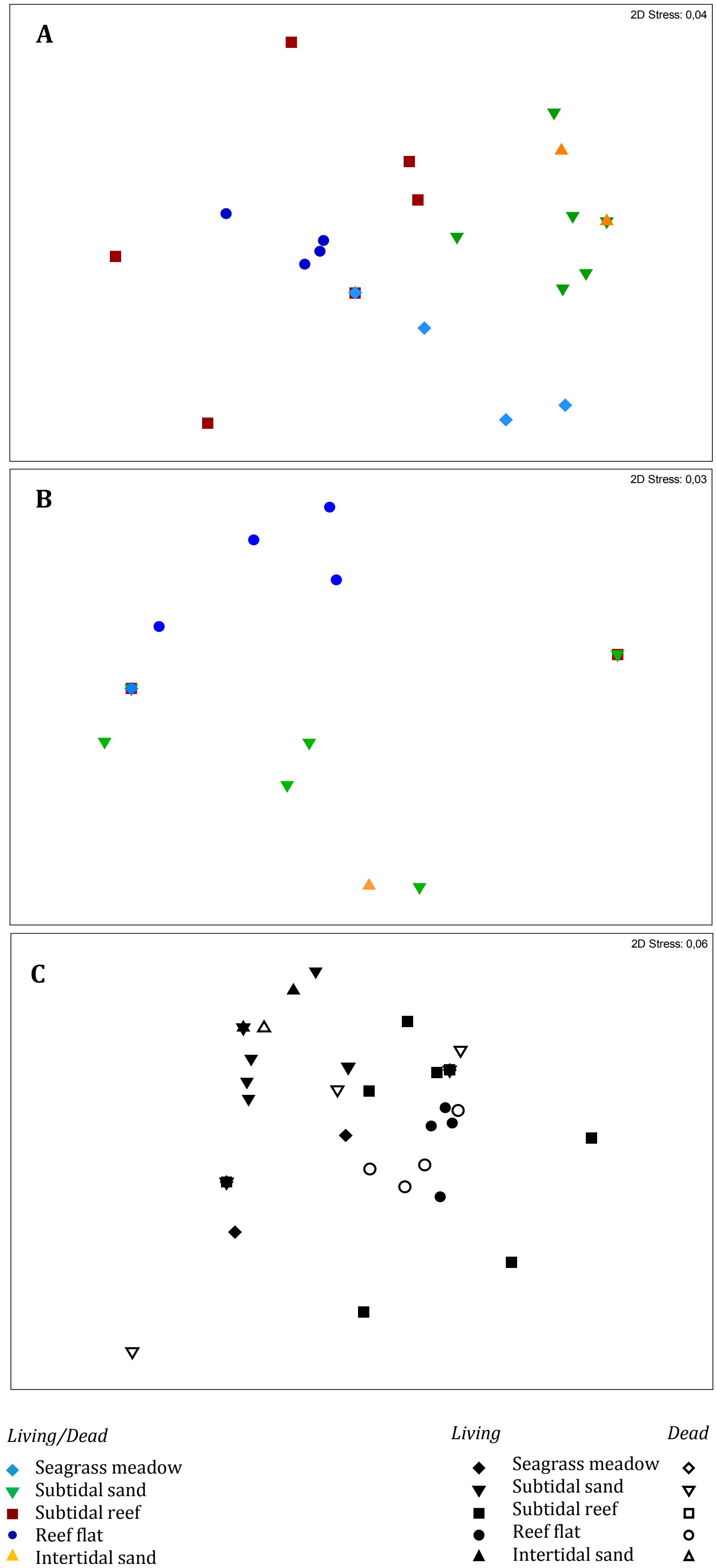


Figure 9. Ordination of *Conus* abundance. **A.** nMDS plot of living *Conus* assemblages from 27 transects at 11 sites. Distances between points correspond to dissimilarities in taxonomic composition. **B.** nMDS plot of dead assemblages from 16 transects at 9 sites. **C.** nMDS plot displaying living (black) and dead (transparent) *Conus* assemblages from 31 transects. The two groups do not show clear separation indicating a rather similar composition.

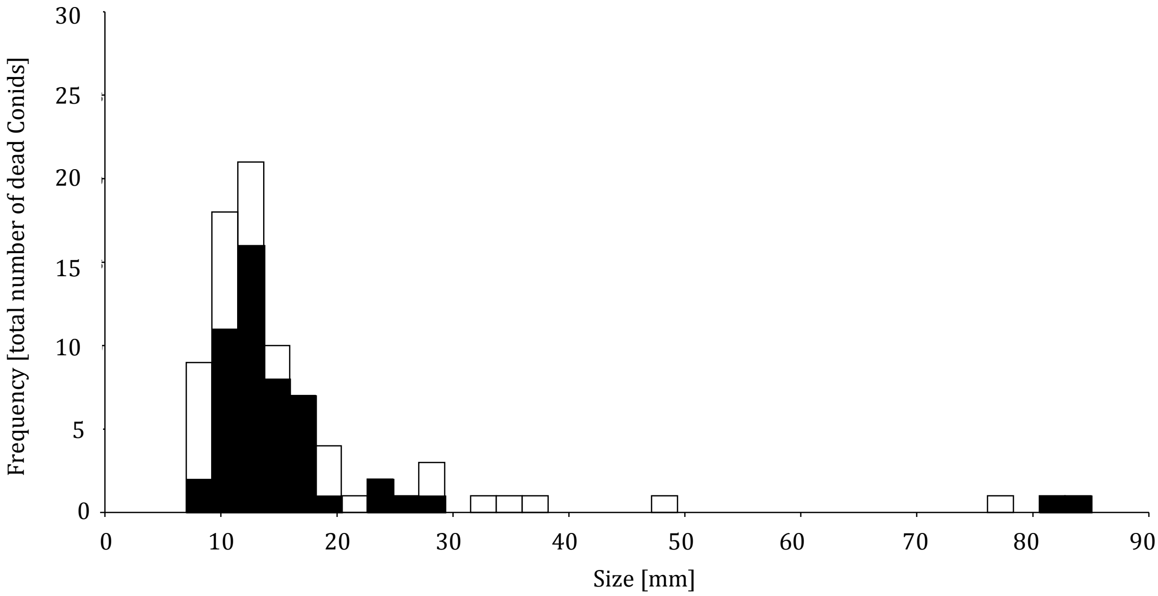


Figure 10. Size frequency distribution of dead conids, including shells that could not be identified to species level. White bars represent the total dead assemblage whereas black bars represent empty shells occupied by hermit crabs.

Table 1. Overview of the five *Conus* habitat types.

Habitat & Sampling location	No. of transects	Sampled area [m²]	Number of transects per sampling depth [m]	Coordinates
Subtidal reef				
Moray Garden	9	45	3 x 5, 3 x 10, 3 x 15	28°26.262’ N 34°27.534' E
Islands South	9	45	3 x 5, 3 x 10, 3 x 15	28°28.655' N 34°30.731' E
Abu Helal	6	30	3 x 5, 3 x 10	28°32.542' N 34°30.998' E
Lighthouse	9	45	3 x 5, 3 x 10, 3 x 15	28°29.944‘ N 34°31.182‘ E
Reef flat				
The Islands	4	20	< 1	28°28.655' N 34°30.731' E
Subtidal sand				
Coral Garden	3	3.75	5, 8, 9	28°33.294' N 34°31.257' E
Golden Blocks	3	3.75	4, 5, 4	28°26.342' N 34°27.812' E
Moray Garden	3	3.75	6, 5, 5	28°26.262’ N 34°27.534' E
Seagrass meadow				
Bannerfish Bay	6	7.5	4, 3, 4, 9, 8, 8	28°29.934' N 34°31.125' E
Mashraba	6	7.5	8, 7, 6, 7, 3, 3	28°29.712' N 34°31.021' E
Lighthouse	6	7.5	5, 6, 7, 4, 5, 4	28°29.944' N 34°31.182' E
Intertidal sand				
Dahab Lagoon	9	11.25	< 1	28°28.593' N 34°30.391' E

Table 2. Basic data on sampling locations. MG = Moray Garden, IS = The Islands, AH = Abu Helal, LH = Lighthouse, GB = Golden Blocks, CG = Coral Garden, BB = Bannerfish Bay, MS = Mashraba.

Transect	*Location*	*Depth [m]*	*Habitat type*	*Number of species*		*Population density*			
						Living [per m^2]		Dead [per m^2]	
				Live	Dead	Mean	Std. Dev	Mean	Std. Dev
1	MG	5	Subtidal reef (Coral carpet)	1	0	0.2	0.4	0	0
2	MG	5	Subtidal reef (Coral carpet)	0	1	0	0	0.2	0.4
3	MG	5	Subtidal reef (Coral carpet)	0	1	0.2	0.4	0	0
4	MG	10	Subtidal reef (Coral carpet)	1	0	0.2	0.4	0	0
5	MG	10	Subtidal reef (Coral carpet)	0	0	0	0	0	0
6	MG	10	Subtidal reef (Coral carpet)	0	0	0	0	0	0
7	MG	15	Subtidal reef (Coral carpet)	0	1	0	0	0.2	0.4
8	MG	15	Subtidal reef (Coral carpet)	1	0	0.2	0.4	0	0
9	MG	15	Subtidal reef (Coral carpet)	0	0	0	0	0	0
10	IS	5	Subtidal reef (Reef slope)	1	1	0.2	0.4	0.2	0.4
11	IS	5	Subtidal reef (Reef slope)	2	0	0.4	0.9	0	0
12	IS	5	Subtidal reef (Reef slope)	0	0	0	0	0	0
13	IS	10	Subtidal reef (Patch reef)	0	0	0	0	0	0
14	IS	10	Subtidal reef (Patch reef)	0	0	0	0	0	0
15	IS	10	Subtidal reef (Patch reef)	0	0	0	0	0	0
16	IS	15	Subtidal reef (Patch reef)	1	0	0.2	0.4	0	0
17	IS	15	Subtidal reef (Patch reef)	0	0	0	0	0	0
18	IS	15	Subtidal reef (Patch reef)	0	1	0.4	0.9	0	0
19	AH	5	Subtidal reef (Coral carpet)	1	0	0.2	0.4	0	0
20	AH	5	Subtidal reef (Coral carpet)	1	0	0.2	0.4	0	0
21	AH	5	Subtidal reef (Coral carpet)	0	0	0	0	0	0
22	AH	10	Subtidal reef (Coral carpet)	0	0	0	0	0	0
23	AH	10	Subtidal reef (Coral carpet)	1	1	0.2	0.4	0.2	0.4
24	AH	10	Subtidal reef (Coral carpet)	0	0	0	0	0	0
25	LH	5	Subtidal reef (Reef slope)	1	0	0.2	0.4	0	0
26	LH	5	Subtidal reef (Reef slope)	3	0	0.7	0.5	0	0
27	LH	5	Subtidal reef (Reef slope)	2	0	0.8	0.4	0	0
28	LH	10	Subtidal reef (Coral patches)	0	0	0	0	0	0
29	LH	10	Subtidal reef (Coral patches)	0	0	0	0	0	0
30	LH	10	Subtidal reef (Coral patches)	0	0	0	0	0	0
31	LH	15	Subtidal reef (Coral patches)	0	0	0	0	0	0
32	LH	15	Subtidal reef (Coral patches)	0	0	0	0	0	0
33	LH	15	Subtidal reef (Coral patches)	0	0	0	0	0	0
34	IS	< 1	Reef flat	4	6	4	5.4	4.2	4.7
35	IS	< 1	Reef flat	2	5	2.8	1.6	1.8	1.8
36	IS	< 1	Reef flat	3	6	4.6	2.1	2.6	1.5
37	IS	< 1	Reef flat	5	3	13.2	5.5	2.0	1.6
38	GB	4	Subtidal sand	3	2	8.0	8.5	3.2	3.3
39	GB	5	Subtidal sand	2	2	2.2	3.2	3.2	4.4
40	GB	4	Subtidal sand	2	3	1.6	2.2	4.8	3.3
41	CG	9	Subtidal sand	1	1	2.4	3.6	0.8	1.8
42	CG	8	Subtidal sand	1	1	0.8	1.8	1.6	2.2

43	CG	5	Subtidal sand	2	1	2.4	3.6	0.8	1.8
44	MG	6	Subtidal sand	0	1	0	0	0.8	1.8
45	MG	5	Subtidal sand	0	0	0	0	0	0
46	MG	5	Subtidal sand	2	0	1.6	3.6	0	0
47	BB	4	Seagrass meadow	0	1	0.0	0.0	0.6	1.3
48	BB	3	Seagrass meadow	1	1	0.8	1.8	0.8	1.8
49	BB	4	Seagrass meadow	1	0	0.8	1.8	0	0
50	BB	9	Seagrass meadow	0	0	0	0	0	0
51	BB	8	Seagrass meadow	0	0	0	0	0	0
52	BB	8	Seagrass meadow	0	0	0	0	0	0
53	MS	8	Seagrass meadow	0	0	0	0	0	0
54	MS	7	Seagrass meadow	0	0	0	0	0	0
55	MS	6	Seagrass meadow	0	0	0	0	0	0
56	MS	7	Seagrass meadow	0	0	0	0	0	0
57	MS	3	Seagrass meadow	0	0	0	0	0	0
58	MS	3	Seagrass meadow	2	0	1.6	2.2	0	0
59	LH	5	Seagrass meadow	0	0	0	0	0	0
60	LH	6	Seagrass meadow	2	0	1.6	2.2	0	0
61	LH	7	Seagrass meadow	0	0	0	0	0	0
62	LH	4	Seagrass meadow	0	0	0	0	0	0
63	LH	5	Seagrass meadow	1	0	0.8	1.8	0	0
64	LH	4	Seagrass meadow	0	0	0	0	0	0
65	Lagoon	< 0.5	Intertidal sand	1	1	1.6	3.6	0.8	1.8
66	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
67	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
68	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
69	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
70	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
71	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
72	Lagoon	< 0.5	Intertidal sand	0	0	0	0	0	0
73	Lagoon	< 0.5	Intertidal sand	2	2	1.6	2.2	1.6	2.2

Table 3. Feeding ecology of the *Conus* species found around Dahab.

Species	Description	Feeding mode
Conus arenatus	Hwass in Burguière, 1792	vermivorous
Conus tessulatus	Born, 1778	vermivorous, piscivorous
Conus parvatus	Walls, 1979	vermivorous
Conus miliaris	Hwass in Bruguière, 1792	vermivorous
Conus pennaceus	Born, 1778	molluscivorous
Conus nussatella	Linnaeus, 1758	vermivorous
Conus rattus	Hwass in Bruguière, 1792	vermivorous
Conus textile	Da Motta, 1982	molluscivorous
Conus nigropunctatus	Sowerby II, 1857	piscivorous
Conus geographus	Linnaeus, 1758	piscivorous
Conus taeniatus	Hwass in Bruguière, 1792	vermivorous
Conus striatus	Linnaeus, 1758	piscivorous
Conus flavidus	Lamarck, 1810	vermivorous
Conus maldivus	Hwass in Bruguière, 1792	vermivorous

Table 4. *Conus* species diversity.

	Living			*Dead*			*Total*	
	S	*N*	H‘	*S*	*N*	H‘	*S*	H‘
Reef flat	5	120	0.9	8	42	1.5	9	1.1
Subtidal reef	6	15	1.5	4	5	1.3	9	1.8
Subtidal sand	4	24	0.9	5	19	1.2	6	1.3
Seagrass meadow	3	7	1.0	2	2	---	3	1.0
Intertidal sand	2	4	0.6	1	1	---	2	0.5

S = species number, *N* = sample size, H‘= Shannon and Weaver Index (1949)
H’ = -Σ (pi) (log pi)

Table 4. Average shell lengths of living and dead Conids per habitat and sampling station.

Habitat	Living		Dead		
	Mean shell length [mm]	*N*	Mean shell length [mm]	*N*	Hermit - crab occupied
Subtidal reef	17.9 ± 7.1	20	50.3 ± 34.8	6	3
Moray Garden	16.7 ± 7.2	3	57.7 ± 39.7	3	1
Islands South	26.5 ± 7.9	4	22.0 ± 14.1	2	1
Abu Helal	17.3 ± 5.0	4	85.0	1	1
Lighthouse	14.8 ± 4.9	9	---	---	---
Reef flat The Islands	12.5 ± 5.0	120	14.4 ± 5.7	53	46
Subtidal sand	14.3 ± 9.8	24	13.5 ± 9	19	1
Coral Garden	16.3 ± 12.8	7	10.8 ± 2.2	4	---
Golden Blocks	13.3 ± 9.4	15	11.8 ± 3.8	14	1
Moray Garden	15.0 ± 1.4	2	48.0	1	---
Seagrass meadow	31.4 ± 21.9	7	20.0 ± 12.7	2	1
Bannerfish Bay	22.0 ± 14.1	2	20.0 ± 12.7	2	1
Mashraba	59.0 ± 22.6	2	---	---	---
Lighthouse	19.3 ± 4.2	3	---	---	---
Intertidal sand Dahab Lagoon	42.3 ± 13.6	4	25.0 ± 7.9	3	---

Table 6. ANOSIM for *Conus* habitats of living assemblages

Living Conidae	*R* statistic	Significance level %	Actual permutations	Number of permuted statistics ≥ 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	0.15	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**	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

Note R-values > 0.5 indicating clearly separable groups (bold values)

Table 7. ANOSIM for *Conus* habitats of dead assemblages

Dead Conidae	*R* statistic	Significance level %	Actual permutations	Number of permuted statistics ≥ observed *R*
Subtidal reef , reef flat	0.146	14.3	35	5
Subtidal reef, subtidal sand	- 0.29	52.9	495	262
Subtidal reef, seagrass meadow	- 0.333	100	5	5
Subtidal reef, intertidal sand	0.036	60	15	9
Reef flat, subtidal sand	0.109	18.8	495	93
Reef flat, seagrass meadow	**0.501**	20	5	1
Reef flat, intertidal sand	**0.964**	6.7	15	1
Subtidal sand, seagrass meadow	- 0.192	77.8	9	7
Subtidal sand, intertidal sand	0.246	11.1	45	5
Seagrass meadow, intertidal sand	**1**	33.3	3	1

Note R-values > 0.5 indicating clearly separable groups (bold values)

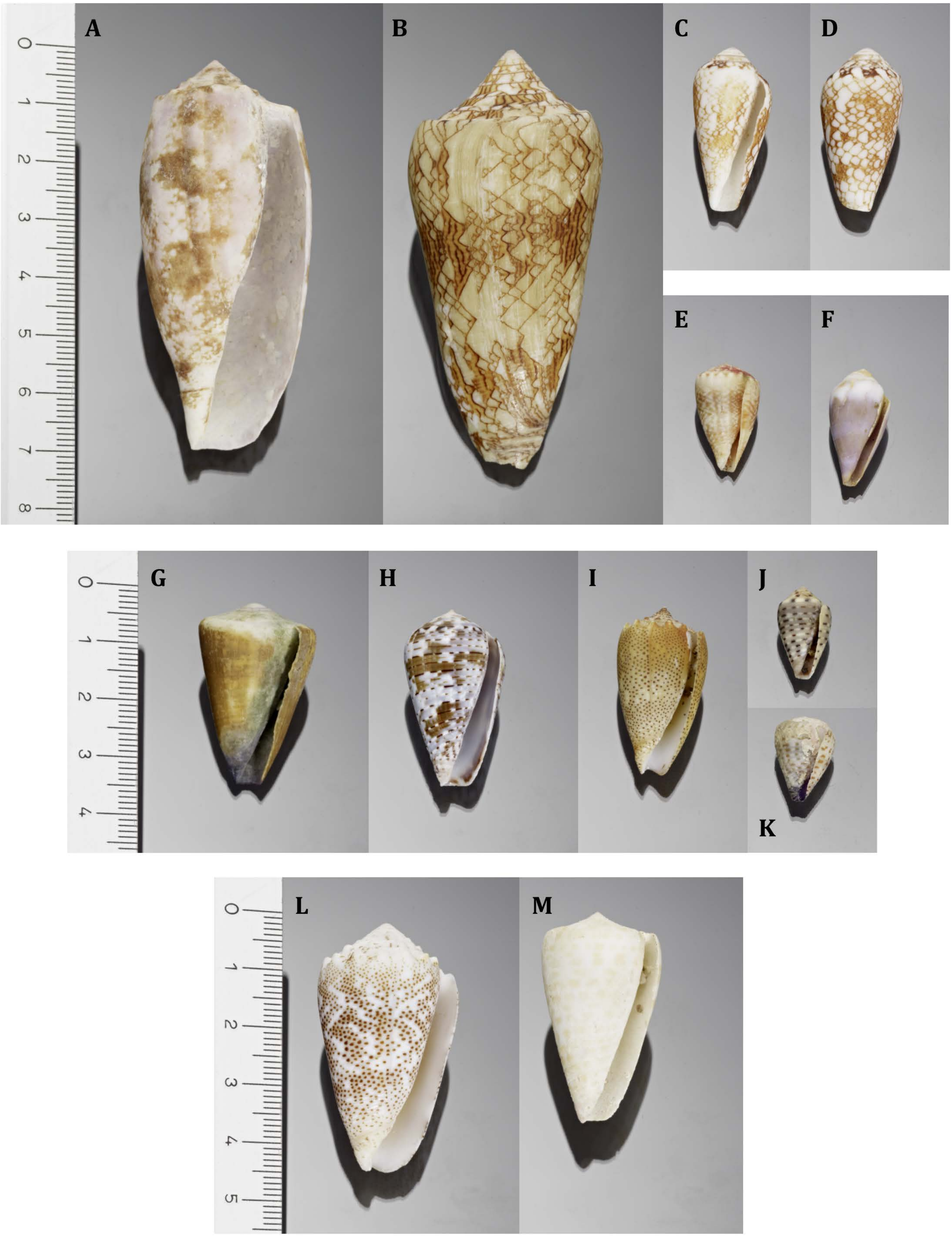
Table 8. ANOSIM for *Conus* habitats separated into living and dead assemblages

Living versus dead *Conidae*	*R* statistic	Significance level %	Actual permutations	Number of permuted statistics ≥ observed *R*
Total assemblage	0.141	0.6	999	5
Subtidal reef	-0.03	57.1	999	570
Reef flat	0.229	20	35	7
Subtidal sand	0.162	5.5	999	54
Seagrass meadow	-0.2	83.3	6	5
Intertidal sand	**0.75**	33.3	3	1

Note R-values > 0.5 indicating clearly separable groups (bold values)

Table 9. Mean shell size (+/- standard deviation) of all species in the studied habitats.

Habitat	Living		Dead	
	Mean shell length [mm]	*N*	*Mean shell length [mm]*	*N*
Subtidal reef				
C. parvatus	13 ± 1.8	7	13 ± 1.4	2
C. taeniatus	12.5 ± 0.7	2		
C. tessulatus	11	1		
C. miliaris	24	1		
C. flavidus	26.7 ± 1.5	3		
C. maldivus	35	1		
C. arenatus			32	1
C. striatus			82	1
C. geographus			77	1
unidentifiable	18.2 ± 5	5	85	1
Total		20		6
Reef flat				
C. parvatus	10.8 ± 1.6	87	11 ± 1.9	19
C. taeniatus	12.6 ± 2.8	19	6.6 ± 3.1	10
C. miliaris	13.5 ± 2.4	4	15.4 ± 6.4	7
C. flavidus	27 ± 5.2	9	20 ± 4.2	2
C. nigropunctatus	33	1		
C. arenatus			37	1
C. nussatella			25	1
C. pennaceus			28	1
C. tessulatus			14	1
unidentifiable			12 ± 2.1	11
Total		120		53
Subtidal sand				
C. parvatus	14	1	12.4 ± 4.1	9
C. arenatus	8.7 ± 3.1	3	8	2
C. maldivus	30.3 ± 3.2	3		
C. tessulatus	12.5 ± 8.8	17	11.3 ± 2.7	6
C. rattus			12	1
C. textile			48	1
Total		24		19
Seagrass meadow				
C. parvatus	15.3 ± 3	3	11	1
C. arenatus	33 ± 9.5	3	29	1
C. textile	75	1		
Total		7		2
Intertidal sand				
C. tessulatus	41.3 ± 16.6	3	19	1
C. maldivus	45	1		
unidentifiable			28 ± 8.5	2
Total		4		3



Supplementary Figure 1. A. *Conus geographus* **B.** *Conus textile* **C-D.** *Conus pennaceus* **E.** *Conus miliaris* **F.** *Conus rattus* **G.** *Conus flavidus* **H.** *Conus nigropunctatus* **I.** *Conus arenatus* **J.** *Conus taeniatus* **K.** *Conus parvatus* **L.** *Conus arenatus* **M.** *Conus tessulatus. C. striatus, C. nussatella* and *C. maldivus* not shown.

Supplementary Figure 2. *C. tessulatus* (left) and *C. arenatus* (right) on the tidal flat.

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