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„Predation intensity of molluscan death assemblages in the Persian (Arabian) Gulf"

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1. Abstract

Drilling predation metrics are a common method of analysing predator-prey interactions. A thorough literature research revealed that drilling predation has not been investigated in potentially contaminated areas. Also, studies in tropical and subtropical areas are rare. Therefore, I investigated whether the presence of oil platforms influences predation patterns in tropical shallow subtidal benthic assemblages. I considered the possible effects of environmental factors such as type of substrate, depth, community structure and composition, and species traits such as epi- or infaunal life habit and size (the latter only in the intertidal). Finally, I assessed whether bivalve species were more often wall drilled (in the centre of the valve) or edge drilled (on the margin of the valve). I studied assemblages around two oil platforms in the Umm al Dalkh (UA) and Zakum (ZK) oilfields, in the southern Persian (Arabian) Gulf, off the coast of the United Arab Emirates. Additionally, I investigated an unspoiled intertidal area to compare results in different habitats. Drill holes in mollusc shells were examined and the two metrics Drilling Frequency (DF) and Prey Effectiveness (PE) were used. DF informs about drilled individuals in the assemblage and PE is the ability of the prey to resist drilling predation.

Predation intensity was higher in the subtidal than in the intertidal (DF was 12.5% and 2.1%, respectively). In both habitats, gastropods were drilled more frequently than bivalves (21.6% and 8.6%, respectively, in the subtidal, and 5.1% and 0.5%, respectively, in the intertidal). Predation intensities did not significantly differ between the two oilfields. No pattern of predation intensity around the platforms was detected, implying little effect of the structures on prey-predator relationships. Environmental factors like depth or substrate did not correlate with the predation metrics.

No significant differences were detected between epi- and infaunal species but in the intertidal, in two out of seven species smaller individuals were more intensively drilled than larger ones. Community structure and richness and predator abundance (muricid and naticid gastropods) did not affect drilling patterns in the subtidal. In the subtidal, finally, all families were more often drilled internally, whereas no significant differences were detected in the intertidal.

2. Zusammenfassung

Die Analyse von Bohrlöchern ist eine weit verbreitete Methode um Räuber-Beute Interaktionen zu bewerten. Bislang kann in der wissenschaftlichen Fachliteratur, trotz diverser Artikel, keine Studie gefunden werden, für die Proben in potentiell kontaminierten Bereichen genommen wurden. Daher habe ich untersucht ob Ölplattformen Prädationsmuster von Mollusken beeinflussen können. Hierzu wurden Stichproben von benthischen Lebensgemeinschaften aus dem Sublittoral des subtropischen Persischen Golfes genommen. Ich habe die Auswirkungen möglicher Einflüsse untersucht, etwa Umweltfaktoren wie Substratbeschaffenheit, Wassertiefe, Zusammensetzung der Lebensgemeinschaft und Merkmale wie Lebensweise (Epi- und Infauna) oder Größe der Schale (nur in der Gezeitenzone). Zuletzt, habe ich analysiert, ob Bivalvenarten häufiger am Rand oder in der Mitte der Schale angebohrt wurden. Die Stichprobengebiete befanden sich neben der beiden Ölplattformen in Umm al Dalkh (UA) und Zakum (ZK), im südlichen Persischen (Arabischen) Golf, vor der Küste der Vereinigten Arabischen Emirate. Zusätzlich wurde eine unberührte Gezeitenzone beprobt um Prädation in unterschiedlichen Lebensräumen vergleichen zu können. Hierzu wurden Bohrlöcher in Molluskenschalen untersucht um Bohrfrequenz (Drilling Frequency, DF) und Beuteerfolg (Prey Effectiveness, PE) zu ermitteln. DF gibt Aufschluss über die Anzahl der Individuen mit Bohrlöchern in einer Probe und PE zeigt die Fähigkeit der Beute den Angriffen des Prädators zu widerstehen.

Die Bohrfrequenz im Sublittoral (DF = 12.5%) war höher als in der Gezeitenzone (DF = 2.1%). In beiden Lebensräumen wurden Gastropoden (Sublittoral: 21.6%; Gezeitenzone: 5.1%) häufiger bebohrt als Bivalven (Sublittoral: 8.6%; Gezeitenzone: 0.5%).Es wurden keine Unterschiede in den Räuber-Beute Beziehungen ermittelt die auf die Präsenz von Ölplattformen zurückgeführt werden konnten. Auch für andere Umweltfaktoren, wie Wassertiefe oder Substratbeschaffenheit, konnten keine Zusammenhänge mit dem Vorhandensein von Bohrlöchern gefunden werden.

Außerdem hatte der Lebensstil, ob Epi- oder Infauna, keine Bedeutung für das Ausmaß der Prädation. Die Größe der Schale hatte in zwei Fällen einen Einfluss auf die Prädationshäufigkeit, denn es wurden kleinere Individuen häufiger erbeutet wurden als größere. In den fünf weiteren untersuchten Arten war jedoch kein Zusammenhang auszumachen. Im Sublittoral konnte auch die Struktur der Lebensgemeinschaften betrachtet werden. Hierbei hatten jedoch weder Artenreichtum, Abundanz, noch die Evenness (Ausgeglichenheit) einen größeren Einfluss auf die Bohrfrequenz oder den Beuteerfolg. Zuletzt wurden im Sublittoral alle Bivalvenfamilien häufiger in der Mitte der Schale angebohrt, jedoch in der Gezeitenzone war kein Trend auszumachen.

3. Introduction

Several predators leave traces on their prey but none are as distinctive as naticid and muricid gastropod drill holes. The analysis of drilling predation has many advantages and is the most widely used method to analyse predatory success among benthic invertebrates. Major benefits of this approach include the study of quantifiable data on biotic interaction and the broad range of environments available (Kowalewski 2002). Indeed, the study of drill holes has engaged many scientist and many studies have been published both on fossil (e.g. Leighton 2003, Hoffmeister et al. 2004, Chattopadhyay and Dutta 2013) as well as recent data (e.g. Garrity and Levings 1981, Sawyer and Zuschin 2010, Pahari et al. 2016).

Environmental factors might influence the predation patterns. There is evidence that drilling predation depends on water depth. Drilling in gastropod species in the Bahamas was found to occur more often in shallow waters than in deep waters (> 70 m) (Walker et al. 2002). Drilling frequency in the Red Sea was higher in the subtidal (25.7%) than in the intertidal zone (1.2%) (Zuschin and Ebner 2015). Likewise, in the Mediterranean Sea, drilling frequency was higher in the sublittoral (27.4%) than in the intertidal (1.4%) (Sawyer and Zuschin 2010). A study from the northern Red Sea showed no significant differences due to substrate types (fine-grained, rock bottom, reef, sandy) (Chattopadhyay et al. 2015). Therefore, I inspected the influence of environmental factors on predation patterns, by asking the following questions:

(1) Are there differences in predation patterns between habitats (intertidal versus subtidal or different sites in the subtidal)?

(2) Do environmental factors (depth, substrate) influence predation patterns?

Another aspect is prey selectivity. Several authors postulate prey size selectivity. Some studies found drilled individuals to be larger than undrilled individuals (e.g. Chattopadhyay and Dutta 2013, Gordillo and Archuby 2012), but others found no preference in prey size (e.g. Grey et al. 2006, Hagadorn and Boyajian 1997). Therefore, during my thesis I addressed also the question:

(3) Does prey size influence predation?

Little is known about how community structure affects predation patterns. In the Gulf of Trieste (Northern Adriatic Sea) no correlation between drilling frequency and diversity indices (e.g., richness) or predator abundance was found (Sawyer and Zuschin 2010). In my study site, I therefore addressed the question:

(4) Are predation metrics correlated with metrics of community structure and composition?

Offshore structures such as the oil platforms are most often investigated in terms of their potential impact on benthic assemblages (e.g., Moore et al. 1987, Olsgard and Gray 1995, Ellis et al 2012) or their function as artificial reefs (e.g., Wolfson et al. 1979, Bomkamp et al. 2004, Bergmark and Jorgensen 2014). No previous studies have investigated the effects of these artificial structures on prey-predator interactions. Therefore, I addressed the question:

(5) Does the presence of oil platforms influence predation patterns?

On larger scale drilling frequency is influenced by latitudinal gradient. There is some evidence that drilling predation increases towards the equator. Bertness (1981) found an increase in predation intensity from the temperate to the tropics in shell-crushing predation. Dudley and Vermeij (1978) detected that gastropod drill holes on *Turritella* sp. are more frequent in the tropics and subtropics (32.0%) than in temperate regions (11.0%). A study on terebrid gastropods showed highest drilling frequency in the tropics and a variety between 43.0% and 0.0% of drilled shells depending on sampling site (Vermeij et al 1980). A latitudinal gradient was also made out along the coast of Brazil, were drilling occurs in 12.0% in the tropics and in 5.0% in the temperate regions (Visaggi and Kelley 2015). A study in Polar Regions found 7.0% drilling frequency in the White Sea in barnacle shells (Yakovis and Artemieva 2015) In contrast, in Micronesian reef snails drilling was an unimportant mode of predation with a drilling frequency of 0.2% and below (Vermeij 1979). Since tropical latitudes have likely a higher predation rate, the study setting in the Persian (Arabian) Gulf is an ideal site to answer the questions above.

4. Material and Methods

4.1. Study areas

Fig. 1: The Persian (Arabian) Gulf; studied fields are indicated by black stars.

The sample sites are located in the Persian (Arabian) Gulf, a semi-enclosed shallow sea in the subtropics. The average water depth is 36 m. This area contains the world's richest oil deposits. The oil is extracted and transported through this water body (Al-Ghadban and Abdali 1998).

Two habitat types were investigated: the subtidal and the intertidal. In the subtidal, field work was conducted in 1999 around two oil platforms in the Umm al Dalkh (UA) and Zakum (ZK) oilfields, in the United Arab Emirates (Fig. 1). Samples were taken within different distances (6.4 km in Umm al Dalkh and 14.3 km in Zakum) from these oil platforms and in different water depths between 6 and 20 meters. In UA, 13 sites were selected and in ZK, 15 sites. Samples were collected manually by scoops and sieved to exclude individuals below 2 mm and bigger than 5 mm. This range was chosen to exclude juveniles which are too difficult to identify in a taxonomically poorly known area while large individuals would have been weakly represented in the sample due to the relatively small area sampled. In addition, the two fields of Umm al Dalkh and Zakum were analyzed individually as they are characterized by different substrates.

In the intertidal, the studied material comes from the localities of Umm al-Quwain (UAQ) and Al Rams (near Ras al-Khaimah (RAK)) in the United Arab Emirates (Fig. 1). Samples were collected in 2003. In both areas, a total of 6 (5 in Al Rams and 1 in Umm al-Quwain) sampling sites were chosen. Bulk samples were taken from the first 1 – 3 cm of the sandy substrate and sieved through a 1 mm mesh.

4.2. Definition and analysis of drill holes

Individuals were analysed in the lab with a binocular microscope. Drill holes are characterized by a circular shape and a conical structure, being larger on the outside of the shell (Kowalewski 2002) (Fig. 2). The holes were categorized into complete drill holes (Fig. 2A), which break through the shell, and incomplete holes (Fig. 2B), which are only on the surface. Incomplete drill holes are recognized as predator failure to kill its preferred prey. In addition, the position of the hole on the shell was taken into account and defined as wall drilling or edge drilling. Wall drilling is done within the margin of the shell and forms a complete circle. Edge drilling is done at the margin of the shell and does not form a circle because it is cut off.

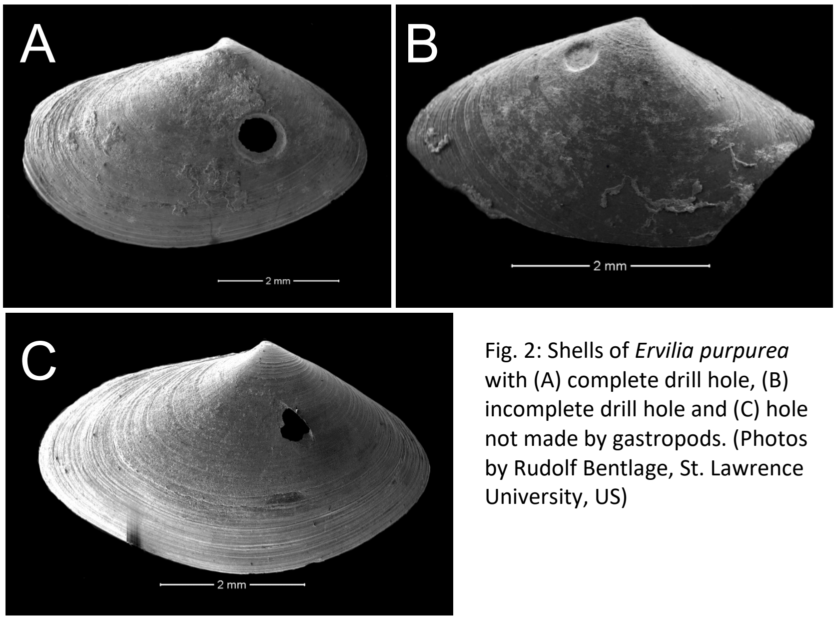

Fig. 2: Shells of *Ervilia purpurea* with (A) complete drill hole, (B) incomplete drill hole and (C) hole not made by gastropods. (Photos by Rudolf Bentlage, St. Lawrence University, US)

The predation of naticids and muricids is very characteristic. The predators leave micro-rasping marks that are identifiable as drilling. These marks are visible as nearly parallel scratches done by the radula teeth (Schiffbauer et al. 2008). The predation follows a stereotyped procedure. The predator-prey interaction includes the accessory boring organ (ABO), the radula and a chemical compound or acid produced by the gastropod. In general, the feeding process follows a consistent pattern and the shell is penetrated with a mixture of mechanical and chemical activities. When the gastropod captures the prey, the anterior propodium of the predator forms a proboscis that enables the radula to rasp a hole into the shell. After some time of rasping, the proboscis is retracted and the accessory boring organ is positioned in the incomplete borehole and places a secret that further removes the shell. This procedure is repeated if necessary. When the borehole breaks through, the gastropod can feed on its prey (Carriker 1981).

4.3. Predation metrics

In order to analyse the predation intensity, indices for Drilling Frequency (DF) and Prey Effectiveness (PE) were calculated. Drilling Frequency is an indication of how many drilled individuals are present in the assemblage. Prey Effectiveness informs about the ability of the prey to resist drilling predation. In favour of keeping it straightforward, I united wall- and edge drilled holes to drill holes in general for the calculations of the predation metrics unless otherwise indicated.

$$Drilling\ Frequency\left(DF\right)=\frac{number\ of\ drilled\ shells}{total\ number\ of\ shells}$$

$$Prey\ Effectiveness\left(PE\right)=\frac{number\ of\ incomplete\ drill\ holes}{total\ number\ of\ drill\ attempts}$$

4.4. Molluscan classes, families and species

We compared drill holes done by naticid and muricid gastropods at different taxonomic levels of prey. Prey organisms were gastropods, bivalves and scaphopods. Only species or families were considered with more than fifty individuals (n > 50) to strengthen the statistical output. Therefore, scaphopods were not analyzed further because of not fulfilling the criteria of more than fifty individuals. The number of bivalve individuals was corrected for disarticulated shells to compute drilling frequencies. Therefore, the number of loose valves found at each site was divided by two (the number of valves of a complete bivalve) and summed up with the number of complete shells (Kowalewski 2002, Sawyer and Zuschin 2010).

4.5. Prey characteristics

In the intertidal area we also considered prey size. Therefore, width and height of five random undrilled individuals per site and the biggest individuals were determined. In addition, all drilled individuals were measured. For bivalves height is defined as the distance between the umbo and the ventral margin and width goes from the anterior to the posterior margin. The height of gastropods is measured from the apex to the base of the aperture and the width from the widest whorl to the edge of the aperture. In the analysis height was used to represent size because in all species this measurement was the bigger one compared to width.

Last, the life habit of the bivalve species was taken into account by comparing epifaunal with infaunal species. Information about life habits of prey species was extracted from Beesley et al (1998) (Tab. 1, Tab. 2, Tab. 3, Tab. 4).

Tab. 1: Subtidal bivalve species list and life habit information**.**

Species name	**Family**	**Epi/infaunal**
Gregariella simplicifilis	Mytilidae	epifaunal
Septifer forskali	Mytilidae	epifaunal
Solamen adamsianum	Mytilidae	epifaunal
Anadara sp.1 (juv)	Arcidae	infaunal
Glycymeris sp.1 (juv)	Glycymerididae	infaunal
Pteria sp.1	Pteriidae	epifaunal
Limatula sp. 2	Limidae	epifaunal
Anomia achaeus	Anomiidae	epifaunal
Chama sp.1 (juv)	Chamidae	epifaunal
Anodontia sp. 1	Lucinidae	infaunal
Cardiolucina semperiana	Lucinidae	infaunal
Pillucina cf. denticula	Lucinidae	infaunal
Pillucina vietnamica	Lucinidae	infaunal
Diplodonta aff. subrotunda sp. 3	Ungulinidae	infaunal
Fulvia fragilis	Cardiidae	infaunal
Parvicardium sueziense	Cardiidae	infaunal
Cadella semen	Tellinidae	infaunal
Loxoglypta rhomboides	Tellinidae	infaunal
Tellidora pellyana	Tellinidae	infaunal
Tellina sp.2	Tellinidae	infaunal
Ervilia purpurea	Semelidae	infaunal
Ervilia scaliola	Semelidae	infaunal
Ervilia sp.1	Semelidae	infaunal
Callista florida	Veneridae	infaunal
Circenita callipyga	Veneridae	infaunal
Gafrarium pectinatum	Veneridae	infaunal
Microcirce dilecta	Veneridae	infaunal
Timoclea cf arakana	Veneridae	infaunal
"venerid" sp. 1	Veneridae	infaunal

Tab. 2: Subtidal gastropod species list and life habit information**.**

Species name	**Family**	**Epi/infaunal**
Bothropoma cf. *munda*	Colloniidae	epifaunal
Cerithium scabridum	Cerithiidae	epifaunal
Viriola corrugata	Triphoridae	epifaunal
Rissoina pachystoma	Rissoidae	epifaunal
Calyptraea pellucida	Calyptraeidae	epifaunal
Cronia sp. 1	Muricidae	epifaunal

Tab. 3: Intertidal bivalve species list and life habit information.

Species name	Family	Epi/infaunal
Pillucina cf. *vietnamica*	Lucinidae	infaunal
Tellina arsinoensis	Tellinidae	infaunal
Ervilia cf. *purpurea*	Semilidae	infaunal
Dosina ceylonica	Veneridae	infaunal

Tab. 4: Intertidal gastropod species list and life habit information.

Species name	Family	Epi/infaunal
Cerithium cf. *scabridum*	Cerithiidae	epifaunal
Clypeomorus bifasciata	Cerithiidae	epifaunal
Diala semistriata	Dialidae	epifaunal
Cerithidea cingulata	Potamididae	epifaunal
Pirenella conica	Potamididae	epifaunal
Clathrofenella cerithina	Scaliolidae	epifaunal
Stenothyra cf. arabica	Stenothyridae	epifaunal
Assiminea sp.	Assimineidae	epifaunal
Acteocina sp. 1	Scaphandridae	epifaunal

4.6. Community indices and environmental factors considered in the subtidal

Community indices were calculated such as species richness, abundance and evenness. Species richness was calculated from the number of counted species and the help of a rarefaction curve to estimate the actual species richness, because of uneven sample sizes. The abundances of muricid and naticid predators were taken from the death and the living assemblage.

Environmental factors and contamination levels were used to look for correlations with predation metrics. Concentrations of arsenic, barium, magnesium, cadmium, copper, nickel, lead, mercury, vanadium, zinc, iron and Total Petroleum Hydrocarbons were analysed in the sediment (Appendix Tab. 17, Appendix Tab. 18). Other environmental factors were the water depth and the substrate type, whether the sample had been taken from hard- or soft substrate. The distance from the platform was also considered using a categorical factor with three levels: proximal, mid or far away from the oil platform. The metric distances ranged from zero to fourteen kilometres.

4.7. Statistical tests

The influences of ecological factors on the data were analysed with ANOVA, for categorical data, like substrate, subtidal fields and wall- and edge drilling. Spearman correlation was used for distance in meter, depth, as well as community indices (species richness, abundance and evenness) and environmental factors mentioned above. In addition, t-tests were performed to analyse differences in predation among species or families and Mann-Whitney tests for prey size. The statistical analyses were done in the R statistical environment (R Core Team 2015) and with the PAST software (Hammer et al 2001).

5. Results

5.1. Predation on assemblage level

The subtidal samples contained approximately 50,000 molluscan shells, of which 6,517 shells had drill holes. The intertidal samples contained about 7,000 shells, of which 159 were drilled. The Drilling Frequency (DF) was 12.5% in the subtidal and 2.1% in the intertidal.

More in detail, the DF was 11.9% for bivalves and 26.4% for gastropods in the subtidal, whereas, in the intertidal area the overall drilling was 2.5% in bivalves and 1.9% in gastropods. The two fields in the subtidal were different. Umm al Dalkh had a DF of 12.0% for bivalves and 20.4% for gastropods. In Zakum bivalves, 11.7% of individuals were drilled and in gastropods 31.0%.

Prey Effectiveness (PE) in the subtidal was higher for bivalves (8.0%) than for gastropods (4.9%). A closer look at the fields reveal that in Umm al Dalkh gastropods (7.4%) were more resistant to drilling than bivalves (5.3%), whereas, in Zakum bivalves (12.8%) escaped three times more often than gastropods (3.6%). In the intertidal, no incomplete drill hole was found; therefore, PE could not be calculated.

Tab. 5: Total number of individuals and of completely drilled individuals by molluscan class in the subtidal oilfields. Number of bivalve valves was corrected for disarticulated shells.

	UA (Individuals)		ZK (Individuals)	
Class	**Total**	**Drilled**	**Total**	**Drilled**
Bivalvia	16130	1935 (12.0%)	8714.5	1018 (11.7%)
Gastropoda	985	201 (20.4%)	1298	402 (31.0%)
Scaphopoda	63	8 (12.7%)	1	0 (0.0%)

Tab. 6: Total number of individuals and of completely drilled individuals by molluscan class in the intertidal. Number of bivalve valves was corrected for disarticulated shells.

Class	Total	Drilled
Bivalvia	1998.5	49 (2.5%)
Gastropoda	3237	61 (1.9%)
Scaphopoda	3	0 (0.0%)

At family level, significant differences in the frequency of predation between the habitats and among families can be observed. The most abundant subtidal bivalve families had all been drilled. The highest DF can be observed in Anomiidae (21.0%), in Chamidae and Lucinidae (19.0% each) (Fig. 3). PE was greatest in Corbulidae (39.9%), followed by Cardiidae (17.1%) and Semelidae (9.4%) (Fig. 4). In the subtidal, drilling is generally higher in families of gastropods than of bivalves. The highest DF can be found in Collonidae (41%), second are Cerithiidae (34.9%) and third are Pyramidellidae (30.1%) (Fig. 5). In contrast, the PE of gastropods is lower than of bivalves. Triphoridae have a PE of 17.4%, followed by Pyramidellidae (9%) and Cerithiidae (7.6%) (Fig. 6). That is, predators are less effective in preying upon bivalves than upon gastropods.

In the intertidal, drilling frequencies are generally lower than in the subtidal. Among bivalve families, Veneridae has the highest DF (5.7%), followed by Lucinidae (1.5%), and Tellinidae (0.5%). Among the analyzed species, Semelidae were not drilled at all (Fig. 7). Among intertidal gastropods, Assimineidae (11.1%), Scaliolidae (4.4%) and Cerithiidae (3.8%) (Fig. 9) were the most frequently drilled families. In the intertidal no incomplete drill holes were found, therefore, PE is zero for all families.

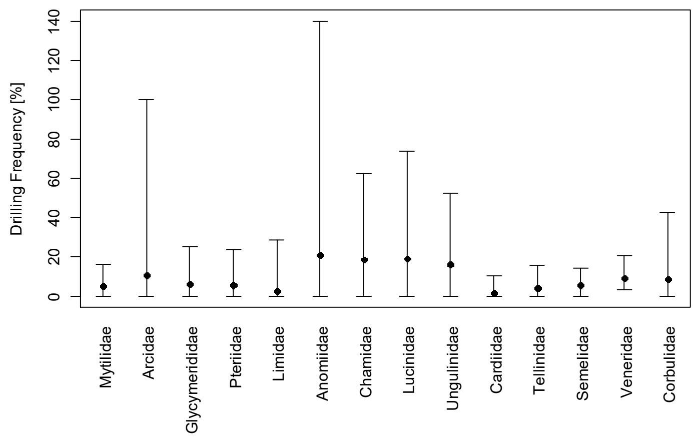

Fig. 3: DF of subtidal bivalve families at regional scale. Error bars indicate 95% confidence intervals. (Figure for Anomiidae is achieved by valves drilled multiple times)

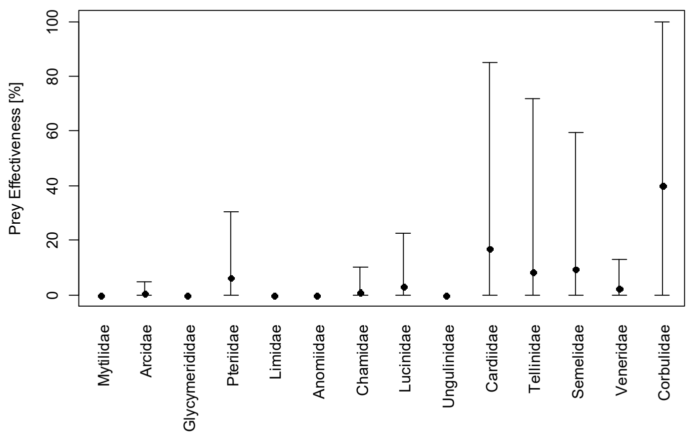

Fig. 4: PE of subtidal bivalve families at regional scale. Error bars indicate 95% confidence intervals.

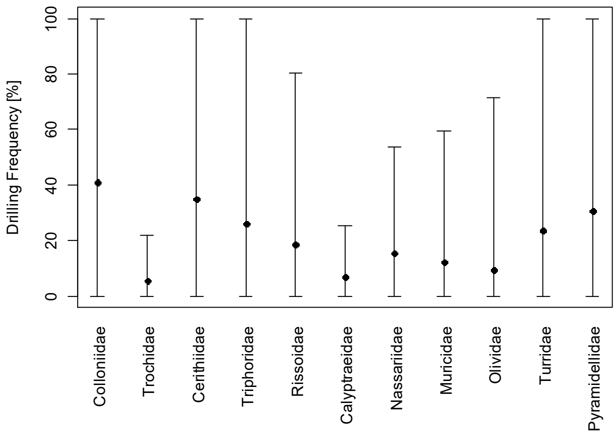

Fig. 5: DF of subtidal gastropod families at regional scale. Error bars indicate 95% confidence intervals.

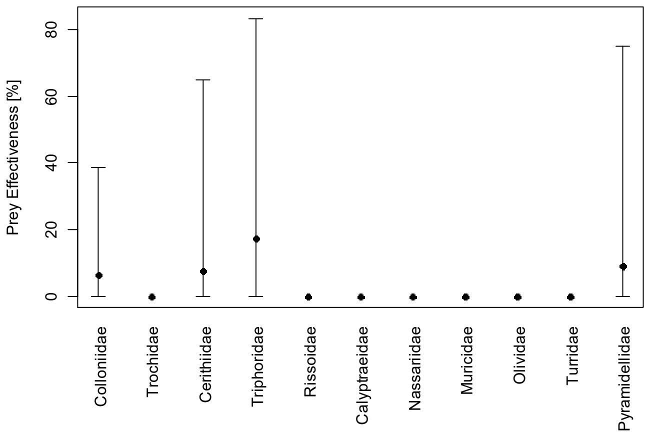

Fig. 6: PE of subtidal gastropod families at regional scale. Error bars indicate 95% confidence intervals.

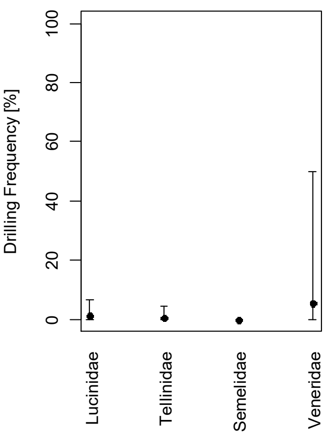

Fig. 7: DF of intertidal bivalve families at regional scale. Error bars indicate 95% confidence intervals.

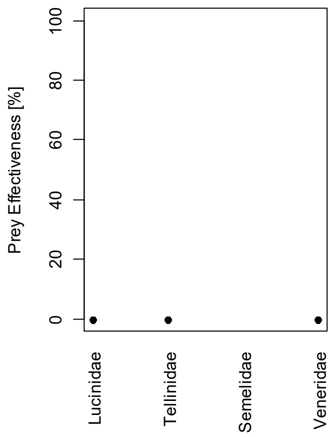

Fig. 8: PE of intertidal bivalve families at regional scale. Error bars indicate 95% confidence intervals. (Figure for Semelidae is achieved by absence of drill holes)

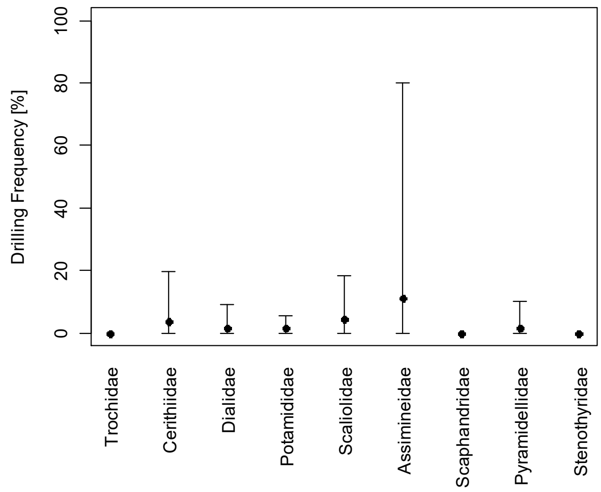

Fig. 9: DF of intertidal gastropod families at regional scale. Error bars indicate 95% confidence intervals.

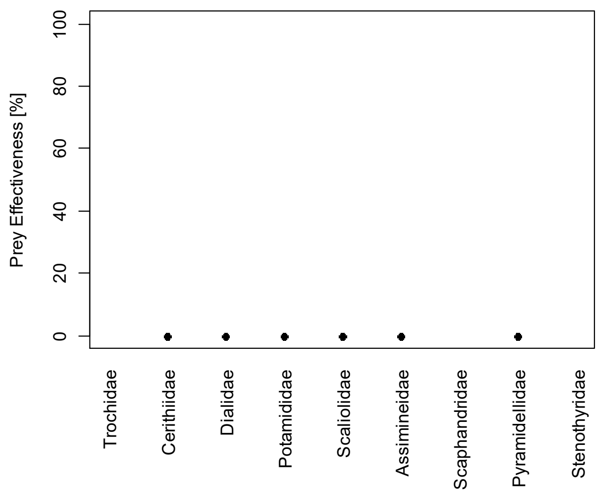

Fig. 10: PE of intertidal gastropod families at regional scale. Error bars indicate 95% confidence intervals.

Tab. 7: Total number of individuals, wall- and edge completely and incompletely drilled valves by bivalve families in the subtidal oilfields. Number of bivalve valves was corrected for disarticulated shells.

	UA (Individuals)				ZK (Individuals)			
Family	Total	Wall	Edge	Incomplete	Total	Wall	Edge	Incomplete
Mytilidae	337	14.5 (4.3%)	3.5 (1.0%)	0 (0.0%)	295	15 (5.1%)	2 (0.7%)	0 (0.0%)
Arcidae	328.5	17 (5.2%)	3.5 (1.1%)	0.5 (0.2%)	64	1.5 (2.3%)	1 (1.6%)	0 (0.0%)
Glycymerididae	26.5	2.5 (9.4%)	0.5 (1.9%)	0 (0.0%)	189	9.5 (5.0%)	4 (2.1%)	0 (0.0%)
Pteriidae	211.5	17.5 (8.3%)	0 (0.0%)	1 (0.5%)	580.5	31.5 (5.4%)	0 (0.0%)	5.5 (0.9%)
Limidae	64	2 (3.1%)	0 (0.0%)	0 (0.0%)	26	0.5 (1.9%)	0 (0.0%)	0 (0.0%)
Anomiidae	49	5 (10.2%)	0 (0.0%)	0 (0.0%)	5	0.5 (10.0%)	0.5 (10.0%)	0 (0.0%)
Chamidae	94.5	6 (6.3%)	2.5 (2.6%)	0 (0.0%)	213	35.5 (16.7%)	24.5 (11.5%)	0.5 (0.2%)
Lucinidae	699.5	93.5 (13.4%)	25.5 (3.6%)	4.5 (0.6%)	77	7 (9.1%)	7 (9.1%)	0 (0.0%)
Ungulinidae	59	6.5 (11.0%)	1 (1.7%)	0 (0.0%)	141	15.5 (11.0%)	1.5 (1.1%)	0 (0.0%)
Cardiidae	469	2.5 (0.5%)	0.5 (0.1%)	0.5 (0.1%)	237.5	6.5 (2.7%)	0.5 (0.2%)	2 (0.8%)
Tellinidae	759	29.5 (3.9%)	10 (1.3%)	1 (0.1%)	79.5	2 (2.5%)	0 (0.0%)	0.5 (0.6%)
Semelidae	9400.5	191 (2.0%)	265 (2.8%)	32.5 (0.3%)	6166.5	250 (4.1%)	17 (0.3%)	64 (1.0%)
Veneridae	3441	197.5 (5.7%)	51.5 (1.5%)	5.5 (0.2%)	576	60.5 (10.5%)	9 (1.6%)	2.5 (0.4%)
Corbulidae	58.5	2.5 (4.3%)	1 (1.7%)	7 (12.0%)	0	0 (NA)	0 (NA)	0 (NA)

Tab. 8: Total number of individuals, wall- and edge completely and incompletely drilled shells by gastropod families in the subtidal oilfields.

	UA (Individuals)				ZK (Individuals)			
Family	Total	Wall	Edge	Incomplete	Total	Wall	Edge	Incomplete
Colloniidae	281	87 (31.0%)	0 (0.0%)	10 (3.6%)	56	25 (44.6%)	0 (0.0%)	3 (5.4%)
Trochidae	125	15 (12.0%)	0 (0.0%)	0 (0.0%)	68	2 (2.9%)	0 (0.0%)	0 (0.0%)
Cerithiidae	76	24 (31.6%)	0 (0.0%)	4 (5.3%)	725	299 (41.2%)	0 (0.0%)	5 (0.7%)
Triphoridae	7	2 (28.6%)	0 (0.0%)	0 (0.0%)	83	14 (16.9%)	0 (0.0%)	4 (4.8%)
Rissoidae	12	2 (16.7%)	0 (0.0%)	0 (0.0%)	69	19 (27.5%)	0 (0.0%)	0 (0.0%)
Calyptraeidae	100	10 (10.0%)	3 (3.0%)	0 (0.0%)	1	0 (0.0%)	0 (0.0%)	0 (0.0%)
Nassariidae	41	10 (24.4%)	0 (0.0%)	0 (0.0%)	9	1 (11.1%)	0 (0.0%)	0 (0.0%)
Muricidae	30	9 (30.0%)	0 (0.0%)	0 (0.0%)	112	10 (8.9%)	0 (0.0%)	0 (0.0%)
Olividae	38	5 (13.2%)	0 (0.0%)	0 (0.0%)	32	1 (3.1%)	0 (0.0%)	0 (0.0%)
Turridae	53	10 (18.9%)	0 (0.0%)	0 (0.0%)	10	2 (20.0%)	0 (0.0%)	0 (0.0%)
Pyramidellidae	25	7 (28.0%)	0 (0.0%)	0 (0.0%)	65	23 (35.4%)	0 (0.0%)	3 (4.6%)

Tab. 9: Total number of individuals, wall- and edge completely and incompletely drilled valves by bivalve families in the intertidal. Number of bivalve valves was corrected for disarticulated shells.

Family	Total	Wall	Edge	Incomplete
Lucinidae	558.5	1 (0.2%)	6.5 (1.2%)	0 (0.0%)
Tellinidae	165	1.5 (0.9%)	0 (0.0%)	0 (0.0%)
Semelidae	94	0 (0.0%)	0 (0.0%)	0 (0.0%)
Veneridae	1100.5	2.5 (0.2%)	11 (1.0%)	0 (0.0%)

Tab. 10: Total number of individuals, wall- and edge completely and incompletely drilled shells by gastropod families in the intertidal.

Family	Total	Wall	Edge	Incomplete
Trochidae	86	0 (0.0%)	0 (0.0%)	0 (0.0%)
Cerithiidae	1047	21 (2.0%)	0 (0.0%)	0 (0.0%)
Dialidae	69	2 (2.9%)	0 (0.0%)	0 (0.0%)
Potamididae	1446	21 (1.5%)	0 (0.0%)	0 (0.0%)
Scaliolidae	113	11 (9.7%)	0 (0.0%)	0 (0.0%)
Assimineidae	70	1 (1.4%)	0 (0.0%)	0 (0.0%)
Scaphandridae	102	0 (0.0%)	0 (0.0%)	0 (0.0%)
Pyramidellidae	72	2 2.8%)	0 (0.0%)	0 (0.0%)
Stenothyridae	57	0 (0.0%)	0 (0.0%)	0 (0.0%)

In the subtidal, the most drilled bivalves are *Anodontia* sp. 1 (DF = 32.4%), followed by *Pillucina* cf. *denticula* (DF = 20.8%) and *Microcirce dialecta* (DF = 19.6%) (Appendix Fig. 22). PE in *Fulvia fragilis* was 100% as only one incomplete and no complete drill holes were found. *Parvicardium sueziense* has a PE of 16% and *Ervilia purpurea* of 12% (Appendix Fig. 23). The most frequently drilled gastropods were *Bothropoma* cf. *munda*, which had the highest DF of 43.5%, followed by *Cerithium scabridum* (24.8%) and *Rissoina pachystoma* (18.4%) (Appendix Fig. 24). The highest PE in subtidal gastropods was found in *Viriola corrugata* (26%), *Cerithium scabridum* (12.9%) and *Bothropoma* cf. *munda* (6.8%) (Appendix Fig. 25).

In the intertidal, no incomplete drill holes were found. Therefore, the PE of all species was zero. DF of bivalves was 1.5% in *Pillucina* cf. *vietnamica* and 0.4% in *Dosina ceylonica* (Appendix Fig. 26). Among gastropods, *Cerithium* cf. *scabridum* was most frequently drilled with 15.6%, followed by *Assiminea* sp. (11.1%) and *Clathrofenella cerithina* (4.5%) (Appendix Fig. 28).

5.2. Differences in predation among habitats

We analyzed differences in DF between the most abundant (n > 50) bivalve and gastropod species in the subtidal and the intertidal (Fig. 11). For both bivalves and gastropods, DF in the subtidal is higher than in the intertidal. The mean DF of bivalves in the subtidal is 8.6% and in the intertidal 0.5%. This difference is significant ($t = -10$, $p < 0.0001$). The mean DF for gastropod species in the subtidal is 21.6% and in the intertidal 5.1%, again showing a significant difference ($t = -5.3$, $p < 0.0001$). Even if bivalves and gastropods are compared within the habitats the difference is significant (subtidal: $t = -4.7$, $p < 0.0001$; intertidal: $t = -2.8$, $p < 0.05$). Because PE in the intertidal is zero, the PE differs also significantly between habitats (for bivalves: intertidal-mean = 0.0%, subtidal-mean = 4.5%, $t = -3.6$, $p < 0.05$; for gastropods: intertidal-mean = 0.0%, subtidal-mean = 9.4%, $t = -3$, $p < 0.05$).

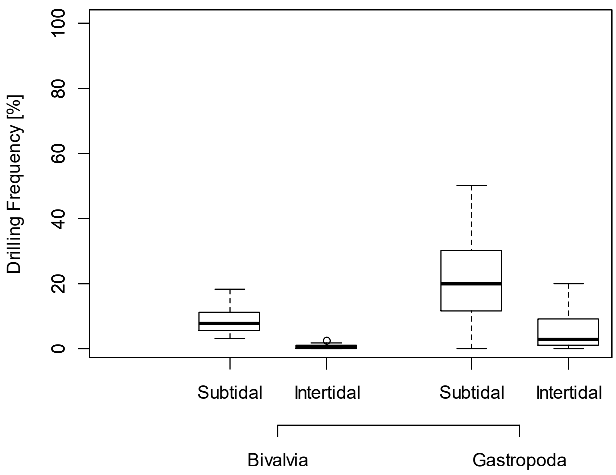

Fig. 11: Comparison of DF between the subtidal and intertidal habitat for bivalve and gastropod species (n > 50).

At the class level, bivalve (7.1% and 10.0%, respectively) and gastropod (21.0% and 22.1%, respectively) Drilling Frequencies do not differ significantly between the two subtidal fields Umm al Dalkh (UA) and Zakum (ZK) (Fig. 12). The same applies for PE, no significant difference between the fields for bivalves (3.1% and 5.7%, respectively) and gastropods (11.4% and 7.6%, respectively)

When it comes to families, Tellinidae and Veneridae were more frequently predated in Zakum (Tellinidae: UA = 6.8%, ZK = 1.9%, $t = 3$, $p < 0.05$, Veneridae: UA = 7.3%, ZK = 11.4%, $t = -2.8$, $p < 0.05$), whereas Trochidae were more predated in Zakum (UA = 9.7%, ZK = 1.6%, $t = 2.9$, $p < 0.05$). When comparing individual species, DF was higher in ZK than in UA for *Chama* sp. 1 (juv) (UA = 11.3%, ZK = 25.6%, $t = -2.3$, $p < 0.05$), whereas DF was higher in UA for *Tellidora pellyana* (UA = 19.6%, ZK = 6.1%,

$t = 3.1$, $p < 0.05$) and *Tellina* sp. 2 (UA = 1.6%, ZK = 0.0%, $t = 3$, $p < 0.05$). PE significantly differs between the fields for *Cardiolucina semperiana* (UA = 12.1%, ZK = 0.06%, $t = 2.9$, $p < 0.05$). No other species showed significant differences.

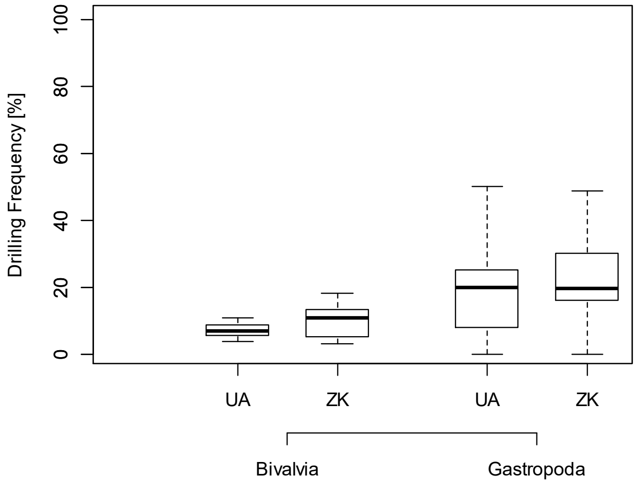

Fig. 12: Comparison of DF between the subtidal UA and ZK fields for bivalve and gastropod species (n > 50).

5.3. Environmental factors in the subtidal

The effect of water depth on DF was analyzed in the subtidal (Fig. 13, Fig. 14). The sample sites were located at depths from 6 to 22 m. No correlation between depth and DF was present for bivalves (Spearman's rho = -0.18, p = 0.36) nor gastropods (Spearman's rho = -0.02, p = 0.9). Also PE did not significantly correlate with depth (bivalves: Spearman's rho = 0.09, p = 0.65; gastropods: Spearman's rho = 0.14, p = 0.46).

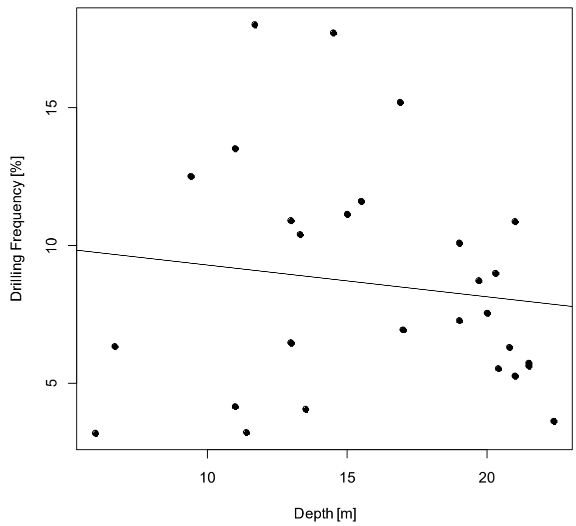

Fig. 13: DF and Depth [m] for bivalve species on regional scale in the subtidal. No significant correlation was found.

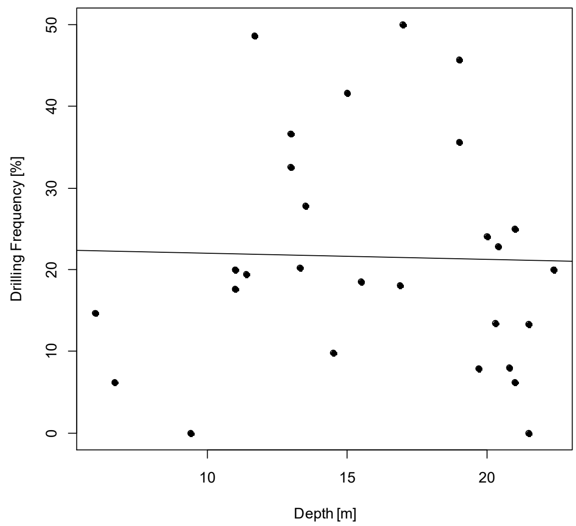

Fig. 14: DF and Depth [m] for gastropod species on regional scale in the subtidal. No significant correlation was found.

Two different substrate types were found in Zakum, as there is a hard substrate bottom (HSB) and a soft substrate bottom (SSB) (Fig. 15). No significant differences in DF were found between these two substrates, neither for bivalves (ANOVA: F = 0.01, p = 0.91) nor for gastropods (ANOVA: F = 0.10, p = 0.76). Also PE was not significantly different between the two substrate types (ANOVA: bivalves: F = 0.20, p = 0.66; gastropods: F = 1.92, p = 0.19).

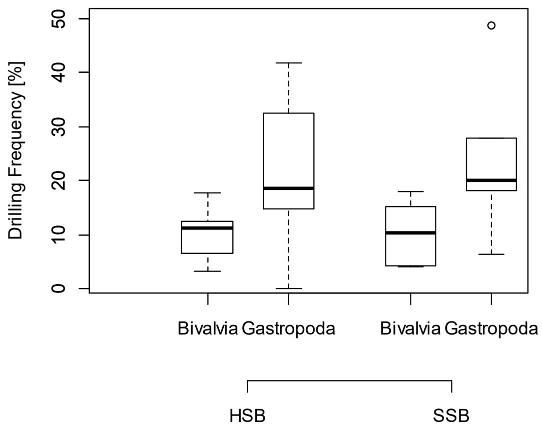

Fig. 15: Comparison of DF at hard- and soft substrate bottom in ZK of bivalve and gastropod species (n > 50) in the subtidal area.

5.4. Prey size in the intertidal

Generally, drilled shells are not significantly different in size from undrilled shells (Fig. 16, Fig. 17). Exceptions are the bivalve *Dosinia* sp. 1 (Mann-Whitney $W = 734$, $p < 0.005$) and the gastropod *Clathrofenella cerithina* (Mann-Whitney $W = 215$, $p < 0.05$), where undrilled individuals were larger.

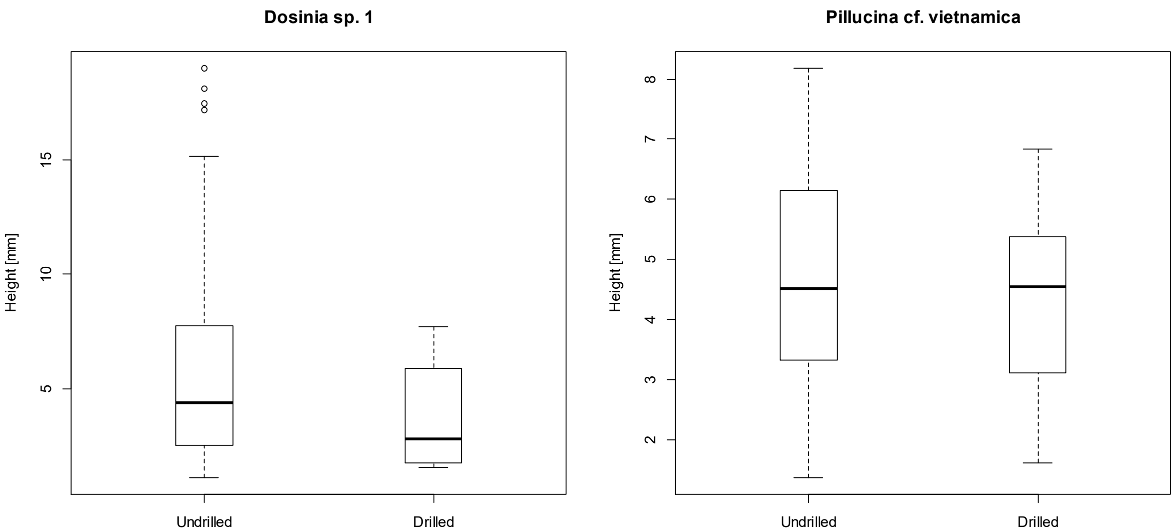

Fig. 16: Size (umbo-ventral height) of undrilled and drilled bivalves in the intertidal.

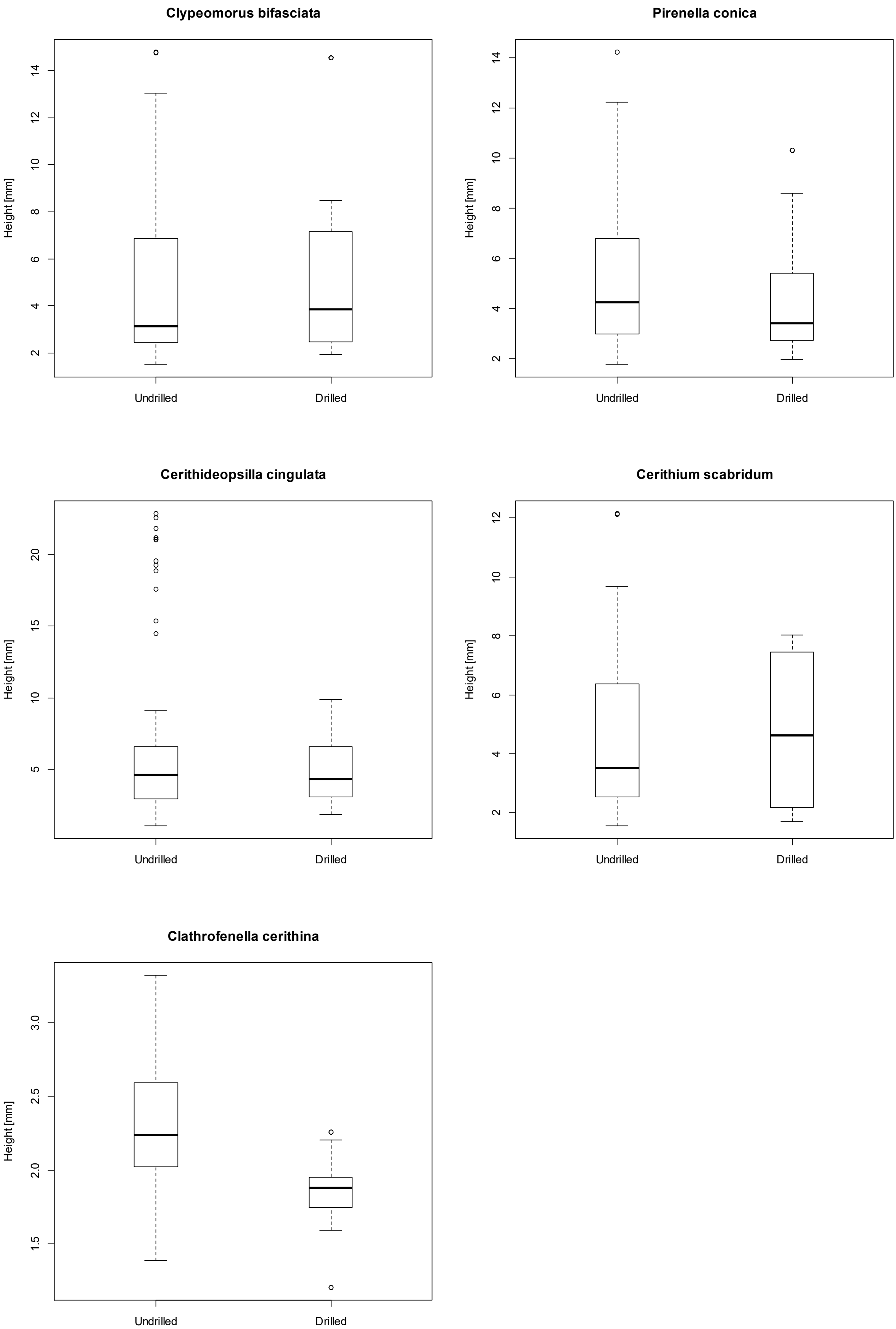

Fig. 17: Size (shell height) of undrilled and drilled gastropods in the intertidal.

5.5. Epifaunal versus infaunal prey

The comparison of epifaunal and infaunal bivalve species in the subtidal reveals no significant differences in DF between life habits (ANOVA: $F = 0.02$, $p = 0.891$) (Fig. 18). PE was not significant either (ANOVA: $F = 0.55$, $p = 0.46$).

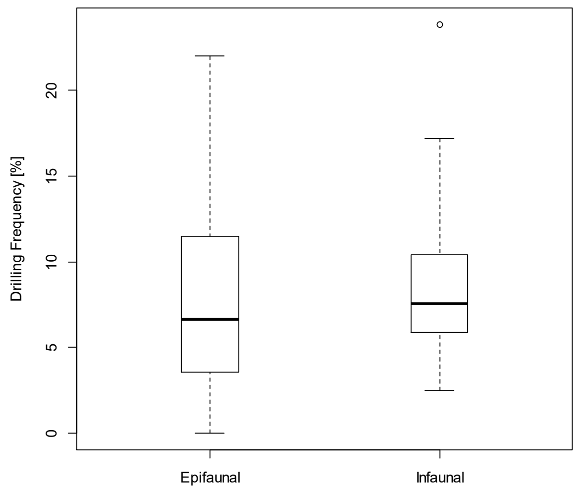

Fig. 18: DF for epifaunal and infaunal bivalve species (n > 50) in the subtidal area.

5.6. Wall drilling versus edge drilling

In the intertidal, Tellinidae and Semelidae are wall drilled. This is opposed to Lucinidae and Veneridae, as they are drilled more often by the edge. Nonetheless, the analysis shows no significance between wall- and edge drilling (Fig. 19). In the subtidal significant differences could be observed (Fig. 20). The family Mytilidae is drilled more often by the wall (wall-drilling-mean = 4.6%, edge-drilling-mean = 0.9%, $t = 4.3$, $p< 0.001$). The same applies for Pteriidae (wall-drilling-mean = 6%, edge-drilling-mean = 0.0%, $t = 4.3$, $p < 0.001$), Lucinidae (wall-drilling-mean = 14.2%, edge-drilling-mean = 4.8%, $t = 2.2$, $p < 0.05$), Ungulinidae (wall-drilling-mean = 14.8%, edge-drilling-mean = 1.3%, $t = 4.3$, $p < 0.001$), Cardiidae (wall-drilling-mean = 1.5%, edge-drilling-mean:0.2%, $t = 2.3$, $p < 0.05$), Tellinidae (wall-drilling-mean = 3.1%, edge-drilling-mean = 1.1%, $t = 2.3$, $p < 0.05$), and Veneridae (wall-drilling-mean = 8.2%, edge-drilling-mean = 1.3%, $t = 7.6$, $p < 0.0001$).

PE could solitarily be calculated for the family Cardiidae (wall-drilling-mean = 0.2%, edge-drilling-mean = 0.3%, t = -0.338, p = 0.762) because only one bivalve was found with an incomplete edge drilling.

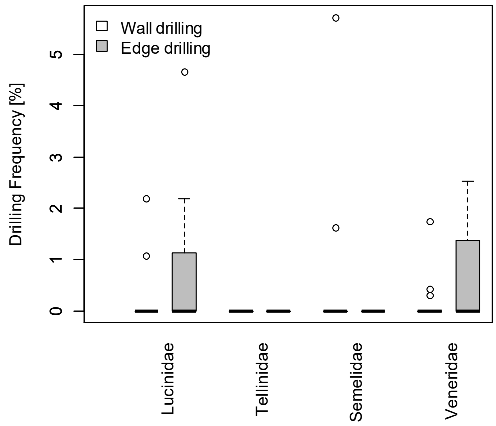

Fig. 19: DF of wall- and edge drilled intertidal bivalve families.

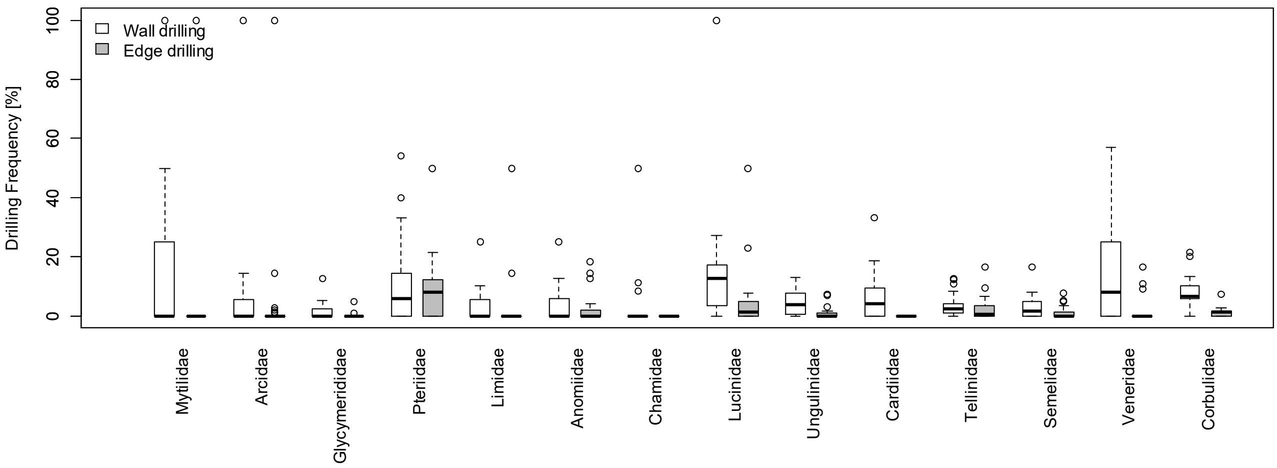

Fig. 20: DF of wall- and edge drilled subtidal bivalve families.

5.7. Community structure and composition in the subtidal

We analyzed the correlation between predation metrics and species richness, overall molluscan abundance, evenness, and predator abundance in living and death assemblages (Tab. 11, Tab. 12, Tab. 13, Tab. 14). There is a slightly positive correlation between PE and species abundance for gastropods in Zakum (Spearman's rho = 0.63, $p < 0.05$). In general, muricids, which are epifaunal predators, were more abundant than naticids, which are infaunal predators, in both fields (Tab. 13, Tab. 14).

Tab. 11: Spearman rank correlation (Spearman's rho) of species richness, overall molluscan abundance and evenness with bivalves and gastropods in UA. Significant values are highlighted in bold.

	Bivalvia				**Gastropoda**			
	DF		**PE**		**DF**		**PE**	
	ρ	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**
Richness	0.188	0.538	-0.158	0.606	-0.216	0.478	-0.209	0.494
Abundance	-0.148	0.629	0.352	0.239	0.151	0.622	-0.114	0.711
Evenness	0.091	0.768	-0.165	0.590	0.136	0.658	-0.106	0.731

Tab. 12: Spearman rank correlation (Spearman's rho) of species richness, overall molluscan abundance and evenness with bivalves and gastropods in ZK. Significant values are highlighted in bold.

	Bivalvia				**Gastropoda**			
	DF		**PE**		**DF**		**PE**	
	ρ	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**
Richness	-0.018	0.949	-0.118	0.676	0.107	0.703	-0.375	0.168
Abundance	-0.279	0.315	0.118	0.676	0.315	0.253	**0.613**	**0.015**
Evenness	0.133	0.638	-0.043	0.879	-0.045	0.875	0.246	0.377

Tab. 13: Spearman rank correlation (Spearman's rho) of predator abundance with bivalves and gastropods in UA. Significant values are highlighted in bold. No living naticids were found in UA. (DA = death assemblage, LA = living assemblage)

	Bivalvia				**Gastropoda**			
	DF		**PE**		**DF**		**PE**	
	ρ	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**
Naticidae - DA	0.123	0.689	-0.209	0.493	-0.209	0.493	-0.170	0.578
Muricidae - DA	0.303	0.315	-0.314	0.295	-0.131	0.670	-0.129	0.675
Naticidae - LA	-	-	-	-	-	-	-	-
Muricidae - LA	0.087	0.777	0.367	0.218	0.070	0.821	-0.419	0.154

Tab. 14: Spearman rank correlation (Spearman's rho) of predator abundance with bivalves and gastropods in ZK. Significant values are highlighted in bold. No dead or living naticids were found in ZK. (DA = death assemblage, LA = living assemblage)

	Bivalvia				**Gastropoda**			
	DF		**PE**		**DF**		**PE**	
	ρ	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**	**ρ**	**p-value**
Naticidae - DA	-	-	-	-	-	-	-	-
Muricidae - DA	0.154	0.584	0.253	0.363	0.249	0.371	0.191	0.495
Naticidae - LA	-	-	-	-	-	-	-	-
Muricidae - LA	0.463	0.082	0.370	0.174	-0.243	0.383	0.384	0.158

5.8. Oil platform and contamination pattern in the subtidal

We considered the distance from the platforms as proxy of influence on predation (Fig. 21). In ZK no correlation was found. In UA, an increased DF can be observed for bivalve species with increasing distance from the platform (Spearman's rho = 0.7, $p < 0.05$). PE did not correlate with distance.

Looking at the influence of sediment contaminants on predation (Tab. 15, Tab. 16), the concentration of zinc is positively correlated with DF in bivalves in UA (Spearman's rho = 0.6, $p < 0.05$). In Zakum, PE of bivalves was weakly correlated with the presence of mercury (Spearman's rho = 0.66, $p < 0.05$) and iron (Spearman's rho = 0.6, $p < 0.05$) and that of gastropods with iron (Spearman's rho = 0.53, $p < 0.05$).

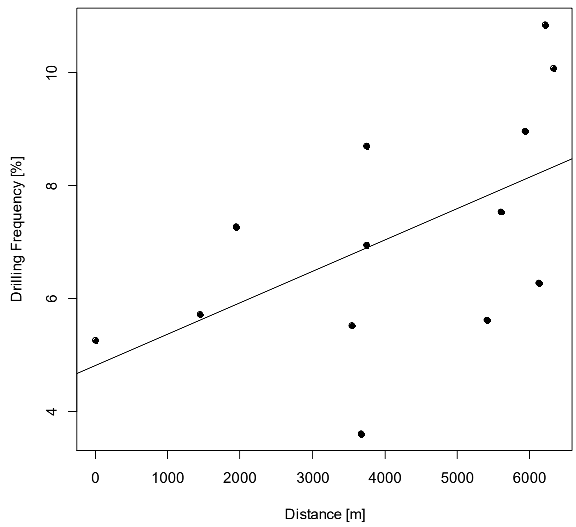

Fig. 21: DF as a function of distance [m] for bivalve species in UA. Correlation was significant (Spearman's rho = 0.6, $p < 0.05$).

Tab. 15: Spearman rank correlation (Spearman's rho) of contaminants with bivalves and gastropods in UA. Significant values are highlighted in bold.

	Bivalvia				Gastropoda			
	DF		PE		DF		PE	
	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value
Arsenic (As)	0.291	0.336	-0.307	0.307	0.349	0.242	-0.182	0.551
Barium (Ba)	0.038	0.901	-0.126	0.681	-0.560	0.046	-0.061	0.844
Magnesium (Mg)	0.019	0.950	-0.325	0.279	-0.190	0.535	-0.042	0.892
Cadmium (Cd)	-0.386	0.193	0.309	0.305	-0.077	0.802	-0.284	0.346
Copper (Cu)	0.309	0.305	0.000	1.000	0.463	0.111	-0.284	0.346
Nickel (Ni)	0.114	0.712	-0.260	0.390	-0.069	0.822	-0.251	0.408
Lead (Pb)	-	-	-	-	-	-	-	-
Mercury (Hg)	0.500	0.082	0.149	0.627	0.273	0.368	0.440	0.133
Vandanium (V)	0.297	0.324	-0.262	0.387	0.524	0.066	-0.225	0.459
Zinc (Zn)	**0.598**	**0.031**	-0.254	0.402	0.399	0.177	0.119	0.699
Iron (Fe)	-	-	-	-	-	-	-	-
Total petroleum hydrocarbons (TPH)	-0.333	0.267	-0.408	0.166	-0.072	0.814	-0.090	0.770

Tab. 16: Spearman rank correlation (Spearman's rho) of contaminants with bivalves and gastropods in ZK. Significant values are highlighted in bold.

	Bivalvia				Gastropoda			
	DF		PE		DF		PE	
	ρ	p-value	ρ	p-value	ρ	p-value	ρ	p-value
Arsenic (As)	0.000	1.000	0.248	0.372	0.124	0.660	0.268	0.333
Barium (Ba)	0.437	0.103	0.147	0.600	-0.225	0.420	0.273	0.325
Magnesium (Mg)	-0.007	0.980	-0.384	0.158	-0.138	0.625	0.244	0.381
Cadmium (Cd)	-0.247	0.374	-0.186	0.506	-0.124	0.660	0.335	0.222
Copper (Cu)	-	-	-	-	-	-	-	-
Nickel (Ni)	-	-	-	-	-	-	-	-
Lead (Pb)	-0.127	0.653	0.279	0.314	-0.030	0.915	0.049	0.862
Mercury (Hg)	0.005	0.985	**0.655**	**0.008**	-0.360	0.188	0.184	0.510
Vandanium (V)	-0.127	0.653	0.279	0.314	-0.030	0.915	0.049	0.862
Zinc (Zn)	-0.105	0.708	0.179	0.522	0.055	0.846	0.030	0.916
Iron (Fe)	0.132	0.639	**0.595**	**0.019**	-0.159	0.571	**0.527**	**0.044**
Total petroleum hydrocarbons (TPH)	0.100	0.722	0.158	0.573	0.203	0.468	-0.233	0.404

6. Discussion

6.1. Intertidal versus subtidal

The most prominent difference in predation pattern was found between subtidal and intertidal habitats. A similar outcome was found by other studies in the Red Sea (Zuschin and Ebner 2015) and in the Mediterranean Sea (Sawyer and Zuschin 2010). Fluctuating conditions (salinity and temperature) in the intertidal environment might be critical for drilling predators due to stress (Sawyer and Zuschin 2010).

Another possible explanation could be taphonomic preservation due to the different extent of hydrodynamics, as a drill hole might weaken a shell and it breaks more easily (Kelley 2007, Roy et al. 1994), though, the analysed tidal flat is no high-energy environment. Shells are transported after the death of the mollusc. Therefore, not all species found in these death assemblages are actually living in same habitat.

6.2. Water depth

No correlation between DF and water depth could be found. This might result from the minor difference in depth (6 - 22m) in our study. A similar conclusion was drawn for the missing correlation in the Red Sea (Chattopadyay et al. 2015). Significant correlation with depth was found in studies addressing a larger depth gradient, such as in a study in the Bahamas, where a higher DF had been observed at the shallow part of the shelf than in a depth of > 70 m (Walker et al. 2002).

6.3. Umm al Dalkh (UA) versus Zakum (ZK)

There are basically no significant differences in DF or PE between the two subtidal fields at class level. At family level, Tellinidae, Veneridae (higher predation in Zakum) and Trochidae (higher predation in Umm al Dalkh) differ and at species level significant distinctions could be made in *Chama* sp. 1 (juv) (higher predation in Zakum), *Tellidora pellyana* and *Tellina* sp. 2 (higher predation in Umm al Dalkh).

A study from the Bahamas found differences in DF between two beaches not far away from each other. They motivated the differences with the fact that the two study areas differed in environmental factors like sedimentation and wave energy (Pruss et al. 2011).

6.4. Bivalves versus gastropods

We found a significantly higher DF in gastropods than in bivalves in both habitats. In addition, PE was higher in gastropods than in bivalves in the subtidal. On closer examination of the two fields we identified a higher PE for gastropods than for bivalves in Umm al Dalkh and a higher PE for bivalves than gastropods in Zakum. This pattern is partly in contrast with a study in the Adriatic Sea where bivalves had significant higher DF and PE than gastropods (Sawyer and Zuschin 2010). Differences in shell thickness and sculpture of the analysed species could be responsible.

6.5. Hard substrate versus soft substrate

No significant difference was found in DF or PE between soft substrate and hard substrate in Zakum. Other studies also found no difference between fine-grained sediments and reefs (Chattopadhyay et al. 2015) and no correlation between DF and sediment grain size (Kelley 1993). Higher DF in biogenic habitats (reefs and seagrasses) than in soft sediments was found in the Caribbean (Leonard-Pingel and Jackson 2016).

6.6. Prey size

A correlation between size and DF was found in two out of seven analysed species in the intertidal. The connection of prey size and predation intensity is highly debated. Some authors found a preference for bigger sized prey (Chattopadhyay and Dutta 2013, DeAngelis et al 1985, Gordillo and Anchuby 2012), others found a preference for medium-sized prey (Pahari et al 2016) or smaller prey (Chattopadhyay et al. 2015). Predator size could also play a role as larger predators might prey on larger prey (Hagadorn and Boyajian 1997) but others found no correlation between prey size and drill hole size, which is an indicator of predator size (Hoffmann et al. 2004).

6.7. Epifaunal versus infaunal prey

Our analysis does not support the hypothesis that the evolution of an infaunal mode of life might be the result of defence to predators (Vermeji 1977, Harper and Skeleton 1993), because no difference was found in subtidal bivalves. A different result was found in the Adriatic Sea where epifaunal prey was drilled more often than infaunal prey (Sawyer and Zuschin 2010).

When higher infaunal DF was found, it is usually related to a higher amount of predators, such as naticid gastropods (Chattopadhyay et al 2015, Pahari et al. 2016). In our study, muricids were more abundant than naticids and this might imply different results.

In addition, epifauna is more likely exposed to taphonomic processes after death. In contrast, the infauna might remain buried and so more protected from breakage. Epifaunally living bivalves often have thicker shells than those living infaunally (Best and Kidwell 2000). Therefore, lift habit of the prey can influence DF and PE but in our study it does not.

6.8. Wall- versus edge drilling

No significant differences in predation site preference were found in the intertidal bivalves: Lucinidae and Veneridae are drilled more often by the edge whereas most other families are drilled more often by the wall. In the subtidal, all families were drilled more often wall drilled. Again this result is not significant.

Dietl et al (2005) found that drilling on the margin of the bivalve is faster because the shell is thinner there but also that it bears the risk of losing the proboscis when the valves close. This implies a trade off between getting faster to feed and the loss of a body part and the metabolic effort to reproduce it.

6.9. Community structure, composition and predators

In general, no correlation between predation intensity and community structure and composition was found. A similar result was found by Sawyer and Zuschin (2010). Therefore, other causes are responsible for the structure of the community.

Predator abundance had no influence on prey abundance. In Zakum not only the relative abundance of living muricid predators (13.7%) was higher than in Umm al Dalkh (3.5%), but also the overall DF was higher with 8.0% compared to 2.0%. In both fields no living naticid was found. Other studies found no correlation between DF and naticid abundance (Kelley and Hansen 1993, Kelley and Hansen 2006, Sawyer and Zuschin 2010).

6.10. Oil platforms

The platform in Zakum has no influence on the extent of drilling predation. In UA, Drilling Frequency increases with distance. Significant differences in DF could be found for zinc, mercury and iron. Due to the low contamination pattern (Appendix Tab. 17, Tab. 18) of the possible contaminants in both fields, the correlation in Umm al Dalkh can hardly be confirmed by the platform alone. Other drivers might be responsible.

6.11. Possible causes of bias

The presence of a complete drill hole does not equal predatory success. Some drilling gastropods may kill their prey without drilling it completely or without any drilling traces. Indeed, up to 10% of the prey can be killed without drilling (Kowalewski 2004), but its frequency is species dependent. In contrast, Visaggi et al (2013) found out that non-drilling predation (e.g. suffocation) might occur but is very rare.

Another risk of biased predation data could be taphonomic degradation of shells. Roy et al. (1994) found out that drilled valves are significantly weaker than undrilled valves and break more easily (see also Zuschin and Stanton 2001). In contrast, Kelley (2007) found no weakening of drilled shells. Epifauna species are more vulnerable than infaunal species because infauna stay buried in the sediment even after death and are less likely exposed to water movement (Lazo 2004). Chojancki and Leighton (2014) tested the influence of taphonomic degradation on shells and found that drill holes are still unmistakably recognizable.

7. Conclusions

(1) The most remarkable distinction in mollusc drilling predation could be found between the intertidal and subtidal habitat. The Drilling Frequency in the intertidal was 2.1% and in the subtidal 12.5%. The differences between the subtidal sites Umm al Dalkh and Zakum were small and only significant at family and species level.

(2) Environmental factors like depth and substrate did not correlate with Drilling Frequency or Prey Effectiveness in our study.

(3) In the intertidal, in two out of seven measured species, undrilled prey was significantly larger than drilled prey.

(4) Community measures (species richness, overall molluscan abundance and evenness) as well as predator abundance had no major influence on drilling predation.

(5) In our case study, the distance from oil platforms did not correlate with predation metrics in Zakum and only slightly in Umm al Dalkh, suggesting no interference of these structures with prey-predator relationships.

8. References

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9. Appendix

This appendix includes figures on species level that are not shown in the main text for better readability. Following these, tables for subtidal environmental data, like measurements of distance, substrate type, depth, contaminants, species richness, evenness, overall molluscan abundance and relative predator abundance per sampling site, are attached.

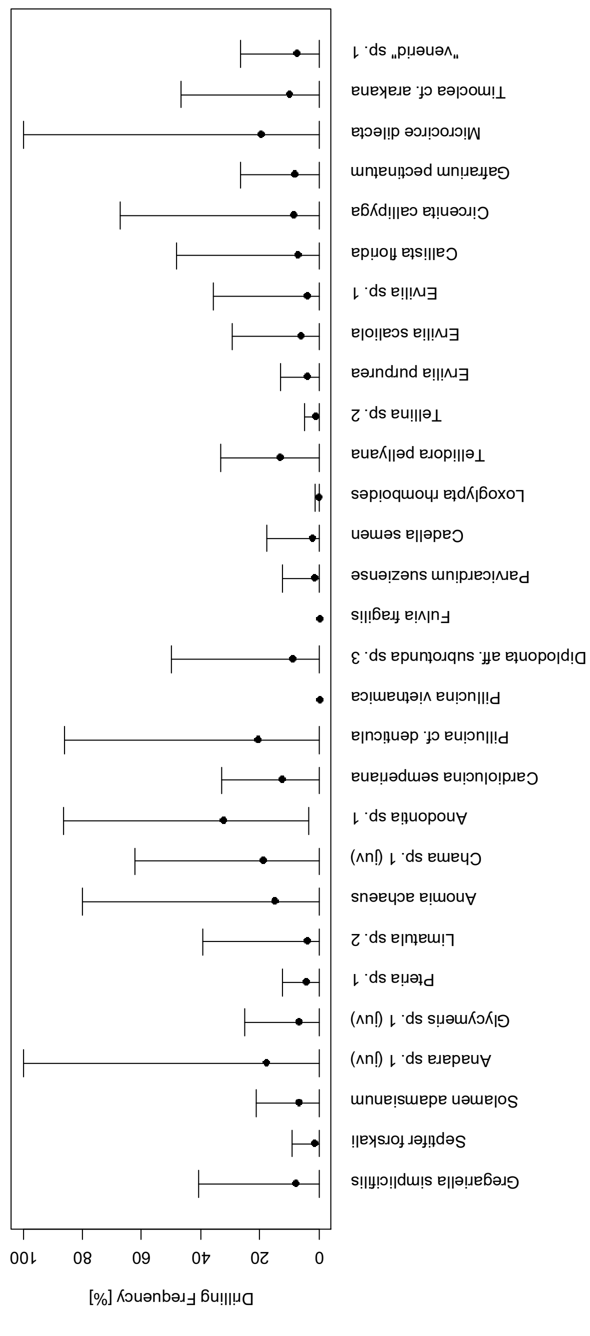

Fig. 22: DF of subtidal bivalve species at regional scale. Error bars indicate 95% confidence intervals.

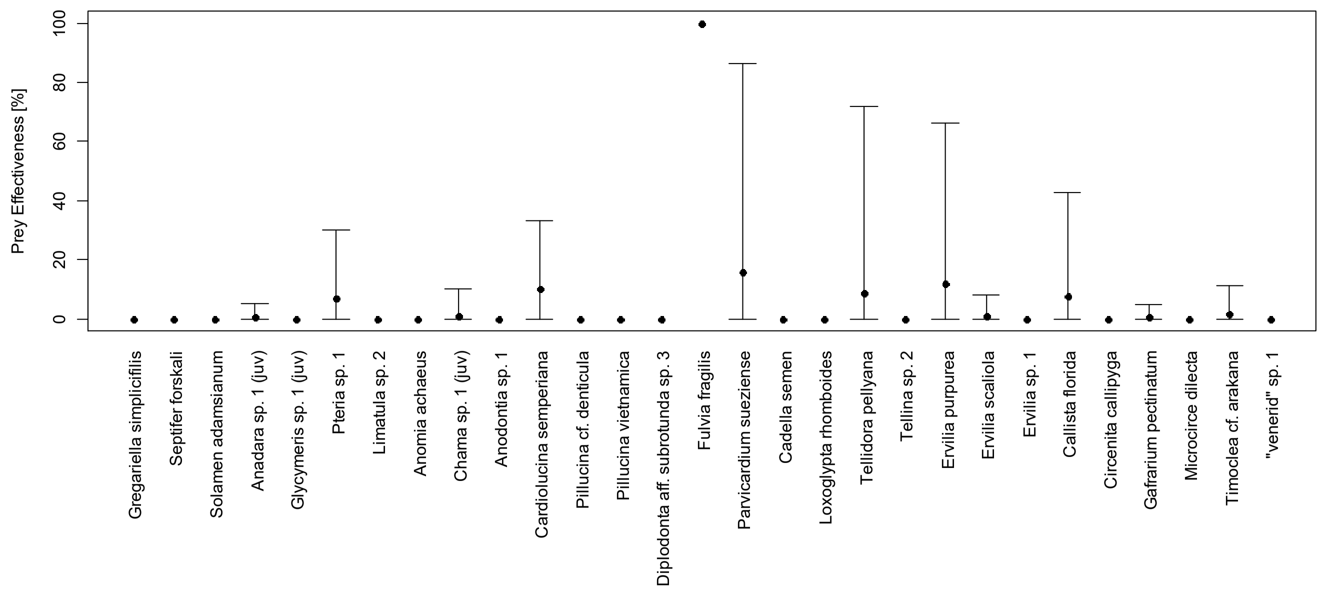

Fig. 23: PE of subtidal bivalve species at regional scale. Error bars indicate 95% confidence intervals.

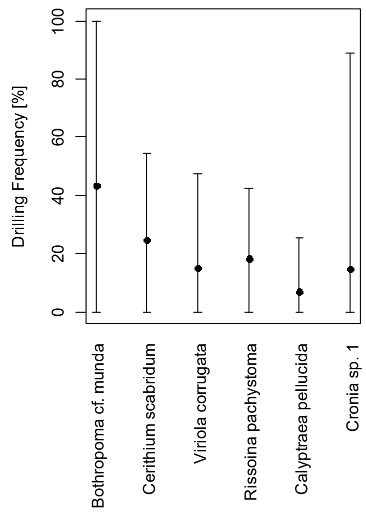

Fig. 24: DF of subtidal gastropod species at regional scale. Error bars indicate 95% confidence intervals.

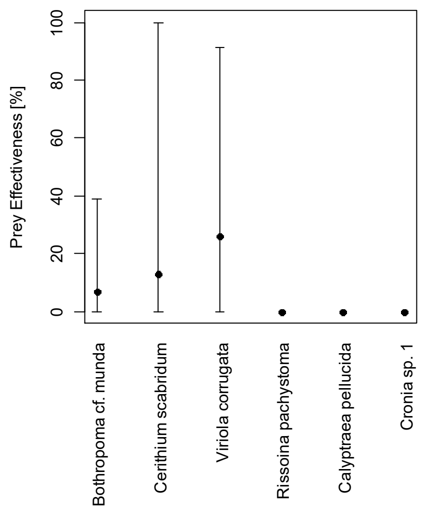

Fig. 25: PE of subtidal gastropod species at regional scale. Error bars indicate 95% confidence intervals.

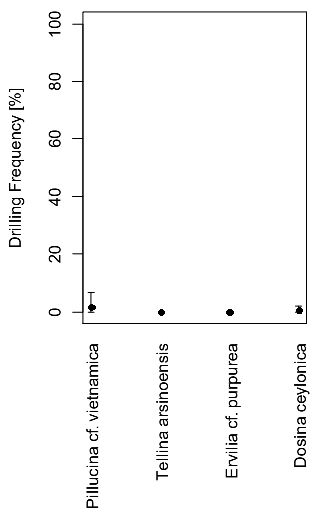

Fig. 26: DF of intertidal bivalve species at regional scale. Error bars indicate 95% confidence intervals.

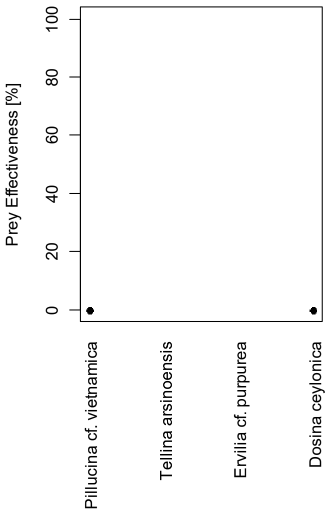

Fig. 27: PE of intertidal bivalve species at regional scale. Error bars indicate 95% confidence intervals.

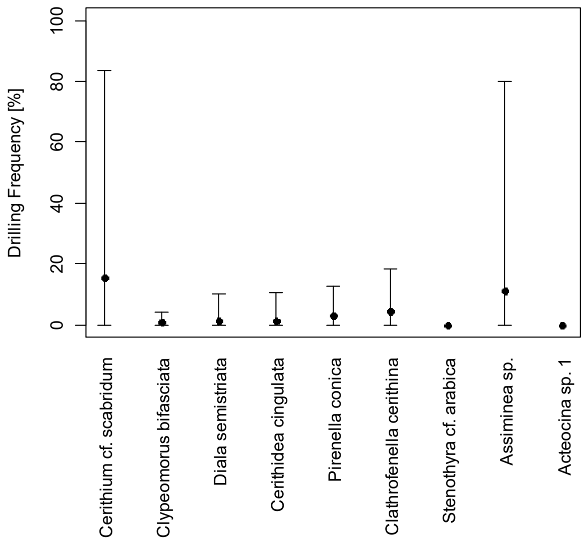

Fig. 28: DF of intertidal gastropod species at regional scale. Error bars indicate 95% confidence intervals.

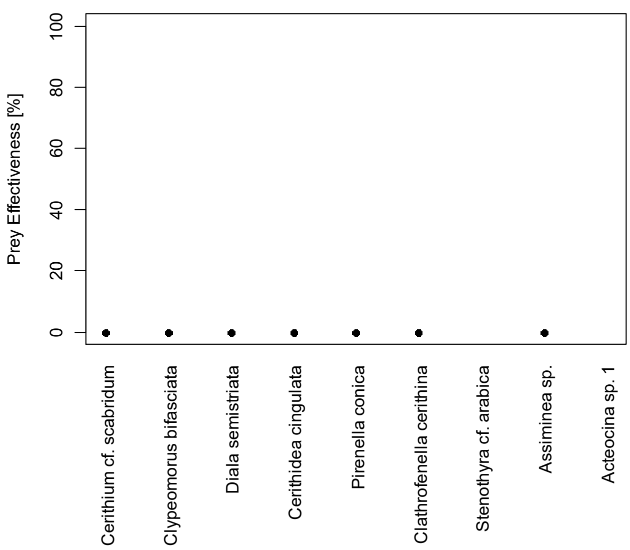

Fig.29: PE of intertidal gastropod species at regional scale. Error bars indicate 95% confidence intervals.

Tab. 17: Biodiversity indices and pollutants (in mg/kg dry weight) of sampling sites in Umm Al Dalkh (UA). SSB = soft substrate.

	UA1	UA2	UA3	UA4	UA5	UA6	UA8	UA10	UA11	UA12	UA13	UA14	UA15
Field	UA	UA	UA	UA	UA	UA	UA	UA	UA	UA	UA	UA	UA
Distance_levels	Far	Mid	Proximal	Mid	Far	Far	Proximal	Far	Far	Mid	Proximal	Mid	Far
Distance_m	6211	3676	1450	3746	6132	5596	0	5405	5937	3546	1947	3744	6336
Substrate	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB	SSB
Depth	21.0	22.4	21.5	19.7	20.8	20.0	21.0	21.5	20.3	20.4	19.0	17.0	19.0
As	6.0	3.3	5.3	4.5	3.3	3.7	6.3	2.5	2.5	5.7	2.5	3.7	2.5
Ba	291	44	63	19	29	54	57	65	78	58	48	15	42
Mg	13667	12333	13633	12300	12267	12667	31600	11733	13900	12733	10433	10800	12333
Cr	9.5	7.1	8.5	7.4	8.1	7.9	14.5	7.0	8.0	9.0	4.9	5.3	10.0
Cd	0.13	0.13	0.13	0.13	2.95	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13
Cu	2.5	2.5	2.5	2.5	2.5	2.5	17.3	2.5	2.5	2.5	2.5	2.5	2.5
Ni	7.3	6.0	7.3	4.2	7.3	6.3	13.7	3.7	6.0	7.0	2.5	2.5	8.0
Pb	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Hg	0.14	0.11	0.11	0.10	0.11	0.13	0.14	0.12	0.12	0.12	0.13	0.21	0.11
Va	2.5	2.5	2.5	11.0	2.5	2.5	17.0	2.5	2.5	2.5	2.5	2.5	2.5
Zn	28.7	5.0	9.0	5.0	5.0	6.7	521.0	5.0	5.0	14.0	8.7	19.7	5.0
Fe	2417	1743	1997	1503	1700	1853	8360	1603	1790	2207	912	1360	2057
TPH	5	12	18	25	17	5	5	5	20	20	5	5	23
DA species richness (rarefied)	11	3	9	2	25	6	4	4	3	8	7	4	7
DA overall molluscan abundance	1305.25	1126.125	1042.5	735.125	1485.5	1227	1136	1783.5	1331	1640	1186.125	1195	1986.125
DA eveness	0.728	0.776	0.607	0.801	0.79	0.781	0.637	0.336	0.529	0.681	0.869	0.282	0.776
DA relative abundance Naticidae	0.2%	0.3%	0.2%	0.1%	0.1%	0.1%	0.0%	0.1%	0.0%	0.1%	0.3%	0.0%	0.2%
DA relative abundance Muricidae	0.2%	0.2%	0.2%	0.3%	0.1%	0.0%	0.2%	0.3%	0.2%	0.0%	0.6%	0.0%	0.2%
LA relative abundance Naticidae	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
LA relative abundance Muricidae	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	25.0%	50.0%	0.0%	0.0%	0.0%	0.0%	0.0%

Tab. 18: Biodiversity indices and pollutants (in mg/kg dry weight) of sampling sites in Zakum (ZK). SSB = soft substrate, HSB = hard substrate.

	ZK16	**ZK24**	**ZK25**	**ZK26**	**ZK27**	**ZK28**	**ZK29**	**ZK31**	**ZK32**	**ZK33**	**ZK34**	**ZK35**	**ZK36**	**ZK37**	**ZK38**
Field	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK	ZK
Distance_levels	Satellite	Proximal	Far	Mid	Proximal	Mid	Far	Far	Mid	Proximal	Mid	Far	Far	Satellite	Satellite
Distance_m	14271	0	3884	2645	2234	2641	4169	4664	2643	2050	2452	3895	3425	11548	13431
Substrate	SSB	SSB	HSB	HSB	HSB	HSB	HSB	SSB	SSB	SSB	HSB	HSB	HSB	HSB	SSB
Depth	16.9	11.0	14.5	13.0	11.4	11.0	9.4	11.7	13.5	13.3	13.0	15.0	15.5	6.0	6.7
As	2.5	2.5	2.5	10.0	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Ba	36	39	31	55	21	23	30	50	77	36	21	31	24	14	14
Mg	8150	9303	9890	10000	8400	8770	10800	9970	12967	9667	9780	8810	10200	10500	8360
Cr	4.5	20.6	3.5	10.8	2.3	1.0	2.4	3.3	5.0	2.5	2.6	2.6	3.2	1.0	2.5
Cd	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.13	0.19	0.13	0.13	0.13	0.13	0.13	0.13
Cu	2.5	9.7	2.5	6.0	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Ni	2.5	8.0	2.5	7.0	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Pb	5.0	14.7	5.0	15.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0	5.0
Hg	0.12	1.43	0.14	0.10	0.12	0.07	0.07	0.08	0.10	0.10	0.08	0.08	0.08	0.08	0.09
Va	2.5	16.0	2.5	21.0	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5	2.5
Zn	5.0	236.0	5.0	63.0	5.0	5.0	5.0	19.0	17.7	5.0	5.0	5.0	5.0	5.0	5.0
Fe	578	12067	530	4310	443	271	365	464	1447	341	467	417	465	207	186
TPH	10	25	26	23	62	23	24	28	23	29	17	12	13	13	18
DA species richness (rarefied)	2	8	12	14	11	14	4	3	10	2	7	9	22	2	2
DA overall molluscan abundance	1649.625	907	212.875	729.5	71	156.25	43	233.125	694.375	1178.125	468	233	615.375	739.125	2088.5
DA eveness	0.157	0.935	0.871	0.852	0.946	0.964	0.936	0.708	0.907	0.251	0.815	0.656	0.939	0.308	0.608
DA relative abundance Naticidae	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
DA relative abundance Muricidae	0.2%	3.2%	4.2%	3.7%	4.2%	0.6%	4.7%	1.3%	0.3%	0.0%	1.1%	2.1%	3.4%	0.1%	0.0%
LA relative abundance Naticidae	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
LA relative abundance Muricidae	40.0%	20.0%	24.0%	23.5%	0.0%	11.1%	0.0%	50.0%	0.0%	0.0%	0.0%	4.3%	15.6%	0.0%	0.0%