DIPLOMARBEIT

Titel der Diplomarbeit

Drilling predation in the northern Adriatic Sea: Spartial variabilities and down-core changes in molluscan assemblages

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1   Abstract

This study deals with predatory drill holes in the bivalve fauna at eight shelf locations in the northern Adriatic Sea. In summer 2013 at each of these sampling stations sediment cores with a length from 140 to 160 cm have been collected. The mollusc assemblages were examined for traces of drilling predation. Several previous studies deal with biotic interactions and their influence on biodiversity. Some studies classify the northern Adriatic Sea as a low-predation setting, whereas others found typical Cenozoic drilling frequencies in subtidal settings.

Almost 54,000 bivalves from eight different sediment cores have been analysed for 1) overall drill frequency (DF), a measure how often bivalves are drilled by predators, most notably gastropods, 2) edge drill frequency (EDF), the quantity of drilling traces at the edge of shells, 3) multiple drill frequency (MDF), the amount of individuals with more than one drill hole, 4) incomplete drill frequency (IDF), the percentage of bivalves which shells are unsuccessfully drilled and 5) prey effectiveness (PE), which shows the proportion of bivalves which resist the predator's attacks.

Total DF across all cores was 18.0 %, but varied strongly between the cores. It was only about 5 % in the Po 3 M13 core (4.6 %) and the Venice M38 core (5.4 %), but reached 15.2 % in the Brijuni core and 22-24 % in the two cores from Panzano.

The EDF was very low with an average of 1.2 % across the total fauna of all analysed cores and differed only slightly between the cores. In the cores from the Po delta, from Venice and Panzano EDFs were close to 0 %, while in the assemblage from Brijuni and Piran M53 frequencies of edge drills reached nearly 2 %.

The amount of multiple drilled bivalves was even lower and ranged from 0-1 % across the cores. The value for the IDF was slightly above 1 % on average for the total fauna sampled. In the assemblage from Brijuni about 4 % of the bivalves were unsuccessfully drilled, while in the cores from Venice, Piran or the Po River delta it was < 1 %.

PE was on average 7.1 % and mostly restricted to very few species in the cores e.g. *Striarca lactea* with 78.2 % at Brijuni and characterized by strong variability between the cores (Piran 2.2 %, Panzano 6.8-10.5 %, Brijuni 19.3 %).

DFs varied not only between the sampling sites, but also along the cores, e.g. from 8 % to 26 % in Brijuni M44. Significant and distinct correlations between drilling intensities and nutrient availability were evident in some cores. Interestingly, DFs were very high in commensals and parasitic bivalves, as well as in suspension feeders. Moreover, in most of the cores infaunal bivalves were drilled more frequently than those with epifaunal life habits. Considering the total bivalve fauna of all cores, DFs of bysally attached bivalves were more than twice as high as DFs of cemented taxa. Actively mobile bivalves with the ability to change

their epifaunal attachment (i.e. bysally attached or reclining bivalves) showed the lowest DFs.

In some assemblages with relatively high diversities, e.g. from Brijuni or Piran, high drilling intensities were found, but drilling intensities in other cores, e.g. from Venice or Panzano, do not correlate with diversity. However, this study may indicate that drilling predation and prey abundance do not principally control diversity, at least not at those sampling sites.

Drilling intensities recorded in the bivalve fauna show strong spatial variation but still suggest typical values for Cenozoic shelf environments.

2   Zusammenfassung

Diese Arbeit beschäftigt sich mit dem Raubdruck bohrender Gastropoden auf Bivalven. Untersucht wurden Bohrspuren auf Muschelschalen von acht Riffstandorten in der Nordadria. Im Sommer 2013 wurden an allen Standorten Sedimentbohrungen durchgeführt und Sedimentkerne mit einer Länge von 140 cm bis 160 cm entnommen. Die in den Sedimentkernen enthaltenen Bivalven wurden auf Bohrlöcher räuberischer Gastropoden untersucht.

Über diese ökologischen Interaktionen und deren Auswirkungen auf die Biodiversität in marinen Ökosystemen gibt es verschiedene Studien. Manche stufen die Bohrintensitäten in der Nordadria als niedrig ein, während andere, insbesondere zum Subtidal deutlich höhere für das Cenozoicum typische Bohrintensitäten festgestellt haben.

Circa 54.000 Bivalven aus acht Sedimentkernen wurden auf folgende Parameter hin untersucht: 1) gesamte Bohrfrequenz, d. h. wie viele der Bivalven wurden von räuberischen Schnecken bebohrt, 2) Häufigkeit von Bohrlöchern, die sich am Rand von Muschelschalen befinden, 3) Häufigkeit von mehrfach bebohrten Muschelschalen, mit zwei oder mehr Bohrlöchern pro Schale, 4) Häufigkeit von unvollständigen Bohrlöchern, bei denen die Bivalvenschale nicht vollständig durchbohrt wurde und 5) Effektivität der Bivalven in der Abwehr bohrender Räuber.

Insgesamt waren 18,0 % der untersuchten Bivalven bebohrt, aber die Bohrintensitäten variierten von Kern zu Kern sehr stark. Im M13-Kern vom Po Delta und im Kern von Venedig hatten nur ca. 5 % der Bivalven Bohrlöcher. Im Vergleich dazu waren 15,2 % Muscheln aus dem Kern von Brijuni und sogar 22-24 % der Bivalven aus den beiden Kernen von Panzano bebohrt.

Die Frequenzen von Bohrspuren am Rand der Bivalvenschalen waren mit durchschnittlich 1,2 % der gesamten Muschelfauna sehr niedrig und schwankten nur gering zwischen den einzelnen Kernen. In den Kernen vom Po Delta, von Venedig und Panzano waren die Frequenzen von Randbohrlöchern nahe zu 0 %, in den Kernen von Brijuni und Piran M53 hatten fast 2 % der Bivalven Bohrlöcher am Schalenrand.

Der Anteil von mehrfach bebohrten Muschelschalen war noch niedriger und erreichte je nach Kern durchschnittlich 0-1 % der Bivalven. Im Schnitt hatten knapp über 1 % der untersuchten Bivalven unvollständige Bohrlöcher. Im Kern von Brijuni waren fast 4 % der Muscheln bebohrt, in den Kernen von Venedig, Piran oder vom Po Delta hatten weniger als 1 % unvollständige Bohrlöcher.

Der Erfolg der Bivalven in der Abwehr bohrender Räuber war im Schnitt 7,1 %. Je nach Muschelart und je nach Kern waren die Ergebnisse sehr unterschiedlich (Piran 2,2 %, Panzano 6,8-10,5 %, Brijuni 19,3 %). *Striarca lactea* hatte im Kern von Brijuni eine besonders hohe Effektivität von 78,2 %. Mehr als drei Viertel aller Bohrlöcher in den Proben von *Striarca* waren in diesem Kern unvollständig und die räuberischen Angriffe demnach nicht erfolgreich.

Die Bohrfrequenzen schwankten aber nicht nur zwischen den einzelnen Kernen, sondern auch zwischen den Sedimentschichten der Bohrkerne. Im Brijuni-Kern variierten die Bohrhäufigkeiten je nach Schichttiefe beispielsweise zwischen 8 % und 26 %. In einigen der untersuchten Kerne korrelierten die Bohrfrequenzen mit dem Nährstoffgehalt bzw. der Primärproduktion am jeweiligen Standort, zB in den Kernen von Venedig oder Panzano, in anderen Kernen, zB von Brijuni jedoch nicht.

Besonders häufig bebohrt waren kommensal und parasitisch lebende Bivalven sowie Suspensionsfresser. Außerdem waren infaunal lebende Bivalven in den meisten Kernen häufiger bebohrt als epifaunal lebende. Epifaunal lebende Muscheln, die mit Hilfe von Byssusfäden am Substrat anhaften, hatten häufiger Bohrlöcher als Bivalven, die am Substrat angewachsen sind, wie zB Ostreidae. Die Gruppe der Bivalven, die sich aktiv fortbewegen und sich sowohl mittels Byssus am Substrat festhalten als auch frei schwimmen können, hatten die wenigsten Bohrlöcher.

Einige Kerne, die eine hohe Diversität aufwiesen, wie zB Brijuni oder Piran, hatten hohe Bohrfrequenzen. In anderen Kernen, zB Venedig oder Panzano, korrelierten Diversität und Bohrfrequenz jedoch nicht. Ein genereller Zusammenhang zwischen Häufigkeit der Bebohrung und der Beutetiere konnte auch nicht festgestellt werden. Denn es waren auch sehr selten vorkommende Bivalvenarten bebohrt und manchmal hatten Arten mit großen Abundanzen relativ wenige Bohrlöcher, zB *Striarca* im Kern von Brijuni.

Insgesamt kann man daraus schließen, dass die Bohrintensitäten der untersuchten Bivalven trotz der großen Variabilität, die zwischen den einzelnen Kernen festgestellt wurde, typischen Bohrintensitäten von Riffen aus dem Cenozoikum entsprechen.

3   Introduction

Competition and predation are essential biological factors debated to limit biodiversity (Karleskint, 2010). A common method to analyse predation rates is to count the traces of predatory attacks on bivalve-shells including drill holes and repair scars. Incomplete drill holes and repair scars represent unsuccessful predatory attacks and are interpreted ambiguously (Leighton, 2002).

The samples for this study were taken from eight different locations and therefore will provide insight into regional variability of drilling intensities that can be compared to local diversity in different habitats. The differences in drilling frequencies along the core may reflect changes of an ecosystem during its history. Temporal variations in drilling predation, however, may not only reflect local species richness and predation pressure but also changes in (paleo)environments in space and time (Kelley and Hansen, 1995, 2007; Zuschin and Sawyer, 2010, 2011; Hoffmeister and Kowalewski, 2001).

In the samples of the Northern Adriatic I examined the drilling intensities and their variability at the scale of decades to millennia at different shelf locations, if there is an effect of feeding strategies and substrate relationships of bivalves on drilling frequencies and prey effectiveness and if there are distinct trends along the sediment cores. Furthermore, it can be tested whether human impact, for example nutrient increase or bottom trawling, influences drilling frequencies. For this reason cores were taken from comparable habitats (depth and sediment type) in areas which were protected from anthropogenic impacts like bottom trawling or on the other hand less protected. Moreover, it may be hypothesised that life habits of both prey and predators affect the drilling intensities. Following these hypotheses it can be examined if there are connections between predation rise and Phanerozoic habitat trends of marine fauna, e. g. infaunalization of benthos (Vermeij, 1977) or cementation in bivalves (Harper, 1991).

Studies from McKinney and Hagemann (2006), Kelley (2006), McKinney (2007) suppose rather low predation intensity in the Northern Adriatic, compared to other Cenozoic shelves at similar latitude. On the other hand Zuschin and Stachowitsch (2009) and Sawyer and Zuschin (2010) came to different conclusions and expect higher drilling intensities in this area. To understand the complexity of drilling predation in the Northern Adriatic I calculated five indices for bivalve assemblages from eight different shelf-locations in the Northern Adriatic: 1) the overall drill frequencies (DF), a measure to quantify how often bivalves are drilled by predators, 2) incomplete drill frequencies (IDF), the proportion of bivalves which shells are unsuccessfully drilled, 3) edge drill frequencies (EDF), the quantity of drills at the edge of shells, 4) multiple drill frequencies (MDF), which account for individuals with more than one drill hole and 5) prey effectiveness (PE), prey's ability to resist drilling predation.

The following hypotheses are tested:
1) DF increases through time (i.e. along the core) because nutrient increase may support more predatory gastropods.

2) DF is higher in nutrient-rich habitats than in more oligotrophic habitats.

3) DF is coherent with life habits of prey. In this context it is analysed if DF is higher on slow-moving and metabolically less active bivalves (suspension feeders) and low on more metabolically active ones (predators). Moreover, it is tested if DF is lower in infaunal and higher in epifaunal molluscs and if cementation can be seen as an efficient defence strategy.

4) DF rises significantly with an increase of diversity.

5) DF and its resulting predation pressure in the Northern Adriatic is on a pre-Cenozoic level.

4 Study area

The sites of the study are located in the Northern Adriatic, which is a semi-enclosed, large sized (> 300 km long) and shallow (on average < 50 m deep) epicontinental sea. That's why its shelf environment is similar to typical Palaeozoic and Mesozoic settings (McKinney, 2007; Zuschin and Stachowitsch, 2009). The modern northern Adriatic Sea was formed in the Holocene by a sea level rise and is therefore a rather young marine area. Its surface circulation is mainly thermohaline and cyclonic, triggered by the freshwater input of the Po River. Moreover, the Po River in addition to other smaller rivers represents not only the primary source of freshwater, but also of sediments and nutrients into the Adriatic Sea (McKinney, 2007). The Northern Adriatic is characterized by its relatively low-energy environment, small tidal range and wave heights. The surface water temperature is 7°C on average in winter and 24°C in summer and the average salinity is 30-35 ‰ (Gačić, 2001; Janeković, 2010). The average sediment accumulation rate in the Northern Adriatic is 0.24 cmy-1 and the gross sedimentation flux is about 0.30-0.88 gcm-2 y-1 (Giordani, 2002). The seafloor in the Northern Adriatic consists of relict Pleistocene sands which are covered by mud from the Holocene (Pigorini, 1968; Goff, 2006). Recent sands spread small costal zones. The inner shelf consists of fine sands, the middle shelf contains silts and clays and the outer shelf is composed of relict sands.

The productivity in the Northern Adriatic is relatively high compared to the rest of the Mediterranean (Zavatarelli, 1998). Due to the enormous sediment and nutrient input from the Po River there is a high primary production in front of the Po delta which leads to a eutrophic or even hypertrophic state in this area and in the north-western region offshore of Venice and in the area of the Gulf of Trieste. The western part of the Northern Adriatic is mesotrophic (Barmawidjaja, 1995).

5   Material and methods

I used drill holes, probably mostly drilled by naticid or muricid snails, for the quantification of the drilling intensities among bivalves in the northern Adriatic Sea, a method also frequently applied by paleoecologists to study predation pressure in the fossil record (Kelley, 2007; Saywer and Zuschin, 2010).

In summer 2013 sediment cores were taken at seven sampling stations along the coast of the Northern Adriatic (Fig. 1). The cores contained sediments to a depth of about 1.5 meters. Station 1 (Piran M1 core) is located at the oceanographic buoy off Piran (Slovenia). This shelf environment features sandy mud with low sediment and nutrient input and is protected from dredging. Station 2 (Piran M53) is located close to station 1, has very similar low sediment and nutrient conditions, but it is further offshore the oceanographic buoy off Piran and not protected from dredging. Stations 3 (Po3 M13) and 4 (Po4 M20) are close to the Po River mouth and characterised by mud

Fig. 1: Map of the study area with sampling locations

with high nutrient and sediment input. Station 5 (Brijuni M44) is located within a marine protected area south of Brijuni Islands (Croatia). In this area the shelf surface consists of relict sands and fishing and dredging is prohibited. Station 6 (Venice M38) is located in the shelf area close to Venice, which contains oligotrophic relict sands along the northern sand belt. This region is highly affected by fishing and dredging. At station 7 two cores were collected (Panzano M28, M29). This station in the Gulf of Triest is characterized by pelitic sediments and is located close to the Isonzo River mouth, near Panzano.

The sediment cores were collected by a UWITEC corer from an oceanographic vessel from an Italian cooperation partner. The diameters of the cores ranged from 9 to 16 cm and the length of the cores differed between 140 and 160 cm depending on the sediment composition at the different locations. (Brijuni M44: 160 cm, Panzano M28 and M29: 150 cm, Piran M1: 145 cm, Piran M53: 155 cm, Venice M38: 140 cm, Po 3 M13: 155 cm and Po 4 M20: 150 cm.) The upper 20 cm of the cores were sliced into 2 cm intervals to receive high-resolution data while the lower parts of the cores were sliced into 5 cm intervals to identify major ecological shifts.

The unbroken shells (> 90 % complete) have been identified to species level, counted and then I examined them for traces of drilling predation. To meet the general accepted criteria

the drill holes had to be circular in cross section with smooth sides, penetrate perpendicularly from the outer shell surface and only one valve is drilled in articulated shells (Carriker & Yochelson, 1968; Rohr, 1991; Baumiller, 1996; Kaplan & Baumiller, 2000; Leighton, 2001).

The examined drill holes were most probably produced by several species of muricid and naticid gastropods. While in many cases the holes drilled by muricids can be clearly distinguished from those drilled by naticids (Bromley, 1981; Kelley and Hansen, 2003), the very abundant muricid gastropod *Hexaplex trunculus* drills holes which are very similar to those of several naticid snails. As the goal of this study was to determine the effects of drilling predation on the bivalve fauna in the Northern Adriatic as a whole and not the effects of a distinct predatory clade, I didn't distinguish between naticid and muricid drill holes.

For evaluation of the overall drilling frequency (DF) - the intensity how often bivalves are attacked by gastropods - the total number of drilled shells (edge and multiple drilled shells included) was divided by the total number of individuals. This calculation was made for each taxon for each layer in the examined cores. To calculate the number of failed predatory attacks and to find out the incomplete drilling frequency (IDF) the number of drill holes which didn't penetrate the shell completely were divided by the number of examined individuals. Bivalves usually disarticulate after death and isolated valves (with or without traces of predation) are preserved. The potential for preservation of both valves is the same and a correction factor of 2 is therefore applied. To evaluate the values for drilling intensities the number of disarticulated valves is usually divided by 2 before the articulated valves are added to the double valved specimens to account for the "adjusted total"-number of individuals (Kowalewski, 2002). But in this study the higher amount of either right or left valves was added to the double valved specimens of each layer. As a measure of predation failure, prey effectiveness (PE) was calculated. This value provides a relative frequency of unsuccessful attacks in form of incomplete drills. To account for the PE the number of incomplete drills was divided by the total number of attacks (complete plus incomplete drills) (Vermeij, 1987; Kowalewskij, 2002).

In most of the cases gastropod predators choose the drilling site on their bivalve prey selectively following a stereotyped behaviour. Based on a cost-benefit ratio model (Kitchell, 1981) it is most likely that the prey shells are drilled centrally (Kelley, 1986). In some cases (especially in the bivalve genus *Corbula*) the gastropods don't follow these stereotyped pattern and we find numerous valves with drill holes on the edge of the shells. These edge drills were then counted and the edge drilling frequency (EDF) was computed by dividing the number of edge drills by the adjusted total number of individuals. A few valves showed not only a single drill hole but even two, three or more complete and incomplete drill holes on a single valve. These cases were counted and a frequency of those multiple drill holes (MDF) as well as a frequency of incomplete drill holes (IDF) was calculated by dividing the number of valves with multiple or incomplete drills by the adjusted total of individuals.

The variation of predation intensities among bivalve families and furthermore among the ecological guilds, e. g. feeding strategies and substrate relationship/attachment, was analysed. The diet categories of the examined bivalves range from suspension and deposit feeders, chemosymbionts to carnivores (microcarnivore), e.g. *Cuspidaria cuspidata* or *Cardiomya costellata*. The substrate relationship categories of the bivalves in the samples include borers, commensals, epifaunal (hard/soft bottom), infaunal (hard/soft bottom), soft bottom semi-infaunal (e.g. *Andara*) and nestlers (hard/soft bottom), e.g. Limidae. The epifaunal categories contain byssal attachers, cementers and recliners (Beesley, 1998; Nevesskaja, 2006; Todd, 2001).

As the total number of shells as well as the number of species and families differs significantly among the cores and especially along the cores, DF, EDF, MDF, IDF and PE were evaluated at different taxonomic levels and for the various ecological guilds. *Corbula gibba* is a common bivalve species in all of the eight sediment cores and is generally frequent in most parts of the northern Adriatic Sea. Therefore in this study *Corbula gibba* is used as a kind of "key species" which is compared with the general trend within and between cores. For statistical analyses and generating graphs the software package R was used.

Rarefaction curves were generated for a representative comparison of diversities. To illustrate the relationship between the bivalve community structure and the predation intensity following values were calculated and examined for correlations to DF: species richness, evenness, overall bivalve abundance and abundances of the most abundant species. For generating these graphs the software package PAST was used.

6 Results

A total of 53,994 individuals of bivalves (87,315 single valves and 1,216 articulated animals) were examined for drill holes from eight different core samples (Table 1). This total fauna consists of 117 bivalve species from 38 families. The drilling intensities were computed for the total drill frequency (DF) which includes drills of disarticulated, articulated valves, edge drilled and multiple drilled valves. Moreover, frequencies for edge-drills (EDF), for multiple drill holes (MDF) and for incomplete drill holes (IDF) were calculated (Table 2-4) and then Prey effectiveness (PE) was generated (Table 5).

6.1 Predation intensities in the total fauna

6.1.1 Overall drill frequency (DF)

The average drilling intensity of the total fauna from all eight cores was 18.0 %, but total drill intensities as well as the abundances of bivalves in the assemblages differ significantly in the analysed sediment cores (Table 1). The highest average overall drill frequency was calculated for the Piran M53 core where more than 24.3 % of the 13,063 examined molluscs were drilled. At the second station close to Piran (M1) the total number of individuals along the core was the highest among the various locations with a total of 14,677, but the DF of this core (Piran M1) is with an average of 18.1 % more than 5 % lower than at Piran M53. In the Po delta and in the area of Venice DFs were the lowest among all cores (Table 1). In the Po3 M13 core in less than 5 % of the 849 bivalves traces of drilling predation were recognized. The samples of the second core from the area close to the Po River (Po4 M20) showed slightly higher predation rates with 8.5 % on average along the core. In the sediment core from the shelf area close to Venice the DF was about 5 %. In comparison to the low rates in the Po and Venice-stations the Panzano cores (M28, M29) which contained 3,000 to 4,000 bivalves show considerably higher drilling intensities of 21.8-23.8 % along the core. In the M44-core from the Brijuni islands on the east coast of the Northern Adriatic 15.2 % of the 12,255 examined molluscs were drilled.

Table 1: Drill frequencies (DF) of the total fauna of all 8 cores

Total fauna - Drill frequency					
Core	Adj. Total	Drills (total)	DF (%)	lCI	uCI
Brijuni M44	12,255	1,865	15.22	0.14	0.16
Piran M1	14,677	2,660	18.12	0.18	0.19
Piran M53	13,063	3,180	24.34	0.24	0.25
Panzano M28	4,040	963	23.84	0.22	0.25
Panzano M29	3,155	688	21.81	0.20	0.23
Venedig M38	5,071	273	5.38	0.05	0.06
Po3 M13	849	39	4.59	0.03	0.06
Po4 M20	884	75	8.48	0.07	0.11
total	53,994	9,743	18.04	0.18	0.18

6.1.2 Occurrence of atypical borehole sites - edge drill frequency (EDF)

As mentioned in Kitchell (1981) and Kelley (1986) gastropod predators drill their bivalve prey not only centrally in one of the valves, but sometimes at the edges of a valve. These cases are relatively rare but nevertheless it is interesting to test if there are environments where more edge drilled shells can be found or if these specific drill preferences are correlated with specific taxa only, for example the genus *Corbula*. The frequency of edge-drills in the total fauna examined was rather low with a mean of 1.2 % (Table 2). The highest EDFs of about 2 % were calculated for the assemblages from Piran M53 and Brijuni M44. The smallest assemblages of the sediment cores from the Po delta have no or only very few edge-drilled valves (0-0.3 %). But in the Panzano cores (M28, M29) and in the samples from the shelf area near Venice (M38) the EDFs were on a similar low level (0.3-0.5 %) although the bivalve assemblages were larger in these cores. In the largest examined assemblage from the shelf area off Piran (M1) EDF was only 0.8 %.

Table 2: Edge drilling frequencies (EDF) of the total fauna of all 8 cores

Total fauna - Edge drill frequency (EDF)					
Core	Adj. Total	ED	EDF (%)	lCI	uCI
Brijuni M44	12,255	232	1.89	0.02	0.02
Piran M1	14,677	119	0.81	0.01	0.01
Piran M53	13,063	256	1.96	0.02	0.02
Panzano M28	4,040	20	0.50	0.00	0.01
Panzano M29	3,155	14	0.44	0.00	0.01
Venice M38	5,071	17	0.34	0.00	0.01
Po3 M13	849	0	0.00	0.00	0.00
Po4 M20	884	3	0.34	0.00	0.01
total	53,994	661	1.22	0.01	0.01

6.1.3 Multiple predator attacks - multiple drill frequency (MDF)

According to my evaluation frequencies of valves with more than one (complete or incomplete) drill holes are very rare in the Northern Adriatic with an average rate of 0.4 % of the total bivalve fauna examined in 8 cores. The highest, but still very low MDF was calculated for the assemblage from the Panzano M29 core collected from the shelf area in the Gulf of Triest with 1.1 % of the total amount of bivalves along the core. In the assemblages from the Brijuni islands (M44), 0.6 % of the examined bivalves showed multiple traces of attacks of gastropod predators. The analysis of the bivalves from the shelf off Piran (M1, M53) and of the second core from the Gulf of Trieste shows MDFs of 0.3-0.5 %. In the assemblages col-

lected from the shelf in the mouth of the Po River (M13, M20) and near Venice (M38) virtually no multiple drilled valves were detected.

Table 3: Multiple drill frequencies (MDF) of the total fauna of all 8 cores

Total fauna - Multiple drill frequency (MDF)					
Core	**Adj. Total**	**MD**	**MDF (%)**	**lCI**	**uCI**
Brijuni M44	12,255	69	0.56	0.00	0.01
Piran M1	14,677	46	0.31	0.00	0.00
Piran M53	13,063	46	0.35	0.00	0.00
Panzano M28	4,040	18	0.45	0.00	0.01
Panzano M29	3,155	35	1.11	0.00	0.02
Venice M38	5,071	1	0.02	0.00	0.00
Po3 M13	849	0	0.00	0.00	0.00
Po4 M20	884	0	0.00	0.00	0.01
total	53,994	215	0.40	0.00	0.00

6.1.4 Predation failure - incomplete drill frequency (IDF)

The analysis of the traces of predation includes not only the successful attacks of the gastropods on bivalve shells, but also signs of failed attempts of drilling - incompletely perforated drill holes. The average rate of incomplete drill holes in the total fauna of all examined sediment cores is rather low (table 4). Only in 1.38 % of the shells of the 53,994 bivalves incomplete bore holes were recorded. The highest IDF was calculated for the assemblage from the Brijuni islands (M44) where 3.65 % of the bivalves had incompletely perforated drill holes. In the core samples collected in Panzano (M28, M29) IDFs range from 1.76 % to 2.57 %. In the largest assemblages from the study collected from the shelf area around Piran (M1, M53) the IDF varied between 0.46 and 0.54 %. In the cores from the shelf close to Venice (M38) and in one of the cores from the Po delta (M13) virtually no shell with incomplete drill holes were detected. In the second Po core in at least 0.90 % of the examined individuals incompletely perforated bore holes were present.

Total fauna - Incomplete drill frequency (IDF)					
Core	**Adj. Total**	**ID**	**IDF (%)**	**lCI**	**uCI**
Brijuni M44	12,255	447	3.65	0.03	0.04
Piran M1	14,677	67	0.46	0.00	0.01
Piran M53	13,063	71	0.54	0.00	0.01
Panzano M28	4,040	71	1.76	0.01	0.02
Panzano M29	3,155	81	2.57	0.02	0.03
Venice M38	5,071	1	0.02	0.00	0.00
Po3 M13	849	0	0.00	0.00	0.00
Po4 M20	884	8	0.90	0.00	0.02
total	53,994	746	1.38	0.01	0.01

6.1.5 Ability to resist predatory attacks - prey effectiveness (PE)

Prey effectiveness, bivalves' ability to resist or deter a predator's attack, was evaluated for the total assemblage. On average more than 7.1 % of the predator attacks (successful plus unsuccessful) on the total fauna of all 8 cores failed. Among the different locations PE varied significantly. The highest average value of PE was computed for the bivalves from the shelf near Brijuni islands (19.3 %). In the samples of one of the cores from the area of the Gulf of Triest (Panzano M29) another very high PE (10.5 %) was recovered. The examined bivalves from the second core from the shelf area located in the river mouth of the Isonzo river (Panzano M28) had a much lower PE (6.9 %). PE was very low (2.2 to 2.5 %) in the samples from the shelf close to Piran (M1, M53). In the samples from Venice (M38) and from one of the cores collected in the Po delta (M13) lowest average values for PE were detected. The computed value for the PE of the samples from the second core from the Po delta (M20) seems rather high (9.6 %), but it has to be considered that the sample size of this core was very low and the PE value is based on only 8 incomplete drill holes out of 83 detected predation attempts.

Table 5: Prey effectiveness (PE) of the total fauna of all 8 cores

Total fauna - Prey effectivenesss (PE)					
Core	**Total Attacks**	**ID**	**PE (%)**	**lCI**	**uCI**
Brijuni M44	2,312	447	19.33	0.19	0.20
Piran M1	2,727	67	2.46	0.02	0.03
Piran M53	3,251	71	2.18	0.02	0.03
Panzano M28	1,034	71	6.87	0.05	0.09

Panzano M29	769	81	10.53	0.08	0.13
Venice M38	274	1	0.36	0.00	0.02
Po3 M13	39	0	0.00	0.00	0.00
Po4 M20	83	8	9.64	0.04	0.18
total	10,489	746	7.11	0.07	0.07

6.2 Predation intensities at different sampling locations

6.2.1 Drilling predation in the samples from Brijuni Islands (M44)

This core (M44) was collected within a marine protected area south of Brijuni Islands (Croatia), where fishing and dredging is prohibited. In this area the shelf surface consists of relict sands. The core had a length of 160 cm and according to the data from Radiocarbon-calibrated amino-acid-racemination (AAR) this core shows the local bivalve fauna and its characteristics from present time to more than 5,000 years into the past.

6.2.1.1 Overall drilling intensity in the samples from Brijuni (M44)

The overall drill frequency (DF) of the total bivalve assemblage from the Brijuni core was 15.2 %. The curve in Fig. 2 shows the variability of the overall DF along the core. A slight rise in predation intensity from the bottom of the core up to a core-length of about 40-50 cm is evident (Fig.2). For this sediment depth a DF of more than 20 % was calculated. In the layer at about 40-45 cm sediment depth the drill frequency stagnates and upwards it declines significantly towards the youngest sediment layers, even though there was a short, albeit relatively sharp increase at a sediment depth of about 15 cm.
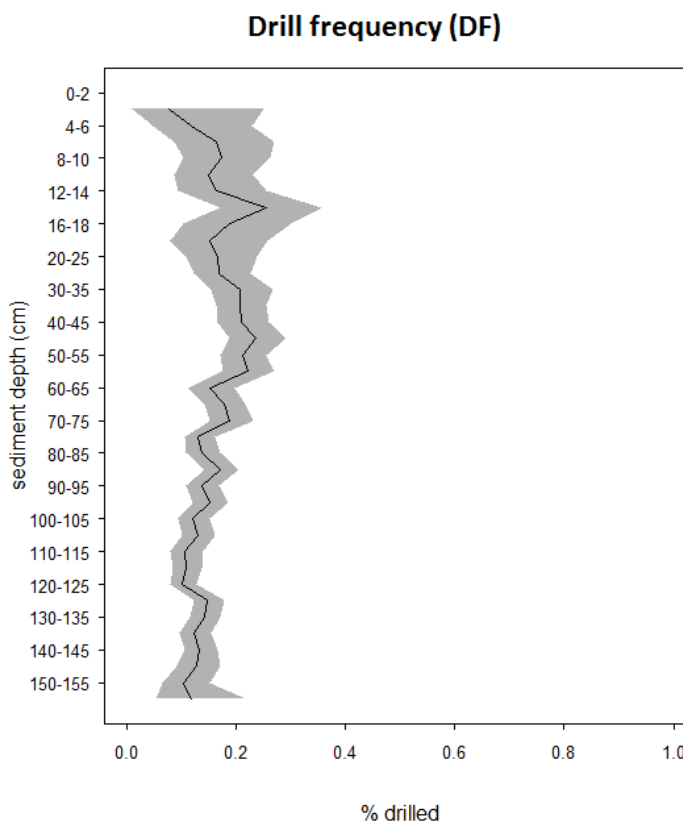
Fig. 2: Overall drill frequency (DF) along Brijuni M44 core

The assemblage from this core represents more than 12,200 bivalves, belonging to 69 species and 27 families. The two most abundant species were *Timoclea ovata* and *Striarca lactea* which account for more than 36.3 % of the total bivalve assemblage from the Brijuni samples. For this reason the analysis of the trends in DFs of these two species appears of particular interest (Fig. 3). For computing these trend lines only species with abundances > 10 individuals were represented in the line graph. That's the cause why the lines end in the upper third of the sediment succession. In the younger sediments these two species are rather rare. Nevertheless the graph shows an exciting comparison of drilling intensities and its trends along the core. DF-
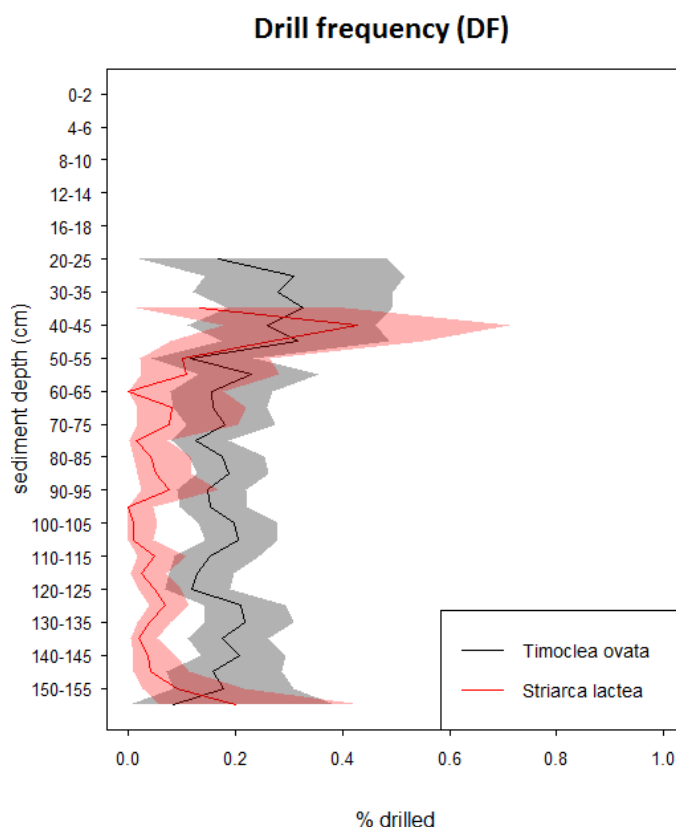
Fig. 3: Overall drill frequencies (DF) of the 2 top-species along Brijuni M44 core

curve of *Timoclea ovata* starts at a rather low level of about 10 % in the oldest layers examined and rises up to nearly 20 % in the samples from the proximate sediment layers. Then the *Timoclea*-curve fluctuates at a level of approximately 20 % until it reaches a sediment depth of 45 cm, where a significant rise up to 30-35 % in drilling intensity is recognized. At a sediment depth of 25 cm DF drops abruptly which may indicate a similar trend as it is seen in the graph for the total assemblage. But as the sample size of this taxon is not representative anymore in the youngest sediment layers the general trend can't be seriously confirmed or verified. On the first sight the trend of the DF for *Striarca lactea* seems very different from that of *Timoclea ovata*, because it starts at a higher level of 20 % at the deepest sediment layers and declines shortly after, exactly at the same layer as the DF for *Timoclea ovata* increases. But after this shift the *Striarca*-curve remains on a low level of 1-10 %, but at a sediment depth of 45 cm it rises considerably - accurately at the same layer as the increase of drilling intensity in *Timoclea* was recovered. At this sediment layer DF of the *Striarca* samples rises to a level of more than 40 % before it drops in a similar abrupt way as the *Timoclea*-curve does. Unfortunately, as well as for *Timoclea,* the sample size for *Striarca* in the upper most sediment layers is again too small to make any serious statements about the development of drilling predation in the youngest past. However, the trend for both *Timoclea* and *Striarca* tend to confirm the general trend (Fig. 2) of declining predation intensity in the youngest history of the mollusc assemblage from the shelf area around Brijuni islands.

In the assemblage from the shelf around Brijuni islands *Corbula gibba* represents 4.0 % of the total bivalve fauna in the core. Even though this proportion is not representative for the whole assemblage the general trend for the drilling frequency of *Corbula gibba* along the core (Fig. 4) has obvious similarities compared to the overall DF-trend of the total fauna for the Brijuni core sample (Fig. 2). First of all in the deepest and oldest sediment layers the *Corbula*-curve remains on a very low level of predation (< 10 %) and gradually rises core-upwards until a sediment depth of approximately 40 cm. At this depth the curve sharply drops. These changes are very similar to the shifts in drilling intensities of *Timoclea* and *Striarca* and accordingly, analysis of *Corbula* once again underlines basic coherence with the general trend of a decreasing drilling intensity of the total fauna in the upper layers.
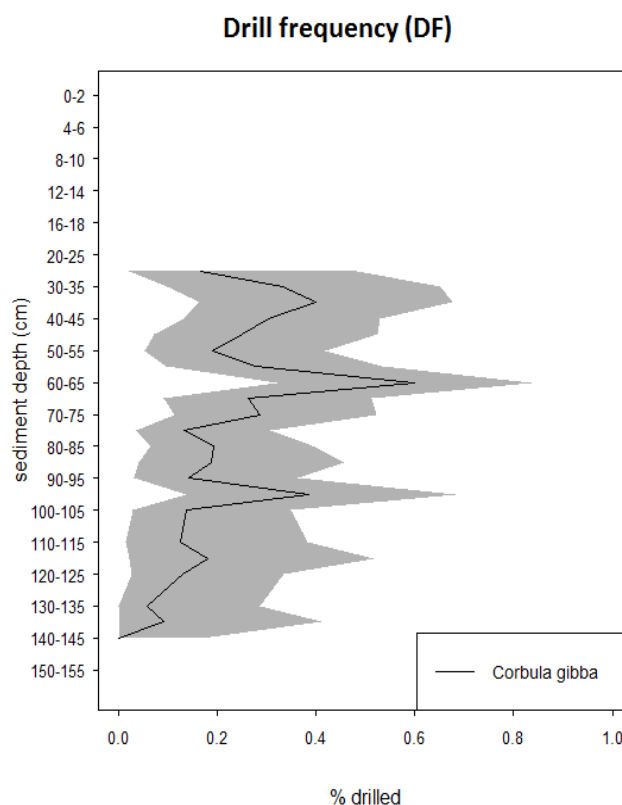
Fig. 4: Overall drill frequency (DF) of *Corbula gibba* along Brijuni M44 core

6.2.1.2 EDF, MDF, IDF and PE in the bivalve fauna from Brijuni (M44)

Edge drilling frequency (EDF) reached about 2 % of the total fauna examined in the Brijuni M44 core. This quota of drills is rather low on average but varies distinctly along the core (Fig. 5). From the bottom layers upwards to a depth of 40 cm the average EDF is only slightly above 0-0.5 %. But from a depth of 40 cm upwards EDF increases noticeably. In the upper 15 cm of the core the EDF-curve shows 2 small peaks at a sediment depth of 15 and 10 cm. In the uppermost layers, however, the EDF decreases again to almost 0 %. In 19 of 69 species edge drills were recovered. Among the abundant species with the highest EDFs are *Timoclea ovata* (2.5 %), *Striarca lactea* (0.8 %) and *Modiolus adriaticus* (19.6 %). *Corbula gibba* has an average EDF of 3.7 %. Considering the trends of the EDFs of these four species along the core (Fig. 6) a general tendency can't be detected, because the curves fluctuate quite strongly. The rise of EDF of *Modiolus adriaticus* starting at a sediment depth of 95 cm with values up to 45 % between 75 and 40 cm is remarkable. But nevertheless high EDF values like those of *Modiolus* are restricted to few species and specimens.
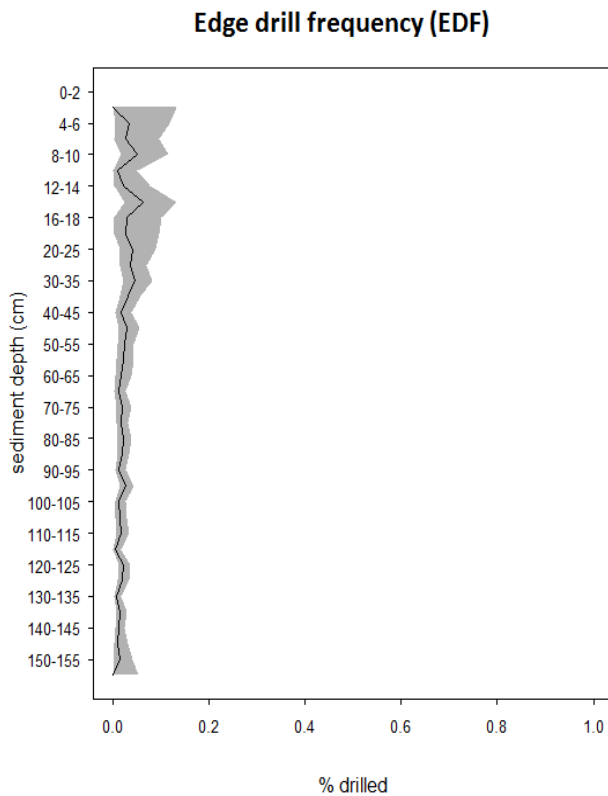
Fig. 5: Edge drill frequency (EDF) along Brijuni M44
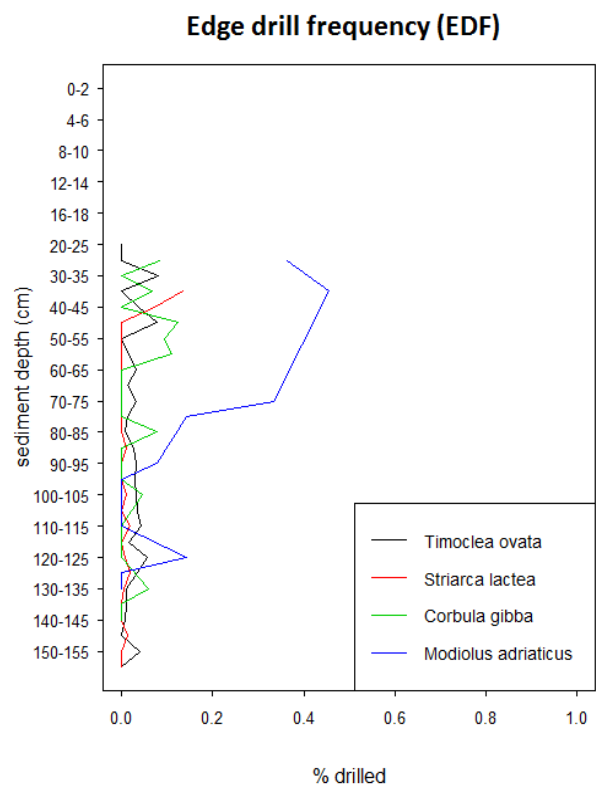
Fig. 6: EDFs of *Timoclea, Striarca, Corbula* and *Modiolus* along Brijuni M44

Multiple drilled shells are even rarer than edge drills and the average MDF among the bivalve fauna in Brijuni is 0.6 %. The general trend along the core is rather stable in the lower half at a level slightly above 0-1.1 % (Fig. 7). Slight fluctuations of the trend can be recovered at layers in a depth of 65 cm (2.2 %), 30 cm (1.4 %) and 20 cm (2.1 %). In the uppermost layers (from 6 cm upwards) another moderate rise can be detected.
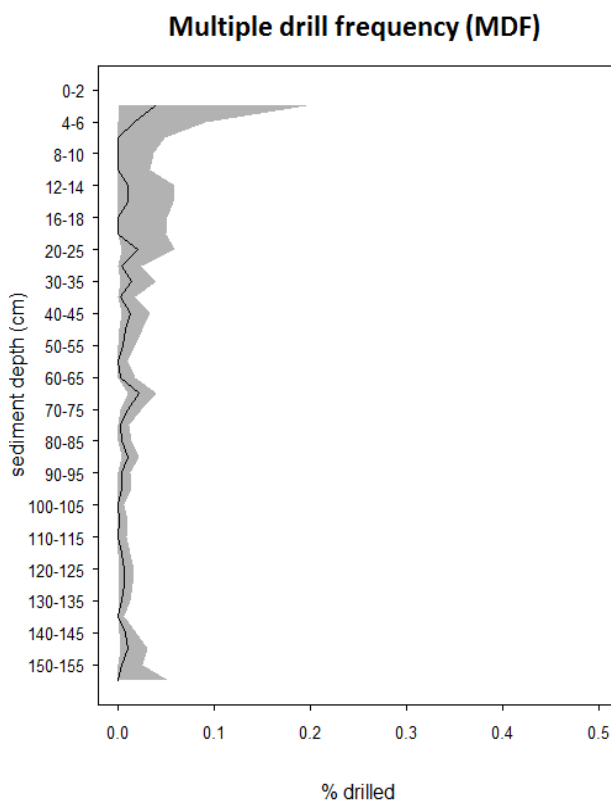
Fig. 7: Multiple drill frequency (MDF) along Brijuni M44
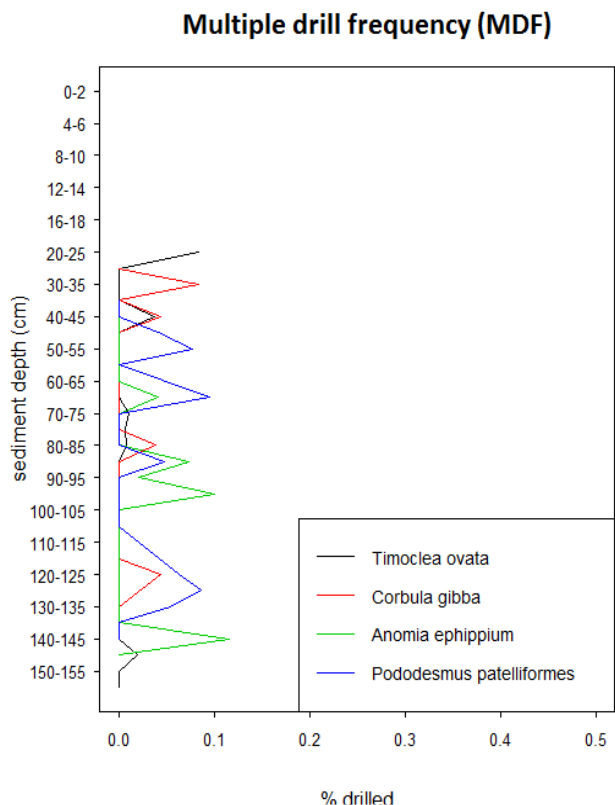
Fig. 8: MDFs of *Timoclea, Anomia, Corbula* and *Pododesmus* along Brijuni M44

Seventeen of the 69 species examined in the Brijuni-assemblage have shells with more than one drill hole. Most of these shells (55.1 %) were recorded among *Timoclea ovata*, *Podo-desmus patelliformes*, *Anomia ephippium* or *Corbula gibba*. *Timoclea ovata* had an average MDF of 2.5 %, *Anomia ephippium* 0.7 %, *Pododesmus patelliformes* 1.0 % and *Corbula gibba* had a MDF of 3.7 % along the core. MDFs of these species influence the general trend of the total assemblage fundamentally (Fig. 8). The species specific curves for example show that the peak at a sediment depth of 30 cm is the result of higher MDFs of *Pododesmus patelli-formes* and *Corbula gibba* and the increase in the upper layers is the consequence of a high MDF of *Anomia ephippium*.

To detect the proportion of predation failure IDFs and PEs were computed. For the assemblage from the shelf near Brijuni islands the average values for IDF and PE were the highest among the 8 cores sampled. In 3.7 % of the bivalves incompletely perforated drill holes were detected. Along the core the IDF varies only slightly. 92.8 % of the incomplete drills were recovered within samples of *Striarca lactea*, *Nucula cf. nucleus* and *Corbula gibba*. IDF of *Striarca lactea* reached even 18.7 %, *Nucula cf. nucleus* had an IDF of 3.8 % and 3.1 % of the specimens of *Corbula gibba* were unsuccessfully drilled.
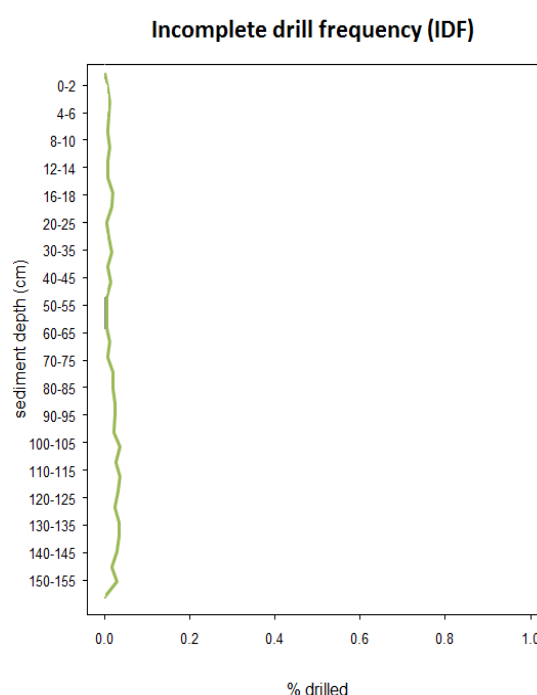
Fig. 9: Incomplete drill frequency (IDF) along Brijuni M44

The proportion of failed predation events out of the total attacks was 19.3 %. The PE was on an exceptional high level in *Striarca lactea* in the samples from the Brijuni M44 core with a computed value of 78.2 %. *Nucula cf. nucleus* had a PE of 15.3 % and *Corbula gibba* 12.5 %. Considering the PE-curves of the total bivalve fauna and of *Striarca lactea* it can be concluded that *Striarca* influences the overall PE-trend significantly, especially in a sediment depth from 150 up to 40 cm. In these layers the total PE trend reflects that of *Striarca,* which ranges on a very high level from the lowermost layers up to 70-80 cm. In layers from 105 cm upwards the general PE-trend decreases gradually, but fluctuates heavily until it reaches a depth of 20 cm. In the uppermost sediment layers the PE of the total assemblage of the Brijuni core declines moderately, just as that of *Striarca* (from 16 cm upwards).
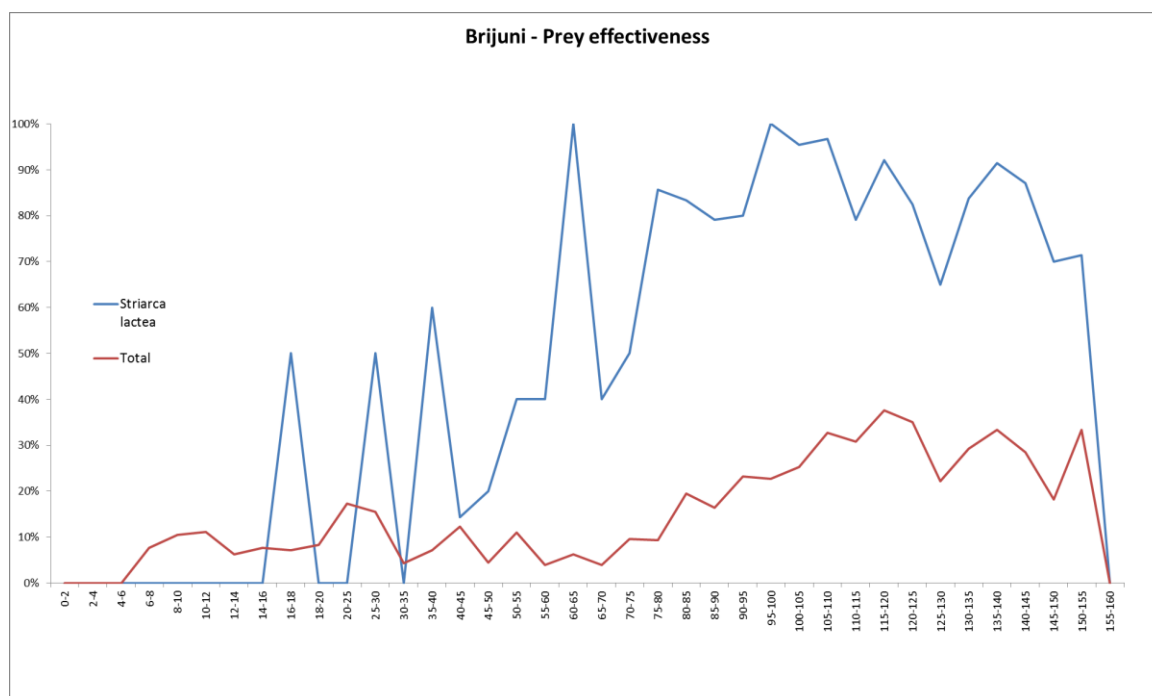
Fig. 10: Prey effectiveness (PE) of the total fauna (total) and *Striarca lactea* along Brijuni M44 core

6.2.2 Drilling predation in the samples from Piran (cores M1, M53)

From the shelf area around the oceanographic buoy off Piran (Slovenia) two sediment cores were collected from areas with different impact by bottom dredging: - in contrast to core M53, core M1 is from a protected region. The evaluated results from drilling intensities of these two core samples are presented in comparison to each other. Both cores have a rather large sample size of 14,677 (M1) and 13,063 (M53) individuals and a core length of 145 cm (M1) and 155 cm (M53).

6.2.2.1 Overall drilling intensity in the samples from Piran (M1, M53)

The M1 core had an overall drill frequency (DF) of 18.1 %, while in the M53 core DF reached 24.3 %. Even though the overall DF of the bivalve assemblage of Piran M53 is more than 6 % higher, the trends along the sediment succession of these two cores show obvious similarities (Fig. 11, 12). A distinct difference is that the DF-curve of the Piran M1 sample fluctuates around values below 20 % almost all along the core while the DF-curve from Piran M53 stays above this value. Similar to each other the curves start on a relative high level in the lowermost layers (145 cm/155 cm) at 19.1 % in M1 and 27.7 % in M53, respectively, and decline significantly to a depth of 125-130 cm. From 125 upwards to 115 cm depth both trends show a considerable rise before they start decreasing almost in parallel at 115 cm depth. From this layer upwards till 60/65 cm the DFs range around 10 % in M1 and 20 % in M53. At a sediment depth of 60/65 cm DFs in both cores increase again and vary at rather high levels around 20 % in M1 and up to 36 % in M53. Moreover, in both assemblages DFs drop again about 5 % in the uppermost 5 cm of the cores.
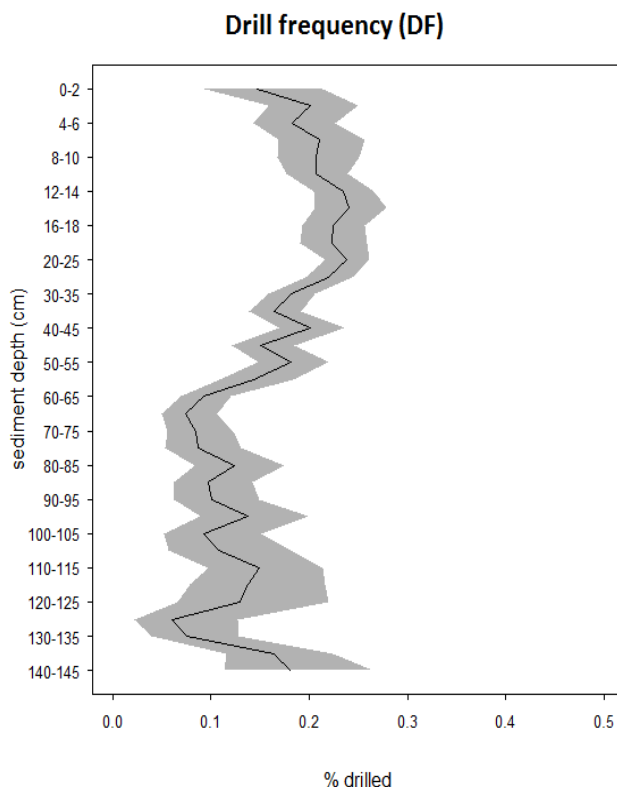
Fig. 11: Overall drill frequency (DF) along Piran M1   **Fig. 12:** Overall drill frequency (DF) along Piran M53 core
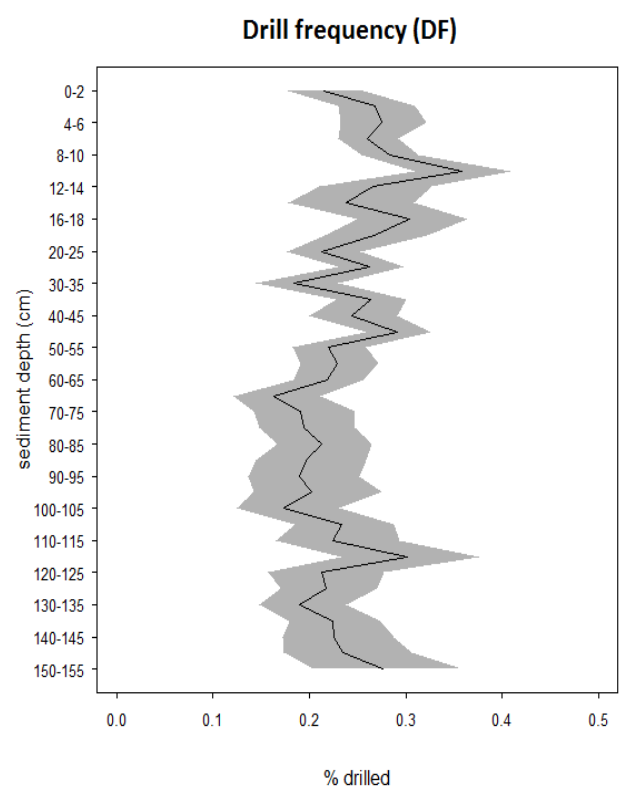
The assemblages of Piran count more than 13,000 bivalves in each core, belonging to 73 (M1)/72 (M53) different species and 31 (M1)/32 (M53) families. In both Piran cores the two most abundant species are *Gouldia minima* and *Corbula gibba*. In Piran M1 these two species represent 45.0 % of the total bivalve fauna of the core and in M53 43.3 %. *Gouldia minima* had average DFs of 36.6 % in M1 and even 39.5 % in M53. For *Corbula gibba* DFs of 18.3 % and 24.9 % were recorded. These values from the evaluations of the *Corbula* samples correlate accurately with the general trends for the total assemblages for Piran.

Considering the DFs of *Gouldia* and *Corbula* side by side in both cores (M1, M53). *Gouldia's* DFs ranges about 10-15 % above the value of *Corbula's* DFs (Fig. 13, 14). Especially in the graph from the Piran M1 core the trend of the curves of these two species is rather similar along the core. Coherent to the general trend the DFs of Gouldia and Corbula are on high levels at the bottom layers of the core and drop sharply in the overlying 10-20 cm (Fig. 13). Above, trends for *Gouldia's* and *Corbula's* DF reflect the general trend of an increase of drilling predation at a sediment depth of 120 as well as a decrease at 115 cm depth and another rise at 60-70 cm is followed by a decrease in the uppermost layers. In the graph showing the samples of the Piran M53 core, the DF trends appear more opposite, because in particular *Gouldia's* DF fluctuates heavily from layer to layer in the lower half of the core. But at a depth of 100-105 cm the curves of both species drop abruptly and from the following rise in the overlying sediment layers onwards the DF trends of *Gouldia* and *Corbula* continue more or less parallel. The trend of both curves captures the short decrease of drilling intensities at 65-70 cm depth similar to the pattern in the general trend (Fig. 12). Compared to the M1 core the drilling intensities in M53 vary much more along the core, but major changes of drilling intensities of the two top species in M53 also clearly follow the general core trend.
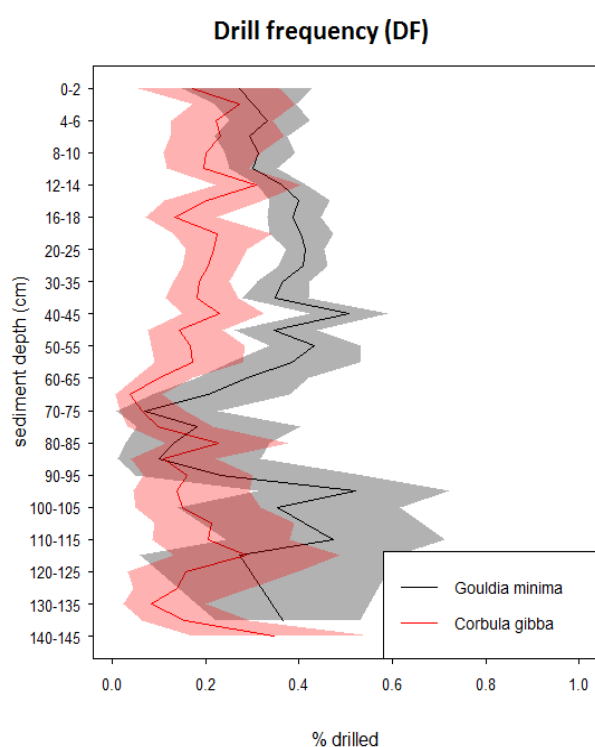
Fig. 13: DFs of *Gouldia minima* and *Corbula gibba* along Piran M1
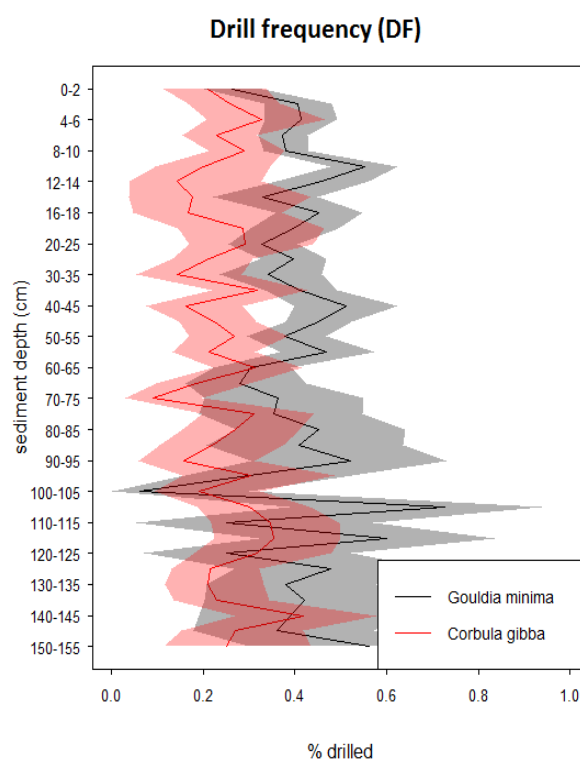
Fig. 14: DFs of *Gouldia minima* and *Corbula gibba* along Piran M53

The trend of drilling predation for *Corbula gibba* along the core once again reflects the overall changes of DF of the total assemblage quite well. Due to its very high abundance in the shelf area off Piran *Corbula* is even more representative for general trends or as an indicator for possible shifts in certain sediment layers.

6.2.2.2 EDF, MDF, IDF and PE in the bivalve fauna from Piran (M1, M53)

The average frequency of edge drills differs between 1.96 % among the bivalves from the M53 core and 0.89 % in the assemblage from the M1 samples. The EDF trend of the assemblage from the M1 core remains rather stable at a value below 1 % all along the core (Fig. 15) and fluctuates only very slightly in the bottom layers (e. g. at 145 cm, 120 cm) as well as in the uppermost sediment layers (at 2-4 cm depth). Among the bivalves from M53 EDF is generally on a moderately higher level (Fig. 16), similar to the overall DF which was also significantly higher in the samples from the M53 core. The EDF trend of the M53 assemblage varies a bit more along the core than in M1. Moreover, some of the little peaks, e.g. at 120-105 cm, 90-80 cm, 50-45 cm or 16-10 cm depth, are not only recovered in the EDF-graph (Fig. 16), but also in the trend of the overall drill intensity of the M53 core (Fig. 12). It seems that in the assemblage from the M1 core increasing edge drilling goes hand in hand with a general rise in drill intensity, at least in the sediment layers mentioned above.
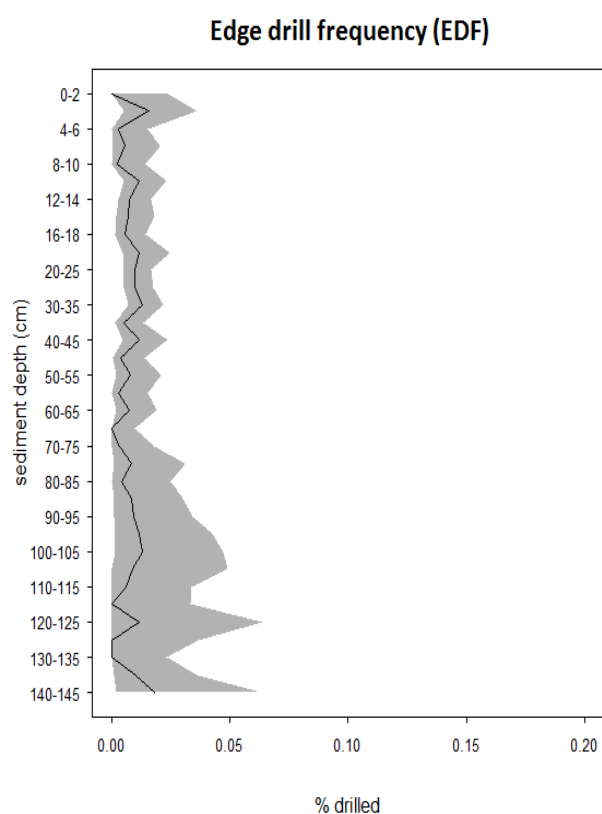
Fig. 15: Edge drill frequency (EDF) along Piran M1
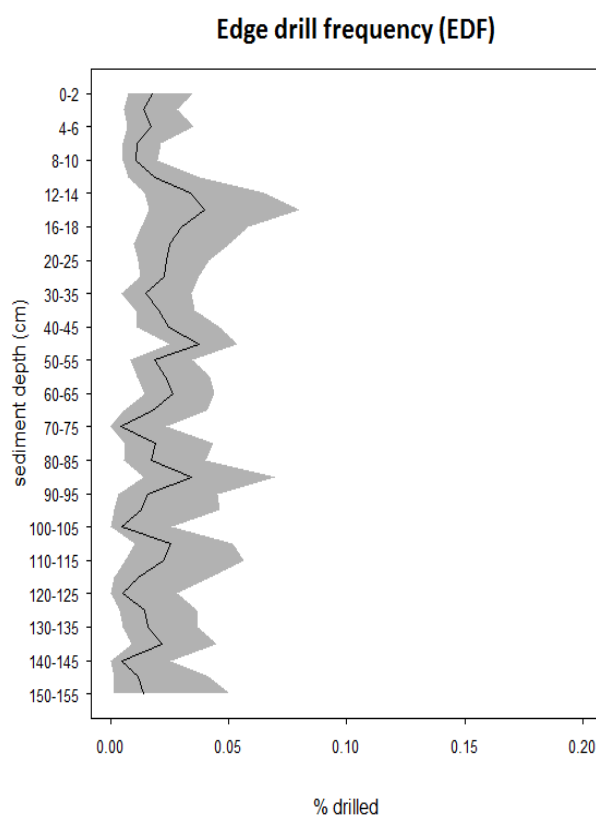
Fig. 16: Edge drill frequency (EDF) along Piran M53

In nine of the 73 species from the M1 core edge drills were recovered. But 85.7 % of all edge drills of the bivalves from M1 were detected in shells belonging to *Gouldia* and *Corbula*. *Gouldia* had an average EDF of 1.2 % and *Corbula* of 2.2 % in the samples of M1. In the other Piran core (M53) 16 of the total 72 species exhibited edge drills, but once again most of these drills (72.3 %) were discovered on specimens of *Gouldia* and *Corbula*. In the samples of *Gouldia* an EDF of 3.4 % was computed and in *Corbula's* specimens EDF reached 3.0 %.

The frequency of multiple drilled shells is on a very low level in both Piran cores. In M1 the average MDF of the total fauna is 0.3 % and in the assemblage of M53 the MDF reaches up to 0.4 %. The trends in Fig. 17 and 18 show that the MDF curves in both cores fluctuate only slightly along the core. In the samples of almost all layers the MDF values vary between 0 and 1 %. In the total assemblage from the Piran M1 core multiple drills were recovered in 7 species. Most of these multiple drills (73.9 %) were found in specimens of *Corbula gibba*. In the second Piran core (M53) the results were similar. In 9 out of 72 species individuals with more than one drill hole were detected, but most of the shells (76.1 %) with multiple traces of drilling predation belong to *Corbula gibba*.
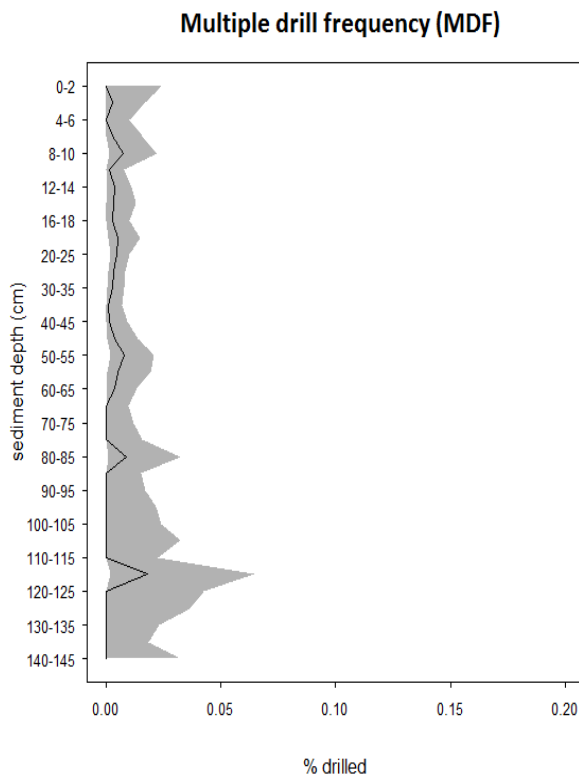
Fig. 17: Multiple drill frequency (MDF) along Piran M1   **Fig. 18:** Multiple drill frequency (MDF) along Piran
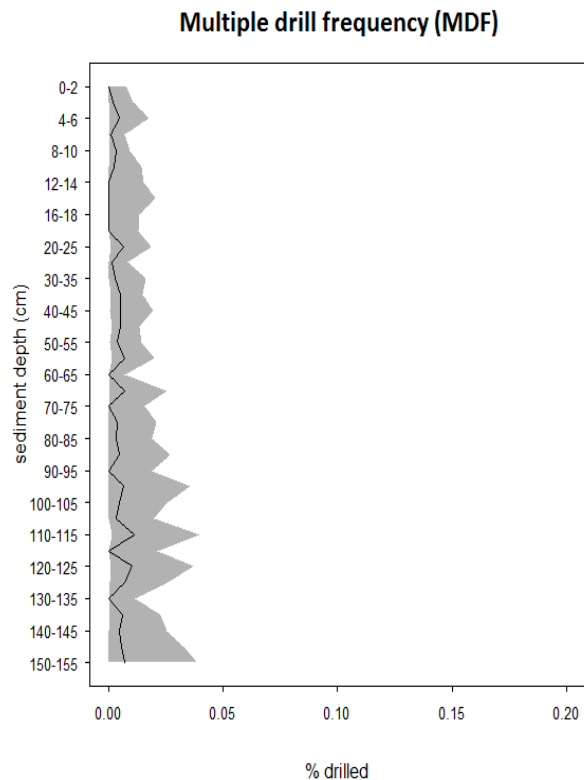
The proportion of predation failure was evaluated by calculating IDFs and PEs. IDFs in the samples from the Piran cores (M1, M53) are very low (around 0.5 %). The trend along the cores keeps rather stable and hardly fluctuates (Fig. 19, 20). Only the IDF trend of bivalves from the M53 core reveals few small peaks, for example at a sediment depth of 85-90 cm, where the IDF reached a level of 2.0 % or at 12-14 cm, where it increased to 1.3 %. In the assemblages of both Piran cores most of the specimens with incomplete drill holes (M1: 91.0 %, M53: 85.9 %) belonged to the species *Corbula gibba*. In the samples of M1 *Corbula's* IDF was 2.5 % and in the second Piran core (M53) *Corbula's* IDF reached 2.8 %.
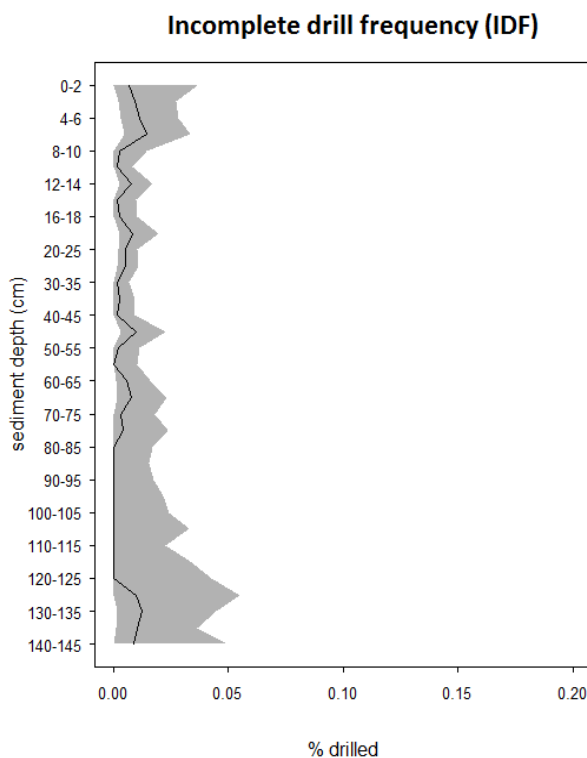
Fig. 19: Incomplete drill frequency (IDF) along Piran M1   **Fig. 20:** Incomplete drill frequency (IDF) along Piran M53
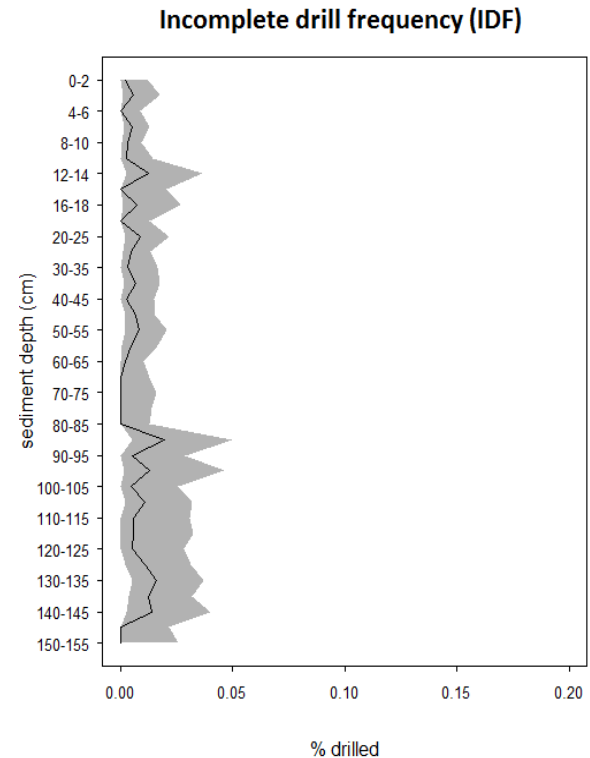
The proportion of unsuccessful predation events among the total number of recorded attacks was much lower in the Piran cores compared to the high PE (19.3 %) in the assemblage of Brijuni (M44). In the sample of Piran M1 PE reached a level of 2.5 %, in the bivalve fauna from the Piran M53 core a slightly lower PE of 2.2 % was computed. Considering the course of the PE trends along the cores a few significant peaks can be recovered (Fig. 21, 22). At the bottom layers from 145 to 125 cm PE rises remarkably up to a level of about 10 % in both cores (M1, M53). In the samples from M1 almost no traces of unsuccessful predation were detected from a sediment depth of 120 to 80 cm. From this layer upwards PE of M1 increases again and fluctuates rather sharply with peaks at 65-70 cm, 45-50 cm, 12-14 cm and in the uppermost sediment layers. The PE-curve of the bivalves from Piran M53 fluctuates in a similar pattern as seen in the M1 core in Fig. 21, but exhibits most of its major peaks at different sediment depth, e. g. 85-90 cm, 50-55 cm, 20-25 cm and 12-14 cm (similar rise as in Fig. 21).

As most of the incompletely perforated bore holes were recovered in specimens of *Corbula gibba*, the general trend of the PE among the total core samples is heavily influenced by *Corbula*'s high PE and its trend curve along the core. In the M1 samples *Corbula* has a PE of 12.1 % on average among the total fauna examined and in the M53 core its PE ranges around 10.0 %.
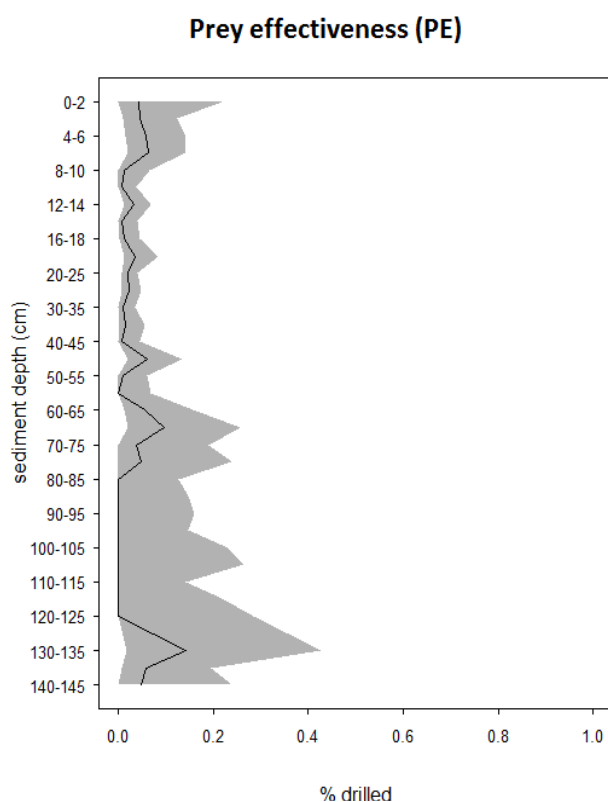
Fig. 21: Prey effectiveness (PE) along Piran M1
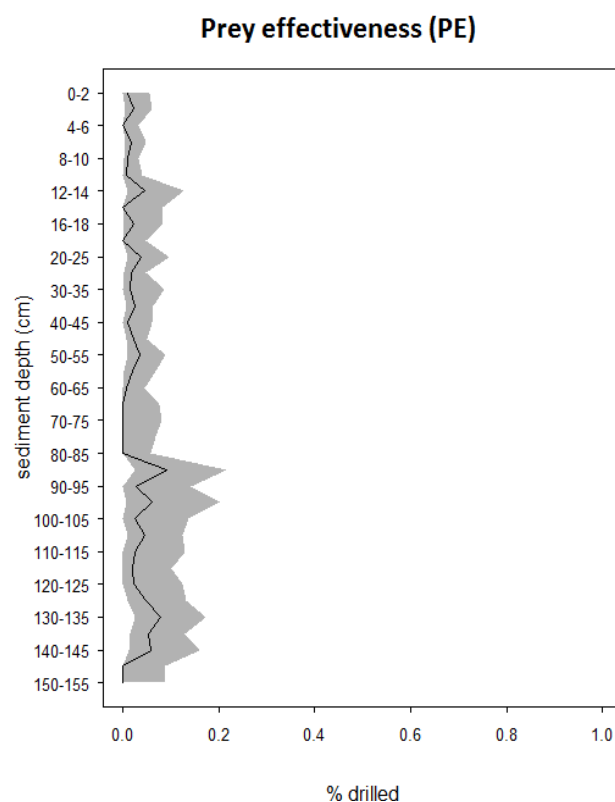
Fig. 22: Prey effectiveness (PE) along Piran M53

6.2.3 Drilling predation in the samples from Panzano (M28, M29)

From the shelf area in the Gulf of Trieste, near Panzano (Italy) two sediment cores (M28, M29) were collected. This area is highly affected by anthropogenic impacts like fishing and dredging. Both cores were 150 cm long and from locations very close to each other, and they are treated together, similar to the core analysis from Piran. The two sediment cores from the station near Panzano represent 4,040 (M28) and 3,155 (M29) bivalves. Compared to the larger assemblages of Brijuni and Piran the sample sizes of these cores seem considerably smaller. In the M28 core the assemblage consists of 44 species, belonging to 23 families, while in the M29 core 39 species from 23 families were recorded.

6.2.3.1 Overall drilling intensity in the samples from Panzano (M28, M29)

The overall drill frequencies among the Panzano cores are quite high in comparison with the other cores. For the total assemblage of the M28 core a DF of 23.8 % was computed and the total fauna from the other Panzano core (M29) reached a DF of 21.8 %. The DF trends of the two Panzano cores show heavy fluctuating drilling intensities along the cores in both assemblages (Fig. 23, 24). Although the trends seem rather different on first glance, there are definitely some similarities. First of all, both curves vary within nearly the same range limits almost all along the core, roughly between 15 and 30 %. Moreover, in both cores a moderate increase of DF can be detected from a sediment depth of 130 cm upwards. Another similarity is the steady decrease of drilling intensities from a depth of approximately 30 cm to the uppermost layers. Even though there is also a short rise in the DF-curve of M28 this declining DF trend in the younger sediment layers is clearly reflected in the graphs (Fig. 23, 24).
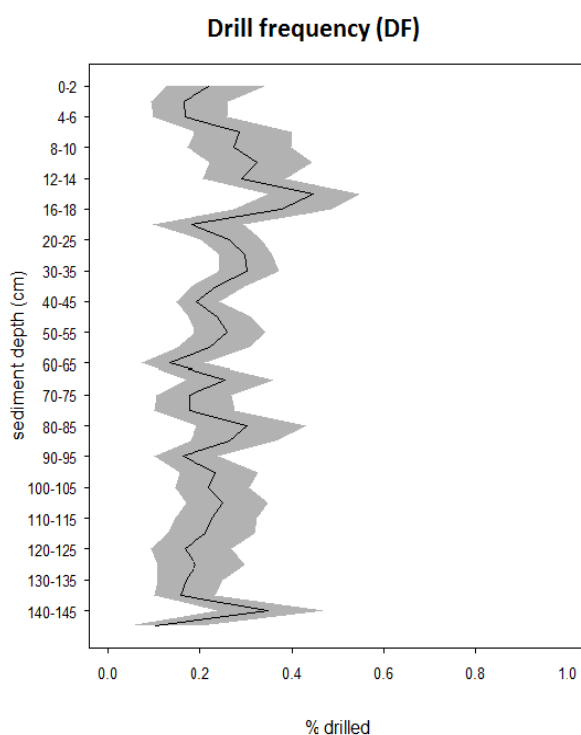
Fig. 23: Overall drill frequency (DF) along Panzano M28   **Fig. 24:** Overall drill frequency (DF) along Panzano M29
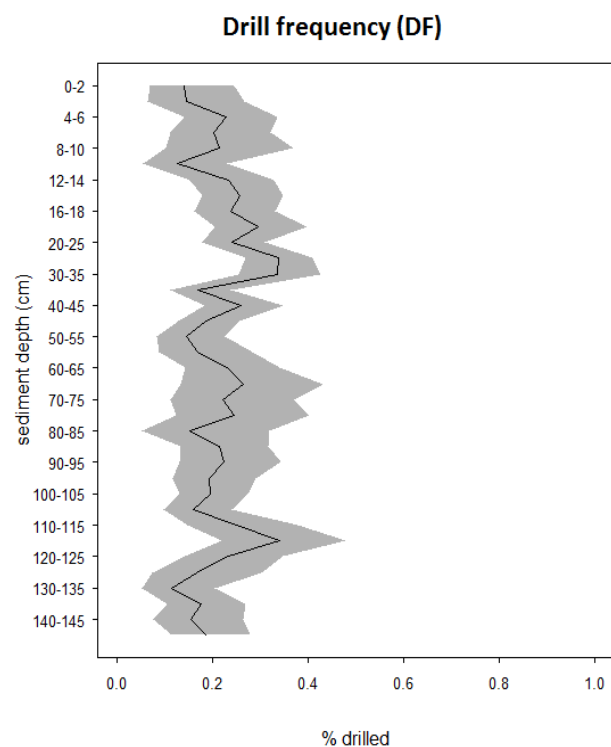
The two most abundant species in the Panzano (M28, M29) cores are *Kurtiella bidentata* and *Corbula gibba*, which account together for 54.3 % (M28) and 52.9 % (M29) of all the individuals from the assemblages. Due to their high abundance in these cores the DF-trends of these two species are considered in detail in Fig. 24 and 25. The average DF of the samples of *Kurtiella* was 40.7 % in M28 and 34.4 % in M29. From the specimens of *Corbula* 30.0 % (in M28) and 31.9 % (in M29) were drilled. Considering the DF-curves of the two top species in the Panzano core M28, the course of the general trend can be detected on the first sight. Especially in the characteristic fluctuations of drilling intensities of *Corbula gibba* frequency patterns of the overall DF (Fig. 24) are noticeably reflected. Moreover, it is interesting to see that the DF-curves of *Kurtiella* and *Corbula* run almost parallel in many parts of the sediment succession, particularly in the upper 70 cm. For instance, at layers of 60-65 cm, 40-45 cm, 18-20 cm or 14-16 cm depth both species show distinct changes in drilling intensities. At a sediment depth of 14-16 cm *Kurtiella* reached a DF of 72.7%. The trends of drilling predation in *Kurtiella* and *Corbula* along the M29 core seem more diverse than in M28, because especially *Corbula's* drilling frequencies tend to vary heavily from one layer to the other. *Kurtiella's* DF-curve fluctuates between 20 % and 40 %. At the layers of 115-120 cm and 65-70 cm depth *Corbula's* DFs rise up to 68.4 % and 75.0 %.
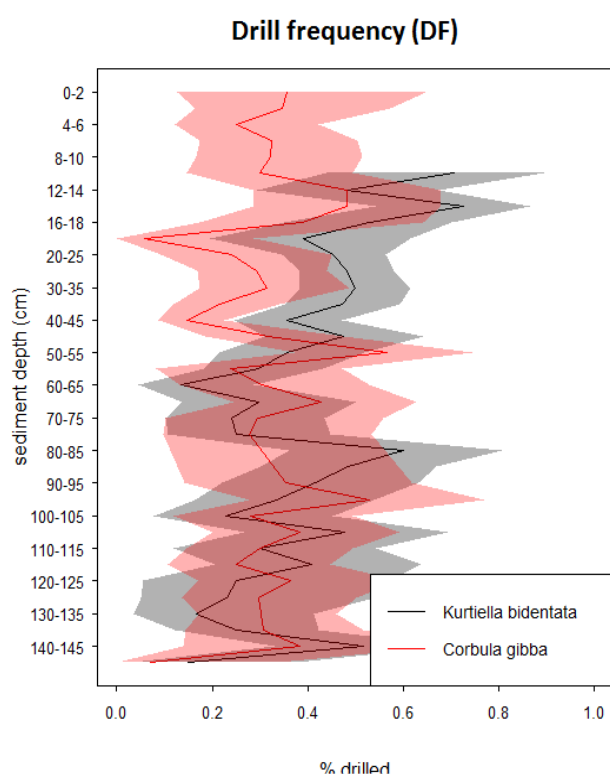
Fig. 25: DFs of *Kurtiella bidentata* and *Corbula gibba* along Panzano M28
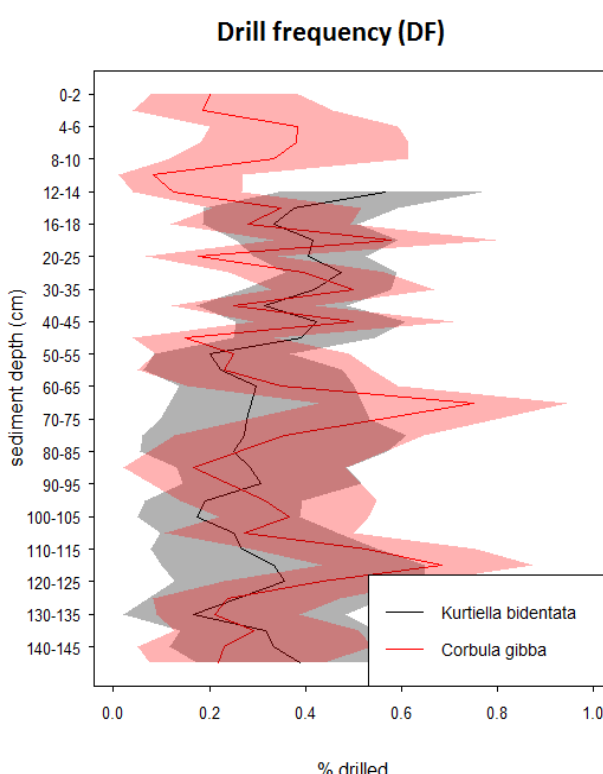
Fig. 26: DFs of *Kurtiella bidentata* and *Corbula gibba* along Panzano M29

Once again, the DF of one particular species (*Corbula gibba*) and its changes in the latest history reflects the trends for the total assemblage collected from a certain shelf area quite good. The high abundance of *Corbula*, near Panzano allows a closer evaluation of its general

trends and remarkable changes in predation intensities along the sediment layers (Fig. 24, 25). But especially the comparison of the DF-curves of *Kurtiella* and *Corbula* in the samples from M29 clearly points out that not each sharp rise in predation seen in *Corbula's* trend line means higher predation intensity for the total fauna. Moreover, it should be kept in mind that the significantly smaller sample size in the cores collected in the river mouth of the Isonzo River (M28, M29) rapidly leads to rather high drill frequencies in certain layers, which should not be overestimated, over-interpreted or generalized.

6.2.3.2   EDF, MDF, IDF and PE in the bivalve fauna of Panzano (M28, M29)

The frequency of drills at atypical shells sites, in particular at the edges of the shells, is very low in the assemblages collected near Panzano. In the samples from M28 the average EDF was 0.5 % and only in 0.4 % of the bivalve fauna from M29 edge drills were recovered. The graphs (Fig. 27, 28) show that this low intensity of edge drillings is not stable all along the core, but fluctuates in certain layers in each of the two considered assemblages. For instance, in both cores a slightly increasing number of edge drills was detected in the layers from 130-120 cm, up to 2.6 % in M28 and 2.1 % in M29. Moreover, at sediment depths of 65-70 cm and 40-30 cm both assemblages exhibit a moderately higher EDF up to 1.1 % in M28 and 1.6 % in M29. Within the bivalve fauna from the M28 core the highest rates of edge drills were computed for the upper layers, e.g. in 14-16 cm and 8-10 cm depth, where EDF ranged at a level of 3.0 %. In the second core from Panzano (M29) the highest EDF with a value of 3.0 % was calculated for the sediment layer at 90-95 cm. Similar to the pattern of the EDF-curve in the uppermost layers of M28 we can also find a little peak of the edge drill intensity (up to 1.8 %) in the upper core layers in the sample of M29.
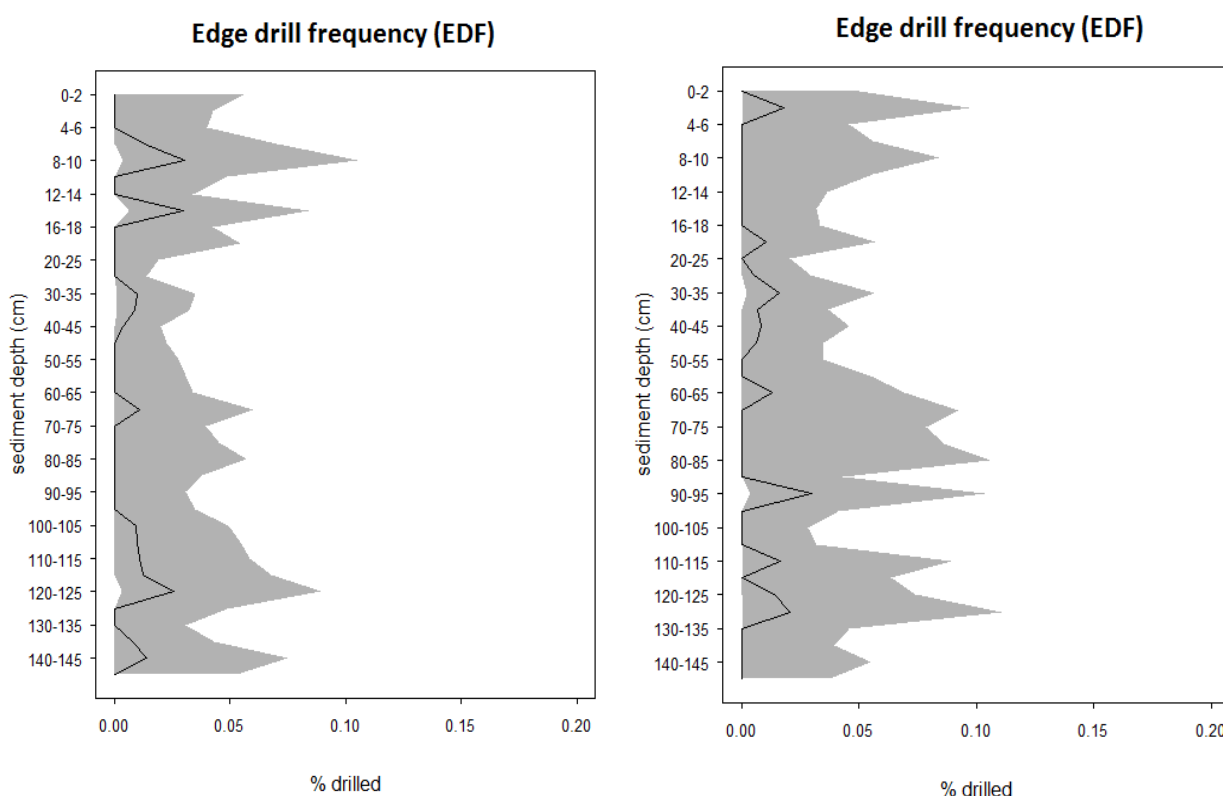
Fig. 27: Edge drill frequency (EDF) along Panzano M28   **Fig. 28:** Edge drill frequency (EDF) along Panzano M29

In the bivalve fauna from Panzano edge drills were recovered only in samples of 2 species, *Corbula gibba* and *Modiolus.* In the assemblage from M28 95 % of the accounted edge drills were found in samples of *Corbula gibba*. In the sample from M29 *Corbula* was the only species where edge drilled specimen were discovered. The average EDFs calculated for *Corbula gibba* in particular were 1.8 % in M28 and 1.7 % in M29.

Multiple drilled shells are rather rare in the samples from Panzano. Among the bivalves from M28 the average MDF is about 0.4 %, which is also exactly the average MDF calculated for the fauna of all cores examined. The MDF computed for the assemblage from M29 reaches a higher level of 1.1 % among all the bivalves. From the M28 core only 2 species, namely the two most abundant *Corbula gibba* and *Kurtiella bidentata* contain multiple drilled individuals in their samples. Most of these multiple drilled specimens belong to the genus *Corbula* (88.8 %). The average MDFs computed for Corbula gibba ranged from 1.6 % in M28 to 4.1 % in M29. These significant differences in the frequency of multiple drilled bivalves are quite well reflected in the trends along the cores (Fig. 29, 30). The highest MDFs of the sample from M28 were recorded in the layers at 130-135 cm (2.5 %), 105-110 cm (2.0 %) and 65-70 cm (1.1 %). In the other Panzano core (M29) at exactly the same sediment depths considerably more multiple drilled bivalves were detected (2.5 %, 4.4 % and 5.3 %). In the upper layers MDFs rise again slightly in both cores, to 1.4 % in M28 and 2.7 % in M29.
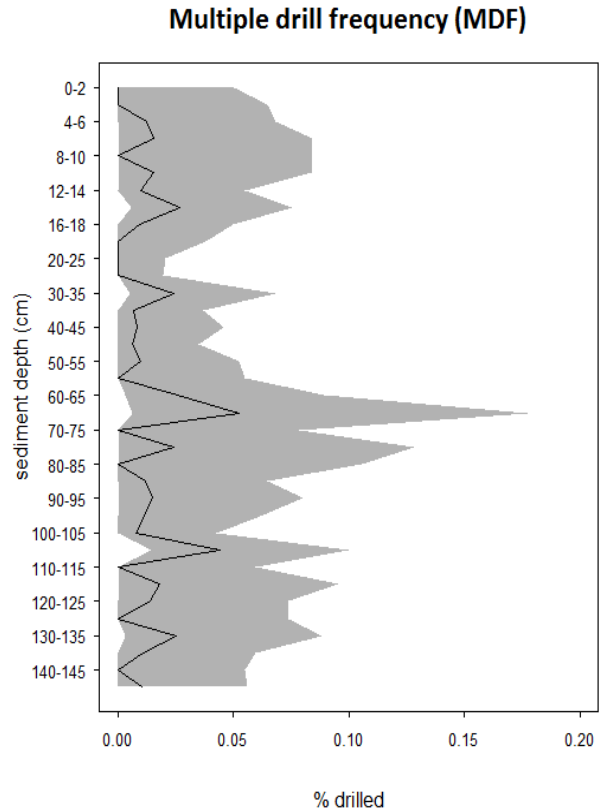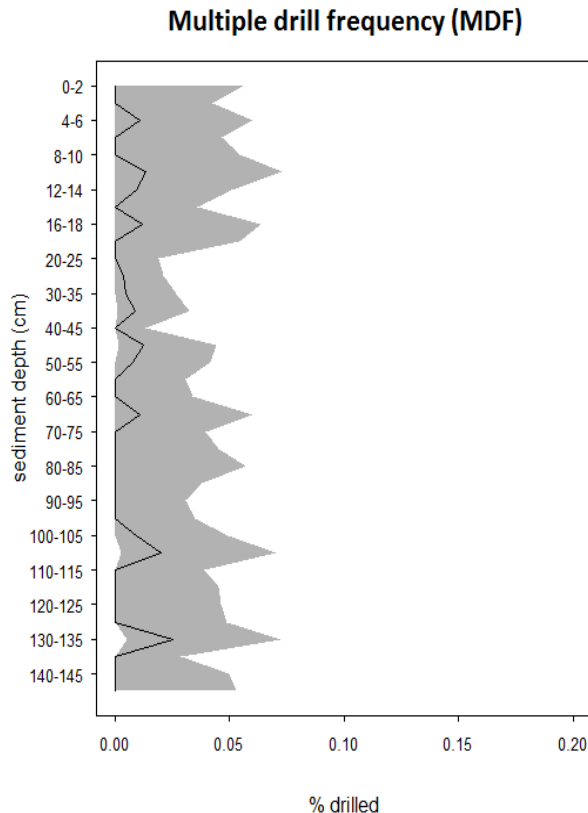
Fig. 29: Multiple drill frequency (MDF) along Panzano M28   **Fig. 30:** Multiple drill frequency (MDF) along Panzano M29

For evaluation of predation failure incomplete drill frequencies (IDFs) and values for prey effectiveness were calculated for the two cores from Panzano (M28, M29). The assemblages from M28 and M29 had an average IDF of 1.8 % and 2.6 %, respectively. In the Pazano M28 core unsuccessful drills were found in 4 different species (*Nucula cf. nucleus, Abra alba, Paphia rhomboides* and *Corbula gibba*), but similar to the other cores, for example Brijuni (M44), Piran (M1, M53), most of these incomplete drills were recovered in specimens of *Corbula gibba* (94.4 %). In the second Panzano core incomplete drills were detected exclusively in samples of *Corbula*. When IDFs are computed on species level *Corbula gibba* has an average IDF of 6.5 % in M28 and 9.8 % in M29. Considering the development of the IDFs along the core three peaks or three zones of increased IDFs attract attention (Fig. 31, 32). First of all, there is a rise of incomplete drills in both assemblages (M28, M29) in the samples at the bottom layers between 130 and 140 cm (up to 4.2 % in M28, 3.3 % in M29). In the middle of the core at a sediment depth of 55-60 cm in M28 and 60-70 cm in M29 the curves reflect increasing IDFs up to 2.5 % in M28 and 5.1 % in M29. But the highest fluctuations are recognised in the samples of the uppermost layers of both Panzano cores, where IDFs reach 9.1 % in M28 and even higher values of 12.5 % in M29.
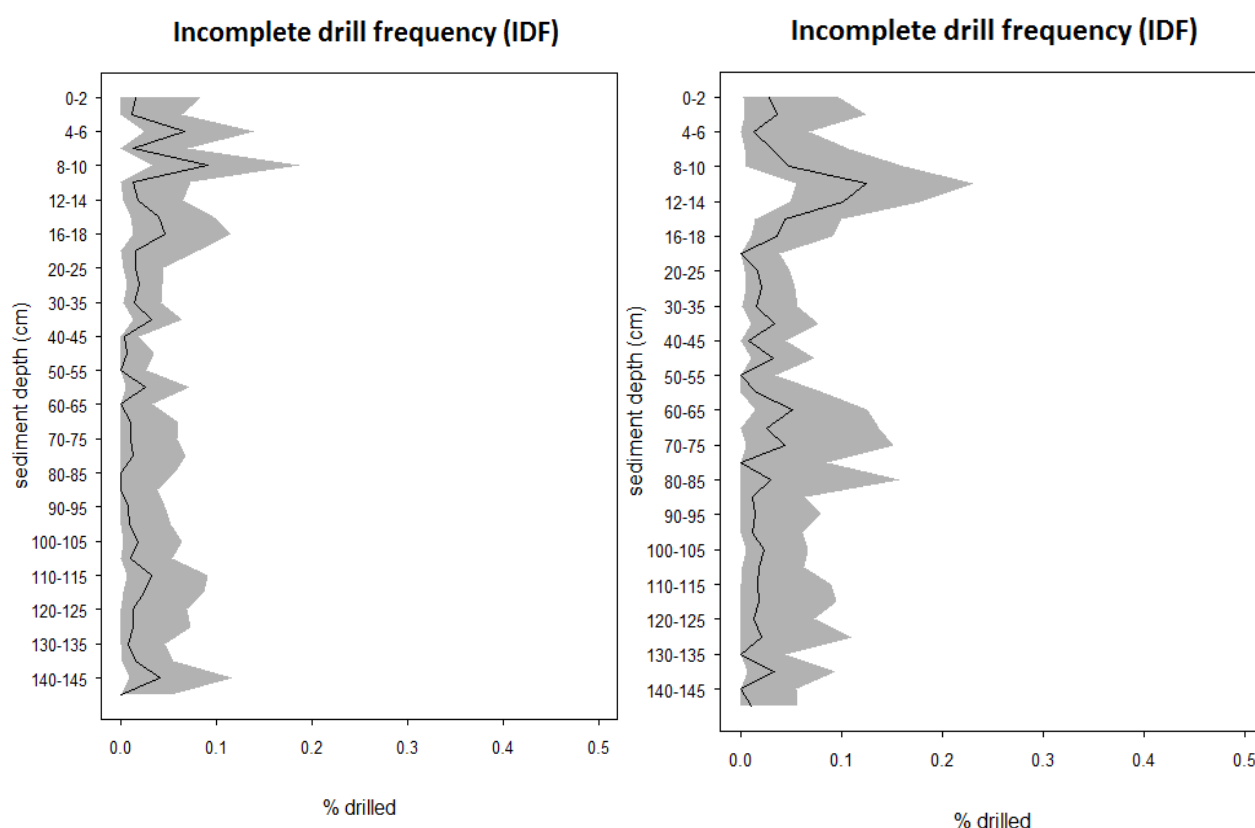
Fig. 31: Incomplete drill frequency (IDF) along Panzano M28   **Fig. 32:** Incomplete drill frequency (IDF) along Panzano M29

Prey effectiveness (PE) in the samples from the sediment cores from Panzano range from 6.9 % for M28 to 10.5 % for M29. Almost all of the incomplete drills were recorded in samples of *Corbula gibba* and *Corbula's* average PEs reached 17.8 % in M28 and 23.5 % in M29. The PE trends are very similar to the IDFs (Fig. 33, 34). The only differences are that the PE-

values generally range on higher levels and therefore the fluctuations seem sharper and more intense, especially the peaks in the uppermost sediment layers, where PEs up to 28.6 % (M28) and 50.0 % (M29) were computed. That means nearly every third (in M28) or every second (in M29) predatory attack on bivalves in these samples failed.
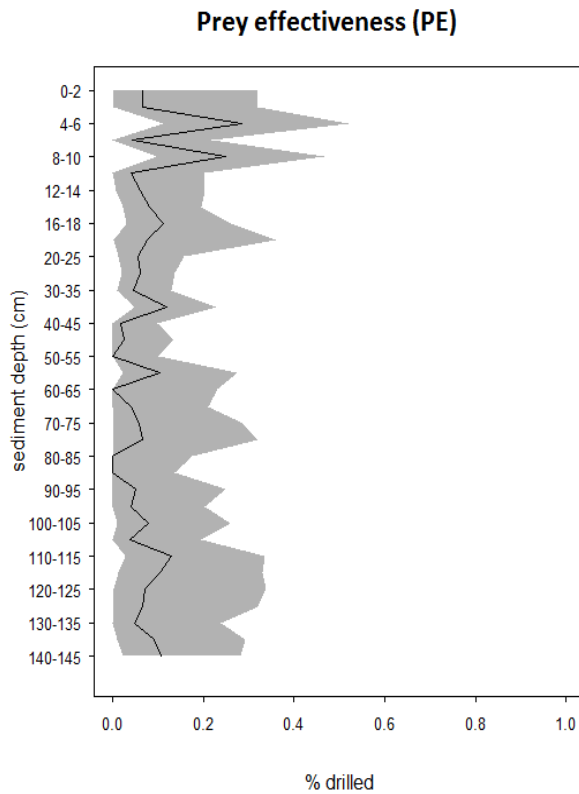
Fig. 33: Prey effectiveness (PE) along Panzano M28
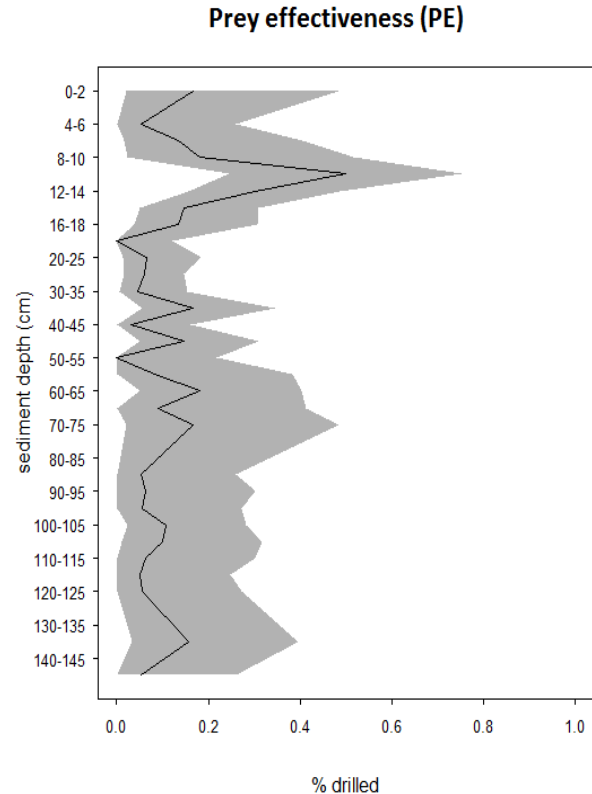
Fig. 34: Prey effectiveness (PE) along Panzano M29

6.2.4 Drilling predation in the samples from Venice (M38)

The core M38 was collected in the shelf area close to Venice. At this location sediment structure is characterized by oligotrophic relict sands and the marine environment at this sampling station is highly affected by anthropogenic impacts, e.g. fishing and dredging. The M38 core had a length of 140 cm represented 5,071 bivalves, belonging to 65 species and 27 families. Compared to the assemblages of the other cores Venice M38 is rather middle-sized, smaller than Brijuni M44 or Piran M1, M53, but larger than Panzano M28, M29 or the Po M13, M20 cores. The diversity in this assemblage is significantly higher than in the samples from Panzano (M28, 29).

6.2.4.1 Overall drilling intensity in the samples from Venice (M38)

Drilling frequency (DF) of the bivalves from M38 is very low (5.4 %). This value suggests a remarkably lower drilling predation than in the cores from other shelf locations, for example Panzano M28, M29 where DFs of 21.8-23.8 % were calculated. Only one of the cores collected from the Po delta exhibited even lower drilling predation. Considering the development of the drilling intensity of the examined assemblage of Venice M38 along the length of the core a moderate variability of drilling intensity can be recognized (Fig. 35). There are only few layers or layer sections were the DFs remain stable. The highest DFs were detected in the bottom layers from 130-135 cm (16.7 %). Moreover, at a depth of 90-120 cm DFs of 5.9 % to 7.7 % were calculated. Further peaks were recognized in the upper half of the core at a sediment depth of 50-50 cm (7.8 %) or in the layers of the upper 20 cm of the core (9.4 % to 10.1 %).

The most abundant species in the assemblage of M38 are *Lucinella divaricata, Anomia cf. ephippium, Parvicardium scabrum* and *Moerella distorta* which account for 45.8 % of the total sample. The DFs of these four species are very different, both the average values and the trends along the core (Fig. 36). The samples of *Lucinella divaricata*, which was the most abundant bivalve species among the assemblage of Venice M38, had an average DF of 11.8 %. *Anomia cf. ephippium's* DF reached 12.6 %, while in only 1.0 % of *Parvicardium scabrum's* and in 3.7 % of *Moerella distorta's* specimens drill holes were recovered. The black line represents the trend of *Lu-*
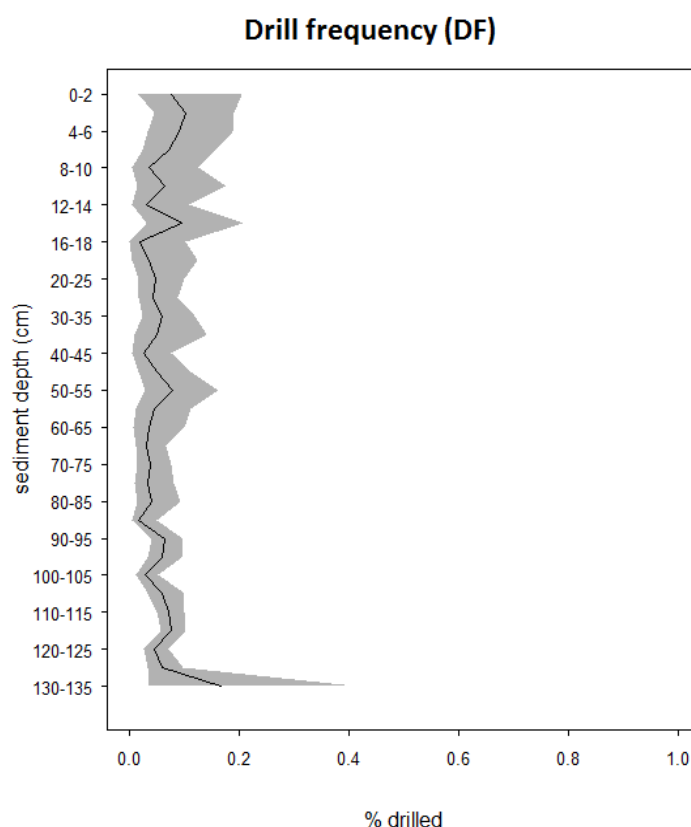
Fig. 35: Overall drill frequency (DF) along Venice M38
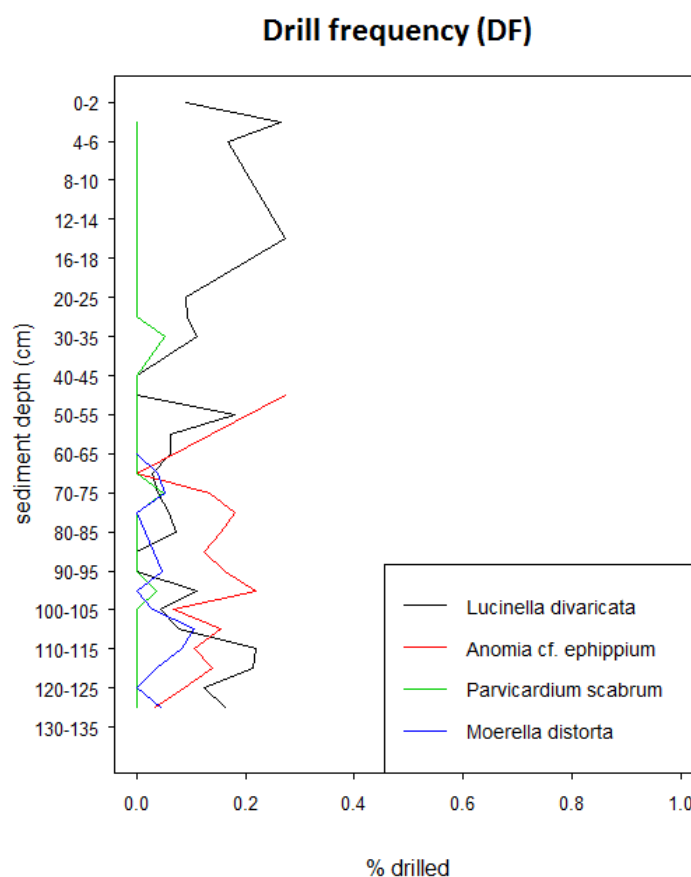
Fig. 36: DFs of *Lucinella divaricata, Anomia cf. ephippium, Parvicardium scabrum, Moerella distorta* along Venice M38

cinella's sample which exhibits high DFs in the bottom layers from 110-130 cm (12.5 %-21.9 %), at a depth of 50-55 cm (18.2 %) and in the uppermost 20 cm of the core (up to 27.3 %). *Anomia* shows high DFs in sediment layers from 70-120 cm (up to 21.9 %) and at 45-50 cm depth (27.3 %). In the uppermost layers *Anomia's* sample size becomes too small for representative conclusions about its drilling intensity. *Parvicardium scabrum's* DF is quite low almost all along the core and in only three sediment layers drilled shells were recovered, at 95-100 cm (3.7 %), 70-75 cm (5.0 %) and 30-35 cm (5.3 %) depth. *Moerella* shows its highest DFs at depth of 105-115 cm (8.3 %-10.5 %) and at 70-75 cm (5.3 %). Although the DF curves of these four species seem rather confuse or disordered at first sight, a few general patterns can be recovered. For instance, there are rising DFs in *Lucinella*, *Anomia* and *Moerella* from 120 cm upwards and declining drilling intensities at a depth of 100-105 cm. From this layer upwards in all of these three species a significant increase is detected. In the samples from 90 cm depth there is a similar tendency of declining drilling predation followed by another rise for these three species in the Venice M38 core. At 65-70 cm depth the DFs of all the four top species from M38 decline considerably and only in the samples of *Lucinella* and *Anomia* rising DFs are recognized in the proximate sediment layers.

Among the assemblage from the Venice M38 core the bivalve species *Corbula gibba* is very rare. Due to its very small sample size in this core it can't be used as a "key species" reflecting any general patterns or trends regarding drilling intensities along the core.

6.2.4.2   EDF, MDF, IDF and PE in the bivalve fauna from Venice (M38)

The frequency of drills located at the edges of the bivalve shells (EDF) was very low in the assemblage from the Venice M38 core. The average EDF among all the examined bivalves was 0.3 %. This frequency fluctuated slightly along the core and reached a few moderate peaks at sediment layers from 125-130 cm (0.8 %), 60-65 cm (1.2 %), 35-40 cm (1.7 %) and 18-20 cm (1.8 %) (Fig.37). In nine of the 65 species edge drills were recovered, but most of these were found on shells of *Anomia cf. ephippium* (23.5 % of all edge drills) and *Glycymeris glycymeris* (29.4 %). The average EDF calculated for *Anomia* was 0.8 % and *Glycymeris* had an EDF of 5.2 %.

The only example of a multiple drilled bivalve in core Venice M38 was detected in
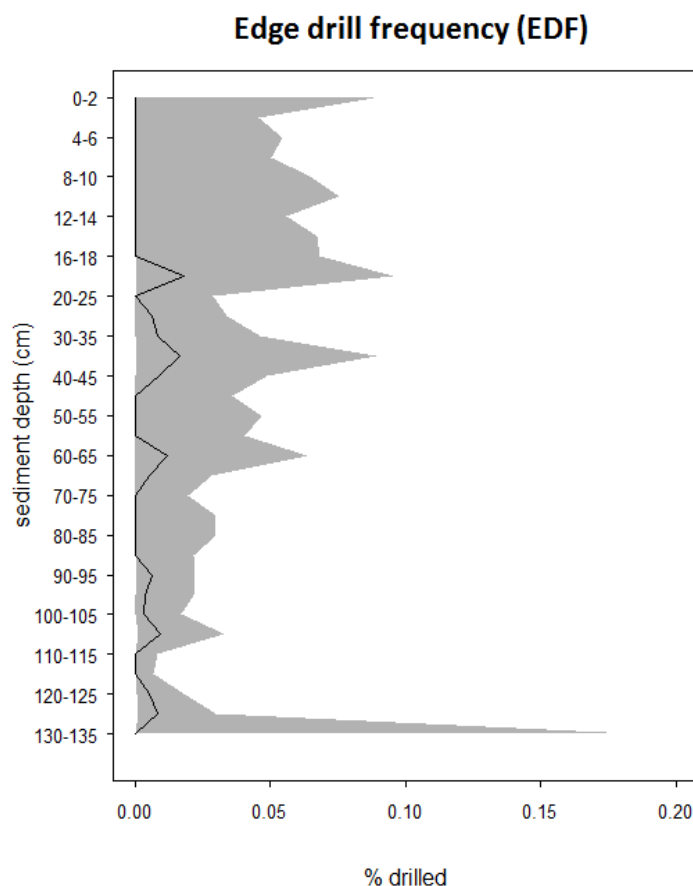
Fig. 37: Edge drill frequency (EDF) along Venice M38

the samples of *Anomia cf. ephippium* and similarly there was only one unsuccessfully drilled shell, belonging to *Corbula gibba*. The occurrence of predation failure was so rare that Prey effectiveness (PE) for the bivalve fauna of Venice M38 was only slightly above 0 %. According to my evaluations only 0.4 % of all the recognized predation attacks of M38 failed. This remarkably low value may correlate with the generally low drilling frequency in the total assemblage at this sampling station.

6.2.5 Drilling predation in the samples from Po (M13, M20)

At the shelf close to the Po River mouth two cores were collected (Po3 M13 and Po4 M20). The sediment composition in this region is characterized by mud with high nutrient and sediment input. The Po3 M13 core had a length of 155 cm, consisted of 849 bivalves, belonging to 27 species and 17 families. Po4 M20 was 150 cm long and 884 bivalves of 29 species and 16 families were counted. Compared to the assemblages of the other cores the Po cores are the smallest and have the lowest diversity.

6.2.5.1 Overall drilling intensity in the samples from Po (M13, M20)

The overall DFs of the assemblages are 4.6 % (Po 3 M13) and 8.5 % (Po 4 M20). The DF trends along the cores show a strong variability (Fig. 38, 39). The highest DFs were detected in the middle of both cores, at a depth from 70-80 cm (26.1 % in M13 and 25.0 % in M20). Increasing drilling intensities were recorded in both cores at a depth of 105-125 cm. In the uppermost and the bottom layers of these two cores DFs are very low.
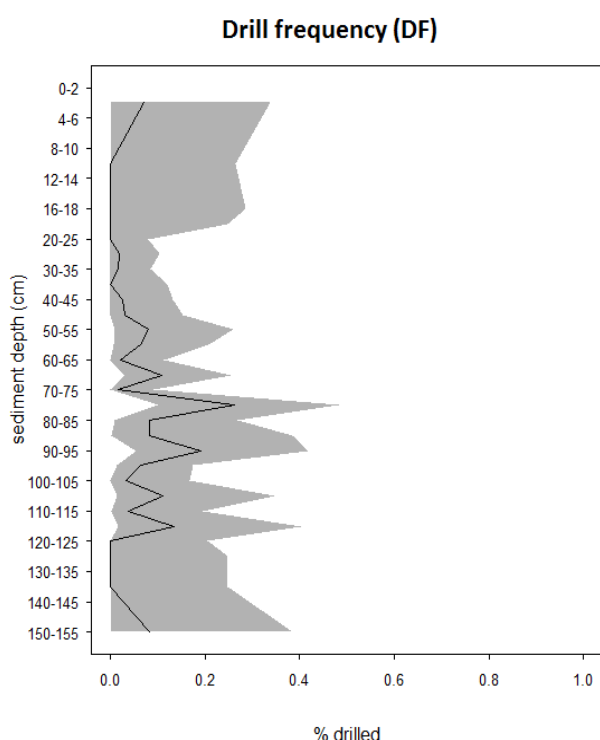
Fig. 38: Overall drill frequency (DF) along Po 3 M13
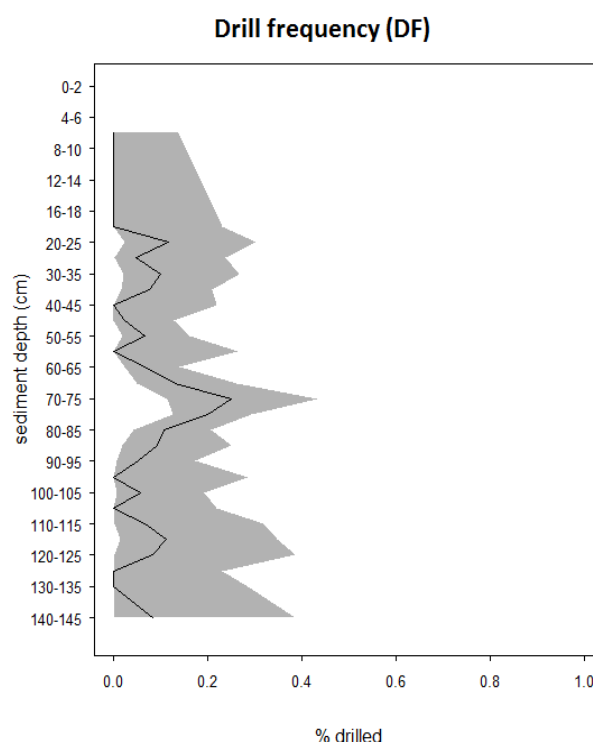
Fig. 39: Overall drill frequency (DF) along Po 4 M20

The two most abundant species of the assemblages from the Po delta were *Corbula gibba* and *Kurtiella bidentata* which account for 71.3 % (M13) and 71.4 % (M20) of all the bivalves from the cores. In both cores (M13, M20) most of the drill holes were recorded among *Corbula gibba* (89.7 % in M13, 94.7 % in M20). Due to that reason the general trends of the two Po cores are based on *Corbula's* drilling intensities. The average DF of *Corbula gibba* was 7.0 % in M13 and 14.1 % in M20. Considering *Corbula's* drilling intensities along the cores the highest DFs (35.3 % in M13, 36.4 % in M20) are reached at a depth of 75-80 cm (M13) and 70-75 cm (M20).

6.2.5.2 EDF, MDF, IDF and PE in the bivalve fauna from Po (M13, M20)

EDFs of the two cores from the Po delta were very low (0 % in M13, 0.3 % in M20). In M13 no edge drills were recovered, whereas in M20 all edge drills were recognized among *Corbula gibba*, which had an average EDF of 0.6 %. The edge drills of M20 were recorded in the middle of the core at sediment depth of 35-40 cm, 60-65 cm and 70-75 cm. Multiple drilled valves were not found in any of the two cores (M13, M20) from the Po delta. A few incompletely perforated shells were detected among *Corbula gibba* in the M20 core. The average IDF of the total fauna from the M20 core was 0.9 %. *Corbula gibba* had an IDF of 1.6 %. These incomplete drills were again found in the middle of the core (from 45 to 85 cm) and in the bottom layers (from 120 to 145 cm) (Fig. 40). *Corbula's* prey effectiveness (PE) reached 10.1 %, while the average PE of the total fauna was 9.6 %.
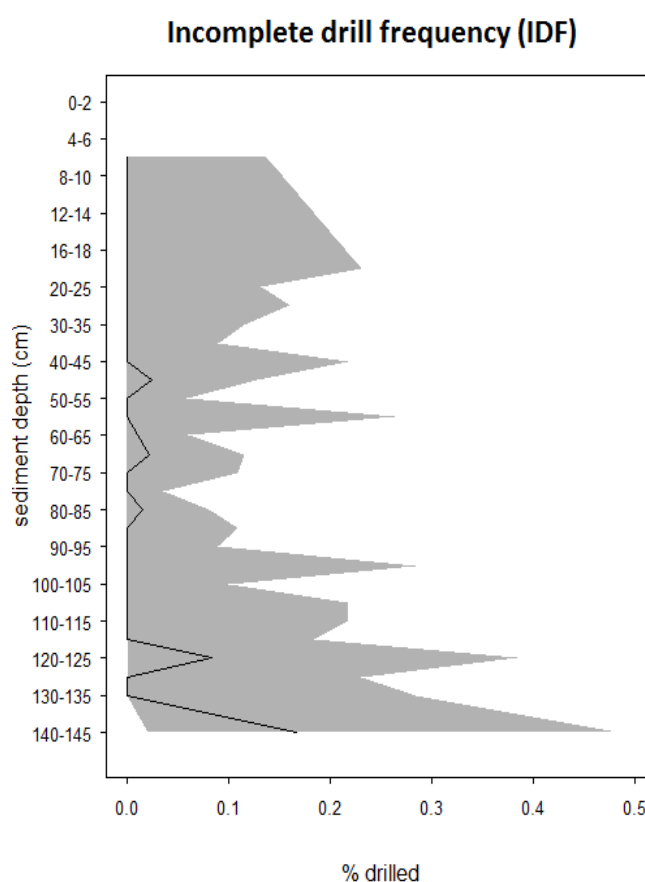
Fig. 40: Incomplete drill frequency (IDF) along Po 4 M20

6.3   Predation intensities at different taxonomic levels

Mean DF, IDF and PE across the total fauna of all 8 cores are 18.0 %, 1.4 % and 7.1 %, respectively (Table 1, 3, 4). Seven of the 38 bivalve families were never drilled, but most of these families were represented by relatively few individuals (n < 20). Among the families which were attacked, DFs range from 0.7 % (Donacidae) to 28.9 % (Veneridae) (Table 6). The five most abundant bivalve families across the total fauna of the 8 cores were all drilled. They had mean DFs from 8.8 % to 28.9 %: Veneridae (28.9 %), Corbulidae (22.1 %), Cardiidae (8.8 %), Montacutidae (27.2 %) and Anomidae (21.7 %). Sixteen of the 36 bivalve families among the eight cores contained incomplete drill holes. Among the abundant families (n > 50) the IDFs ranged between 0.1 % (e.g. Ostreidae, Lucinidae, Cardiidae, Semelidae) and 17.6 % (Noetiidae). The five most abundant bivalve families had IDFs from 0.1 % (Veneridae, Anomidae, Cardiidae) to 3.6 % (Corbulidae). Among the 11 species of the Montacutidae no incomplete drill holes were found. The PEs of the families with incomplete drill holes in their samples ranged from 0.2 % (Veneridae) to 77.9 % (Noetiidae). The most abundant families had PEs which range from 0.2 % (Veneridae) to 14.2 % (Corbulidae).

Table 6: Mean DF, IDF and PE of abundant bivalve families (n > 50), pooled across all 8 cores

Total fauna							
Family	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Nuculanidae	2	339	43	1	12.7	0.3	2.3
Nuculidae	2	1,770	331	31	18.7	1.8	8.6
Arcidae	6	365	20	3	5.5	0.8	13.0
Noetiidae	1	2,124	106	373	5.0	17.6	77.9
Glycymerididae	2	480	30	5	6.3	1.0	14.3
Crenellinae	3	1,523	136	3	8.9	0.2	2.2
Pectinidae	6	2,064	134	10	6.5	0.5	6.9
Anomidae	3	2,691	583	3	21.7	0,1	0.5
Limidae	6	226	9	0	4.0	0.0	0.0
Ostreidae	2	1,619	136	1	8.4	0.1	0.7
Chamidae	2	261	38	0	14.6	0.0	0.0
Lucinidae	6	1,734	253	1	14.6	0.1	0.4
Thyasiridae	1	138	12	0	8.7	0.0	0.0
Montacutidae	11	3,523	958	0	27.2	0.0	0.0
Kellidae	2	82	6	0	7.3	0.0	0.0
Basterotiidae	1	94	0	0	0.0	0.0	0.0
Cardiidae	11	6,795	595	5	8.8	0.1	0.8
Mactridae	1	215	5	0	2.3	0.0	0.0
Semelidae	4	2,330	230	2	9.9	0.1	0.9
Tellinidae	9	2,222	274	0	12.3	0.0	0.0
Solecurtidae	2	138	4	0	2.9	0.0	0.0
Donacidae	1	281	2	0	0.7	0.0	0.0
Veneridae	12	13,668	3,956	8	28.9	0.1	0.2

Corbulidae	2	8,080	1,783	294	22.1	3.6	14.2
Pharidae	2	129	2	0	1.6	0.0	0.0
Gastrochaenidae	1	121	2	1	1.7	0.8	33.3
Hiatellidae	1	656	72	5	11.0	0.8	6.5
Thraciidae	3	188	2	0	1.1	0.0	0.0

All five of the most abundant bivalve species across the 8 cores (*Corbula gibba*, *Gouldia minima*, *Kurtiella bidentata*, *Parvicardium scabrum* and *Timoclea ovata* were drilled. DFs range from 0.7 % (*Donax venustus*) to 37.0 % (*Gouldia minima*) (Table 7). *Saxicavella jeffreysi* is the only species among the most abundant (n > 50) which had no drill holes. Twenty five of the abundant species (n > 50) were incompletely drilled. Among the species with incomplete drill holes, IDFs range from 0.1 % (e.g. *Musculus subpictus*, *Anomia ephippium*) to 17.6 % (*Striarca lactea*). In the species with incomplete perforated drill holes, PE ranged from 0.2 % (*Gouldia minima, Timoclea ovata*) to 77.9 % (*Striarca lactea*).

Table 7: Mean DF, IDF and PE of the most abundant bivalve species (n > 50), pooled across all 8 cores

Total fauna						
Species	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Nuculana pella	279	27	1	9.7	0.4	3.6
Sacculla commutata	60	16	0	26.7	0.0	0.0
Nucula cf. Nucleus	1,608	302	29	18.8	1.8	8.8
Nucula sulcata	162	29	2	17.9	1.2	6.5
Arca noae	202	3	2	1.5	1.0	40.0
Arca tetragona	102	17	1	16.7	1.0	5.6
Striarca lactea	2,123	106	373	5.0	17.6	77.9
Glycymeris glycymeris	451	28	5	6.2	1.1	15.2
Musculus subpictus	747	56	1	7.5	0.1	1.8
Modiolus adriacus	523	82	2	15.7	0.4	2.4
Aequipecten opercularis	655	35	3	5.3	0.5	7.9
Mimachlamys varia	373	23	2	6.2	0.5	8.0
Chlamys multistriatus	77	17	4	22.1	5.2	19.0
Flexopecten glaber	907	66	0	7.3	0.0	0.0
Anomia ephippium	1,653	326	2	19.7	0.1	0.6
Heteranomia squamula	428	104	0	24.3	0.0	0.0
Pododesmus patelliformes	610	153	1	25.1	0.2	0.6
Limaria loscombi	56	4	0	7.1	0.0	0.0
Limatula gwyni	82	3	0	3.7	0.0	0.0
Ostrea sp.	1,608	135	1	8.4	0.1	0.7
Chama gryphoides	249	36	0	14.5	0.0	0.0
Anodontia fragilis	751	140	0	18.7	0.0	0.0
Lucinella divaricata	896	107	0	11.9	0.0	0.0
Myrtea spinifera	60	5	1	8.3	1.7	16.7

Thyrasira biplicata	138	12	0	8.7	0.0	0.0
Kurtiella bidentata	2,805	922	0	32.9	0.0	0.0
Lepton squamosum	122	2	0	1.6	0.0	0.0
Hemilepton nitidium	317	19	0	6.0	0.0	0.0
Kellia suborbicularis	84	12	0	14.3	0.0	0.0
Saxicavella jeffreysi	94	0	0	0.0	0.0	0.0
Acanthocardia paucicostata	485	15	0	3.1	0.0	0.0
Acanthocardia aculeata	159	2	0	1.3	0.0	0.0
Papillicardium papillosum	2,110	150	3	7.1	0.1	2.0
Parvicardium exiguum	443	65	1	14.7	0.2	1.5
Parvicardium scriptum	451	47	0	10.4	0.0	0.0
Parvicardium scabrum	2,490	296	0	11.9	0.0	0.0
Parvicardium minimum	417	18	0	4.3	0.0	0.0
Spisula subtruncata	215	5	0	2.3	0.0	0.0
Abra alba	1,431	168	2	11.7	0.1	1.2
Abra nitida	869	62	0	7.1	0.0	0.0
Morella distorta	1,667	253	0	15.2	0.0	0.0
Tellina fabula	265	10	0	3.8	0.0	0.0
Azorinus chamasolen	136	4	0	2.9	0.0	0.0
Donax venustus	281	2	0	0.7	0.0	0.0
Mysia undata	60	8	0	13.3	0.0	0.0
Callista chione	205	5	0	2.4	0.0	0.0
Gouldia minima	7,995	2,957	6	37.0	0.1	0.2
Pitar rudis	1,696	347	0	20.5	0.0	0.0
Paphia rhomboides	392	75	1	19.2	0.3	1.3
Dosinia lupinus	210	17	0	8.1	0.0	0.0
Venus verrucosa	205	27	0	13.2	0.0	0.0
Timoclea ovata	2,560	449	1	17.5	0.0	0.2
Clausinella fasciata	274	67	0	24.5	0.0	0.0
Corbula gibba	8,066	1,783	294	22.1	3.6	14.2
Phaxas adriaticus	106	2	0	1.9	0.0	0.0
Gastrochaena dubia	121	2	1	1.7	0.8	33.3
Hiatella arctica	656	72	5	11.0	0.8	6.5
Thracia phaseolina	184	2	0	1.1	0.0	0.0

In the bivalve assemblage from the Brijuni M44 core all of the abundant families (n > 50) were drilled (Table 8). The DFs of these bivalve families ranged from 5.2 % (Noetiidae) to 29.9 % (Anomidae). Twelve of the abundant families contained incomplete drill holes. Within these families IDFs ranged from 0.1 % (Anomidae) and 18.7 % (Noetiidae). Among the families with unsuccessful perforated drills PEs ranged from 0.2 % (Veneridae) to 78.2 % (Noetiidae). Chamidae, Kellidae, Limidae, Montacutidae, Nuculanidae and Ostreidae were never incompletely drilled in Brijuni M44.

Table 8: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Brijuni M44

Brijuni M44							
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Family							
Anomidae	3	1,443	431	2	29.9	0.1	0.5
Arcidae	4	152	17	3	11.1	2.0	15.0
Cardiidae	5	1,615	121	3	7.5	0.2	2.4
Chamidae	2	74	11	0	14.9	0.0	0.0
Corbulidae	1	487	105	15	21.6	3.1	12.5
Crenellinae	2	310	65	2	21.0	0.6	3.0
Glycymerididae	1	354	21	5	5.9	1.4	19.2
Hiatellidae	1	274	44	3	16.1	1.1	6.4
Kellidae	2	59	4	0	6.8	0.0	0.0
Limidae	4	151	8	0	5.3	0.0	0.0
Montacutidae	4	192	22	0	11.5	0.0	0.0
Noetiidae	1	2,000	104	373	5.2	18.7	78.2
Nuculanidae	2	76	17	0	22.4	0.0	0.0
Nuculidae	1	709	149	27	21.0	3.8	15.3
Ostreidae	1	193	41	0	21.2	0.0	0.0
Pectinidae	5	461	42	10	9.1	2.2	19.2
Semelidae	1	99	14	1	14.1	1.0	6.7
Veneridae	9	3,455	621	1	18.0	0.0	0.2

All of the most abundant bivalve species (n > 50) from the Brijuni M44 core contained drill holes (Table 9). The DFs ranged from 2.5 % (*Lepton squamosum)* to 30.8 % *(Pododesmus patelliformes).* Sixteen of the abundant species had no incomplete drills. The others had at least 1 incompletely perforated bore hole. IDFs among these species ranged from 0.1 % (*Anomia ephippium*) to 18.7 % (*Striarca lactea*) and the PEs from 0.5 % (*Anomia ephippium*) to 78.2 % (*Striarca lactea*).

Table 9: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Brijuni M44

Brijuni M44						
	n	D	ID	DF (%)	IDF (%)	PE (%)
Species						
Sacculla commutata	57	16	0	28.1	0.0	0.0
Nucula cf. Nucleus	709	149	27	21.0	3.8	15.3
Arca tetragona	91	17	1	18.7	1.1	5.6
Striarca lactea	1,999	104	373	5.2	18.7	78.2
Glycymeris glycymeris	354	21	5	5.9	1.4	19.2
Modiolus adriacus	286	65	2	22.7	0.7	3.0
Aequipecten opercularis	240	18	3	7.5	1.3	14.3
Mimachlamys varia	109	13	2	11.9	1.8	13.3
Chlamys multistriatus	75	17	4	22.7	5.3	19.0

Anomia ephippium	726	215	1	29.6	0.1	0.5
Heteranomia squamula	311	91	0	29.3	0.0	0.0
Pododesmus patelliformes	406	125	1	30.8	0.2	0.8
Limaria loscombi	56	4	0	7.1	0.0	0.0
Limatula gwyni	82	3	0	3.7	0.0	0.0
Ostrea sp.	188	40	0	21.3	0.0	0.0
Chama gryphoides	71	11	0	15.5	0.0	0.0
Lepton squamosum	81	2	0	2.5	0.0	0.0
Hemilepton nitidium	57	4	0	7.0	0.0	0.0
Kellia suborbicularis	70	12	0	17.1	0.0	0.0
Papillicardium papillosum	448	36	3	8.0	0.7	7.7
Parvicardium scriptum	382	41	0	10.7	0.0	0.0
Parvicardium scabrum	375	28	0	7.5	0.0	0.0
Parvicardium minimum	398	16	0	4.0	0.0	0.0
Abra alba	99	14	1	14.1	1.0	6.7
Gouldia minima	331	56	0	16.9	0.0	0.0
Pitar rudis	242	44	0	18.2	0.0	0.0
Venus verrucosa	140	19	0	13.6	0.0	0.0
Timoclea ovata	2,450	433	1	17.7	0.0	0.2
Clausinella fasciata	264	67	0	25.4	0.0	0.0
Corbula gibba	487	105	15	21.6	3.1	12.5
Hiatella arctica	274	44	3	16.1	1.1	6.4

Among the bivalve assemblage from the Piran M1 core, two of the most abundant families (Arcidae, Gastrochaenidae) never had drill holes (Table 10). All the other abundant families (n > 50) contained at least one drill hole. The DFs of these bivalve families ranged from 1.3 % (Noetiidae) to 33.3 % (Veneridae). Five of the abundant families had incomplete drill holes; Veneridae had the lowest IDF (0.1 %) and Corbulidae the highest (2.5 %). Among the families with incompletely drilled bore holes PEs ranged from 0.2 % (Veneridae) to 14.3 % (Hiatellidae).

Table 10: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Piran M1

Piran M1						
Family	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Anomidae	3	368	26	1	7.1	0.3	3.7
Arcidae	4	102	0	0	0.0	0.0	0.0
Cardiidae	8	2,158	187	0	8.7	0.0	0.0
Chamidae	2	116	11	0	9.5	0.0	0.0
Corbulidae	2	2,427	443	61	18.3	2.5	12.1
Crenellinae	2	335	5	0	1.5	0.0	0.0
Gastrochaenidae	1	54	0	0	0.0	0.0	0.0
Hiatellidae	1	121	6	1	5.0	0.8	14.3

Lucinidae	4	346	72	0	20.8	0.0	0.0
Montacutidae	8	316	27	0	8.5	0.0	0.0
Noetiidae	1	78	1	0	1.3	0.0	0.0
Nuculidae	1	393	55	1	14.0	0.3	1.8
Ostreidae	1	960	46	0	4.8	0.0	0.0
Pectinidae	5	413	11	0	2.7	0.0	0.0
Semelidae	3	656	41	0	6.3	0.0	0.0
Solecurtidae	1	66	1	0	1.5	0.0	0.0
Tellinidae	4	644	67	0	10.4	0.0	0.0
Veneridae	9	4,964	1,651	3	33.3	0.1	0.2

In two of the abundant bivalve species (n > 50) from the Piran M1 core (*Arca noae, Abra nitida*) no drill holes were found (Table 11). The other highly abundant species contained at least one drill hole and their DFs ranged from 1.3 % (*Striarca lactea, Acanthocardia aculeata*) to 36.6 % *(Gouldia minima).* Five of the abundant species had incomplete drill holes (*Nucula cf. nucleus*, *Anomia cf. ephippium, Gouldia minima, Corbula gibba, Hiatella arctica*). For these families, IDFs ranged from 0.1 % (*Gouldia minima*) to 2.5 % (*Corbula gibba*) and the PEs from 0.2 % (*Gouldia minima*) to 14.3 % (*Hiatella arctica*).

Table 11: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Piran M1

Piran M1						
Species	n	D	ID	DF (%)	IDF (%)	PE (%)
Nucula cf. nucleus	393	55	1	14.0	0.3	1.8
Arca noae	95	0	0	0.0	0.0	0.0
Striarca lactea	78	1	0	1.3	0.0	0.0
Musculus subpictus	130	4	0	3.1	0.0	0.0
Mimachlamys varia	142	3	0	2.1	0.0	0.0
Flexopecten glaber	231	7	0	3.0	0.0	0.0
Anomia cf. ephippium	184	8	1	4.3	0.5	11.1
Heteranomia cf. squamula	62	6	0	9.7	0.0	0.0
Pododesmus cf. patelliformis	122	12	0	9.8	0.0	0.0
Ostrea sp.	960	46	0	4.8	0.0	0.0
Chama gryphoides	112	10	0	8.9	0.0	0.0
Anodontia fragilis	326	69	0	21.2	0.0	0.0
Kurtiella bidentata	163	25	0	15.3	0.0	0.0
Hemilepton nitidum	111	2	0	1.8	0.0	0.0
Acanthocardia aculeata	157	2	0	1.3	0.0	0.0
Papillocardium papillosum	913	37	0	4.1	0.0	0.0
Parvicardium exiguum	127	20	0	15.7	0.0	0.0
Parvicardium scabrum	847	123	0	14.5	0.0	0.0
Abra alba	600	41	0	6.8	0.0	0.0
Abra nitida	55	0	0	0.0	0.0	0.0

Moerella distorta	624	67	0	10.7	0.0	0.0
Azorinus chamasolen	66	1	0	1.5	0.0	0.0
Gouldia minima	4,172	1,528	3	36.6	0.1	0.2
Pitar rudis	641	110	0	17.2	0.0	0.0
Corbula gibba	2,426	443	61	18.3	2.5	12.1
Gastrochaena dubia	54	0	0	0.0	0.0	0.0
Hiatella arctica	121	6	1	5.0	0.8	14.3

Among the bivalves from the Piran M53 core, all of the most abundant families (n > 50) had drill holes (Table 12). For these families DFs ranged from 4.9 % (Arcidae) to 36.5 % (Veneridae). Seven of the abundant families contained incomplete drill holes, of these families Cardiidae and Veneridae had the lowest IDF (0.1 %) and Corbulidae the highest (2.8 %). Among the families with incomplete drills PEs ranged from 0.2 % (Veneridae) to 10.0 % (Corbulidae).

Table 12: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Piran M53

Piran M53						
	S	n	D	ID	DF	IDF	PE
Family					(%)	(%)	(%)
Anomidae	3	208	49	0	23.6	0.0	0.0
Arcidae	3	61	3	0	4.9	0.0	0.0
Cardiidae	8	1,950	261	2	13.4	0.1	0.8
Chamidae	2	71	16	0	22.5	0.0	0.0
Corbulidae	2	2,204	547	61	24.8	2.8	10.0
Crenellinae	2	413	56	1	13.6	0.2	1.8
Hiatellidae	1	120	10	1	8.3	0.8	9.1
Lucinidae	5	363	73	0	20.1	0.0	0.0
Montacutidae	9	675	135	0	20.0	0.0	0.0
Nuculidae	1	286	74	1	25.9	0.3	1.3
Ostreidae	1	315	40	1	12.7	0.3	2.4
Pectinidae	3	436	68	0	15.6	0.0	0.0
Semelidae	4	752	107	0	14.2	0.0	0.0
Tellinidae	3	613	160	0	26.1	0.0	0.0
Veneridae	8	4,276	1,561	3	36.5	0.1	0.2

In all of the abundant bivalve species (n > 50) from the Piran M53 core (*Arca noae*, *Abra nitida*) drill holes were found (Table 13). Drilling frequencies ranged from 4.0 % (*Acanthocardia paucicostata)* to 36.6 % *(Gouldia minima).* Seven of the abundant species contained at least one incomplete drill hole (*Nucula cf. nucleus*, *Musculus subpictus*, *Ostrea sp.*, *Parvicardium exiguum, Gouldia minima, Corbula gibba, Hiatella arctica*). For these families, IDFs ranged from 0.1 % (*Gouldia minima*) to 2.8 % (*Corbula gibba*) and the PEs from 0.2 % (*Gouldia minima*) to 10.0 % (*Corbula gibba*).

Piran M53						
Species	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Nucula cf. nuclaeus	286	74	1	25.9	0.3	1.3
Arca noae	56	3	0	5.4	0.0	0.0
Musculus subpictus	217	40	1	18.4	0.5	2.4
Modiolus adriaticus	196	16	0	8.2	0.0	0.0
Aequipecten opercularis	62	15	0	24.2	0.0	0.0
Flexopecten glaber	325	49	0	15.1	0.0	0.0
Anomia ephippium	152	34	0	22.4	0.0	0.0
Ostrea sp.	315	40	1	12.7	0.3	2.4
Chama gryphoides	66	15	0	22.7	0.0	0.0
Anodontia fragilis	347	71	0	20.5	0.0	0.0
Kurtiella bidentata	349	123	0	35.2	0.0	0.0
Hemilepton nitidum	108	5	0	4.6	0.0	0.0
Acanthocardia paucicostata	174	7	0	4.0	0.0	0.0
Papillicardium papillosum	703	77	0	11.0	0.0	0.0
Parvicardium exiguum	155	32	1	20.6	0.6	3.0
Parvicardium scabrum	781	140	0	17.9	0.0	0.0
Abra alba	573	93	0	16.2	0.0	0.0
Abra nitida	173	14	0	8.1	0.0	0.0
Moerella distorta	526	157	0	29.8	0.0	0.0
Gouldia minima	3,464	1,370	3	39.5	0.1	0.2
Pitar rudis	651	170	0	26.1	0.0	0.0
Timoclea ovata	57	9	0	15.8	0.0	0.0
Corbula gibba	2,198	547	61	24.9	2.8	10.0
Hiatella arctica	120	10	1	8.3	0.8	9.1

All of the most abundant families (n > 50) from the Panzano M28 core were drilled (Table 14). Drilling frequencies ranged from 0.6 % (Crenellinae) to 40.2 % (Montacutidae). In four of the abundant families incomplete drill holes were recovered (Corbulidae, Nuculidae, Semelidae, Veneridae). Of these families Semelidae had the lowest IDF (0.2 %) and Corbulidae the highest (6.5 %). Among the families with incomplete drills PEs ranged from 2.1 % (Veneridae) to 17.8 % (Corbulidae).

Table14: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Panzano M28

Panzano M28							
Family	**S**	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Anomiidae	3	67	3	0	4.5	0.0	0.0
Cardiidae	5	230	14	0	6.1	0.0	0.0
Corbulidae	2	1,030	309	67	30.0	6.5	17.8

Crenellinae	2	178	1	0	0.6	0.0	0.0
Montacutidae	3	1,190	478	0	40.2	0.0	0.0
Nuculanidae	2	69	9	0	13.0	0.0	0.0
Nuculidae	1	160	29	2	18.1	1.3	6.5
Ostreidae	1	82	6	0	7.3	0.0	0.0
Pectinidae	3	184	6	0	3.2	0.0	0.0
Semelidae	2	419	41	1	9.8	0.2	2.4
Veneridae	5	230	47	1	20.4	0.4	2.1

All of the abundant bivalve species (n > 50) from the Panzano M28 core had drill holes (Table 15) and their DFs ranged from 2.2 % (*Flexopecten glaber)* to 40.7 % *(Kurtiella bidentata).* In four of the abundant species at least one incomplete drill hole was detected (*Nucula cf. nucleus*, *Abra alba*, *Paphia rhomboids, Corbula gibba*). For these families, IDFs ranged from 0.6 % (*Paphia rhomboides*) to 6.5 % (*Corbula gibba*) and the PEs from 3.3 % (*Paphia rhomboides*) to 17.8 % (*Corbula gibba*).

Table 15: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Panzano M28

Panzano M28						
	n	D	ID	DF	IDF	PE
Species				(%)	(%)	(%)
Nuculana pella	68	9	0	13.2	0.0	0.0
Nucula cf. nuclaeus	160	29	2	18.1	1.3	6.5
Musculus subpictus	168	4	0	2.4	0.0	0.0
Flexopecten glaber	138	3	0	2.2	0.0	0.0
Ostrea sp.	76	6	0	7.9	0.0	0.0
Kurtiella bidentata	1,165	474	0	40.7	0.0	0.0
Acanthocardia paucicostata	159	6	0	3.8	0.0	0.0
Parvicardium exiguum	61	8	0	13.1	0.0	0.0
Abra alba	67	14	1	20.9	1.5	6.7
Abra nitida	352	27	0	7.7	0.0	0.0
Paphia rhomboides	158	29	1	18.4	0.6	3.3
Corbula gibba	1,029	309	67	30.0	6.5	17.8

Only one of the most abundant families (n > 50) from the Panzano M29 core never had drill holes (Ostreidae) (Table 16). Among families that were attacked, Corbulidae had the highest DF (31.9 %) and Crenellinae the lowest (2.9 %). Only one bivalve family from the Panzano M29 core had incomplete drill holes (Corbulidae). For Corbulidae the mean IDF was 9.8 % and PE 23.5 %.

Table 16: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Panzano M29

					Panzano M29			
Family	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Cardiidae	4	198	6	0	3.0	0.0	0.0
Corbulidae	1	824	263	81	31.9	9.8	23.5
Crenellinae	2	172	5	0	2.9	0.0	0.0
Montacutidae	3	863	294	0	34.1	0.0	0.0
Nuculanidae	1	62	3	0	4.8	0.0	0.0
Nuculidae	1	140	23	0	16.4	0.0	0.0
Ostreidae	1	54	0	0	0.0	0.0	0.0
Pectinidae	3	113	5	0	4.4	0.0	0.0
Semelidae	2	324	26	0	8.0	0.0	0.0
Veneridae	5	213	52	0	24.4	0.0	0.0

Except *Ostrea sp.* all of the abundant bivalve species (n > 50) from the Panzano M29 core contained drill holes (Table 17). Drilling frequencies ranged from 2.9 % (*Musculus subpictus*) to 34.4 % *(Kurtiella bidentata).* Only one species in the assemblage from the Panzano M29 core had incompletely perforated drill holes (*Corbula gibba*). Its IDF and PE were 9.5 % and 23.5 %.

Table 17: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Panzano M29

				Panzano M29		
Species	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Nuculana pella	62	3	0	4.8	0.0	0.0
Nucula cf. nuclaeus	140	23	0	16.4	0.0	0.0
Musculus subpictus	170	5	0	2.9	0.0	0.0
Flexopecten glaber	88	4	0	4.5	0.0	0.0
Ostrea sp.	54	0	0	0.0	0.0	0.0
Kurtiella bidentata	844	290	0	34.4	0.0	0.0
Acanthocardia paucicostata	124	2	0	1.6	0.0	0.0
Parvicardium exiguum	62	4	0	6.5	0.0	0.0
Abra alba	64	5	0	7.8	0.0	0.0
Abra nitida	256	21	0	8.2	0.0	0.0
Paphia rhomboides	161	40	0	24.8	0.0	0.0
Corbula gibba	824	263	81	31.9	9.8	23.5

All of the most abundant families (n > 50) from the Venice M38 core were drilled (Table 18). Lowest drilling frequencies occurred in Pectinidae (0.6 %) and highest in Hiatellidae (16.7 %). Only one incomplete drill hole was recovered, which was detected in Corbulidae. IDF and PE for Corbulidae were 1.0 % and 9.1 %, respectively.

Venice M38							
Family	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Anomidae	3	553	71	0	12.8	0.0	0.0
Cardiidae	7	611	6	0	1.0	0.0	0.0
Corbulidae	1	99	10	1	10.1	1.0	9.1
Crenellinae	2	107	4	0	3.7	0.0	0.0
Donacidae	1	280	2	0	0.7	0.0	0.0
Glycymerididae	2	124	9	0	7.3	0.0	0.0
Hiatellidae	1	54	9	0	16.7	0.0	0.0
Lucinidae	3	982	105	0	10.7	0.0	0.0
Mactridae	1	157	4	0	2.5	0.0	0.0
Pectinidae	3	357	2	0	0.6	0.0	0.0
Tellinidae	6	838	26	0	3.1	0.0	0.0
Thraciidae	1	164	2	0	1.2	0.0	0.0
Veneridae	10	467	19	0	4.1	0.0	0.0

Among the abundant bivalve species (n > 50) from the Venice M38 core, fourteen were drilled (Table 19). *Aequipecten opercularis* and *Anodontia fragilis* never had drill holes. Among species that were attacked, DFs ranged from 0.7 % (*Donax venustus)* to 16.7 % *(Hiatella arctica).* From the bivalve assemblage of the Venice M38 core, only *Corbula gibba* contained incompletely perforated drill holes. *Corbulas* IDF and PE were 1.0 % and 9.1 %.

Table 19: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Venice M38

Venice M38						
Species	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Glycymeris glycymeris	97	7	0	7.2	0.0	0.0
Aequipecten opercularis	249	0	0	0.0	0.0	0.0
Flexopecten glaber	85	2	0	2.4	0.0	0.0
Anomia cf. ephippium	508	64	0	12.6	0.0	0.0
Anodontia fragilis	75	0	0	0.0	0.0	0.0
Lucinella divaricata	892	105	0	11.8	0.0	0.0
Parvicardium scabrum	485	5	0	1.0	0.0	0.0
Spisula subtruncata	157	4	0	2.5	0.0	0.0
Moerella distorta	436	16	0	3.7	0.0	0.0
Tellina fabula	265	10	0	3.8	0.0	0.0
Donax venustus	280	2	0	0.7	0.0	0.0
Callista chione	195	4	0	2.1	0.0	0.0
Dosinia lupinus	155	9	0	5.8	0.0	0.0
Corbula gibba	99	10	1	10.1	1.0	9.1
Hiatella arctica	54	9	0	16.7	0.0	0.0
Thracia phaseolina	164	2	0	1.2	0.0	0.0

The assemblages from the two Po cores (M13 and M20) were both very small. Among the bivalves from Po 3 M13 only Corbulidae, Montacutidae contained more than 50 individuals (Table 20). Both of these families were drilled in M13 and had drilling frequencies from 1.8 % (Montacutidae) to 7.0 % (Corbulidae). The most abundant species among these families (*Kurtiella bidentata* and *Corbula gibba*) were the only drilled bivalves in M13 and had very similar DFs (Table 21). No incomplete drill holes were recorded in the assemblage from Po 3 M13. The most abundant families from Po 4 M20 were Corbulidae, Montacutidae and Pectinidae and among these families only Corbulidae had drill holes (Table 22). Among the Corbulidae only the species *Corbula gibba* was drilled, therefore DFs were nearly the same both on family and species level (14.0 %). Moreover, *Corbula gibba* was the only species with incomplete drill holes, and had an IDF of 1.6 % and a PE of 10.1 % (Table 23).

Table 20: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Po 3 M13

Po 3 M13						
Family	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Corbulidae	2	503	35	0	7.0	0.0	0.0
Montacutidae	3	114	2	0	1.8	0.0	0.0

Table 21: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Po 3 M13

Po 3 M13						
Species	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Kurtiella bidentata	107	2	0	1.9	0.0	0.0
Corbula gibba	498	35	0	7.0	0.0	0.0

Table 22: Mean DF, IDF and PE of the most abundant bivalve families (n > 50) from Po 4 M20

Po 4 M20						
Family	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Corbulidae	2	506	71	8	14.0	1.6	10.1
Montacutidae	2	133	0	0	0.0	0.0	0.0
Pectinidae	4	66	0	0	0.0	0.0	0.0

Table 23: Mean DF, IDF and PE of the most abundant bivalve species (n > 50) from Po 4 M20

Po 4 M20						
Species	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Kurtiella bidentata	126	0	0	0.0	0.0	0.0
Corbula gibba	505	71	8	14.1	1.6	10.1

6.4 Life habits and drilling predation

6.4.1 Feeding strategies

The five categories for bivalve feeding strategies are carnivores, chemosymbionts, commensals, deposit feeders and suspension feeders. In terms of number of species and individuals, the total bivalve fauna of all cores was strongly dominated by suspension feeders, followed by deposit feeders and commensals (Table 24). Chemosymbiotic bivalves accounted for 3.5 % of the total fauna, while carnivores were even rarer, represented by only 2 species. Mean DF across the total fauna was 18.0 %, in suspension feeders drilling intensities almost meet this average value with a mean DF of 18.3 %. In deposit feeders DF is lower (13.1 %) than in chemosymbiotic bivalves (14.2 %). Commensals and carnivores show the highest drilling intensities among the different feeding categories (24.3 % and 27.3 %), although the sample size of the carnivore bivalves was very low (n = 11). In carnivores no incomplete drill hole was found. Among the other feeding guilds, at least one incompletely perforated valve was recovered and IDFs ranged from 0.0 % (commensals) to 1.7 % (suspension feeders). Moreover, suspension feeders had the highest PE (8.6 %), followed by deposit feeders (3.7 %) and commensals had the lowest (0.1 %).

Table 24: Bivalve feeding strategies and drill hole data across the total fauna

Total fauna							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Carnivore	2	11	3	0	27.3	0.0	0.0
Chemosymbiotic	7	1,872	265	1	14.2	0.1	0.4
Commensal	10	4,130	1,005	1	24.3	0.0	0.1
Deposit feeding	20	6,701	879	34	13.1	0.5	3.7
Suspension feeding	81	41,288	7,576	709	18.3	1.7	8.6

Among the assemblage from the Brijuni M44 core, in terms of number of species and individuals, bivalves were also dominated by suspension feeders and deposit feeders (Table 25). Mean DF across the core was 15.2 %. In deposit feeders a higher DF was recorded (19.9 %), while in suspension feeders DF is distinctly lower (14.8 %). Highest drilling intensities were recorded in carnivores, which are, however, represented by very few individuals. Chemosybiotic bivalves had the lowest DF among the bivalve fauna from the Brijuni M44 core (5.3 %). Carnivores and commensals never had incomplete drill holes in the Brijuni core. In the other guilds, IDF ranged from 1.8 % (chemosymbiotics) to 3.8 % (suspension feeders). In chemosymbiotic bivalves the highest PE was recovered (25.0 %), while PE was significantly lower in deposit feeders (12.9 %).

Table 25: Bivalve feeding strategies and drill hole data from Brijuni M44 core

Brijuni M44							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Carnivore	2	7	3	0	42.9	0.0	0.0
Chemosymbiotic	4	57	3	1	5.3	1.8	25.0
Commensal	4	215	22	0	10.2	0.0	0.0
Deposit feeding	12	948	189	28	19.9	3.0	12.9
Suspension feeding	47	11,032	1,637	417	14.8	3.8	20.3

In both Piran cores (M1, M53), suspension feeders dominate the bivalve fauna, followed by deposit feeders (Table 26, 27). In M1 no carnivores were recorded. The mean DF across the core was 24.3 % in M53 and 18.1 % in M1. Chemosymbiotic bivalves in both Piran cores have similar DFs (18.8 % in M53 and 19.5 % in M1), while suspension feeders were more frequently drilled in M53 (25.4 %) than in M1 (19.7 %). In commensals from the Piran M53 core a mean DF of 21.7 % was recorded, which is significantly higher than the average DF of the other Piran core (7.1 %) or of the total fauna across all the cores (10.2 %). Among carnivores and commensal bivalves no incomplete drill holes were detected, while the other guilds contain at least one incompletely perforated valve. Both Piran cores had similar IDFs of 0.1 % in deposit feeders and commensals to 0.5 % (M1) and 0.7 % (M53) in suspension feeders. Highest PE was recorded for suspension feeders (2.7 % in M1 and 2.6 % in M53), while commensals and deposit feeders both had an effectiveness of 0.6 % against predators.

Table 26: Bivalve feeding strategies and drill hole data from Piran M1 core

Piran M1							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Carnivore	0	0	0	0	0.0	0.0	0.0
Chemosymbiotic	5	390	76	0	19.5	0.0	0.0
Commensal	8	437	31	0	7.1	0.0	0.0
Deposit feeding	10	1,737	169	1	9.7	0.1	0.6
Suspension feeding	50	12,116	2,386	66	19.7	0.5	2.7

Table 27: Bivalve feeding strategies and drill hole data from Piran M53 core

Piran M53							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Carnivore	1	1	0	0	0.0	0.0	0.0
Chemosymbiotic	6	409	77	0	18.8	0.0	0.0
Commensal	9	784	170	1	21.7	0.1	0.6
Deposit feeding	9	1,700	349	2	20.5	0.1	0.6
Suspension feeding	47	10,168	2,582	68	25.4	0.7	2.6

In terms of abundance, suspension feeding bivalves dominate the Panzano M28 core, followed by commensals (Table 28). Mean DF across the core was 23.8 %. Among the different feeding guilds, highest drilling frequencies were recorded in commensals (35.2 %) and lowest in deposit feeders (12.6 %). In carnivores, chemosymbiotic bivalves and commensals no incomplete drill holes were found. Most of the incompletely perforated drill holes were detected in suspension feeders, in which IDF reached 3.4 % and PE was 14.8 %. Deposit feeders had an IDF of 0.4 % and effectiveness against predators was also significantly lower than in suspension feeding bivalves (3.4 %).

Table 28: Bivalve feeding strategies and drill hole data from Panzano M28 core

Panzano M28							
Feeding strategies	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Carnivore	1	1	0	0	0.0	0.0	0.0
Chemosymbiotic	2	18	3	0	16.7	0.0	0.0
Commensal	4	1,358	478	0	35.2	0.0	0.0
Deposit feeding	7	688	87	3	12.6	0.4	3.4
Suspension feeding	30	1,976	391	68	19.8	3.4	14.8

With respect to feeding categories the composition of the bivalve assemblage of the second Panzano core (M29) is rather similar to M28. In M29 suspension feeders and commensals also dominate the bivalve fauna (Table 29). Mean DF across the core was 21.8 %. In carnivores no drill holes were recovered. The highest DF (28.9 %) was recorded in commensals, which was still more than 6 % lower than in commensals from the Panzano M28 core (35.2 %). In the other guilds, drilling intensities were very similar to the results of M28. In deposit feeders the lowest DF was computed (10.3 %). Incomplete drill holes were found only among suspension feeders, which had an IDF of 5.2 % and a PE of 19.7 %.

Table 29: Bivalve feeding strategies and drill hole data from Panzano M29 core

Panzano M29							
Feeding strategies	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Carnivore	1	2	0	0	0.0	0.0	0.0
Chemosymbiotic	1	7	1	0	14.3	0.0	0.0
Commensal	4	1,033	299	0	28.9	0.0	0.0
Deposit feeding	5	555	57	0	10.3	0.0	0.0
Suspension feeding	28	1,559	331	81	21.2	5.2	19.7

In Venice M38 suspension feeders strongly dominate, followed by chemosymbiotic bivalves and deposit feeders (Table 30). The Venice M38 core did not contain carnivores. Mean DF across the core was very low with 5.4 %. Chemosymbiotic bivalves had the highest DF (10.7 %) among the feeding guilds, while the lowest DF (2.8 %) was recorded in deposit feeders.

Incomplete drill holes were only found in suspension feeders, in which IDF was only slightly above 0 % and the effectiveness against predators was 0.7 %.

Table 30: Bivalve feeding strategies and drill hole data from Venice M38 core

Venice M38							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Carnivore	0	0	0	0	0.0	0.0	0.0
Chemosymbiotic	3	982	105	0	10.7	0.0	0.0
Commensal	6	48	3	0	6.3	0.0	0.0
Deposit feeding	11	952	27	0	2.8	0.0	0.0
Suspension feeding	45	3,089	138	1	4.5	0.0	0.7

The bivalve fauna of both Po cores (M13, M20) was dominated by suspension feeders, followed by commensals. Carnivores were not found among the bivalves of the Po cores and chemosymbiotics were very rare (Table 31, 32). Mean DF across the Po 3 M13 core was 4.6 %. Chemosymbiotic bivalves in this core did not contain drill holes, while in the other guilds at least one drill hole was recovered. DFs range from 1.7 % in commensals to 5.4 % in suspension feeders. No incomplete drill hole was found among the total bivalve fauna of the M13 core.

Table 31: Bivalve feeding strategies and drill hole data from Po 3 M13 core

Po 3 M13							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF (%)**	**IDF (%)**	**PE (%)**
Carnivore	0	0	0	0	0.0	0.0	0.0
Chemosymbiotic	1	7	0	0	0.0	0.0	0.0
Commensal	4	117	2	0	1.7	0.0	0.0
Deposit feeding	4	55	1	0	1.8	0.0	0.0
Suspension feeding	18	670	36	0	5.4	0.0	0.0

The mean DF across the Po 4 M20 core was higher (8.5 %) than in the other core from the Po delta (M13). Among the feeding guilds of the bivalves from the Po 4 M20 core, only suspension feeders contain drill holes (Table 32). Their drilling frequency was 11.1 %. Incompletely perforated drill holes were recovered only in suspension feeders, which had an IDF of 1.2 % and a PE of 9.6 %.

Po 4 M20							
Feeding strategies	**S**	**n**	**D**	**ID**	**DF** (%)	**IDF** (%)	**PE** (%)
Carnivore	0	0	0	0	0.0	0.0	0.0
Chemosymbiotic	1	2	0	0	0.0	0.0	0.0
Commensal	3	138	0	0	0.0	0.0	0.0
Deposit feeding	5	66	0	0	0.0	0.0	0.0
Suspension feeding	20	678	75	8	11.1	1.2	9.6

6.4.2 Substrate relationships and mobility

The six substrate relationship categories are borer, commensals, epifaunal bivalves, infaunal bivalves, nestler and semiinfaunal bivalves. In terms of number of species and individuals, the total bivalve fauna across all 8 cores was strongly dominated by infaunal bivalves, followed by epifaunal and commensal taxa (Table 33). Among the very rare semiinfaunal bivalves (e.g. *Diplodonta*) no drill holes were found, while in all the other groups referring to substrate relationships drill holes were recovered. In the groups, which were attacked, DFs range from 2.3 % in the rare borers to 24.3 % in commensals. Infaunal bivalves had higher DFs (19.5 %) than epifaunal taxa (11.6 %). Among nestler and semiinfaunal bivalves no incomplete drill holes were detected, while the other groups contained at least one. IDFs range from slightly above 0 % in commensals to 3.4 % in epifaunal taxa. The lowest PE was recorded in commensals, while among borers the effectiveness against predators was 25.0 %. Moreover, epifaunal bivalves had a much high PE (22.6 %) than infaunal taxa (4.5 %).

Referring to the epifaunal attachment categories of the examined bivalves, most individuals were recliners or lived bysally attached to the substrate (e.g. rocks) in their marine environments. In all four groups of epifaunal attachment drill holes were recovered. The highest drilling frequencies were recorded in bysally attached bivalves (19.0 %) and recliners (18.5 %), while in cemented bivalves (e. g. *Ostrea*) DF was significantly lower (9.3 %). The lowest DF (5.4 %) was evaluated for bivalves which can change their epifaunal attachment and live either bysally attached or reclining. IDFs were lowest in cemented taxa (0.1 %) and highest in bysally attached bivalves (3.4 %). PE ranged from 0.6 % in cemented bivalves to 15.1 % in bysally attached taxa. Concerning the mobility categories among bivalves, the assemblage was divided into actively mobile, facultatively mobile and immobile taxa. In terms of number of species and individuals, the total bivalve fauna was dominated by facultatively mobile taxa, followed by actively mobile bivalves. The highest DFs were recorded in facultatively mobile bivalves (20.4 %), while in actively mobile taxa only 11.3 % were drilled. All groups contained incomplete drill holes and their IDFs ranged from 0.2 % in immobile bi-

valves to 1.9 % in facultatively mobile taxa. Effectiveness against predators was highest in facultatively mobile bivalves (8.3 %) and lowest in immobile taxa (1.2 %).

Total fauna							
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Substrate relationships							
Borer	4	131	3	1	2.3	0.8	25.0
Commensal	11	4,131	1,005	1	24.3	0.0	0.1
Epifaunal	23	11,789	1,362	398	11.6	3.4	22.6
Infaunal	69	37,614	7,348	345	19.5	0.9	4.5
Nestler	9	261	10	0	3.8	0.0	0.0
Semiinfaunal	4	76	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	29	20,234	3,849	682	19.0	3.4	15.1
Cemented	4	1,880	174	1	9.3	0.1	0.6
Recliner	73	30,462	5,628	53	18.5	0.2	0.9
Recliner/Bysally	14	1,426	77	10	5.4	0.7	11.5
Mobility							
Actively mobile	44	11,402	1,294	45	11.3	0.4	3.4
Facultatively mobile	65	37,249	7,603	691	20.4	1.9	8.3
Immobile	11	5,351	831	10	15.5	0.2	1.2

In terms of number of species and individuals, the bivalve assemblage from Brijuni M44 core was also dominated by infaunal taxa, followed by epifaunal bivalves (Table 34). Not considering the very rare semiinfaunal bivalves, which did not contain any drill holes, DFs ranged from 5.3 % in nestlers to 15.6 % in infaunal taxa. Epifaunal bivalves had slightly lower DFs (15.0 %) than infaunal, but significantly higher DFs than commensals and borers (10.2 % and 8.3 %, respectively). The highest IDF was recorded in epifaunal bivalves (7.4 %), while commensals, nestler and semiinfaunal taxa never had incomplete drill holes among the assemblage from Brijuni M44. The lowest IDF occurred for infaunal taxa (0.8 %). The highest PEs were recovered in the relatively rare borers (33.3 %), but their effectiveness against predators did not significantly differ to that of epifaunal bivalves (32.9 %). The infaunal taxa had the lowest PE (4.8 %).

Most of the epifaunal bivalves from the M44 core were represented by reclining or bysally attached taxa. Among epifaunal attachment categories, highest DFs were detected in cemented bivalves (19.5 %). In bysally attached and reclining taxa DFs did not differ strongly (15.7 % and 15.1 %). Most of the incomplete drill holes were found in bysally attached bivalves, which had an IDF of 7.5 % and a PE of 32.3 %. In the cemented bivalves from the M44

core no incomplete drill holes were recorded. Among the attachment groups with incomplete drill holes, reclining bivalves had the lowest IDFs and PE (0.6 % and 4.1 %, respectively).

In terms of number of species and individuals, the facultatively mobile taxa dominated the bivalve fauna of Brijuni M44. In immobile bivalves DFs (26.4 %) were significantly higher than in facultatively (12.5 %) and actively mobile taxa (15.0 %). Most of the incomplete drill holes were detected in facultatively mobile bivalves, which had an average IDF of 4.7 % and a PE of 27.1 %. Significantly lower IDFs and PEs were evaluated for immobile bivalves (0.3 % and 1.1 %) and actively mobile taxa (2.4 % and 13.9 %, respectively).

Table 34: Comparison of DF, IDF and PE across ecological categories from Brijuni M44 core

Brijuni M44							
	S	n	D	ID	DF	IDF	PE
Substrate relationships					(%)	(%)	(%)
Borer	3	24	2	1	8.3	4.2	33.3
Commensal	5	216	22	0	10.2	0.0	0.0
Epifaunal	20	5,323	800	393	15.0	7.4	32.9
Infaunal	35	6,543	1,022	52	15.6	0.8	4.8
Nestler	4	151	8	0	5.3	0.0	0.0
Semiinfaunal	2	2	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	18	5,302	834	398	15.7	7.5	32.3
Cemented	3	267	52	0	19.5	0.0	0.0
Recliner	38	6,080	919	39	15.1	0.6	4.1
Recliner/Bysally	10	610	49	10	8.0	1.6	16.9
Mobility							
Actively mobile	26	1,618	242	39	15.0	2.4	13.9
Facultatively mobile	35	8,642	1,084	402	12.5	4.7	27.1
Immobile	8	1,999	528	6	26.4	0.3	1.1

Infaunal bivalves strongly dominate the assemblage from Piran M1 in terms of number of species and individuals (Table 35). The second largest group in terms of abundance were epifaunal taxa. The relatively rare borers and semiinfaunal bivalves had no drill holes. In the groups which were attacked, drilling frequencies ranged from 2.6 % in nestlers to 21.5 % in infaunal bivalves. Epifaunal and commensal taxa from the Piran M1 core showed significantly lower DFs of 4.4 % and 7.1 %. Incomplete drill holes were recorded only in infaunal and epifaunal bivalves among the Piran M1 core. Infaunal taxa had IDFs of 0.6 % and PE of 2.5 %, while in epifaunal bivalves from Piran M1 IDF and PE were lower (0.1 % and 1.9 %, respectively).

Referring to the epifaunal attachment categories, reclining taxa dominate the bivalve fauna from the Piran M1 core, followed by bysally attached and cemented taxa. Recliners had significantly higher DFs (21.8 %) than bysally attached taxa (13.5 %). In cemented bivalves very low DFs (5.3 %) were recognized among the Piran M1 core. Incomplete drill holes were found in recliners and bysally attached taxa. While DFs and PE were only slightly above 0 % in recliners, bysally attached bivalves had IDFs of 1.7 % and PE of 11.0 %. In terms of abundance, most of the bivalves from the assemblage of Piran M1 belong to facultatively mobile taxa. Referring to mobility categories, DFs ranged from 5.5 % in immobile to 22.1 % in facultative mobile taxa. Actively mobile bivalves from the Piran M1 core had DFs of 10.0 %.

Table 35: Comparison of DF, IDF and PE across ecological categories from Piran M1 core

Piran M1							
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Substrate relationships							
Borer	1	54	0	0	0.0	0.0	0.0
Commensal	8	437	31	0	7.1	0.0	0.0
Epifaunal	20	2,390	104	2	4.4	0.1	1.9
Infaunal	39	11,746	2,526	65	21.5	0.6	2.5
Nestler	2	39	1	0	2.6	0.0	0.0
Semiinfaunal	3	14	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	24	3,795	511	63	13.5	1.7	11.0
Cemented	3	1,076	57	0	5.3	0.0	0.0
Recliner	40	9,604	2,090	4	21.8	0.0	0.2
Recliner/Bysally	6	205	4	0	2.0	0.0	0.0
Mobility							
Actively mobile	23	2,571	257	1	10.0	0.0	0.4
Facultatively mobile	41	10,488	2,316	64	22.1	0.6	2.7
Immobile	9	1,621	89	2	5.5	0.1	2.2

Similar to the other Piran core, the assemblage from Piran M53 was also dominated by infaunal bivalves, followed by epifaunal taxa and commensals (Table 36). Borers, nestler and semiinfaunal bivalves were relatively rare in this core (M53). Among the semiinfaunal bivalves no drill holes were detected, while in all other groups at least one drill hole was recorded. In the attacked groups, DFs ranged from 2.6 % in borers to 26.7 % in infaunal taxa. Commensals had higher DFs (21.7 %) than epifaunal bivalves (15.4 %), the next lowest category. Nestlers had very low DFs of 3.1 %. In infaunal, epifaunal and commensal taxa at least one incomplete drill hole was recovered. In these groups, IDFs range from 0.1 % in commensals and epifaunal bivalves to 0.7 % in infaunal taxa. PE was lowest in commensals (0.6 %) and highest in infaunal bivalves (2.5 %).

Referring to epifaunal attachment categories, the bivalve assemblage from Piran M53 was also dominated by reclining and bysally attached bivalves, which showed high DFs of 26.0 % and 20.0 %. In cemented taxa significantly lower DFs were recognized (11.1 %). Bysally attached, cemented and reclining taxa all contained at least one incomplete drill hole. IDFs ranged from 0.1 % in recliners to 1.4 % in bysally attached bivalves. Effectiveness against predators was about 0 % in cemented and reclining taxa and reached 4.9 % in bysally attached bivalves.

Regarding to mobility categories, in terms of number of species and individuals, facultatively mobile bivalves dominated also the assemblage from Piran M53. Immobile taxa showed lower DFs (15.4 %) than actively mobile bivalves (19.0 %). In facultatively mobile taxa the highest DFs were detected (26.5 %). Incomplete drill holes were found in taxa of all mobility groups. In actively mobile taxa IDF and PE (0.1 % and 0.4 %) were lower than in immobile bivalves (0.3 % and 1.7 %), while facultatively mobile taxa showed highest IDFs and PE (0.7 % and 2.5 %).

Table 36: Comparison of DF, IDF and PE across ecological categories from Piran M53 core

Piran M53							
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Substrate relationships							
Borer	2	38	1	0	2.6	0.0	0.0
Commensal	9	784	170	1	21.7	0.1	0.6
Epifaunal	16	2,239	345	3	15.4	0.1	0.9
Infaunal	40	9,951	2,661	67	26.7	0.7	2.5
Nestler	2	32	1	0	3.1	0.0	0.0
Semiinfaunal	3	18	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	23	4,527	943	64	20.0	1.4	4.9
Cemented	3	386	56	1	11.1	0.3	0.0
Recliner	42	8,018	2,159	6	26.0	0.1	0.1
Recliner/Bysally	4	131	20	0	10.0	0.0	0.0
Mobility							
Actively mobile	22	2,611	495	2	19.0	0.1	0.4
Facultatively mobile	41	9,699	2,567	67	26.5	0.7	2.5
Immobile	9	752	116	2	15.4	0.3	1.7

In terms of abundance, infaunal taxa dominated the bivalve assemblage from the Panzano M28 core, followed by commensals (Table 37). Borers, nestler and semiinfaunal taxa were relatively rare and did not contain any drill holes. Commensals had higher DFs (35.2 %) than infaunal taxa (20.2 %) and that of epifaunal bivalves was distinctly lower (4.5 %). Incomplete-

ly perforated drill holes were recorded only in infaunal taxa, in which IDF reached 3.1 % and PE was 13.3 %.

Concerning epifaunal attachment categories, bysally attached bivalves dominated the assemblage from the Panzano M28 core in terms of abundance. Lowest DFs of 5.6 % were evaluated for taxa which can live bysally attached or reclining. In cemented bivalves lower DFs (7.3 %) were recognized than in reclining taxa (11.2 %) and highest DFs were recovered in bysally attached bivalves (31.7 %). In cemented taxa no incomplete drill hole was detected, while most of these unsuccessful predation attempts were recorded in bysally attached bivalves, in which IDF reached 2.7 % and PE was 7.8 %. In reclining taxa from the Panzano M28 core lower IDFs and PE were recovered (0.3 % and 2.5 %).

Regarding to the mobility categories of bivalves, similar to the other cores, facultatively mobile taxa dominate also the bivalves from Panzano M28 core in terms of number of species and individuals. And similar to the results from the two Piran cores, highest DFs were evaluated for the facultatively mobile bivalves (28.9 %). Among the assemblage from M28 immobile taxa had lower DFs (5.3 %) than actively mobile bivalves (10.7 %). Incomplete drill holes were detected only in actively and facultatively mobile bivalves, with IDFs of 0.3 % and 2.3 %, respectively. Moreover, PE was higher in facultatively mobile bivalves (7.4 %) than in actively mobile taxa (3.1 %).

Table 37: Comparison of DF, IDF and PE across ecological categories from Panzano M28 core

Panzano M28							
	S	**n**	**D**	**ID**	**DF**	**IDF**	**PE**
Substrate relationships					(%)	(%)	(%)
Borer	1	2	0	0	0.0	0.0	0.0
Commensal	4	1,358	478	0	35.2	0.0	0.0
Epifaunal	9	379	17	0	4.5	0.0	0.0
Infaunal	26	2,294	464	71	20.2	3.1	13.3
Nestler	2	3	0	0	0.0	0.0	0.0
Semiinfaunal	2	5	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	11	2,501	792	67	31.7	2.7	7.8
Cemented	1	82	6	0	7.3	0.0	0.0
Recliner	27	1,405	158	4	11.2	0.3	2.5
Recliner/Bysally	5	53	3	0	5.6	0.0	0.0
Mobility							
Actively mobile	15	897	96	3	10.7	0.3	3.1
Facultatively mobile	23	2,957	853	68	28.9	2.3	7.4
Immobile	6	187	10	0	5.3	0.0	0.0

Similar to the other Panzano core (M28), the assemblage from Panzano M29 was also dominated by infaunal and commensal bivalves (Table 38). Borers were not found, nestling and semiinfaunal bivalves were relatively rare and had no drill holes. All other groups contained drill holes. In the attacked groups, DFs ranged from 4.1 % in epifaunal to 28.9 % in commensal taxa. Similar to M28, the infaunal bivalves from M29 had lower DFs (20.3 %) than commensals. As well as in M28, also among the second Panzano core incomplete drill holes were recovered only in infaunal taxa. Their IDFs reached 4.3 % and mean PE was 17.6 %.

Referring to epifaunal attachment categories, the bivalve assemblage from Panzano M29 was also dominated by bysally attached and reclining bivalves. While in the relatively rare cemented bivalves no drill holes were detected, in all other groups at least one drill hole was recognized. Of the two most abundant groups, bysally attached bivalves had significantly higher DFs (29.3 %) than recliners (10.6 %). Similar results are seen in the other Panzano core. Incomplete drill holes were found only among bysally attached taxa, in which IDFs of 4.2 % and PE of 12.5 % were calculated.Regarding mobility categories, in terms of number of species and individuals, facultatively mobile bivalves strongly dominated also the assemblage from Panzano M29. Relatively rare immobile taxa showed the lowest DFs (3.8 %). Actively mobile bivalves were the next-highest category with DFs of 9.2 %. In facultatively mobile taxa the highest DFs were detected (26.5 %). Incomplete drill holes were found only in facultatively mobile taxa, in which IDFs of 3.5 % were recorded and PE reached 11.6 %.

Table 38: Comparison of DF, IDF and PE across ecological categories from Panzano M29 core

Panzano M29							
	S	**n**	**D**	**ID**	**DF**	**IDF**	**PE**
Substrate relationships					**(%)**	**(%)**	**(%)**
Borer	0	0	0	0	0.0	0.0	0.0
Commensal	4	1,033	299	0	28.9	0.0	0.0
Epifaunal	9	246	10	0	4.1	0.0	0.0
Infaunal	24	1,869	379	81	20.3	4.3	17.6
Nestler	1	5	0	0	0.0	0.0	0.0
Semiinfaunal	1	3	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	10	1,936	567	81	29.3	4.2	12.5
Cemented	1	54	0	0	0.0	0.0	0.0
Recliner	24	1,133	120	0	10.6	0.0	0.0
Recliner/Bysally	4	33	1	0	3.0	0.0	0.0
Mobility							
Actively mobile	12	687	63	0	9.2	0.0	0.0
Facultatively mobile	22	2,338	620	81	26.5	3.5	11.6
Immobile	5	131	5	0	3.8	0.0	0.0

In terms of number of species and individuals, infaunal taxa dominated the bivalve assemblage from the Venice M38 core, followed by epifaunal taxa; semiinfaunal bivalves were not found (Table 39). Borer, nestler and commensals were relatively rare in this assemblage (M38) and nestler and borer did not contain any drill holes. Mean DFs were very low in the Venice M38 core (5.4 %). Among the attacked groups DFs ranged from 4.7 % in infaunal to 7.9 % in epifaunal taxa. In commensals DFs were slightly lower than in epifaunal bivalves (6.1 %). Incomplete drill holes were very rare in the assemblage from M38 and only found among infaunal taxa, with IDF only slightly above 0 % and PE of 0.5 %.

Concerning epifaunal attachment categories, reclining bivalves strongly dominated the assemblage from the Venice M38 core in terms of abundance, followed by bysally attached taxa. No drill holes were recovered in taxa which can live bysally attached or reclining. In the relatively rare cemented bivalves higher DFs (23.1 %) were recognized than in bysally attached taxa (10.6 %). Lowest DFs were evaluated for reclining bivalves (4.5 %). Incomplete drill holes were detected only in bysally attached bivalves, in which IDF reached 0.1 % and PE was 1.0 %.

Regarding mobility categories of bivalves, similar to the other cores, facultatively mobile taxa dominated the bivalve assemblage from Venice M38 core in terms of number of species. However, in terms of abundance the actively mobile bivalve dominated the assemblage of M38. Immobile forms had significantly higher DFs (13.1 %) than actively mobile bivalves (5.1 %), while in facultatively mobile taxa the lowest DFs (3.0 %) were found. Incomplete drill holes were recovered only in facultatively mobile bivalves, with IDF of 0.1 % and PE of 2 %.

Table 39: Comparison of DF, IDF and PE across ecological categories fromVenice M38 core

Venice M38						
	S	n	D	ID	DF	IDF	PE
Substrate relationships					(%)	(%)	(%)
Borer	1	13	0	0	0.0	0.0	0.0
Commensal	6	48	3	0	6.3	0.0	0.0
Epifaunal	15	1,084	86	0	7.9	0.0	0.0
Infaunal	41	3,896	184	1	4.7	0.0	0.5
Nestler	2	30	0	0	0.0	0.0	0.0
Semiinfaunal	0	0	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	19	883	94	1	10.6	0.1	1.0
Cemented	1	13	3	0	23.1	0.0	0.0
Recliner	41	3,873	176	0	4.5	0.0	0.0
Recliner/Bysally	4	302	0	0	0.0	0.0	0.0
Mobility							
Actively mobile	21	2,758	140	0	5.1	0.0	0.0
Facultatively mobile	38	1,680	50	1	3.0	0.1	2.0
Immobile	6	633	83	0	13.1	0.0	0.0

In terms of abundance, infaunal taxa dominated the bivalve assemblage from both Po cores (M13, M20), followed by commensals (Table 40). The Po 3 M13 core did not contain any borers and nestlers were very rare. Drill holes were recovered only in the two most abundant groups from M13. Of these two attacked groups, DFs were higher in infaunal taxa (5.7 %) than in commensals (1.7 %). No incomplete drill holes were detected among the bivalve assemblage from M13.

Concerning epifaunal attachment categories, bysally attached bivalves strongly dominated the assemblage from Po 3 M13 core in terms of abundance, followed by recliners. No drill holes were recorded in the rare cementers or in taxa which can live bysally attached or as recliners. In bysally attached taxa higher DFs (5.9 %) were recognized than in reclining bivalves (1.2 %). Referring to the mobility categories of bivalves, facultatively mobile taxa dominated the bivalve assemblage from Po 3 M13 in terms of number of species and individuals. In the relatively rare immobile forms no drill holes were found. Moreover, facultatively mobile bivalves had higher DFs (5.3 %) than actively mobile bivalves (0.8 %) in M13.

Table 40: Comparison of DF, IDF and PE across ecological categories from Po 3 M13 core

Po 3 M13						
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Substrate relationships							
Borer	0	0	0	0	0.0	0.0	0.0
Commensal	4	117	2	0	1.7	0.0	0.0
Epifaunal	5	46	0	0	0.0	0.0	0.0
Infaunal	15	652	37	0	5.7	0.0	0.0
Nestler	1	1	0	0	0.0	0.0	0.0
Semiinfaunal	2	33	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	8	631	37	0	5.9	0.0	0.0
Cemented	1	1	0	0	0.0	0.0	0.0
Recliner	15	168	2	0	1.2	0.0	0.0
Recliner/Bysally	3	49	0	0	0.0	0.0	0.0
Mobility							
Actively mobile	9	125	1	0	0.8	0.0	0.0
Facultatively mobile	15	712	38	0	5.3	0.0	0.0
Immobile	3	12	0	0	0.0	0.0	0.0

Similar to the other Po core (M13), the assemblage from Po 4 M20 was also dominated by infaunal and commensal bivalves (Table 41). Borers and nestlers were not found among the M20 core and semiinfaunal bivalves were very rare. Concerning substrate relationship categories, only the infaunal taxa contained drill holes and their DFs reached 11.3 %. Moreover,

incomplete drill holes were discovered also only among infaunal taxa, in which IDFs of 1.2 % and PE of 9.6 % was recorded.

Referring to epifaunal attachment categories, the bivalve assemblage from Po 4 M20 was also dominated by bysally attached and reclining bivalves. Only in these two abundant drill holes were recognized and bysally attached bivalves had significantly higher DFs (10.8 %) than recliners (2.2 %). Incomplete drill holes were found only among bysally attached taxa, with IDFs of 1.2 % and PE of 10.1 %.

Regarding mobility categories, in terms of number of species and individuals, facultatively mobile bivalves strongly dominated also the assemblage from Po 4 M20. Moreover, only in this group, complete and incomplete drill holes were found. Drilling frequency reached 10.2 %, while IDFs and PE of the facultatively mobile bivalves was 1.1 % and 9.6 %, respectively.

Table 41: Comparison of DF, IDF and PE across ecological categories from Po 4 M20 core

Po 4 M20							
	S	n	D	ID	DF (%)	IDF (%)	PE (%)
Substrate relationships							
Borer	0	0	0	0	0.0	0.0	0.0
Commensal	3	138	0	0	0.0	0.0	0.0
Epifaunal	8	82	0	0	0.0	0.0	0.0
Infaunal	17	663	75	8	11.3	1.2	9.6
Nestler	0	0	0	0	0.0	0.0	0.0
Semiinfaunal	1	1	0	0	0.0	0.0	0.0
Epifaunal attachment							
Bysally	8	659	71	8	10.8	1.2	10.1
Cemented	1	1	0	0	0.0	0.0	0.0
Recliner	18	181	4	0	2.2	0.0	0.0
Recliner/Bysally	2	43	0	0	0.0	0.0	0.0
Mobility							
Actively mobile	11	135	0	0	0.0	0.0	0.0
facultatively mobile	14	733	75	8	10.2	1.1	9.6
Immobile	4	16	0	0	0.0	0.0	0.0

6.7 Diversity and predation intensities

At standardized sample size, the assemblages from the Po cores (M13, M20) showed the lowest and the assemblages from the Piran (M1, M53) and Brijuni M44 the highest species diversities of the sampling sites (Fig. 41-42).
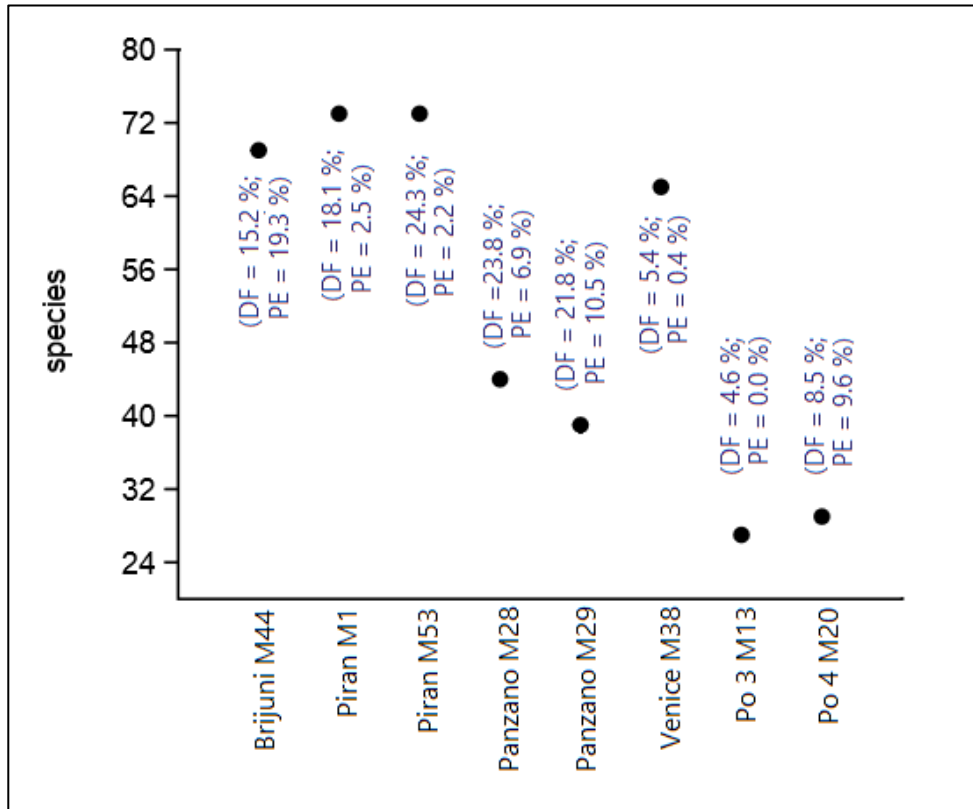
Fig. 41: Species diversities of the sampling locations and drilling data (DF, PE)

The rarefaction curves in Fig. 42 a) and b) show that all cores contain relatively high numbers of species with only few individuals. Fig. 42 a) demonstrates that the two cores from Piran (M1, M53) and from Brijuni (M44) had similar high diversities, sample sizes and relatively high DFs. Venice M38 shows a high diversity and a moderate number of bivalves, but very low DFs and PE. The rarefaction trends for the Po cores (M13, M20) reflect the lowest diversities, smallest assemblage size and lowest diversities among the sampling sites. The curves for Panzano M28 and M29 demonstrate moderate diversities and sample sizes and had the highest DFs of all the cores. Fig. 42 b) provides a detailed view into the rarefaction trends of the cores.
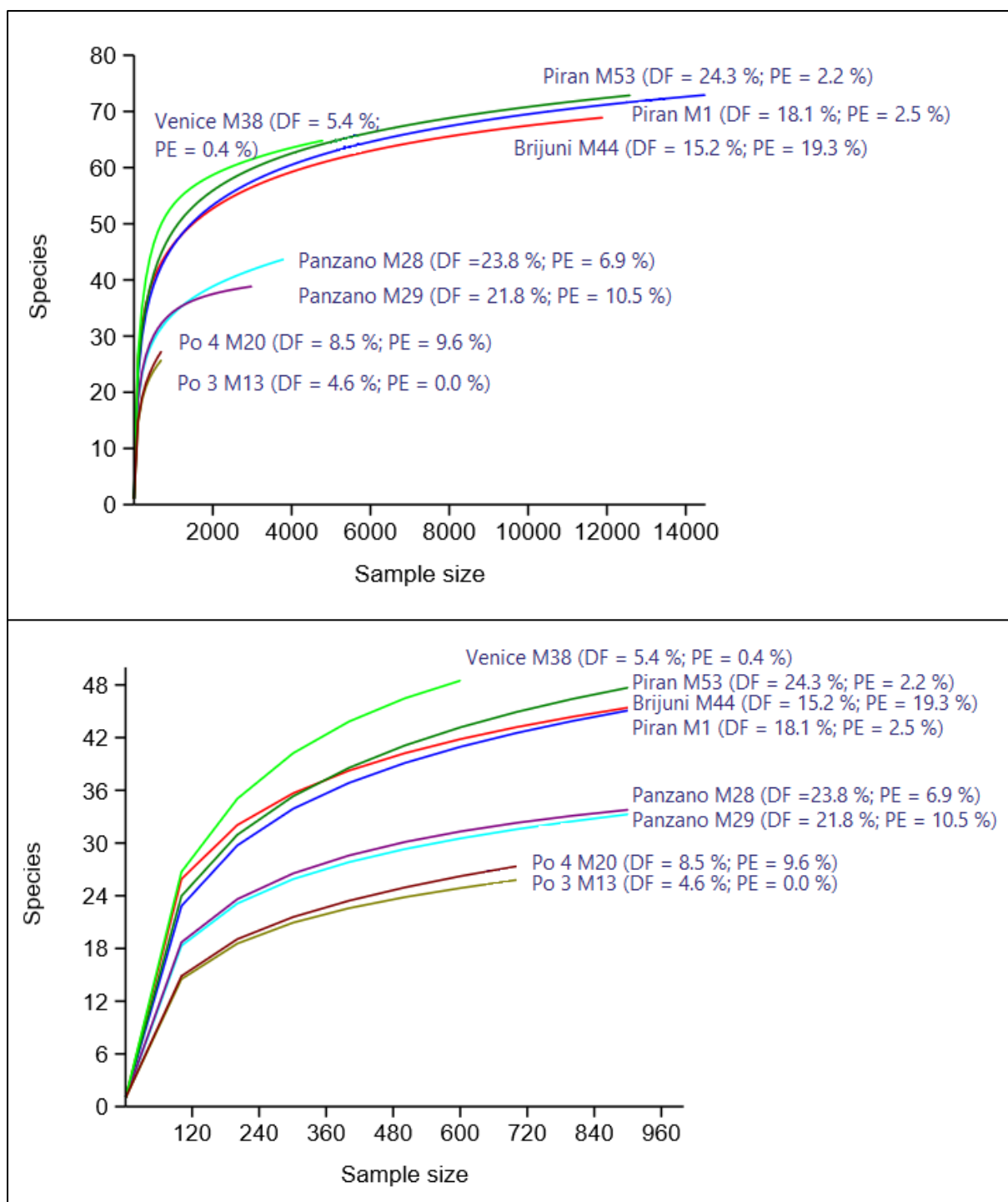
Fig. 42: Rarefaction curves of all cores with drilling data (DF, PE) a) max. sample size = 14.000;
  b) max. sample size = 1000

Mean DFs and PE of all cores were tested for correlations with following diversity indices:
Simpson's diversity, Shannon-Wiener diversity, Margalef's Richness and Fischer's alpha. In
several cores (Brijuni M44, Piran M1, M53, Po 3 M13 and Po 4 M20) the average DFs corre-
lated with measures of diversity, but for other cores (Venice M38, Panzano M28, M29) cor-
relations completely failed.

The Shannon-Wiener Index (Fig. 43) is a measure of evenness of the assemblages from the eight sampling sites. Fig. 43 demonstrates that evenness and drilling frequencies correlate in the cores from Brijuni M44, Piran M1 and M53 and the two Po cores (M13, M20). But in the Panzano cores (M28 and M29) and in Venice M38 DFs and evenness did not agree.
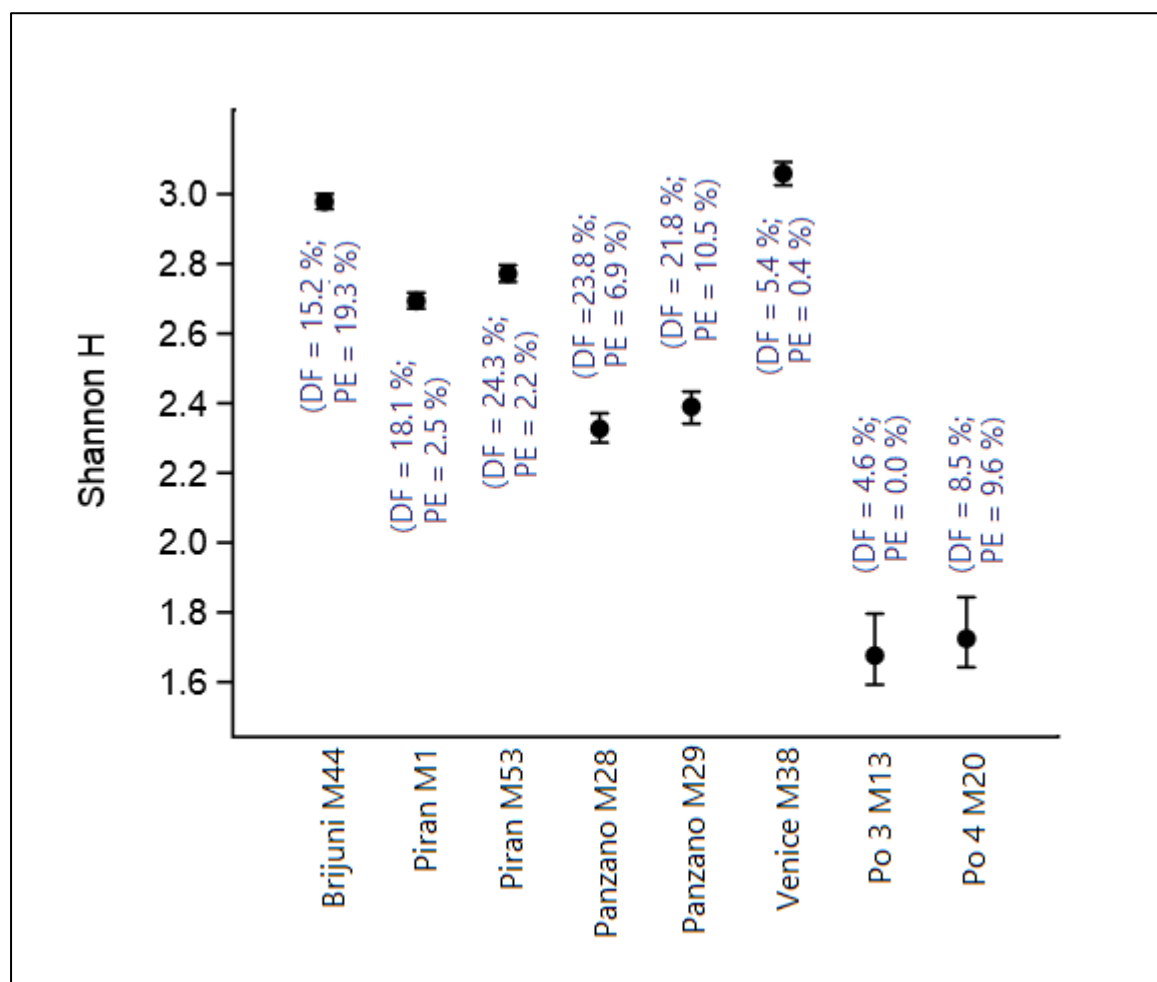
Fig. 43: Comparison of Shannon-Wiener Index of all cores with drilling data (DF, RE)

The Margalef Index (Fig. 44) is a measure of species richness of the assemblages from the eight sediment cores. Fig. 44 reflects similar results as the Shannon-Wiener index. Species richness correlates with drilling intensities in the cores from Brijuni M44, Piran M1 and M53 and Po M13 and M20, but for Venice M38 and the Panzano cores (M28, M29) correlations failed.
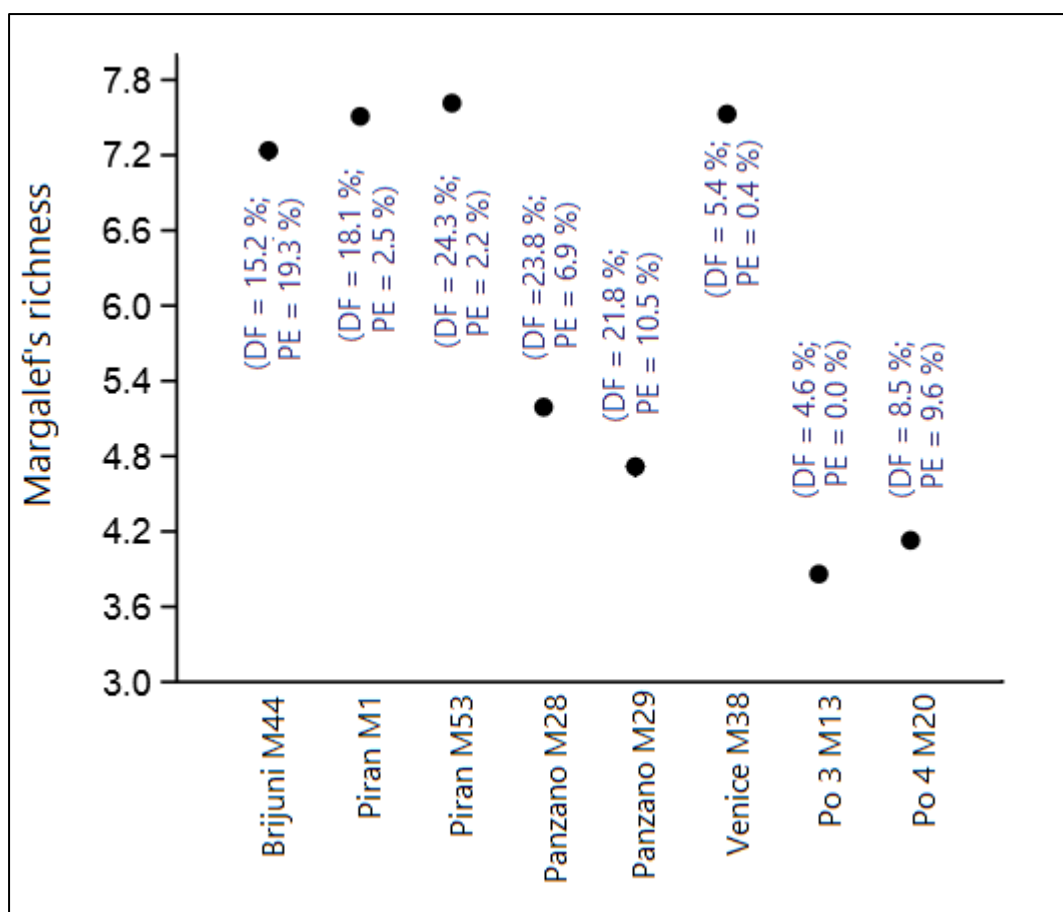
Fig. 44: Comparison of Margalef Index of all cores with drilling data (DF, PE)

Moreover, DFs correlated negatively with dominance. The DFs of the most abundant species of each core did sometimes, but not always correlate with that species' abundance. For instance, in Brijuni M44 the second most abundant species was *Striarca lactea*, which had a mean DF of only 5.0 %.

7 Discussion

7.1 Predation increase through time (along the core) due to increased nutrient input

During the Mesozoic several marine ecosystems changed fundamentally. McKinney and Hageman (2007) suggest a profound change in the dominance of life habits in the marine fauna, from sedentary, epibenthic suspension-feeding communities of the Paleozoic to endobenthic modern communities. One hypothesized reason for this transformation in marine ecosystems may be an increase of nutrients, from oligotrophic (low-nutrient) Paleozoic seas to more nutrient-rich (eutrophic) conditions on and within the modern sea floor (Vermeij, 1987; Bambach, 1983, 1999). The Northern Adriatic with its shallow and flat sedimentary sea floor provides ideal localities to test ecosystem modifications. Its long history of intense human impacts, e.g. pollution of main tributaries (Po River) led to eutrophication and intense fishery, including bottom trawling, strongly affected benthic invertebrate communities (Franceschini et al., 1999, Thrush and Dayton, 2002). The northern Adriatic Sea hosts both types of soft-bottom benthic communities, "Paleozoic" epifaunal and "modern" infaunal-dominated (Sepkoski, 1981). Therefore this marine basin is a "living laboratory" for palaeobiological approach. Sedimentation rate, sediment type and particularly nutrient content are variables which influence ecological changes towards a modern marine fauna (McKinney and Hageman, 2007). McKinney and Hageman (2007) hypthesize a tendency to sedentary suspension-feeding epibenthic communities in areas with low nutrient levels and low predation intensities, i. e. in the northeastern Adriatic. In shallow, nutrient-rich waters with high predation intensity McKinney (2007) expects an endobenthos-rich modern ecosystem.

The environmental conditions at the sampling location of this study varied strongly, in particular sedimentation rates and nutrient availability. Among the eight sediment cores different trends of drilling predation on bivalves have been detected, both among the cores and along the sediment layers. In Brijuni M44, for instance, where sedimentation (0.15 cm/year) and nutrient content is rather low, the core shows the local bivalve fauna and its characteristics from present time to more than 5,000 years into the past. DFs rise from the bottom layers to about 50 cm depth, but from 50 cm upwards DFs decrease strongly. This general trend is clearly reflected in the most abundant species of this assemblage (e.g. *Timoclea ovata*, *Striarca lactea* and *Corbula gibba*). In the shelf area near Piran sedimentation rates are also rather low (0.16-0.26 cm/year) and the two cores (M1, M53) cover a similar time span as Brijuni M44 core. In M1 and M53 increased drilling frequencies were recognized in the middle of the core, at about 60 cm, but in the uppermost layers (from 10 cm upwards) DFs decrease again. DF-trends of abundant species (e.g. *Corbula gibba*, *Gouldia minima*) confirm this trend. The results from the assemblages of Panzano (M28, M29) do also not agree with the hypothesis of a significant predation increase in the recent past. In contrary, except for the slight DF-rise in the uppermost 5 cm of the M28 core, in both cores (M28, M29) moderate, but steadily decreasing drilling frequencies in the upper 20-30 cm of the cores were found. The general trend of drilling frequencies in the assemblage from Venice shows a

moderate increase in the upper 20 cm of the core (primarily due to DF-rise in *Lucinella*) and therefore M38 is the only core which might agree with the hypothesis of increasing DF with increasing nutrient content. However, the mean DF of M38 is generally very low, the peaks in the upper layers reached only 9-10 % and there occurred similar DF peaks in the middle and the bottom layers of the core. In the Po delta particularly high sedimentation rates (1.94-2.54 cm/year) and nutrient contents were recorded and the assemblages (M13, M20) cover the smallest time span of a few decades only. In both cores (M13, M20) a heavy increase of DF was recorded in the middle of the core, at 70-100 cm depth, upwards DFs decreased gradually and in the uppermost layers DFs were very low.

7.2 Comparison of nutrient-rich and nutrient-poor sites

Nutrient availability (reflected in chlorophyll *a* content of the water) is hypothesized to primarily determine the distribution of "Paleozoic" or "modern" ecosystem structure in the mollusc shelfs from the northern Adriatic Sea (McKinney and Hageman, 2007). Through the Otranto Strait oligotrophic waters enter the Adriatic See from the Mediterranean and follow an overall cyclonic path, up the Balkan coast with secondary cyclonic gyres in the southern, middle and in the northern Adriatic Sea (Artegiani et al., 1997). Most of the freshwater which is supplemented to the Adriatic, is added along the Italian coast, especially from the Po River (Raicich, 1994). Sediment and terrigenous nutrients derived from the Apenines and western Italian Alps enter the Adriatic Sea primarily through the Po River. While small portions of these sediments remain in the river delta, most of them are swept southward and accumulate along the Italian coast (Cattaneo et al., 2003; Frignani et al., 2005). From the Po River and other Italian rivers primary nutrients (N, P, Si) stream primarily southward along the Italian coast. In the Northern Adriatic the cyclonic flow is less intense than elsewhere in the Adriatic Sea and while it is stronger developed in winters, it almost stops in summer due to high temperatures, diminished winds and high river discharges, for instance of the Po River (McKinney and Hageman, 2007).

Environmental conditions varied heavily between the sampling locations of this study, which are located both at the west and the east coast of the northern Adriatic Sea. In the shelf area near Venice the sediment composition consists of oligotrophic relict sands. The assemblage from this core (M38) showed very low DFs and therefore conforms to the hypothesis that low nutrient content leads to low predation frequencies. The marine environment around the Po delta is influenced by very high sedimentation rates, primarily muddy sediments and high nutrient input from the Po River. The assemblages from the two Po cores (M13, M20) contained the smallest bivalve assemblages, with only 850-880 individuals, respectively, and DFs were among the lowest in the dataset. This low predation intensities despite high nutrient contents may be the consequence of sensitivity to freshwater in drilling gastropods. The shelf area around Piran is characterized by sandy mud and minor nutrient input, but the mean DFs of the assemblages from M1 and M53 were relatively high with 18 % and 25 %,

respectively. In the two cores from the area close to Panzano (M28, M29) the highest DFs were detected. Nutrient input from the Isonzo River is relatively high. The shelf environment near Brijuni islands is formed by relict sands and rather low nutrient input. DFs of 15 % were recognized in this assemblage (M44). These results show distinct correlations between drilling intensities and nutrient availability in some cores (i.g. Venice, Panzano), but not in all.

7.3   Specific features of unsuccessful predation

Cases of unsuccessful predation may happen when the size of the prey is too large for the predator to handle or when the shell of the bivalve prey is very thick, as is the case in the genus *Corbula*. Bivalves of this taxonomic group have a conchiolin layer within their shell which is discussed to act like a deterrent to predators. Failures in prey-manipulation result in nonfunctional, incompletely perforated drill holes or very unusual drill hole sites (Kitchell, 1981; Kelley, 1986).

Interestingly, rather high frequencies of incomplete drill holes were recovered not only in the genus *Corbula*, where most of the edge drills or multiple drills were discovered, but also in *Striarca*. Among the assemblage from Brijuni M44, where *Striarca lactea* was the second highest abundant bivalve species, *Striarca* had rather low DFs of 5.0 %, while uncommonly high IDFs of 17.6 % and a PE of 77.9 % were detected. Most of these incomplete drill holes correspond with the pattern of nonfunctional boreholes specified by Kelley (1986). These nonfunctional drill holes reach the shell interior, but different from successful drill holes, these are characterized by a rather wide outer drill hole diameter, which indicates the predator size, and a narrow inner drill hole diameter, which is not large enough for the proboscis to penetrate and therefore feeding fails (Kelley, 1986). Drill holes of this type were found only among *Striarca* in the assemblage from Brijuni. *Corbula* usually contained incomplete boreholes, which did not completely perforate the shell and therefore did not reach the shell interior. The conchiolin layer of Corbulids appears to deter drilling predators (Kelley, 1986).

7.4   Life habits of prey and drilling predation

Previous studies (e.g. Vermeij, 1977, 1987) emphasize the key role of predation in regulating life habits in marine ecosystems. However, the relevance of feeding strategies, substrate relationships and attachment for drilling intensities has been rarely considered in former research works (e.g. Sawyer and Zuschin, 2010).

Concerning the total bivalve fauna of the eight sediment cores from the northern Adriatic Sea, the relatively rare carnivores had the highest DFs, but the sample size for this group is very low. Apart from carnivores, DFs on commensal and parasitic bivalves were the highest, followed by suspension feeders. The high drilling intensities in commensals are of special interest, because these bivalves usually live attached to invertebrates and should not be a

typical subject to common gastropod drillers. Especially in the assemblages from the river mouth of the Isonzo River in the Gulf of Trieste (Panzano M28, M29), their attack frequencies reached up to 35.2 %. In a study of Sawyer and Zuschin (2010) on surface samples from the same area, similar results were detected and it was hypothesized that these commensal or parasitic bivalves may be exposed and attacked by drilling predators after death, deterioration or consumption of their host. Adapted to a cryptic life-style commensal bivalves have very thin shells and therefore may be easy prey for opportunistic drillers.

Considering the total assemblage, suspension feeding bivalves had lower DFs than commensals and carnivores, but significantly higher predation intensities than deposit feeders. A possible reason for the higher risk of predation in filter feeders may be their availability to the predators, because they are the most abundant guild in all the assemblages and therefore may have a high encounter frequency with predatory gastropods (Leighton, 2002; compare also Saywer and Zuschin, 2010). In deposit feeders and chemosymbiotic bivalves the lowest DFs were detected, at least concerning the total bivalve fauna. Vermeij (1987) expects that both infaunal life-style and the ability to move quickly through the sediment could reduce the risk of predation. This hypothesis may explain the lower drilling intensities among deposit feeders. But in the assemblages from Brijuni M44, and Piran M53 deposit feeders reached DFs around 20 %.

Reduced drilling intensities in chemosymbiotic bivalves are discussed to be associated with toxic reducing compounds in their tissues (Amano and Jenkins, 2007). This would deter predatory drillers in presence of other abundant prey. But in the assemblages from Piran (M1, M53) where chemosymbiotics were relatively rare (2.7 % and 3.1% of the total number of individuals), DFs reached almost 20 %. In the assemblage from Venice M38 chemosymbiotics even had the highest DFs among the feeding guilds. These results conform to other studies on the Northern Adriatic (Saywer and Zuschin, 2010) or from the Red sea (Zuschin and Ebner, 2015) or on deposits of the American Gulf Coastal Plain (Kelley and Hansen, 1993, 2006), which all discovered rather high drilling frequencies among the chemosymbiontic family Lucinidae.

Moreover, it has been hypothesized that rising predation pressure during the Mesozoic contributed to increased infaunalization of bivalves (Vermeij, 1987). According to this theory, infaunal life habits could reduce the risk of predation and result in lower DFs on infaunal bivalves. Life habits of the predatory gastropods also play a major role in this case. Naticid gastropods for instance, are infaunal predators and commonly prey upon infaunal bivalves and gastropods (Yochelson et al., 1983; Dietl, 2002). Only on rare occasions, it is reported that naticids hunt and drill their prey epifaunally (Savazzi and Reyment, 1989; Dietl, 2002). Muricid gastropods, in contrast, typically prey at the sediment surface, although sometimes, they dig up and drill also shallow-infaunal prey. In this context, it seems obvious that a prey's position in the substrate largely predicts which predator it might encounter (e.g. Chattopadhvay et al, 2014).

Contrary to other assumtions (e.g. Sawyer and Zuschin, 2010), the results of this study only partly support this hypothesis. Only in one assemblage from Venice M38 infaunal bivalves had significantly lower drilling frequencies than epifaunal taxa. In all other cores and particularly regarding to the total bivalve fauna examined, infaunal bivalves were drilled far more frequently than those with epifaunal life habits; considering the total fauna, nearly twice as often. Considering the dominance of infaunal bivalves in terms of abundance in most of the examined assemblages, a prey's availability to the predator, again, might play an important role in case of prey selection. In the Brijuni M44 core, for instance, where epi- and infaunally living bivalves are similarly abundant, both groups show similar drilling frequencies (15 % and 15.6 %, respectively). Most heavily drilled bivalves of this core were from the epifaunal Anomidae and Noetiidae (with particularly high IDFs) and the infaunal Veneridae. In the Piran cores (M1, M53), which contained four to five times more infaunal than epifaunal bivalves, DF of infauna strongly exceeds that of epifauna.

An interesting aspect concerning substrate relationships are high drilling intensities among commensal bivalves. Considering the total fauna and particularly the two cores from Panzano (M28, M29), commensals had the highest drilling frequencies among the substrate relationship categories. As mentioned in the discussion about feeding strategies, these high DFs may be the consequence of their - due to very thin shells rather defenceless - exposure to predatory drillers after death, consumption or deterioration of the host.

Referring to epifaunal attachment categories, it has been hypothesized that cementation was adopted in several bivalve families in the Mesozoic as a measure to hamper grappling predators the manipulation of their prey (Harper, 1991). Although this theory is discussed controversially, muricids, for instance, need only little manipulation for hunting and drilling their prey. Furthermore, studies of Sawyer and Zuschin (2010) detected considerably higher DFs in cemented bivalves, than in bysally attached or reclining animals in the Gulf of Trieste. On the other hand, Stone (1998) expected that cementing bivalves may have responded morphologically to drilling predators in the Cenozoic and demonstrated that spines on epifaunal cementers effectively deter muricids.

Regarding the drilling data of the total fauna examined in this study, cemented bivalves had significant lower DFs than recliners or bysally attached bivalves. This general trend and also similar results from the cores Piran (M1, M53), Panzano (M28, M29) and Po (M13, M20) may confirm with the theory of cementation as a predation deterrent strategy, but in cemented bivalves from Brijuni M44 and Venice M38 relatively high drilling frequencies of about 20 % were found in this life habit group.

Compared to cemented bivalves, bysally attached animals can vary the strength of attachment seasonally, may detach voluntarily for mobility or for secondary larval settlement and reattach if dislodged (Price, 1980). As handling time and manipulation of the prey is supposed to be more essential for predatory gastropods than energetic gain (Rovero et al. 2000), byssal attachment is discussed to prevent predators, because manipulating may be

hampered and therefore the risk of exposure to their own enemies might be enhanced. Moreover, some mussels react with greater byssus production in case of exposure to damaged conspecific or heterospecific cues (Shin et al., 2008). Similar to other studies from the northern Adriatic Sea (e.g. Sawyer and Zuschin, 2010) the bysally attached bivalves of the total fauna across all cores were drilled rather frequently (about 20 %) and compared to cementers, DFs of bysally attached bivalves was significantly higher (more than twice as high as in cementers). But the drilling intensities among the epifaunal attachment groups varied heavily among the cores. In the assemblages from Brijuni M44 and Venice M38, for instance, bysally attaching bivalves seem more effective at deterring drillers compared to cementers, but on the other hand, in the cores from Piran (M1, M53) and Panzano (M28, M29) DFs of bysally attaching bivalves are significantly higher than those of cementers.

Actively mobile bivalves had the lowest DFs across the total fauna of all cores, but these include not only the typical recliners, for instance pectinids, but also bivalve taxa, which can change their epifaunal attachment and live bysally attached or reclining, for instance *Andara* or Limidae. This epifaunal-attachment-group had the lowest drilling frequencies of all. Considering the total fauna, drilling frequencies on common recliners are not significantly lower than on byssaly attached bivalves. But again, results vary among the cores. In the Brijuni M44 core, recliners had significantly lower DFs than cementers, but only slightly lower DFs than bysally attaching bivalves (less than 1 % difference). In the Piran cores (M1, M53) recliners are drilled even more frequently than bysally attached or cemented bivalves. In other cores, for instance, Panzano (M28, M29), Venice (M38) and Po (M13, M20) recliners had lower DFs than bysally attaching animals. These results would conform to the hypothesis that recliners, for instance pectinids, 'jump' or 'swim' and therefore may escape when they are encountered by predators (Thomas and Gruffydd, 1971; Brand, 1991). Moreover, it is discussed that evolutionary trends in shell morphology of several scallop lineages may reflect adaptions which encourage the mobility of these bivalves, probably as a consequence of increased predatory pressure (Beu, 1995; Jonkers, 2000).

7.4   DFs did not correlate with diversity

The influence of local ecological interactions, in particular predation, on biodiversity over evolutionary timescales is an essential paleoecological issue (Eldredge and Could, 1972; Vermej, 1987). Intermediate predation intensities are supposed to increase diversity in modern benthic communities, probably caused by reduced competition for space, as studies from the Pacific North-West of the USA show (e.g. Connell, 1961). But the comparison of predation frequencies and measures of diversity often yield contradictory results. For instance, in a study from Kelley and Hansen (2009) about local molluscan assemblages from the US coastal plain, DFs did not correlate with prey diversity. On the other hand, in other fossil assemblages from North America, which include molluscs from Maastrichtian (Harries

and Schopf, 2007) or Eocene (Hansen and Kelley, 1995) correlations between diversity and DFs were detected.

In this study, mean DF of several cores correlated with measures of diversity, but for other cores (e.g. Venice M38) correlations completely failed. One explanation for the very low diversity in the cores (M13, M20) from the shelf around the Po River delta is that physiological constraints (e.g. extremely high sedimentation and freshwater discharges from the Po) probably exclude both predators and non-drilling ("prey") taxa.

In most of the common molluscivorous gastropods trophic polymorphisms were recovered, which means that they hunt different prey types and therefore exhibited different prey-capture methods to handle a variety of prey species (Winberger, 1994; Walker, 2007). As a result, factors such as prey abundances and encounter rates are supposed to control DFs (Leighton, 2002). In the examined assemblages from the Northern Adriatic, most of the bivalve families with n > 50 included at least some drilled specimens. As nearly all, even particularly rare species, e.g. the carnivore *Cardiomya costellata* were attacked, the drilling predators appear to be generalists. DFs and prey abundances, however, did not correlate in each core. For instance, in the small assemblages from the Po cores (M13, M20), where very low diversity and numbers of bivalve individuals were recorded, only the most abundant species (e.g. *Corbula gibba*) were drilled and the mean DFs of the cores were relatively low. On the other hand, in Brijuni M38, which represents one of the largest assemblages with high diversity and rather high mean DFs, the two most abundant species, the infaunal *Timoclea ovata* and the epifaunal *Striarca lactea* show very different DFs of 17.7 % and 5.2 %. Interestingly, particularly high IDFs and PE were discovered in *Striarca lactea* from Brijuni M44. Moreover, the Panzano cores (M28, M29) which have moderate bivalve diversity and abundances show the highest DFs among the cores. Furthermore, Venice M38 had a very high diversity, but despite that DFs were among the lowest of all cores.

7.5 DFs in the Northern Adriatic and the low predation hypothesis

Kelley (2006) and McKinney (2007) suggested low predation pressure in the northern Adriatic Sea due to bulk sample analyses from a single shelf location near Venice, where drilling frequencies showed a rather low (Cretaceous) level (< 10 %), and low occurrence and diversity of high-energy predators (e.g. balistid fish, echinoids with advanced dentition or durophagous crabs). Others reported that wide areas of the Northern Adriatic are strongly affected by fishing and probably have predation levels within the mean scope of the Mediterranean and not similar to the pre-Cenozoic (Zuschin and Stachowitsch, 2009).

Kowalewski et al. (1998) distinguished three phases of Phanerozoic drilling predation. The Mesozoic phase is characterized by very rare, while in the Cenozoic phase significantly increased drilling intensities are recognized. The Cretaceous phase shows moderate drilling intensities, such as reported from Kelley and Hansen (2006), who evaluated DFs of 13.2 % to

16.2 % for bivalves from Creatceous deposits of the North American Gulf Coastal Plain. In this study, the overall drilling frequencies across all cores reach about 20 % and can be classified as typical Cenozoic. However, DFs varied strongly (5-24 %) between the cores; while in assemblages from the Po River delta (M13, M20) and Venice (M38), very low DFs of about 5-10 % were recorded, all the other assemblages had DFs of 15-24 %.

The overall PE evaluated for the total bivalve fauna examined in this study (7.1 %) is also comparable to other Cenozoic basins. Kojumbdjiera (1974) reported PE of < 1 % for key species of the Miocene of Bulgaria and Culotta (1988) evaluated a PE about 5 % in Plio-Pleistocene deposits of Florida. A study from Zuschin and Sawyer (2010) reported PE of 10.3 % for Northern Adriatic bivalves, which appear similar to those from the Cenozoic Gulf Coastal Plain of North America (1-19 %) reported from Kelley and Hansen (2006). In this study, PE on *Corbula gibba* was 14.2 % across all cores (up to 23.5 % in Panzano M29) and therefore ranges on a similar level as PE of corbulids from the Cenozoic Gulf Coastal Plain which ranged from 11 % to 59 % (Kelley and Hansen, 2006).

Considering these comparisons of Cenozoic DFs and PE from other regions with the examined bivalve assemblages from the Northern Adriatic, this study does not agree with the hypothesis that drilling intensity in the northern Adriatic Sea is at a pre-Cenozoic level or particularly low compared to other Cenozoic basins, although the spartial variability is remarkably high.

8   Conclusion

Environmental conditions and life habits of prey appear to play a major role in predation intensities. Drilling intensities and prey effectiveness varied strongly between the sampling locations and also along the cores. Highest DFs were detected in the assemblages from Panzano and the lowest in the cores from the Po delta and Venice. Multiple drill holes and drill holes at the edge of the bivalve shells were rather rare in the assemblages and primarily occurred in *Corbula gibba*. Moreover, most of the cores also contained incompletely perforated valves, but except for the cores from Brijuni and Piran, IDFs did not exceed 1 %. A significant increase of drilling frequencies in the youngest past did not occur in any of the assemblages, but slightly increasing drilling frequencies in the uppermost sediment layers were found in Venice.

The sampling locations differed in environmental conditions, e.g. sedimentation rate, sediment composition and nutrient content. Although in some cores (e.g. Panzano) drilling frequencies correlated positively in others (e.g. Venice) negatively with nutrient availability, predation intensities did not always follow this trend (e.g. Brijuni).

Considering feeding strategies, this study found high drilling frequencies in commensal and parasitic bivalves, as well as in suspension feeders. But again, the results varied significantly between the sampling sites. Furthermore, the hypothesis that infaunal life style may be an effective defence strategy in marine invertebrates can't be supported in this study. Apart from Venice, infaunal bivalves were drilled far more frequently than those with epifaunal life habits. The general trend of lower drilling intensities in cemented bivalves in the total fauna agrees with the theory of cementing as a deterrence strategy in bivalves. However, considering the assemblages separately the results are again ambiguous. Nevertheless, actively mobile bivalves clearly showed the lowest drilling intensities.

In some of the assemblages, DFs correlated positively with common measures of diversity, but in others (e.g. Venice) correlations clearly failed. Although predators appear to be generalists and attack nearly all prey encountered, DFs and prey abundances did not principally conform in all cores. Finally, this study definitely supports the hypothesis that DFs strongly vary between and within environments in the northern Adriatic Sea and that in addition to drilling predators, also other predators, e.g. durophages, as well as human impacts may affect molluscan diversity in the Northern Adriatic.

In contrast to other assumptions, drilling intensities recorded in the bivalve fauna of the assemblages of several sampling sites show higher DFs and PE than those typically found in Cretaceous molluscs. The overall drilling frequencies investigated in this study reject the hypothesis of pre-Cenozoic drilling predation in molluscs of the northern Adriatic Sea, although a very wide spartial variability was recognized.

9 Acknowledgements

10   Appendix

10.1 Drilling intensities of all species across the total fauna and from all cores

Table 42: DF, IDF, PE, EDF and MDF of all species across the total fauna of all cores

Species	n	D	ID	ED	MD	DF (%)	IDF (%)	PE (%)	EDF (%)	MDF (%)
Nuculana pella	279	27	1	1	0	9.7	0.4	3.6	0.4	0.0
Sacculla commutata	60	16	0	1	0	26.7	0.0	0.0	1.7	0.0
Nucula cf. Nucleus	1,608	302	29	5	1	18.8	1.8	8.8	0.3	0.1
Nucula sulcata	162	29	2	0	0	17.9	1.2	6.5	0.0	0.0
Arca noae	202	3	2	1	0	1.5	1.0	40.0	0.5	0.0
Arca tetragona	102	17	1	12	0	16.7	1.0	5.6	11.8	0.0
Barbatia barbata	17	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Andara transversa	43	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Striarca lactea	2,123	106	373	16	2	5.0	17.6	77.9	0.8	0.1
Glycymeris glycymeris	451	28	5	7	0	6.2	1.1	15.2	1.6	0.0
Glycymeris violacescens	29	2	0	0	0	6.9	0.0	0.0	0.0	0.0
Mytilus sp.	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	747	56	1	10	0	7.5	0.1	1.8	1.3	0.0
Modiolus adriacus	523	82	2	65	0	15.7	0.4	2.4	12.4	0.0
Modiolus barbatus	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Aequipecten opercularis	655	35	3	1	0	5.3	0.5	7.9	0.2	0.0
Mimachlamys varia	373	23	2	1	0	6.2	0.5	8.0	0.3	0.0
Palliolum incomparabile	31	5	1	0	0	16.1	3.2	16.7	0.0	0.0
Chlamys multistriatus	77	17	4	0	1	22.1	5.2	19.0	0.0	1.3
Flexopecten glaber	907	66	0	7	0	7.3	0.0	0.0	0.8	0.0
Pecten jacobaeus	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anomia ephippium	1,653	326	2	16	13	19.7	0.1	0.6	1.0	0.8
Heteranomia squamula	428	104	0	3	9	24.3	0.0	0.0	0.7	2.1
Pododesmus patelliformes	610	153	1	6	17	25.1	0.2	0.6	1.0	2.8
Lima lima	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lima cf. Hians	3	1	0	0	0	33.3	0.0	0.0	0.0	0.0
Limaria loscombi	56	4	0	0	0	7.1	0.0	0.0	0.0	0.0
Limatula gwyni	82	3	0	0	0	3.7	0.0	0.0	0.0	0.0
Limatula subauriculata	11	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Limaria tuberculata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea edulis	11	1	0	0	0	9.1	0.0	0.0	0.0	0.0
Ostrea sp.	1,608	135	1	9	3	8.4	0.1	0.7	0.6	0.2
Glans aculeata	35	1	0	0	0	2.9	0.0	0.0	0.0	0.0
Chama gryphoides	249	36	0	18	1	14.5	0.0	0.0	7.2	0.4
Pseudochama gryphina	12	2	0	0	0	16.7	0.0	0.0	0.0	0.0
Anodontia fragilis	751	140	0	1	1	18.7	0.0	0.0	0.1	0.1

Ctena decussata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lucinella divaricata	896	107	0	0	0	11.9	0.0	0.0	0.0	0.0
Lucinoma borealis	5	1	0	0	0	20.0	0.0	0.0	0.0	0.0
Loripes lucinalis	20	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Myrtea spinifera	60	5	1	0	0	8.3	1.7	16.7	0.0	0.0
Thyrasira biplicata	138	12	0	0	0	8.7	0.0	0.0	0.0	0.0
Neolepton obliquatum	18	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	2,805	922	0	0	6	32.9	0.0	0.0	0.0	0.2
Tellimya ferruginosa	17	2	0	0	0	11.8	0.0	0.0	0.0	0.0
Litigiella glabra	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Montacuta goudi	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Montacuta phascolionis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Scacchia oblonga	46	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton squamosum	122	2	0	0	0	1.6	0.0	0.0	0.0	0.0
Lepton subtrigonum	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Arculus cf. sykesii	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidium	317	19	0	0	1	6.0	0.0	0.0	0.0	0.3
Kellia suborbicularis	84	12	0	0	3	14.3	0.0	0.0	0.0	3.6
Bornia geoffroyi	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	94	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostata	485	15	0	0	0	3.1	0.0	0.0	0.0	0.0
Acanthocardia deshayesii	50	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia aculeata	159	2	0	0	0	1.3	0.0	0.0	0.0	0.0
Papillicardium papillosum	2,110	150	3	0	1	7.1	0.1	2.0	0.0	0.0
Parvicardium exiguum	443	65	1	0	0	14.7	0.2	1.5	0.0	0.0
Parvicardium scriptum	451	47	0	0	6	10.4	0.0	0.0	0.0	1.3
Parvicardium scabrum	2,490	296	0	3	0	11.9	0.0	0.0	0.1	0.0
Parvicardium minimum	417	18	0	0	0	4.3	0.0	0.0	0.0	0.0
Cerastoderma edule	26	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cerastoderma glaucum	35	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Laevicardium crassum	31	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	215	5	0	0	0	2.3	0.0	0.0	0.0	0.0
Abra alba	1,431	168	2	0	1	11.7	0.1	1.2	0.0	0.1
Abra nitida	869	62	0	0	0	7.1	0.0	0.0	0.0	0.0
Abra prismatica	25	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra tenuis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Morella distorta	1,667	253	0	0	0	15.2	0.0	0.0	0.0	0.0
Tellina serata	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina pulchella	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina donacina	7	1	0	0	0	14.3	0.0	0.0	0.0	0.0
Tellina fabula	265	10	0	0	0	3.8	0.0	0.0	0.0	0.0
Tellina pygmaea	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina incarnata	28	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrana fragilis	31	3	0	0	0	9.7	0.0	0.0	0.0	0.0

Arcopagia balaustina	36	6	0	0	0	16.7	0.0	0.0	0.0	0.0
Gari costulata	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gari fervensis	30	1	0	0	0	3.3	0.0	0.0	0.0	0.0
Gari depressa	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Azorinus chamasolen	136	4	0	0	0	2.9	0.0	0.0	0.0	0.0
Solecurtus candidus	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Donax venustus	281	2	0	0	0	0.7	0.0	0.0	0.0	0.0
Mysia undata	60	8	0	0	0	13.3	0.0	0.0	0.0	0.0
Callista chione	205	5	0	0	0	2.4	0.0	0.0	0.0	0.0
Gouldia minima	7,995	2,957	6	175	9	37.0	0.1	0.2	2.2	0.1
Pitar rudis	1,696	347	0	31	1	20.5	0.0	0.0	1.8	0.1
Pitar mediterraneus	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Paphia rhomboides	392	75	1	0	1	19.2	0.3	1.3	0.0	0.3
Venerupis aurea	11	1	0	0	0	9.1	0.0	0.0	0.0	0.0
Dosinia lupinus	210	17	0	1	0	8.1	0.0	0.0	0.5	0.0
Venus verrucosa	205	27	0	3	0	13.2	0.0	0.0	1.5	0.0
Venus casina	38	3	0	1	0	7.9	0.0	0.0	2.6	0.0
Timoclea ovata	2,560	449	1	61	7	17.5	0.0	0.2	2.4	0.3
Clausinella fasciata	274	67	0	12	1	24.5	0.0	0.0	4.4	0.4
Coralliophaga	6	1	0	0	1	16.7	0.0	0.0	0.0	16.7
Diplodonta brocchii	18	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Diplodonta trigona	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	8,066	1,783	294	174	124	22.1	3.6	14.2	2.2	1.5
Lentidium mediterraneum	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Barnea candida	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	106	2	0	0	0	1.9	0.0	0.0	0.0	0.0
Ensis ensis	23	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrochaena dubia	121	2	1	1	0	1.7	0.8	33.3	0.8	0.0
Hiatella arctica	656	72	5	15	3	11.0	0.8	6.5	2.3	0.5
Pandora pinna	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pandora inaequivalvis	27	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cuspidaria cuspidata	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cardiomya costellata	3	3	0	0	0	100.0	0.0	0.0	0.0	0.0
Thracia phaseolina	184	2	0	0	0	1.1	0.0	0.0	0.0	0.0
Thracia corbuloides	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia cf disorta	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cochlodesma praetenue	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pisidium sp.	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 43: DF, IDF, PE, EDF and MDF of all species from Brijuni M44

Brijuni M44										
Species	**n**	**D**	**ID**	**ED**	**MD**	**DF (%)**	**IDF (%)**	**PE (%)**	**EDF (%)**	**MDF (%)**
Nuculana pella	19	1	0	0	0	5.3	0.0	0.0	0.0	0.0
Sacculla commutata	57	16	0	1	0	28.1	0.0	0.0	1.8	0.0
Nucula cf. Nucleus	709	149	27	2	1	21.0	3.8	15.3	0.3	0.1
Arca noae	44	0	2	0	0	0.0	4.5	100.0	0.0	0.0
Arca tetragona	91	17	1	12	0	18.7	1.1	5.6	13.2	0.0
Barbatia barbata	15	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Andara transversa	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Striarca lactea	1,999	104	373	16	2	5.2	18.7	78.2	0.8	0.1
Glycymeris glycymeris	354	21	5	2	0	5.9	1.4	19.2	0.6	0.0
Musculus subpictus	24	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Modiolus adriacus	286	65	2	56	0	22.7	0.7	3.0	19.6	0.0
Aequipecten opercularis	240	18	3	0	0	7.5	1.3	14.3	0.0	0.0
Mimachlamys varia	109	13	2	0	0	11.9	1.8	13.3	0.0	0.0
Palliolum incomparabile	30	5	1	0	0	16.7	3.3	16.7	0.0	0.0
Chlamys multistriatus	75	17	4	0	1	22.7	5.3	19.0	0.0	1.3
Flexopecten glaber	5	1	0	0	0	20.0	0.0	0.0	0.0	0.0
Anomia ephippium	726	215	1	5	12	29.6	0.1	0.5	0.7	1.7
Heteranomia squamula	311	91	0	2	8	29.3	0.0	0.0	0.6	2.6
Pododesmus patelliformes	406	125	1	4	14	30.8	0.2	0.8	1.0	3.4
Lima lima	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lima cf. Hians	3	1	0	0	0	33.3	0.0	0.0	0.0	0.0
Limaria loscombi	56	4	0	0	0	7.1	0.0	0.0	0.0	0.0
Limatula gwyni	82	3	0	0	0	3.7	0.0	0.0	0.0	0.0
Ostrea edulis	5	1	0	0	0	20.0	0.0	0.0	0.0	0.0
Ostrea sp.	188	40	0	0	0	21.3	0.0	0.0	0.0	0.0
Chama gryphoides	71	11	0	7	0	15.5	0.0	0.0	9.9	0.0
Pseudochama gryphina	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anodontia fragilis	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ctena decussata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Myrtea spinifera	39	3	1	0	0	7.7	2.6	25.0	0.0	0.0
Thyrasira biplicata	15	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	40	8	0	0	2	20.0	0.0	0.0	0.0	5.0
Lepton squamosum	81	2	0	0	0	2.5	0.0	0.0	0.0	0.0
Arculus cf. sykesii	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidium	57	4	0	0	1	7.0	0.0	0.0	0.0	1.8
Kellia suborbicularis	70	12	0	0	3	17.1	0.0	0.0	0.0	4.3
Bornia geoffroyi	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Papillicardium papillosum	448	36	3	0	1	8.0	0.7	7.7	0.0	0.2
Parvicardium scriptum	382	41	0	0	6	10.7	0.0	0.0	0.0	1.6

Parvicardium scabrum	375	28	0	0	0	7.5	0.0	0.0	0.0	0.0
Parvicardium minimum	398	16	0	0	0	4.0	0.0	0.0	0.0	0.0
Laevicardium crassum	12	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	99	14	1	0	0	14.1	1.0	6.7	0.0	0.0
Morella distorta	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina serata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina pulchella	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina donacina	7	1	0	0	0	14.3	0.0	0.0	0.0	0.0
Arcopagia balaustina	20	6	0	0	0	30.0	0.0	0.0	0.0	0.0
Gari costulata	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gari fervensis	8	1	0	0	0	12.5	0.0	0.0	0.0	0.0
Gari depressa	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Callista chione	10	1	0	0	0	10.0	0.0	0.0	0.0	0.0
Gouldia minima	331	56	0	8	0	16.9	0.0	0.0	2.4	0.0
Pitar rudis	242	44	0	7	0	18.2	0.0	0.0	2.9	0.0
Pitar mediterraneus	1	0	0			0.0	0.0	0.0	0.0	0.0
Venerupis aurea	11	1	0	0	0	9.1	0.0	0.0	0.0	0.0
Venus verrucosa	140	19	0	3	0	13.6	0.0	0.0	2.1	0.0
Timoclea ovata	2,450	433	1	61	7	17.7	0.0	0.2	2.5	0.3
Clausinella fasciata	264	67	0	12	1	25.4	0.0	0.0	4.5	0.4
Coralliophaga juv	6	1	0	0	1	16.7	0.0	0.0	0.0	16.7
Diplodonta trigona	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	487	105	15	18	5	21.6	3.1	12.5	3.7	1.0
Phaxas adriaticus	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrochaena dubia	15	1	1	1	0	6.7	6.7	50.0	6.7	0.0
Hiatella arctica	274	44	3	13	2	16.1	1.1	6.4	4.7	0.7
Cuspidaria cuspidata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cardiomya costellata	3	3	0	0	0	100.0	0.0	0.0	0.0	0.0
Thracia phaseolina	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia cf disorta	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 44: DF, IDF, PE, EDF and MDF of all species from Piran M1

Species	n	D	ID	ED	MD	DF (%)	IDF (%)	PE (%)	EDF (%)	MDF (%)
Nuculana pella	42	6	0	0	0	14.3	0.0	0.0	0.0	0.0
Saccella commutata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Nucula cf. nucleus	393	55	1	1	0	14.0	0.3	1.8	0.3	0.0
Arca noae	95	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Arca tetragona	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Barbatia barbata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anadara transversa	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Striarca lactea	78	1	0	0	0	1.3	0.0	0.0	0.0	0.0
Glycymeris violacescens	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mytilus sp.	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	130	4	0	0	0	3.1	0.0	0.0	0.0	0.0
Aequipecten opercularis	25	1	0	0	0	4.0	0.0	0.0	0.0	0.0
Mimachlamys varia	142	3	0	0	0	2.1	0.0	0.0	0.0	0.0
Palliolum incomparabile	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Chlamys multistriata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Flexopecten glaber	231	7	0	0	0	3.0	0.0	0.0	0.0	0.0
Anomia cf. ephippium	184	8	1	0	0	4.3	0.5	11.1	0.0	0.0
Heteranomia cf. squamula	62	6	0	0	0	9.7	0.0	0.0	0.0	0.0
Pododesmus cf. patelliformis	122	12	0	0	2	9.8	0.0	0.0	0.0	1.6
Limaria tuberculata	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea sp. (cf. stentina)	960	46	0	2	1	4.8	0.0	0.0	0.2	0.1
Glans aculeata	21	1	0	0	0	4.8	0.0	0.0	0.0	0.0
Chama gryphoides	112	10	0	4	1	8.9	0.0	0.0	3.6	0.9
Pseudochama gryphina	4	1	0	0	0	25.0	0.0	0.0	0.0	0.0
Anodontia fragilis	326	69	0	1	0	21.2	0.0	0.0	0.3	0.0
Lucinella divaricata	3	1	0	0	0	33.3	0.0	0.0	0.0	0.0
Loripes lucinalis	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Myrtea spinifer	13	2	0	0	0	15.4	0.0	0.0	0.0	0.0
Thyasira biplicata	44	4	0	0	0	9.2	0.0	0.0	0.0	0.0
Neolepton obliquatum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	163	25	0	0	0	15.3	0.0	0.0	0.0	0.0
Tellimya ferruginosa	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Litigiella glabra	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Montacuta phascolionis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Scacchia oblonga	9	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton squamosum	20	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidum	111	2	0	0	0	1.8	0.0	0.0	0.0	0.0
Kellia suborbicularis	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia aculeata	157	2	0	0	0	1.3	0.0	0.0	0.0	0.0

Papillocardium papillosum	913	37	0	0	0	4.1	0.0	0.0	0.0	0.0
Parvicardium exiguum	127	20	0	0	0	15.7	0.0	0.0	0.0	0.0
Parvicardium scriptum	28	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium scabrum	847	123	0	1	0	14.5	0.0	0.0	0.1	0.0
Parvicardium minimum	9	2	0	0	0	22.2	0.0	0.0	0.0	0.0
Cerastoderma edule	25	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Laevicardium crassum	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	8	1	0	0	0	12.5	0.0	0.0	0.0	0.0
Abra alba	600	41	0	0	1	6.8	0.0	0.0	0.0	0.2
Abra nitida	55	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra prismatica	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Moerella distorta	624	67	0	0	0	10.7	0.0	0.0	0.0	0.0
Tellina serrata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrana fragilis	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Arcopagia balaustina	12	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Azorinus chamasolen	66	1	0	0	0	1.5	0.0	0.0	0.0	0.0
Mysia undata	13	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gouldia minima	4,172	1,528	3	49	6	36.6	0.1	0.2	1.2	0.1
Pitar rudis	641	110	0	7	1	17.2	0.0	0.0	1.1	0.2
Paphia rhomboides	25	1	0	0	0	4.1	0.0	0.0	0.0	0.0
Dosinia lupinus	26	1	0	0	0	3.9	0.0	0.0	0.0	0.0
Venus verrucosa	36	4	0	0	0	11.1	0.0	0.0	0.0	0.0
Venus casina	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Timoclea ovata	36	7	0	0	0	19.7	0.0	0.0	0.0	0.0
Clausinella fasciata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Diplodonta brocchii	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	2,426	443	61	53	34	18.3	2.5	12.1	2.2	1.4
Lentidium mediterraneum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrochaena dubia	54	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	121	6	1	1	0	5.0	0.8	14.3	0.8	0.0
Pandora inaequivalvis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia phaseolina	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 45: DF, IDF, PE, EDF and MDF of all species from Piran M53

Species	n	D	ID	ED	MD	DF (%)	IDF (%)	PE (%)	EDF (%)	MDF (%)
Nuculana pella	49	8	1	1	0	16.3	2.0	11.1	2.0	0.0
Nucula cf. nuclaeus	286	74	1	2	0	25.9	0.3	1.3	0.7	0.0
Arca noae	56	3	0	1	0	5.4	0.0	0.0	1.8	0.0
Arca tetragona	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anadara transversa	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Striarca lactea	42	1	0	0	0	2.4	0.0	0.0	0.0	0.0
Musculus subpictus	217	40	1	8	0	18.4	0.5	2.4	3.7	0.0
Modiolus adriaticus	196	16	0	8	0	8.2	0.0	0.0	4.1	0.0
Aequipecten opercularis	62	15	0	1	0	24.2	0.0	0.0	1.6	0.0
Mimachlamys varia	49	4	0	1	0	8.2	0.0	0.0	14.3	0.0
Flexopecten glaber	325	49	0	7	0	15.1	0.0	0.0	2.2	0.0
Anomia ephippium	152	34	0	7	0	22.4	0.0	0.0	4.6	0.0
Heteranomia squamula	14	4	0	0	1	28.6	0.0	0.0	0.0	7.1
Pododesmus patelliformes	42	11	0	1	1	26.2	0.0	0.0	2.4	2.4
Ostrea sp.	315	40	1	6	2	12.7	0.3	2.4	1.9	0.6
Glans aculeata	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Chama gryphoides	66	15	0	7	0	22.7	0.0	0.0	10.6	0.0
Pseudochama gryphina	5	1	0	0	0	20.0	0.0	0.0	0.0	0.0
Anodontia fragilis	347	71	0	0	1	20.5	0.0	0.0	0.0	0.0
Lucinella divaricata	1	1	0	0	0	100.0	0.0	0.0	0.0	0.0
Lucinoma borealis	5	1	0	0	0	20.0	0.0	0.0	0.0	0.0
Loripes lucinalis	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Myrtea spinifera	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thyasira biplicata	46	4	0	0	0	8.7	0.0	0.0	0.0	0.0
Neolepton obliquatum	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	349	123	0	0	1	35.2	0.0	0.0	0.0	0.3
Tellimya ferruginosa	11	2	0	0	0	18.2	0.0	0.0	0.0	0.0
Litigiella glabra	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Montacuta goudi	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Scacchia oblonga	15	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton squamosum	20	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton subtrigonum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidum	108	5	0	0	0	4.6	0.0	0.0	0.0	0.0
Kellia suborbicularis	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostata	174	7	0	0	0	4.0	0.0	0.0	0.0	0.0
Papillicardium papillosum	703	77	0	0	0	11.0	0.0	0.0	0.0	0.0
Parvicardium exiguum	155	32	1	0	0	20.6	0.6	3.0	0.0	0.0
Parvicardium scriptum	40	6	0	0	0	15.0	0.0	0.0	0.0	0.0

Parvicardium scabrum	781	140	0	2	0	17.9	0.0	0.0	0.3	0.0
Parvicardium minimum	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cerastoderma glaucum	35	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Laevicardium crassum	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	45	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	573	93	0	0	0	16.2	0.0	0.0	0.0	0.0
Abra nitida	173	14	0	0	0	8.1	0.0	0.0	0.0	0.0
Abra prismatica	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra tenuis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Moerella distorta	526	157	0	0	0	29.8	0.0	0.0	0.0	0.0
Gastrana fragilis	25	3	0	0	0	12.0	0.0	0.0	0.0	0.0
Arcopagia balaustina	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Azorinus chamasolen	25	1	0	0	0	4.0	0.0	0.0	0.0	0.0
Donax venustus	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	20	3	0	0	0	15.0	0.0	0.0	0.0	0.0
Gouldia minima	3,464	1,370	3	118	3	39.5	0.1	0.2	3.4	0.1
Pitar rudis	651	170	0	17	0	26.1	0.0	0.0	2.6	0.0
Paphia cf. rhomboides	32	3	0	0	1	9.4	0.0	0.0	0.0	3.1
Dosinia lupinis	17	2	0	1	0	11.8	0.0	0.0	5.9	0.0
Venus verrucosa	28	4	0	0	0	14.3	0.0	0.0	0.0	0.0
Venus casina	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Timoclea ovata	57	9	0	0	0	15.8	0.0	0.0	0.0	0.0
Diplodonta brocchii	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	2,198	547	61	67	35	24.9	2.8	10.0	3.0	1.6
Lentidium mediterraneum	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Barnea candida	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrochaena dubia	37	1	0	0	0	2.7	0.0	0.0	0.0	0.0
Hiatella arctica	120	10	1	0	1	8.3	0.8	9.1	0.0	0.8
Pandora pinna	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cuspidaria cuspidata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia phaseolina	9	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 46: DF, IDF, PE, EDF and MDF of all species from Panzano M28

	n	D	ID	ED	MD	DF (%)	IDF (%)	PE (%)	EDF (%)	MDF (%)
Species										
Nuculana pella	68	9	0	0	0	13.2	0.0	0.0	0.0	0.0
Saccella commutata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Nucula cf. nuclaeus	160	29	2	0	0	18.1	1.3	6.5	0.0	0.0
Anadara transversa	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	168	4	0	0	0	2.4	0.0	0.0	0.0	0.0
Modiolus barbatus	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Aequipecten opercularis	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mimachlamys varia	32	3	0	0	0	9.4	0.0	0.0	0.0	0.0
Flexopecten glaber	138	3	0	0	0	2.2	0.0	0.0	0.0	0.0
Anomia ephippium	50	3	0	0	0	6.0	0.0	0.0	0.0	0.0
Heteranomia squamula	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pododesmus patelliformis	13	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Limatula subauriculata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Limaria tuberculata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea edulis	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea sp.	76	6	0	0	0	7.9	0.0	0.0	0.0	0.0
Anodontia fragilis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thyasira biplicata	17	3	0	0	0	17.6	0.0	0.0	0.0	0.0
Neolepton obliquatum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	1,165	474	0	0	2	40.7	0.0	0.0	0.0	0.2
Hemilepton nitidum	23	4	0	0	0	17.4	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostat	159	6	0	0	0	3.8	0.0	0.0	0.0	0.0
Papillicardium papillosum	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium exiguum	61	8	0	0	0	13.1	0.0	0.0	0.0	0.0
Parvicardium scabrum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Laevicardium crassum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	67	14	1	0	0	20.9	1.5	6.7	0.0	0.0
Abra nitida	352	27	0	0	0	7.7	0.0	0.0	0.0	0.0
Moerella distorta	39	8	0	0	0	20.5	0.0	0.0	0.0	0.0
Tellina pulchella	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Azorinus chamasolen	28	2	0	0	0	7.1	0.0	0.0	0.0	0.0
Solecurtus candidus	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	6	3	0	0	0	50.0	0.0	0.0	0.0	0.0
Gouldia minima	14	3	0	0	0	21.4	0.0	0.0	0.0	0.0
Pitar rudis	45	9	0	0	0	20.0	0.0	0.0	0.0	0.0
Paphia rhomboides	158	29	1	0	0	18.4	0.6	3.3	0.0	0.0
Dosinia lupinus	6	3	0	0	0	50.0	0.0	0.0	0.0	0.0
Corbula gibba	1,029	309	67	19	16	30.0	6.5	17.8	1.8	1.6

Lentidium mediterraneum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	45	2	0	0	0	4.4	0.0	0.0	0.0	0.0
Gastrochaena dubia	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	36	1	0	0	0	2.8	0.0	0.0	0.0	0.0
Pandora inaequivalvis	18	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cuspidaria cuspidata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 47: DF, IDF, PE, EDF and MDF of all species from Panzano M29

Species	n	D	ID	ED	MD	DF (%)	IDF (%)	PE (%)	EDF (%)	MDF (%)
Nuculana pella	62	3	0	0	0	4.8	0.0	0.0	0.0	0.0
Nucula cf. nuclaeus	140	23	0	0	0	16.4	0.0	0.0	0.0	0.0
Anadara transversa	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	170	5	0	0	0	2.9	0.0	0.0	0.0	0.0
Modiolus adriaticus	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Aequipecten opercularis	6	1	0	0	0	16.7	0.0	0.0	0.0	0.0
Mimachlamys varia	19	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Flexopecten glaber	88	4	0	0	0	4.5	0.0	0.0	0.0	0.0
Anomia ephippium	26	2	0	0	0	7.7	0.0	0.0	0.0	0.0
Heteranomia squamula	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pododesmus patelliformis	8	1	0	0	0	12.5	0.0	0.0	0.0	0.0
Ostrea sp.	54	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thyasira biplicata	7	1	0	0	0	14.3	0.0	0.0	0.0	0.0
Kurtiella bidentata	844	290	0	0	1	34.4	0.0	0.0	0.0	0.1
Montacuta goudi	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidum	15	4	0	0	0	26.7	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostata	124	2	0	0	0	1.6	0.0	0.0	0.0	0.0
Papillicardium papillosum	11	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium exiguum	62	4	0	0	0	6.5	0.0	0.0	0.0	0.0
Laevicardium crassum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	64	5	0	0	0	7.8	0.0	0.0	0.0	0.0
Abra nitida	256	21	0	0	0	8.2	0.0	0.0	0.0	0.0
Moerella distorta	29	5	0	0	0	17.2	0.0	0.0	0.0	0.0
Azorinus chamasolen	17	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	9	2	0	0	0	22.2	0.0	0.0	0.0	0.0
Pitar rudis	35	7	0	0	0	20.0	0.0	0.0	0.0	0.0
Paphia rhomboides	161	40	0	0	0	24.8	0.0	0.0	0.0	0.0
Dosinia lupinus	6	2	0	0	0	33.3	0.0	0.0	0.0	0.0
Venus casina	1	1	0	0	0	100.0	0.0	0.0	0.0	0.0
Corbula gibba	824	263	81	14	34	31.9	9.8	23.5	1.7	4.1
Phaxas adriaticus	22	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	33	2	0	0	0	6.1	0.0	0.0	0.0	0.0
Pandora inaequivalvis	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cuspidaria cuspidata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia phaseolina	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thracia corbuloides	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 48: DF, IDF, PE, EDF and MDF of all species from Venice M38

Venice M38										
Species	**n**	**D**	**ID**	**ED**	**MD**	**DF (%)**	**IDF (%)**	**PE (%)**	**EDF (%)**	**MDF (%)**
Nuculana pella	39	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Nucula cf. nucleus	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Arca noae	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Arca tetragona	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Barbatia barbata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Striarca lactea	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Glycymeris glycymeris	97	7	0	5	0	7.2	0.0	0.0	5.2	0.0
Glycymeris violacescens	27	2	0	0	0	7.4	0.0	0.0	0.0	0.0
Musculus subpictus	30	3	0	2	0	10.0	0.0	0.0	6.7	0.0
Modiolus adriaticus	39	1	0	1	0	2.6	0.0	0.0	2.6	0.0
Aequipecten opercularis	249	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mimachlamys varia	21	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Flexopecten glaber	85	2	0	0	0	2.4	0.0	0.0	0.0	0.0
Anomia cf. ephippium	508	64	0	4	1	12.6	0.0	0.0	0.8	0.2
Heteranomia cf. squamula	27	3	0	1	0	11.1	0.0	0.0	3.7	0.0
Pododesmus cf. patelliformis	18	4	0	1	0	22.2	0.0	0.0	5.6	0.0
Limatula subauriculata	9	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea sp. (cf. stentina)	13	3	0	1	0	23.1	0.0	0.0	7.7	0.0
Anodontia fragilis	75	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lucinella divaricata	892	105	0	0	0	11.8	0.0	0.0	0.0	0.0
Loripes lucinalis	15	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	11	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellimya ferruginosa	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Scacchia oblonga	22	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton squamosum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Lepton subtrigonum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hemilepton nitidum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kellia suborbicularis	10	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia deshayesii	50	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia aculeata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Papillocardium papillosum	28	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium exiguum	38	1	0	0	0	2.6	0.0	0.0	0.0	0.0
Parvicardium scriptum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium scabrum	485	5	0	0	0	1.0	0.0	0.0	0.0	0.0
Laevicardium crassum	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	157	4	0	0	0	2.5	0.0	0.0	0.0	0.0
Abra alba	20	1	0	0	0	5.0	0.0	0.0	0.0	0.0
Abra prismatica	19	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Moerella distorta	436	16	0	0	0	3.7	0.0	0.0	0.0	0.0

Tellina pulchella	8	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina fabula	265	10	0	0	0	3.8	0.0	0.0	0.0	0.0
Tellina pygmaea	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Tellina incarnata	28	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrana fragilis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gari fervensis	22	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Donax venustus	280	2	0	0	0	0.7	0.0	0.0	0.0	0.0
Mysia undata	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Callista chione	195	4	0	0	0	2.1	0.0	0.0	0.0	0.0
Gouldia minima	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pitar rudis	47	4	0	0	0	8.5	0.0	0.0	0.0	0.0
Paphia rhomboides	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Dosinia lupinus	155	9	0	0	0	5.8	0.0	0.0	0.0	0.0
Venus verrucosa	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Venus casina	19	2	0	1	0	10.5	0.0	0.0	5.3	0.0
Timoclea ovata	17	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Clausinella fasciata	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	99	10	1	0	0	10.1	1.0	9.1	0.0	0.0
Phaxas adriaticus	12	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ensis ensis	23	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Gastrochaena dubia	13	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	54	9	0	1	0	16.7	0.0	0.0	1.9	0.0
Thracia phaseolina	164	2	0	0	0	1.2	0.0	0.0	0.0	0.0
Cochlodesma praetenue	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pisidium sp.	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 49: DF, IDF, PE, EDF and MDF of all species from Po 3 M13

Po 3 M13									
Species	**n**	**D**	**ID**	**ED**	**MD**	**DF (%)**	**IDF (%)**	**PE (%)**	**EDF (%)**	**MDF (%)**
Nucula cf. nucleus	30	1	0	0	0	3.3	0.0	0.0	0.0	0.0
Anadara transversa	28	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Aequipecten opercularis	18	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Flexopecten glaber	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anomia ephippium	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Limatula subauriculata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea juvenil	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thyasira biplicata	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Neolepton obliquatum	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	107	2	0	0	0	1.9	0.0	0.0	0.0	0.0
Hemilepton nitidum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	45	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostata	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra nitida	19	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Moerella distorta	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pitar rudis	15	1	0	0	0	6.7	0.0	0.0	0.0	0.0
Paphia rhomboides	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Venus casina	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Corbula gibba	498	35	0	0	0	7.0	0.0	0.0	0.0	0.0
Lentidium mediterraneum	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	4	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	6	0	0	0	0	0.0	0.0	0.0	0.0	0.0

Table 50: DF, IDF, PE, EDF and MDF of all species from Po 4 M20

Po 4 M20									
Species	**n**	**D**	**ID**	**ED**	**MD**	**DF (%)**	**IDF (%)**	**PE (%)**	**EDF (%)**	**MDF (%)**
Nucula cf. nuclaeus	36	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Nucula sulcata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Musculus subpictus	5	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Aequipecten opercularis	41	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mimachlamys varia	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Flexopecten glaber	21	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pecten jacobaeus	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Anomia ephippium	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pododesmus patelliformis	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Ostrea juvenil	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Thyasira biplicata	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Neolepton obliquatum	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Kurtiella bidentata	126	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Saxicavella jeffreysi	29	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Acanthocardia paucicostata	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Papillicardium papillosum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Parvicardium minimmum	2	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Cerastoderma edule	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Spisula subtruncata	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra alba	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Abra nitida	14	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Moerella distorta	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Mysia undata	3	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Pitar rudis	20	2	0	0	0	10.0	0.0	0.0	0.0	0.0
Paphia rhomboides	10	2	0	0	0	20.0	0.0	0.0	0.0	0.0
Corbula gibba	505	71	8	3	0	14.1	1.6	10.1	0.6	0.0
Lentidium mediterraneum	1	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Phaxas adriaticus	7	0	0	0	0	0.0	0.0	0.0	0.0	0.0
Hiatella arctica	12	0	0	0	0	0.0	0.0	0.0	0.0	0.0

10.2   Pictures of drilled bivalves

Plate 1
1) a-d) Drilled valves of *Timoclea ovata* from Brijuni M44
2) a-d) Incompletely drilled valves of *Striarca lactea* from Brijuni M44
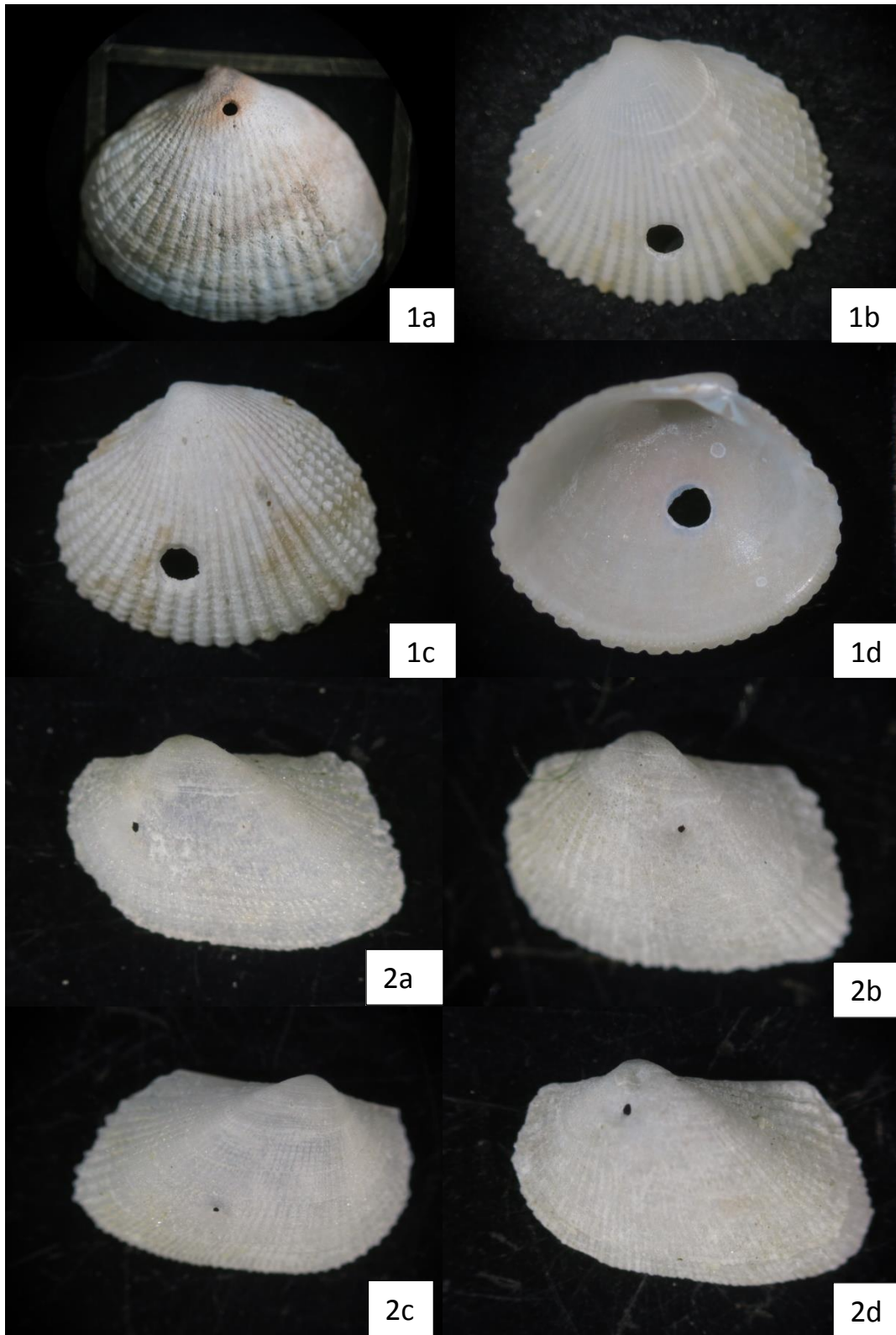
Plate 2
1) a-d) Drilled valves of *Corbula gibba* from Panzano M28
2) a) Edge drilled valve of *Corbula gibba* from Panzano M28
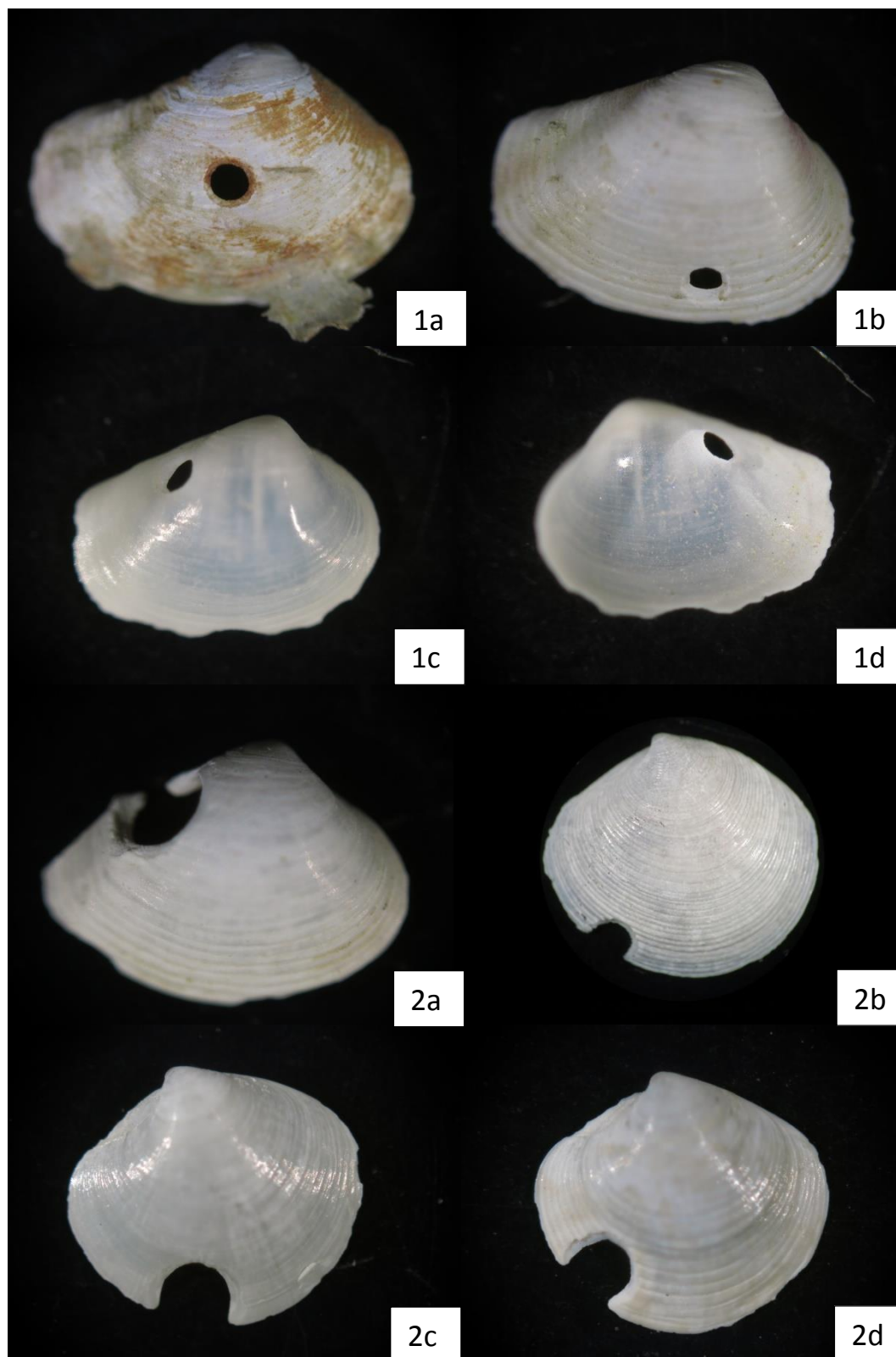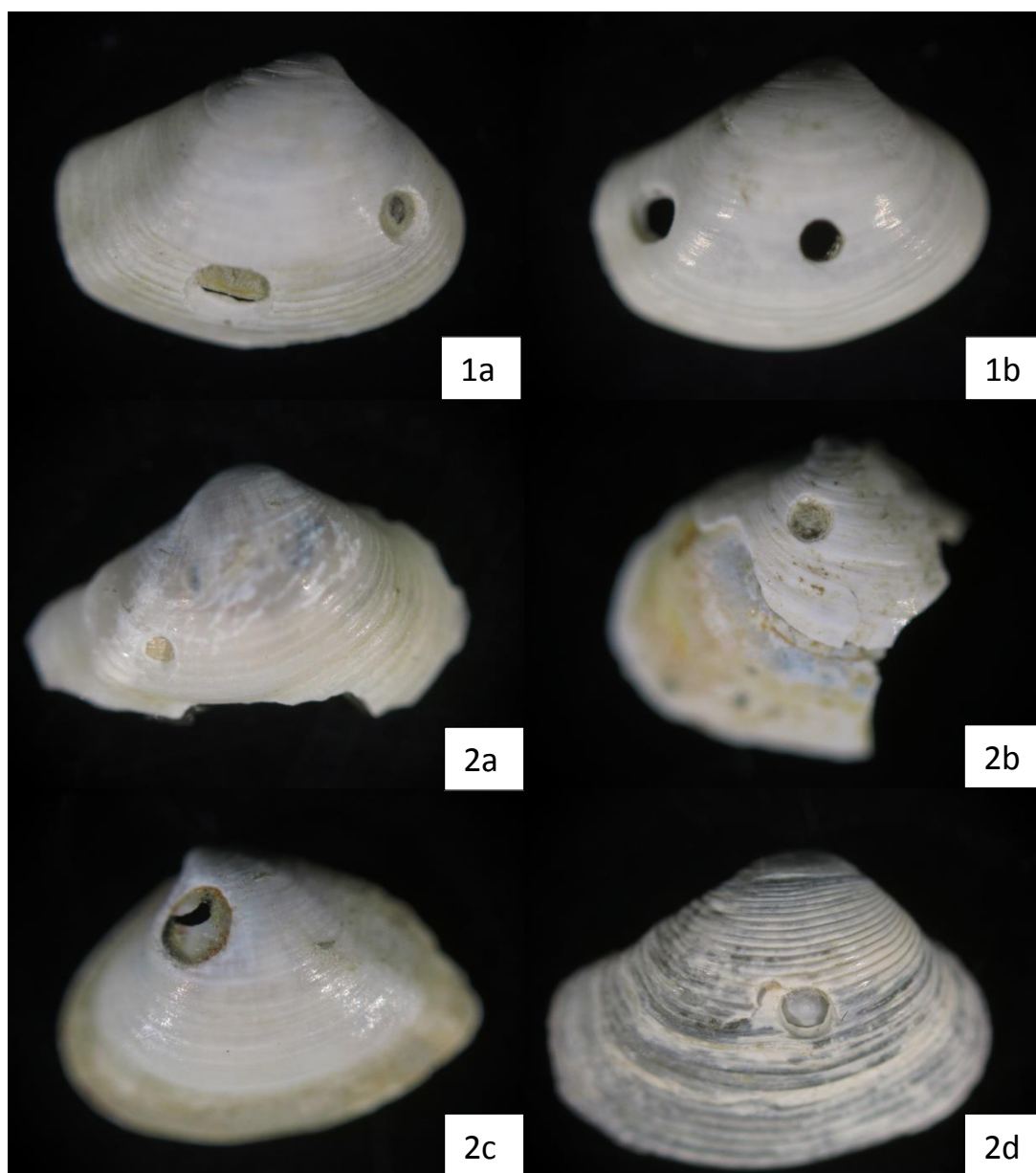2) b-d) Edge drilled valves of *Corbula gibba* from Piran M53

Plate 3
1) a-b) Multiple drilled valves of *Corbula gibba* from Panzano M28
2) a-d) Incompletely drilled valves of *Corbula gibba* from Panzano M28

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