



universität  
wien

# DISSERTATION

Titel der Dissertation

Quantitative studies of drilling predation on  
Cenozoic and Recent marine molluscs from  
Europe

Verfasserin

Jennifer A. SAWYER, B.Sc., M.Sc.

Angestrebter akademischer Grad

Doktorin der Naturwissenschaften (Dr. rer. nat.)

Wien, im März 2010

Studienkennzahl lt. Studienblatt: A 091 434

Dissertationsgebiet lt. Studienblatt: Paläontologie

Betreuer: Ao. Univ. -Prof. Mag. Dr. Martin ZUSCHIN



*For Helmut*



# Acknowledgements

I would like to extend my deepest gratitude to my supervisor Martin Zuschin, without whose patience, guidance and endless support writing this dissertation would have been utterly impossible. I would also like to thank all of the reviewers for the published portions of this dissertation: Patricia Kelley, Greg Dietl, Michal Kowalewski and Liz Harper. In every case their reviews were thorough, detailed, stimulating and resulted in greatly improved publications. Patricia Kelley and Michał Kowalewski deserve further thanks for agreeing not only to review my dissertation, but also to fly all the way to Vienna to act as reviewers for my Defensio.

Bettina Riedel and Michael Stachowitsch offered invaluable advice and support for the Northern Adriatic studies by helping collect samples, allowing me to use EAGU to photograph the seafloor during their already hectic field season, reading late versions of manuscripts, being amazing co-authors and introducing me to the magic of Adria.

Stefano Dominici spent days in the field and weeks at the binocular identifying species, but perhaps most importantly introducing me to some of the best Chianti and panino al prosciutto Italy has to offer!

Peter Peresler provided samples for use in one of the studies and useful discussions. Johann Hohenegger offered very helpful statistical advice and discussions. Thanks also to Mathias Harzhauser, Oleg Mandic, and Lovrenc Lipej for important discussions. Enzo Campani, Maurizio Forli, Mathias Harzhauser, and Oleg Mandic helped with identifications. Manfred Fritz helped in data acquisition. Alexandra Haselmair, Philipp Steiner, Didier Merle and Reinhard Roetzel supported field work.

I am very grateful for financial support provided through projects P19013-B17 and P17655-B03 of the Austrian Science Fund (FWF).

Very deep appreciation has been earned by Antonello Brigulio for a seemingly endless supply of the world's best limoncello, coffee and his constantly optimistic outlook. Benjamin Sames has also earned my gratitude. Benj has been an enormous help with translations, helping me to navigate through the bureaucratic offices of the City of Vienna and the University, introducing me to colleagues at conferences and always offering a few moments of support when I was feeling a bit lost. Monika Rockenschaub and Joyce Ampong-Gyasi, you have been my biggest cheerleaders. Thanks for forcing me to take time for myself every once in a while.

I would like to extend special thanks to the Semmelmayer family for their unbelievable support over the past three years! You have taken me into your home, fed me every Saturday, treated me on birthdays and holidays, given me a place to relax whether I needed it or not and tried your absolute hardest to teach me German!

I am very fortunate to be able to claim one of the most supportive, loving and caring families in the whole entire world. Caroline and Thomas, Wesley and Lynn-Anne, Laura and Michael, I love you all and thank you for your endless support! Mom, thanks for encouraging me to move to Austria to complete my doctorate work. Though I miss you and everyone else back home, I have grown so much as person and as a researcher here. I would not replace the experiences I've had during the past three years with any others. Dad, do you remember the hikes we would take when we wanted to collect rose quartz and any other rocks we could find when I was a little girl? What about all of those times you pointed out the foxes or the deer on the side of the road when we were driving down the highway? Or when we collected sea shells at the beach and I found one with a perfect round little hole straight through the middle and I asked you how it got there? You gave me an undying curiosity for nature and a passion for science. Thank you for opening my eyes to the world around me.

Helmut, many things have contributed to the completion of my thesis, but nothing compares to your love and support. Thanks for having so much patience for me over the past three years.

# Table of Contents

<b>Acknowledgements</b>	i
<b>List of Figures</b>	vii
<b>List of Tables</b>	xi
<b>Abstract</b>	xiii
<b>Zusammenfassung</b>	xv
<b>Chapter 1: Predator-prey interactions from <i>in situ</i> time lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic)</b>	1
1.1. Abstract	1
1.2. Introduction	2
1.3. Materials and Methods	5
1.3.1. <i>In situ</i> images	6
1.3.2. Quantitative samples	7
1.3.3. Size frequency of <i>Mytilus</i> and <i>Hexaplex</i>	7
1.3.4. Overall predation frequency	8
1.3.5. Prey effectiveness	8
1.3.6. Size refuge	10
1.4. Results	10
1.4.1. Composition of the mussel bed	10
1.4.2. <i>In situ</i> images	12
1.4.3. Size frequency distribution of prey and predator	14
1.4.4. Overall predation frequency	16
1.4.5. Mode of attack	16
1.4.6. Prey effectiveness	16
1.4.7. Size refuge	17
1.5. Discussion	17
1.6. Conclusions	28
1.7. References	30

**Chapter 2: Intensities of drilling predation of molluscan assemblages along a transect through the Northern Gulf of Trieste (Adriatic Sea) 39**

2.1. Abstract	39
2.2. Introduction	41
2.3. Study Area and Benthic Assemblages	44
2.4. Methods	46
2.5. Drilling Predators in the Northern Adriatic Sea	50
2.6. Results	51
2.6.1. Basic structure of the molluscan assemblages	51
2.6.2. Predation intensities in size categories	52
2.6.3. Predation intensities at different taxonomic levels	56
2.6.4. Life habits of molluscs and drilling predation	57
2.6.5. Environmental variation in drilling frequency	62
2.6.6. Diversity and predation intensities	76
2.7. Discussion	79
2.7.1. Drilling intensities of bivalves, gastropods and scaphopods	79
2.7.2. Life habits of prey and drilling predation	81
2.7.3. Environmental variation and drilling predation	86
2.7.4. Diversity and drilling predation	90
2.7.5. Size selectivity	92
2.7.6. Northern Adriatic drilling intensities and the low predation hypothesis	93
2.8. Conclusions	95
2.9. References	98

**Chapter 3: Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the Early and Middle Miocene marine fossil record of the Central Paratethys 115**

3.1. Abstract	115
3.2. Introduction	116
3.3. Geologic Setting	117
3.4. Methods	123
3.5. Results	126
3.5.1. Basic structure of molluscan assemblages	126
3.5.2. Drilling intensities at different taxonomic levels	126
3.5.3. Variation in drilling predation within localities	128
3.5.4. Variation in drilling predation between localities	135
3.5.5. Karpatian and Badenian drilling predation	138
3.5.6. Drilling predation in Central Paratethys environments	142
3.5.7. Drilling predation in other Miocene basins	151
3.6. Discussion	152
3.7. Conclusions	160
3.8. References	161

<b>Chapter 4: Size filtering fossils: Effects of sieve size on diversity and drilling intensity estimates in Eocene and Miocene molluscs of Central Europe</b>	<b>171</b>
4.1. Abstract	171
4.2. Introduction	172
4.3. Geologic Overview	176
4.4. Materials and Methods	177
4.4.1. Material collection and processing	177
4.4.2. Diversity estimates	178
4.4.3. Drilling intensities	179
4.5. Results	180
4.5.1. Diversity estimates	180
4.5.2. Drilling intensities	185
4.6. Discussion	192
4.6.1. Previous and new suggestions for sieving approaches	198
4.7. Conclusions	200
4.8. References	201
<b>Appendix A</b>	<b>209</b>
<b>Appendix B</b>	<b>219</b>
<b>Curriculum Vita</b>	<b>227</b>



# List of Figures

## Chapter 1: Predator-prey interactions from *in situ* time lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic):

- Fig. 1.1.** Study area: mussel bed located about 2 km off coast of Piran, Slovenia (Northern Adriatic Sea; 45° 32.69 N; 13° 34.94 E). 6
- Fig. 1.2.** *Hexaplex trunculus* and *Mytilus galloprovincialis* with traces of successful predatory attempts. 9
- Fig. 1.3.** Size-frequency distributions of *Mytilus galloprovincialis* and *Hexaplex trunculus*. 18
- Fig. 1.4.** Chipping frequency (mean and 95 % confidence intervals) of small, medium and large *Mytilus galloprovincialis*. 19
- Fig. 1.5.** Size distribution of all *Mytilus galloprovincialis*, and Marginally chipped *M. galloprovincialis* in 5 mm size intervals. 20

## Chapter 2: Intensities of drilling predation of molluscan assemblages along a transect through the Northern Gulf of Trieste (Adriatic Sea)

- Fig. 2.1.** Study area in the Northern Adriatic Sea, the Gulf of Trieste, Bay of Panzano and subtidal transect showing the positions of the sublittoral samples 00-8. 46
- Fig. 2.2.** Drilled and undrilled epifaunal and infaunal mollusc species common in sublittoral habitats in the Gulf of Trieste in three size categories. 55
- Fig. 2.3.** Mean drill frequencies of abundant mollusc families pooled across all samples. 58
- Fig. 2.4.** Comparison of drill frequencies and prey effectiveness across ecological categories. 60
- Fig. 2.5.** Environmental analysis of predation parameters for tidal flat, pooled sublittoral, and sublittoral environments. 64
- Fig. 2.6.** Tidal flat and sublittoral drill frequencies of two *Bittium* species common in both intertidal and sublittoral samples. 65
- Fig. 2.7.** Predation intensities of the total assemblage per sample for drill frequency and prey effectiveness. 67

<b>Fig. 2.8.</b> Drill frequency and prey effectiveness from each studied environment.	68
<b>Fig. 2.9.</b> Comparison of drill frequencies and prey effectiveness for families with $n > 10$ in at least three environments.	69
<b>Fig. 2.10.</b> Inter-environmental comparison of drilling predation across bivalve feeding strategies for drill frequencies and prey effectiveness.	73
<b>Fig. 2.11.</b> Inter-environmental comparison of drill frequencies and prey effectiveness for gastropod feeding strategies.	74
<b>Fig. 2.12.</b> Inter-environmental comparison of drill frequencies and prey effectiveness for bivalve substrate relationships.	74
<b>Fig. 2.13.</b> Inter-environmental comparison of drill frequencies and prey effectiveness across epifaunal bivalve attachment strategies.	77
<b>Fig. 2.14.</b> Rarefaction of molluscan faunas from samples collected along a transect in the Gulf of Trieste.	80

### **Chapter 3: Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the Early and Middle Miocene marine fossil record of the Central Paratethys**

<b>Fig. 3.1.</b> Lower (Burdigalian) to Upper (Tortonian) Miocene geochronology and biostratigraphy with stratigraphic positions of sampled localities in the Central Paratethys.	118
<b>Fig. 3.2.</b> Map of sample localities in Austria and Slovakia.	118
<b>Fig. 3.3.</b> Drilling predation pooled across all samples and all taxa, and the classes Bivalvia, Gastropoda and Scaphopoda.	127
<b>Fig. 3.4.</b> Drilling predation of common bivalve and scaphopod families in the Central Paratethys.	131
<b>Fig. 3.5.</b> Drilling predation of common gastropod families in the Central Paratethys	132
<b>Fig. 3.6.</b> Drilling predation within Karpatian and Badenian localities.	134
<b>Fig. 3.7.</b> Variation in drilling predation for the total assemblage and mollusc classes between each Karpatian locality sampled.	136
<b>Fig. 3.8.</b> Variation in drilling predation for the total assemblage and mollusc classes between each Badenian locality sampled.	137

<b>Fig. 3.9.</b> Drilling predation for the Karpatian and Badenian assemblages of the Central Paratethys for the total molluscan assemblage, mollusc classes, and abundant families.	139
<b>Fig. 3.10.</b> Ordination of family-level drill frequencies of Central Paratethys fossil mollusc assemblages using non-metric Multidimensional Scaling (nMDS).	141
<b>Fig. 3.11.</b> Drilling predation for intertidal and sublittoral assemblages of the Central Paratethys for the total molluscan fauna, mollusc classes, and abundant families.	144
<b>Fig. 3.12.</b> Drilling predation for shallow sublittoral and inner shelf assemblages of the Central Paratethys for the total molluscan fauna, mollusc classes, and abundant families.	146
<b>Fig. 3.13.</b> Species-level drilling predation for the family Neritidae from intertidal, shallow sublittoral and inner sand environments.	147
<b>Fig. 3.14.</b> Species-level drilling predation for the family Potamididae from intertidal, shallow sublittoral and inner sand environments.	148
<b>Fig. 3.15.</b> Drilling predation for inner shelf mud and sand assemblages of the Central Paratethys for the total molluscan fauna, molluscan classes, and abundant families.	150

#### **Chapter 4: Size filtering fossils: Effects of sieve size on diversity and drilling intensity estimates in Eocene and Miocene molluscs of Central Europe**

<b>Fig. 4.1.</b> Analyses of molluscan diversity among size fractions within the Paris and Korneuburg Basins.	182
<b>Fig. 4.2.</b> Molluscan diversity analyses using different sieve treatments to process samples within the Paris and Korneuburg Basins.	184
<b>Fig. 4.3.</b> Molluscan drilling frequencies for each size fraction within the Paris and Korneuburg Basins.	187
<b>Fig. 4.4.</b> Drilling frequencies of common families calculated from each size fraction within the Paris and Korneuburg Basins.	189
<b>Fig. 4.5.</b> Molluscan drilling frequencies derived from using different sieve sizes to process samples within the Paris and Korneuburg Basins.	191
<b>Fig. 4.6.</b> Drilling frequencies of common families derived from using different sieve sizes to process samples within the Paris and Korneuburg Basins.	193

## Appendix B

- Appendix B Fig. 1.** Mean drill frequencies and prey effectiveness of the total assemblage and among classes pooled across all samples. 221
- Appendix B Fig. 2.** Mean drilling frequencies of the five most abundant bivalve and gastropod species pooled across all samples. 222
- Appendix B Fig. 3.** Significantly different intra-environmental drill frequencies for families ( $n > 20$ ) from level bottom mud samples and intra-environmental prey effectiveness for Corbulidae. 223
- Appendix B Fig. 4.** Intra-environmental drill frequencies for the family Cerithiidae, and intra-environmental prey effectiveness for families in both level bottom sand samples. 224
- Appendix B Fig. 5.** Intra-environmental comparison of drill frequencies and prey effectiveness for ecological categories with significant differences among level bottom mud samples. 225
- Appendix B Fig. 6.** Intra-environmental comparison of drill frequencies and prey effectiveness for ecological categories with significant differences between level bottom sand samples. 226

# List of Tables

## Chapter 1: Predator-prey interactions from *in situ* time lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic)

<b>Table 1.1.</b> Species composition and abundances of live material from each sample collected from the mussel bed	11
<b>Table 1.2.</b> Summary of <i>Hexaplex trunculus</i> activity compiled from 22.9 h of time-lapse photography at 6 min intervals on a subtidal mussel bed in the Gulf of Trieste	13
<b>Table 1.3.</b> ANOVA summary of differences in mean shell lengths of <i>Mytilus galloprovincialis</i> and <i>Hexaplex trunculus</i>	15
<b>Table 1.4.</b> Tukey's pair-wise comparisons of mean shell lengths among samples	15
<b>Table 1.5.</b> Marginal chipping and drilling frequencies per sample	19

## Chapter 2: Intensities of drilling predation of molluscan assemblages along a transect through the Northern Gulf of Trieste (Adriatic Sea)

<b>Table 2.1.</b> Summary of drill hole data for each sample and for environments	52
<b>Table 2.2.</b> Taxonomic summary of drill hole data pooled across all samples for classes, families/subfamilies and the 5 most abundant species of bivalves and gastropods	53
<b>Table 2.3.</b> Ecological summary of drill hole data pooled across all samples	61
<b>Table 2.4.</b> Intra-environmental drill frequency variation in level bottom mud samples for the total assemblage, classes, families, genera and species	70
<b>Table 2.5.</b> Intra-environmental drill frequency variation in level bottom sand samples for the total assemblage, classes, families, genera and species	71
<b>Table 2.6.</b> Intra-environmental drill frequency variation among ecological categories within level bottom mud samples	78
<b>Table 2.7.</b> Intra-environmental drill frequency variation among ecological categories within level bottom sand samples	79
<b>Table 2.8.</b> Correlation between diversity indices, total shell abundance,	81

predator abundances, prey effectiveness and drill frequency

### **Chapter 3: Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the Early and Middle Miocene marine fossil record of the Central Paratethys**

<b>Table 3.1.</b> Summary of environments, numbers of shells studied and predation data from Karpatian and Badenian samples.	120
<b>Table 3.2.</b> Taxonomic summary of drill hole data from Karpatian and Badenian aged molluscs from the Central Paratethys for the overall assemblage, classes and families	129
<b>Table 3.3.</b> Average drill frequencies and standard variations calculated from individual samples pooled into time, environment, and locality categories	135
<b>Table 3.4.</b> Results of ANOSIM (analysis of similarity) for Karpatian versus Badenian environments	140
<b>Table 3.5.</b> Statistical comparison of Central Paratethys drill frequencies published data from other Miocene basins using Chi-squared test	152

### **Chapter 4: Size filtering fossils: Effects of sieve size on diversity and drilling intensity estimates in Eocene and Miocene molluscs of Central Europe**

<b>Table 4.1.</b> Summary of drill frequency data for the total assemblage, bivalves, gastropods and abundant families for each size fraction in the Eocene Paris Basin and Miocene Korneuburg Basin	186
<b>Table 4.2.</b> Summary of drill frequency data calculated for the total assemblage, bivalves, gastropods and abundant families for each sieve treatment in the Eocene Paris Basin and the Miocene Korneuburg Basin	190

### **Appendix A**

<b>Appendix A Table 1.</b> Summary of living and dead molluscs pooled across all samples	211
<b>Appendix A Table 2.</b> Summary of drill hole data for ecological categories across environments	215

## Abstract

Direct evidence of ecological interactions between fossil organisms is generally rare, but one exception is predatory drill holes on hard-shelled prey. Few studies have accounted for spatial variation in drilling predation when exploring trends through time, data on predation from European molluscs are scarce and predation intensities have rarely been studied for ecological guilds. Natural variation through space, however, may confound temporal trends. To address these issues, four studies involving drilling predation on Cenozoic and Recent molluscs from Central Europe are presented.

Examination of >85,000 molluscs from 134 bulk samples suggests that variation in drilling predation can be drastic within and between environments. Drill frequency of Miocene storm bed samples at the locality Immendorf varied between 0 and 57.5%, and values from the modern Northern Adriatic ranged from 1.4% to 27.4% from intertidal to sublittoral deposits, suggesting careful environmental determinations are necessary to ensure sampling protocols account for spatial variation in predation intensities.

Overall drilling predation from Miocene deposits of the Central Paratethys is lower than that from contemporary deposits from North America, suggesting large-scale differences in predation pressure. Comparison of Eocene samples from the Paris Basin and Miocene samples from the Central Paratethys revealed assemblage-level drilling frequencies were sensitive to the sieve-size used for sample processing, highlighting potential problems when comparing studies using different methodologies.

In the Northern Adriatic Sea, highest drilling intensities were seen in suspension feeding, epifaunal and cementing taxa, supporting long-held paleoecological theories relating predation to changes in ecological guilds through the Phanerozoic. A case-study of predation on *Mytilus galloprovincialis* by the muricid *Hexaplex trunculus* on a sublittoral mussel bed in the Gulf of Trieste indicates facultative feeding activity, with the gastropod often chipping rather than drilling its prey, suggesting that multiple modes of predation should be considered whenever possible.



# Zusammenfassung

Direkte Nachweise ökologischer Interaktionen zwischen fossilen Organismen sind eher selten. Eine Ausnahme bilden jedoch durch Prädatoren verursachte Bohrlöcher an hartschaliger Beute. Wenige Studien berücksichtigen bei der Untersuchung zeitlicher Trends die räumliche Verteilung von räuberischen Bohrlöchern. Von europäischen Mollusken gibt es nur spärliche Daten über solche räuberische Aktivitäten und Bohrintensitäten für ökologische Gilden sind überhaupt selten untersucht worden. Räumliche Schwankungen können jedoch zeitliche Trends überprägen. Hier werden vier Studien präsentiert, die Bohrprädatoren an känozoischen und rezenten Mollusken unter diesen Fragestellungen behandeln.

Die Auswertung von mehr als 85 000 Mollusken aus 134 quantitativen Sedimentproben legt nahe, dass Veränderungen der Bohr-Prädation innerhalb und zwischen Ökosystemen drastisch sein können. Die Bohr-Häufigkeit in miozänen Sturmablagerungen der Lokalität Immendorf variierte zwischen 0 und 57.5% und Werte aus der modernen Nordadria reichten von 1.4% bis 27.4% von intertidalen bis sublittoralen Ablagerungen. Sorgfältige Bestimmungen der Paläoenviroments sind also notwendig, um räumliche Verteilungsmuster sinnvoll interpretieren zu können.

Insgesamt ist die Bohrintensität miozäner Ablagerungen der zentralen Paratethys geringer als die zeitgleicher Ablagerungen Nordamerikas, was auf grosse regionale Unterschiede im Raubdruck hinweist. Der Vergleich von Proben aus dem Eozän des Pariser Beckens mit solchen aus dem Miozän der zentralen Paratethys zeigte, dass Bohr-Häufigkeiten von Vergesellschaftungen stark von der Siebgrösse bei der Probenaufbereitung beeinflusst werden, Trends zwischen Siebfraktionen jedoch ähnlich sind. Beim Vergleich zwischen Studien müssen solche methodischen Unterschiede berücksichtigt werden.

In der Nordadria wurden die höchsten Bohrintensitäten bei filtrierenden, epifaunalen und festgehefteten Taxa beobachtet. Dies unterstützt paläoökologische Theorien, die Raubdruck mit Veränderungen ökologischer Gilden während des Phanerozoikums in Verbindung setzen. Eine Fallstudie über Prädation an der Muschel *Mytilus galloprovincialis* durch die Raubschnecke *Hexaplex trunculus* auf einer sublittoralen Muschelbank im Golf von Triest zeigt fakultative Fressaktivität, wobei der Gastropode oft eher die Schale der Beute mechanisch aufbrach, anstatt hineinzubohren. Wann immer möglich, sollten also alle Prädationsmodi in Betracht gezogen werden.



**CHAPTER 1:**  
**PREDATOR-PREY INTERACTIONS FROM *IN SITU* TIME-LAPSE  
OBSERVATIONS OF A SUBLITTORAL MUSSEL BED IN THE GULF  
OF TRIESTE (NORTHERN ADRIATIC)<sup>1</sup>**

**1.1. Abstract**

*Hexaplex trunculus* (Linnaeus, 1758) is one of the most abundant and widespread muricid gastropods in the Northern Adriatic Sea, but relatively little is known about the feeding ecology of this predator. We examined the activity of *H. trunculus* on a sublittoral mussel bed at 24 m depth through *in situ* time-lapse observations and bulk samples. The camera photographed a 0.25 m<sup>2</sup> section of the mussel bed at 6-min intervals for ~23 h. Photos were examined frame-by-frame for gastropod movement and activities, especially interactions between *H. trunculus* and *Mytilus galloprovincialis* (Lamarck, 1819). Our survey indicates high activity-levels of *H. trunculus* on the seafloor: all gastropods made minor movements, most made major movements, and most left the field of view during the study interval. On average, individuals remained stationary for only 7.3 h. Two predation attempts on *Mytilus* involving conspecific competition were documented, and one *Hexaplex* was consuming a mussel at the onset of the deployment. Additionally, 487 *M. galloprovincialis* from four diver-taken 0.25 m<sup>2</sup> quadrates were measured and examined for traces of marginal chipping and drilling predation. *Mytilus* from surface samples ranged from 11.1 mm to 95.5 mm in length, and one of the four samples had a significantly different average

---

<sup>1</sup> Published in: Sawyer, J.A., Zuschin, M., Riedel, B., Stachowitsch, M., 2009. Predator-prey interactions from *in situ* time-lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic). *Journal of Experimental Marine Biology and Ecology* 371, 10-19.

shell length from the others. 114 *H. trunculus* were collected and measured. *Hexaplex* ranged from 22.1 mm to 86.1 mm and the mean shell length did not differ among samples, though they were overwhelmingly medium and large. Predation frequency (the ratio of successfully preyed upon bivalves to the total number of bivalves sampled) is high at the studied site (> 55 %), and large gastropods preferred a chipping mode of predation to drilling, supporting earlier laboratory studies showing a preference for *M. galloprovincialis* and this predation strategy. Prey effectiveness (the ratio of failed predatory attacks to total predatory attacks) is also high (63.8 %), and no evidence of a size refuge was found. Feeding in *H. trunculus* is highly facultative, calling for caution when using drill holes to estimate predation intensities; whenever possible, traces of multiple predation modes should be considered.

## **1.2. Introduction**

Predator–prey interactions are frequently investigated in laboratory experiments e.g., Freeman and Byers, 2006; Peharda and Morton, 2006; Chattopadhyay and Baumiller, 2007). While this approach allows a high level of control, it often does not accurately reflect the same interactions in the natural environment: natural settings are complex, and most laboratory experiments are designed to eliminate such complexities. Moreover, most field data tend to be from more accessible intertidal habitats (e.g., Sanford et al., 2003; Meyer and Byers, 2005; Edgell and Rochette, 2008) than from the methodologically more demanding subtidal settings (e.g., Breen et al., 1982; Wahle and Steneck, 1992). We build upon recent laboratory studies on the predatory behavior of

*Hexaplex trunculus* (Peharda and Morton, 2006; Morton et al., 2007) to better understand its ecology in its natural setting.

Three modes of predatory attack are documented in muricid gastropods: drilling (Harper and Peck, 2003; Peharda and Morton, 2006; Harding et al., 2007), marginal chipping (Peharda and Morton, 2006) and wedging (Vermeij and Kool, 1994). Moreover, at least one laboratory study has documented muricids killing mussels without producing any visible damage to the prey shell (Kowalewski, 2004). Drill holes are preserved in the shell and can be easily quantified in bulk samples. Marginal chipping leaves characteristic damage on the shell's exterior (Warren, 1916; Carriker, 1951) that can easily be quantified in complete shells with limited marginal damage from other sources.

Predation is a key process in structuring benthic communities (MacArthur, 1972; Holt, 1977; Palmer, 1979; Bohannan and Lenski, 2000), and recent literature proposes low predation pressure as a general background condition in the Northern Adriatic (e.g., McKinney and Hageman, 2006; McKinney, 2007). McKinney (2007) lists asteroids, bottom-feeding fish, cephalopods, crustaceans, gastropods and polychaetes as carnivores in the Adriatic basin, but few studies have examined the effects of these predators. Muricid gastropods play an important role in regulating the population dynamics of mussel, barnacle, tubeworm and limpet prey (Menge, 1974; Morton, 2004). *H. trunculus* is one of the most abundant and widespread muricid gastropods in the Northern Adriatic, where it is fished for human consumption and used as fish bait. Also, *Hexaplex's* heavy consumption of cultured bivalve prey has rendered it a pest species (Benović, 1997). Densities up to 120 individuals/m<sup>2</sup> have been reported at black mussel (*Mytilus galloprovincialis*) and European flat oyster (*Ostrea edulis*,

Linnaeus, 1758) aquaculture fisheries (Zavodnik and Šimunović, 1997). Wurzian (1982) studied the function of carnivores from epifaunal communities in the Northern Adriatic and determined that *H. trunculus* has a homogeneous distribution there (average density  $0.2 \pm 0.1$  individuals/m<sup>2</sup>). In a baiting experiment using a dead fish, 39 individuals were attracted, equivalent to every *H. trunculus* within 200 m<sup>2</sup>. The gastropod's diet consisted of *Arca noae* (Linnaeus, 1758), *Chlamys varia* (Linnaeus, 1758), *Corbula gibba* (Olivi, 1792), *Venus* sp. (Linnaeus, 1758), and *Ophiothrix quinquemaculata* (DelleChiaje, 1828); it also grazed on sponges.

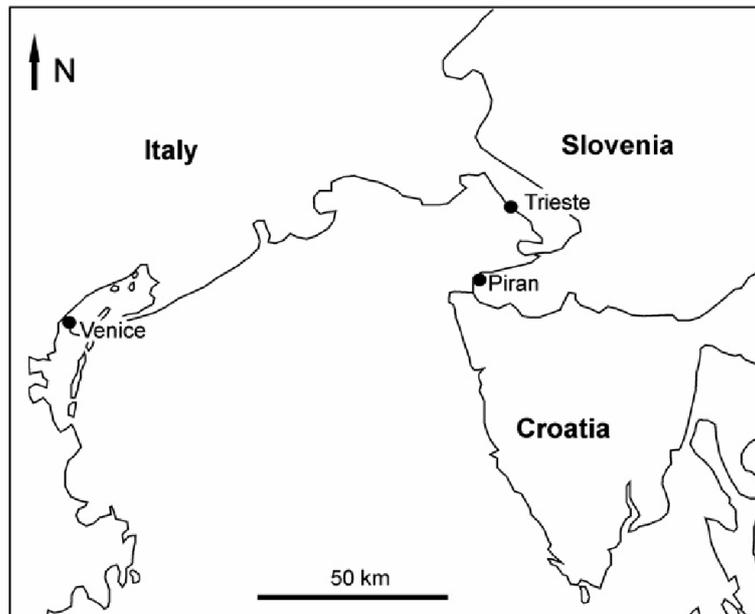
Despite its abundance and relative importance as a consumer of cultured bivalves, little is known about the ecology of *H. trunculus*. Most studies deal with the occurrence of imposex (Axiak et al., 1995; Terlizzi et al., 1998; Chiavarini et al., 2003) and its purple dye (Andreotti et al., 2004). Peharda and Morton (2006) and Morton et al. (2007) studied a variety of aspects of *H. trunculus* feeding behavior in laboratory settings, including predator size, mode of attack, prey choice, handling time and feeding rates using three species of bivalves common in the Northern Adriatic: *A. noae*, *M. galloprovincialis* and *Modiolus barbatus* (Linnaeus, 1758). According to their results, *H. trunculus* is capable of two modes of attack: drilling a hole through the shell and chipping, in which the gastropod uses a labral spine to chip or wedge the posterior portion of the bivalve shell. *M. galloprovincialis* was the preferred prey, and medium and large-sized predators (~ 55 mm and ~ 70 mm shell length, respectively) chose chipping over drilling when attacking these mussels (Peharda and Morton, 2006). The authors calculated that a medium sized *H. trunculus* consumes approximately 18 large *M. galloprovincialis* (~ 65 mm long) per year.

According to Morton et al.'s (2007) results, *H. trunculus* tended to chip thin-shelled prey, but drilled bivalves with thicker shells. *H. trunculus* attacked *M. galloprovincialis* by drilling (either marginally or laterally) or chipping, based on the predator and prey size (Peharda and Morton, 2006; Morton et al., 2007). Small gastropods tended to drill at the valve margin, medium gastropods tended to chip or drill (at the valve margin) in about equal proportions, and in contrast to Peharda and Morton (2006), large gastropods tended to laterally drill medium and large-sized *Mytilus*.

### **1.3. Materials and Methods**

A mussel bed of *M. galloprovincialis* on a subtidal muddy sand bottom in the Gulf of Trieste, Northern Adriatic (Fig. 1.1) offers a unique setting in which to examine *H. trunculus* predatory behavior. The mussel bed has a diameter of approximately 17 m and is located about 2 km off Piran (Slovenia, Northern Adriatic Sea, N 45° 32.69 E 13°34.94) below the oceanographic buoy of the Marine Biology Station Piran. All data were collected using SCUBA.

Time-lapse photography on a 0.25 m<sup>2</sup> section of the mussel bed provides information on the gastropod's activity at 24 m water depth. In addition, quantitative samples allow us to evaluate prey size preference and mode of attack (drilling or marginal chipping). Prey effectiveness — a metric used to determine the frequency of survival of predatory attack within a prey population (Vermeij,



**Fig. 1.1.** Study area: mussel bed located about 2 km off coast of Piran, Slovenia (Northern Adriatic Sea; 45° 32.69 N; 13° 34.94 E).

1987; e.g., Walker and Yamada, 1993; Kelley et al., 2001) — is examined for *M. galloprovincialis*, and we look for evidence of a size refuge.

### 1.3.1. *In situ* Images

A specially designed underwater camera system (for a detailed description see Stachowitsch et al., 2007), positioned atop a 50 × 50 × 50 cm aluminum frame, was deployed on the mussel bed to document a 0.25 m<sup>2</sup> quadrat. 229 *in situ* photographs were taken at 6-min intervals for approximately 23 h from 12:13 on 24 September 2007 to 11:01 on 25 September 2007. These photographs were examined frame-by-frame to document *H. trunculus* activity, including mobility, prey consumption, and potential predatory attempts. Every individual gastropod was also examined for minor movements (less than one body-length), major movements (greater than one body-length), conspecific interactions, predatory behavior, and time spent consuming prey. Peharda and Morton's (2006)

illustration of a *Hexaplex* drilling a *Mytilus* shows the gastropod positioned atop the posterior portion of the mussel's shell. Those individuals that made movements ending in such prey grappling and manipulation were interpreted to be actively searching for prey. These activities were noted, as were potential attempts to chip or drill the prey shell, and prey consumption. A short time-lapse film was created from the full series of photographs.

### **1.3.2. Quantitative Samples**

To evaluate predation frequency, size preference, and prey effectiveness, four bulk samples of *H. trunculus* and *M. galloprovincialis* were collected by hand from the mussel bed. One sample was collected in July and another in September 2006, and two samples were collected in September 2007. For each sample, a 0.25 m<sup>2</sup> quadrat was placed randomly on the mussel bed and all living molluscs and dead shells on the surface collected.

All living organisms were identified, and living and dead *M. galloprovincialis* and *H. trunculus* were measured. To avoid potential taphonomic bias, only whole specimens with otherwise intact shell margins were evaluated. Dead mussels consisted of both articulated and disarticulated valves. Disarticulated *M. galloprovincialis* within each sample were matched based on valve size and shape, growth lines and repairs. Perfectly matched valve-pairs and articulated mussels were measured (length and width) and examined for traces of marginal chipping and drilling predation.

### **1.3.3. Size-Frequency of *Mytilus* and *Hexaplex***

The length, width and wet weight (including shell) of live *H. trunculus* and *M. galloprovincialis* were measured using vernier callipers ( $\pm 0.1$  mm) and an

electronic scale ( $\pm 0.01$  g). In contrast with Peharda and Morton's (2006) study, in which bivalves of three exact sizes were used, our study examines *M. galloprovincialis* of all sizes encountered. Peharda and Morton (2006) represented small *Mytilus* with  $20 \text{ mm} \pm 1 \text{ mm}$ , medium with  $35 \text{ mm} \pm 1 \text{ mm}$ , and large with  $65 \text{ mm} \pm 1 \text{ mm}$  long individuals. To simplify comparison with their study, we assigned *M. galloprovincialis* to the following size classes (by length): small  $< 27.5 \text{ mm}$ ; medium  $27.5 \text{ mm} - 50 \text{ mm}$ ; large  $> 50 \text{ mm}$ . The boundary between small and medium *Mytilus* is exactly halfway between Peharda and Morton's (2006) small and medium values, and the boundary between medium and large is exactly halfway between their medium and large values.

Similarly, Peharda and Morton (2006) utilized exact sizes to represent small ( $40 \text{ mm} \pm 1 \text{ mm}$ ), medium ( $55 \text{ mm} \pm 1 \text{ mm}$ ), and large ( $70 \text{ mm} \pm 1 \text{ mm}$ ) *H. trunculus* in the laboratory. To simplify comparison with their study, we assigned *H. trunculus* to the following size classes: small  $< 47.5 \text{ mm}$ ; medium  $47.5 \text{ mm} - 62.5 \text{ mm}$ ; large  $> 62.5 \text{ mm}$ . Analogous to *Mytilus*, our boundaries were exactly halfway between Peharda and Morton's (2006) categories.

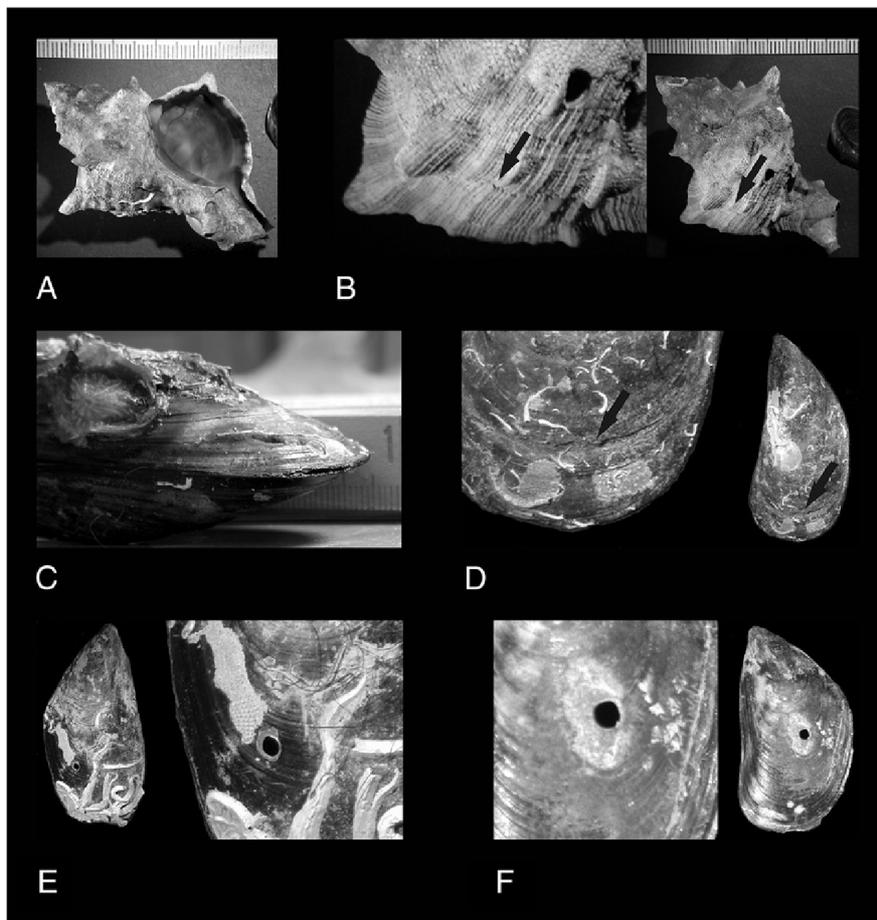
#### **1.3.4. Overall Predation Frequency**

Lethal predation frequency is calculated by dividing the number of mussels with evidence of lethal chipping and/or lethal drilling (Fig. 1.2.) by the total number of dead valve-pairs in the sample population (e.g., Dietl, 2004). Here, we examine the frequency of drilling and marginal chipping.

#### **1.3.5. Prey Effectiveness**

Repair scars (Vermeij, 1983, 2002; Kowalewski, 2002; Zuschin et al., 2003) and incomplete drill holes (Vermeij, 1983; Kowalewski, 2002; Dietl, 2003)

are often cited as evidence of unsuccessful predatory attempts on bivalves. Nonetheless, not all incomplete drill holes indicate unsuccessful predation (Kowalewski, 2004). Here, we examined each bivalve pair for evidence of failed (repair scars, incomplete drill holes) and successful (lethal chipping traces, complete drill holes) attacks. Prey effectiveness is calculated by dividing the number of unsuccessful predatory attacks by the total number of predatory attacks in a population (Vermeij, 1987). This number represents the frequency with which *M. galloprovincialis* survived predation attempts by *H. trunculus*.



**Fig. 1.2.** *Hexaplex trunculus* and *Mytilus galloprovincialis* with traces of successful predatory attempts. A) *H. trunculus* in apertural view; B) *H. trunculus* with repair scar, possibly formed during failed chipping attack; C) *M. galloprovincialis* with traces of successful chipping predation; D) *M. galloprovincialis* (length: 80.3 mm) with repair scar; E-F) *M. galloprovincialis* with complete drill hole (Lengths: E. = 70.8 mm; F. = 71.6 mm).

### 1.3.6. Size refuge

We compared the size–frequency distribution of the collected samples of *M. galloprovincialis* to the frequency distribution of marginally chipped and drilled individuals at 5 mm length intervals to identify potential size refuges, i.e., the size at which the frequency of attacks drops significantly (Boulding, 1984; Leighton, 2002).

## 1.4. Results

### 1.4.1. Composition of the mussel bed

*M. galloprovincialis* and their predators *H. trunculus* were by far the dominant species in the 4 quadrates taken at the sampling site (Table 1.1). *Mytilus* were byssally attached to other shells and to each other, forming dense clumps of up to 32 individuals. Living and dead mussels provided a substratum for encrusting taxa, including macroscopically conspicuous sponges, ascidians (*Microcosmus* spp., *Phallusia mammilata*), and anthozoans (*Cereus pedunculatus*). These were accompanied by the more inconspicuous encrusting molluscs (small oysters and anomiids), balanids (*Balanus* sp., *Chthalamus depressus*), bryozoans (e.g., *Schizoporella longirostris*) and serpulids (e.g., *Pomatoceros triqueter*). Other byssally-attached bivalves in the mussel bed included *M. barbatus* and *C. varia*. The nestling bivalve *Lima hians* was abundant in one of the samples; other nestlers included *Hiatella arctica*. An interesting component was the typically infaunal common nut clam *Nucula nucleus*, which was abundant among the byssus threads of mussels, potentially feeding on their fecal pellets. Vagile elements included galatheid (*Galathea* spp., *Pisidia* spp.) and

xanthid (*Pilumnus spinifer*) crabs, hermit crabs (*Paguristes eremita*), unidentified shrimps and scavenging gastropods (*Nassarius coronatus*), ophiurids (mostly *Ophiothrix quinquemaculata*, *Ophiura* spp.), echinoids (*Psammechinus microtuberculatus*) and a holothurian (*Ocnus planci*).

**Table 1.1.** Species composition and abundances of live material from each sample collected from the mussel bed

Taxa	Sample 1	Sample 2	Sample 3	Sample 4
Porifera				
Sponges (unidentified)	1	6	2	3
<i>Suberites domuncula</i>	–	–	–	1
Anthozoa				
<i>Cereus pedunculatus</i>	1	–	–	4
Platyhelminthes				
Turbellaria (unidentified)	–	–	1	–
Gastropoda				
<i>Hexaplex trunculus</i>	18	5	68	21
<i>Nassarius coronatus</i>	–	–	25	3
Bivalvia				
<i>Nucula nucleus</i>	14	7	–	5
<i>Mytilus galloprovincialis</i>	159	12	91	20
<i>Modiolus barbatus</i>	–	1	–	–
<i>Chlamys varia</i>	1	–	3	–
<i>Anomia ephippium</i>	2	–	–	–
<i>Lima hians</i>	–	1	9	1
<i>Ostrea</i> sp.	–	–	–	1
<i>Hiatella arctica</i>	–	–	1	1
Polychaeta				
Serpulids ( <i>Pomatoceros triqueter</i> )	–	–	1	–
Polychaetes (unidentified)	–	–	1	–
Crustacea				
<i>Chthamalus depressus</i>	–	–	5	–
<i>Balanus</i> sp.	–	–	1	–
Shrimp (unidentified)	2	–	10	–
<i>Paguristes eremita</i>	–	–	3	1
<i>Galathea</i> spp.	5	1	6	20
<i>Pisidia</i> spp.	9	1	11	20
<i>Pilumnus spinifer</i>	5	1	7	3
Bryozoa				
Various species (e.g., <i>Schizoporella longirostris</i> )	1	1	1	1
Holothuroidea				
<i>Ocnus planci</i>	1	–	3	–
Echinoidea				
<i>Psammechinus microtuberculatus</i>	1	–	3	2
Ophiuroidea				
<i>Ophiothrix quinquemaculata</i>	12	15	5	7
<i>Ophiura</i> spp.	–	–	1	2
Ascidiacea				
<i>Phallusia mammilata</i>	–	–	1	–
<i>Microcosmus</i> spp.	–	–	2	2

For colonial organisms the numbers of colonies were counted.

### 1.4.2. In situ images

Thirty-nine *H. trunculus* were observed over the course of 22.9 h of in situ images. Most gastropods had characteristic epibiont growth, so it was possible to recognize individuals that left and later re-entered the frame. Twenty-five individuals were present in the quadrat at the beginning of observations. Thereafter, 19 *Hexaplex* entered and 29 left the quadrat. The last frame contained 12 individuals. Eight *H. trunculus* remained within the field of view for the entire duration of observations (Table 1.2).

All gastropods moved during the deployment: 38 of the 39 made minor movements, and 35 made major movements. On average, each *Hexaplex* made many more minor movements (29.9), than major movements (4.4). On average, an individual remained completely stationary for 7.3 h. 74 % of the gastropods remained stationary for at least 1 h, 44 % for at least 6 h, 31 % for at least 12 h, 23 % for at least 16 h, and 8 % for at least 20 h.

Two *H. trunculus* were flipped over during observations. The causes of these disruptions were not documented in either case. The first individual spent 8.0 h attempting to flip itself back to its natural position; the second was able to right itself in less than 12 min.

One gastropod was feeding on a *M. galloprovincialis* as photography began. That individual continued to feed for an additional 10.5 h. Two gastropods manipulated prey after a series of major moves. In both cases, the gastropods positioned themselves over the posterior margin of the same *Mytilus* shell, similarly to the drilling *H. trunculus* diagrammed in Peharda and Morton (2006). Minor wiggles between frames indicate slight movement, presumably attempts to access the mussel. The first searched for 0.3 h and then spent 5.2 h

**Table 1.2.** Summary of *Hexaplex trunculus* activity compiled from 22.9 h of time-lapse photography at 6 min intervals on a subtidal mussel bed in the Gulf of Trieste

Hexaplex	Presence in quadrat			Movement			Predation				
	On first photo	Entered	Exited	On last photo	Minor	Major	Stationary (h)	Overturned (h)	Searching (h)	Manipulating (h)	Feeding (h)
1	1	0	0	1	13	0	20.9	0	0	0	0
2	1	0	1	0	18	2	12.8	8.0	0	0	0
3	1	0	0	1	33	0	17.7	0	0	0	0
4	1	0	0	1	56	2	16.9	0	0	0	10.5
5	1	1	1	0	20	6	3.8	0	0	0	0
6	1	1	1	1	54	3	16.9	0	0	0	0
7	1	1	1	1	31	0	19.5	0	0	0	0
8	1	0	0	1	19	3	20.3	0	0	0	0
9	1	0	1	0	41	13	8.0	0	0	0	0
10	1	0	0	1	14	1	21.0	0	0	0	0
11	1	1	1	0	60	1	4.3	0.2	0	0	0
12	1	1	1	0	78	14	6.2	0	0	0	0
13	1	0	1	0	2	3	5.1	0	0	0	0
14	1	0	0	1	58	4	16.5	0	0	0	0
15	1	0	1	0	87	8	12.6	0	0	0	0
16	1	0	0	1	99	8	12.0	0	0	0	0
17	1	0	1	0	1	1	4.7	0	0	0	0
18	1	0	1	0	6	2	3.1	0	0	0	0
19	1	0	1	0	13	2	3.8	0	0	0	0
20	1	0	1	0	13	1	3.9	0	0	0	0
21	1	0	1	0	20	5	7.8	0	0	0	0
22	1	0	1	0	20	3	0.5	0	0	0	0
23	1	0	1	0	20	3	6.3	0	0	0	0
24	1	0	1	0	25	2	9.3	0	0	0	0
25	0	1	1	0	21	5	2.4	0	0	0	0
26	0	1	1	0	29	12	0.2	0	0	0	0
27	0	1	1	0	5	3	0.3	0	0	0	0
28	0	1	1	0	21	7	3.2	0	0	0	0
29	0	1	1	0	7	9	0.0	0	0	0	0
30	0	1	1	0	21	1	0.0	0	0	0	0
31	0	1	1	0	7	12	0.0	0	0	0	0
32	0	1	1	0	0	3	0.0	0	0	0	0
33	0	1	1	0	1	2	0.0	0	0	0	0
34	1	0	0	1	52	3	17.3	0	0	0	0
35	0	1	1	0	49	2	0.0	0	0	0	0
36	0	1	1	0	9	2	0.0	0	0	0	0
37	0	1	1	0	25	2	3.6	0	0	0	0
38	0	1	0	1	33	11	0.0	0	1.2	2.9	0
39	0	1	0	1	86	12	3.1	0	0.3	5.2	0
Total	25	19	29	12	1167	173	284.0	8.2	1.5	8.1	10.5
% total	64.1%	48.7%	74.4%	30.8%	-	-	-	-	-	-	-
Moves/individual	-	-	-	-	29.9	4.4	-	-	-	-	-
Average time	-	-	-	-	-	-	7.3	0.2	<0.1	0.2	0.3

Explanation: Minor and major moves are counts. Stationary (h) represents the time in hours a *Hexaplex* spent not moving. Overturned (h) represents the amount of time in hours a *Hexaplex* spent flipped onto its back. Searching (h), Manipulating (h) and Feeding (h) represent the time (in hours) a *Hexaplex* spent searching for, manipulating and eating prey.

manipulating and presumably attempting to chip or drill the prey. The second attacker interrupted the manipulations by the first *H. trunculus*, which then abandoned the prey. The second animal appeared in the quadrat and searched for a minimum of 1.2 h and spent 2.9 h manipulating. The photographic series ended before the result of the attack (completion or abandonment) could be documented. The behavior of these two gastropods differed from that of the non-attacking individuals observed in the photographs: most, when not actively moving, were nestled between *Mytilus* on the shell bed. In fact, it was initially difficult to see particular gastropods until they emerged from between or underneath the mussels.

#### **1.4.3. Size-frequency distribution of prey and predator**

A total of 487 (282 living and 205 dead) *M. galloprovincialis* were collected from the four samples. The mean shell length varied among samples ( $F = 19.94$ ,  $p < 0.0001$ , ANOVA), with sample 3 having a significantly different mean shell length than the other samples based on Tukey's post hoc comparisons (Tables 1.3 and 4, Fig. 1.3). *M. galloprovincialis* ranged from 11.1 to 95.2 mm in length. Overall, the samples contained two small ( $< 27.5$  mm), 45 medium (27.5 mm – 50 mm), and 235 large ( $> 50$  mm) living mussels, and 12 small, 41 medium, and 152 large dead mussels. The smallest live individual was 15.2 mm, the smallest dead was 11.1 mm. The largest live individual was 95.2 mm, the largest dead was 93.6 mm.

A total of 111 live and three dead *H. trunculus* were collected among the four samples. The mean shell length did not vary among samples ( $F = 2.396$ ,  $p < 0.05$ , ANOVA, Tables 1.3 and 1.4, Fig. 1.3). Live specimens ranged from 22.1 to 86.1 mm in length. The three empty shells measured 76.7 mm, 78.0 mm and 78.0

**Table 1.3.** ANOVA summary of differences in mean shell lengths of *Mytilus galloprovincialis* and *Hexaplex trunculus*

	S of S	df	ms	F	p
<i>Differences in mean length of Mytilus galloprovincialis tested among four samples</i>					
Between samples	12,778.7	3	4,259.6	19.9	<0.0001
Within samples	103,203.0	483	213,671.0		
Total	115,982.0	486			
<i>Differences in mean length of Hexaplex trunculus tested among four samples</i>					
Between samples	435,806.0	3	145,269.0	2,396.0	0.072
Within samples	6,607.4	109	606,182.0		
Total	7,043.2	112			

Key: S of S = Sum of Squares, *df* = degrees of freedom, ms = mean square, *F* = *F*-value, *p* = *p*-value.

**Table 1.4.** Tukey's pair-wise comparisons of mean shell lengths among samples

	Sample 1		Sample 2		Sample 3		Sample 4	
	<i>Q</i>	<i>p</i>	<i>Q</i>	<i>p</i>	<i>Q</i>	<i>p</i>	<i>Q</i>	<i>p</i>
<i>Mytilus galloprovincialis</i>								
Sample 1	-	-	-	-	-	-	-	-
Sample 2	0.9923	0.8965	-	-	-	-	-	-
Sample 3	6,894	<0.0001	5,902	<0.001	-	-	-	-
Sample 4	0.9259	0.9139	0.06639	1.0	5,968	<0.001	-	-
<i>Hexaplex trunculus</i>								
Sample 1	-	-	-	-	-	-	-	-
Sample 2	4,609	<0.01	-	-	-	-	-	-
Sample 3	1,372	0.7666	3,237	0.1071	-	-	-	-
Sample 4	0.769	0.9481	3,840	<0.05	1.0	0.9738	-	-

Key: *Q* = *Q*-value, *p* = *p*-value

mm. The living gastropods were represented by one small (< 47.5 mm), ten medium (47.5 – 62.5 mm), and 100 large (> 62.5 mm) individuals.

#### **1.4.4. Overall predation frequency**

The overall frequency of lethal marginal chipping measured in bulk samples was 53.2 % (range: 41.6 % to 69.8 %), the overall frequency of lethal drilling 3.9 % (range: 0 % to 9.3 %) (Table 1.5). Through combined modes of predation, *H. trunculus* exerted an overall predation frequency of 57.1 % here.

#### **1.4.5. Mode of attack**

109 (53 %) of the 205 dead *Mytilus* showed evidence of lethal chipping, whereas only 8 individuals (4 %) were drilled. Gastropods clearly preferred marginal chipping to drilling ( $\chi^2 = 87.118$ ,  $p \ll 0.0001$ ). Twenty-five percent of the small, 61 % of the medium, and 53 % of the large *M. galloprovincialis* were killed through marginal chipping; these rates did not differ significantly ( $\chi^2 = 48.3$ ,  $p = 0.18$ ; Fig. 1.4). One small (8 %), three medium (7 %), and four (3 %) large *M. galloprovincialis* were killed through drilling; again, these rates were not significantly different ( $\chi^2 = 25.6$ ,  $p = 0.46$ ).

#### **1.4.6. Prey effectiveness**

Prey effectiveness against chipping predation attempts ranged among samples from 56.4 % to 68.1 %. The overall value across all samples was 63.8 % (Table 1.5). For drilling, this effectiveness for each sample and for all samples combined is 0 % because no incomplete drill holes were observed in any sample, and only 8 complete drill holes were found.

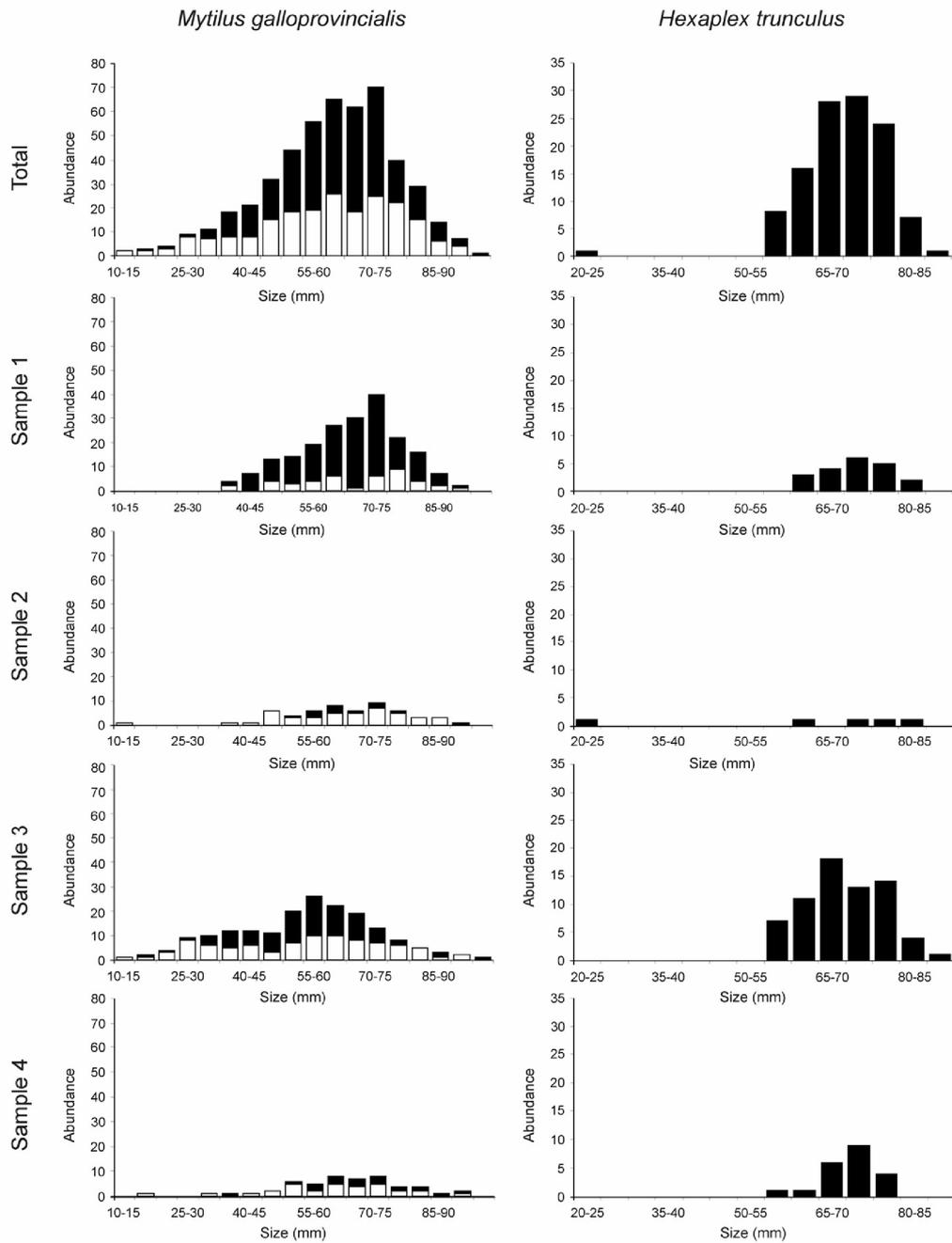
#### **1.4.7. Size refuge**

No evidence of a size refuge in *M. galloprovincialis* was found based on size- frequency and chipping distributions (Fig. 1.5). No successful chipping was recorded in the smallest size categories (15 – 20 mm, 20 – 25 mm), although unsuccessful chipping did occur. The frequency of chipping predation increased with bivalve length until an intermediate size was attained (50- to 55 mm). This frequency was then variable in intermediate and large *M. galloprovincialis*. Chipping occurred at all larger sizes, suggesting no size refuge in this population.

#### **1.5. Discussion**

*Mytilus* is a key molluscan ecosystem engineer in modern temperate seas: mussel aggregations usually provide space for epifauna that otherwise would be unable to colonize soft substrata, and they provide refuge to numerous cryptic species (for a review see Gutiérrez et al., 2003). *Mytilus* occurs regularly in the rocky intertidal, where it can be very abundant, and mass occurrences are a typical feature of harbors. However, mussel beds are not a typical feature on the widespread soft bottoms of the Northern Adriatic. *H. trunculus*, on the other hand, occurs regularly here on all hard and soft substrata from the intertidal to deeper water (Riedl, 1983).

In the Northern Adriatic, diverse macroepifauna communities are widely distributed on soft bottoms (Fedra, 1978; Zuschin et al., 1999; McKinney, 2007). The epifauna largely consists of decimeter-scale, interspecific, high-biomass aggregations termed multi-species clumps (Fedra et al., 1976) or bioherms: one or

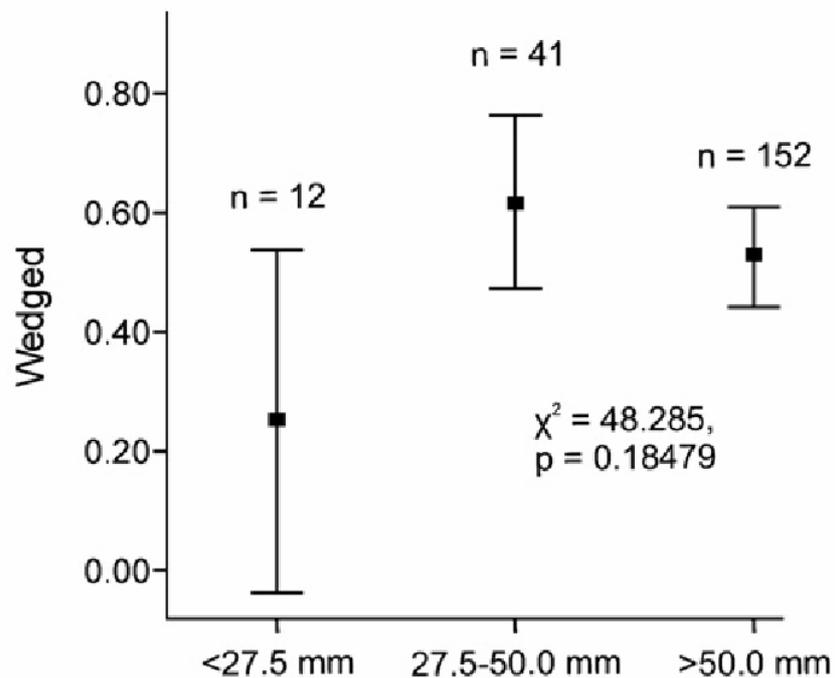


**Fig. 1.3.** Size-frequency distributions of *Mytilus galloprovincialis* and *Hexaplex trunculus*. *M. galloprovincialis* is represented by live (black) and dead (white) individuals. *H. trunculus* is represented by only living individuals. Note that predator and prey densities are correlated.

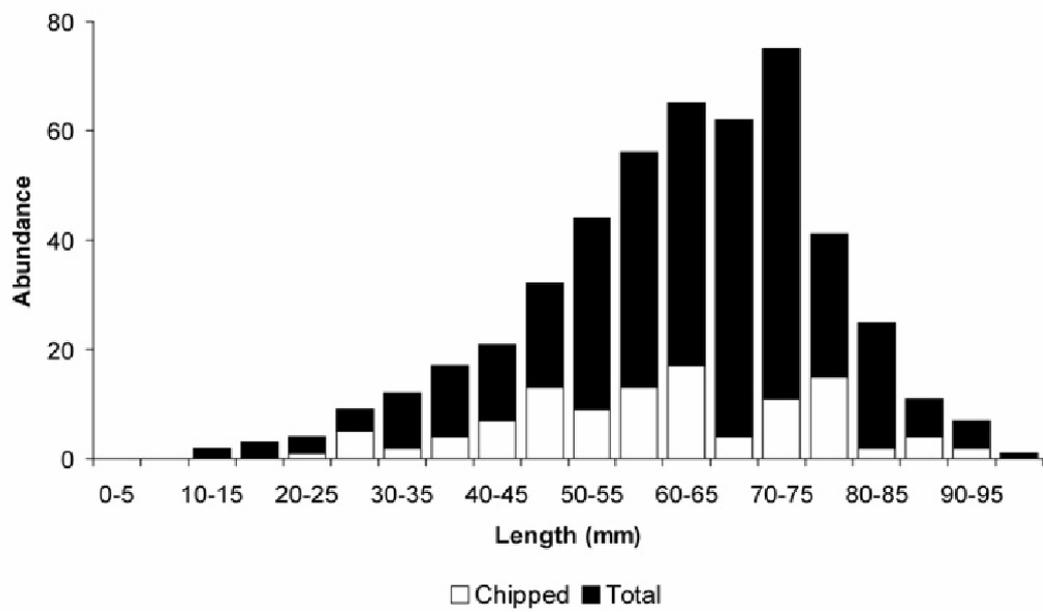
**Table 1.5.** Marginal chipping and drilling frequencies per sample

Sample	<i>n</i>	MC	RS	D	ID	CF	DF	CPE	DPE
1	42	24	31	1	0	57.1%	2.4%	56.4%	0.0%
2	43	30	53	4	0	69.7%	9.3%	63.9%	0.0%
3	89	37	79	3	0	41.6%	3.4%	68.1%	0.0%
4	31	18	29	0	0	58.1%	0.0%	61.7%	–
Total	205	109	192	8	0	53.2%	3.9%	63.8%	0.0%

Key: *n* = number of *Mytilus galloprovincialis* examined for traces of predation, MC = individuals with traces of marginal chipping, RS = repair scars, D = drill holes, ID = incomplete drill holes, CF = chipping frequency, DF = drill frequency, CPE = prey effectiveness against chipping predation, DPE = prey effectiveness against drilling predation.



**Fig. 1.4.** Chipping frequency (mean and 95 % confidence intervals) of small, medium and large *Mytilus galloprovincialis*.



**Fig. 1.5.** Size distribution of all *Mytilus galloprovincialis* (black), and marginally chipped *M. galloprovincialis* (white) in 5 mm size intervals. No major decrease in attacks occurs at any size, indicating no size refuge against chipping predation.

more shelly hard substrates provide the base for sessile, suspension-feeding colonizers (mostly sponges, ascidians, anemones or bivalves), which in turn serve as an elevated substrate for additional vagile and semi-sessile organisms (mostly brittle stars and crabs; Zuschin and Pervesler, 1996). Therefore, virtually all taxa found in the samples from the mussel bed — except the mussels themselves — are well known components of the epifauna on soft bottoms in the study area.

Our in situ observations document that *H. trunculus* is a mobile and active member of the benthic community. All individuals moved during the ~ 23 h observation period and most left the field of view. Two gastropods (5 %) moved and apparently handled prey after major movements, which we interpreted as involving searching behavior, and one was observed feeding at the onset of the deployment. Aquarium-kept individuals can survive up to six months without being fed; adults feed on juveniles, and cannibalism among adults also occurs (Zuschin, personal observation; Fig. 1.2b). Peharda and Morton (2006) calculated that a medium *H. trunculus* probably feeds on 18 large *M. galloprovincialis* each year; therefore, considering the high mussel densities (prey available ad libitum) and the relatively short observation period, as well as other sources of available food both inside and outside the frame, it was surprising we were able to view any predatory events. Based on Peharda and Morton's (2006) calculation, 39 *Hexaplex* observed for approximately 24 h would be expected to consume ~ 1.9 *Mytilus*. We only observed one feeding *Hexaplex*, but as most gastropods left the frame during the deployment, other predatory attempts by these individuals may have gone unrecorded. Also, considering that both drilling and chipping require, on average, more than 24 h (Peharda and Morton, 2006), capturing the entire attack and

consumption sequence during the deployment would have been even more surprising.

*M. galloprovincialis* were more normally distributed in terms of size, but the sample population is also clearly skewed towards large specimens (Fig. 1.3). We explain this population structure by the site specific conditions. The mussel population has reached a size and density that enables it to survive autonomously on the sediment bottom. One source of new individuals, however, is from the anchoring chains of the adjoining oceanographic buoy, either naturally during storms or when these chains are cleaned. Based on visual inspections, this input will involve a full range of mussel sizes, although larger individuals may predominate. The dense mussel bed and potential episodic input of fresh individuals, in turn, clearly attract mussel predators in larger numbers. Muricids in the Northern Adriatic are known to aggregate around prey falls and to spawn together around communal egg cases (Stachowitsch, personal observations). In both cases, smaller *H. trunculus* are rare. Most gastropods and mussels in our study were medium and large individuals. The bulk samples only yielded one small *H. trunculus*. In addition, frequent SCUBA diving at the site over several years reveals that small *Hexaplex* are exceedingly rare. Accordingly, small *H. trunculus* do not contribute significantly to the predation within the mussel bed. This is supported by hermit-crab occupied shells: the largest *P. eremita* individuals solely inhabit shells of adult *Murex brandaris* and *H. trunculus*, with smaller crabs in *Aporrhais pes-pelecani* but rarely in smaller muricids (Stachowitsch, 1980). Smaller living *H. trunculus* are rarely observed on the sediment in the surrounding benthic community as well, but may be hidden in multispecies clumps/bioherms. Since every intact empty gastropod shell is

occupied, such small shells are either destroyed during predation or have very low natural mortality rates and thus do not enter the hermit crab population in larger numbers.

No other predators on the mussel bed are likely to leave similar chipping traces. While fish could also be preying upon the mussels, they have no mechanism for grappling, thus they are more likely to crush shells between their teeth or dermal plates than to chip and scrape shell margins. Morton and Harper (2008) describe mandibular chipping by juvenile shore crabs on small *M. galloprovincialis* from the southeast coast of England. Although similar to marginal chipping traces of *H. trunculus*, such predators are unlikely to be the culprits here, because mandibular chipping tends to be used by aechelate crustaceans and by juveniles of chelate taxa (Lau, 1987). The decapod taxa at the studied mussel bed are always small (carapace width < 2 or 3 cm) and thus probably leave no chipping traces in any but the smallest mussels in our data set. Furthermore, Morton and Harper (2008) report that juvenile shore crabs did not attack any mussels > 25 mm, and only ~ 2 % of our mussels fall within this limit. Finally, aechelate decapods have never been collected or observed at this locality.

Peharda and Morton (2006) report that small *H. trunculus* preferred small and medium mussels, while medium and large gastropods fed randomly on small, medium and large prey. This agrees with our Northern Adriatic data, where *H. trunculus* also displayed no size preferences for *Mytilus*.

Drill holes are especially appealing for studies of predation in the fossil record because they are preserved in a wide variety of hard-shelled prey, are easily recognizable, and can be used to distinguish between successful and unsuccessful predatory attempts (but see Kowalewski, 2004). They have played a

critical role in the study of evolutionary, ecological and behavioral aspects of predation (e.g., Kitchell et al., 1981; Baumiller et al., 1999; Kowalewski et al., 2000; Kelley and Hansen, 2003). Using such drill holes to estimate predation intensity often assumes obligatory drilling behavior. Our, Peharda and Morton's (2006) and Morton et al.'s (2007) results, however, show multiple strategies in *H. trunculus*, and this gastropod may more frequently choose chipping over drilling in its natural environment. This is supported by facultative drilling in several other muricid species (e.g., *Nucella lamellose*, drilling and other methods, Kowalewski, 2004; *Trophon longstaffi*, drilling and wedging, Harper and Peck, 2003; and *Chorus giganteus*, drilling and pulling prey apart with its foot, Gutiérrez and Gallardo, 1999). Accordingly, predation intensities calculated solely based on drill holes probably yield underestimates. In the mussel bed examined, the infrequent occurrence of drilling would grossly underestimate predation intensity if marginal chipping were not also evaluated. This calls for caution when using drill holes alone to estimate predation intensity, and underlines the importance of identifying traces of multiple predatory modes when addressing predation of hard-shelled prey in both recent and fossil systems.

Several considerations might explain the preference of chipping over drilling. Drilling is a slow process and handling prey may expose predators to a greater risk of interruption or attack (Vermeij, 1987). The main shell-crushing predator of *H. trunculus* is the gilthead bream *Sparus auratus*, but several batoid species, most notably *Pteromylaeus bovinus*, are also known to prey extensively on this gastropod (Lovrenc Lipej, personal communication). The two gastropods flipped during the deployment may have been overturned by such predators. Alternatively, *Mytilus* can flip predatory gastropods by attachment to the snail and

subsequent retraction of byssus threads (Petraitis, 1987); the longer the attack, the greater the opportunity for such byssus attachment. Considering that two (5 %) of the 39 snails were flipped over during the ~ 23 h film sequence, such disturbance may be common on the mussel bed. Finally, the competition we observed between conspecifics would favor the faster, chipping mode of predation. Chipping, however, also harbors a potential threat: in whelks this strategy can damage or break the gastropod's own shell (Nielsen, 1975), and similar damage may occur in *H. trunculus* (Fig. 1.2b). The snapping valves of prey can also amputate the whelk's proboscis (Dietl, 2004), and similar hazards could affect other gastropods. When predators are exposed to crushed conspecifics, drilling frequencies are reduced and prey is increasingly abandoned (e.g., *Nucella lamellosa* on *Mytilus trossulus*; Chattopadhyay and Baumiller, 2007). The high density of large gastropods in our mussel bed entails a high possibility of interruption of predatory activity by conspecifics. This scenario would additionally favor a quick (chipping) predatory strategy (despite the potential risks). The fact that the bulk samples contain much more chipping than drilling damage indicates that *H. trunculus* chooses speed over safety.

The prey effectiveness reported here, determined from chipping traces, is relatively high (56.4 % – 68.1 %). *Mytilus* can therefore survive such marginal chipping attacks. Bivalves and mussels in particular, are thought to poorly withstand and subsequently repair shell damage caused by durophages (shell-crushing predators; Vermeij, 1983). Conversely, several studies point to high prey effectiveness and durophage-resistance in bivalves. For example, only 17 of the 38 observed attacks involving mandibular chipping by juvenile *Carcinus maenas* on *M. galloprovincialis* were successful (Morton and Harper, 2008). Most attacks

they observed or inferred based on marginal damage to the posterior of shell were unsuccessful, and many of those could have resulted in later repair scars. Accordingly, the prey effectiveness in their study would have been quite high (max. 55 %). Alexander and Dietl (2001) report prey effectiveness in *Mytilus edulis* from the New Jersey coast up to 19 %. In addition, Zuschin and Stanton (2001) report high resistance of experimentally crushed *Mytilus edulis*. Values for Plio-Pleistocene *Mercenaria* from southwestern Florida, marginally chipped by the whelk *Sinistrofulgur* ranged between 47 and 69 %, depending on the stratigraphic unit sampled (Dietl, 2003). The razor clams *Tagelus plebeius* from the Mar Chiquita coastal lagoon, Argentina, show repair frequencies from American oystercatcher attack as high as 73 % (Lomovaski et al., 2005). Some very resistant bivalves in the present study bore the marks of several predatory attempts; one medium-sized individual survived six attempts at marginal chipping before apparently succumbing to *H. trunculus* on the seventh attack.

Prey effectiveness and repair frequencies, while useful metrics for evaluating predation intensity, do require a caveat: they are only reliable if the predation traces are faithfully represented in a sample. It is unlikely that dead *Mytilus* shells are transported from our study site, but mussels killed by large durophagous predators that are likely to destroy the shell may not be represented: we considered only whole shells with intact margins. Removal of a proportion of a living prey population by a secondary predator would alter our perception of repair frequency and prey effectiveness. Such shell destruction would artificially increase the repair frequency of the prey population while artificially decreasing prey effectiveness. The degree of the inflation of the former and deflation of the latter depends on the proportion of the prey population removed by other

predators. A modeling approach simulating several such scenarios is currently being developed. Although prey effectiveness on our mussel bed is rather high, it is a conservative estimate even if other predators are attacking the *Mytilus* population and destroying their shells.

Prey selectivity has been studied in modern and fossil populations by examining frequency distributions of organisms with various predation traces (e.g., Ansell, 1960; Allmon et al., 1990). Durophagous predators are limited by the size of their attack- or grappling structures (Vermeij, 1987). Accordingly, potential prey organisms can sometimes obtain a size refuge by increasing overall body size. Our observations confirm the results of Peharda and Morton (2006), who found that large size does not provide a refuge for *M. galloprovincialis*. Though no mussels grew large enough to avoid chipping attempts by *Hexaplex*, small size may provide a refuge; the smallest mussels were not attacked in our study. This may reflect their more concealed positions. For example, Stewart and Creese (2004) reported that two species of whelk preferred small clams in laboratory experiments, but more often consumed medium-sized individuals in the field, reflecting the size of clams available.

Predation frequencies are the most widely used metric for evaluating predation intensity in both modern and ancient marine environments (e.g., Sander and Lalli, 1982; Vermeij et al., 1989; Hoffmeister and Kowalewski, 2001). Increased predation has been forwarded as one of several hypotheses to explain the evolutionary shift from macroepi- to macroinfauna- dominated benthic communities (Vermeij, 1987). This aspect therefore merits critical examination. In contrast to recent assumptions for the Northern Adriatic in general (e.g., McKinney and Hageman, 2006; McKinney, 2007), the overall predation

frequency for the predator–prey system on this mussel bed is relatively high (> 55 %). This indicates that if prey densities are high, predator densities can also be high in the Northern Adriatic (see Fig. 1.3). This calls for further study in this region to better understand overall intensity and patchiness of predation, and its effect on community structure.

*M. galloprovincialis* at our study site formed aggregations ranging from 2 to 32 individuals. Although densely aggregated bivalves must compete for resources (e.g., Okamura, 1986), they are often found in clumps. Despite increased competition, mussels living inside the outer margins of the clump are less susceptible to predation (Bertness and Grosholz, 1985; Okamura, 1986). Predators that need to manipulate their prey during attacks are hindered by such clumping behavior (Bertness and Grosholz, 1985; Côté and Jelnikar, 1999). The effect of clump-size on the predatory behavior and performance of *H. trunculus* would be an interesting topic for future studies.

## 1.6. Conclusions

We corroborate, in the field, key aspects of earlier laboratory studies on *H. trunculus* and *M. galloprovincialis*, including no preference for prey size, marginal chipping as the preferred mode of predation in large snails, and no size-refuge in the bivalve. In addition, *M. galloprovincialis* is highly effective against predatory attempts by *H. trunculus*. The *in situ* observations enhance laboratory studies by providing a base of reference regarding prey preferences, overall mobility, and how the predator interacts with its natural environment. As the dominant component of the studied mussel bed, *M. galloprovincialis* provides

hard substrate for a variety of encrusting taxa. Our *in situ* photography and surface samples show that the gastropods were highly active on the sea floor, may experience frequent disturbance and exert high levels of predation on their bivalve prey. Finally, multiple predation strategies by *H. trunculus* and many other muricids should be considered in studies of both modern and fossil communities in which drill holes alone are used to estimate predation intensity.

## 1.7. References

- Alexander, R.R., Dietl, G.P., 2001. Shell repair frequencies in New Jersey bivalves: A recent baseline for tests of escalation with Tertiary, mid-Atlantic congeners. *Palaios* 16, 354-371.
- Allmon, W.D., Nieh, J.C., Norris, R.D., 1990. Predation in time and space revisited: drilling and peeling in turritelline gastropods. *Palaeontology* 33, 595-611.
- Andreotti, A., Bonaduce, A., Colombini, M.P., Ribechini, E., 2004. Characterization of natural indigo and shellfish purple by mass spectrometric techniques. *Rapid Communications in Mass Spectrometry* 18, 1213-1220.
- Ansell, A.D., 1960. Observations on predation of *Venus striatella* (Da Costa) by *Natica alderi* Forbes. *Proceedings of the Malacological Society* 34, 157-164.
- Axiak, V., Vella, A.J., Micallef, D., Chircop, P., Mintoff, B., 1995. Imposex in *Hexaplex trunculus* (Gastropoda, Muricidae)—first results from biomonitoring of tributyltin contamination in Mediterranean. *Marine Biology* 121, 686-691.
- Baumiller, T.K., Leighton, L.R., Thompson, D., 1999. Boreholes in brachiopods of the Fort Payne Formation (Lower Mississippian, central USA). *Palaeogeography Palaeoclimatology Palaeoecology* 147, 283-289.
- Benović, A., 1997. The history, present condition, and future of the molluscan fisheries of Croatia. *In*: MacKenzie, C.L. Jr., Burrell, V.G. Jr., Rosenfield, A., Hobart, W.L. (eds). *The history, present condition, and future of the*

- molluscan fisheries of North and Central America and Europe, vol. 3, Europe. NOAA Technical Report NMFS 129. U.S. Department of Commerce, pp 217-226.
- Bertness, M.D., Grosholz, E., 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: the costs and benefits of a clumped distribution. *Oecologia* 67, 192-204.
- Bohannon, J.M., Lenski, R.E., 2000. The relative importance of competition and predation varies with productivity in a model community. *American Naturalist* 156, 329-340.
- Boulding, E.G., 1984. Crab-resistant features of shells of burrowing bivalves: decreasing vulnerability by increasing handling time. *Journal of Experimental Marine Biology and Ecology* 76, 201-223.
- Breen, P.A., Carson, T.A., Foster, J.B., Stewart, E.A., 1982. Changes in subtidal community structure associated with British Columbia sea otter transplants. *Marine Ecology Progress Series* 7, 13-20.
- Carriker, M.R., 1951. Observations on the penetration of tightly closed bivalves by *Busycon* and other predators. *Ecology* 32, 73-83.
- Chattopadhyay, D., Baumiller, T.K., 2007. Drilling under threat: and experimental assessment of the drilling behavior of *Nucella lamellosa* in the presence of a predator. *Journal of Experimental Marine Biology and Ecology* 352, 257-266.
- Chiavarini, S., Massanisso, P., Nicolai, P., Nobili, C., Morabito, R., 2003. Butyltins concentration levels and imposex occurrence in snails from the Sicilian coasts (Italy). *Chemosphere* 50, 311-319.

- Côté, I.M., Jelnikar, E., 1999. Predator-induced clumping behavior in mussels (*Mytilus edulis* Linnaeus). *Journal of Experimental Marine Biology and Ecology* 235, 201-211.
- Dietl, G.P., 2003. Coevolution of a marine gastropod predator and its dangerous bivalve prey. *Biological Journal of the Linnean Society* 80, 409-436.
- Dietl, G.P., 2004. Origins and circumstances of adaptive divergence in whelk feeding behavior. *Palaeogeography Palaeoclimatology Palaeoecology* 208, 279-291.
- Edgell, T.C., Rochette, R., 2008. Differential snail predation by an exotic crab and the geography of shell-claw covariance in the northwest Atlantic. *Evolution* 62, 1216-1228.
- Fedra, K., 1978. On the ecology of the North Adriatic Sea—wide range investigations on the Benthos: the Gulf of Trieste. *Memorie di Biogeografia Adriatica* IX, 69-87
- Fedra, K., Olscher, E.M., Scherubel, C., Stachowitsch, M., Wurzian, R.S., 1976. On the ecology of a North Adriatic benthic community: distribution, standing crop and composition of the macrobenthos. *Marine Biology* 38, 129-145.
- Freeman, A.S., Byers, J.E., 2006. Divergent induced responses to an invasive predator in marine mussel populations. *Science* 313, 831-833.
- Gutiérrez, R.M., Gallardo, C.S., 1999. Prey attack, food preference and growth in juveniles of the edible muricid snail, *Chorus giganteus*. *Aquaculture* 174, 69-79.

- Gutiérrez, J.L., Jones, C.G., Strayer, D.L., Iribarne, O.O., 2003. Molluscs as ecosystem engineers: the role of shell production in aquatic habitats. *Oikos* 101, 79-90.
- Harding, J.M., Kingsley-Smith, P., Savini, D., Mann, R., 2007. Comparison of predation signatures left by Atlantic oyster drills (*Urosalpinx cinerea* Say, Muricidae) and veined rapa whelks (*Rapana venosa* Valenciennes, Muricidae) in bivalve prey. *Journal of Experimental Marine Biology and Ecology* 352, 1-11.
- Harper, E.M., Peck, L., 2003. Predatory behavior and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology* 26, 208-217.
- Hoffmeister, A.P., Kowalewski, M., 2001. Spatial and environmental variation in the fossil record of drilling predation: A case study from the Miocene of Central Europe. *Palaios* 16, 566-579.
- Holt, R.D., 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12, 197-229.
- Kelley, P.H., Hansen, T.A., 2003. The fossil record of drilling predation on bivalves and gastropods. *In*: Kelley, P.H., Kowalewski, M., Hansen, T.A. (eds.), *Predator-prey interactions in the fossil record: Topics in Geobiology Series 20*. Plenum Press/Kluwer, New York, pp. 113-133
- Kelley, P.H., Hansen, T.A., Graham, S.E., Huntoon, A.G., 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. *Palaeogeography Palaeoclimatology Palaeoecology* 166, 165-176.

- Kitchell, J.A., Boggs, C.H., Kitchell, J.F., Rice, J.A., 1981. Anomalies in naticid predatory behavior: a critique and experimental observations. *Malacologia* 27, 291-298.
- Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods. *In*: Kowalewski, M., Kelley, P.H. (eds.), *The fossil record of predation*. Paleontological Society Special Papers, vol. 8. Yale University, New Haven, pp. 3-42.
- Kowalewski, M., 2004. Drill holes produced by the predatory gastropod *Nucella lamellose* (Muricidae): Palaeobiological and ecological implications. *Journal of Molluscan Studies* 70, 359-370.
- Kowalewski, M., Simões, M.G., Torello, F.F., Mello, L.H.C., Ghilardi, R.P., 2000. Drill holes in shells of Permian benthic invertebrates. *Journal of Paleontology* 74, 532-543.
- Lau, C.J., 1987. Feeding behavior of the Hawaiian slipper lobster *Scyllarides squammosus*, with a review of decapod crustacean feeding tactics on molluscan prey. *Bulletin of Marine Science* 41, 378-391.
- Leighton, L.R., 2002. Inferring predation intensity in the marine fossil record. *Paleobiology* 28, 328-342.
- Lomovaski, B.J., Gutiérrez, J.L., Iribarne, O.O., 2005., Identifying repaired shell damage and abnormal calcification in the stout razor clam *Tagelus plebeius* as a tool to investigate its ecological interactions. *Journal of Sea Research* 54, 163-175.
- MacArthur, R.H., 1972. *Geographical Ecology*. Princeton University Press, Princeton.

- McKinney, F.K., 2007. The Northern Adriatic Ecosystem: deep time in a shallow sea. Columbia University Press, New York.
- McKinney, F.K., Hageman, S.J., 2006. Paleozoic to modern marine ecological shift displayed in the northern Adriatic Sea. *Geology* 34, 881-884.
- Menge, J.L., 1974. Prey selection and foraging period of the predaceous rocky intertidal snail, *Acanthina punctulata*. *Oecologia* 17, 293-316.
- Meyer, J.J., Byers, J.E., 2005. As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam. *Ecology Letters* 8, 160-166.
- Morton, B., 2004. Predator-Prey interactions between *Lepsiella vinosa* (Gastropoda: Muricidae) and *Xenostrobus inconstrans* (Bivalvia: Mytilidae) in a southwest Australian marsh. *Journal of Molluscan Studies* 70, 237-245.
- Morton, B., Harper, E.M., 2008. Predation upon *Mytilus galloprovincialis* (Mollusca: Bivalvia: Mytilidae) by juvenile *Carcinus maenas* (Crustacea: Decapoda) using mandibular chipping. *Journal of the Marine Biological Association of the United Kingdom* 87, 933-940.
- Morton, B., Peharda, M., Harper, E.M., 2007. Drilling and chipping patterns of bivalve prey shell penetration by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae). *Journal of the Marine Biological Association of the United Kingdom* 87, 933-940.
- Nielsen, C., 1975. Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a short review of attack methods of other prosobranchs. *Ophelia* 13, 87-108.
- Okamura, B., 1986. Group living and the effects of spatial position in aggregations of *Mytilus edulis*. *Oecologia* 69, 341-347.

- Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. *Evolution* 33, 697-713.
- Petratis, P.S., 1987. Immobilization of the predatory gastropod *Nucella lapillus* by its prey *Mytilus edulis*. *Biological Bulletin* 172, 307-314.
- Peharda, M., Morton, B., 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator-prey interactions with the black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). *Marine Biology* 148, 1011-1019.
- Riedl, R., 1983. *Fauna und Flora des Mittelmeeres*. Verlag Paul Parey, Hamburg und Berlin.
- Sander, F., Lalli, C.M., 1982. A comparative study of the mollusk communities on the shelf-slope margin of Barbados, West Indies. *Veliger* 24, 309-318.
- Sanford, E., Roth, M.S., Johns, G.C., Wares, J.P., Somero, G.N., 2003. Local selection and latitudinal variation in a marine predator-prey interaction. *Science* 300, 1135-1137.
- Stachowitsch, M., 1980. The epibiotic and endolithic species associated with gastropod shells inhabited by the hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. *P.S.Z.N.I: Marine Ecology* 1, 73-101.
- Stachowitsch, M., Riedel, B., Zuschin, M., Machan, R., 2007. Oxygen depletion and benthic mortalities: the first in situ experimental approach to documenting an elusive phenomenon. *Limnology and Oceanography: Methods* 5, 344-352.
- Stewart, M.J., Creese, R.G., 2004. Feeding ecology of whelks on an intertidal sand flat in north-eastern New Zealand. *New Zealand Journal of Marine and Freshwater Research* 38, 819-831.

- Terlizzi, A., Geraci, S., Minganti, V., 1998. Tributyltin (TBT) pollution in the coastal waters of Italy as indicated by imposex in *Hexaplex trunculus* (Gastropoda, Muricidae). *Marine Pollution Bulletin* 36, 141-165.
- Vermeij, G.J., 1983. Traces and trends of predation with special reference to bivalved animals. *Palaeontology* 26, 455-465.
- Vermeij, G.J., 1987. *Evolution and Escalation, an Ecological History of Life*. Princeton, Princeton.
- Vermeij, G.J., 2002. Evolution in the consumer age: Predators and the history of life. *In*: Kowalewski, M., Kelley, P.H. (eds.), *The fossil record of predation*. Paleontological Society Special Paper, vol. 8. Yale University, New Haven, pp. 375-393.
- Vermeij, G.J., Dudley, E.C., Zipser, E., 1989. Successful and unsuccessful drilling predation in Recent pelecypods. *Veliger* 32, 266-273.
- Vermeij, G.J., Kool, P.S., 1994. Evolution of the labral spines of *Acanthais*, new genus and other rapanine muricid gastropods. *Veliger* 37, 414-424.
- Wahle, R.A., Steneck, R.S., 1992. Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology* 157, 91-114.
- Walker, S.E., Yamada, S.B., 1993. Implications for the gastropod fossil record of mistaken crab predation on empty mollusk shells. *Palaeontology* 36, 735-741.
- Warren, S., 1916. The feeding habits of *Busycon*. *The Nautilus* 30, 66-68.

- Wurzian, R.S., 1982. Die Funktion der Räuber der Makro-Epifauna in einer sublitoralen Benthos Gemeinschaft im Golf von Triest. Unpublished PhD Thesis, University of Vienna, Vienna.
- Zavodnik, D., Šimunović, A., 1997. Beekralješnjaci morskog dna Jadrana. Svjetlost, Sarajevo.
- Zuschin, M., Pervesler, P., 1996. Secondary hard ground-communities in the Northern Gulf of Trieste, Adriatic Sea. *Senckenbergiana maritima*, 28, 53-63
- Zuschin, M., Stachowitsch, M., Pervesler, P., Kollmann, H., 1999. Structural features and taphonomic pathways of a high-biomass epifauna in the northern Gulf of Trieste, Adriatic Sea. *Lethaia* 32, 299-317.
- Zuschin, M., Stachowitsch, M., Stanton, R.J., Jr., 2003. Patterns and processes of shell fragmentation in modern and ancient marine environments. *Earth-Science Reviews* 63, 33-82.
- Zuschin, M., Stanton, R.J. Jr., 2001. Experimental measurement of shell strength and its taphonomic interpretation. *Palaios* 16, 161-170.

**CHAPTER 2:**  
**INTENSITIES OF DRILLING PREDATION OF MOLLUSCAN**  
**ASSEMBLAGES ALONG A TRANSECT THROUGH THE NORTHERN**  
**GULF OF TRIESTE (ADRIATIC SEA)<sup>1</sup>**

**2.1. Abstract**

Drilling predation is one of the most studied biotic interactions in the fossil record and potentially controls biodiversity, but its history may be confounded by natural patchiness across environments. This aspect has been inconsistently evaluated. The current study contributes to our understanding of drilling predation in the Northern Adriatic, which has been previously classified as a low-predation setting, and examines the roles of environment, patchiness, and ecology of prey organisms in modern seas. Nearly 49,000 molluscs from two intertidal and six sublittoral bulk samples along a transect in the Gulf of Trieste were analyzed for drill frequency (DF) and prey effectiveness (PE), a measure of prey's ability to resist predatory attacks.

DF across all samples was 20.6 %, but varied between the intertidal (1.4 %) and sublittoral (27.4 %). Amongst the latter, DF differed between the delta foreset beds (18.1 %) and level bottom muds and sands (~28 % each). PE was low in the intertidal (1.1 %) and sublittoral (4.5 %). Overall DF, and PE amongst the three mud samples varied by nearly 10 %, while that within the two sand samples varied little; however, significantly different DFs were observed only

---

<sup>1</sup> Published as: Sawyer, J., Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeography, Palaeoclimatology, Palaeoecology* 285, 152-173.

among the families Nuculidae, Galeommatidae and Corbulidae in level bottom mud and Cerithiidae in level bottom sand samples. Only Corbulidae displayed significant variation in PE among level bottom mud samples (16.5 - 43.7 %). PE varied significantly between level bottom sand samples only within the families Cerithiidae and Trochidae.

Suspension feeding bivalves and gastropods had the highest DFs (24.3 % and 39.1 %, respectively), and the value of epifaunal bivalves (32.0 %) was nearly twice as high as that of infaunal bivalves (17.9 %). DFs of cementing (43.0 %) and byssate (27.0 %) bivalves were higher than that of recliners (9.9 %). Considering their cryptic life habits, parasitic gastropods (20.3 %) and commensal bivalves (40.6 %) had exceptionally high DFs. For each ecological category, PE was highest on suspension-feeding (11.1 %), infaunal (15.8 %) and cementing (10.5 %) bivalves, and on parasitic gastropods (11.9 %).

DF did not correlate with diversity indices or predator abundance in the sublittoral; therefore, drilling predation probably does not control diversity on the local scale here. DFs support paleoecological theory relating predation to changes in ecological guilds through the Phanerozoic. DFs were highest on suspension feeders, parasites and sessile prey, and were lowest on predators, recliners, and endobenthic molluscs. While cementation likely reduces bivalve susceptibility to durophages, it apparently does not impede drilling predators. Finally, DF did not vary across size classes in any species examined except *Venerupis rhomboides*, where the smallest fraction was drilled more often. Additionally, as the proportion of large individuals in our samples was small, disparities in DF across size classes probably did not influence our results. With respect to predation intensity the relatively high DF in the sublittoral, as well as high DF and PE for

various taxa and guilds, place the Northern Adriatic Sea among typical Cenozoic shelf environments.

## **2.2. Introduction**

In light of the current biodiversity crisis (Wilson, 2003), a key task of paleoecologists is to determine what controls biodiversity (Leighton, 2004). Predation has long been recognized as a major control on local diversity (e.g. Connell, 1961; Paine, 1966), but its role as a major control on the global scale has been hotly debated (e.g., Dietl and Vermeij, 2006; Madin et al., 2006; Roopnarine et al., 2006). One of the most common methods of analyzing predation in the fossil record is to quantify traces of predatory attacks on hard-shelled prey in the form of drill holes and repair scars. Because the latter indicate unsuccessful predatory attempts, their interpretation can be ambiguous (Leighton, 2002). As a result, paleoecologists tend to use drill holes, especially those attributed to naticid and muricid gastropods, to quantify predation in the fossil record (Allmon et al., 1990; Roopnarine and Beussink, 1999; Taylor and Glover, 1999; Kaplan and Baumiller, 2000; Hoffmeister and Kowalewski, 2001; Kelley et al., 2001; Harper, 2003; Harper and Peck, 2003; Baumiller and Bitner, 2004). Although drilling predation is therefore a well-documented biotic interaction in fossil ecosystems (Vermeij, 2002), its history is debated (Kelley and Hansen, 2007): Vermeij (2002) reports that the time-span from the Eocene to Recent is characterized by stable predation intensities at a high modern level, while Kelley and Hansen (2003) document highly variable predation frequencies throughout the Cenozoic. This disparity may reflect a lack of focus on local patchiness in both diversity and

predation intensities. In fact, most assemblage-level drilling predation studies have focused on changes in DF through time as a test of Vermeij's (1987) escalation hypothesis; however, contemporaneous variation in drilling intensities through space may confound the interpretation of temporal patterns (Kelley and Hansen, 2007). Such patchiness in local species richness and predation pressure has been well established (e.g. MacArthur, 1965; Hansen and Kelley, 1995; Hoffmeister and Kowalewski, 2001; Zuschin et al., 2004, 2006; Kelley and Hansen, 2007). In contrast, researchers have not consistently evaluated paleoenvironments when studying temporal drilling trends. Understanding such trends requires examining the amount of spatial variation within and between environments at any locality and/or time. This study is part of a larger project that aims to characterize regional Cenozoic drilling frequencies throughout Central Europe. We aim to provide a modern baseline for these regional comparisons of drilling intensities from intertidal to sublittoral habitats. Most marine fossil assemblages formed in sublittoral shelf settings that are logistically more difficult to sample in modern oceans, and the taxonomic resolution in most temporal analyses of drilling predation is the genus or family. We address these problems by using SCUBA to collect and analyse molluscs from sublittoral habitats at the species-level to improve our understanding of modern drilling predation.

Life habits may restrict encounters between some predators and their potential prey. For instance, infaunal burrowing naticid gastropods are not likely to encounter epifaunal, bysally-attaching *Mytilus* bivalves, and epifaunal muricid gastropods are unlikely to feed on deep infaunal prey. Therefore, increased predation intensity has been hypothesized as the driving mechanism for several Phanerozoic trends in life habits of marine organisms, including the

infaunalization of the marine benthos (Vermeij, 1977) and cementation in bivalves (Harper, 1991). The modern fauna is regarded as more metabolically active than its Paleozoic counterparts (e.g. carnivorous and predatory feeding strategies vs. active and passive suspension feeding; Bambach, 1999), but only a few assemblage-level predation studies have evaluated the life habits of constituent taxa (see Kelley and Hansen, 2006; Harries and Schopf, 2007). Gastropod and bivalve feeding strategies, as well as bivalve-substrate relationships and epifaunal bivalve attachment in the Gulf of Trieste are examined to improve our knowledge of life habits and their effects on drilling intensities.

Prey size can affect predation rates through predator selection of specific size-classes (Kitchell, 1986; Allmon et al., 1990), while our perception of drill frequencies can be altered by sieve size (Kowalewski and Hoffmeister, 2003). The proportion of drilled shells within size-classes is examined in selected species to determine if prey-size affects drilling predation in the Northern Adriatic Sea.

Predation intensity has been hypothesized to be much lower in the Northern Adriatic than would be expected from a Cenozoic shelf at similar latitude (McKinney and Hageman, 2006; Kelley, 2006; McKinney, 2007), but relatively few studies have directly examined predation there. Drilling predation has been assessed from beach deposits near Venice, Italy (Kelley, 2006), but no analyses of sublittoral drilling frequencies are available. Kelley's (2006) study, in conjunction with the apparent lack of durophages (e.g. balistid fish and crabs), suggests that the Northern Adriatic experiences low levels of predation (McKinney and Hageman, 2006; McKinney, 2007; but see Zuschin & Stachowitsch, 2009). While Kelley's (2006) study revealed unusually low DFs, we suspect that drilling intensities are higher in the sublittoral, based on an

expected greater diversity of drilling gastropod species there (Savini et al., 2004; Peharda and Morton, 2006; Sawyer et al., 2009).

To contribute to the overall understanding of drilling predation in the Adriatic, the drill frequencies (DF), incomplete drill frequencies (IDF), and prey effectiveness (PE, a measure of a prey's ability to resist drilling predation) are analyzed from molluscan samples collected along a transect in the Gulf of Trieste. The following hypotheses are tested: 1) DF relates predictably to life habits of prey: a) DF is highest on slow-moving and metabolically less active guilds (e.g. suspension feeders) and lowest on the more metabolically active guilds (e.g. predators), b) DF is lowest on infaunal and highest on epifaunal molluscs, c) cementation is an effective defensive strategy against drilling predators; 2) DF decreases with prey size; 3) DF increases from the intertidal to the sublittoral; 4) drilling frequency and PE differ between and within level bottom environments; 5) DF is positively correlated with diversity; 6) predation pressure exerted by drilling predators in the Northern Adriatic Sea is pre-Cenozoic in intensity.

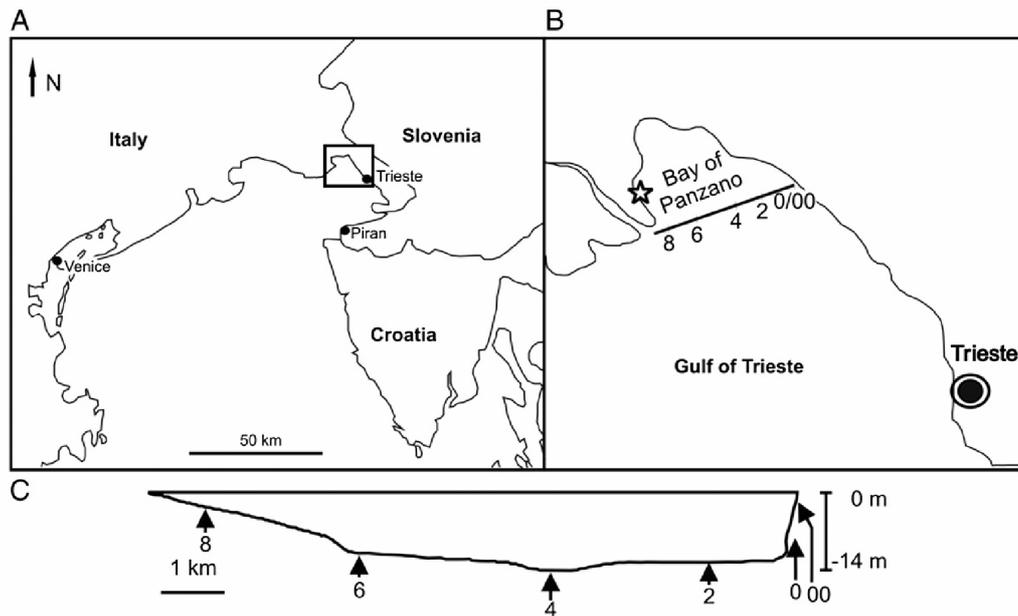
### **2.3. Study area and benthic assemblages**

The Northern Adriatic is one of the world's largest modern epicontinental seas and is semi-enclosed, with an average water depth of < 50 m and a length of > 300 km. This makes it comparable in extent to a typical Paleozoic or Mesozoic shelf environment (McKinney, 2007; Zuschin and Stachowitsch, 2009). The shelf is relatively low-energy with small tidal range and wave heights (Nelson, 1970). The Po River, along with several smaller rivers, serves as the primary source of freshwater, sediments and nutrients into the Adriatic and accounts for nearly one-

third of the entire freshwater input into the Mediterranean (for an overview, see McKinney, 2007).

Historical studies on the Northern Adriatic seafloor, based on grab samples, define the general benthic assemblage of the Gulf of Trieste according to infauna species (“*Schizaster chiajei*” community, Vatova 1949; see also McKinney, 2007). However, the fauna in the Gulf of Trieste has also been extensively studied by underwater camera sled and intensive SCUBA-supported fieldwork from the 1970s until today (Fedra et al., 1976; Stachowitsch et al., 2007, Riedel et al., 2008). These studies document widespread, high biomass, macroepibenthic communities characterized by highly patchy distribution. This reflects the presence of epifaunal multispecies clumps on shell grounds on an otherwise muddy soft bottom (Zuschin et al., 1999; Zuschin and Stachowitsch, 2009).

The Gulf of Trieste and particularly the Bay of Panzano (Fig. 2.1) have hosted numerous actuopalaeontological studies, including the spatial distribution of intertidal and sublittoral foraminifera (Hohennegger et al., 1989, 1993), the spatial distribution and orientation of crustacean burrows (Hohennegger and Pervesler, 1985; Pervesler and Dworschak, 1985; Pervesler and Hohennegger, 2006) and the distribution, structure and taphonomy of macroepifauna (Zuschin and Piller, 1994; Zuschin and Pervesler, 1996, Zuschin et al., 1999). These studies all sampled the benthos along the same transect in the Gulf of Trieste, whose sediment distribution, composition and facies zonation was determined by Zuschin and Piller (1994). This study extends the above work, using the same sublittoral transect and adjoining tidal flat to evaluate the molluscan composition and focuses on drilling predation.



**Fig. 2.1.** Study area in A) the Northern Adriatic Sea, B) the Gulf of Trieste, Bay of Panzano and C) subtidal transect showing the positions of the sublittoral samples 00-8. The star marks the position of the tidal flat.

## 2.4. Methods

Standardized bulk samples were collected from two tidal flat and six sublittoral locations along a transect in the Gulf of Trieste in the Northern Adriatic Sea (Fig. 2.1) in May 1985 (sublittoral samples) and October 1999 (intertidal samples; Table 2.1). Tidal flat samples were collected near the mouth of the Isonzo River, one each from the outer and inner tidal flat. Each sample consisted of 31,500 cm<sup>3</sup> of muddy-sand collected using a 30 cm by 30 cm by 35 cm boxcore. Sublittoral samples were collected using SCUBA from depths of 4 m to 15 m. Each sample consisted of 19,242 cm<sup>3</sup> of sediment collected with a cylindrical core of 35 cm (diameter) by 20 cm (height) from the delta foreset bed,

and level bottom muds and sands. All sediment was washed through a 1 mm sieve using freshwater. Living individuals were separated and preserved in ethanol. Molluscs were sorted and identified to species level (D'angelo and Gargiullo, 1979; Cossignani et al., 1992).

Unbroken shells (> 90 % complete) were counted and examined for traces of drilling predation. Drill holes were considered to be predatory in nature if they met widely accepted criteria: holes that are circular in cross section with smooth sides, penetrate perpendicular to and from the outside of the shell surface, and penetrate one valve only in articulated shells (Carriker and Yochelson, 1968; Rohr, 1991; Baumiller, 1996; Kaplan and Baumiller, 2000; Leighton, 2001). Several species of muricid and naticid gastropods produce drill holes with distinct morphologies that can easily be distinguished (Bromley, 1981; see Kelley and Hansen, 2003 for review). We did not distinguish between *Oichnus paraboloides* (made by naticids) and *O. simplex* (made by muricids). One of the most common and voracious muricid gastropods in the study area, *Hexaplex trunculus* (Sawyer et al., 2009), leaves drill holes that are often indistinguishable from those left by naticid gastropods. Our approach was to determine the effects of drilling predation as a whole on molluscan communities in the Northern Adriatic, rather than the effects of a single predatory clade on its prey.

Drilling frequency (DF), the measure of how often organisms are attacked by drilling predators, was calculated by dividing the total number of drilled shells by the total number of individuals examined. Incomplete drilling frequency (IDF), a measure of how frequently predatory attacks failed, was calculated by dividing the total number of incomplete drill holes by the number of shells examined. To account for disarticulated valves, DF and IDF values for all

bivalves were corrected: the number of valves with complete or incomplete drill holes was divided by half the total number of valves examined (e.g. Kowalewski, 2002). Prey Effectiveness (PE) was calculated by dividing the number of incomplete drill holes in the population by the total number of drills attempted (incomplete plus complete drill holes; e.g. Vermeij, 1987).

To test if variation in prey size affects calculated DFs, three infaunal and one epifaunal species were measured from all sublittoral samples and the proportions with predatory drill holes from various size-classes were compared using chi-square tests. *Chama gryphoides*, *Venerupis rhomboides*, *Lucinella divaricata* and *Turritella communis* were chosen because they are very abundant, frequently drilled, and have large size-variations compared to other molluscs from our samples. For statistical analysis, the larger two categories of *Venerupis rhomboides* were combined to increase the number of drilled shells to > 5, a requirement of the chi-square test.

Predation parameters were also compared among families across ecological guilds (bivalve and gastropod prey feeding strategies, bivalve substrate relationships and attachment strategies). For bivalves, feeding categories included chemosymbionts, deposit- and suspension-feeders, and carnivores. For gastropods, diet categories included browsing carnivores, detritivores, herbivores, parasites, predators and suspension feeders. Bivalve substrate relationship categories included borers, commensals, epifauna, infauna and nestlers. Bivalve epifaunal attachment categories included byssal attachers, cementers and recliners. Information on life habits was compiled from Beesley et al. (1998), Nevesskaja (2006), and from the Neogene Marine Biota of Tropical America molluscan life habits databases (Todd, 2001).

Environmental parameters may affect predator and prey performance; therefore, drilling predation is compared graphically (using 95 % confidence intervals) and statistically (using chi-square test) between the tidal flat and sublittoral habitats (delta foreset beds, level bottom muds and level bottom sands), among sublittoral environments, and within level bottom mud and sand samples to further document potential patchiness in predation between and within specific environments in modern seas.

The number of shells differs strongly between samples (range: 1,179 - 19,038) and rarefaction curves were used to compare diversities. To determine how community structure may relate to predation intensity, the following were tested for correlations with sample DF using Spearman's rho: species richness, overall molluscan abundance, the abundance of the five most abundant species, and various diversity indices. Because of the relatively low diversity and DF on the tidal flat, these tests were performed using all samples (including those from the tidal flat) and on the sublittoral samples only. In addition, the abundances of naticid and muricid gastropods, and other potential drillers, were tested for correlations with DFs.

DF, IDF and PE were calculated at various taxonomic levels and for ecological guilds using SAS/IML codes. Graphics were generated using the software package SPSS 10.0 (SPSS, 1999). All other statistical analyses were performed in PAST (Hammer et al., 2001).

## 2.5. Drilling predators in the Northern Adriatic Sea

Several potential drillers were identified from the recovered samples. *Hexaplex trunculus* is one of the most common muricid gastropods in the Northern Adriatic Sea and the naticid *Euspira macilenta* was fairly common in the sublittoral samples. Although *H. trunculus* is capable of exerting intense predation pressure on bivalves in the region, drilling is relatively rare in adults (Peharda and Morton, 2006; Morton et al., 2007; Sawyer et al., 2009). *Ocenebra edwardsi* is reported to drill small *Mytilus galloprovincialis* (Tongiorgi et al., 1981); therefore, the *Ocenebra* sp. found in our samples may also be capable of drilling. Juveniles of the invasive gastropod *Rapana venosa* could also drill in the Northern Adriatic (Kingsley-Smith et al., 2003), although this species was not recovered in our samples. Additionally, potential drillers include juvenile nassariids (Morton and Chan, 1997), marginellids (Ponder and Taylor, 1992) and buccinids (Peterson and Black, 1995), though little knowledge exists of drilling in these groups (for review see Walker, 2007). Most of the known drillers we recovered were the naticid gastropod *Euspira macilenta* (n = 390) and several species of muricids (n = 181). Of the other potential drillers, the nassariids were quite abundant (n = 2745). Buccinids (n = 68) and marginellids (n = 77) were less abundant components of the recovered fauna and probably not important contributors to drilling predation here.

In addition to drilling gastropods, the cephalopod *Octopus vulgaris* (Lamarck) is known to drill oysters and gastropods (Nixon, 1979; Arnold and Arnold, 1969) and is common in the Adriatic (Riedl, 1983). Also, certain nematodes are predatory drillers of Foraminifera and could potentially drill small

and juvenile molluscs (Sliter, 1965, 1975), and certain flatworms have been reported to drill oysters (Woelke, 1957; for review see Kowalewski, 2002).

## **2.6. Results**

### **2.6.1. Basic structure of the molluscan assemblages**

A total of 48,906 complete individual molluscs (calculated from 700 articulated bivalves and 60,480 disarticulated valves, and the shells of scaphapods and gastropods) were collected, identified to species level and examined for drill holes from two intertidal and six sublittoral bulk samples (Table 2.1). These shells represent 67 species from the intertidal and 172 from the sublittoral, totaling 178 species from 72 families (Table 2.2). The five most abundant bivalve species account for 57.3 % of the total bivalve assemblage, and the five most abundant gastropod species accounted for 54.4 % of the total gastropod assemblage.

Only 0.8 % of all shells were collected live, although due to the small size of some species, many living molluscs were likely overlooked (especially gastropods). Only 6 species with abundances > 10 were represented by more than 10 % live individuals (*Loripes lacteus*, *Tapes decussates*, *Nassarius incrassatus*, *N. reticulatus*, *Cyclope neritea* and *Haminoea navicula*) and two species only occurred living (*Pharus legumen*, n = 3; and *Pholas dactylus*, n = 1; Appendix A Table 2.1).

**Table 2.1.** Summary of drill hole data for each sample and for environments

Summary of drill hole data								
	Description	S	n	D	ID	DF (%)	IDF (%)	PE (%)
<i>Sample</i>								
0	Level bottom gravely sand	137	19,038	5528	121	29.0	0.6	2.1
00	Level bottom gravely sand	119	4294	1125	8	26.2	0.2	0.7
2	Level bottom silt-clay	58	5855	1315	97	22.5	1.7	6.9
4	Level bottom silt-clay	49	2867	928	89	32.4	3.1	8.8
6	Level bottom silt-clay	51	2867	792	140	27.6	4.9	15.0
8	Level bottom silt-clay from delta slope	68	1179	221	13	18.1	1.1	5.6
Boxcore 1	Littoral muddy sand from inner tidal flat	28	5701	79	0	1.4	0.0	0.0
Boxcore 2	Littoral muddy sand from outer tidal flat	47	7069	96	2	1.4	0.0	2.0
<i>Environment</i>								
Tidal flat	Total mollusc fauna	66	12,770	175	2	1.4	0.0	1.1
Subtidal (pooled)	Total mollusc fauna	172	36,136	9909	468	27.4	1.3	4.5
Delta foreset beds	Total mollusc fauna	75	1224	221	13	18.1	1.1	5.6
Level bottom mud	Total mollusc fauna	74	6913	1941	242	28.1	3.5	11.1
Level bottom sand	Total mollusc fauna	148	23,332	6653	129	28.5	0.6	1.9
Tidal flat	Bivalves	36	3437	71	3	2.1	0.1	4.1
Subtidal (pooled)	Bivalves	74	9718	3064	350	31.5	3.6	10.3
Delta foreset beds	Bivalves	36	733	142	13	19.4	1.8	8.4
Level bottom mud	Bivalves	36	5167	1759	273	34.0	5.3	13.4
Level bottom sand	Bivalves	56	3827	1163	64	30.4	1.7	5.2
Tidal flat	Gastropods	30	9333	175	0	1.9	0.0	0.0
Subtidal (pooled)	Gastropods	98	24,845	6804	114	27.4	0.5	1.6
Delta foreset beds	Gastropods	31	442	79	0	17.9	0.0	0.0
Level bottom mud	Gastropods	37	7363	1857	144	25.2	2.0	7.2
Level bottom sand	Gastropods	91	19,426	5487	63	28.2	0.3	1.1
Tidal flat	Scaphopods	0	0	0	0	-	-	-
Subtidal (pooled)	Scaphopods	1	1573	41	4	2.6	0.3	8.9
Delta foreset beds	Scaphopods	1	5	0	0	0.0	0.0	0.0
Level bottom mud	Scaphopods	1	1489	38	2	2.6	0.1	5.0
Level bottom sand	Scaphopods	1	79	3	2	3.8	2.5	40.0

S = species richness, n = abundance (corrected to account for disarticulated bivalves), D = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, IDF = incomplete drill frequency, and PE = prey effectiveness.

### 2.6.2. Predation intensities in size categories

No significant differences were found between the proportions of drilled shells across size-categories in the four measured species, except in *Venerupis rhomboides* (Fig. 2.2): it was drilled more frequently in the smallest compared to the two larger size categories ( $\chi^2 = 26.162$ ,  $p < 0.0001$ ). Although this bivalve is among the largest in the Northern Adriatic, with a maximum measured length of 33 mm (compared to 11 mm and 7 mm for *Chama gryphoides* and *Lucinella divaricata*, respectively), most *V. rhomboides* in our study (66.2 %) were small (< 5 mm) individuals. The epifaunal cementing bivalve *C. gryphoides* showed no significant differences in DF between size classes. The largest specimens (> 3mm) make up only 18.7 % of the population, while the intermediate size (2 – 3 mm) contains 55.2 %, and the smallest (1 – 2mm) 26.1 %. In contrast, the infaunal *L. divaricata*'s first two size categories (1 – 2 mm and 2 – 3 mm) make up similar

**Table 2.2.** Taxonomic summary of drill hole data pooled across all samples for classes, families/subfamilies and the 5 most abundant species of bivalves and gastropods

	<i>n</i>	<i>D</i>	ID	DF (%)	IDF (%)	PE (%)
Total assemblage	48,906	10,084	470	20.6	1.0	4.5
<i>Class</i>						
Bivalvia	13,155	3080	352	23.4	2.7	10.3
Gastropoda	34,178	6963	114	20.4	0.3	1.6
Scaphopoda	1573	41	4	2.6	0.3	8.9
<i>Family</i>						
<i>Bivalvia</i>						
Nuculanidae	197	37	1	18.8	0.5	2.6
Nuculidae	228	81	1	35.5	0.4	1.2
Arcidae	155	81	2	52.3	1.3	2.4
Noetinae	56	38	0	67.9	0.0	0.0
Glycymerididae	1	0	0	0.0	0.0	-
Crenellinae	55	19	0	34.5	0.0	0.0
Mytilinae	300	48	2	16.0	0.7	4.0
Modiolinae	124	13	1	10.5	0.8	7.1
Pectinidae	206	20	0	9.7	0.0	0.0
Spondylidae	4	0	0	0.0	0.0	-
Anomiidae	235	81	0	34.5	0.0	0.0
Limidae	4	0	0	0.0	0.0	-
Ostreidae	193	55	4	28.5	2.1	6.8
Chamidae	180	127	27	70.6	15.0	17.5
Lucinidae	530	121	4	22.8	0.8	3.2
Thyasiridae	1	0	0	0.0	0.0	-
Galeommatidae	2102	857	2	40.8	0.1	0.2
Cardiidae	1528	166	0	10.9	0.0	0.0
Mactridae	208	27	1	13.0	0.5	3.6
Solenidae	2	0	0	0.0	0.0	-
Pharellidae	7	2	0	28.6	0.0	0.0
Semelidae	384	27	0	7.0	0.0	0.0
Tellinidae	380	44	0	11.6	0.0	0.0
Psammobiidae	1	0	0	0.0	0.0	-
Solecurtiidae	16	0	0	0.0	0.0	-
Donacidae	11	0	0	0.0	0.0	-
Petricolidae	4	0	0	0.0	0.0	-
Veneridae	1881	521	17	27.7	0.9	3.2
Corbulidae	3897	628	286	16.1	7.3	31.3
Gastrochaenidae	3	0	0	0.0	0.0	-
Hiatellidae	242	85	4	35.1	1.7	4.5
Pandoridae	12	0	0	0.0	0.0	-
Cuspidariidae	4	2	0	50.0	0.0	0.0
Thraciidae	2	0	0	0.0	0.0	-
<i>Gastropoda</i>						
Patellidae	9	0	0	0.0	0.0	-
Fissurellidae	91	0	0	0.0	0.0	-
Scissurellidae	21	4	0	19.0	0.0	0.0
Haliotidae	27	1	0	3.7	0.0	0.0
Phasianellidae	214	16	0	7.5	0.0	0.0
Trochidae	2497	283	6	11.3	0.2	2.1
Iravadiidae	157	36	1	22.9	0.6	2.7
Rissoidae	9107	2299	22	25.2	0.2	0.9
Hydrobiidae	2645	23	0	0.9	0.0	0.0
Truncatellidae	21	2	0	9.5	0.0	0.0
Cerithiidae	11,482	2456	8	21.4	0.1	0.3
Turritellidae	2209	973	0	44.0	0.0	0.0
Aporrhaidae	412	35	1	8.5	0.2	2.8
Calyptraeidae	299	8	1	2.7	0.3	11.1
Naticidae	390	31	2	7.9	0.5	6.1
Tonnoidae	7	0	0	0.0	0.0	-
Muricidae	181	34	1	18.8	0.6	2.9
Buccinidae	68	8	0	11.8	0.0	0.0
Nassariidae	2745	396	52	14.4	1.9	11.6
Marginellidae	77	6	0	7.8	0.0	0.0
Mitridae	1	0	0	0.0	0.0	-
Costellariidae	27	8	0	29.6	0.0	0.0
Conidae	36	2	0	5.6	0.0	0.0
Turridae	498	187	1	37.6	0.2	0.5
Cerithiopsidae	35	6	1	17.1	2.9	14.3
Triphoridae	182	32	12	17.6	6.6	27.3
Epitoniidae	81	23	0	28.4	0.0	0.0
Aclididae	1	0	0	0.0	0.0	-
Eulimidae	64	12	0	18.8	0.0	0.0

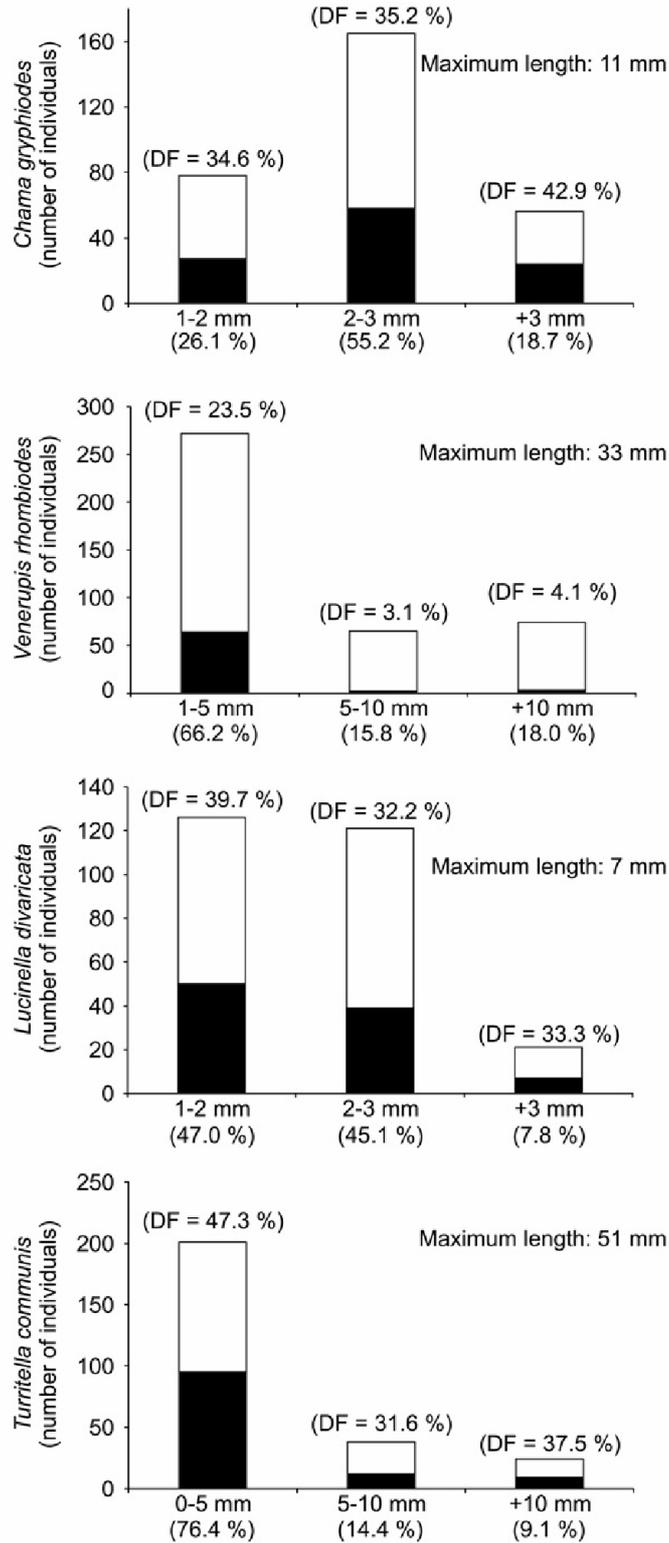
*n* = abundance (corrected to account for disarticulated bivalves), *D* = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, IDF = incomplete drill frequency and PE = prey effectiveness.

**Table 2.2 (Continued).** Taxonomic summary of drill hole data pooled across all samples for classes, families/subfamilies and the 5 most abundant species of bivalves and gastropods.

	<i>n</i>	<i>D</i>	ID	DF (%)	IDF (%)	PE (%)
Gastropoda						
Pyramidellidae	331	68	6	20.5	1.8	8.1
Acteonidae	17	3	0	17.6	0.0	0.0
Haminoeidae	65	4	0	6.2	0.0	0.0
Philinidae	20	0	0	0.0	0.0	–
Scaphandridae	58	4	0	6.9	0.0	0.0
Retusidae	98	3	0	3.1	0.0	0.0
Ellobiidae	6	0	0	0.0	0.0	–
Scaphopoda						
Dentaliidae	1572	41	6	2.6	0.4	12.8
<i>Most abundant species</i>						
Bivalvia						
<i>Mysella bidentata</i>	2001	852	4	42.6	0.2	0.5
<i>Parvicardium papillosum</i>	933	159	0	17.0	0.0	0.0
<i>Chamelea gallina</i>	711	193	11	27.1	1.5	5.4
<i>Corbula gibba</i>	1878	563	530	30.0	28.2	48.5
<i>Lentidium mediterraneum</i>	2019	45	1	2.2	0.0	2.2
Pooled abundant bivalves	13,155	3073	603	23.4	4.6	16.4
Gastropoda						
<i>Hydrobia ulvae</i>	2754	21	0	0.8	0.0	0.0
<i>Bittium reticulatum</i>	2296	1362	6	59.3	0.3	0.4
<i>Bittium latreilli</i>	8934	463	4	5.2	0.0	0.9
<i>Turritella communis</i>	2209	973	0	44.0	0.0	0.0
<i>Nassarius cf. pygmaeus</i>	2387	338	53	14.2	2.2	13.6
Pooled abundant gastropods	34136	6979	122	20.4	0.4	1.7
Scaphopoda						
<i>Dentalium sp.</i>	1572	41	6	2.6	0.4	12.8

*n* = abundance (corrected to account for disarticulated bivalves), *D* = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, IDF = incomplete drill frequency and PE = prey effectiveness.

proportions (47.0 % and 45.1 %, respectively), but larger specimens (> 3 mm) are relatively rare (7.8 %). No significant differences in DF were found between size categories of *L. divaricata*. *Turritella communis*, a shallow-infaunal suspension feeding gastropod, is strongly represented by small (length < 5 mm) individuals (76.4 %), but no statistically significant differences in DF between size categories were observed. Although the maximum length of *T. communis* was 51 mm, the proportion of individuals > 10 mm was only 9.1 %.



**Fig. 2.2.** Drilled (black) and undrilled (white) epifaunal (*Chama gryphoides*) and infaunal (*Venerupis rhomboides*, *Lucinella divaricata*, and *Turritella communis*) mollusc species common in sublittoral habitats in the Gulf of Trieste in three size categories. Proportions of total population within each size class are listed below each column, and drill frequencies (DF) are shown above.

### 2.6.3. Predation intensities at different taxonomic levels

Pooled DF, IDF and PE across all samples are 20.6 %, 1.0 % and 4.5 %, respectively (Table 2.2). Bivalve DF was slightly higher than that of gastropods ( $\chi^2 = 52.53$ ,  $p \ll 0.0001$ ), which in turn was much higher than scaphopods' DF ( $\chi^2 = 300.31$ ,  $p \ll 0.0001$ ). IDF was low ( $< 3 \%$ ) in all three molluscan classes. PE was indistinguishable between bivalves and scaphopods ( $\chi^2 = 0.0904$ ,  $p = 0.956$ ), but gastropods had a lower PE (1.6 %) than both bivalves ( $\chi^2 = 407.6$ ,  $p \ll 0.0001$ ) and scaphopods ( $\chi^2 = 14.537$ ,  $p < 0.001$ ; see also Appendix B Fig. 1).

Eleven of the 34 bivalve families never had drill holes, but these families were represented by relatively few individuals ( $n < 20$ ). Among families that were attacked, DFs ranged from 7.0 % (Semelidae) to 70.6 % (Chamidae; Table 2.2, Fig. 2.3a). Thirteen bivalve families contained incomplete drill holes. For these families, IDF ranged from 0.1 % (Galeommatidae) to 15.0 % (Chamidae). PE ranged from 0.2 % (Galeommatidae) to 31.3 % (Corbulidae) across bivalve families with incomplete drill holes.

Seven of the 36 gastropod families never had drill holes, although except the Fissurellidae ( $n = 91$ ) these families were represented by  $< 20$  individuals. Among families that were attacked, DF ranged from 0.9 % (Hydrobiidae) to 44.0 % (Turritellidae; Table 2.2, Fig. 2.3b). Thirteen gastropod families contained incomplete drill holes, of which cerithiids had the lowest IDF (0.1 %) and PE (0.3 %), while triphorids had the highest (6.6 % and 27.3 %, respectively).

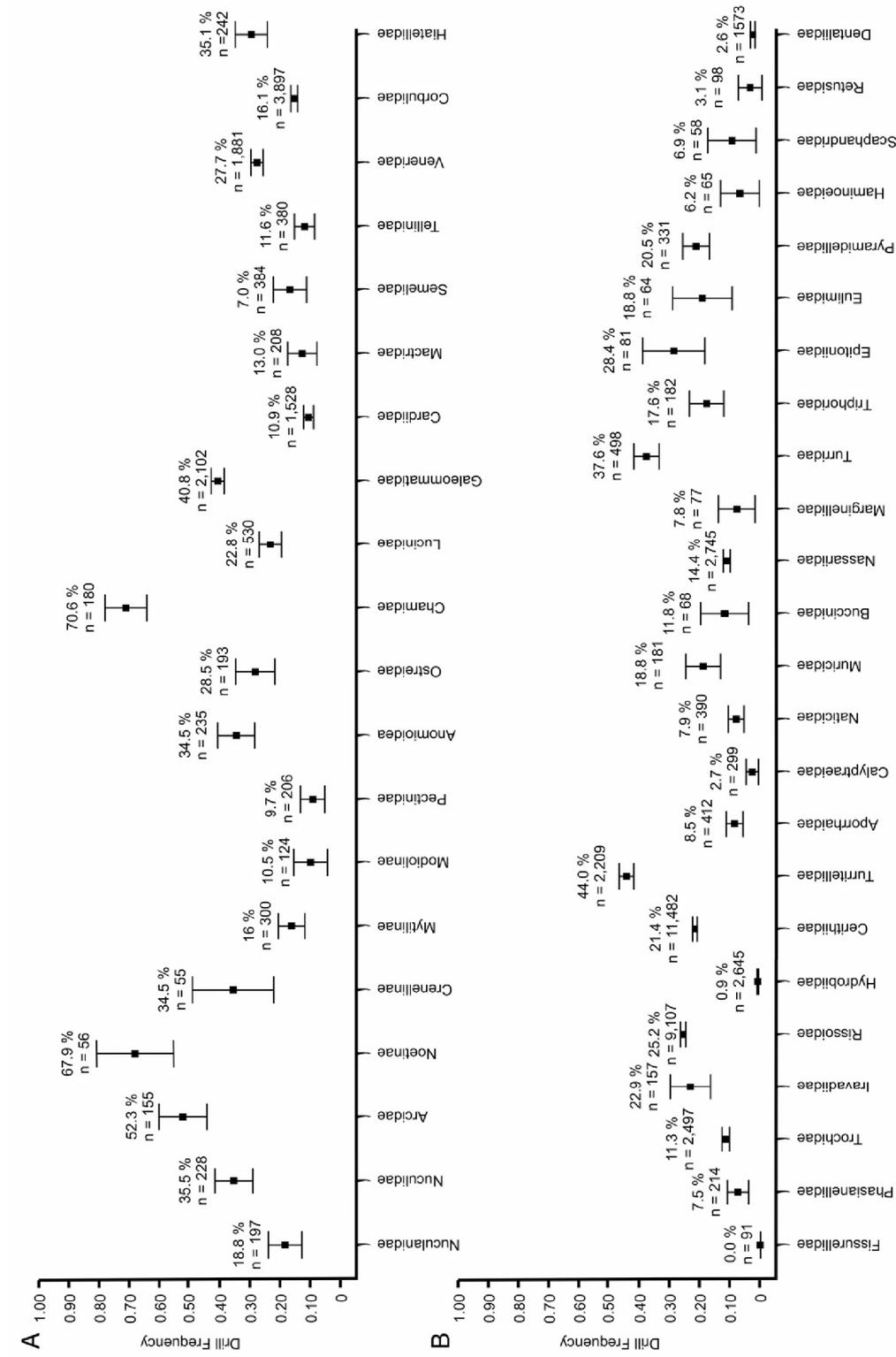
All five of the most abundant bivalve species were drilled. Drilling frequencies ranged from 2.2 % (*Lentidium mediterraneum*) to 42.6 % (*Mysella bidentata*; Table 2.2, see also Appendix B Fig. 2.2). *Parvicardium*

*papillosum* was never incompletely drilled, while the others had at least one incomplete drill hole. For these species with incomplete drill holes, IDFs ranged from 0.2 % (*Mysella bidentata*) to 28.2 % (*Corbula gibba*). In species with incomplete drill holes, PE ranged from 0.5 % (*Mysella bidentata*) to 48.5 % (*Corbula gibba*; Table 2.2).

All five of the most abundant gastropod species were drilled, with frequencies ranging from 0.8 % (*Hydrobia ulvae*) to 44.0 % (*Turritella communis*; Table 2.2, see also Appendix B Fig. 2.2). *Hydrobia ulvae* and *Turritella communis* were never incompletely drilled, while the others had at least one incomplete drill hole. For species with incomplete drill holes, IDFs ranged from 0.3 % (*Bittium reticulatum*) to 2.2 % (*Nassarius cf. pygmaeus*) and PE from 0.4 % (*Bittium reticulatum*) to 13.6 % (*Nassarius cf. pygmaeus*).

#### **2.6.4. Life habits of mollusks and drilling predation**

*Feeding strategies.*—In terms of number of species and individuals, bivalves were strongly dominated by suspension feeders, followed by deposit feeders (Table 2.3). DF was > 15 % in all categories and was lower in deposit feeders than in chemosymbionts ( $\chi^2 = 12.731$ ,  $p = 0.0017$ ) and suspension feeders ( $\chi^2 = 44.865$ ,  $p < 0.0001$ ), but not statistically different between the latter ( $\chi^2 = 0.603$ ,  $p = 0.7397$ ; Fig. 2.4). Carnivores had no incomplete drill holes. In other guilds, PE ranged from 1 % (deposit feeders) to 11.1 % (suspension feeders). PE was significantly higher among suspension feeders than among chemosymbionts ( $\chi^2 = 7.8037$ ,  $p = 0.02$ ) and deposit feeders ( $\chi^2 = 19.348$ ,  $p < 0.0001$ ), but was not significantly different ( $\chi^2 = 1.88$ ,  $p = 0.391$ ) between the

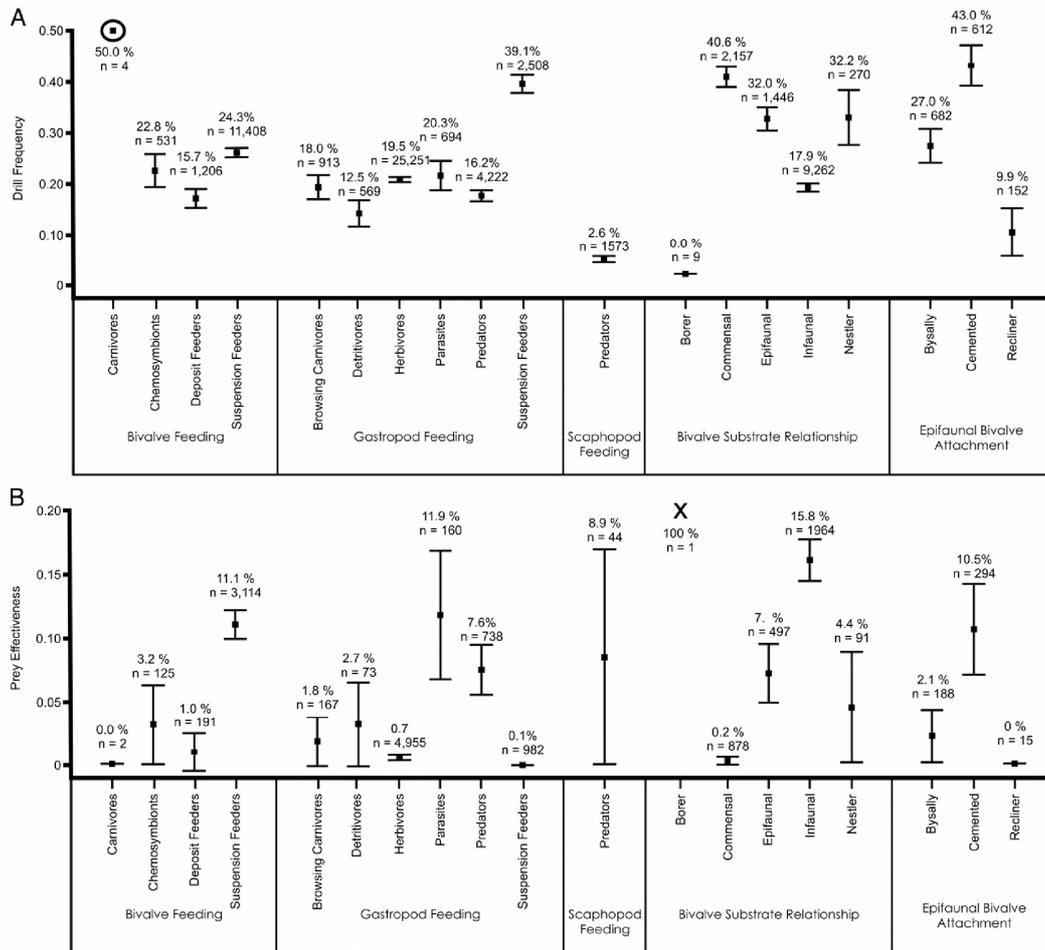


**Fig. 2-3.** Mean drill frequencies of abundant mollusc families (n > 50) pooled across all samples. A) Bivalves and B) gastropods and scaphopods. Error bars are 95 % confidence intervals.

latter two guilds (Table 2.3). Although rare, carnivorous bivalves were drilled, but no incomplete drill holes were found.

In terms of number of species, gastropods were strongly dominated by herbivores and predators followed by parasites; however, in terms of abundance, suspension feeders are more important than parasites (Table 2.3). DFs ranged from 12.5 % (detritivores) to 39.1 % (suspension feeders) and were significantly higher in suspension feeders than in the next-highest category (parasites,  $\chi^2 = 84.4$ ,  $p < 0.0001$ ; Fig. 2.4). The drill frequency of detritivores (< 15 %) was significantly lower than that of parasites ( $\chi^2 = 13.8$ ,  $p < 0.001$ ) and herbivores ( $\chi^2 = 17.6$ ,  $p < 0.001$ ), but not different from predators ( $\chi^2 = 5.1$ ,  $p = 0.07$ ; Fig. 2.4a). PE ranged from 0.1 % (suspension feeders) to 11.9 % (parasites). Parasites and predators had the highest PE (not statistically distinguishable;  $\chi^2 = 3.2$ ,  $p = 0.21$ ). Suspension feeders had lower PE than browsing carnivores ( $\chi^2 = 11.8$ ,  $p = 0.003$ ). Detritivores were not significantly different in effectiveness against their predators than parasites ( $\chi^2 = 5.1$ ,  $p = 0.078$ ), predators ( $\chi^2 = 2.35$ ,  $p = 0.308$ ), browsing carnivores ( $\chi^2 = 0.22$ ,  $p = 0.90$ ), or herbivores ( $\chi^2 = 4.48$ ,  $p = 0.11$ ), but were more effective than suspension feeders ( $\chi^2 = 16.63$ ,  $p < 0.001$ ).

*Substrate relationships.*—In terms of number of species, bivalves were strongly dominated by infaunal taxa, followed by epifaunal taxa; however, in terms of abundance, commensals were the second largest group. Excluding the relatively rare borers (Fig. 2.4, Table 2.3), DFs ranged from 17.9 % (infaunal) to 40.6 % (commensal). Commensal bivalves had higher DFs than nestlers ( $\chi^2 = 7.06$ ,  $p = 0.03$ ), the next lowest category. Infaunal bivalves had significantly lower DFs than nestlers ( $\chi^2 = 36.26$ ,  $p < 0.0001$ ), the next highest category.



**Fig. 2.4.** Comparison of A) drill frequencies and B) prey effectiveness across ecological categories: bivalve, gastropod and scaphopod feeding strategies, bivalve substrate relationships, and epifaunal bivalve attachment. Error bars are 95 % confidence intervals. Circled data point represents confidence intervals that exceed the y-axis. Note—in a) 'n' = number of molluscs (adjusted to account for disarticulated bivalves), in b) 'n' = complete plus incomplete drill holes. Boring bivalves (marked with an X) contained only 1 incomplete drill hole, resulting in a PE of 100 %.

**Table 2.3.** Ecological summary of drill hole data pooled across all samples

	<i>S</i>	<i>n</i>	<i>D</i>	ID	DF (%)	IDF (%)	PE (%)
<i>Bivalve feeding strategies</i>							
Carnivore	1	4	2	0	50.0	0.0	0.0
Chemosymbiotic	5	531	121	4	22.8	0.8	3.2
Deposit feeding	14	1206	189	2	15.7	0.2	1.0
Suspension feeding	57	11,408	2768	346	24.3	3.0	11.1
<i>Gastropod feeding strategies</i>							
Browsing carnivore	3	913	164	3	18.0	0.3	1.8
Detritivore	2	569	71	2	12.5	0.4	2.7
Herbivore	45	25,251	4922	33	19.5	0.1	0.7
Parasite	17	694	141	19	20.3	2.7	11.9
Predator	30	4222	682	56	16.2	1.3	7.6
Suspension feeding	2	2508	981	1	39.1	0.0	0.1
<i>Scaphopod feeding strategies</i>							
Predator	1	1573	41	4	2.6	0.3	8.9
<i>Bivalve substrate relationship</i>							
Borer	5	9	0	1	0.0	11.1	100.0
Commensal	9	2157	876	2	40.6	0.1	0.2
Epifaunal	12	1446	462	35	32.0	2.4	7.0
Infaunal	44	9262	1654	310	17.9	3.3	15.8
Nestler	5	270	87	4	32.2	1.5	4.4
<i>Epifaunal bivalve attachment</i>							
Bysally	6	682	184	4	27.0	0.6	2.1
Cemented	4	612	263	31	43.0	5.1	10.5
Recliner	2	152	15	0	9.9	0.0	0.0

*S* = species richness within ecological category, *n* = abundance (corrected to account for disarticulated bivalves), *D* = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, IDF = incomplete drill frequency, and PE = prey effectiveness.

Epifaunal bivalves and nestlers did not have significantly different DFs ( $\chi^2 = 0.0007$ ,  $p = 0.996$ ). PE ranged from 0.2 % (commensal) to 15.8 % (infaunal), and was higher in infaunal than epifaunal bivalves ( $\chi^2 = 25.147$ ,

$p \ll 0.0001$ ; the next highest group), which were each higher than in commensals ( $\chi^2 = 23.275$ ,  $p \ll 0.0001$  and  $\chi^2 = 56.281$ ,  $p \ll 0.0001$ , respectively). The PE of nestlers and epifaunal bivalves did not differ significantly ( $\chi^2 = 0.87$ ,  $p = 0.647$ ).

In terms of number of species and abundance, epifaunal bivalves were dominated by bysally attaching and cementing forms. DFs ranged from 9.9 % (recliners) to 43.0 % (cementers), and were higher in cementers than bysally attaching bivalves ( $\chi^2 = 36.493$ ,  $p \ll 0.0001$ ), which in turn were higher than in recliners ( $\chi^2 = 20.032$ ,  $p \ll 0.0001$ ; Fig. 2.4, Table 2.3). PE ranged from 0 % (recliners) to 10.5 % (cementers) and was significantly higher in cementers than bysally attaching bivalves ( $\chi^2 = 12.063$ ,  $p = 0.0024$ ), but was not significantly different between bysally attaching and reclining bivalves ( $\chi^2 = 0.326$ ,  $p = 0.85$ ).

#### **2.6.5. Environmental variation in drilling frequency**

*Taxa.*—DFs of the total assemblage differed significantly between tidal flat (1.4 %) and all sublittoral (27.4 %) samples ( $\chi^2 > 3000$ ,  $p \ll 0.0001$ ; Fig. 2.5a). IDFs and PE (Fig. 2.5) also differ significantly between tidal flat and sublittoral samples ( $\chi^2 = 161.45$ ,  $p \ll 0.0001$  and  $\chi^2 = 4.67$ ,  $p = 0.03$ , respectively). Two species, *Bittium latreillii* and *B. reticulatum*, were abundant in both the intertidal and sublittoral. For each, drilling intensities were higher in the sublittoral than on the tidal flat ( $\chi^2 = 408.63$ ,  $p \ll 0.0001$ ,  $\chi^2 = 1047.7$ ,  $p \ll 0.0001$ , respectively; Fig. 2.6).

DFs among samples ranged from 1.4 % (inner and outer tidal flat) to 32.4 % (sample 4 from level bottom mud; Table 2.1, Fig. 2.7). No incomplete drill holes were recovered from the inner tidal flat. Of the other samples, IDFs were also low and ranged from  $< 0.1$  % (outer tidal flat) to 4.9 % (sample 6 from level

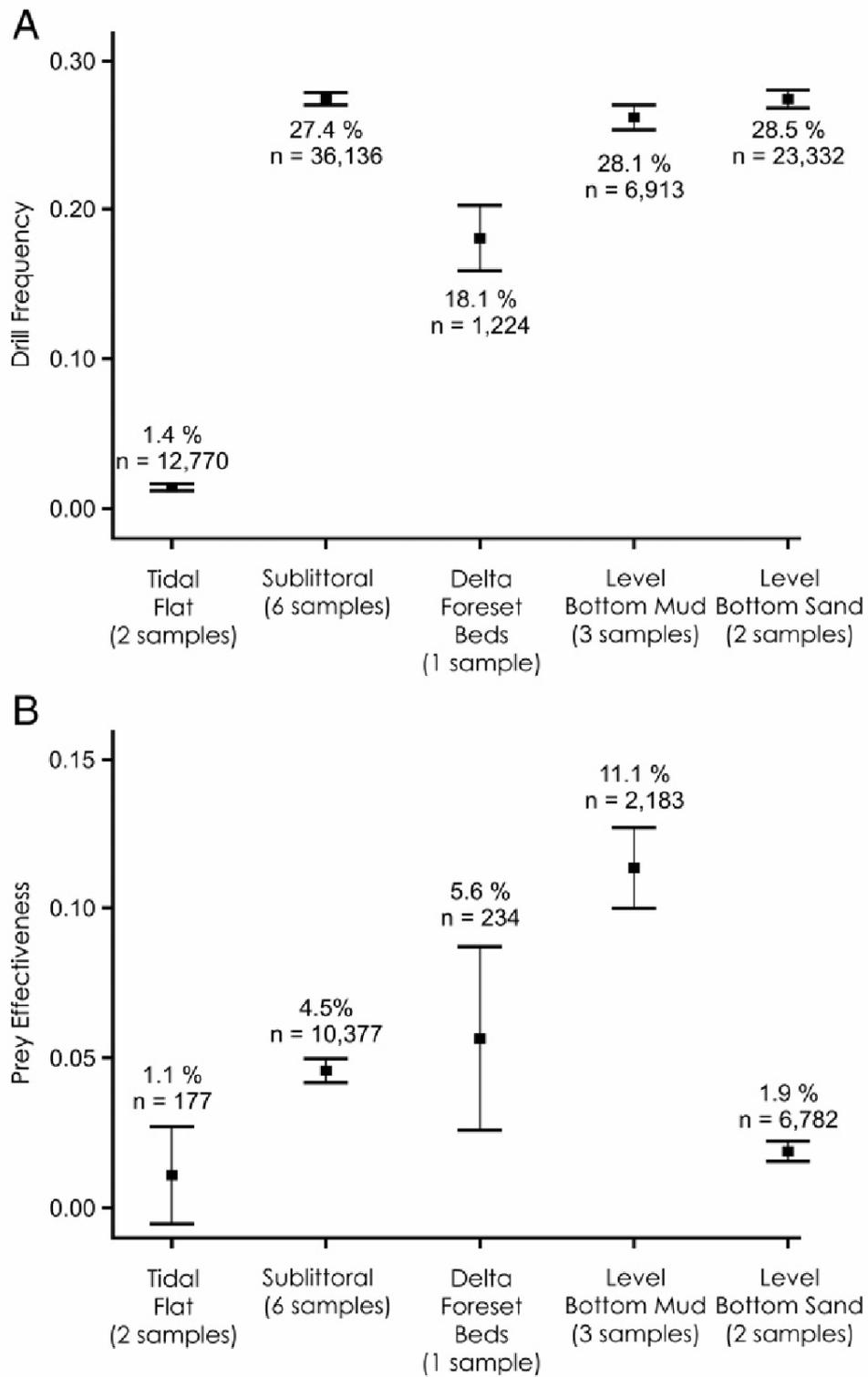
bottom mud). PE ranged from 0.7 % (sample 00 level bottom sand) to 15.0 % (sample 6 level bottom mud).

DF was significantly higher in the delta foreset beds than the tidal flat ( $\chi^2 = 1130.8$ ,  $p \ll 0.0001$ ), which in turn had a significantly higher value than the level bottom muds ( $\chi^2 = 53.53$ ,  $p \ll 0.0001$ ); the values were approximately equal in level bottom muds and sands ( $\chi^2 = 0.50$ ,  $p = 0.779$ ; Fig. 2.5). PE was not significantly different between the tidal flat and the delta foreset beds ( $\chi^2 = 5.613$ ,  $p = 0.0604$ ), but increased from the delta to level bottom muds ( $\chi^2 = 6.845$ ,  $p = 0.033$ ) and was higher on mud than on level bottom sands ( $\chi^2 = 351.09$ ,  $p \ll 0.0001$ ).

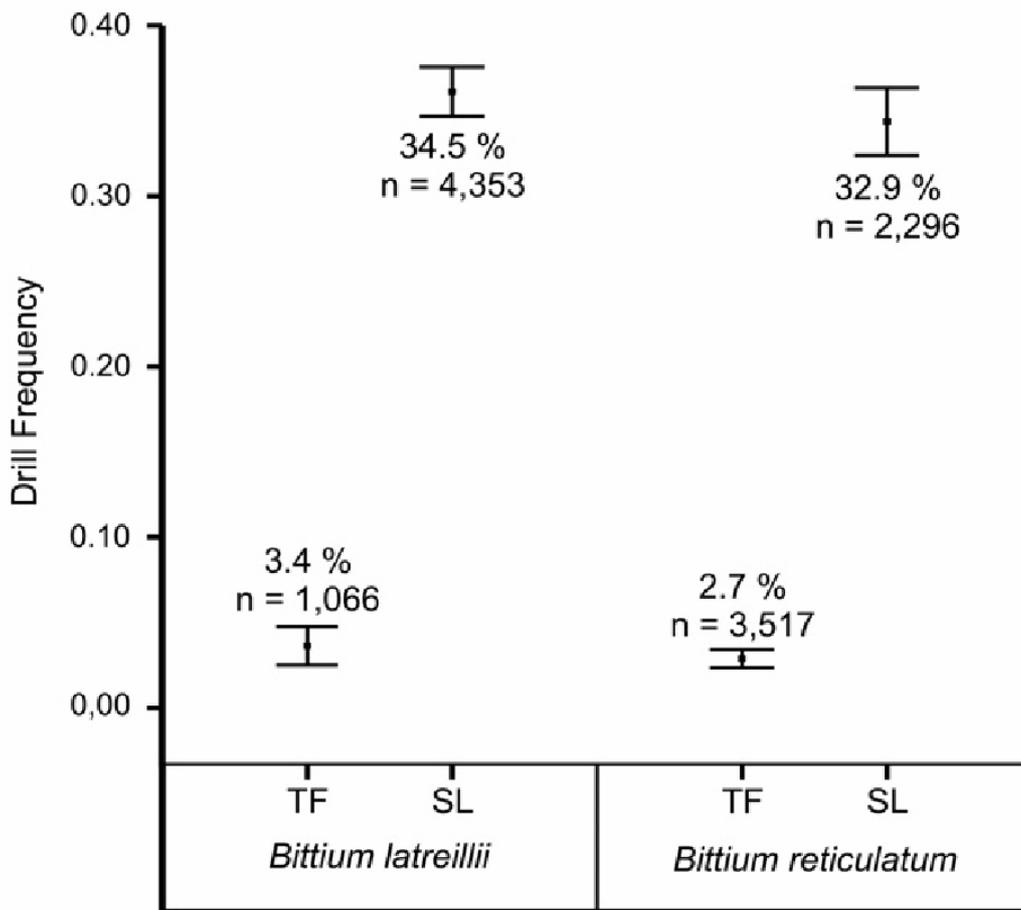
With respect to the spatial distribution of DFs, bivalves and gastropods followed a similar pattern: in both taxa, DF increased from the tidal flat to the sublittoral. Moreover, bivalves had a slightly higher DF than gastropods in all environments, but significantly so in level bottom muds. Sublittoral environmental differences in DF are also apparent, with higher frequencies in level bottom muds and sands than in the delta foreset beds (Fig. 2.8). In bivalves, IDF was highest in level bottom muds (5.3 %) and below 2 % elsewhere (Table 2.1). No incomplete drill holes were found in gastropods from the tidal flat or the delta foreset beds, and IDF was highest in level bottom mud (though only 2.0 %). Bivalves had higher PEs in all environments than did gastropods. Also, both taxa had higher PEs in level bottom muds than in level bottom sands.

In general, bivalve families had higher DFs in mud than in sand or delta environments, though this pattern is not always significant. Galeommatids, for example, were drilled less frequently in the delta foreset beds and level bottom

sands than in level bottom muds (Fig. 2.9a). PE in galeommatids was very low (0.2 % in level bottom muds and 0 % in all other environments). In contrast,



**Fig. 2.5.** Environmental analysis of predation parameters for tidal flat, pooled sublittoral, and sublittoral environments for A) drill frequency, and B) prey effectiveness. Error bars are 95 % confidence intervals.



**Fig. 2.6.** Tidal flat (TF) and sublittoral (SL) drill frequencies of two *Bittium* species common in both intertidal and sublittoral samples.

venerids had a PE of 0 % in level bottom muds versus 5.9 % in the delta foreset beds sample and 3.1 % in level bottom sands (Fig. 2.9b). Corbulid PEs ranged from 2.2 % on the tidal flat to 32.4 % on level bottom muds, though this pattern could be partially controlled by two different corbulid species. *Corbula gibba*, the key corbulid in the sublittoral, has a much thicker shell than *Lentidium mediterraneum*, the tidal flat species. Additionally, generally low DFs on the tidal flat likely contribute substantially to this pattern.

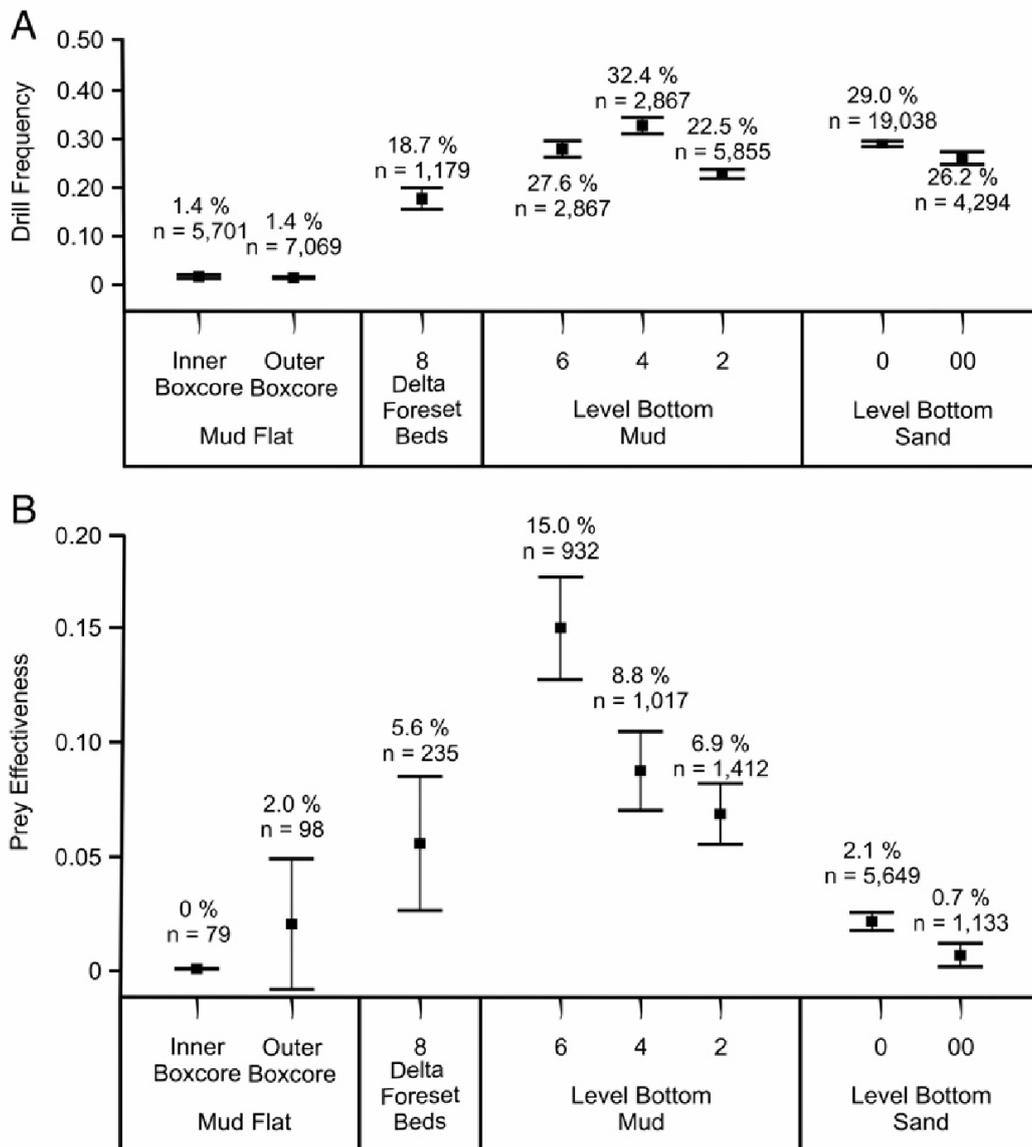
At the family level, gastropods had a higher DF in level bottom sand than in level bottom mud (significant only in nassariids; Fig. 2.9a). DF was generally

lower on the delta foreset beds than in level bottom muds and sands (except nassariids). All gastropod families had very low PEs (< 2 %) in level bottom sands, but values of 0 % in all other environments (Fig 2.9b).

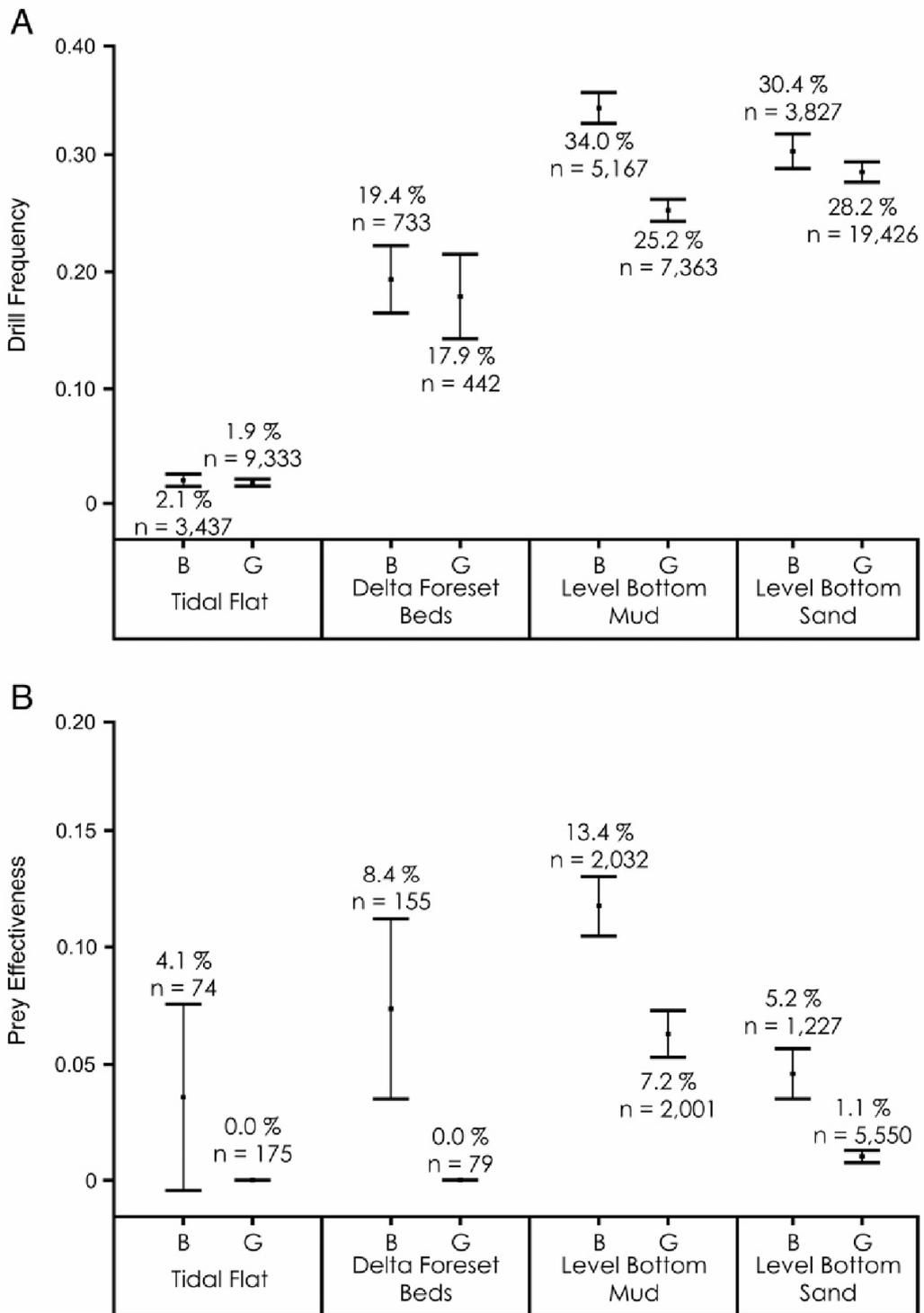
Some samples within environments differed significantly in drilling frequencies and PE (Fig. 2.7). In level bottom muds, DFs varied by nearly 10 %, and the values of samples 2 and 6 differed significantly from sample 4 ( $\chi^2 = 99.01$ ,  $p \ll 0.0001$ , and  $\chi^2 = 15.36$ ,  $p \ll 0.0001$ , respectively). PE of sample 6 differed significantly from that of samples 2 and 4 ( $\chi^2 = 44.09$ ,  $p \ll 0.0001$ ) and varied by nearly 8 %. Both DF and PE differed significantly between the two level bottom sands samples (DF,  $\chi^2 = 16.78$ ,  $p \ll 0.0001$ , Fig. 2.7a; PE,  $\chi^2 = 10.43$ ,  $p < 0.01$ , Fig. 2.7b).

DFs for the classes Bivalvia and Gastropoda, and the families Nuculidae, Galeommatidae and Corbulidae, differed significantly among level bottom mud samples (Table 2.4, see also Appendix B Fig. 2.3). The genera *Nucula* and *Corbula* (each consisting of one species in our samples) differed significantly in DFs among level bottom mud samples. Large differences in PE among these samples existed only in the family Corbulidae.

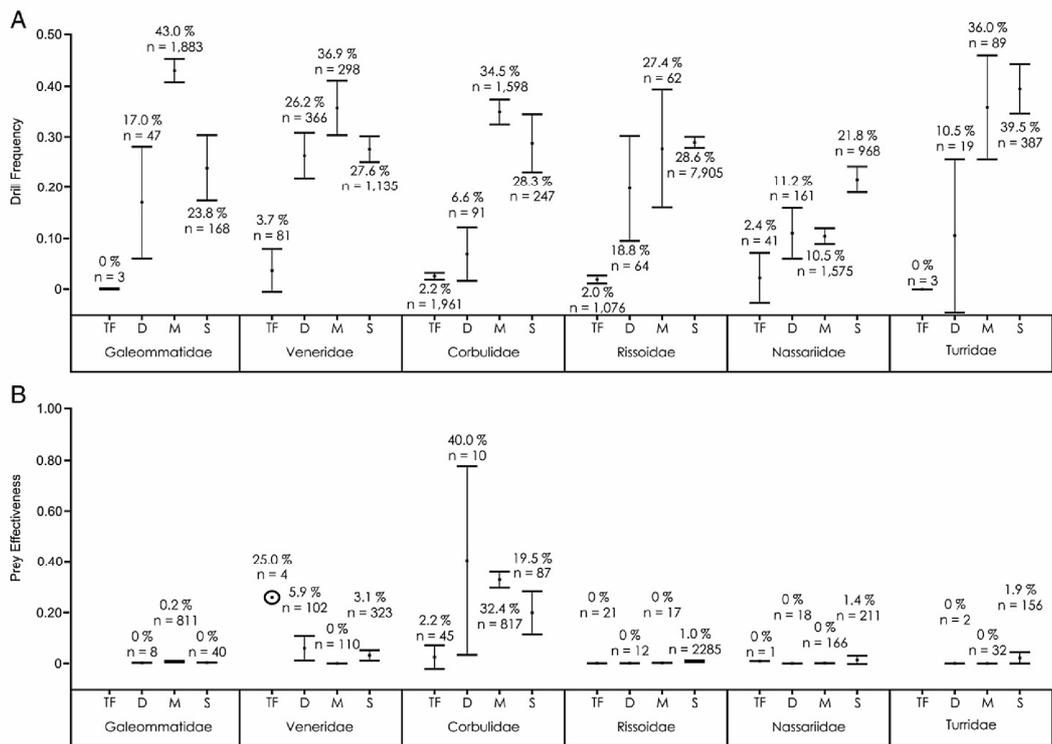
DFs of the class Bivalvia and the gastropod family Cerithiidae differed significantly between level bottom sand samples (Table 2.5, Appendix B Fig. 2.4). On the genus level, *Mytilus*, *Alvania* and *Bittium* and at the species level, *Hiatella arctica* and *Bittium latreilli* differed between samples. The families Trochidae and Cerithiidae differed in PE between level bottom sand samples. Other families have consistent PE across the samples.



**Fig. 2.7.** Predation intensities of the total assemblage per sample for A) drill frequency and B) prey effectiveness. Samples are grouped by environment. Error bars are 95 % confidence intervals.



**Fig. 2.8.** A) Drill frequency and B) prey effectiveness from each studied environment. B = bivalves and G = gastropods. Error bars are 95 % confidence intervals.



**Fig. 2.9.** Comparison of A) drill frequencies and B) prey effectiveness for families with  $n > 10$  in at least three environments. ‘ $n$ ’ for prey effectiveness is complete plus incomplete drill holes. TF = tidal flat, D = delta foreset beds, M = level bottom mud, and S = level bottom sand. Error bars are 95 % confidence intervals.

*Ecological categories.*—In general, DF was low in all ecological categories on the tidal flat and higher in sublittoral habitats. Also, DF was generally higher on level bottom mud and sands than on the delta foreset beds within ecological categories. Likewise, PE tended to be higher in level bottom sands and muds than in the delta foreset beds (when the total of incomplete and complete drill holes was large enough to justify a comparison;  $n > 20$ ; Figs. 2.10-2.13).

Chemosymbiotic bivalves had an overall DF of 22.8 % (Fig. 2.4a), but when compared among environments, those from pooled sublittoral samples (DF = 51.5 %) had significantly higher DFs than any other group in any other

environment (Fig. 2.10, supplementary Table 2.2). Sublittoral chemosymbiont DF is controlled by that from level bottom sands, which contain > 90 % of all such individuals. Both deposit and suspension feeders have lower DFs on the delta than in both level bottom muds and sands. PE was generally low (< 5 %) in chemosymbionts and carnivores in all environments (Fig. 2.10; Appendix A

**Table 2.4.** Intra-environmental drill frequency variation in level bottom mud samples for the total assemblage, classes, families, genera and species ( $n > 20$ )

	Sample 2 (%)	Sample 4 (%)	Sample 6 (%)	$\chi^2$	$p$ -value
Total assemblage	22.5	32.4	27.6	112.09	<b><math>\ll 0.0001</math></b>
Class					
Bivalvia	25.5	45.7	38.1	167.47	<b><math>\ll 0.0001</math></b>
Gastropoda	27.0	26.3	19.7	23.54	<b><math>\ll 0.0001</math></b>
Scaphopoda	3.0	0.7	2.8	4.81	0.09
Family					
Nuculanidae	9.0	13.0	10.3	4.99	0.17
Nuculidae <sup>a</sup>	7.6	45.5	56.8	13.35	<b>&lt; 0.01</b>
Pectinidae	7.3	12.9	15.0	1.94	0.58
Anomiidae <sup>a</sup>	6.0	17.7	19.2	0.67	0.88
Ostreidae <sup>a</sup>	7.2	28.3	13.3	2.95	0.40
Galeommatidae	9.2	48.6	50.6	52.35	<b><math>\ll 0.0001</math></b>
Cardiidae	12.1	15.6	13.2	0.30	0.96
Veneridae	32.3	39.0	45.8	4.07	0.25
Corbulidae <sup>a</sup>	5.9	65.5	33.3	49.74	<b><math>\ll 0.0001</math></b>
Hiatellidae	13.5	6.5	20.0	2.79	0.43
Nassariidae	9.9	11.8	10.4	0.95	0.81
Genera					
<i>Nucula</i> <sup>a</sup>	7.6	45.5	56.8	13.35	<b>&lt; 0.001</b>
<i>Venerupis</i> <sup>a</sup>	6.6	37.1	48.2	6.59	0.09
<i>Corbulae</i> <sup>a</sup>	5.9	65.5	33.3	49.74	<b><math>\ll 0.0001</math></b>
<i>Turritella</i> <sup>a</sup>	45.7	44.7	43.7	0.46	0.93
<i>Aporrhais</i> <sup>a</sup>	5.8	12.0	6.1	3.54	0.32
<i>Calyptraea</i> <sup>a</sup>	2.2	1.7	3.8	0.71	0.87
<i>Euspira</i> <sup>a</sup>	6.9	5.5	6.8	0.15	0.99
<i>Nassarius</i>	9.9	11.8	10.4	0.95	0.81
<i>Dentalium</i> <sup>a</sup>	3.0	0.7	2.8	4.81	0.09
Species					
<i>Nuculana pella</i>	9.0	11.3	10.3	5.81	0.12
<i>Nucula cf. nucleus</i>	7.6	45.5	56.8	13.35	<b>&lt; 0.001</b>
<i>Anomia epphipium</i>	6.0	17.7	19.2	0.67	0.88
<i>Ostrea edulis</i>	7.2	28.3	13.3	2.95	0.40
<i>Parvicardium papillosum</i>	3.4	15.8	41.7	7.13	0.07
<i>Corbula gibba</i>	5.9	65.5	33.3	49.74	<b><math>\ll 0.0001</math></b>

Sample 2-6 columns list drill frequencies,  $\chi^2$  = chi-squared value and  $p$  =  $p$ -value. Bold  $p$ -values are significant at a level of alpha = 0.05.

<sup>a</sup> Indicates monospecific families and genera.

**Table 2.5.** Intra-environmental drill frequency variation in level bottom sand samples for the total assemblage, classes, families, genera and species ( $n > 20$ )

	Sample 0 (%)	Sample 00 (%)	$\chi^2$	$p$ -value
Total assemblage	29.0	26.2	13.84	<b>&lt;0.001</b>
Class				
Bivalvia	32.2	20.5	66.09	<b>≪0.0001</b>
Gastropoda	28.5	27.1	2.81	0.25
Family				
Arcidae	54.8	35.1	4.43	0.11
Modiolinae	17.8	4.6	5.25	0.07
Lucinidae	51.3	54.8	0.13	0.94
Galeommatidae	25.3	13.6	1.44	0.49
Cardiidae	16.4	16.5	0.00	1.00
Veneridae	27.7	25.4	0.16	0.92
Fissurellidae	0.0	0.0	.	.
Phasianellidae	6.7	4.8	1.47	0.48
Trochidae	17.5	16.4	0.17	0.92
Iravidiidae	22.6	23.7	0.01	0.99
Rissoidae	28.5	29.2	0.25	0.88
Cerithiidae	34.9	29.5	15.83	<b>&lt;0.001</b>
Muricidae	20.3	12.0	0.94	0.62
Nassariidae	21.1	27.1	2.23	0.33
Triphoridae	18.8	12.0	0.68	0.71
Pyramidellidae	22.8	16.3	0.98	0.61
Genera				
<i>Mytilus</i> <sup>a</sup>	25.4	10.3	11.49	<b>&lt;0.01</b>
<i>Gouldia</i> <sup>a</sup>	28.1	36.8	0.68	0.71
<i>Venerupis</i>	35.8	23.8	1.11	0.58
<i>Alvania</i>	28.0	24.3	31.64	<b>≪0.0001</b>
<i>Rissoa</i>	39.9	42.5	0.46	0.79
<i>Bittium</i>	35.1	29.7	15.58	<b>&lt;0.001</b>
<i>Nassarius</i>	21.1	27.1	2.23	0.33
Species				
<i>Parvicardium papillosum</i>	16.6	23.6	2.20	0.33
<i>Hiatella arctica</i>	60.8	33.3	6.98	<b>&lt;0.05</b>
<i>Alvania</i> sp. 2	29.3	26.1	0.83	0.66
<i>Pussilina marginata</i>	26.8	23.8	0.91	0.64
<i>Bittium latreilli</i>	35.9	30.2	11.79	<b>&lt;0.01</b>
<i>Bittium reticulatum</i>	33.9	28.7	4.54	0.10

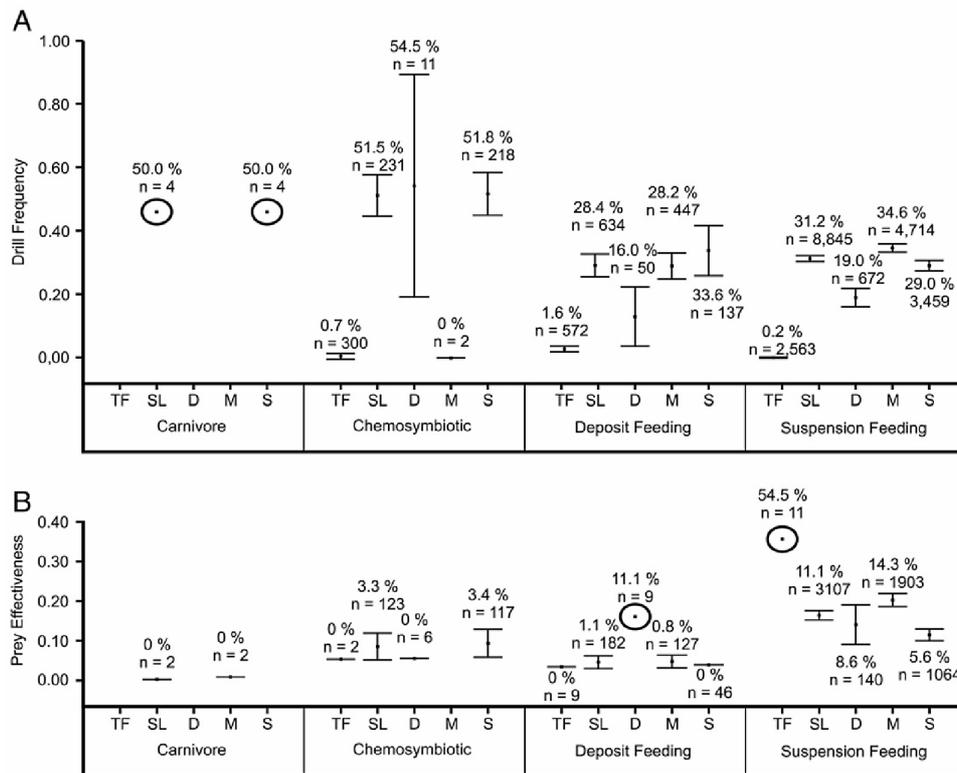
Sample 0 and 00 columns list drill frequencies,  $\chi^2$  = chi-squared value and  $p$  =  $p$ -value. Bold  $p$ -values are significant at the level of alpha = 0.05.

<sup>a</sup> Indicates monospecific genera.

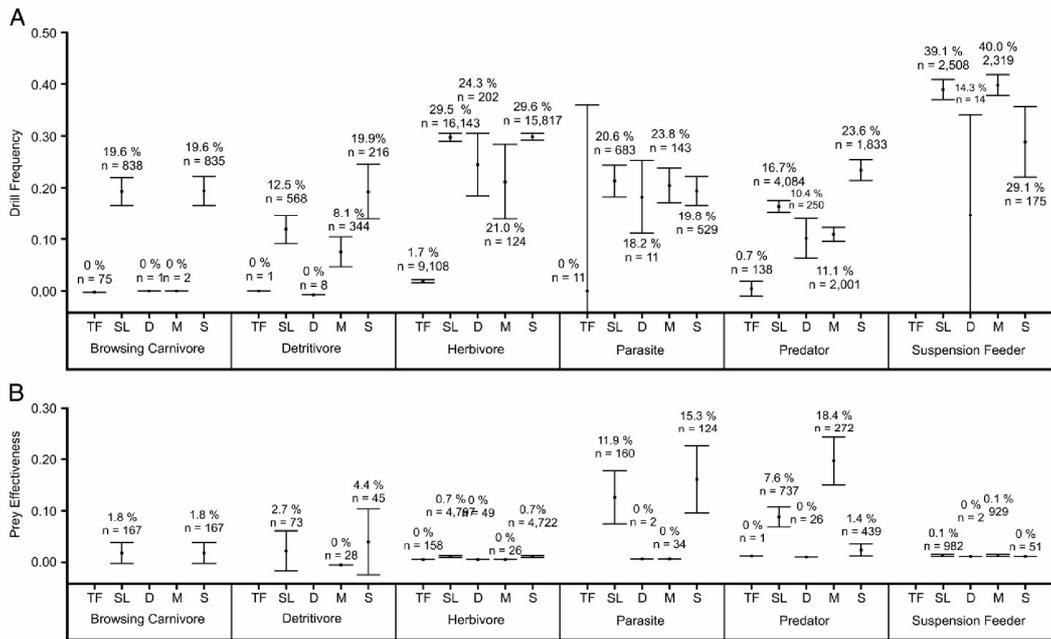
Table 2.2). Deposit feeders had 11.1 % on the delta foreset beds, though this is calculated from < 10 drilled shells. In all other environments, deposit feeders had values < 2 %. Suspension feeders had the lowest and highest PE in level bottom sands (5.6 %) and muds (14.3 %), respectively (Fig. 2.10).

Drilling frequency within all gastropod feeding categories was always higher on level bottom muds and sands than on the delta or tidal flat. Parasites had similar DFs across all sublittoral environments. All other gastropod feeding categories had highest DFs in level bottom sands, except suspension feeders, which had a much higher DF in level bottom muds (Fig. 2.11, Appendix A Table 2.2). Browsing carnivores were frequently attacked in level bottom sands, but were virtually absent in level bottom muds and on the delta foreset beds. Herbivores were attacked frequently in all sublittoral environments, but were much more abundant in level bottom sands.

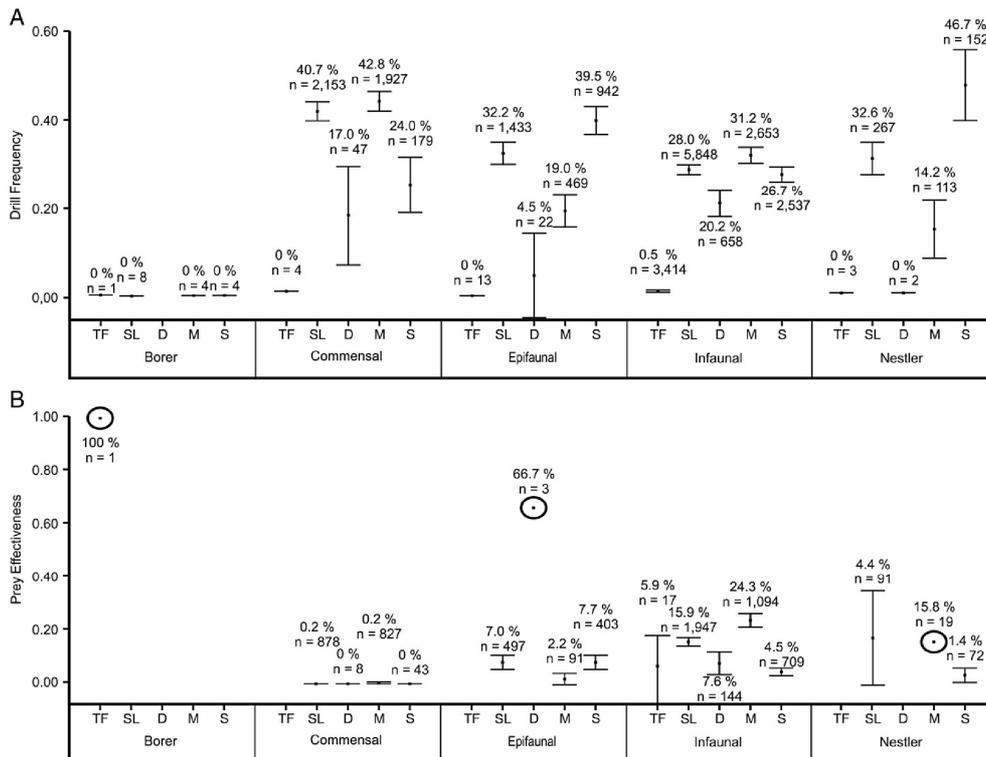
DF was lower in predators and detritivores than other gastropod feeding categories. Gastropods within parasitic, carnivorous, herbivorous and detritivorous guilds had PEs of 0 % in all environments except level bottom sands. Predators and had highest PEs in level bottom muds (18.4 %). Suspension feeder PE was very low in all environments (< 0.1 %). Overall, predators and parasites had the highest PE (Fig. 2.11, see Appendix A Table 2). Drilling frequencies of all bivalve categories according to substrate relationships were significantly different between mud and sand environments (exception: the relatively rare borers, n = 8; Fig. 2.12, see also Appendix A Table 2). Commensal and infaunal bivalves had higher DFs in level bottom muds (42.8 % and 31.2 %, respectively), and epifaunal and nestling bivalves had higher DFs in level bottom sands (39.5 % and 46.7 %, respectively).



**Fig. 2.10.** Inter-environmental comparison of drilling predation across bivalve feeding strategies for A) drill frequencies and B) prey effectiveness. TF = tidal flat, SL = total sublittoral, D = delta foreset beds, M = level bottom mud and S = level bottom sand. Error bars are 95 % confidence intervals. Circled data point represents confidence intervals that exceed the y-axis.



**Fig. 2.11.** Inter-environmental comparison of A) drill frequencies and B) prey effectiveness for gastropod feeding strategies. TF = tidal flat, SL = total sublittoral, D = delta foreset beds, M = level bottom mud, and S = level bottom sand. Error bars = 95 % confidence intervals.



**Fig. 2.12.** Inter-environmental comparison of A) drill frequencies and B) prey effectiveness for bivalve substrate relationships. TF = tidal flat, SL = total sublittoral, D = delta foreset beds, M = level bottom mud and S = level bottom sand. Error bars = 95 % confidence intervals. Circled data points are confidence intervals that exceed the y-axis.

Excluding commensals (very low PE, < 1 %, in every environment) and the relatively rare epifaunals from the delta, PE in level bottom muds ranged from 2.2 % in epifaunal to 24.3 % in infaunal bivalves. PE was higher in level bottom sands than level bottom muds for epifaunal bivalves. Infaunal bivalves showed the opposite pattern: PE was higher in the muds than sands and delta foreset beds (Fig. 2.12, see Appendix A Table 2).

DF in epifaunal bivalve attachment categories ranged from 9.0 % (recliners from level bottom muds) to 64.6 % (cementers from level bottom sands) in individual-rich categories ( $n > 50$ ). Values were higher in cementers from level bottom sands than any other category from any other environment (Fig. 2.13). Also, DF was higher in level bottom sands than level bottom muds in bysally attaching and reclining bivalves (not statistically different in the latter). In general, DF was lower in recliners and varied less between environments (Fig. 2.13, see also Appendix A Table 2).

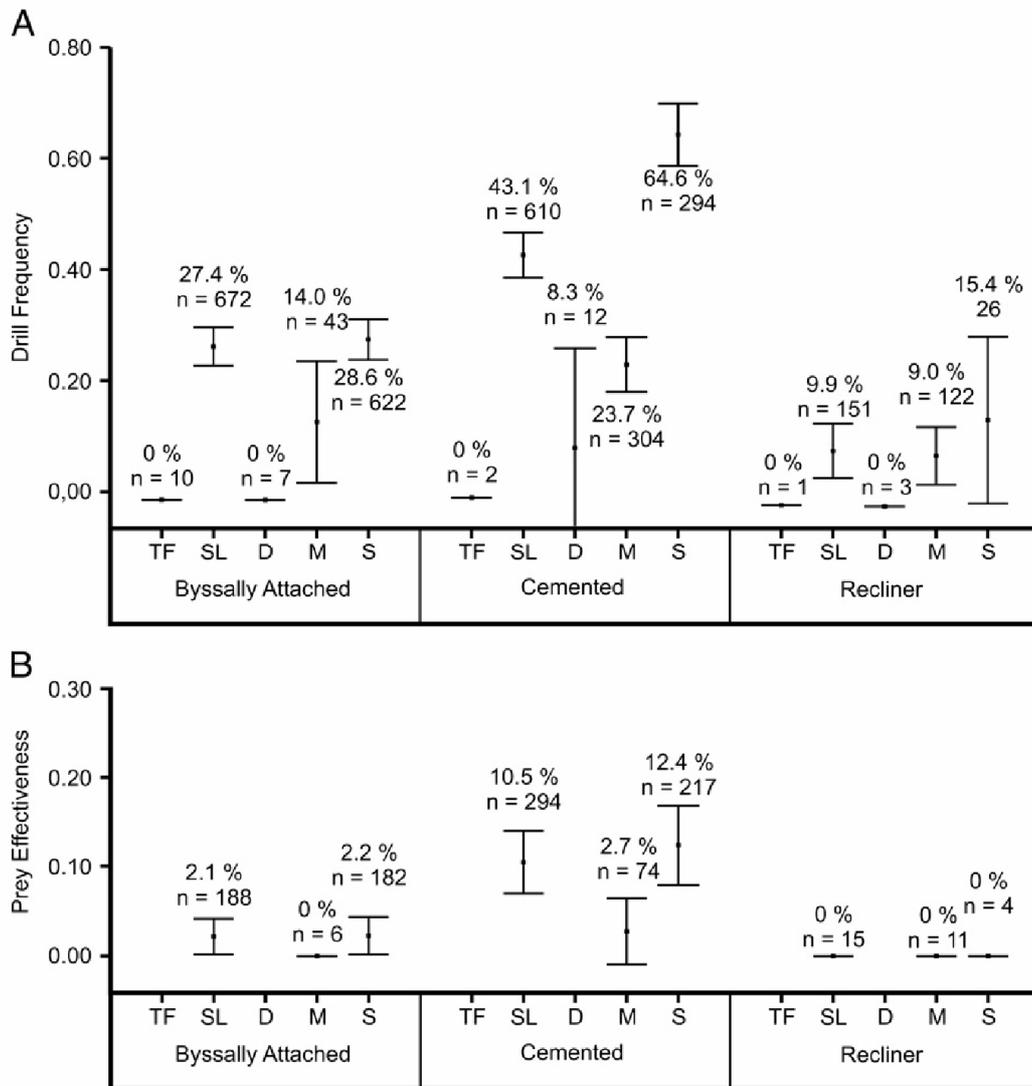
PE was generally low in bysally attaching and reclining bivalves (< 3 %) in all environments. Cementing bivalves had higher PE in level bottom sands (12.4 %) than level bottom muds (2.7 %; Fig. 2.13, see also Appendix A Table 2).

DFs were significantly different within level bottom mud samples in deposit- and suspension-feeding, commensal, and infaunal bivalves, as well as in parasitic gastropods (Table 2.6, Appendix B Fig. 5). No such differences were observed among epifaunal bivalve attachment categories. PEs also differed significantly in suspension feeding and infaunal bivalves, but not in any other ecological category.

DFs differed significantly between level bottom sand samples in suspension-feeding, epifaunal and bysally attaching bivalves, and in browsing carnivorous gastropods (Table 2.7, Appendix B Fig. 6), whereas significant differences in PE occurred only in suspension-feeding and epifaunal bivalves.

#### **2.6.6. Diversity and predation intensities**

At standardized sample size, the tidal flat showed the lowest and sublittoral sands the highest diversities (Fig. 2.14). DF correlated weakly but significantly with species richness and the following diversity indices: Simpson's diversity, Shannon-Wiener diversity, Margalef's Richness and Fischer's alpha; it correlated negatively with dominance. However, restricting the analyses to sublittoral samples did not yield any significant correlations (Table 2.8). This suggests that the much lower DF and diversities in the tidal flat samples drive the overall pattern. Also, the DF of the most abundant species from each sample did not correlate with that species' abundance, but did correlate with combined naticid and muricid abundances, as well as with that of nassariid abundance. Again, these correlations failed when the tidal flat samples were removed.



**Fig. 2.13.** Inter-environmental comparison of A) drill frequencies and B) prey effectiveness across epifaunal bivalve attachment strategies. TF = tidal flat, SL = total sublittoral, D = delta foreset beds, M = level bottom mud, and S = level bottom sand. Error bars are 95 % confidence intervals.

**Table 2.6.** Intra-environmental drill frequency variation among ecological categories within level bottom mud samples

	Sample 2 (%)	Sample 4 (%)	Sample 6 (%)	$\chi^2$	p-value
<i>Bivalve feeding strategies</i>					
Carnivore	50.0	0.0	100.0	–	–
Chemosymbiotic	–	0.0	–	–7.94	–
Deposit feeding	23.1	32.1	37.6	7.94	<b>&lt;0.05</b>
Suspension feeding	25.8	47.4	38.3	165.56	<b>≪0.0001</b>
<i>Gastropod feeding strategies</i>					
Browsing carnivore	0.0	–	–	–	–
Detritivore	6.4	12.5	6.1	3.80	0.28
Herbivore	17.6	42.9	44.4	5.76	0.12
Parasite	29.2	3.0	33.3	10.35	<b>&lt;0.05</b>
Predator	11.1	11.2	10.9	0.03	1.00
Suspension	40.9	40.9	35.7	3.77	0.29
<i>Scaphopod feeding strategies</i>					
Predator	3.0	0.7	2.8	4.81	0.19
<i>Bivalve substrate relationship</i>					
Borer	0.0	–	0.0	–	–
Commensal	33.0	48.5	50.5	51.78	<b>≪0.0001</b>
Epifauna	20.0	18.0	15.3	1.16	0.76
Infaunal	22.6	50.8	33.4	142.53	<b>≪0.0001</b>
Nestler	13.5	6.7	20.0	2.64	0.45
<i>Bivalve attachment</i>					
Bysally	17.9	0.0	14.3	1.46	0.69
Cemented	26.2	24.1	16.1	2.38	0.50
Recliner	3.3	14.8	14.3	4.65	0.20

Sample 2-6 list drill frequencies (%),  $\chi^2$  = chi-squared value, and  $p$  = p-value. Bold  $p$ -values are significant at the level of alpha = 0.05.

## 2.7. Discussion

### 2.7.1. Drilling intensities of bivalves, gastropods and scaphopods

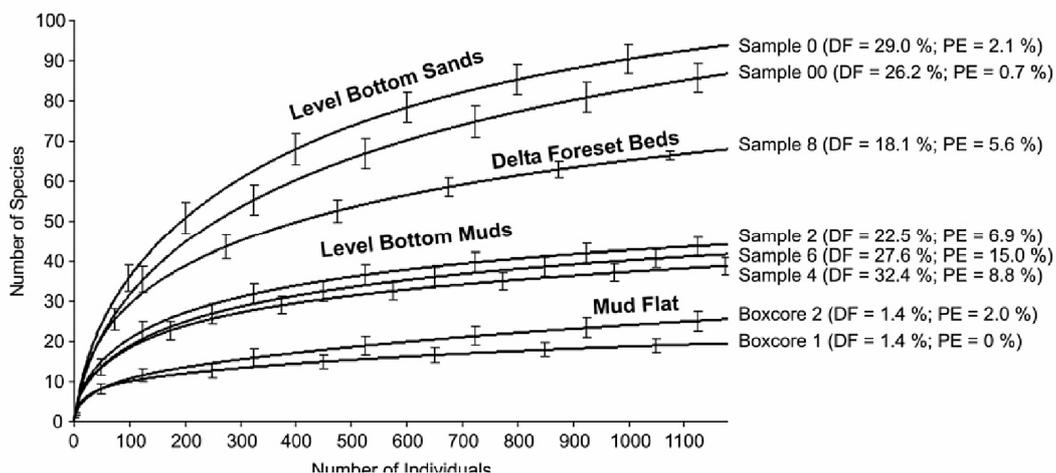
Vermeij (1987 p. 308-311) stated that Cenozoic bivalves are more resistant to drilling predation than gastropods, potentially through adaptation

**Table 2.7.** Intra-environmental drill frequency variation among ecological categories within level bottom sand samples

	Sample 0 (%)	Sample 00 (%)	$\chi^2$	<i>p</i> -value
<i>Bivalve feeding strategies</i>				
Carnivore	–	–	–	–
Chemosymbiotic	26.9	54.8	0.03	0.98
Deposit feeding	35.2	14.3	0.74	0.69
Suspension feeding	31.0	19.6	16.86	<b>&lt;0.001</b>
<i>Gastropod feeding strategies</i>				
Browsing carnivore	19.2	24.6	126.49	<b>≪0.00001</b>
Detritivore	17.2	23.4	0.85	0.65
Herbivore	30.1	27.8	3.71	0.16
Parasite	20.9	13.9	1.43	0.49
Predator	23.5	24.6	0.06	0.97
Suspension	28.9	50.0	–	–
<i>Scaphopod feeding strategies</i>				
Predator	3.8	–	–	–
<i>Bivalve substrate relationship</i>				
Borer	0.0	0.0	–	–
Commensal	26.0	14.8	1.01	0.60
Epifauna	50.3	17.5	44.01	<b>≪0.00001</b>
Infaunal	26.9	26.3	0.02	0.99
Nestler	52.2	30.6	2.02	0.36
<i>Bivalve attachment</i>				
Bysally	40.2	13.0	31.78	<b>&lt;0.00001</b>
Cemented	67.2	50.0	0.94	0.62
Recliner	14.3	20.0	0.07	0.96

Sample 0 and 00 list drill frequencies,  $\chi^2$  = chi-squared value and *p* = *p*-value. Bold *p*-values are significant at the level of alpha = 0.05.

involving thick shells and strong sculpture (Vermeij, 1980; Kitchell et al., 1981). Our data largely support this view. In general, bivalves in this study have significantly higher DFs and PEs, than gastropods. Kelley and Hansen (1993) found that PE from naticid predators is consistently higher in bivalves than gastropods from Cretaceous to Oligocene deposits of the North Atlantic Coastal Plain. The authors also reported that bivalve and gastropod PE increased from the Cretaceous to the Oligocene (1.6 % - 18.9 % and 5 % - 11 %, respectively). Drilling predation on scaphopods has rarely been reported, but was low (1 – 5 %) in Cretaceous to Holocene deposits from the southern Louisiana Gulf Coast, USA (Yochelson et al., 1983). The DFs for scaphopods in the Bay of Panzano are within this range (2.6 %). Nearly all of the common families in the Gulf of Trieste were heavily drilled; 10 of the 18 bivalve families and 13 of the 23 gastropod families (n > 50) had DFs > 10 % (Fig. 2.3).



**Fig. 2.14.** Rarefaction of molluscan faunas from samples collected along a transect in the Gulf of Trieste. Samples and their environments are listed with pooled drill frequencies (DF) and prey effectiveness (PE). Error bars are standard deviations around the mean.

**Table 2.8.** Correlation between diversity indices, total shell abundance, predator abundances, prey effectiveness and drill frequency

	All samples		Sublittoral samples	
	Spearman's <i>r</i>	<i>p</i> -value	Spearman's <i>r</i>	<i>p</i> -value
Species richness	0.74	<b>0.037</b>	0.43	0.397
Dominance index	−0.79	<b>0.021</b>	−0.28	0.596
Simpson index	0.79	<b>0.021</b>	0.28	0.596
Shannon index	0.79	<b>0.021</b>	0.49	0.329
Buzas and Gibson's evenness	0.43	0.289	−0.20	0.704
Menhinicks Richness index	0.67	0.071	0.26	0.623
Margalef's Richness index	0.71	<b>0.047</b>	0.37	0.468
Equitability	0.69	0.058	0.26	0.623
Fischer's alpha	0.71	<b>0.047</b>	0.37	0.468
Berger–Parker dominance	−0.69	0.058	−0.31	0.544
Most abundant species (per sample)	−0.48	0.233	−0.03	0.957
Total shell abundance	0.02	0.955	0.60	0.208
Naticid abundance	0.55	0.157	−0.14	0.785
Muricid abundance	0.57	0.143	0.29	0.579
Nassariid abundance	0.71	<b>0.050</b>	0.37	0.473
Marginellid abundance	0.15	0.721	0.30	0.560
Buccinid abundance	0.41	0.316	0.30	0.568
Naticid and muricid abundance	0.71	<b>0.050</b>	0.09	0.859
Prey effectiveness	0.60	0.117	0.15	0.774

Bold *p*-values are significant at the level of alpha = 0.05.

### 2.7.2. Life habits of prey and drilling predation

Although basic life habit data is widely available for molluscs, the roles of feeding strategy, substrate relationship and attachment on drilling intensities have rarely been considered in modern or fossil assemblage-level predation analyses. This is surprising considering the emphasis placed on predation's role in regulating life habits in marine ecosystems (e.g. Vermeij, 1977, 1987).

In the Gulf of Trieste, suspension-feeding bivalves and gastropods had the highest DFs. It is possible that suspension feeders are attacked more frequently because of their availability to the predators (i.e. they are the most abundant guild); alternatively, predators may preferentially choose them because they are

easy prey. In general, DF was higher for epifaunal than infaunal suspension-feeders (Fig. 2.4). The most heavily drilled gastropod family was the suspension-feeding Turritellidae. These results are consistent with those of Kelley and Hansen (1993), who also noted a preference for turritellids by naticid gastropods. They argue that due to this family's suspension-feeding lifestyle, turritellids can only move sluggishly, reducing their capacity to escape from predators once an attack has commenced. Furthermore, these gastropods typically live buried directly under the sediment surface and are therefore susceptible to both muricid and naticid drillers.

Both infaunal life habit and the ability to move quickly through and on top of the sediment have been hypothesized to reduce marine invertebrate's risk of predation (e.g. Vermeij, 1987). Indeed, deposit feeders, detritivores and predators had the lowest DFs. The relatively high drilling frequencies on browsing carnivores, however, contrast with the assertion that these guilds benefit from their uninhibited movement.

Drilling predators may be expected to avoid chemosymbionts due to toxic reducing compounds in their tissues (Amano and Jenkins, 2007); this would lower their DF in the presence of other abundant prey. In the Northern Adriatic, where their drilling frequencies exceed 20 %, this does not appear to be the case. Similarly, members of the chemosymbiotic family Lucinidae from Cretaceous to Pleistocene deposits of the American Gulf Coastal Plain were also heavily drilled (Kelley and Hansen, 1993, 2006).

Increasing predation pressure during the Mesozoic has been hypothesized as a driving mechanism for the infaunalization of bivalves (Vermeij, 1987). If an infaunal life habit reduces the risk of predation, then lower DFs on infaunal

bivalves are expected. Naticid gastropods typically prey upon infaunal bivalves and gastropods, and rarely do they also attack scaphopods (Yochelson et al., 1983). These infaunal predators seldom hunt on the surface in the laboratory (Guerrero and Reymont, 1988) or in the field (Dietl, 2002). Savazzi and Reymont (1989) do, however, report sub-aerial hunting at low tide, followed by drilling within the substrate. On rare occasions, epifaunal drilling also occurs (Dietl, 2002). Muricids, on the other hand, search for and drill prey epifaunally (although some may dig up shallow-infaunal prey). This indicates that a mollusc's position within the substrate should largely control which predators it encounters.

As hypothesized, epifaunal bivalves were drilled more frequently (nearly twice as often) than infaunal species in the Northern Adriatic. The most heavily drilled bivalves were from the epifaunal Noetinae and Chamidae. The fossil record reveals similar trends: naticid drilling intensities in the less-abundant epifaunal taxa of the Maastrichtian Fox Hills Formation (Western Interior Seaway) were nearly twice those of infaunal taxa but are attributed to naticids (Harries and Schopf, 2007).

One interesting result of this study was the exceptionally high DF on commensal and parasitic bivalves and gastropods. These species typically live attached to invertebrates and should not normally be subject to predation by drillers. Nonetheless, their attack frequencies are as high as 40.6 % and 20.3 %, respectively. These molluscs are adapted to a cryptic life-style and have very thin shells. One hypothesis for such high drilling frequencies is that once the host dies and is consumed or deteriorates, these commensals/parasites are exposed and consequently attacked by opportunistic drilling predators. Interestingly, typical

muricid and naticid drill holes are much larger than the holes found on our commensal and predatory taxa. One potential explanation is that their predators are juvenile gastropods — or an entirely different group of organisms.

Harper (1991) hypothesized that cementation was adopted in multiple families of bivalves in the Mesozoic in response to increased predation pressure from grappling predators, noting that decreased manipulability leads to reduced predator success in asteroids and crustaceans. It seems unlikely; however, that predation by gastropods, particularly muricids, would be hampered by cementation because little manipulation is required (note that naticids do manipulate their prey). Furthermore, the appearance of muricids in the Cretaceous was not marked by further rise of cemented taxa (Harper, 1991). In concurrence, cementing bivalves in the Gulf of Trieste had considerably higher DFs (43.0 %) than bysally attaching (27.0 %) and reclining (9.9 %) bivalves. The frequency is exaggerated, however, by the analytical methods used. Many of the cementers, including chamids and oysters, were dominated by top valves in our samples, yet the valve-correction was performed on all bivalves. DFs calculated solely from top valves show values of 23.9 % (DFs of top valves for *Ostrea edulis*, *Anomia ephippium*, *Chama gryphoides*, and *Spondylus* sp. are 16.4 %, 20.8 %, 34.9 % and 0 %, respectively). Nonetheless, this still indicates that drillers are clearly not deterred by cementation. Cementing bivalves may have responded morphologically to drilling predators in the Cenozoic. Stone (1998) demonstrated that spines on epifaunal cementing species effectively deter muricid predation, but not starfish. Accordingly, PE on cementers was quite high compared to other taxa, perhaps in part due to the spiny morphology and thick shells of many such taxa in the Northern Adriatic.

Byssal attachment has several advantages over cementation, including seasonally variable attachment strength, voluntary detachment for mobility, secondary larval settlement, and the ability to re-attach if dislodged (Price, 1980). For marine invertebrates, handling time may be a more important factor than energetic gain in predator food choice (e.g. Rovero et al., 2000). It may be difficult for predators to manipulate byssally attached prey into preferred orientations for attack, possibly increasing exposure to their own enemies. Furthermore, greater byssus production occurs when some mussels are exposed to damaged conspecific and heterospecific cues (Shin et al., 2008). Interestingly, byssally attaching bivalves in the Gulf of Trieste seem relatively ineffective at deterring drillers; although their DF is over 25 %, their PE is only 2.1 % (versus 10.5 % for cementing forms).

Clumping by mussels through byssal threads reduces drilling frequency in laboratory experiments (Casey and Chattopadhyay, 2008). Additionally, mussels can attach byssal threads to predatory gastropods, then flip and immobilize them with further byssal production (Petraitis, 1987; Day et al., 1991). This is a dangerous deterrent to drillers. Mussels were relatively rare along the transect; however, Sawyer et al. (2009) report low occurrences of drill holes in *Mytilus galloprovincialis* in a nearby mussel bed in the Gulf of Trieste. Further comparison of clumping and non-clumping epifaunal, byssally attached bivalves would help clarify the effects of byssal attachment on drilling intensity.

Recliners, consisting mostly of pectinids, had the lowest DF and PE among epifaunal bivalves. Many pectinids ‘jump’ or ‘swim’ when encountered by predators (Thomas and Gruffydd, 1971; Brand, 1991; Himmelman et al., 2009). Such escape responses may contribute to the lower DF in these taxa.

Indeed, evolutionary trends in the shell morphology of various scallop lineages are thought to reflect adaptations that increase mobility, probably in response to predatory pressures (e.g. Beu, 1995; Jonkers, 2000).

### **2.7.3. Environmental variation and drilling predation**

The lowest DFs in bivalves and gastropods were mostly found amongst families that were uncommon on sublittoral soft substrates. For example, Hydrobiidae and Retusidae had very low DFs and were common only on the tidal flat, and the hard-substrate-dwelling fissurellids were never drilled (though predators could presumably access these ‘keyhole’ limpets through their anal pores). Considering that the infrequently drilled family Semelidae was common only on the tidal flat, its DF of 7.0 % was actually relatively high (significantly higher than other tidal flat bivalves; DF = 2.1 %;  $\chi^2 = 30.04$ , p-value  $\ll 0.0001$ ). All of the five most abundant bivalve and gastropod species were heavily drilled, except those that were environmentally limited to the tidal flat (i.e. *Lentidium mediterraneum* and *Hydrobia ulvae*).

Several studies have examined the relationship between depth and drilling predation (e.g. Sander and Lalli, 1982; Hansen and Kelley, 1995; von Rützen-Kositzkau, 1999; Walker, 2001; Tomašových and Zuschin, 2009), but the overall depth-range of our transect (0 to 14 m) was relatively small. The freshwater influence from the Isonzo may have affected DFs here more than depth. DF appears to be lower in the more extreme intertidal environments than their sublittoral counterparts in the Gulf of Trieste. For instance, drilling frequencies were significantly lower on the tidal flat and on the delta foreset beds than in sublittoral settings further from the mouth of the Isonzo. Kelley (2006) found DFs

similarly low to those from our tidal flat on a beach near Venice, Italy. This points to regionally low predation levels in intertidal settings. Perhaps the strongly fluctuating abiotic conditions (temperature and salinity) inherent in intertidal settings are unfavourable to the drilling gastropods in this region.

Predatory molluscs can play a significant ecological role on soft (unconsolidated) shores (e.g. Vermeij, 1980; Berry, 1982; Broom, 1982), but studies specifically examining the effects of soft substrate-dwelling muricids are generally lacking because most such muricids are typical of less accessible subtidal settings (Ponder and Vokes, 1988; but see recent studies by Prinkrakoon and Tëmkin (2008) and Tan (2008) from the Kungkrabaen Bay, Thailand, and by Stewart and Creese (2004) on predatory whelks from North-Eastern New Zealand). *Hexaplex trunculus*, one of the most abundant predatory drillers in the Adriatic (Peharda and Morton, 2006; Sawyer et al., 2009), cannot survive long periods of desiccation and is probably not adapted to life in habitats occasionally exposed to air (Rilov et al., 2004). Likewise, extreme increases in body temperature are known to reduce feeding rates in marine invertebrates (e.g. Pincebourde et al., 2008), and significant decreases in predation rates at high temperatures have been observed in the muricid *Thais haemastoma* (Garton and Stickle, 1980). Aerial exposure and high temperatures may prevent the presence of drilling predators on the studied tidal flat in the Gulf of Trieste. This is supported by the scarceness of potential drillers we recovered from the inner and outer tidal flat samples. A total of 6 naticids were recovered from the two tidal flat samples, compared to 397 from the six sublittoral samples (range: 5 to 174). No muricids were recovered from the tidal flat samples, compared to 181 from sublittoral samples (range: 2 to 138).

Salinity on the studied tidal flat ranges from 18 ‰ (spring) to 33 ‰ (early autumn) and is lower, on average (26.8 ‰), than in the open Gulf of Trieste (38.3 ‰) (Hohenegger et al., 1989). Average bottom salinities along the entire transect ranged from 26 to 40 ‰, but more narrowly (37 - 39 ‰) at our sublittoral sample localities (Zuschin and Piller, 1994). Decreased salinity in the sublittoral is caused by freshwater influx from the Isonzo River, which mostly affects the delta forest beds. Salinity changes can negatively affect the predation rates of several muricid species (e.g. Manzi, 1970; Garton and Stickle, 1980). When the drilling muricids *Urosalpinx cinerea* and *Eupleura caudata* are exposed to fluctuating salinities, they exhibit lower levels of general activity and survival than those under constant salinity (Zachary and Haven, 1973). At constantly high salinities, activity increases. Garton and Stickle (1980) demonstrated that, in *Thais haemastoma*, moderate decreases and increases of salinity both decreased feeding rates, whereas intermediate salinities increased the rates. Lowered salinity may also offer a predation refuge for barnacles and mussels when a shallow low-salinity layer is formed (e.g. southwestern New Zealand; Witman and Grange, 1998). Finally, decreased DF has been postulated as an environmental effect of brackish water environments in naticid predation on corbulid bivalves from Neogene deposits in the Dominican Republic and Florida (Anderson, 1992).

Predation is strongly controlled by habitat (Vermeij et al., 1981; Hansen and Kelley, 1995; Cadée et al., 1997); therefore, differences in predation frequencies are expected across different sublittoral substrates. In the Gulf of Trieste, DFs are considerably lower in the delta than in level bottom muds and sands. While differences in DF between muds and sands vary by less than 5 % in both bivalves (mud = 34.0 %, sand = 30.4 %) and gastropods (mud = 25.2 %, sand = 20.4 %).

sand = 28.2 %), they are more pronounced at the family level (e.g. DF for galeommatids from muds = 43.0 %, but from sands = 23.8 %, Fig. 2.9).

DFs in the Gulf of Trieste can vary as much spatially within similar substrates as between substrates. For example, DF varies by as much as 10 % among the three level bottom mud samples (Fig. 2.7), while variation between the delta foreset bed sample and that from pooled level bottom muds is also about 10 % (Fig. 2.5). However, the total variation in DF between the two sand samples is only 2.8 %. Within the two mollusc classes, variations within substrates can vary even more than between substrates. For example, bivalve DF varies by nearly 15 % between the delta foreset bed sample and level bottom muds, but by nearly 20 % among level bottom mud samples. On the other hand, gastropod DFs vary by about 10 % between the delta foreset beds and level bottom sands, but are not significantly different between sand samples.

Hoffmeister and Kowalewski (2001) report significant spatial variations in drilling predation on molluscs, both locally and regionally, among facies in the Miocene of Central Europe. Those variations could either be exaggerated or masked when samples were pooled into coarser analytical groupings, but regardless of the taxonomic resolution of the analysis, inter-regional and facies variation between samples was significant and could exceed 20 % (up to 3-fold differences). Likewise, Yochelson et al. (1983) reported that scaphopods showed higher DFs in coarser than in finer sediments in Cretaceous through Holocene deposits. In the Adriatic, scaphopod DFs were low overall and only varied by 1.2 % between level bottom mud and sand substrates; the values here did not significantly differ among level bottom mud samples.

Overall, DFs along the transect were fairly consistent between families within both mud and sand environments, but when variation occurred, it could be as much as three-fold. Likewise, Vermeij (1980) reported molluscan DFs from 10 localities in Guam (12 species) to range from 7.4 to 24.6 %. Baumiller and Bitner (2004) showed that brachiopod DFs from four Central-European Miocene species ranged from 2 to 39.9 %. Finally, Simões et al. (2007) report DFs on bivalves (from brachiopod-bivalve mixed assemblages) from similar sublittoral substrates on the Southern Brazilian shelf to range as much as 10 %, and between habitats from 0 – 14 %.

#### **2.7.4. Diversity and drilling predation**

A fundamental paleoecological question is whether local ecological interactions, such as predation, “scale up” to influence global biodiversity over evolutionary timescales (Eldredge and Gould, 1972; Gould, 1985; Vermeij, 1987; Kowalewski et al., 1998; Madin et al., 2006; Huntley and Kowalewski, 2007, Stanley, 2008). Intermediate levels of predation are known to increase diversity in modern benthic communities (e.g. predatory reduction of competitive exclusion for space in the Pacific North-West of the USA; e.g. Connell, 1961; Paine, 1966; Connell, 1978). Several methods have been used to determine this, including comparing predator proportions and abundances with those of prey, and comparing measures of predation intensities and frequencies with measures of diversity. These methods yield contradictory results. For example, Madin et al. (2006) compared long-term patterns in the proportion of carnivorous marine invertebrates with those of infaunal or mobile prey, and between the proportion of bioturbators and immobile epifauna. They found no significant correlations (but

see Dietl and Vermeij, 2006; Roopnarine et al., 2006). In contrast, Huntley and Kowalewski (2007) report remarkable concordance between predation intensities and genus-level assemblage diversity estimates across geologic periods through the Phanerozoic; they do, however, caution that such historical patterns are often scale-dependent and should not be extrapolated to finer resolutions. Accordingly, they could not reproduce their result at finer time resolution, and Kelley and Hansen (2009) also found no correlation between prey diversity and DFs for Cretaceous through Pleistocene local molluscan assemblages from the US coastal plain. Nonetheless, correlations between diversity and DF have been found in local fossil assemblages from North America, including molluscs from Maastrichtian (Harries and Schopf, 2007) and Eocene deposits (Hansen and Kelley, 1995). In this study, DF correlated with several measures of diversity, but when the sublittoral samples were examined alone, those correlations failed. One explanation is that the very low diversity, predator abundance and DFs in the tidal flat controlled the overall correlation, as physiological constraints probably exclude both predators and non-drilling taxa.

Trophic polymorphisms – eating more than one prey type and exhibiting more than one prey-capture method (Winberger, 1994) – are common amongst molluscivorous gastropods (Walker, 2007). In those predators capable of handling a wide variety of prey species, factors such as encounter rate are likely controls of DF (Leighton, 2002). In the Northern Adriatic, all members of bivalve-, and most gastropod families, with  $n > 20$  had DFs of  $> 5\%$ . Hydrobiids were the only abundant gastropod family with  $DF < 5\%$ , and, along with haliotids and retusids, were only common on the tidal flat. As drilling predators in this study attacked all but the rarest sublittoral species, they appear to be generalists.

Although it would, therefore, be reasonable to expect DFs and relative prey abundance to correlate, no such correlation was found between DF and the most abundant species per sample.

#### **2.7.5. Size selectivity**

Naticids attack larger prey as they grow larger (Edwards and Huebner, 1977; Berry, 1982; Kingsley-Smith et al., 2003). For most species examined here, no differences in the proportion of drilled individuals existed across size-categories, with the exception of *Venerupis rhomboides*. Larger specimens of this infaunal bivalve are likely to be outside the size range that the relatively small naticids found in our samples could handle. *Lucinella divaricata*, on the other hand, was drilled as much in the larger size classes as in the smaller. *Chama gryphoides* was also much smaller than *V. rhomboides*. This epifaunal cementer would be susceptible to muricids, which require little manipulation to drill their prey and can thus drill larger shells. Finally, most *Turritella communis* were small, but those in the largest size classes (shell lengths much larger than the naticids in our samples) had similar DFs to those in smaller size classes. Turritellids are shallow-infaunal suspension feeders, which may be susceptible to a large range of naticid and muricid predators.

Most sublittoral bivalves and gastropods were smaller than those represented by the species described above. In fact, the overwhelming majority belongs to small species or are juveniles of larger species (< 5 mm). It is therefore unlikely that non-standardization of molluscs by size class biased our results or interpretations.

### **2.7.6. Northern Adriatic drilling intensities and the low predation hypothesis**

Kelley (2006) reported Cretaceous-level drilling frequencies (< 10 %) and PE (0.03 %) from bulk samples collected on a beach near Venice, Italy (Northern Adriatic). This report of Cretaceous-level drilling frequencies from a single locality has been used, in conjunction with the apparent absence or low diversity of high-energy predators (e.g. balistid fish, echinoids with advanced dentition, durophagous crabs), as evidence of low predation pressure throughout the Northern Adriatic (McKinney, 2007). Others have argued that the Northern Adriatic is a key fishing ground in the Mediterranean and therefore is likely to have predation levels that are Mediterranean in scope, and not similar to the pre-Cenozoic or to northern latitudes (Zuschin and Stachowitsch, 2009).

Kowalewski et al. (1998) identified three phases of Phanerozoic drilling predation. The Mesozoic phase is marked by very rare drilling predators that typically are documented by single or very few holes, though localized areas of unusually good preservation have yielded high levels of drilling predation in Mesozoic molluscan assemblages (Harper et al., 1998, 1999). In contrast, increasingly common drilling (dominated by prosobranch gastropods) and much greater drilling intensities than previously documented mark the Cenozoic phase. While drilling frequencies from this study are very low on the tidal flat, overall drilling frequencies pooled across all intertidal and sublittoral settings exceed 20 % and in the subtidal approach 30 %. Such intensities are clearly at Cenozoic levels. DFs as low as ~ 5 % or less are known from other Cenozoic mollusc assemblages (Simões et al., 2007); thus, the overall and sublittoral frequencies here should not be considered low.

Kelley and Hansen (2006) report overall gastropod DFs from Cretaceous deposits of the North American Gulf Coastal Plain to range from 3.7 % to 6.0 %, and for bivalves from 13.2 % to 16.2 %; drilling frequencies for Cenozoic gastropods ranged from 6.0 % to 46.5 % and for bivalves from 0 % to 41.5 %. In this study, overall gastropod and bivalve DFs (20.4 % and 23.4 %, respectively) fall within their Cenozoic ranges.

Allmon et al. (1990) reported DFs of Late Cretaceous turrnellid gastropods from the New World to be 1.9 % to 4.5 %, while those of the Cenozoic ranged from 1.5 % to 27.6 % (23.5% in Recent). The respective Cretaceous turrenellid values reported by Kelley and Hansen (2006) were 4.2 % and 12.6 %, and in the Cenozoic were 0 % to 57.6 %. Turrnellid DFs in the current study ranged from 31.2 % to 45.7% (44.0 % pooled across all samples), and were as high as those of the North and South American and Gulf Coastal Plain Cenozoic turrnellids.

The overall PE determined here (4.5 %) is also comparable to other Cenozoic basins. For example, in the Miocene of Bulgaria, PE was < 1 % for key species (Kojumdjiera, 1974); in the Plio-Pleistocene deposits of Florida, it was ~ 5 % or less for all species (Culotta, 1988), in the Pleistocene of Fiji 3 % (Kohn and Aura, 1999) and in deep-water Pliocene gastropods from Ecuador < 5 % for species that were drilled (Walker, 2001). The PE of Northern Adriatic bivalves (10.3 %) is similar to those from the Cenozoic Gulf Coast Plain (1 % to 19 %), though that of gastropods (1.6 %) is low in comparison (0 % to 17 %; Kelley and Hansen, 2006). PE is as high as 48.5 % on *Corbula gibba* in the Gulf of Trieste; the corbulids from the Cenozoic Gulf Coastal Plain range from 11 % to 59 % (Kelley and Hansen, 2006).

Several authors have examined how drilling frequency correlates with latitude (e.g. Dudley and Vermeij, 1978; Alexander and Dietl, 2001). The sublittoral DF we calculated (27.4 %) is slightly higher than – though not significantly different from ( $\chi^2 = 1.22$ , p-value = 0.269) – that calculated from the latitudinally equivalent beach deposits of the Nova Scotian Province of the eastern United States (22.2 %; Kelley and Hansen, 2007).

Based on these comparisons of Cenozoic DFs and PE from other regions with the Gulf of Trieste, we reject the hypothesis that drilling intensity in the Northern Adriatic Sea is at a pre-Cenozoic level, or that it is anomalously low compared to other Cenozoic basins.

## **2.8. Conclusions**

The life habits of prey apparently play a major role in their predation intensities. Drilling intensity is highest on slow-moving and metabolically less active guilds. This hypothesis is supported by high drilling frequencies of suspension-feeding turrnellid and parasitic gastropods, and of cementing and commensal bivalves, along with the relatively low drilling frequencies of recliners and predators. In addition, our results support the long-held hypothesis that an infaunal life habit is an effective strategy against predation in marine invertebrates. The high drilling frequencies on parasitic and commensal molluscs were unexpected, and the small size of the drill holes in these taxa raises the question of what organisms are drilling these cryptic forms. Finally, cementation and byssal attachment do not seem to deter drilling predators based on the high

drilling frequencies reported in these guilds. This analysis supports the view that ecological details of predators and their prey must be considered to fully understand predation in modern and fossil habitats.

The most striking differences in drilling intensities occurred between the intertidal and sublittoral in the Gulf of Trieste. Drilling was consistently rare on the tidal flat and was substantially and significantly higher in all sublittoral samples. DFs in the sublittoral were relatively similar, but the depth range examined was too narrow to make strong predictions about a depth gradient.

Inter- and intra-environmental variation in predation can be quite pronounced in level bottom communities. DFs significantly varied among all environments, although the differences were small between the level bottom mud and sand. Within muds however, predation intensities varied by as much as 10 % across assemblages, and up to 20 % among classes, supporting the hypothesis that DF significantly varies between and within environments in the Northern Adriatic Sea. These results emphasize the importance of rigorous analysis of spatial variation in studies of modern and fossil drilling predation.

DF correlated with several diversity measures across the entire region, but all correlations failed when only sublittoral habitats were tested. As such, the very low predator abundances and mollusc diversity on the tidal flat probably controlled the diversity correlations. Low predation pressure may reduce diversity on the tidal flat, but it is more likely that physiological constraints prevent many Northern Adriatic molluscs from living there. We therefore conclude that drilling predators are not a major control of molluscan diversity along the studied transect. Other predators and the combined effects of drilling,

durophagous and human predation, however, may still play a major role in overall diversity in this region.

Large specimens of infaunal and epifaunal taxa were generally rare, and where size-selectivity by drillers was observed, it was skewed to smaller individuals. Furthermore, for most taxa examined, the proportions of drilled shells were not statistically different across size categories. Accordingly, our results are not likely to be significantly affected by size-selectivity of drilling predators.

Contrary to previous assumptions, drilling predators are capable of exerting strong pressure on molluscan prey in the Gulf of Trieste. The DFs and PEs recorded in this study are substantially higher than those typical of Cretaceous molluscs. Based on the overall predation parameters investigated here, we reject the hypothesis that drilling predation is pre-Cenozoic in intensity in the Northern Adriatic Sea.

## 2.9. References

- Alexander, R.R., Dietl, G.P., 2001. Latitudinal trends in naticid predation on *Anadara ovalis* (Vrugiere, 1789) and *Divalinga quadrisulcata* (Orbigny, 1842) from New Jersey to the Florida Keys. *American Malacological Bulletin* 16, 179-194.
- Allmon, W.D., Nieh, J.C., Norris, R.D., 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. *Palaeontology* 33, 595-611.
- Amano, K., Jenkins, R.G., 2007. Eocene drill holes in cold-seep bivalves of Hokkaido, northern Japan. *P.S.Z.N.I.: Marine Ecology* 27, 108-114.
- Anderson, L.C., 1992. Naticid gastropod predation on corbulid bivalves: effects of physical factors, morphological features, and statistical artifacts. *Palaios* 7, 602-620.
- Arnold, J.M., Arnold, K.O., 1969. Some aspects of hole-boring predation by *Octopus vulgaris*. *American Zoologist* 9, 991-996.
- Bambach, R.K., 1999. Energetics in the global marine fauna: a connection between terrestrial diversification and change in the marine biosphere (Energétique de la faune marine globale: relation entre les diversifications et les changements de la biosphère marine). *Geobios* 32, 131-144.
- Baumiller, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123, 343-351.
- Baumiller, T.K., Bitner, M.A., 2004. A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 85-95.

- Beesley, P.L., Ross, G.J.B., Wells, A., 1998. Mollusca: a Southern Synthesis: Fauna of Australia. Vol. 5 CSIRO Publishing. Melbourne.
- Berry, A.J., 1982. Predation by *Natica maculosa* Lamarck (Naticidae: Gastropoda) upon the trochacean gastropod *Umbonium bestiarum* (L.) on a Malaysian shore. *Journal of Experimental Marine Biology and Ecology* 64, 71-89.
- Beu, A.G., 1995. Pliocene limestones and their scallops—lithostratigraphy, pectinid biostratigraphy and paleogeography of eastern North Island Late Neogene limestone. Institute of Geological and Nuclear Sciences Monograph 10, New Zealand Geological Survey Paleontological Bulletin 68, 1-243.
- Brand, A.R., 1991. Scallop ecology: distributions and behaviour. *In*: Shumway, S.E. (ed.), *Scallops: biology, ecology and aquaculture*. Elsevier, Amsterdam, pp. 517-584.
- Bromley, R.G., 1981. Concepts in ichnotaxonomy illustrated by small round holes in shells. *Acta Geologica Hispanica* 16, pp. 55-64.
- Broom, M.J., 1982. Size-selection, consumption rates and growth of the gastropods *Natica maculosa* (Lamarck) and *Thais carinifera* (Lamarck) preying upon the bivalve, *Anadara granosa* (L.). *Journal of Experimental Marine Biology and Ecology* 56, 213-233.
- Cadee, G.C., Walker, S.E., Flessa, K.W., 1997. Gastropod shell repair in the intertidal of Bahia la Choya (N. Gulf of California). *Palaeogeography, Palaeoclimatology, Palaeoecology* 136, 67-78.

- Carriker, M.R., Yochelson, E.L., 1968. Recent gastropod boreholes and Ordovician cylindrical borings. Contributions to Paleontology, Geological Survey Professional Paper, 593(B), B1-B26.
- Casey, M.M., Chattopadhyay, D., 2008. Clumping behavior as a strategy against drilling predation: implications for the fossil record. Journal of Experimental Marine Biology and Ecology 367, 174-179.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42, 710-723.
- Connell, J.H., 1978. Diversity in tropical rain forest and coral reefs. Science 199, 1302-1310.
- Cossignani, T., Cossignani, V., Di Nisio, A., Passamonti, M., 1992. Atlante Delle Conchiglie del Medio Adriatico (Atlas of shells from the Central Adriatic Sea). L'Informatore, Piceno.
- Culotta, E., 1988. Predators and available prey: naticid predation during a Neogene molluscan extinction event. MS Thesis, Univ. Michigan, Ann Arbor, Michigan.
- D'angelo, G., Gargiullo, S., 1979. Guida alle Conchiglie Mediterranee: Conoscerle Cercarle Collezionarle. Fabbri Editori, S.p.A., Milano.
- Day, R.W., Barkai, A., Wickens, P.A., 1991. Trapping of three drilling whelks by two species of mussel. Journal of Experimental Marine Biology and Ecology 149, 109-122.
- Dietl, G.P., 2002. Traces of naticid predation on the gryphaeid oyster *Pycnodonte dissimularis*: epifaunal drilling of prey in the Paleocene. Historical Biology 16, 13-19.

- Dietl, G.P., Vermeij, G.J., 2006. Comment on “Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates”. *Science* 314, 925e.
- Dudley, E.C., Vermeij, G.J., 1978. Predation in time and space: drilling in the gastropod *Turritella*. *Paleobiology* 4, 436-441.
- Edwards, D.G., Huebner, J.D., 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbour, Massachusetts, USA. *Ecology* 58, 1218-1236.
- Eldredge, N., Gould, S.J., 1972. Punctuated equilibria: an alternative to phyletic gradualism. *In*: Schopf, T.J.M. (ed), *Models in Paleobiology*. Freeman, Cooper and Co., San Fransisco, CA, pp. 82-115.
- Fedra, K., Ölscher, E.M., Scherubel, C., Stachowitsch, M., Wurzian, R.S., 1976. On the ecology of a North Adriatic benthic community: distribution, standing crop and composition of the macrobenthos. *Marine Biology* 38, 831-833.
- Garton, D., Stickle, W.B., 1980. Effects of salinity and temperature on the predation rate of *Thais haemastoma* on *Crassostrea virginica* spat. *Biological Bulletin* 158, 49-57.
- Gould, S.J., 1985. The paradox of the first tier: an agenda for paleobiology. *Paleobiology* 11, 2-12.
- Guerrero, S., Reyment, R.A., 1988. Predation and feeding in the naticid gastropod *Naticarius intricatoides* (Hidalgo). *Palaeogeography, Palaeoclimatology, Palaeoecology* 68, 49-52.

- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics Software Package for education and data analysis. *Palaeontologia Electronica* 4: 9, [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm).
- Hansen, T.A., Kelley, P.H., 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *Palaios* 10, 268-278.
- Harper, E.M., 1991. The role of predation in the evolution of cementation in bivalves. *Palaeontology* 34, 455-460.
- Harper, E.M., 2003. Assessing the importance of drilling predation over the Palaeozoic and Mesozoic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 210, 185-198.
- Harper, E.M., Peck, L., 2003. Predatory behaviour and metabolic costs in the Antarctic muricid gastropod *Trophon longstaffi*. *Polar Biology* 26, 208-217.
- Harper, E.M., Forsythe, G.T.W., Palmer, T., 1998. Taphonomy and the Mesozoic Marine Revolution: preservation state masks the importance of boring predators. *Palaios* 13, 352-360.
- Harper, E.M., Forsythe, G.T.W., Palmer, T., Kowalewski, M., Dulai, A., Fürsich, F.T., 1999. A fossil record full of holes: the Phanerozoic history of drilling predation: comment and reply. *Geology* 27, 959-960.
- Harries, P.J., Schopf, K.M., 2007. Late Cretaceous gastropod drilling intensities: data from the Maastrichtian Fox Hills Formation, Western Interior Seaway, USA. *Palaios* 22, 35-46.
- Himmelman, J.H., Guderley, H.E., Duncan, P.F., 2009. Responses of the saucer scallop *Amusium balloti* to potential predators. *Journal of Experimental Marine Biology and Ecology* 378, 58-61-

- Hoffmeister, A.P., Kowalewski, M., 2001. Spatial and environmental variation in the fossil record of drilling predation: a case study from the Miocene of central Europe. *Palaios* 16, 566-579.
- Hohenegger, J., Pervesler, P., 1985. Orientation of crustacean burrows. *Lethaia* 18, 323-339.
- Hohenegger, J., Piller, W., Baal, C., 1989. Reasons for spatial microdistributions of foraminifers in an intertidal pool (Northern Adriatic Sea). *PSZNI: Marine Ecology* 10, 43-78.
- Hohenegger, J., Piller, W.E., Baal, C., 1993. Horizontal and vertical microdistribution of foraminifers in the shallow subtidal Gulf of Trieste, Northern Adriatic Sea. *Journal of Foraminiferal Research* 23, 79-101.
- Huntley, J.W., Kowalewski, M., 2007. Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences* 104, 15006-15010.
- Jonkers, H.A., 2000. Gastropod predation patterns in Pliocene and Recent pectinid bivalves from Antarctica and New Zealand. *N. Z. Journal of Geology and Geophysics* 43, 247-254.
- Kaplan, P., Baumiller, T.K., 2000. Taphonomic inferences on boring habit in the Richmondian *Onniella meeki* Epibole. *Palaios* 15, 499-510.
- Kelley, P.H., 2006. Low frequency of drilling predation in the northwest Adriatic: Cretaceous rather than Paleozoic analog. Geological Society of America Southeastern Section—55<sup>th</sup> Annual Meeting, Geological Society of America Abstracts with Programs 38, p. 22.

- Kelley, P.H., Hansen, T.A., 1993. Evolution of the naticid gastropod predator-prey system: an evaluation of the hypothesis of escalation. *Palaios* 8, 358-375.
- Kelley, P.H., Hansen, T.A., 2003. The fossil record of drilling predation on bivalves and gastropods. *In: Kelley, P.H., Kowalewski, M., Hansen, T.A. (eds.), Predator-Prey Interactions in the Fossil Record. Kluwer Academic/Plenum Press, New York, pp. 113-139.*
- Kelley, P.H., Hansen, T.A., 2006. Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. coastal plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 236, 302-320.
- Kelley, P.H., Hansen, T.A., 2007. Latitudinal patterns in naticid gastropod predation along the East coast of the United States: a modern baseline for interpreting temporal patterns in the fossil record. *In: Bromley, R.G., Buatois, L.A., Mangano, G., Genise, J.F., Melchor, R.N. (eds.), Sediment-Organism Interactions: A Multifaceted Ichnology. SEPM Special Publication No. 88, Tulsa, p.287-299. SEPM (Society for Sedimentary Geology), Tulsa.*
- Kelley, P.H., Hansen, T.A., 2009. Evolutionary effects of Cretaceous – Pleistocene naticid gastropod predation: drilling frequency, prey diversity, and predator diversity. 9<sup>th</sup> North American Paleontological Convention—Cincinnati Museum Center Scientific Contributions 3, 301-302.
- Kelley, P.H., Hansen, T.A., Graham, S.E., Huntoon, A.G., 2001. Temporal patterns in the efficiency of naticid gastropod predators during the

- Cretaceous and Cenozoic of the United States Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166, 165-176.
- Kingsley-Smith, P.R., Mann, R., Harding, J., 2003. A predation signature-based key to attribute predation upon bivalves to native versus invasive gastropods. *Proceedings of the Third International Conference on Marine Bioinvasions*, La Jolla, California, pp. 72.
- Kingsley-Smith, P.R., Richardson, C.A., Seed, R., 2003. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropods: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology* 295, 173-190.
- Kitchell, J.A., 1986. The evolution of predator-prey behavior: naticid gastropods and their molluscan prey. *In*: Nitecki, M., and Kitchell, J.A. (eds.), *Evolution of Animal Behavior: Paleontological and Field Approaches*, Oxford University Press, Oxford, pp. 88-110.
- Kitchell, J.A., Boggs, C.H., Kitchell, J.F., Rice, J.A., 1981. Prey selection by naticid gastropods: experimental tests and application to the fossil record. *Paleobiology* 7, 533-552.
- Kohn, A.J., Arua, I., 1999. An early Pleistocene molluscan assemblage from Fiji: gastropod faunal composition, paleoecology and biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 146, 99-145.
- Kojumdjiera, E., 1974. Les gasteropodes perceurs et leurs victimes du Miocene de Bulgarie du Nord-Ouest. *Bulgarian Academy of Sciences, Bulletin of Geological Institute, Series Paleontology* 23, 5-24.
- Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods. *In*: Kowalewski, M., Kelley, P.H. (eds.), *The Fossil Record of*

- Predation. Paleontological Society Papers 8, Yale University, New Haven, pp. 3-42.
- Kowalewski, M., Dulai, A., Fürsich, F., 1998. A fossil record full of holes: the Phanerozoic history of drilling predation. *Geology* 26, 1091-1094.
- Kowalewski, M., Hoffmeister, A.P., 2003. Sieves and fossils: effects of mesh size on paleontological patterns. *Palaios* 18, 460-469.
- Leighton, L.R., 2001. Evaluating the accuracy of drilling frequency as an estimate of prey preference and predation intensity. *PaleoBios* 21, supplement to number 2, pp. 83.
- Leighton, L.R., 2002. Inferring predation intensity from the marine fossil record. *Paleobiology* 28, 328-342.
- Leighton, L.R., 2004. Are we asking the right question? *Palaios* 19, 313-315.
- MacArthur, R.H., 1965. Patterns of species diversity. *Biological Reviews* 40, 510-533.
- Madin, J.S., Alroy, J., Aberhan, M., Fürsich, F.T., Kiessling, W., Kosnik, M.A., Wagner, P.J., 2006. Statistical independence of escalatory ecological trends in Phanerozoic marine invertebrates. *Science* 312, 897-900.
- Manzi, J.J., 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Biological Bulletin* 138, 35-46.
- McKinney, F.K., 2007. *The Northern Adriatic Ecosystem: deep time in a shallow sea*. Columbia University Press, New York.
- McKinney, F.K., Hageman, S.J., 2006. Paleozoic to modern marine ecological shift displayed in the northern Adriatic Sea. *Geology* 34, 881-884.

- Morton, B., Chan, K., 1997. First report of shell boring predation by a member of the Nassariidae (Gastropoda). *Journal of Molluscan Studies* 63, 476-478.
- Morton, B., Peharda, M., Harper, E.M., 2007. Drilling and chipping patterns of bivalve prey shell penetration by *Hexaplex trunculus* (Mollusca: Gastropoda: Muricidae). *Journal of the Marine Biological Association of the United Kingdom* 87, 933-940.
- Nelson, B.W., 1970. Hydrography, sediment dispersal, and recent historical development of the Po River Delta, Italy. *In: Morgan, J.P. Shaver, R.H. (eds.), Deltaic Sedimentation, Modern and Ancient. The Society of Economic Paleontologists and Mineralogists Special Publication* 15, pp. 152-184.
- Neveškaja, L.A., 2006. Ethological-trophic groups of bivalve molluscs and their distribution in the Phanerozoic. *Palaeontological Journal* 40, 375-390.
- Nixon, M., 1979. Hole-boring in shells by *Octopus vulgaris* Cuvier in the Mediterranean. *Malacologia* 18, 431-443.
- Paine, R.T., 1966. Food web complexity and species diversity. *American Naturalist* 100, 65-75.
- Peharda, M., Morton, B., 2006. Experimental prey species preferences of *Hexaplex trunculus* (Gastropoda: Muricidae) and predator-prey interactions with the black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae). *Marine Biology* 148, 1011-1019.
- Pervesler, P., Dworschak, P.C., 1985. Burrows of *Jaxea nocturna* NARDO in the Gulf of Trieste. *Senckenbergiana maritima* 17, 33-53.
- Pervesler, P., Hohenegger, J., 2006. Orientation of crustacean burrows in the Bay of Panzano (Gulf of Trieste, Northern Adriatic Sea). *Lethaia* 39, 173-186.

- Peterson, C.H., Black, R., 1995. Drilling by buccinid gastropods of the genus *Cominella* in Australia. *The Veliger* 38, 37-42.
- Petratis, P.S., 1987. Immobilization of the predatory gastropod, *Nucella lapillus*, by its prey, *Mytilus edulis*. *Biological Bulletin* 172, 307-314.
- Pincebourde, S., Sanford, E., Helmuth, B., 2008. Body temperature during low tide alters the feeding performance of a top intertidal predator. *Limnology and Oceanography* 23, 1562-1573.
- Ponder, W.F., Vokes, E.H., 1988. A revision of the Indo-West Pacific fossil and Recent species of *Murex* s. s. and *Haustellum* (Mollusca: Gastropoda: Muricidae). *Records of the Australian Museum, supplement* 8, 1-160.
- Ponder, W.F., Taylor, J.D., 1992. Predatory shell drilling by two species of *Austroginella* (Gastropoda; Marginellidae). *Journal of Zoology* 228, 317-328.
- Price, H.A., 1980. Seasonal variation in the strength of byssal attachment of the common mussel *Mytilus edulis*. *Journal of the Marine Biological Association of the United Kingdom* 60, 147-155.
- Printrakoon, C., Tëmkin, I., 2008. Comparative ecology of two parapatric populations of *Isognomon* (Bivalvia: Isognomonidae) of Kungkrabaen Bay, Thailand. *The Raffles Bulletin of Zoology Supplement* No. 18, 75-94.
- Riedel, B., Zuschin, M., Stachowitsch, M., 2008. Oxygen depletion under glass: behavioural responses of benthic macrofauna to induced anoxia in the Northern Adriatic. *Journal of Experimental Marine Biology and Ecology* 367, 17-27.

- Riedl, R., 1983. Fauna and Flora des Mittelmeeres, Verlag Paul Parey, Hamburg und Berlin.
- Rilov, G., Benayahu, Y., Gasith, A., 2004. Life on the edge: do biomechanical and behavioral adaptations to wave-exposure correlate with habitat partitioning in predatory whelks? Marine Ecology Progress Series 282, 193-204.
- Rohr, D.M., 1991. Borings in the shell of an Ordovician (Whiterockian) gastropod. Journal of Paleontology 65, 687-688.
- Roopnarine, P.D., Beussink, A., 1999. Extinction and naticid predation of the bivalve *Chione* von Mühlfeld on the late Neogene of Florida. Palaeontologia Electronica 2(1).
- Roopnarine, P.D., Angielczyk, K.D., Hertog, R., 2006. Comment on "Statistical independence of escalatory trends in Phanerozoic marine invertebrates. Science, 314, 925d.
- Rovero, F., Hughes, R.N., Chelazzi, G., 2000. When time is of the essence: choosing a currency for prey-handling costs. Journal of Animal Ecology 69, 683-698.
- Sander, F., Lalli, C.M., 1982. A comparative study of the mollusk communities on the shelf-slope margin of Barbados, West Indies. The Veliger 24, 309-318.
- Savazzi, E., Reyment, R.A., 1989. Subaerial hunting behaviour in *Natica gualteriana* (naticid gastropod). Palaeogeography, Paleoclimatology, Paleoecology 74, 355-364.
- Savini, D., Castellazzi, M., Favruzzo, M., Occhipinti-Ambrogi, A., 2004. The alien mollusc *Rapana venosa* (Valenciennes, 1864; Gastropoda,

- Muricidae) in the Northern Adriatic Sea: population structure and shell morphology. *Chemical Ecology* 20, 411-424.
- Sawyer, J.A., Zuschin, M., Riedel, B., Stachowitsch, M., 2009. A predator-prey interaction from *in situ* studies on a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic). *Journal of Experimental Marine Biology and Ecology* 371, 10-19.
- Shin, P.K.S., Liu, C.C., Liu, Z.X., Cheung, S.G., 2008. Marine mussels *Brachidontes variabilis* selected smaller places of refuge and enhanced byssus production upon exposure to conspecific and heteropsecific cues. *Journal of Experimental Marine Biology and Ecology* 361, 16-20.
- Simões, M.G., Rodrigues, S.C., Kowalewski, M., 2007. Comparative analysis of drilling frequencies in recent brachiopod-mollusc associations from the Southern Brazillian Shelf. *Palaios* 22, 143-154.
- Sliter, W.V., 1965. Laboratory experiments on the life cycle and ecologic controls of *Rosalina globularis* d'Orbigny, *Journal of Protozoology* 12, 210-215.
- Sliter, W.V., 1975. Foraminiferal life and residue assemblages from Cretaceous slope deposits. *Geological Society of America Bulletin* 86, 897-906.
- SPSS, 1999. *SPSS base 10 applications guide*. Prentice-Hall, Chicago.
- Stachowitsch, M., Riedel, B., Zuschin, M., Machan, R., 2007. Oxygen depletion and benthic mortalities: the first *in situ* experimental approach to documenting an elusive phenomenon. *Limnology and Oceanography: Methods* 5, 344-352.
- Stanley, S.M., 2008. Predation defeats competition on the seafloor. *Paleobiology* 34, 1-21.
- Stewart, M.J., Creese, R.G., 2004. Feeding ecology of whelks on an intertidal sand flat in north-eastern New Zealand. *N.Z. Journal of Marine and Freshwater Research* 38, 819-831.

- Stone, H.M.I., 1998. On predator deterrence by pronounced shell ornament in epifaunal bivalves. *Palaeontology* 41, 1051-1068.
- Tan, K.S., 2008. Mudflat predation on bivalves and gastropods by *Chicoreus capucinus* (Neogastropoda: Muricidae) at Kungkrabaen Bay, Gulf of Thailand. *The Raffles Bulletin of Zoology* 18, 235-245.
- Taylor, J.D., Glover, E.A., 1999. Penetrating the defences: opercular drilling by *Dicathais orbita* (Mollusca: Gastropoda: Muricidae) on the turbinid gastropod *Ninella torquata*. In: Walker, D.I., Wells, F.E. (eds.), *The seagrass flora and fauna of Rottnest Island, Western Australia*. Western Australian Museum, Perth, pp. 177-198.
- Thomas, G.E., Gruffydd, L.D., 1971. The types of escape reactions elicited in the scallop *Pecten maximus* by selected sea-star species. *Marine Biology* 10, 87-93.
- Todd, J.A., 2001. Neogene Marine Biota of Tropical America: Molluscan Life Habit Databases. Last updated 27 March, 2001, accessed January 2008. <http://eusmilia.geology.uiowa.edu/database/mollusc/mollusclifestyles.htm>.
- Tomašových, A., Zuschin, M., 2009. Variation in brachiopod preservation along a carbonate shelf-basin transect (Red Sea and Gulf of Aden): environmental sensitivity of taphofacies. *Palaios* 24, 697-716.
- Tongiorgi, P., Nardi, P., Galleni, L., Nigro, M. Salghetti, U., 1981. Feeding habits of *Ocenebrina edwardsi* (Mollusca: Prosobranchia) a common mussel drill of the Italian coasts. *Marine Ecology* 2, 169-180.
- Vatova, A., 1949. La fauna bentonica dell' alto e medio Adriatico. *Nova Thalassia* 1, 1-110.

- Vermeij, G.H., 1977. The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology* 3, 245-258.
- Vermeij, G.J., 1980. Drilling predation in a population of the edible bivalve *Anadara granosa* (Arcidae). *The Nautilus* 94, 123-125.
- Vermeij, G.J., 1987. *Evolution and Escalation: an ecological history of life*. Princeton University Press, Princeton, New Jersey.
- Vermeij, G.H., 2002. Evolution in the consumer age: predators in the history of life. *In: Kowalewski, M., Kelley, P.H. (eds.), The Fossil Record of Predation*. Paleontological Special Papers 8, Yale University, New Haven, pp. 375-394.
- Vermeij, G.J., Schindel, D.E., Zipser, E., 1981. Predation through geological time: evidence from gastropod shell repair. *Science* 214, 1024-1026.
- von Rützen-Kositzkau, B., 1999. Taphonomie und Biogeographie des hartteiltragenden Makrobenthos im Tiefwasser des Roten Meeres. *Beringeria* 24, 2-150.
- Walker, S.E., 2001. Paleocology of gastropods preserved in turbiditic slope deposits from the Upper Pliocene of Ecuador. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166, 141-163.
- Walker, S.E., 2007. Traces of gastropod predation on molluscan prey in tropical reef environments. *In: Miller, W. III (ed.), Trace Fossils Concepts, Problems, Prospects*. Elsevier, Amsterdam, pp. 324-344.
- Woelke, C.E., 1957. The flatworm *Pseudostylochus ostreophagus* Hyman, a predator of oysters. *Proceedings of the National Shellfisheries Association* 47, 62-67.
- Wilson, E.O., 2003. *The future of life*. Vintage Books, New York.

- Winberger, P.H., 1994. Trophic polymorphisms, plasticity, and speciation in vertebrates. *In*: Stouder, D.J., Fresh, K.L., Feller, R.J. (eds.), Theory and Application in Fish Feeding Ecology, University of South Carolina Press, Columbia, SC, pp. 19-43.
- Witman, J.D., Grange, K.R., 1998. Links between rain, salinity, and predation in a rocky subtidal community. *Ecology* 79, 2429-2447.
- Yochelson, E.L., Dockery, D., Wolf, H., 1983. Predation of sub-Holocene scaphopod mollusks from Southern Louisiana. U.S. Geological Survey Professional Paper 1282.
- Zachary, A., Haven, D.S., 1973. Survival and activity of the oyster drill *Urosalpinx cinerea* under conditions of fluctuating salinity. *Marine Biology* 22, 45-52.
- Zuschin, M., Piller, W.E., 1994. Sedimentology and facies zonation along a transect through the Gulf of Trieste, Northern Adriatic Sea. *Beiträge zur Paläontologie* 18, 75-114.
- Zuschin, M., Pervesler, P., 1996. Secondary hardground communities in the Northern Gulf of Trieste, Adriatic Sea. *Senckenbergiana maritima* 28, 53-63.
- Zuschin, M., Stachowitsch, M., 2009. Epifauna-dominated benthic shelf assemblages: Lessons for the modern Adriatic Sea. *Palaios* 24, 211-221.
- Zuschin, M., Harzhauser, M., Mandic, O., 2004. Spatial variability within a single parautochthonous Paratethyan tidal flat deposit (Karpatian, Lower Miocene - Kleinebersdorf, Lower Austria). *Courier Forschungsinstitut Senckenberg* 246, 153-168.

Zuschin, M., Harzhauser, M., Sauer Moser, K., 2006. Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of the Paratethys. *Lethaia* 39, 66-78.

Zuschin, M., Stachowitsch, M., Pervesler, P., Kollmann, H., 1999. Structural features and taphonomic pathways of a high-biomass epifauna in the northern Gulf of Trieste, Adriatic Sea. *Lethaia* 32, 299-317.

**CHAPTER 3:**  
**SPATIAL VARIATION IN DRILLING PREDATION FROM**  
**INTERTIDAL, SHALLOW SUBLITTORAL AND SHELF**  
**ENVIRONMENTS FROM THE EARLY AND MIDDLE MIOCENE**  
**MARINE FOSSIL RECORD OF THE CENTRAL PARATETHYS<sup>1</sup>**

**3.1. Abstract**

Drilling predation is among the most studied biotic interactions in the fossil record, and its overall patterns are well established on Cenozoic molluscs from North America. Few studies have examined such predation in Europe. This study aims to evaluate molluscan drilling intensities from the Burdigalian, Langhian and Serravallian of the Central Paratethys. Using drill frequency (DF) and prey effectiveness (PE), a measure of prey's ability to survive predatory attacks, we examine taxonomic and environmental effects on drilling predation, evaluate local and regional spatial variation, and compare Central Paratethys values to other contemporaneous basins using > 38,500 whole shells from 162 Karpatian (Upper Burdigalian) and Badenian (Langhian and Lower Serravallian) bulk samples from Austria and Slovakia. DF and PE were slightly higher in bivalves than gastropods, and DF could vary drastically within single environments at single localities (maximum at Immendorf: mean = 10.9 %, standard deviation = 12.9 %). Both DF and PE were more variable in the Karpatian than Badenian. Higher overall DFs, but lower PEs were seen in the Badenian than in the Karpatian. A similar pattern was observed between intertidal

---

<sup>1</sup> In review as: Sawyer, J.A., Zuschin, M., *In Review*. Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the early and middle Miocene marine fossil record of the Central Paratethys. *Palaios* (accepted with moderate revisions).

and sublittoral deposits. We interpret the increase in predation from the Lower to Middle Miocene to reflect environmental shifts from restricted estuarine to deeper, normal marine conditions. Regional predation intensities from the Central Paratethys are distinctly lower than those of other Miocene seas, potentially due to lower predator abundance, differences in faunal composition, and/or fluctuating salinities typical of inland seas.

### **3.2. Introduction**

Predatory drilling traces are among the most widely studied biotic interactions in the fossil record (Vermeij, 1982, 1987; Vermeij and Dudley, 1982; Alexander, 1986; Hoffmeister and Kowalewski, 2001), and assemblage-level patterns of drilling predation are well established in the Cenozoic deposits along the East and Gulf Coasts of the U.S.A. (Kelley and Hansen, 1993, 1996, 2007). Relatively few studies have, however, analyzed Cenozoic drilling predation in European deposits. Furthermore, the majority of studies have focused on temporal patterns in shell drilling (Kelley, 1989, 1992; Kabat, 1990; Kelley and Hansen, 1996), but data regarding environmental and spatial variation are generally lacking (Hoffmeister and Kowalewski, 2001). Disparities in drilling intensity due to spatial and environmental variation can confound temporal trends (Kelley and Hansen, 2003), highlighting the importance of intensive sampling to accurately characterize drilling predation in any given environment at any given time (Sawyer and Zuschin, 2010).

Hoffmeister and Kowalewski (2001) examined drilling predation in Miocene molluscs from Central Europe. They noted highly variable predation

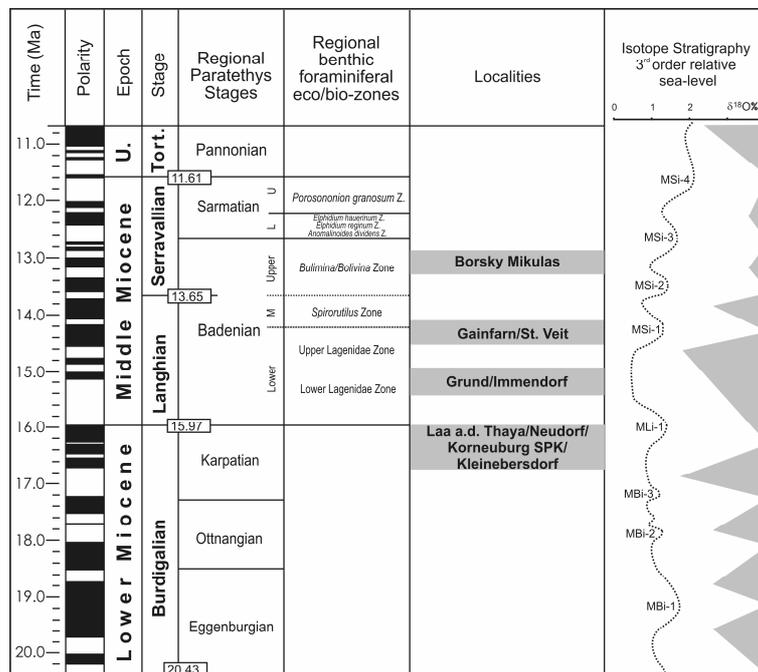
intensities from clay and sand facies in Central Paratethys and Boreal deposits, and noted that Paratethyan drill frequencies were notably lower than those from other contemporaneous provinces. Here, we expand upon Hoffmeister and Kowalewski's (2001) Central Paratethys work. The goals of this paper are to: (1) evaluate drilling intensity patterns in Lower and Middle Miocene molluscan assemblages from the Central Paratethys; (2) evaluate drilling intensity across environments; (3) evaluate spatial variation in drilling intensity within similar environments and within single localities; and (4) expand upon Hoffmeister and Kowalewski's (2001) data to compare Paratethys drill frequencies with those of other contemporaneous Provinces.

### **3.3. Geologic Setting**

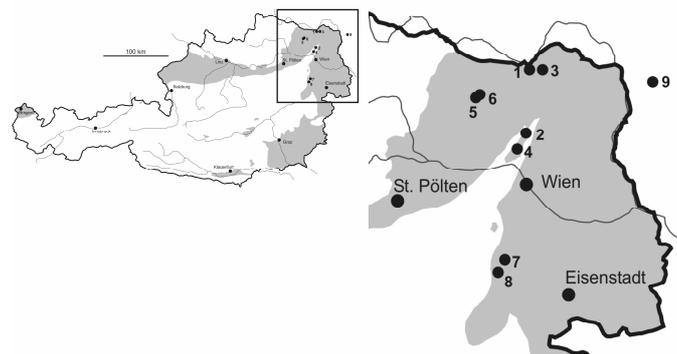
The Miocene sequences of the Central Paratethys have been widely studied and biostratigraphic zonations have been well established regionally and cross-correlated to global chronostratigraphic stages (e.g., Steininger et al., 1976; Rögl and Steininger 1984; Rögl, 1996, 1998, 1999). Our samples are from the local stages Karpatian (Latest Burdigalian) and Badenian (Langhian and Lower Serravallian, Fig. 3.1). A total of 232 bulk samples were collected from four Early Miocene (Burdigalian) and five Middle Miocene (Langhian) localities in Austria and Slovakia (Fig. 3.2). Of those, 162 had molluscan abundances of  $n > 20$ , and were used in this study (Table 3.1).

The Paratethys was a typical epicontinental sea with a diverse and well-preserved molluscan fauna. During the Oligocene and Miocene, the Paratethys extended to the northern boundary of the Mediterranean, from which it was

separated by landmasses formed by the Alps, Dinarides, Hellenids and the Anatolian Massif (Rögl, 1998). The early Middle Miocene is marked by a



**Fig. 3.1.** Lower (Burdigalian) to Upper (Tortonian) Miocene geochronology and biostratigraphy with stratigraphic positions of sampled localities in the Central Paratethys. Modified from *Zuschin, M., Harzhauser, M., Mandic, O., 2007. The stratigraphic and sedimentologic framework of fine-scale faunal replacements in the Middle Miocene of the Vienna Basin (Austria). Palaios 22, 285-895.*



**Fig. 3.2.** Map of sample localities in Austria and Slovakia. Shaded areas represent Neogene deposits. Karpatian (i.e. Burdigalian) localities include: 1 = Laa a.d. Thaya; 2 = Kleinebersdorf; 3 = Neudorf bei Staats; 4 = Korneuburg SPK. Badenian (i.e. Langhian and Lower Serravallian) localities include: 5 = Grund; 6 = Immendorf; 7 = Gainfarn; 8 = St. Veit; 9 = Borský Mikuláš.

widespread marine transgression following a major drop in sea level at the Burdigalian/Langhian transition (Haq et al., 1988; Hardenbol et al., 1998). During the transgression, a broad connection opened between the Mediterranean and the Paratethys, through which free faunal exchange occurred (Rögl, 1998; Studencka et al., 1998; Harzhauser et al., 2002; Harzhauser and Piller, 2007). The rising sea level and the Middle Miocene climatic optimum strongly influenced marine life in the Central Paratethys (Harzhauser et al., 2003). Based on faunal lists, Harzhauser et al. (2003) reported a major faunal turnover at the boundary between the Early and Middle Miocene (Burdigalian/Langhian), which is also characterized by a major environmental shift from shallow, near shore and estuarine to deeper, inner shelf/open marine conditions. Subsequent fine-scale paleocommunity studies of species-abundance patterns suggest, however, that the molluscan assemblages came from largely persistent paleocommunities that tracked environments as facies changed (Zuschin et al., 2007, 2009).

Karpatian (Upper Burdigalian) deposits were collected from the Korneuburg Formation in the Korneuburg Basin (Korneuburg SPK, Kleinebersdorf), from the Laa Formation in the Molasse Zone (Laa a.d. Thaya) and from Neudorf bei Staats. The studied deposits are dated at latest Early Miocene (mammal zone MN5 and nannoplankton zone NN4; e.g., Daxner-Höck, 2001, Harzhauser et al., 2002), spanning from about 16.5 to 16.7 my (Fig. 3.1).

The shell bed sampled at locality Kleinebersdorf is interpreted to be from a parautochthonous or slightly transported tidal flat deposit (Zuschin et al., 2004a). Large *Crassostrea gryphoides* shells in the exposure suggest a nutrient-rich, lower intertidal to upper-most sublittoral environment, likely from a sheltered embayment or lagoon with a partially restricted circulation pattern adjacent to an

**Table 3.1.** Summary of environments, numbers of shells studied and predation data from Karpatian (i.e. Burdigalian) and Badenian (i.e. Langhian and Lower Serravalian) samples.

Age	Locality	facies	number samples (n > 20)	Number molluscs	Number drillholes	Number Bivalves	Number drilled bivalves	Number Gastropods	Number drilled		number scaphopods	number Drilled Scaphopods	Mollusc DF		Bivalve DF	
									Gastropods	Bivalves			Gastropods	Bivalves	Gastropods	Bivalves
Karpatian	Laa a.d. Thaya	I	4	2233	129	258	22	1975	107	0	0	0	5.8%	8.5%		
	Kleinebersdorf	I	6	1266	226	190	12	1076	214	0	0	0	17.9%	6.3%		
	Neudorf	SM	5	214	27	41	0	172	27	1	0	0	12.6%	0.0%		
	Korneuburg	I	41	8562	296	293	3	8247	293	22	0	0	3.5%	1.0%		
		Sh	35	2325	102	606	5	1701	97	18	1	1	4.4%	0.8%		
Badenian	Grund	SS	5	2512	228	1721	141	787	86	4	1	1	9.1%	8.2%		
	Immendorf	SS	25	2223	181	1232	90	977	91	14	0	0	8.1%	7.3%		
	Gainfarn	SM	7	3034	359	2959	357	75	2	0	0	0	11.8%	12.1%		
		SS	11	2074	197	484	42	1581	155	9	0	0	9.5%	8.7%		
	St. Veit	I	6	2411	126	24	0	2387	126	0	0	0	5.2%	0.0%		
		SS	2	1356	151	28	2	1328	149	0	0	0	11.1%	7.1%		
	Borsky Mikulas	I	4	1060	152	25	0	1035	152	0	0	0	14.3%	0.0%		
		SS	11	1497	94	506	36	931	77	60	0	0	6.3%	7.1%		

I = intertidal, Sh = shallow sublittoral, SM = inner shelf mud, SS = inner shelf sand.

estuary (Harzhauser et al., 2002; Zuschin et al., 2004a). Based on their molluscan compositions, we interpret samples from the locality Laa a.d. Thaya to come from a tidal-flat setting, and samples from the locality Neudorf bei Staatz from a shallow sublittoral muddy environment. Samples from Korneuburg SPK come from an extensively sampled section along a roadcut for a new highway (S1) crossing the Korneuburg Basin. We interpret the paleoenvironment for Korneuburg SPK to be a restricted estuary with a nearby large freshwater source from the southwest. Shell beds from this locality are interpreted to come from intertidal to shallow sublittoral settings.

The Badenian (Langhian and Lower Serravallian) deposits were collected from the Grund Formation in the Mollase Basin, and from the Lanzhot & Jakubov and Studienka Formations in the Vienna Basin. Strata from the Lower Lagenidae Foraminifera zone were sampled from the Grund Formation at the localities Grund and Immendorf, which correspond to the nannoplankton zone NN5. Strata from the Upper Lagenidae Foraminifera zone were collected from the Lanzhot & Jakubov Formation at the localities Gainfarn and St. Veit, which also correspond to the nannoplankton zone NN5. Strata from the *Bulimina-Bolivina* Foraminifera Zone were sampled at the locality Borský Mikuláš from the Studienka Formation, which corresponds to the nannoplankton zone NN6. These formations primarily consist of intertidal and fully marine assemblages from siliciclastic, pelitic and sandy-to-gravelly shallow-water deposits (Fig. 3.1, Table 3.1; see also Rögl et al., 2002).

Samples from the locality Grund were taken from highly diverse, densely packed tempestitic shell beds extracted from artificial outcrops dug into the

farmland north of Grund, Lower Austria. Molluscs in these beds were typically abraded and size-sorting indicates that they were transported from agitated shallow-water habitats into somewhat deeper pelitic, dysaerobic environments with monospecific assemblages of *Thyasira* found in life position (Zuschin et al., 2001, 2004b, 2005).

Samples from the locality Immendorf were extracted from an artificial outcrop parallel to the main road connecting Immendorf and Wullersdorf near the town of Hollabrunn in Lower Austria. The shell beds are similar to those of the locality Grund, and are interpreted as allochthonous tempestitic deposits with very high diversity of abraded shells from a mixed soft- and hard bottom shelf environment. The beds have a sandy matrix, and are preserved in deeper-water mudstones (Zuschin et al., 2006).

Samples were collected from an artificial trench near the village of Gainfarn, Lower Austria. Samples from the locality Gainfarn come from three fully marine depositional units that consist of siliciclastic, pelitic, and sandy-to-gravelly shallow-water deposits. The fully marine benthic molluscs in this succession occur primarily as autochthonous and storm-influenced, level-bottom assemblages, but a distinct oyster-vermitid boundstone near the base of the uppermost stratigraphic unit was also included (Zuschin et al., 2007).

Samples collected from the locality St. Veit were also from an artificial trench in the farm land near St. Veit in the Vienna Basin. The beds at St. Veit are contemporaneous to Gainfarn but we interpreted them to be from a more restricted intertidal to shallow sublittoral environment, with intercalations of fully marine sands (M. Zuschin unpublished data, 2008).

The Slovakian locality Borský Mikuláš is located about 90 km northeast of Vienna, Austria (~ 65 km north of Bratislava, Slovakia) in the north-eastern part of the Vienna Basin. The upper Badenian (Lower Serravallian) strata were sampled from an artificial outcrop located just south of the town on the hill Vinohrádky. We interpret the mollusc-rich sandy clay strata from this locality to come from intertidal and shallow sublittoral deposits with intercalated fully marine sands (Švagrovský, 1981).

### **3.4. Methods**

Samples were processed using a 1 mm mesh sieve. Molluscs were removed and identified to species level. Unbroken shells (> 90 % complete) were counted and examined for traces of drilling predation. Round, smooth-sided holes that were circular in cross section, penetrated perpendicular to and from the outside, and were limited to one-valve of an articulated shell, were considered to be predatory in nature (Carriker and Yochelson, 1968; Rohr, 1991; Baumiller, 1996; Kaplan and Baumiller, 2000; Leighton, 2001, Kowalewski, 2002). All families and all samples containing fewer than 20 individuals were removed from the data set for family- and species-level analyses, resulting in analysis of 98.8 % of all whole shells in the dataset. Each shell was examined under a LEICA MZ12 binocular microscope at magnifications ranging from 8 to 30x.

Drilling frequency (DF), a measure of the rate of prey mortality due to drilling predation, was calculated by dividing the number of shells with complete drill holes by the total number examined. DF for bivalves, which tend to disarticulate after death, was calculated by dividing the total number of valves

with a complete drill hole by half the total number of valves examined (Hoffmeister and Kowalewski, 2001; Kowalewski, 2002). Prey effectiveness (PE), a measure of a prey's ability to resist drilling predation, was calculated by dividing the number of incomplete drill holes by the total number of drilling attempts (i.e., complete plus incomplete drill holes; Vermeij, 1987). DF and PE were compared: (1) between Karpatian (i.e., Burdigalian) and Badenian (i.e., Langhian and Lower Serravalian) assemblages; (2) between classes, abundant families and species; (3) between the intertidal, shallow sublittoral and shallow shelf, as well as between shelf muds and sands; and (4) between our samples from the Central Paratethys and data from various other contemporaneous deposits from other basins.

Paleoenvironments were based on paleogeographic position and independent data from foraminifera suggest water depths ranging from intertidal to several tens of meters. Ordination methods suggest the benthic molluscan assemblages developed along this depth-related environmental gradient (Zuschin et al., 2009).

Drilling predation was compared graphically (using 95 % confidence intervals) and statistically. Standard deviations about mean DFs were compared to evaluate variation in DF within single environments, localities and between the Karpatian and Badenian. Chi-squared test was used to compare DFs from the Central Paratethys with those determined for other Miocene basins by previous researchers (e.g., Hoffmeister and Kowalewski, 2001; Kelley and Hansen, 2006; Fortunato, 2007). In addition, explorative multivariate methods were applied to DF data to identify ecological gradients and determine significantly different assemblage-level DFs between environments and localities.

Ordination methods have often been used to identify ecological gradients in modern and fossil ecosystems (e.g., Olszewski and Patzkowsky, 2001; Zuschin et al., 2006, 2007). Non-metric multidimensional scaling (nMDS) was performed on family-level DFs to determine if environmental gradients act as a control of drilling predation in our data set. All outliers (samples with DFs of 0 or 100 %) were removed from the nMDS and analysis to aid in the identification of environmental gradients. Most such outliers came from samples with low abundances or with single families. Additionally, samples in which  $n < 40$  or that consisted of one dominant family and few additional families, each with low abundances ( $n < 20$ ) were also removed from the nMDS and analysis of similarity (ANOSIM) tests. DF is a proportional value, therefore, the addition or removal of a single drill hole in small samples can drastically affect its value. Because DFs in the Central Paratethys are generally low ( $< 10\%$ ), removal of such outliers was deemed necessary to limit the effect of small samples in the multivariate analyses. In all, 14 samples consisting of 856 molluscs, and 2.8 % of the total, were removed from the dataset.

ANOSIM based on Bray-Curtis similarity coefficient (Bray and Curtis, 1957; Clarke and Warwick, 1994) was used to identify significant differences in faunal composition between the Karpatian and Badenian, and among environmental categories. The p-values reported by ANOSIM are often quite low due to few replicates in each group. The more interesting result is the R-value, which gives an absolute measure of how separated the groups are on a scale of zero (indistinguishable) to one (all similarities within groups are less than similarities between groups). R-values  $> 0.75$  indicate well separated groups,  $> 0.5$  indicate overlapping but clearly different groups,  $> 0.25$  indicate strongly

overlapping groups and  $< 0.25$ , indicate barely separable groups (Clarke and Gorley, 2001).

All statistical analyses were performed using PAST 1.93 (Hammer et al., 2001). A significance criterion 5 % ( $\alpha = 0.05$ ) was applied to all statistical analyses. Graphics were generated using the software package SPSS 10.0 (SPSS, 1999).

### **3.5. Results**

#### **3.5.1. Basic structure of molluscan assemblages**

A total of 39,234 mollusc shells, consisting of 8,473 bivalves (corrected), 22,292 gastropods, 128 scaphopods and 31 polyplacophora plates from 42 bivalve, 50 gastropod, two scaphopod and one polyplacophora families (Table 3.2) were identified. These shells represent 149 bivalve, 354 gastropod, two scaphopod and one polyplacophora species.

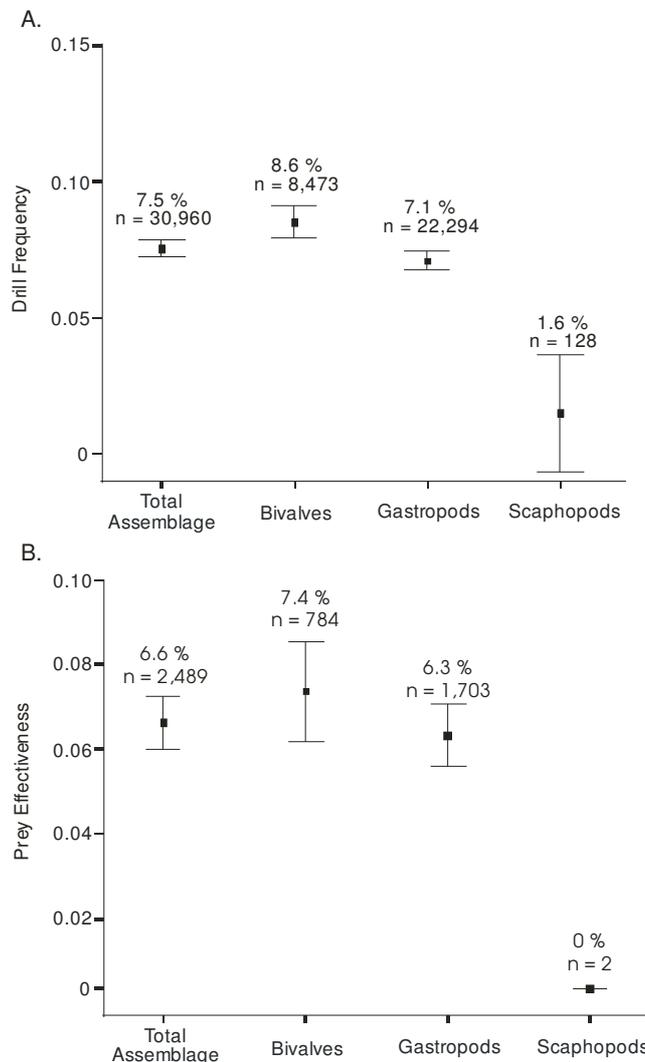
Karpatian samples came from intertidal (51 samples from 3 localities), shallow sublittoral (35 samples from 1 locality) and inner shelf muds (5 samples from 1 locality, Table 3.1). Badenian samples came from intertidal (10 samples from 2 localities), inner shelf muds (7 samples from 1 locality) and inner shelf sands (54 samples from 5 localities, Table 3.1).

#### **3.5.2. Drilling intensities at different taxonomic levels**

Pooled DF and PE for all samples across all Central Paratethys localities are 7.5 % and 6.6 %. DF is slightly higher in bivalves (8.6 %) than gastropods (7.1 %), and much lower in scaphopods (1.6 %). No drill holes were observed in

polyplacophora plates. PE is slightly higher in bivalves (7.4 %) than gastropods (6.3 %), but these values are not significantly different. No incomplete and only 2 complete drill holes were found in scaphopods (Fig. 3.3).

Nineteen of 42 bivalve families were never drilled, but only three of those had abundances greater than 20 (Pectinidae, Mesodesmatidae, Thraciidae, Table 3.2). Among families that were attacked, DFs ranged from 2.3 % (Semelidae) to 15.4 % (Anomiidae). Seven bivalve families have incomplete drill holes, but of those three were attacked fewer than 20 times (complete plus incomplete drill



**Fig. 3.3.** Drilling predation pooled across all samples and all taxa, and the classes Bivalvia, Gastropoda and Scaphopoda. A) Drill frequencies. B) Prey effectiveness. Black squares = means; error bars = 95 % confidence intervals.

holes < 20; Arcidae, Pectinidae, Mesodesmatitidae). PE of the others ranged from 2.8 % (Lucinidae) to 16.7 % (Ostreidae, Fig. 3.4, and Table 3.2).

Twenty-two of 50 gastropod families were never drilled, only two of which had abundances greater than 20 (Phasianellidae, Skeneidae, Table 3.2). Among families that were attacked, DFs ranged from 0.6 % (Hydrobiidae) to 20.0 % (Terebreidae). Thirteen gastropod families had incomplete drill holes; of those, six were attacked fewer than 20 times (complete plus incomplete drill holes < 20; Melanopsidae, Vermetidae, Muricidae, Olividae, Terebridae, and Pyramidellidae). PE for the others ranged from 0.9 % (Turritellidae) to 23.2 % (Neritidae, Fig. 3.5, and Table 3.2).

All five of the most abundant species were drilled; their DFs ranged from 2.2 % (*Agapilia pachii*) to 12.1 % (*Corbula gibba*). All five of the most abundant species also had incomplete drill holes. Their incomplete drill frequencies ranged from 1.7 % (*Granulolabium bicinctum*) to 25.7 % (*Agapilia pachii*, Table 3.2).

### **3.5.3. Variation in drilling predation within localities**

Drilling frequencies could fluctuate drastically within similar environments at single localities in the Central Paratethys (Fig. 3.6; Table 3.3). The locality Grund showed the least overall variation in drilling frequencies between samples (mean DF: 9.3 %, standard deviation: 1.6 %, total range: 7.3 – 11.2 %), while the locality Immendorf showed the greatest (mean DF: 10.9 %, standard deviation: 12.9 %, total range: 0 – 57 %). In general, drilling intensities were more variable in Karpatian localities (mean standard deviation: 5.22 %) than

Badenian localities (mean standard deviation: 4.99 %; Fig. 3.6, Table 3.3).

Likewise, DF pooled across all samples was somewhat constrained in the

**Table 3.2.** Taxonomic summary of drill hole data from Karpatian (i.e. Burdigalian) and Badenian (i.e. Langhian and Lower Serravalian) aged molluscs from the Central Paratethys for the overall assemblage, classes and families

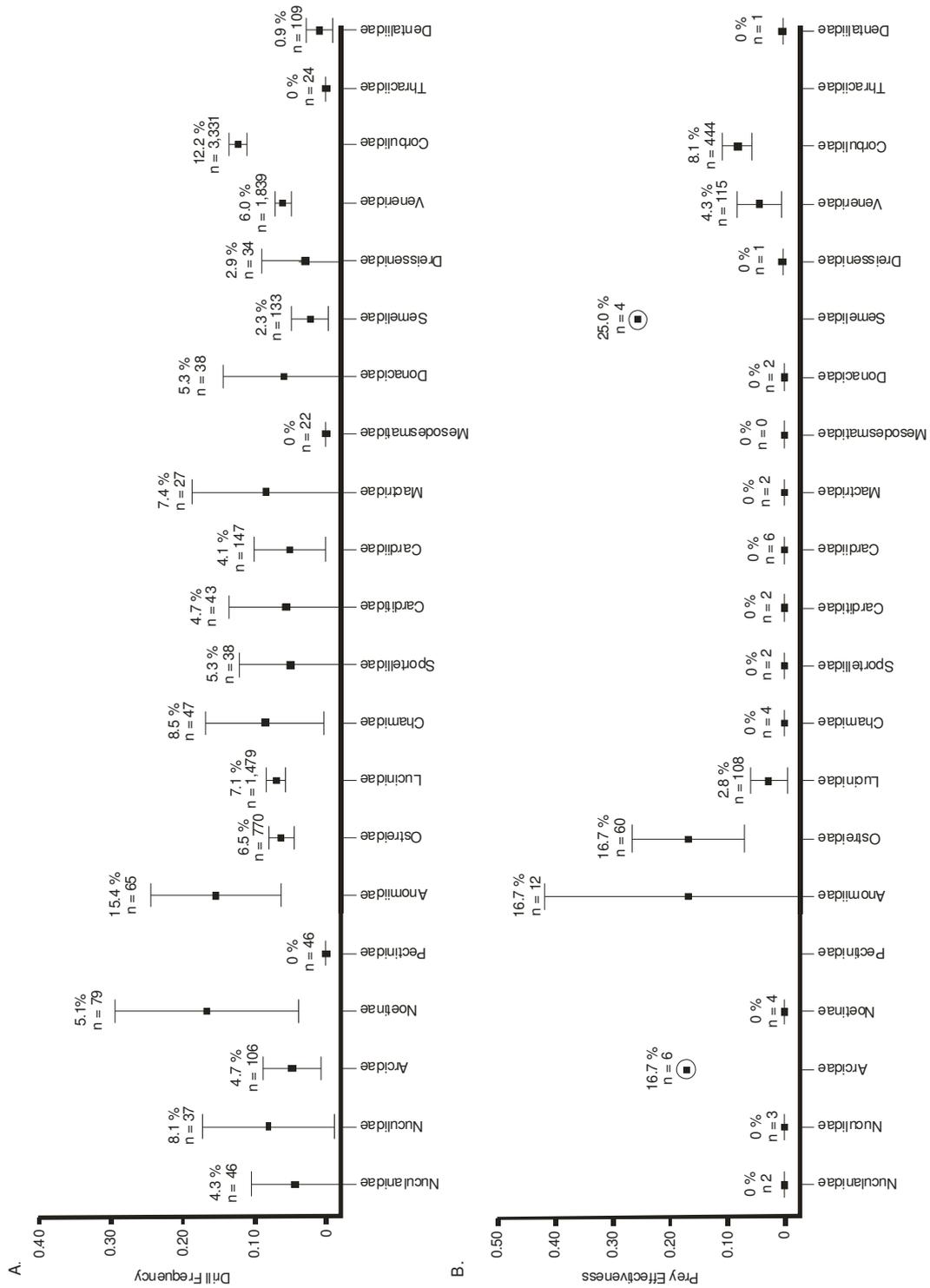
	n	D	ID	DF (%)	PE (%)
Total Assemblage	30960	2324	165	7.5%	6.6%
Class					
Bivalvia	8473	726	58	8.6%	7.4%
Gastropoda	22294	1596	107	7.2%	6.3%
Scaphopoda	128	2	0	1.6%	0.0%
Polyplacophora	31	0	0	0.0%	.
Families					
Bivalvia					
Nuculanidae	46	2	0	4.3%	0.0%
Nuculidae	37	3	0	8.1%	0.0%
Arcidae	106	5	1	4.7%	16.7%
Noetiidae	79	4	0	5.1%	0.0%
Glycymerididae	17	1	0	5.9%	0.0%
Mytilinae	3	0	0	0.0%	.
Crenellinae	2	0	0	0.0%	.
Pectinidae	46	0	0	0.0%	.
Plicatulidae	15	1	0	6.7%	0.0%
Limidae	1	0	0	0.0%	.
Anomiidae	65	10	2	15.4%	16.7%
Ostreidae	770	50	10	6.5%	16.7%
Gryphaeidae	1	0	0	0.0%	.
Lucinidae	1479	105	3	7.1%	2.8%
Thyasiridae	2	0	0	0.0%	.
Ungulinidae	17	1	0	5.9%	0.0%
Chamidae	47	4	0	8.5%	0.0%
Galeommatidae	3	0	0	0.0%	.
Kelliidae	4	0	0	0.0%	.
Lasaeidae	3	0	0	0.0%	.
Leptonidae	2	0	0	0.0%	.
Sportellidae	38	2	0	5.3%	0.0%
Carditidae	43	2	0	4.7%	0.0%
Cardiidae	147	6	0	4.1%	0.0%
Crassatellidae	1	0	0	0.0%	.
Mactridae	27	2	0	7.4%	0.0%
Mesodesmatidae	22	0	0	0.0%	.
Donacidae	38	2	0	5.3%	0.0%
Psammobiidae	6	0	0	0.0%	.
Semelidae	133	3	1	2.3%	25.0%
Tellinidae	11	2	0	18.2%	0.0%
Dreissenidae	34	1	0	2.9%	0.0%
Kelliellidae	16	1	0	6.3%	0.0%
Glossidae	1	0	0	0.0%	.
Petricolidae	4	0	0	0.0%	.
Veneridae	1839	110	5	6.0%	4.3%
Rzehakiidae	2	1	0	50.0%	0.0%
Corbulidae	3331	408	36	12.2%	8.1%
Gastrochaenidae	2	0	0	0.0%	.
Hiatellidae	5	0	0	0.0%	.
Pholadidae	4	0	0	0.0%	.
Thraciidae	24	0	0	0.0%	.

n = abundance (corrected to account for disarticulated bivalves), D = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, PE = prey effectiveness.

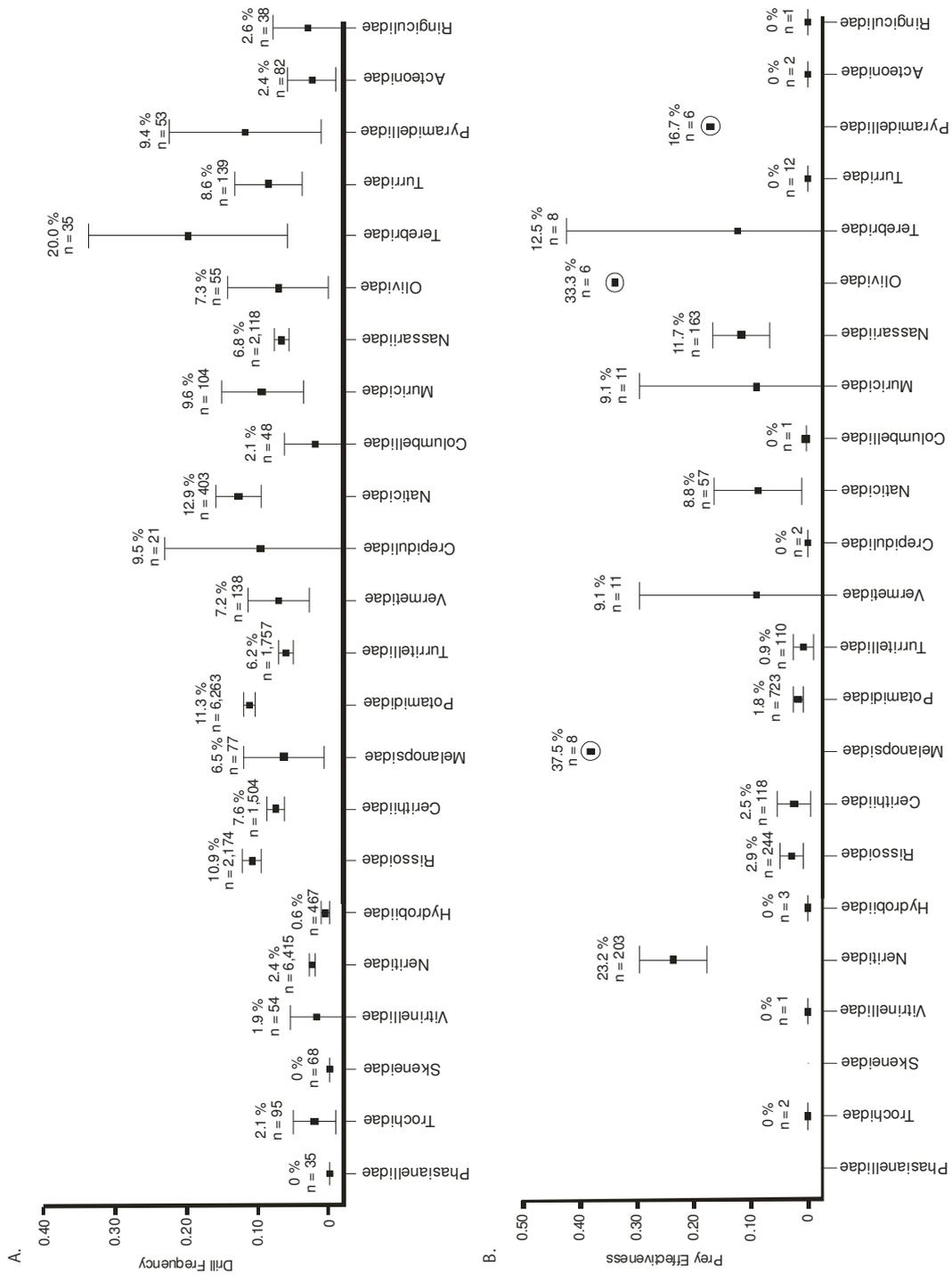
**Table 3.2. (continued).** Taxonomic summary of drill hole data from Karpatian (i.e. Burdigalian) and Badenian (i.e. Langhian and Lower Serravalian) aged molluscs from the Central Paratethys for the overall assemblage, classes and families

	n	D	ID	DF (%)	PE (%)
Gastropoda					
Fissurellidae	12	0	0	0.0%	.
Phasianellidae	35	0	0	0.0%	.
Trochidae	95	2	0	2.1%	0.0%
Turbinidae	6	0	0	0.0%	.
Skeneidae	68	0	0	0.0%	.
Vitrinellidae	54	1	0	1.9%	0.0%
Neritidae	6415	156	47	2.4%	23.2%
Caecidae	1	0	0	0.0%	.
Hydrobiidae	467	3	0	0.6%	0.0%
Rissoidea	2174	237	7	10.9%	2.9%
Rissoinidae	12	0	0	0.0%	.
Cerithiidae	1504	115	3	7.6%	2.5%
Battillariidae	3	1	0	33.3%	0.0%
Litiopidae	4	0	0	0.0%	.
Melanopsidae	77	5	3	6.5%	37.5%
Potamididae	6263	710	13	11.3%	1.8%
Turritellidae	1757	109	1	6.2%	0.9%
Vermetidae	138	10	1	7.2%	9.1%
Aporrhaidae	7	0	1	0.0%	100.0%
Crepidulidae	21	2	0	9.5%	0.0%
Triviidae	3	0	0	0.0%	.
Naticidae	403	52	5	12.9%	8.8%
Cymatiidae	2	0	0	0.0%	.
Ficidae	1	1	0	100.0%	0.0%
Buccinidae	5	0	0	0.0%	.
Columbellidae	48	1	0	2.1%	0.0%
Fasciolaridae	1	0	0	0.0%	.
Muricidae	104	10	1	9.6%	9.1%
Nassariidae	2118	144	19	6.8%	11.7%
Vasidae	5	1	0	20.0%	0.0%
Cancellariidae	15	1	0	6.7%	0.0%
Costellariidae	2	0	0	0.0%	.
Mitridae	5	0	0	0.0%	.
Olividae	55	4	2	7.3%	33.3%
Volutidae	1	0	0	0.0%	.
Conidae	13	1	1	7.7%	50.0%
Terebridae	35	7	1	20.0%	12.5%
Turridae	139	12	0	8.6%	0.0%
Neogastropoda indet.	3	0	0	0.0%	.
Cerithiopsidae	7	2	1	28.6%	33.3%
Triphoridae	3	0	0	0.0%	.
Epitoniidae	14	0	0	0.0%	.
Eulimidae	2	0	0	0.0%	.
Amathinidae	10	1	0	10.0%	0.0%
Pyramidellidae	53	5	1	9.4%	16.7%
Acteonidae	82	2	0	2.4%	0.0%
Cylichnidae	3	0	0	0.0%	.
Retusidae	4	0	0	0.0%	.
Ringiculidae	38	1	0	2.6%	0.0%
Scaphandridae	7	0	0	0.0%	.
Scaphopoda					
Dentaliidae	109	1	0	0.9%	0.0%
Gadiliidae	2	0	0	0.0%	.
Scaphopoda indet.	17	1	0	5.9%	0.0%
Polyplacophora					
Ischnochitonidae	31	0	0	0.0%	.
Most Abundant Species					
<i>Agapilia pachii</i> (Hörnes, 1848)	6049	136	47	2.2%	25.7%
<i>Granulolabium bicinctum</i> (Brocchi, 1814)	6016	693	12	11.5%	1.7%
<i>Corbula (Varicorbula) gibba</i> (Olivi)	3284	397	36	12.1%	8.3%
<i>Timoclea marginata</i>	1168	73	5	6.3%	6.4%
<i>Loripes (Microloripes) dentatus</i> (Defrance)	1130	104	3	9.2%	2.8%

n = abundance (corrected to account for disarticulated bivalves), D = number of complete drill holes, ID = number of incomplete drill holes, DF = drill frequency, PE = prey effectiveness.



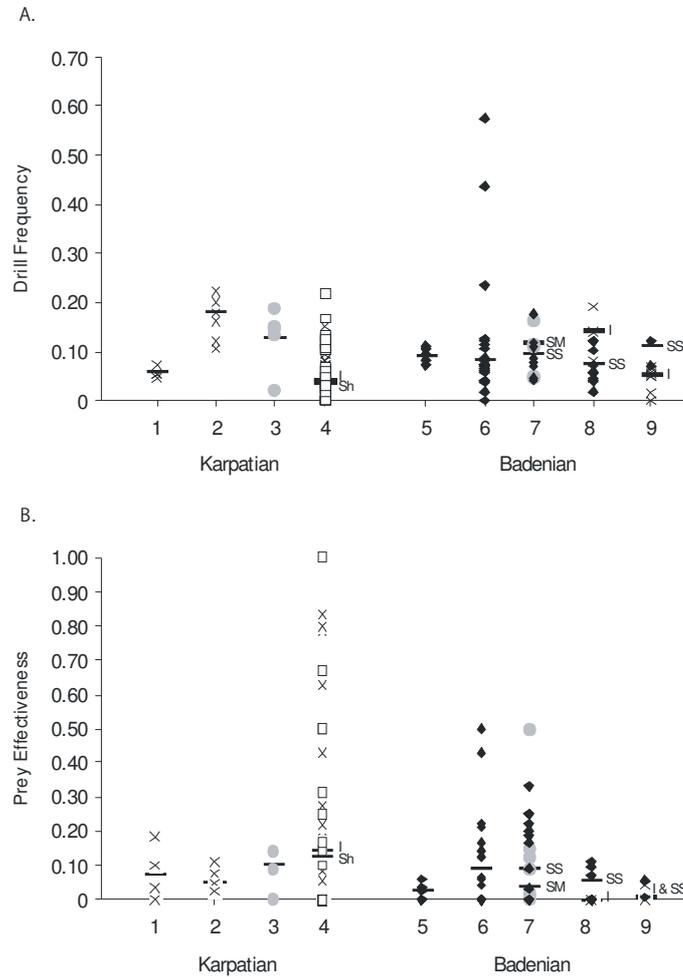
**Fig. 3.4.** Drilling predation of common bivalve and scaphopod families in the Central Paratethys ( $n > 20$ ). A) Drill frequency. B) Prey effectiveness. Dentaliidae is the only scaphopod family represented. Black squares = means; error bars = 95 % confidence intervals.



**Fig. 3.5.** Drilling predation of common gastropod families in the Central Paratethys (n > 20). A) Drill frequency. B) Prey effectiveness. Black squares = means; error bars = 95 % confidence intervals.

Badenian when compared to the Karpatian localities. The highest DF was seen in intertidal Karpatian shell beds from the locality Kleinebersdorf, while the lowest (albeit highly variable) were found at Korneuburg SPK. Samples from muddy shelf sediments occurred in the Karpatian at the locality Neudorf bei Staatz, and in the Badenian at the locality Gainfarn. In both, DFs were variable but approximately the same. Samples from the sandy shelf were only found in Badenian localities, and varied drastically at the locality Immendorf. Sandy shelf samples from other localities had less variable DFs, but values ranged by more than 10 % at localities Gainfarn and Borský Mikuláš (Fig. 3.6, Table 3.3).

Prey effectiveness generally varied more within Badenian localities, though the Karpatian locality Korneuburg SPK had the greatest range overall (0 – 100 %; Fig. 3.6). Korneuburg SPK's high variation in PE was also reflected in samples from the two distinct environments at the locality (ranges: intertidal 0 – 100 %; shallow subtidal 5.4 – 83.3 %). In addition, pooled PE was generally higher in Badenian than Karpatian sample sites. PE from intertidal samples in the Karpatian varied drastically (ranging nearly 10 % or more in every locality), while those from the Badenian locality St. Veit varied little (range: 0 % to 4 %). PE from the muddy shelf ranged from about 0 – 14 % in the Karpatian and from 0 – 50 % in the Badenian, though the sample size (n) was rather low in the Badenian sample with the higher PE, and more typical values were similar to that of the Karpatian samples. The highest pooled PEs in the Badenian, as well as the greatest variation within single localities, was found on the sandy shelf (Fig. 3.6).



**Fig. 3.6.** Drilling predation within Karpatian (i.e., Burdigalian) and Badenian (i.e., Langhian and Lower Serravalian) localities. A) Drilling frequency. B) Prey effectiveness. Each point represents the pooled drilling frequency or prey effectiveness for a single sample. Symbols: X = intertidal; open squares = shallow sublittoral; gray circles = muddy inner shelf; black diamonds = sandy inner shelf; Black bars = pooled DF or PE for all samples pooled from the same environment at the same locality. When multiple environments occur at the same locality, the environments for pooled DFs are indicated by: I = intertidal; Sh = shallow sublittoral; SM = inner shelf mud; SS = inner shelf sand. Karpatian localities: 1 = Laa a.d. Thaya, 2 = Kleinebersdorf, 3 = Neudorf bei Staatz, and 4 = Korneuburg SPK. Badenian localities: 5 = Grund; 6 = Immendorf; 7 = Gainfarn; 8 = St. Veit; and 9 = Borský Mikuláš.

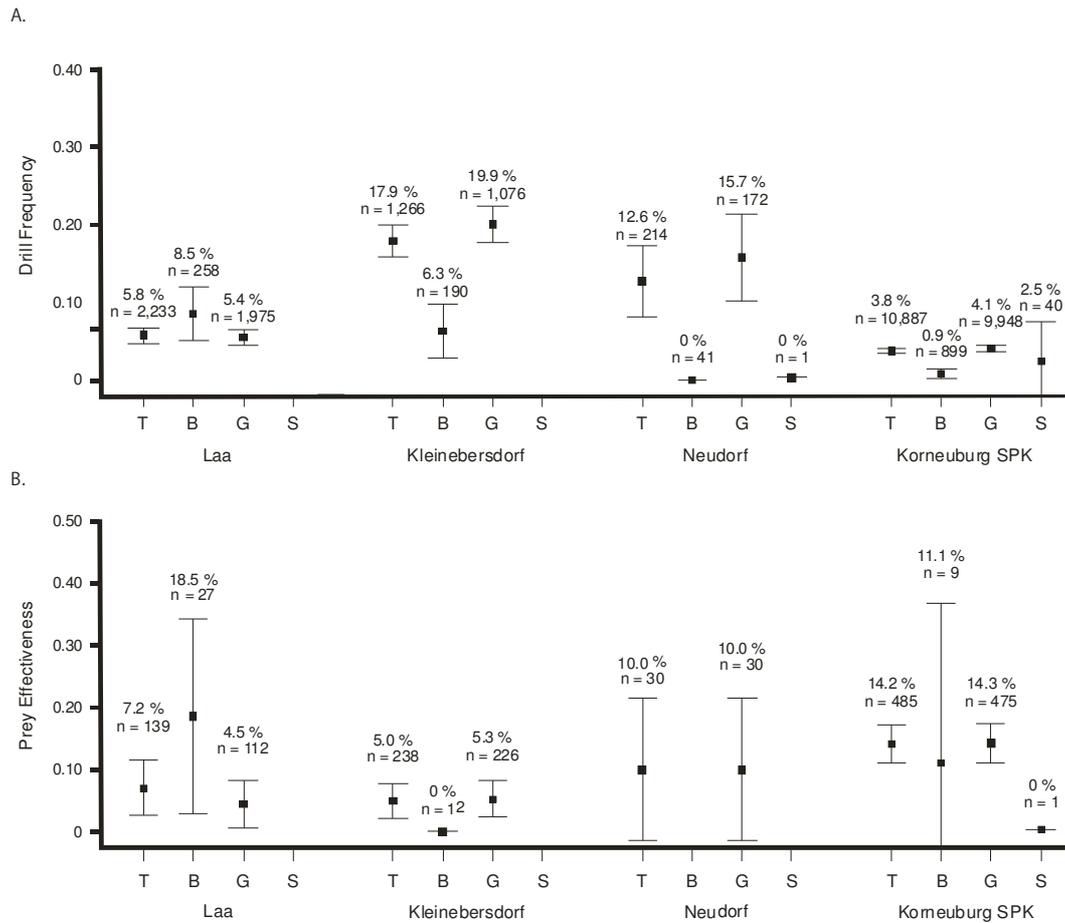
**Table 3.3.** Average drill frequencies and standard variations calculated from individual samples pooled into time, environment, and locality categories

	Facies	number of samples	mean DF (%)	St. Dev. (%)
Total Pooled				
Lower/Middle Miocene	I, Sh, M, S	162	7.4	7.2
Karpatian	I, Sh, M	91	6	5.8
Badenian	I, M, S	71	9.1	8.4
Environment				
Intertidal	I	61	5.9	5.5
Shallow Sublittoral	Sh	35	5.4	5.6
Inner Shelf Mud	M	12	10.7	5.4
Inner Shelf Sand	S	54	9.5	9.2
Locality				
Laa a.d. Thaya	I	4	5.7	5.8
Kleinebersdorf	I	6	16.5	4.5
Neudorf	M	5	12.8	6.3
Korneuburg SPK	I	41	4.1	3.9
Korneuburg SPK	Sh	35	5.4	5.6
Grund	S	5	9.3	1.6
Immendorf	S	25	10.9	12.9
Gainfarn	M	7	9.3	4.5
Gainfarn	S	11	9.3	4.8
St. Veit	I	6	4	2.6
St. Veit	S	2	9.5	3.7
Borsky Mikulas	I	4	11.4	6.4
Borsky Mikulas	S	11	6.6	3.4
Pooled Environments				
Karpatian	I	51	5.7	5.5
Badenian	I	10	6.9	5.7
Karpatian	Sh	--	--	--
Badenian	Sh	--	--	--
Karpatian	M	5	12.8	6.3
Badenian	M	7	9.3	4.5
Karpatian	S	--	--	--
Badenian	S	--	--	--

DF = drill frequency, St. Dev. = standard deviation, I = intertidal, Sh = shallow sublittoral, M = inner shelf mud, S = inner shelf sand.

### 3.5.4. Variation in drilling predation between localities

Among the Karpatian localities, DF pooled across all samples was highest at the locality Kleineberdorf and lowest at Korneuburg SPK. Gastropods were much more abundant than bivalves at all Karpatian localities except Laa a.d. Thaya, and scaphopods were rare and restricted to Korneuburg SPK (Fig. 3.7, Table 3.1). Bivalves had the highest DF at Laa a.d. Thaya. Bivalves were



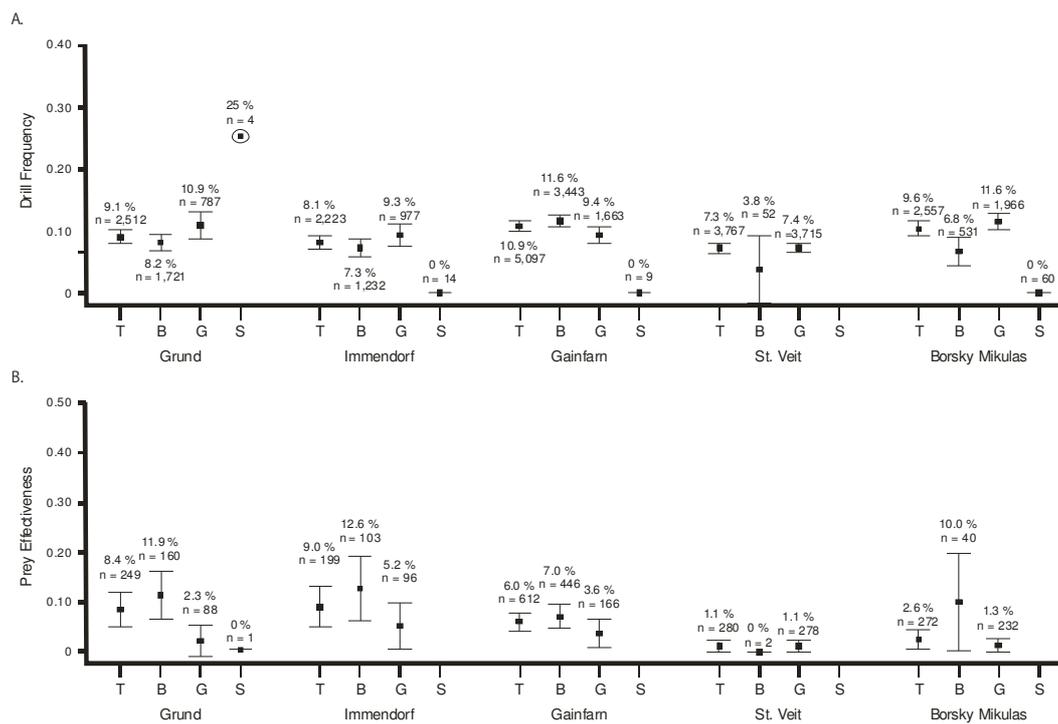
**Fig. 3.7.** Variation in drilling predation for the total assemblage and mollusc classes between each Karpatian (i.e., Burdigalian) locality sampled. A) Drilling frequency. B) Prey effectiveness. T = total assemblage; B = bivalves; G = gastropods; S = scaphopods. Black squares = means; error bars = 95 % confidence intervals.

relatively rare ( $n = 41$ ) and were never drilled at Neudorf bei Staatz. Amongst the other localities, bivalves had the lowest DF at Korneuburg SPK (Fig. 3.7). Scaphopods were only recovered from Neudorf bei Staatz ( $n = 1$ ) and Korneuburg SPK ( $n = 40$ ), and were rarely drilled (Fig. 3.7).

In contrast to DF, the highest pooled PEs occurred at the locality Korneuburg SPK, and the lowest at Kleinebersdorf. Drill holes in bivalves were generally rare, resulting in PE of 0 % at Kleinebersdorf and Neudorf bei Staatz. PE was highest in bivalves from Laa a.d. Thaya (Fig. 3.7). Gastropods had the highest PE at Korneuburg SPK and the lowest at Laa a.d. Thaya. Only one

scaphopod was drilled among all Karpatian localities and no incomplete drill holes were found, resulting in PEs of 0 %.

Overall, pooled DFs from Badenian localities were < 10 %, except at the locality Gainfarn (10.9 %, n = 5,109; Fig. 3.8, Table 3.1). St. Veit had the lowest DFs for the overall assemblages, as well as for bivalves and scaphopods. The highest bivalve DF was observed at Gainfarn, and the highest for gastropods at Borský Mikuláš. Scaphopods were only drilled at the locality Grund (n = 4), and were rare or absent in all other localities (n < 60; Fig. 3.8). Overall, pooled drill frequencies were less restricted in Karpatian (range: 3.8 – 17.9 %) than Badenian (range: 7.3 – 10.9 %) deposits, where DF was generally < 11 % (Figs. 3.7-3.8).



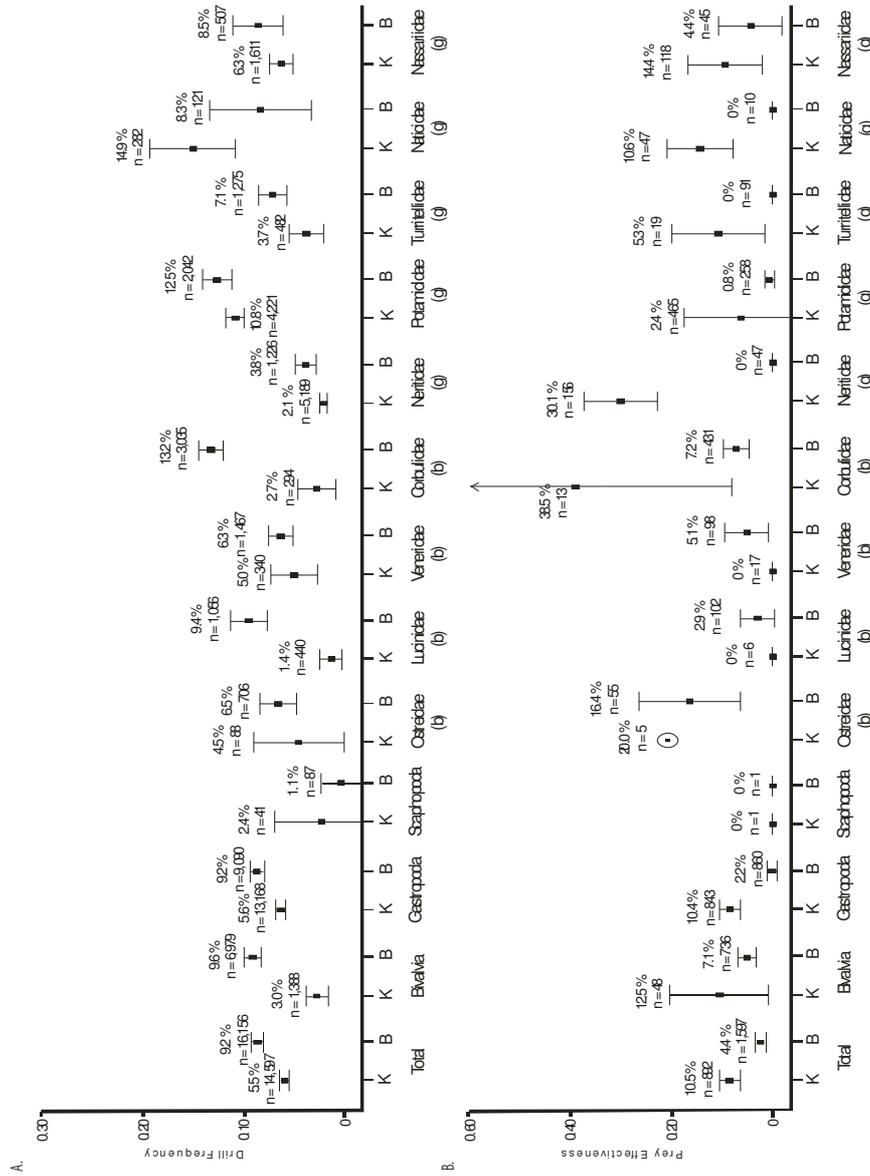
**Fig. 3.8.** Variation in drilling predation for the total assemblage and mollusc classes between each Badenian (i.e., Langhian and Lower Serravalian) locality sampled. A) Drilling frequency. B) Prey effectiveness. T = total assemblage; B = bivalves; G = gastropods; S = scaphopods. Black squares = means; error bars = 95 % confidence intervals.

Overall, pooled PE from Badenian localities was lowest at St. Veit and highest at Immendorf (Fig. 3.8). Bivalve PE was lowest at St. Veit, but the total number of drill holes was also very low there ( $n = 2$ ). Of the other localities, PE was lowest in bivalves from Gainfarn, and highest at Immendorf. Similarly, PE was lowest in gastropods from St. Veit, and highest in those from Immendorf. Scaphopods only occurred at the Badenian locality Grund, and had one complete and no incomplete drill holes (Fig. 3.8).

### **3.5.5. Karpatian and Badenian drilling predation**

In general, DF was higher in the Badenian than in the Karpatian of the Central Paratethys for all assemblages pooled, as well as for bivalves and gastropods (Fig. 3.9). Only DF for scaphopods was higher in the Karpatian than in the Badenian. Among bivalve families, DF was always higher in the Badenian than in the Karpatian. In the Karpatian, the bivalve family with the lowest DF was Lucinidae, and the highest, Veneridae. In contrast, Veneridae had the lowest DF in the Badenian, and Corbulidae the highest (Fig. 3.9). Amongst gastropod families, DF was generally higher in the Badenian than in the Karpatian, with the exception of the Naticidae. The lowest DF among gastropods from the Karpatian were from the Neritidae, and the highest from the Naticidae. Likewise, the Neritidae had the lowest gastropod DF in the Badenian, and the Potamididae the highest. In contrast to bivalves and gastropods, the scaphopod family Dentaliidae had Lower DFs in the Badenian, despite also having a slightly higher abundance (Fig. 3.9).

ANOSIM analysis results in an R-value of 0.2786 between Karpatian and Badenian drill frequencies (Table 3.4), which indicates strongly overlapping but



**Fig. 3.9.** Drilling predation for the Karpatian (i.e., Burdigalian) and Badenian (i.e., Langhian and Lower Serravalian) assemblages of the Central Paratethys for the total molluscan assemblage, mollusc classes, and abundant families. A) Drilling frequency. B) Prey effectiveness. K = Karpatian; B = Badenian; b = bivalve families; g = gastropod families. Black squares = means; error bars = 95 % confidence intervals.

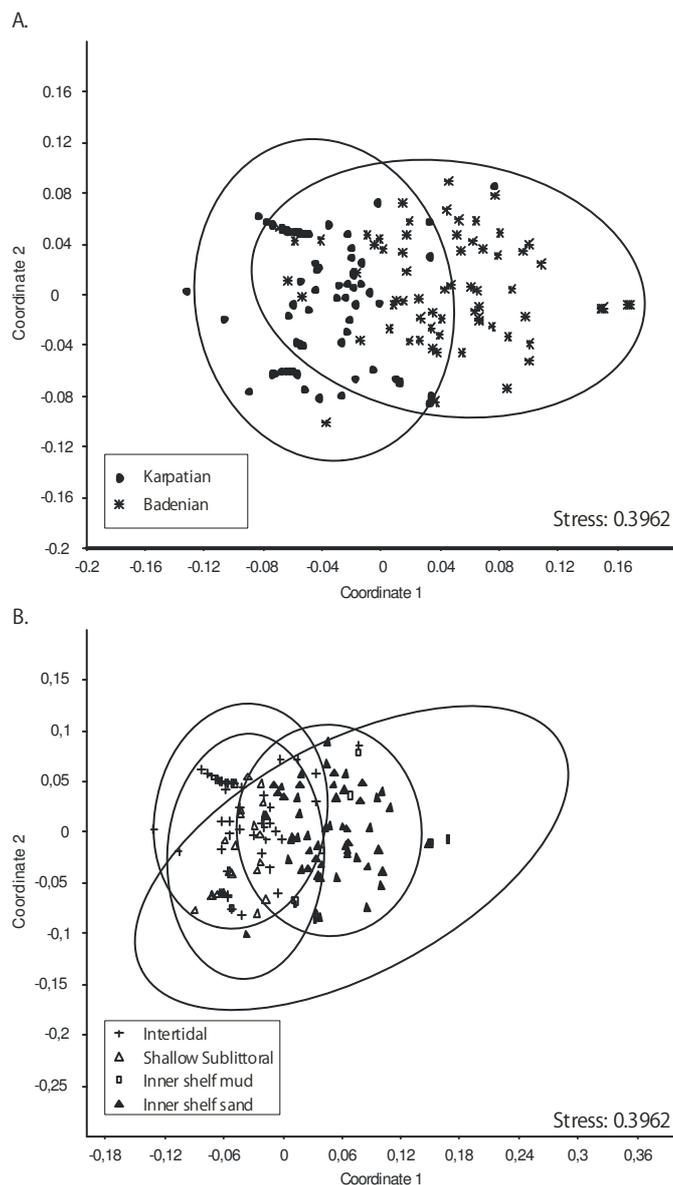
distinguishable groups. Figure 3.10a shows the nMDS ordination plot for family-level DF data with Karpatian and Badenian samples indicated. A weak time-gradient can be seen between samples from the two times, with strongly overlapping, but distinguishable 95 % ellipses. The stress-value in this analysis shows how reliably the high-dimensional relationships among samples are represented in the 2-dimensional plot. Useful plots have stress values < 0.2. The stress-value in our analysis of 0.3962 indicates that caution should be taken when drawing conclusions from the nMDS.

Overall pooled PE, as well as that of bivalves and gastropods, was lower in the Badenian than in the Karpatian (Fig. 3.9). The scaphopods were rarely drilled and had no incomplete drill holes, resulting in PE of 0 %. Between bivalve and gastropod families, the highest PE was seen in the Karpatian in the bivalve families Ostreidae and Corbulidae, and the lowest in the Badenian in the gastropod families Neritidae, Potamididae, Turritellidae and Naticidae. For bivalve families, no clear differences were observed between the Karpatian and Badenian. The lowest bivalve family PEs occurred in the Karpatian in the

**Table 3.4.** Results of ANOSIM (analysis of similarity) for Karpatian (i.e., Burdigalian) versus Badenian (i.e., Langhian and Lower Serravalian) environments

	R-stat	p-value
Time		
K vs B	0.2786	< 0,0001
Environment		
I vs S	0.1819	< 0,0001
I vs Sh vs IS	0.3155	< 0,0001
M vs S	0.4014	< 0,0001
I vs Sh vs M vs S	0.3855	< 0,0001

K = Karpatian, B = Badenian, I = intertidal, S = sublittoral, Sh = shallow sublittoral, IS = inner shelf, M = inner shelf mud, S = inner shelf Sand.



**Fig. 3.10.** Ordination of family-level drill frequencies of Central Paratethys fossil mollusc assemblages using non-metric Multidimensional Scaling (nMDS). Points close to one another indicate samples that are more similar to one another in terms family-level drilling predation than points that are further apart. A. Comparing Karpatian (i.e., Burdigalian) and Badenian (i.e., Langhian and Lower Serravalian) drill frequencies. Circles are 95 % ellipses.

Lucinidae and Veneridae (though  $n < 20$  for both), and in the Badenian in the Lucinidae. The highest PEs among bivalve families in the Karpatian were in the Ostreidae and Corbulidae (though  $n < 20$ ), and in the Badenian in the Ostreidae (Fig. 3.9). Despite generally higher DFs in the Badenian, PEs for gastropod

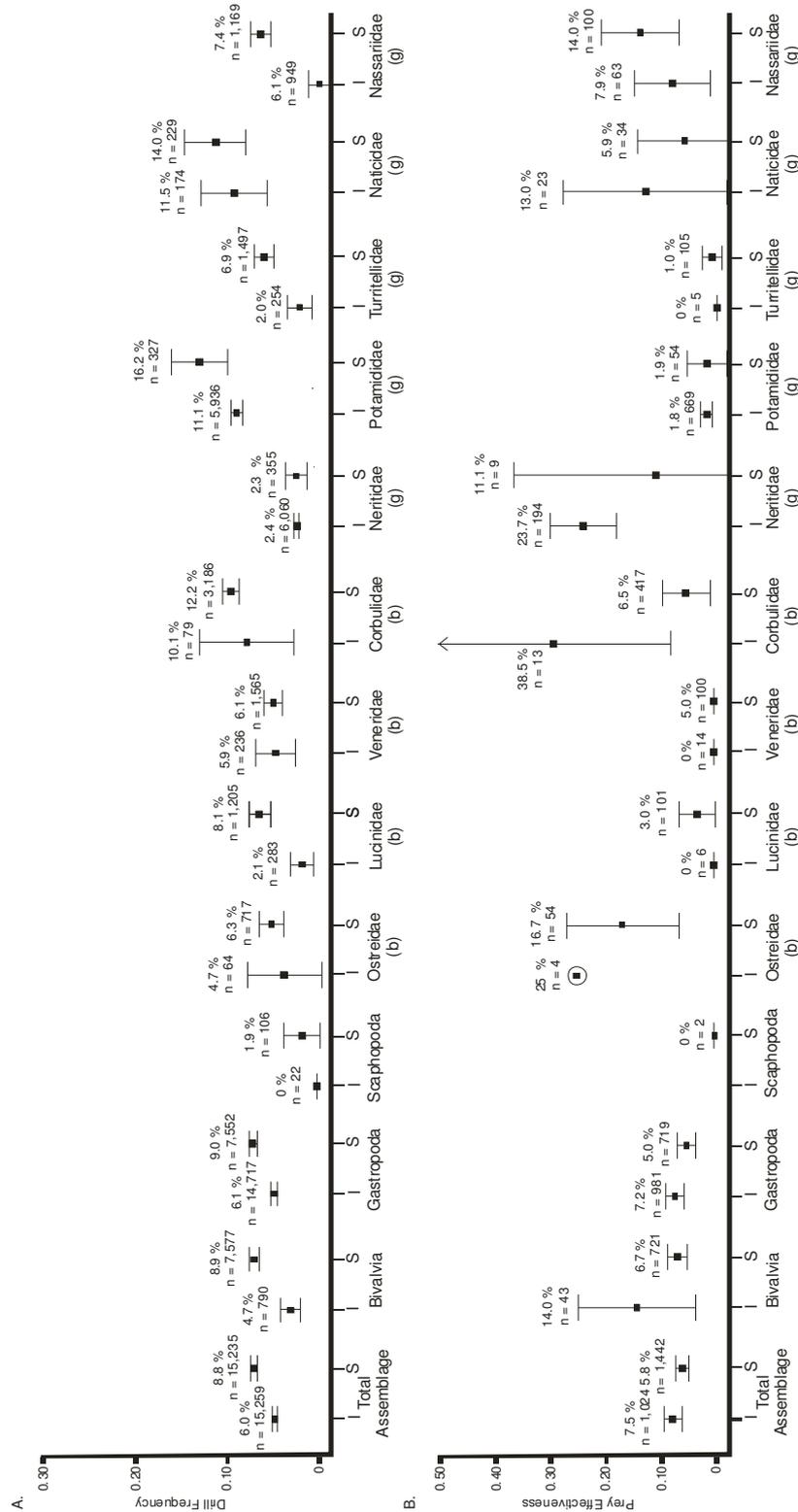
families were always higher in the Karpatian (Fig. 3.9). The gastropod family with the lowest PE in the Karpatian was Potamididae, and the highest Neritidae. In contrast, Neritidae (along with Naticidae) had the lowest PE in the Badenian, while Nassariidae had the highest (although their PE was very low at 0.8 %, Fig. 3.9).

### **3.5.6. Drilling predation in Central Paratethys environments**

*Intertidal and Sublittoral Drilling Predation.*—Intertidal samples from the localities Laa a.d. Thaya, Kleinebersdorf, Korneuburg SPK, St. Viet and Borský Mikuláš were compared to sublittoral samples from the localities Neudorf bei Staatz, Korneuburg SPK, Grund, Immendorf, Gainfarn, St. Veit and Borský Mikuláš (Table 3.1). DF was higher in the sublittoral shell beds of the Central Paratethys for all samples pooled, as well as all classes and families except the gastropod family Neritidae (Fig. 3.11). At the class level, DF was highest in the sublittoral gastropods and lowest in the intertidal bivalves, excluding the rare scaphopods. Scaphopods were never drilled in the intertidal and rarely in the sublittoral. Among bivalve families, intertidal DFs were highest in the Corbulidae and lowest in the Lucinidae. Corbulidae also had the highest DF of bivalve families in the sublittoral, and Veneridae the lowest. Among gastropod families, Naticidae had the highest intertidal DF, and Turritellidae the lowest. In the sublittoral, the highest gastropod DFs were seen in the potamidids and the lowest in the Neritidae (Fig. 3.11). ANOSIM analysis comparing intertidal and sublittoral samples resulted in an R-value of 0.1819 (Table 3.4), indicating that these groups are indistinguishable in terms of their family-level DFs.

No consistent increases or decreases in PE occurred from the intertidal to the sublittoral in the Central Paratethys, although a general decrease was observed at the class level (Fig. 3.11). PE was highest in intertidal bivalves and lowest in sublittoral gastropods. Scaphopods were drilled too rarely to permit comparisons. Among bivalve families, intertidal PEs were lowest for Lucinidae and Veneridae and highest for Corbulidae. In the sublittoral, however, Lucinids had the lowest PE, and Ostreidae the highest. Among gastropod families, intertidal PE was highest in the Neritidae and lowest in the Turritellidae ( $n = 5$ ) and the Potamididae. In the sublittoral, the gastropod family with the highest PE was Nassariidae, and the lowest was Turritellidae (Fig. 3.11).

*Shallow Sublittoral and Inner-Shelf Drilling Predation.*—Shallow sublittoral samples from Korneuburg SPK were compared to inner shelf samples from Neudorf bei Staatz, Grund, Immendorf, Gainfarn, St. Veit and Borský Mikuláš (Table 3.1). DF increased from the shallow sublittoral to the inner shelf for all samples pooled, the classes Bivalvia and Gastropoda, and all bivalve and gastropod families except Naticidae (Fig. 3.12). In contrast, Scaphopod DF decreased from the shallow sublittoral to the inner shelf, despite increased abundances. In the shallow sublittoral, DFs were lowest for the bivalve families Lucinidae and Corbulidae, and for the gastropod family Neritidae. Highest DFs were found in the bivalve family Ostreidae and the gastropod family Naticidae. On the inner shelf, DFs were lowest for the bivalve families Ostreidae and Veneridae, and the gastropod family Neritidae. Highest DFs were seen in the bivalve family Corbulidae and the gastropod family Potamididae (Fig. 3.12). ANOSIM analysis of intertidal versus shallow sublittoral versus inner shelf samples resulted in an R-value of 0.3155, indicating strongly overlapping but

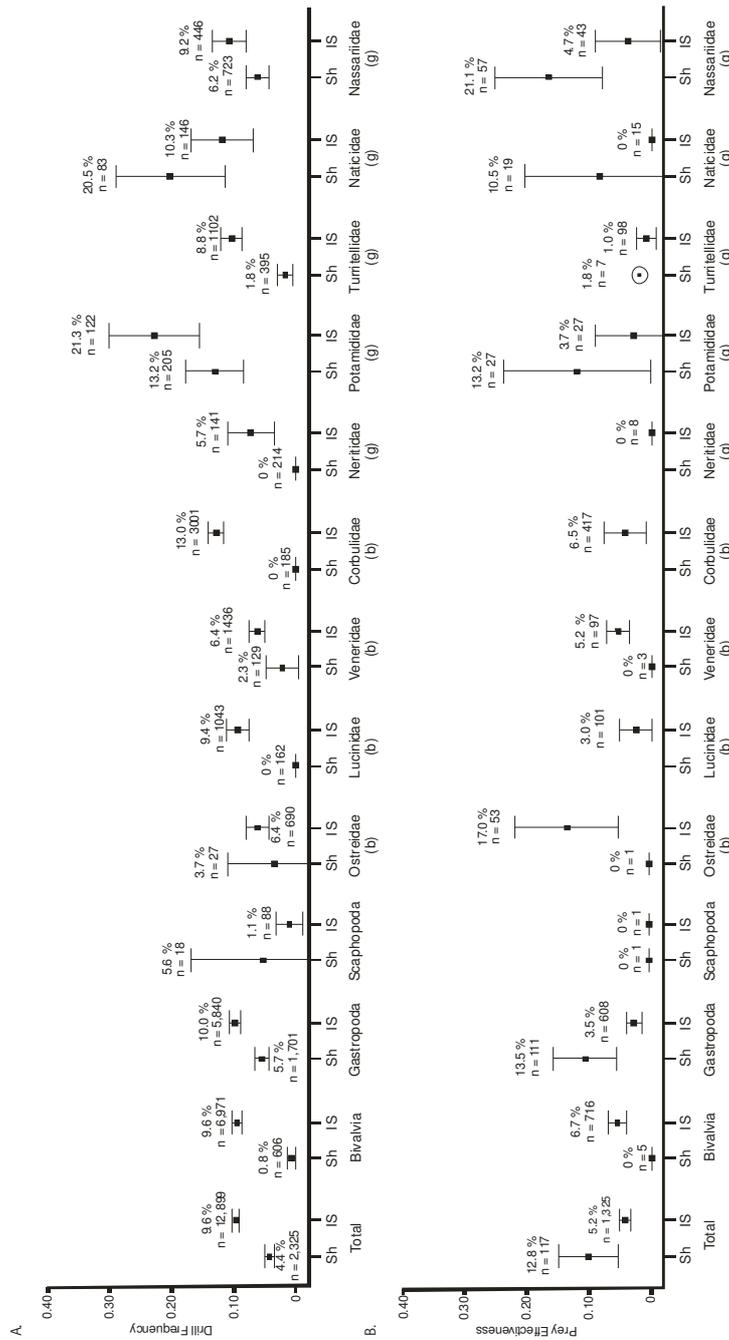


**Fig. 3.11.** Drilling predation for intertidal and sublittoral assemblages of the Central Paratethys for the total molluscan fauna, mollusc classes, and abundant families. A) Drilling frequencies. B) Prey effectiveness. I = intertidal; S = sublittoral; b = bivalve families; g = gastropod families. Black squares = means; error bars = 95 % confidence intervals.

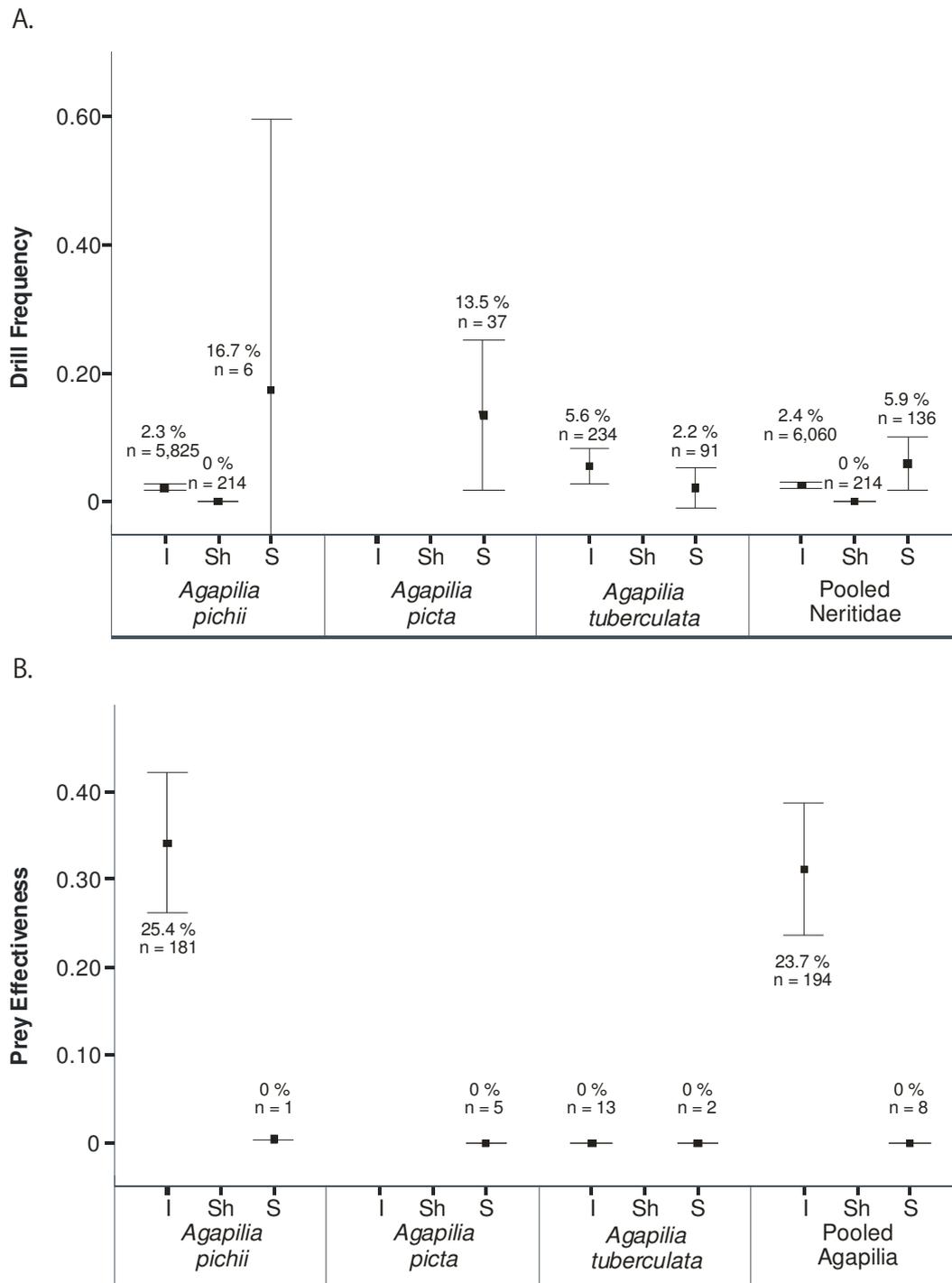
distinguishable groups (Table 3.4). Interestingly, the typically intertidal gastropod families Neritidae and Potamididae both had higher DFs in the deeper shelf deposits than the shallow sublittoral, despite higher abundances in intertidal environments. Figures 3.13-3.14 show Dfs for the common species of the Neritidae and Potamididae within intertidal, shallow sublittoral and inner shelf sand environments. These species were all but absent from inner shelf muds and were not included. The Neritidae consisted primarily of the species *Agapilia pachii*, *A. picta* and *A. tuberculata*. The most abundant of these was *A. pachii*, which existed almost exclusively in the intertidal, and was the only neritidid in the shallow sublittoral. In contrast, *A. picta* was restricted to inner shelf sands. *A. tuberculata* was more common in the intertidal but was present in inner shelf sands. The higher DF in the deeper sand environments for the family Neritidae is probably controlled by high DFs in the species *A. picta* (Fig. 3.13). Only *A. pachii* was attacked enough to evaluate PE at the species-level for the neritids.

The family Potimididae mostly consists of the species *Granulolabrium bicinctum*, *Potamides theodiscus* and *Terebralia bidendata*. Of these, only *G. bicinctum* occurs in large numbers in the shallow sublittoral or inner shelf sand environments (Fig. 3.14). *G. bicinctum* is drilled more frequently in inner shelf sands than in the intertidal, despite drastically reduced abundance in the deeper environment. Interestingly, *G. bicinctum* had a higher PE in the inner shelf sands than in the intertidal, though not significantly so. No other potamidid species were attacked frequently enough to evaluate species-level differences between environments.

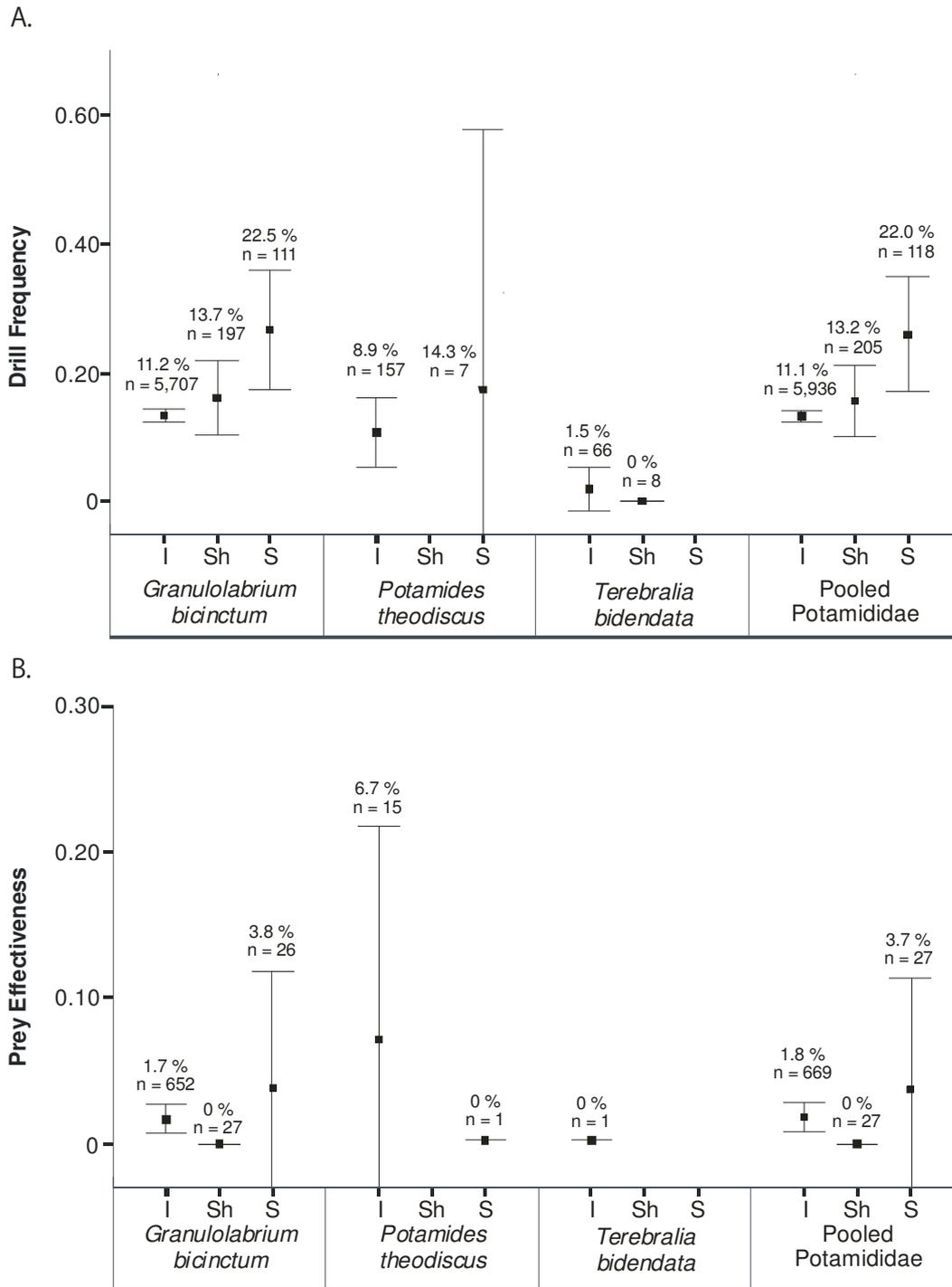
In general, PE decreased from the shallow sublittoral to the inner shelf for all taxa pooled and gastropods, but among bivalves higher values were typically



**Fig. 3.12.** Drilling predation for shallow sublittoral and inner shelf assemblages of the Central Paratethys for the total molluscan fauna, mollusc classes, and abundant families. A) Drilling frequencies. B) Prey effectiveness. Sh = shallow sublittoral; IS = inner shelf; b = bivalve families; g = gastropod families. Black squares = means; error bars = 95% confidence intervals.



**Fig. 3.13.** Species-level drilling predation for the family Neritidae from intertidal, shallow sublittoral and inner sand environments. A. Drill frequencies. B. Prey effectiveness. Black squares = means; error bars = 95 % confidence intervals.

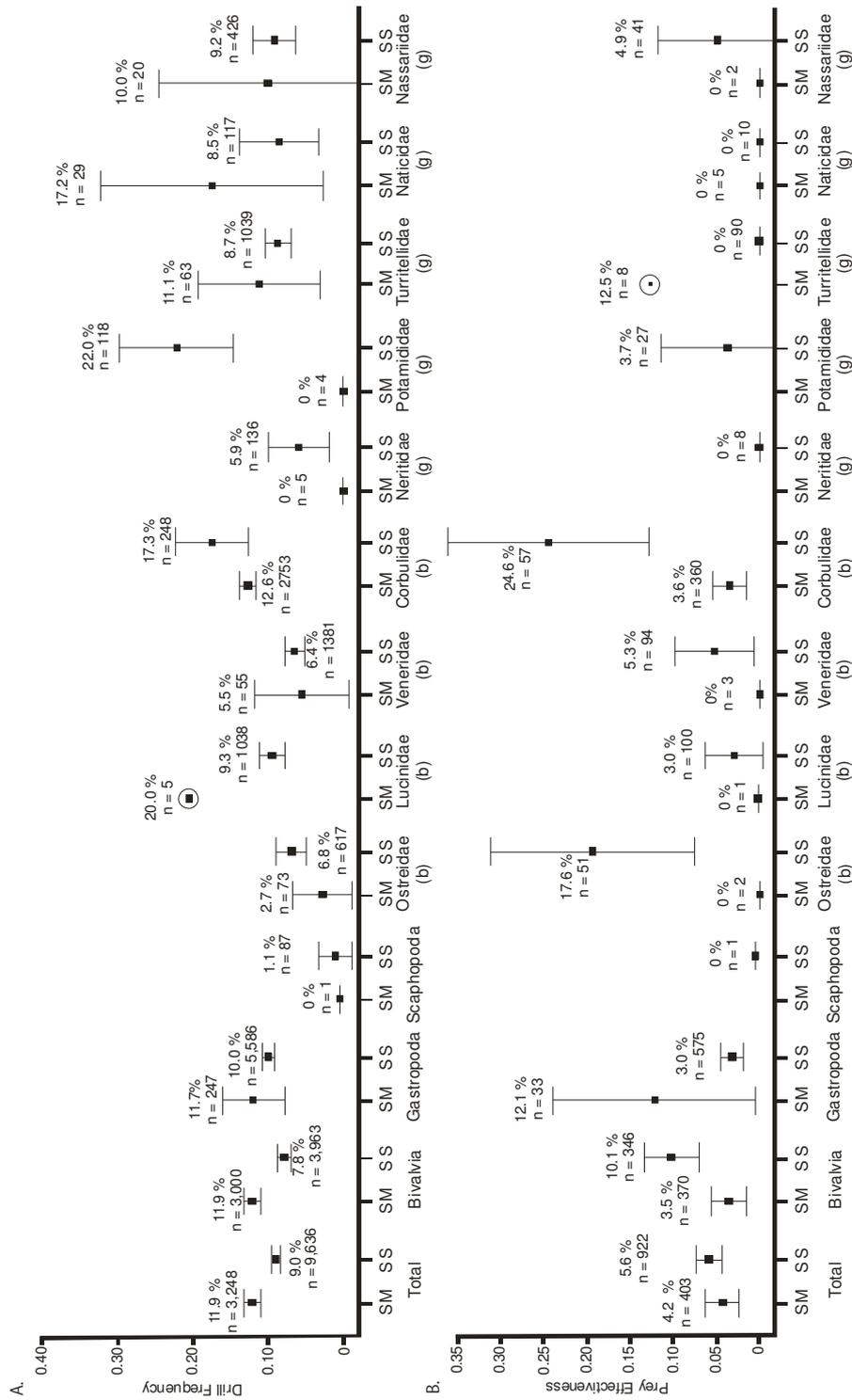


**Fig. 3.14.** Species-level drilling predation for the family Potamididae from intertidal, shallow sublittoral and inner sand environments. A. Drilling frequencies. B. Prey effectiveness. Black squares = means; error bars = 95 % confidence intervals.

observed on the inner shelf (Fig. 3.12). PE was always 0 % in the shallow sublittoral for bivalve families. The gastropod families Potamididae and Nassariidae had the highest PEs in the shallow sublittoral, and Turritellidae had the lowest. The lowest PEs on the inner shelf were found in the bivalve family Lucinidae, and the gastropod families Naticidae, Neritidae and Turritellidae. The highest values were observed in the Ostreidae and the Nassariidae (Fig. 3.12).

*Inner Shelf Mud and Sand Drilling Predation.*—Inner shelf mud samples from Neudorf bei Staatz and Gainfarn were compared to inner shelf sand samples from Grund, Immendorf, Gainfarn, St. Veit and Borský Mikuláš. In general, overall and class-level DFs were higher on inner shelf muds, although scaphopods were attacked more frequently on inner shelf sands. In contrast, common bivalve families had higher DFs in sands than muds (except the lucinids; Fig. 3.15). The lowest inner shelf mud DFs occurred in the Ostreidae, Neritidae and Potamididae, while the highest were seen in the Lucinidae, Corbulidae and Naticidae. The lowest DFs on inner shelf sands were found in the Veneridae and Neritidae, while the highest occurred in the Corbulidae and Potamididae. ANOSIM analysis of mud versus sand samples resulted in the highest R-value among all groups tested (R-value: 0.4014), which indicated strongly overlapping but distinguishable groups (Table 3.4).

Pooled assemblage and bivalve PEs were higher in sandy deposits, whereas gastropod PE was highest in muddy inner shelf deposits, and scaphopods had no difference (Fig. 3.15). The families with the highest PE in inner shelf muds were the Corbulidae and Turritellidae. All others had a PE of 0 %. The families with the highest PEs in inner shelf sands were the Ostreidae, Corbulidae,



**Fig. 3.15.** Drilling predation for inner shelf mud and sand assemblages of the Central Paratethys for the total molluscan fauna, molluscan classes, and abundant families. A) Drilling frequencies. B) Prey effectiveness. SM = inner shelf mud; SS = inner shelf sand; b = bivalve families; g = gastropod families. Black squares = means; error bars = 95 % confidence intervals.

Potamididae, and Nassariidae. The lowest PEs were seen in the Lucinidae, Neritidae, Turritellidae and Naticidae (Fig. 3.15).

*Intertidal vs Shallow Sublittoral vs Inner Shelf Mud vs Inner Shelf Sand.—*

Comparison of all environments using ANOSIM resulted in an R-value of 0.3855, indicating that groups are strongly overlapping but distinguishable (Table 3.4). Figure 3.10b shows an nMDS ordination of family-level DF data with outliers removed. On the plot, an environmentally-related depth gradient can be seen with intertidal and shallow sublittoral samples plotting to the left and the deeper shelf sand and mud samples plotting to the right. Strong overlap between environments is illustrated with 95 % ellipses (Fig. 3.10).

### **3.5.7. Drilling predation in other Miocene Basins**

The DFs reported here are lower than, and significantly different from, those reported for the greater Paratethys Province, as well as for other Miocene basins (Table 3.5). In particular, assemblage-level drilling frequencies from this sample are significantly different from those of the Boreal, Paratethys and South-eastern North Atlantic provinces in Europe, and from those of the North American Atlantic and Gulf Coastal Plain. Assemblage-level DFs for bivalves are significantly lower in the Central Paratethys than for all of the above provinces with the exception of the South-eastern North Atlantic. All differences are significant for assemblage-level gastropod data. Additionally, gastropods from Panama also had statistically different DFs than those reported here (Table 3.5).

**Table 3.5.** Statistical comparison of Central Paratethys drill frequencies published data from other Miocene basins using chi-squared test

Provincance	drilled	undrilled	DF	Chi-sq.	p-value	Source
<b>Total</b>						
Central Paratethys	2324	28636	7.5%	.	.	This Study
Boreal	386	1336	22.4%	476.84	<<0,0001	Hoffmeister & Kowalewski, 2001
Paratethys	156	868	15.2%	82.761	<<0,0001	Hoffmeister & Kowalewski, 2002
Southeastern North Atlantic	27	88	23.5%	41.795	<<0,0001	Hoffmeister & Kowalewski, 2003
US Atlantic & Gulf Coast	11483	21945	34.4%	6876.3	<<0,0001	Kelley & Hansen, 2006
<b>Bivalves</b>						
Central Paratethys	726	7747	8.6%	.	.	This Study
Boreal	102	461	18.1%	57.83	<<0,0001	Hoffmeister & Kowalewski, 2001
Paratethys	72	353	16.9%	34.751	<<0,0001	Hoffmeister & Kowalewski, 2001
Southeastern North Atlantic	5	43	10.4%	0.2079	0.90127	Hoffmeister & Kowalewski, 2001
US Atlantic & Gulf Coasts	7435	14372	34.1%	2019.5	<<0,0001	Kelley & Hansen, 2006
<b>Gastropods</b>						
Central Paratethys	1596	20698	7.2%	.	.	This Study
Boreal	284	875	24.5%	449.52	<<0,0001	Hoffmeister & Kowalewski, 2001
Paratethys	84	515	14.0%	40.423	<<0,0001	Hoffmeister & Kowalewski, 2001
Southeastern North Atlantic	22	45	32.8%	65.613	<<0,0001	Hoffmeister & Kowalewski, 2001
US Atlantic & Gulf Coasts	4048	7573	34.8%	4217.5	<<0,0001	Kelley & Hansen, 2006
Panama	789	3573	18.1%	534.89	<<0,0001	Fortunato, 2007

DF = drill frequency, Chi-sq. = chi-square.

### 3.6. Discussion

Assemblage level analyses of drilling predation have been criticized because they often mix habitats, and generally do not account for variations in the abundances of prey taxa with specific morphologies, adaptive syndromes, and preservation potentials (Leighton, 2002; Vermeij, 2002). Kowalewski (2002) argued, however, that most lower taxa are restricted to relatively short geological time spans with varying abundances. Therefore, they are generally of limited use for analyses spanning large amounts of time. As such assemblage-level analyses have the advantage that they can provide an important baseline that can be compared to individual lineages. He also noted assemblage-level predation data can be computed for any fossil assemblage, meaning that such data, though of limited biological meaning, can be used for analytical comparisons throughout the fossil record. Furthermore, assemblage level predation data offers a proxy for overall predation pressure across ecosystems. Kelley and Hansen (2006) report

good concordance between assemblage-level and lower taxon drill frequencies of molluscs from the North American Gulf Coastal Plain from the Cretaceous to the Pleistocene. In contrast, PE of lower taxa did not correspond well to assemblage level values. Further work is necessary to determine if Kelley and Hansen's (2006) results also apply to other datasets. This research is part of a broader study that aims to examine molluscan diversity and drilling predation from Eocene to Recent marine deposits in Europe.

Gastropods in the studied samples generally had slightly higher DFs than bivalves. Our values are similar to those of previous researchers on molluscan drilling predation in the Central Paratethys, and contrast with those from the Miocene Boreal in Europe (Hoffmeister and Kowalewski, 2001) and the North American Gulf Coastal Plain (Kelley and Hansen, 2006). Modern DFs from the Northern Adriatic are also higher on bivalves than gastropods (Sawyer and Zuschin, 2010). Drilling predation on scaphopods has rarely been documented, but our values were similarly low to those of Cretaceous to Holocene deposits from the southern Louisiana Gulf Coast, USA (Yochelson et al., 1983). Bivalves and gastropods were also drilled less frequently in the Central Paratethys than in the US Gulf Coastal Plain at the family level: lucinids (7.1 %), corbulids (12.2 %), naticids (12.9 %), and turritellids (6.2 %) from the Paratethys each had lower DFs than their Gulf Coast counterparts (ranges: lucinids 40 – 66 %, corbulids 14.6 – 43 %, naticids 18 – 32 %, turritellids 23 – 34 %; Kelley and Hansen, 2006).

PEs of gastropods and bivalves in the US Gulf Coastal Plain ranged from 0 – 16.7 % and 1.4 – 9 % in Miocene samples (Kelley et al., 2001; Kelley and Hansen, 2006). Our Central Paratethys values were in the same range. At the family level, lucinids, corbulids and turritellids from the US Gulf Coastal Plain

each had higher PEs (ranges: lucinids 0 – 10 %, corbulids 8 – 28 %, turritellids 1 – 9 %; Kelley and Hansen, 2006) than their Paratethyan counterparts (2.8 %, 8.1 %, 0.9 %, respectively). In contrast, Paratethyan naticids had a higher PE (8.8 %) than those from the U.S. Gulf Coast (range 0 – 3 %). Abundance of incomplete drill holes in Hoffmeister and Kowalewski's (2001) Paratethys samples was too low allow comparisons with the PEs reported here.

Most assemblage-level drilling predation studies have focused on changes in DF through time as a test of Vermeij's (1987) escalation hypothesis; however, contemporaneous variation in drilling intensities through space may confound the interpretation of temporal patterns (Kelley and Hansen, 2007). Such patchiness in local species richness and predation pressure has been well established (e.g., MacArthur, 1965; Hansen and Kelley, 1995, 2007; Hoffmeister and Kowalewski, 2001; Zuschin et al., 2004a, 2006). In contrast, researchers have not consistently evaluated paleoenvironments when studying temporal predation trends. Understanding such trends requires examining spatial variation within and between environments at single horizons at single localities. Vermeij (1980) reported molluscan DFs from 10 localities in Guam to range from 7.4 – 24.6 %. Baumiller and Bitner (2004) showed that brachiopod DFs from four Central-European Miocene species ranged from 2 – 39.9 %. Simões et al. (2007) reported DFs on bivalves from brachiopod-bivalve mixed assemblages from similar sublittoral substrates on the Southern Brazilian shelf to vary as much as 10 % between habitats. In this study, DF varied drastically within similar environments at single localities. The most extreme case was the locality Immendorf where mean drill frequency was 10.9 % +/- 12.9 % with samples ranging from 0 - 57.5 % (Table 3.3). The results of ANOSIM and nMDS multivariate analyses,

however, suggest that differences between environments are relatively small in our dataset.

With few exceptions, DF is lower and PE is higher in the Karpatian (i.e., Burdigalian) than in the Badenian (i.e., Langhian and Lower Serravalian) at both the class and family levels. It is possible that drilling predators are becoming more efficient in attacking their prey over this time span. Alternatively, the more normal marine conditions typical of the Badenian may be more conducive to drilling predators than the more near-shore, estuarine environments of the Karpatian. Indeed, the same patterns in DF and PE observed between Karpatian and Badenian are also seen between the intertidal and sublittoral overall, for classes and for most families. This suggests that changes in environments at the Lower/Middle Miocene Boundary probably account for the majority of temporal variation in drilling predation in the Central Paratethys. Furthermore, the generally higher variation in DF in Karpatian localities could also result from the potential for greater environmental variability in the intertidal, which was better exposed (and therefore sampled more frequently) in the Karpatian. Additionally, the larger number of Karpatian than Badenian samples could also presumably increase the likelihood of variability in the former.

Predation is strongly controlled by habitat (Vermeij et al., 1981; Hansen and Kelley, 1995; Cadee et al., 1997); therefore, differences in predation frequencies are expected across different paleoenvironments. Intertidal and inner shelf mud samples were collected from both Karpatian and Badenian localities. DFs were greater on inner shelf mud than the intertidal in both the Karpatian and Badenian. The overall variation from inner shelf muds at Neudorf bei Staatz was a little greater than the equivalent Badenian facies at Gainfarn, but the drill

frequencies were approximately equal between the two. Hoffmeister and Kowalewski (2001) report significant variations in drilling predation on molluscs both locally and regionally among facies in the Miocene Boreal and Paratethys provinces. Such variation could either be exaggerated or masked when samples were pooled into coarser analytical groupings, but regardless of the taxonomic resolution of the analysis, inter-regional and facies variations between samples were significant and could exceed 20 % (up to three-fold differences).

Korneuburg SPK had the greatest variation in sample DFs of Karpatian deposits, but also had the lowest pooled DFs compared to all other localities sampled. Based on regional paleoenvironmental reconstructions (Harzhauser et al., 2002), Korneuburg SPK was located within an estuarine environment with large fresh-water input in the late Early Miocene. Lowered and fluctuating salinities have been demonstrated to negatively affect predation by reducing predator activity and feeding rates, and increasing their mortality (Manzi, 1970; Zachary and Haven, 1973; Garton and Stickle, 1980) and low-salinity layers in south-western New Zealand have been hypothesized to create a predation refuge for barnacles and mussels (Whitman and Grange, 1998).

Interesting components of the sublittoral samples were the Neritidae and Potamididae. These gastropods, while much more abundant in intertidal than in sublittoral deposits, had greater DFs on inner shelf sands than the intertidal. Potamidids had particularly high DF on the inner shelf sands, approaching twice that of some of the more typical shelf taxa (e.g., Turritellidae and Corbulidae), and double the intertidal value. A similar pattern is observed for all potamidid species, except *Terebralia bidentata*, which only occurs in the intertidal (Fig. 3.14). *Granulolabrium bicinctum* is the most abundant potamidid in both the

intertidal and sublittoral, and based on its abundance probably contributes most to the family-level pattern. The Neritidae also show a family-level increase in DF from the intertidal to inner shelf sands, though species level comparisons reveal that different species in these environments may control the family-level trend (Fig. 3.13a). For example, *Agapilia tuberculata* is more common and has a higher DF in the intertidal than in inner shelf sands. *A. picta*, which is absent in the intertidal, probably contributes most to the higher DFs on inner shelf sands than in the intertidal. It is possible that these taxa were carried into deeper environments during storm-events (e.g., Zuschin et al., 2004b, 2005). Opportunistic drillers may then have attacked the foreign, and likely weakened, potamitids.

Limited evidence exists for a depth-gradient in drilling predation (Sander and Lalli, 1982; Kelley and Hansen, 1995; Hoffmeister and Kowalewski, 2001; Tomašových and Zuschin, 2009). In this study, the shallow sublittoral environment only occurred at the locality Korneuburg SPK. DFs from the intertidal were lower than in the shallow sublittoral at Korneuburg SPK, but shallow sublittoral DFs were lower than all intertidal samples pooled across the entire region. In fact, pooled intertidal DFs were lower in all classes and families, except the Naticidae, than their inner shelf contemporaries. These results reflect those of the modern Northern Adriatic Sea, where DFs on a tidal flat near the Isonzo River are drastically lower than on the inner shelf (Sawyer and Zuschin, 2010).

The regional DFs reported here are rather low compared to other contemporaneous basins. Miocene DFs from the Boreal province are two- to three times as high as those of the Central Paratethy (22.4 % for all molluscs, 18.1 % for bivalves, 24.5 % for gastropods; Hoffmeister and Kowalewski, 2001).

Likewise, a single sample from Serravallian (early middle Miocene, ~ 14 ma) deposits from the South-eastern North Atlantic had a drill frequency that was higher for the total assemblage (23.6 %) and for gastropods (32.8 %; Hoffmeister and Kowalewski, 2001). Kelley and Hansen (2006) report an abrupt increase in molluscan DFs (27 % for all molluscs, 35 % for bivalves, 20 % for gastropods) from the North American Gulf Coastal Plain during the Miocene. Finally, gastropods from the late Middle Miocene Gatun Fm., Panama had DFs of 18 % (Table 3.5; see also Fortunato, 2007). Our results corroborate those of earlier researchers who also reported regionally low Paratethyan drilling intensities; however, the overall molluscan DF reported here (7.5 % for all molluscs, 8.6 % for bivalves, 7.1 % for gastropods) is roughly half that previously reported (15.8 % for all molluscs, 16.9 % for bivalves, 14.0 % for gastropods; Hoffmeister and Kowalewski, 2001). Low DFs are also seen in the Wimer Fm in Del Norte County California (Upper Miocene), which is interpreted to be a protected coastal mudflat environment that is intertidal or very shallow sublittoral with potentially brackish water conditions and was situated in a temperate climatic zone (DFs were under 6 %; Watkins, 1974).

Several biotic and abiotic factors could influence the low levels of drilling predation observed in the Central Paratethys. Biotic causes may include differences in predator behaviour, faunal composition of predatory and prey taxa (discussed above), relative abundance of drillers, or some combination of the above. Hoffmeister and Kowalewski (2001) found remarkable similarities between size frequency distributions of drill holes and other behaviour patterns based on site selectivity and prey- versus drill hole size-correlations and determined that variation in predatory behaviour between the Boreal and

Paratethys provinces were less likely to cause different predation intensities than other potential factors.

Naticid and muricid gastropods are the most likely drillers in our samples, and make up 1.3 % and 0.4 % of the total molluscan fauna. Percent abundance of naticids calculated from Kelley and Hansen's (2006) data from the US East and Gulf Coastal Plains is 4.2 % of the total molluscan fauna; more than three times that found in the Central Paratethys. Their data did not include drill holes attributed to muricids and no abundance data for that group was included. Presumably the overall drill frequencies and predator abundances would be even higher in the North American data had both groups of drillers been reported. The relative abundance of predatory drillers remains lower in our samples than those of the previous study, even when muricids are included (1.6 % of all molluscs).

Potential abiotic factors influencing drilling predation include water depth, substrate, and salinity. Although limited evidence for a depth-related trend in drilling predation was found in this study, others have found conflicting patterns both within and between basins (e.g., Sander and Lalli, 1982; Hansen and Kelley, 1995; Hoffmeister and Kowalewski, 2001). Hoffmeister and Kowalewski (2001) concluded based on inconsistencies between the Boreal and Paratethys that substrate and depth do not necessarily control predation rates, and that differences may exist in the primary influences of predation intensity from region to region.

Fluctuating salinities in the Central Paratethys during the Miocene (Steininger and Rögl, 1984; Rögl, 1998) may have negatively affected drilling predation rates either by decreasing general activity of predators, or increasing their mortality rates (Manzi, 1970; Zachary and Haven, 1973; Garton and Stickle, 1980). The Boreal and North American Miocene drilling intensities reported by

Hoffmeister and Kowalewski (2001) and Kelley and Hansen (2006) were conducted along passive margins with fully marine conditions that probably experienced more consistent salinities than their Paratethyan counterparts. Changes in salinity have also been hypothesized as an influence on low predation pressure in the Paratethys by Hoffmeister & Kowalewski (2001), and in the modern Northern Adriatic Sea (Sawyer and Zuschin, 2010).

### **3.7. Conclusions**

Variations in drilling intensities were observed across time, environments and localities in the Central Paratethys. This variation occurred at various taxonomic levels, but in general, lower taxa exhibited similar patterns to those of higher-level taxonomic data. Differences in drilling predation within some localities were greater than between localities, and spatial variation in the Central Paratethys could exceed assemblage-level temporal trends observed in other basins. These results emphasize the importance of rigorous sampling protocols in studies of predation in the fossil record. Temporal patterns in drilling predation likely reflect environmental shifts that occurred due the major marine transgression at the Lower/Middle Miocene Boundary as the faunal compositions of predators and prey, climatic and environmental conditions changed. Finally, our results support the hypothesis that predation intensities in the Central Paratethys are markedly low compared to values from other contemporary basins. Differences in predator abundance, faunal composition of sampled basins, salinity or a combination of these factors likely contribute to the low predation intensities in the Central Paratethys.

### 3.8. References

- Alexander, R.R., 1986. Resistance to repair of shell breakage induced by durophages in Late Ordovician brachiopods. *Journal of Paleontology* 60, 273-285.
- Baumiller, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123, 343-351.
- Baumiller, T.K., and Bitner, M.A., 2004. A case of intense predatory drilling of brachiopods from the Middle Miocene of southeastern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 214, 85-95.
- Bray, J.R., and Curtis, J.T., 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs* 27, 325-349.
- Cadee, G.C., Walker, S.E., and Flessa, K.W., 1997. Gastropod shell repair in the intertidal of Bahia la Choya (N. Gulf of California). *Palaeogeography, Palaeoclimatology, Palaeoecology* 136, 67-78.
- Carriker, M.R., and Yochelson, E.L., 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *Contributions to Paleontology, Geological Survey Professional Paper 593(B)*, B1-B26.
- Clarke, K.R., and Gorley, R.N., 2001. *Primer v5. User Manual/Tutorial: Primer-E*, Plymouth, 91 p.
- Clarke, K.R., and Warwick, R.M., 1994. Similarity-based testing for community pattern—the 2-way layout with no replication. *Marine Biology* 118, p. 167-176.

- Daxner-Höck, G., 2001. Early and late Miocene correlations (Central Paratethys):  
Beiträge zur Paläontologie 23, 367-408, Vienna.
- Fortunato, H., 2007. Naticid gastropod predation in the Gatun Formation (late  
Middle Miocene), Panama—preliminary assessment. Paläontologische  
Zeitschrift 81, 356-364.
- Garton, D., and Stickle, W.B., 1980. Effects of salinity and temperature on the  
predation rate of *Thais haemastoma* on *Crassostrea virginica* spat.  
Biological Bulletin 158, 49-57.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001. PAST—Paleontological  
Statistics Software Package for education and data analysis.  
Palaeontologia Electronica vol. 4, issue 1, 178kb, [http://palaeo-  
electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm). Checked March 2007.
- Hansen, T.A., and Kelley, P.H., 1995. Spatial variation of naticid gastropod  
predation in the Eocene of North America. Palaios 10, 268-278.
- Haq, B.U., Hardenbol, J., and Vail, P.R., 1988. Mesozoic and Cenozoic  
chronostratigraphy and cycles of sea level changes, *In*: Wilgus, C.K.,  
Hastings, B.S., Kendall, C.G., St. C., Posamentier, H.W., Ross, C.A.,  
and Van Wagoner, J.C., (eds.), Sea-level changes—an integrated  
approach. SEMP (Society for Sedimentary Geology) Special  
Publications 42, Tulsa, p. 71-108.
- Hardenbol, J., Thierry, J., Farley, M.B., Jacquin, T., Craciansky, P.C., and Vail,  
P.R., 1998. Mesozoic and Cenozoic sequence chronostratigraphic  
framework of European basins, *In*: Graciansky, C.-P., Hardenbol, J.,  
Jacquin, T., and Vail, P.R., (eds.), Mesozoic and Cenozoic Sequence

- Stratigraphy of European Basins. SEPM (Society for Sedimentary Geology) Special Publications 60, Tulsa, p. 3-13.
- Harzhauser, M., Böhme, M., Mandic, O., and Hofman Ch.-Ch., 2002. The Karpatian (Late Burdigalian) of the Korneuburg Basin—A palaeoecological and biostratigraphical synthesis. *Beiträge zur Paläontologie* 27, 441-456, Vienna.
- Harzhauser, M., Mandic, O., and Zuschin, M., 2003. Changes in Paratethyan marine palaeoclimate. *Acta Geologica Polonica* 53, 323-339.
- Harzhauser, M., and Piller, W.E., 2007. Benchmark data of a changing sea—palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 235, 8-31.
- Hoffmeister, A.P., and Kowalewski, M., 2001. Spatial and environmental variation in the fossil record of drilling predation: a case study from the Miocene of central Europe. *Palaios* 16, 566-579.
- Kabat, A., 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologica* 32, 155-193.
- Kaplan, P., and Baumiller, T.K., 2000. Taphonomic inferences on boring habit in the Richmondian *Onniella meeki* Epibole. *Palaios* 15, 499-510.
- Kelley, P.H., 1989. Evolutionary trend within bivalve prey of Chesapeake Group naticid gastropods. *Historical Biology* 2, 139-156.
- Kelley, P.H., 1992. Evolutionary patterns of naticid gastropods of the Chesapeake Group—An example of coevolution. *Journal of Paleontology* 65, 794-800.

- Kelley, P.H., and Hansen, T.A., 1993. Evolution of the naticid gastropod predator-prey system—an evaluation of the hypothesis of escalation. *Palaios* 8, 358-375.
- Kelley, P.H., and Hansen, T.A., 1995. Spatial variation of naticid gastropod predation in the Eocene of North America. *Palaios* 10, 268-278.
- Kelley, P.H., and Hansen, T.A., 1996. Recovery of the naticid gastropod predator-prey system from the Cretaceous-Tertiary and Eocene-Oligocene extinctions. *Geological Society Special Publication* 102, 373-386.
- Kelley, P.H., Hansen, T.A., Graham, S.E., and Huntoon, A.G., 2001. Temporal patterns in the efficiency of naticid gastropod predators during the Cretaceous and Cenozoic of the United States Coastal Plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166, 165-176.
- Kelley, P.H., and Hansen, T.A., 2003. The fossil record of drilling predation on bivalves and gastropods, *In*: Kelley, P.H., Kowalewski, M., and Hansen, T.A. (eds.), *Predator-Prey Interactions in the Fossil Record*. Kluwer Academic/Plenum Press, New York, p. 113-139.
- Kelley, P.H., and Hansen, T.A., 2006. Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. coastal plain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 236, 302-320.
- Kelley, P.H., and Hansen, T.A., 2007. Latitudinal patterns in naticid gastropod predation along the East coast of the United States—a modern baseline for interpreting temporal patterns in the fossil record. *SEPM (Society for Sedimentary Geology) Special Publication* 88, 287-299, Tulsa.

- Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods, *In*: Kowalewski, M., and Kelley, P.H., (eds.), *The Fossil Record of Predation*. Paleontological Society Papers vol. 8, Yale University, New Haven, p. 3-42.
- Leighton, L.R., 2001. Evaluating the accuracy of drilling frequency as an estimate of prey preference and predation intensity. *PaleoBios* 21, supplement to number 2, p. 83.
- Leighton, L.R., 2002. Inferring predation intensity from the marine fossil record. *Paleobiology* 28, 328-342.
- MacArthur, R.H., 1965. Patterns of species diversity. *Biological Reviews* 40, 510-533.
- Manzi, J.J., 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Biological Bulletin* 138, 35-46.
- Olszewski, T., and Patzkowsky, M.E., 2001. Measuring recurrence of marine biotic gradients—A case study from the Pennsylvanian-Permian mid-continent. *Palaios* 16, 444-460.
- Rögl, F., 1996. Stratigraphic correlation of the Paratethys Oligocene and Miocene. *Mitteilungen der Gesellschaft Geologie Bergbaustudenten in Österreich* 41, 65-73.
- Rögl, F., 1998. Palaeogeographic considerations for the Mediterranean and Paratethys Seaways (Oligocene to Miocene). *Annalen des Naturhistorischen Museums in Wien* 99A, 279-310.

- Rögl, F., 1999. Mediterranean and Paratethys—Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geologica Carpathica* 50, 339-349.
- Rögl, F., Spezzaferri, S., and Coric, S., 2002. Micropaleontology and biostratigraphy of the Karpatian-Badenian transition (Early-Middle Miocene boundary) in Austria (Central Paratethys). *Courier Forschungsinstitut Senckenberg* 237, 47-67.
- Rögl, F., and Steininger, F.F., 1984. Neogene Paratethys, Mediterranean and Indo-Pacific seaways—Implications for the paleobiogeography of marine and terrestrial biotas, *In: Brenchley, P.J., (ed.), Fossils and Climate.* Wiley, New York, p. 171-200.
- Rohr, D.M., 1991. Borings in the shell of an Ordovician (Whiterockian) gastropod. *Journal of Paleontology* 65, 687-688.
- Sander, F., and Lalli, C.M., 1982. A comparative study of the mollusk communities on the shelf-slope margin of Barbados, West Indies. *The Veliger* 24, 309-318.
- Simões, M.G., Rodrigues, S.C., and Kowalewski, M., 2007. Comparative analysis of drilling frequencies in recent brachiopod-mollusc associations from the Southern Brazilian Shelf. *Palaios* 22, 143-154.
- SPSS, 1999, *SPSS base 10 Applications Guide.* Prentice-Hall, Chicago, 426 p.
- Sawyer, J.A., and Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea): Palaeogeography, Palaeoclimatology, Palaeoecology 285, 152-173. DOI: 10.1016/j.palaeo.2009.11.007.

- Steininger, F.F., Rögl, F., and Martini, E., 1976. Current Oligocene/Miocene biostratigraphic concept of the Central Paratethys (Middle Europe). *Newsletters on Stratigraphy* 4, 174-202.
- Steininger, F.F., and Rögl, F., 1984. Paleogeography and palinspastic reconstruction of the Neogene of the Mediterranean and Paratethys, *In*: Dixon, J.E., and Robertson, A.H.F., (eds.), *The geological evolution of the eastern Mediterranean*. Geological Society of London Special Publications, No. 17, p. 659-668.
- Studencka, B., Gontsharova, I.A., and Popov, S.V., 1998. The bivalve faunas as a basis for reconstruction of the Middle Miocene history of the Paratethys. *Acta Geologica Polonica* 48, 285-342.
- Švagrovský, J., 1981. Lithofazielle Entwicklung und Molluskenfauna des oberen Badeniens (Miozän M4d) in dem Gebiet Bratislava Devinska Nová Ves. *Západné Karpaty, Seria Paleontológia* 7, 1-203.
- Tomašových, A., and Zuschin, M., 2009. Variation in brachiopod preservation along a carbonate shelf-basin transect (Red Sea and Gulf of Aden): environmental sensitivity of taphofacies: *Palaios* 24, 697-716. DOI: 10.2110/palo.2009.p09-018r.
- Vermeij, G.J., 1980. Drilling predation in a population of the edible bivalve *Anadara granosa* (Arcidae). *The Nautilus* 94, 123-125.
- Vermeij, G.J., 1982. Gastropod shell form, repair, and breakage in relation to predation by the crab *Calappa*. *Malacologica* 23, 329-334.
- Vermeij, G.J., 1987. *Evolution and Escalation—an ecological history of life*. Princeton University Press, Princeton, New Jersey, 527 p.

- Vermeij, G.H., 2002. Evolution in the consumer age—predators in the history of life, *In*: Kowalewski, M., and Kelley, P.H., (eds.), *The Fossil Record of Predation: Paleontological Special Papers*, v. 8, Yale University, New Haven, p. 375-394.
- Vermeij, G.J., Schindel, D.E., and Zisper, E., 1981. Predation through geological time: evidence from gastropod shell repair. *Science* 214, 1024-1026.
- Vermeij, G.J., and Dudley, E.C., 1982. Shell repair and drilling in some gastropods from the Ripley Formation (Upper Cretaceous) of the southeastern U.S.A. *Cretaceous Research* 3, 397-403.
- Watkins, R., 1974. Molluscan Paleobiology of the Miocene Wimer Formation, Del Norte County, California. *Journal of Paleontology* 48, 1264-1282.
- Whitman, J.D., and Grange, K.R., 1998. Links between rain, salinity, and predation in a rocky subtidal community. *Ecology* 79, 2429-2447.
- Yochelson, E.L., Dockery, D., and Wolf, H., 1983. Predation of sub-Holocene scaphopod mollusks from Southern Louisiana. U.S. Geological Survey Professional Paper, no. 1282, 13 p.
- Zachary, A., and Haven, D.S., 1973. Survival and activity of the oyster drill *Urosalpinx cinerea* under conditions of fluctuating salinity. *Marine Biology* 22, 45-52.
- Zuschin, M., Harzhauser, M., and Mandic, O., 2004a. Spatial variability within a single parautochthonous Paratethyan tidal flat deposit (Karpatian, Lower Miocene - Kleinebersdorf, Lower Austria). *Courier Forschungsinstitut Senckenberg* 246, 153-168.
- Zuschin, M., Harzhauser, M., and Mandic, O., 2004b. Taphonomy and paleoecology of the lower Badenian (Middle Miocene) molluscan

- assemblages at Grund (Lower Austria). *Geologica Carpathica* 55, 117-128.
- Zuschin, M., Harzhauser, M., and Sauermoser, K., 2006. Patchiness of local species richness and its implication for large-scale diversity patterns: an example from the middle Miocene of the Paratethys. *Lethaia* 39, 66-78.
- Zuschin, M., Harzhauser, M., and Mandic, O., 2007. The stratigraphic and sedimentologic framework of fine-scale faunal replacements in the Middle Miocene of the Vienna Basin (Austria). *Palaios* 22, 285-295.
- Zuschin, M., Harzhauser, M., and Mandic, O., 2009. Palaeocommunity dynamics across the lower to middle Miocene boundary of the Central Paratethys. 9th North American Paleontological Convention—Cincinnati Museum Center Scientific Contributions 3, 363-364.
- Zuschin, M., Mandic, O., Harzhauser, M., and Pervesler, P., 2001. Fossil evidence for chemoautotrophic bacterial symbiosis in the thyasirid bivalve *Thyasira michelottii* from the Middle Miocene (Badenium) of Austria. *Historical Biology* 15, 223-234.
- Zuschin, M., Harzhauser, M., and Mandic, O., 2005. Influence of size-sorting on diversity estimates from tempestitic shell beds in the middle Miocene of Austria. *Palaios* 20, 142-158.



**CHAPTER 4:**  
**SIZE FILTERING FOSSILS: EFFECTS OF SIEVE-SIZE ON DIVERSITY**  
**AND DRILLING INTENSITY ESTIMATES IN EOCENE AND MIOCENE**  
**MOLLUSCS OF CENTRAL EUROPE**

**4.1. Abstract**

Several workers have noted the sensitivity of ecological patterns to mesh size, but little is known of such effects on fossil data. This study builds upon earlier research to examine sieve-size effects on diversity and drilling predation on molluscs from the Paris (PB) and Korneuburg (KB) Basins using 1 mm, 2 mm and 4 mm sieves. Twelve bulk samples from four localities in the PB, and 118 bulk samples from a transect through the KB, were collected and processed using stacked 1 mm, 2 mm and 4 mm sieves. Molluscs were picked from sieved fractions, sorted to species level, counted, and examined for predatory drill holes. Analyses were performed on size fractions and sieve treatments in which larger fractions were added to smaller fractions to mimic the effects of sieving. Rarefaction curves, species richness, and the Shannon-Wiener and Simpson's indices were used to characterize diversity. The PB had a much higher diversity than the KB regardless of the size fraction or sieve treatment used. Loss of small individuals in coarser size fractions resulted in significantly underestimated species richness in both basins. The Shannon-Wiener index is statistically similar at all size fractions and sieve treatments in the PB, but discrepancies appear in the KB. The Simpson's index is stable across all fractions/sieve treatments in both

basins. Drill frequencies (DF) are higher in the PB than in the KB for all fractions/sieve treatments at the assemblage and class levels, though disagreements occur at the family level. In the PB, no significant differences in DFs were observed between sieve sizes; however, Miocene DFs were significantly different between all size categories. In both the PB and KB, bivalve DFs were not statistically different between sieve sizes, while gastropods had significantly higher values at 4 mm. At the family level, no differences were seen between sieve treatments within, but sometimes occurred between, basins. Based on these and previous results, we suggest future researchers conduct pilot studies to determine the most efficient sieve size to adequately sample species in their samples. Whenever possible, fine mesh sizes should be initially used, and data further sieved into size fractions to ease future comparisons.

## **4.2. Introduction**

Body size is among the most fundamental properties of life (LaBarbara 1986, Jablonski 1996) and as such is correlated with many types of ecological data (Kowalewski and Hoffmeister, 2003). Paleoecological data may be further linked to body size because fossil size affects taphonomic and hydrodynamic properties as well (Martin, 1999). Many palaeontological studies rely on bulk samples of unconsolidated sediment that is processed with sieves, resulting in datasets that are biased towards certain size classes. Despite many studies that have sought to evaluate the importance of sieve size in order to find the most efficient, yet robust, methods for sample collection in the ecological (e.g. Battle et al., 2007; Rodrigues et al., 2007, Lewis and Stoner, 1981) and archaeological (e.g.

Vale and Gargett, 2002; Gobalet, 2005; Zohar and Belmaker, 2005) literature, relatively few studies have examined the effects of utilizing various filtering methods to collect paleontological data (Kidwell, 2001; Kidwell et al., 2001, Kowalewski and Hofmeister, 2003; Bush et al., 2007). As a result, inconsistent sampling protocols are employed by many working groups, which may affect meta analyses of secular trends. Furthermore, recommended mesh size for ecological community characterization studies (e.g. Warwick, 1993; James et al., 1995; Rodrigues et al., 2007) are markedly smaller than those typically recommended by palaeoecologists (e.g. Kidwell et al., 2001; Bush et al., 2007). If one of the goals of palaeoecology is to use the deep time perspective offered by the fossil record to aid modern ecologists in their conservation efforts, the degree to which data collection by these disciplines differs is of fundamental importance. The goal of the present study is to build upon recent research to further evaluate the effects of sieve size on palaeoecological data, in particular community diversity and drilling intensity in Cenozoic molluscan assemblages from the Paris Basin (Eocene) and Central Paratethys (Miocene).

A series of recent studies (Kidwell, 2001; Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003; Bush et al., 2007), have emphasized some of the effects of size filtering on quantitative data collected on molluscs in paleontological studies. Kidwell (2001) reported that use of coarser sieve mesh sizes (> 2 mm) resulted in greater taxonomic fidelity of molluscan death communities to living communities in terms of rank abundances of species. Kidwell et al. (2001) tested a variety of sampling and data-acquisition techniques for taphonomic measurements of molluscs. They reported strong size fraction effects for all types of taphonomic damage. Kowalewski and Hoffmeister (2003)

and Bush et al. (2007) tested the importance of sieve sizes on several paleontological measurements, including the species richness, evenness, encrustation rate, drilling intensities and taxonomic composition by virtually filtering a dataset of pre-measured Miocene molluscs from the Boreal and Paratethys provinces in Europe using a computer model to simulate sieved datasets. Kowalewski and Hoffmeister (2003) report that sieve size affected many paleoecological parameters, and that some were highly volatile. For example, taphonomic grade was significantly different when a 2 mm vs a 3 mm sieve mesh size was used, despite that the two fractions shared more than 90 % of the total specimens. More importantly, they also found that even when the same filtering methods were used for comparative analyses, results were dependent upon the mesh size chosen. Finally, Bush et al. (2007) sought to determine the effects of size-filtering on ecologic composition (using the relative abundance of tiering, motility and feeding categories) of the Miocene molluscs studied by Kowalewski and Hoffmeister (2003). They report that averaging samples from pre-existing datasets reduced the effects of size filtering as long as patchiness was introduced by the samples.

The effects of size filtering on studies of ecological interactions may be quite important in some settings. Due to size-specific selection of predators on their prey (either directly or indirectly by selecting specific species that fall within certain limits), biases due to sieving can be severe (Kowalewski, 2002). Naticids (one of the most important drillers of Cenozoic prey) in particular are known to attack larger organisms as they grow (Edwards and Huebner, 1977; Berry, 1982; Kitchell, 1986; Allmon et al, 1990; Kingsley-Smith et al, 2003a, b). Such effects could be especially strong in assemblages dominated by either large or small

predatory drillers. For example, naticid gastropods in the Northern Adriatic Sea tend to be small and attack smaller prey (e.g. Sawyer and Zuschin, 2010). If drilling frequency were evaluated from the Northern Adriatic Sea using larger sieve mesh sizes, many drilled shells, as well as their drillers, would be discarded. This would result in low drilling frequencies when in fact drilling predation could be high. Likewise, removal of small shells in communities dominated by large predators may artificially inflate drilling frequencies by removing small shells that were not drilled by larger predators. Despite the vulnerability of predation frequencies to size-selection, few studies have examined the effects of size filtering on drilling intensities (see Kowalewski, 2001; Kowalewski and Hoffmeister, 2003).

This study builds upon earlier research (Kidwell, 2001; Kidwell et al., 2001; Kowalewski and Hoffmeister, 2003; Bust et al., 2007) to further examine the effects of sieve-size on palaeoecological data, but differs in several fundamental aspects. We use three sieve sizes (1 mm, 2 mm and 4 mm) to physically process bulk samples rather than virtually sieving or conducting meta-analyses. Where previous researchers have focused on rank abundances and taphonomic grades, as well as ecological niches, evenness and taxonomic proportions, we examine diversity statistics (species richness, Shannon-Wiener and Simpson's indices) and drilling predation between two geographically and temporally separate regions (the Eocene-aged Paris Basin, and the Miocene-aged Korneuburg Basin). We test the following hypotheses: 1) mesh size significantly affects measures of diversities within the Paris and Korneuburg Basins; 2) mesh size significantly effects comparative analyses of diversity between the Paris and Korneuburg Basins; 3) mesh size significantly effects drilling frequencies within

the Paris and Korneuburg Basins; and 4) mesh size significantly effects comparative analyses of drilling frequencies between the Paris and Korneuburg Basins.

### **4.3. Geologic Overview**

The Lutetian strata of the Paris Basin are extremely diverse and were deposited around the time of the early Eocene climatic optimum (Gely and Lorenz, 1991). The middle Lutetian beds are loosely- to densely-packed calcareous sandstones with little cement and are interpreted to have formed in a tropical, oligotrophic shoreface environment. The molluscan diversity decreases in *Batillaria* and Potamidae-dominated beds at the top of the succession at the locality La Ferme de l'Orme. These families of gastropods are typical of an intertidal or lagoonal setting. The lower Bartonian was exposed at Le Guépelle by excavation and contains a somewhat less diverse, although still quite species rich, molluscan assemblage (Gely and Lorenz, 1991).

Samples from the Korneuburg Basin are Upper Burdigalian in age, and were collected from an extensively sampled section along a roadcut for new highway (S1). The Korneuburg Basin is a sub-basin of the Vienna Basin, Austria. The depositional setting for the sampled beds is interpreted to be that of an intertidal to shallow sublittoral restricted estuary with a nearby freshwater source (Harzhauser et al., 2002).

## **4.4. Materials and methods**

### **4.4.1. Material Collection and Processing**

Twelve bulk samples were collected from shell beds at three classic middle Lutetian localities (Grignon, La Ferme de l'orme, Fleury la Riviere) and one Lower Bartonian locality (la Guepelle) in the Paris Basin of France. 118 bulk samples were collected from the locality Korneuburg SPK in the Korneuburg Basin. All samples were processed using stacked 1 mm, 2 mm and 4 mm sieves. Because of overwhelming shell densities in many of the samples, between one half and one sixteenth of the total shell material was used for the 1 mm and 2 mm size fractions from 11 of the Paris Basin samples and 38 of the Korneuburg samples. Typically, for any given sample, the 1 mm fraction was split one more time than the 2 mm fraction, and the entire 4 mm fraction was counted. For example, if  $\frac{1}{2}$ th of the 2 mm size fraction for a sample was used for analyses, only  $\frac{1}{4}$ th of the 1 mm fraction was used. Counts from these split samples were adjusted accordingly for diversity analyses, but such adjustment was not deemed necessary for drilling predation analyses because these are based on proportional data that should not be affected by differences in sample size. Furthermore, drilling frequencies calculated from adjusted data would have gained unreasonable statistical power.

Mollusc shells (including identifiable fragments) were removed, sorted, and identified to species-level using Cossmann and Pissarro (1904-1906; 1910-1913), Harzhauser (2002), and Čytroký (2002). Shells were counted using different criteria for diversity and drilling intensity analyses. For the diversity studies, all individuals were counted, including identifiable fragments. Bivalve

fragments were counted if the umbo was intact, and gastropod fragments if the apex was intact. Fragments were excluded from drilling frequency analyses. For drilling analyses, shells were considered whole if they were approximately 90% or more complete.

Analyses were performed on both the individual size fractions (a proxy for body size) and on sieve treatments (a proxy for methodological size filtering). In other words, in the size fraction approach all shells in the 1 mm sieve (1-2 mm fraction) were counted for both diversity and drilling analyses and compared to all of the shells in the 2 mm (2-4 mm fraction) and the 4 mm (>4 mm fraction) sieves. Then, in the sieve treatment approach the counts from the 2 mm and 4 mm sieves were added to those from the 1 mm sieve to determine the ‘total’ counts (>1 mm sieve treatment). The counts from the 2 mm sieve were added to those from the 4 mm sieve to determine the >2 mm sieved counts, and the remaining individuals in the 4 mm sieve accounted for the >4 mm counts.

#### **4.4.2. Diversity Estimates**

Rarefaction curves were computed by the program Past (Hammer et al., 2001, 2004) to compare species richness between fractions and sieve treatments. 95% confidence intervals were used to determine statistical significance between curves.

Species richness and evenness (based on proportional abundances of species) were used to describe diversities of the Paris and Korneuburg Basins within each size fraction and sieve treatment using the program EstimateS (Colwell, 2009). The Simpson’s index, which is strongly controlled by the 2-3 most abundant species in a dataset, and the Shannon-Wiener index, which is

strongly controlled by the species in the middle of the rank distribution, were used as proxies for evenness. The Shannon-Wiener index is calculated as

$$H' = - \sum p_i \ln p_i$$

Where  $p_i = n_i/N$ ;  $n_i$  = the abundance of the  $i$ th species; and  $N$  = the total abundance (Magurran, 2004, p. 238).

The Simpson's index is calculated as

$$D = \sum \{[n_i(n_i-1)]/[N(N-1)]\}$$

Where  $n_i$  = the abundance of the  $i$ th species; and  $N$  = the total abundance.  $D$  is the probability that any two individuals drawn from the assemblage would be the same species. In order to express the Simpson's index as the diversity, it should be presented as either the compliment (1- $D$ ) or the reciprocal (1/ $D$ ) (Magurran, 2004, p. 239). The reciprocal value expresses the number of equivalent, equally abundant species (Colwell, 2009) and is the form presented here.

#### **4.4.3. Drilling Intensities**

Each complete shell was examined for predatory drill holes. The following widely accepted criteria were used to identify such drills as being predatory in nature: holes should have smooth sides and be circular in cross section, penetrate from the outside of the shell, penetrate perpendicularly to the shell surface, and penetrate only one valve in articulated bivalves (Carriker and Yochelson, 1968; Rohr, 1991; Baumiller, 1996; Kaplan and Baumiller, 2000; Leighton, 2001). Drilling frequency was calculated by dividing the number of complete drill holes by the total number of shells. Regional drill frequencies were determined by pooling shell and drill hole counts from all samples within each basin, as well as for all bivalves, gastropods, and families that were common in both basins.

Additionally, families that were common in one Basin, but rare or absent in the other, were also examined. Comparisons between size fractions, as well as between the Paris and Korneuburg Basins, were not conducted at finer taxonomic resolution because of constraints on sample sizes at the genus and species levels. Significant differences between drilling frequencies were determined by comparing 95 % confidence intervals. Only families with significant differences either within basins when comparing size fractions/sieve treatments, or between basins when comparing the same size fraction/sieve treatment are reported as graphs. All other families are reported in Tables 4.1 and 4.2.

## **4.5. Results**

### **4.5.1. Diversity estimates**

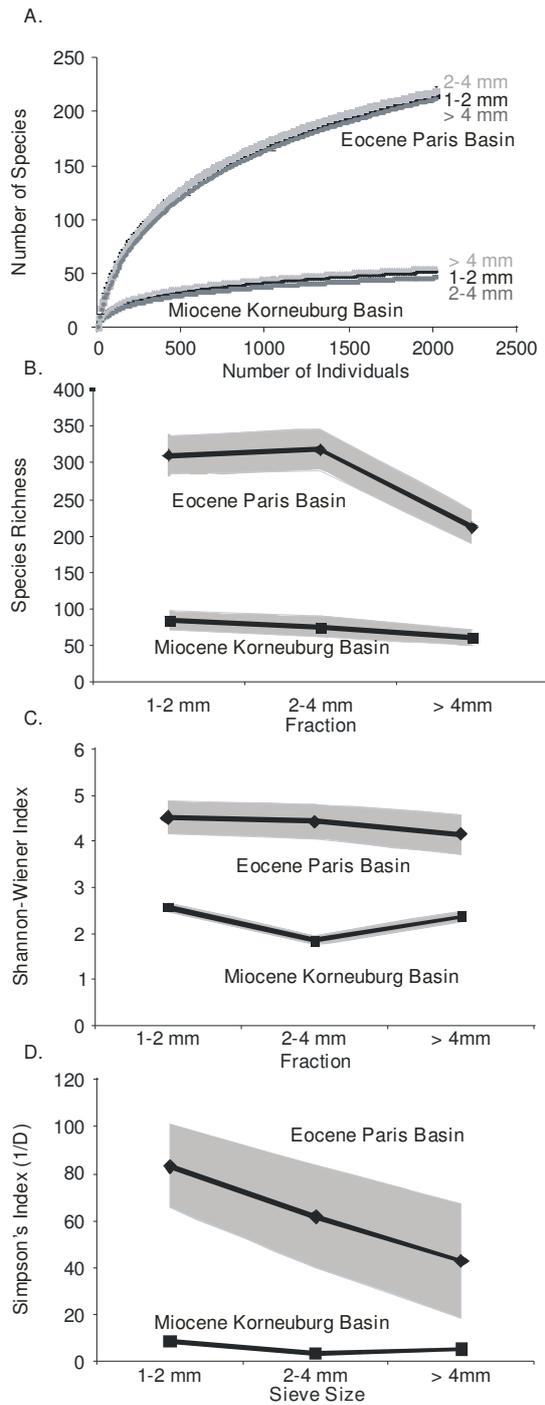
Based on rarefaction curves, species richness, Shannon-Wiener and Simpson's diversity indices, the Paris Basin is much more diverse than the Korneuburg Basin. There are no overlaps between 95 % confidence intervals at any size fraction or sieve-size treatment between the two basins (Figs. 4.1a and 4.2a).

*Size Fractions.*—Rarefaction curves of the 1-2 mm, 2-4 mm and >4 mm fractions of the Paris Basin do not reach an asymptote as more individuals are added, indicating that further sampling would result in greater species richness. In the Paris Basin, the intermediate size fraction (2-4 mm) is marginally more diverse than the smallest and largest size fractions (Fig. 4.1a). Rarefaction curves of the 1-2 mm, 2-4 mm and >4 mm fractions of the Korneuburg Basin reveal that all fractions sufficiently sample species richness at the basin scale. Shells occurred

more often in the largest and smallest size fractions compared to the intermediate fraction. Note that in both basins, confidence limits generally do not exceed the width of the rarefaction curves plotted in Figures 4.1a and 4.2a.

In the Paris Basin samples, the majority of species are found in the 1-2 mm and 2-4 mm size fractions. The number of species in the 1-2 mm and 2-4 mm fractions are nearly equal, but the value drops drastically in the >4 mm fraction. In the Korneuburg basin, species richness in the intermediate size fraction (2-4 mm) is not significantly different from the smaller (1-2 mm) or larger (>4 mm) fractions, but significant differences between the smallest and largest fractions are apparent.

Species in all three size fractions appear to be similarly equitable in the Paris Basin based on the Shannon-Wiener index (Fig. 4.1c). In contrast, the intermediate size fraction in the Korneuburg basin appears to be least diverse. The Simpson's values reported here (reciprocal form) estimate the number of equivalent, equally abundant species. In other words, the number of species that would have been encountered had all been equally common. Simpson's values in the Paris basin are much higher in successively smaller size fractions, but these differences are not significantly different, most likely due to the fact that most species in samples are represented by singletons (Fig. 4.1d). Simpson's values in each fraction of the Korneuburg basin are statistically similar and much lower than those of the Paris Basin.

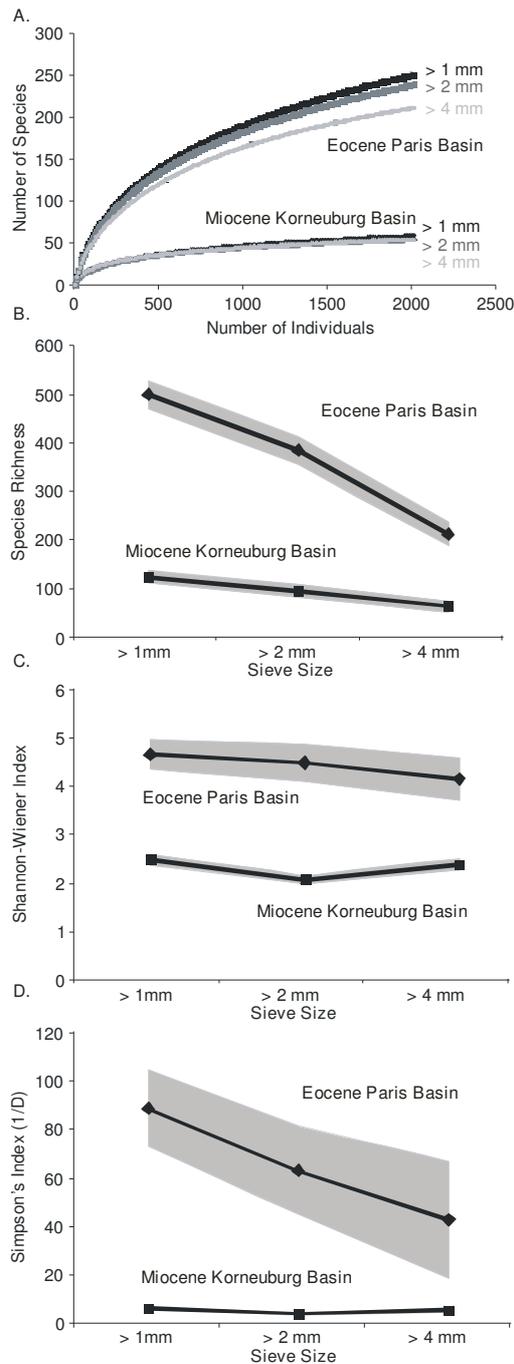


**Fig. 4.1.** Analyses of molluscan diversity among size fractions within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Upper Burdigalian, Miocene) Basins. A, rarefaction curves (note—95% confidence limits are generally smaller than the width of the curves); B, species richness; C, Shannon-Wiener index; D, Simpson index (represented as the reciprocal of D, see methods). In B-D, gray shading represents 95 % confidence intervals.

*Sieve Treatments.*—Rarefaction curves of the >1 mm, >2 mm and >4 mm fractions of the Paris Basin do not level off to the right, indicating that further sampling would likely result in greater species richness. In both the Paris and Korneuburg Basins, diversity decreases with increasing sieve mesh size. These differences are significant in the Paris Basin, but minimal in the Korneuburg Basin (Fig. 4.2a).

In the Paris Basin, loss of smaller species in larger sieve treatments results in species richness values that are significantly underestimated in the >2 mm and >4 mm datasets (Fig. 4.2b) compared to the >1 mm dataset. Though not nearly as drastic as in the Paris Basin, species richness in the Korneuburg Basin is also significantly higher in the >1 mm assemblage than in the >2 mm portion, which is significantly higher than the >4 mm portion.

The Shannon-Wiener index suggests similar diversities regardless of the sieve size used in the Paris Basin. Interestingly, in the Korneuburg Basin, the total assemblage and the >4 mm sieves have similar Shannon-Wiener values, but the >2 mm portion of the assemblage has significantly lower values (Fig. 4.2c). Simpson's values of assemblages are drastically, albeit not statistically, different between sieve-sizes in the Paris basin. No statistical differences are observed in Simpson's value across sieve sizes in the Korneuburg basin, where values are more constrained (Fig. 4.2d).



**Fig. 4.2.** Molluscan diversity analyses using different sieve treatments to process samples within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Upper Burdigalian, Miocene) Basins. A, rarefaction curves (note—95% confidence limits are generally smaller than the width of the curves); B, species richness; C, Shannon-Wiener index; D, Simpson's diversity (represented as the reciprocal of D, see methods). In B-D, gray shading represents 95 % confidence intervals.

#### 4.5.2. Drilling intensities

In general, drilling frequencies are higher in the Paris Basin than in the Korneuburg Basin, in both individual size fractions and sieve treatments. No overlaps in 95 % confidence intervals occur at the assemblage or class levels, though at finer taxonomic resolution some discrepancies occur.

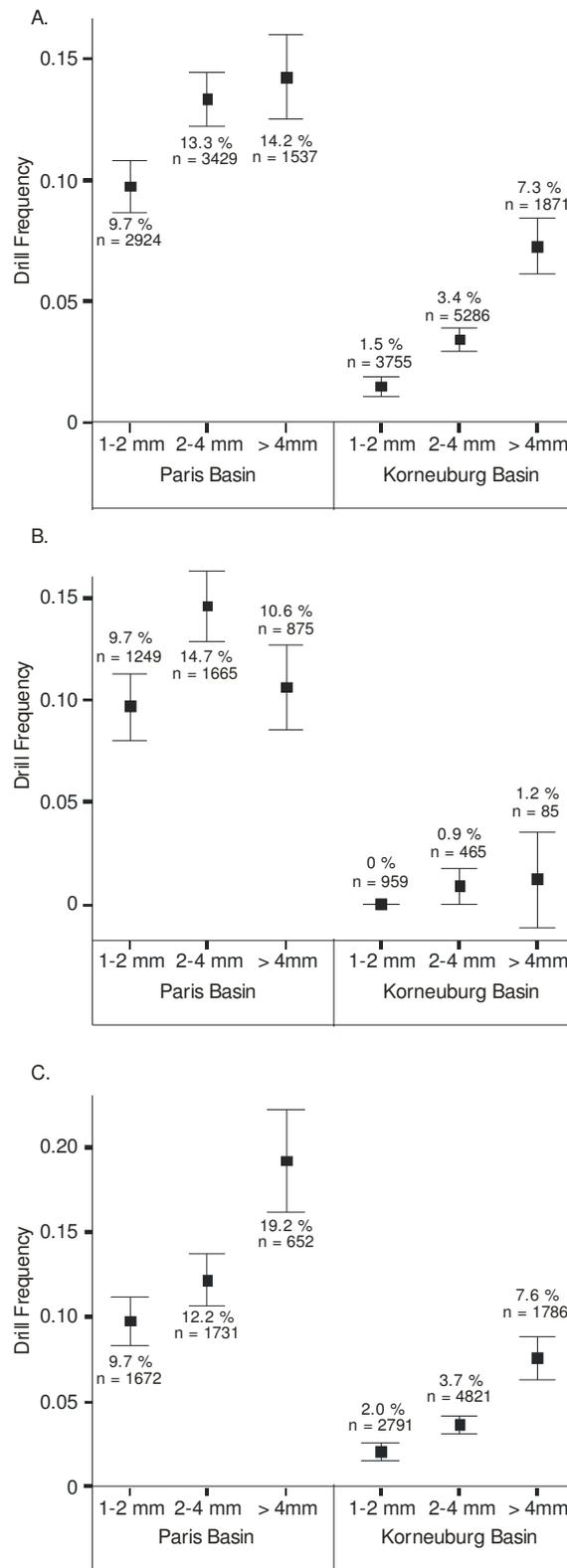
*Size Fraction.*—Assemblage-level drill frequencies in the Paris Basin are significantly higher in the 2-4 mm and >4 mm size classes than in the 1-2 mm fraction. In the Korneuburg Basin, assemblage-level drill frequencies are significantly higher in each successively higher size fraction (Table 4.1, Fig. 4.3a).

The patterns of drill frequencies across size fractions are not consistent across classes in either basin. For example, bivalves from the 2-4 mm fraction are drilled significantly more than those from both the 1-2 mm and >4 mm fractions, which are not statistically different from one another (Fig. 4.3b). In contrast, gastropods from the Paris Basin are drilled significantly more in the >4 mm size fraction than in the smaller fractions, which experience similar drilling frequencies to one another (Fig. 4.3c). No significant differences in drilling frequencies are apparent between size classes of bivalves from the Korneuburg basin (Fig. 4.3b); however, Korneuburg Basin gastropods are drilled significantly more frequently in the 1-2 mm than the 2-4 mm fractions, and again more frequently in the 2-4 mm to than the >4 mm fractions (Table 4.1, Fig. 4.3c).

**Table 4.1.** Summary of drill frequency data for the total assemblage, bivalves, gastropods and abundant families for each size fraction In the Eocene Paris Basin and Miocene Korneuburg Basin

Classes	Eocene Paris Basin			Miocene Korneuburg Basin			
	1-2 mm DF (%)	n	2-4 mm DF (%)	> 4 mm DF (%)	1-2 mm DF (%)	2-4 mm DF (%)	> 4 mm DF (%)
Total Assemblage	2924	9.7	3429	13.3	1537	3755	1871
Bivalvia	1249	9.7	1665	14.7	875	959	85
Gastropoda	1672	9.7	1731	12.2	652	2791	1786
Bivalve Families							
Arcidae	68	5.9	133	18.0	31		
Noetidae	182	7.1	237	14.3	2	39	6
Glycymeriidae	58	15.5	71	25.4	63		
Ostreidae	181	7.7	129	7.0	103	10	59
Lucinidae	59	13.6	35	8.6	17	513	11
Carditidae	302	12.6	493	20.3	374		
Veneridae	145	6.9	282	9.6	99	303	9
Corbulidae	115	10.4	65	15.4	47	295	3
Gastropod Families							
Neritidae						988	187
Hydrobiidae						372	0
Rissoiidae	232	6.5	28	10.7	0	1	0
Cerithiidae	183	21.3	111	14.4	24	213	0
Batillariidae	271	2.2	481	1.2	60	271	24
Potamididae	68	7.4	93	10.8	39		
Turritellidae	290	19.0	347	23.1	234	640	931
Naticidae	46	6.5	60	5.0	61	171	178
Nassariidae						20	73
Turridae	40	2.5	27	14.8	9	194	550
						6	38

n = number of shells, DF (%) = drill frequency.



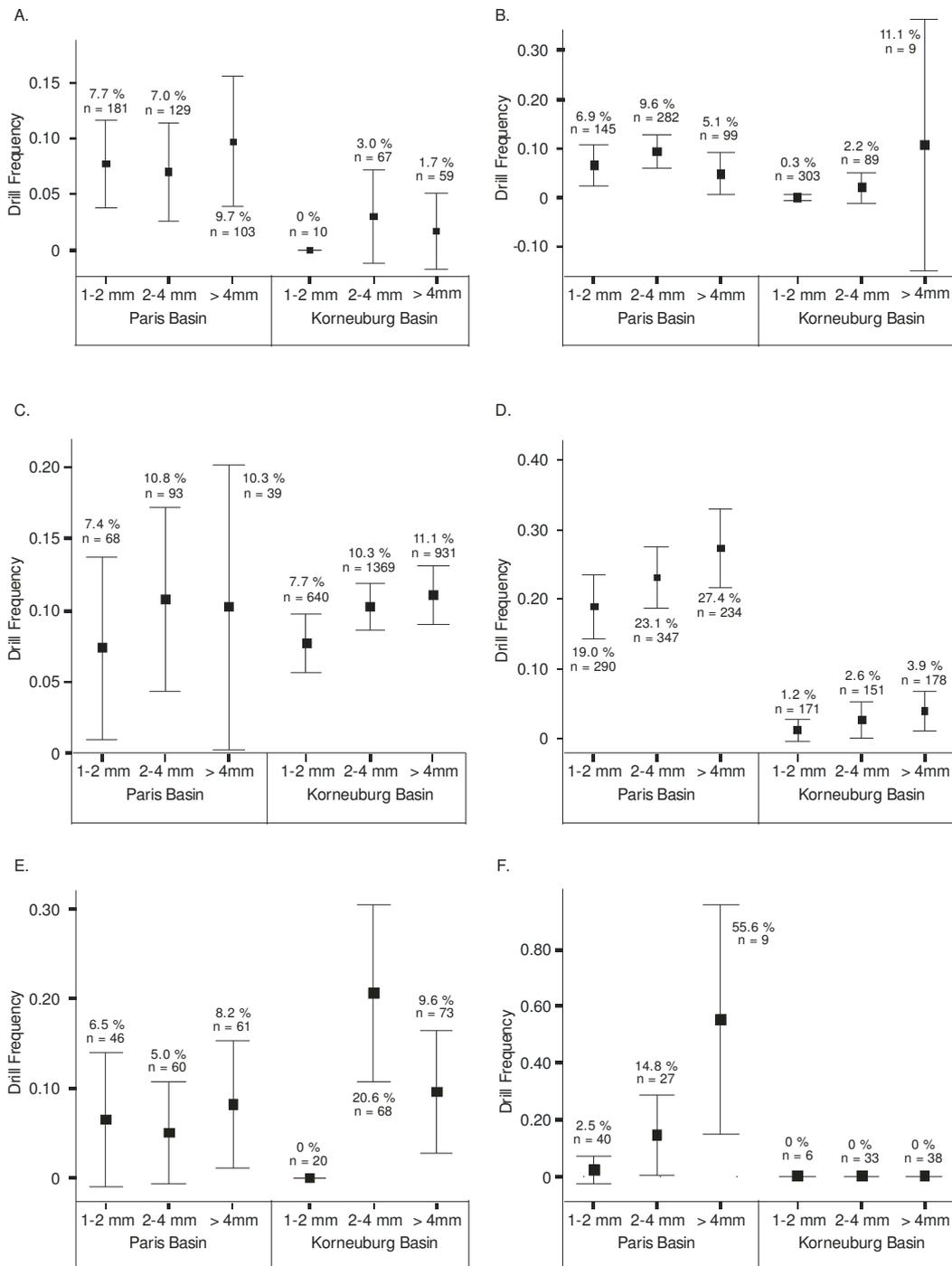
**Fig. 4.3.** Molluscan drilling frequencies for each size fraction within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Upper Burdigalian, Miocene) Basins. A, total assemblage; B, Bivalvia; C, Gastropoda. Error bars represent 95 % confidence intervals.

At the family-level, Paris basin drilling frequencies are not significantly different between size fractions except for the Turridae, which are drilled more frequently in the >4 mm than in the 1-2 mm fraction. No significant differences, however, are observed between the 1-2 mm and the 2-4 mm, or between the 2-4 mm and the > 4 mm sieve fractions (Fig. 4.4). In the Korneuburg Basin, family-level drilling frequencies are similar across all size fractions except in the Naticidae, which were never drilled in the 1-2 mm size fraction (Fig. 4.4).

At the assemblage and class-levels, drill frequencies are always significantly higher within single size classes in the Paris Basin than in the Korneuburg Basin (Fig. 4.3). But at finer taxonomic resolution, differences in drill frequencies between the two basins vary based on the family and size-fraction examined. For example, Veneridae drilling frequencies are significantly higher in the Paris than in the Korneuburg Basin in the 1-2 mm and 2-4 mm size fractions, but not so in the >4 mm fraction (Fig. 4.4b). In the Ostreidae, the 1-2 mm size fraction is drilled significantly more frequently in the Paris Basin samples than in the Korneuburg Basin samples, but not so in the larger fractions (Fig. 4.4a). In contrast, naticids in the 2-4 mm fraction are drilled significantly more in the Korneuburg Basin than in the Paris Basin, but not so in the 1-2 mm or the >4 mm fractions (Fig. 4.4e). Finally, turritellids from all size classes have significantly higher drill frequencies in the Paris Basin than in the Korneuburg Basin (Fig. 4.4f), while values for the potamidids within all size fractions are similar in the Paris and Korneuburg Basins (Fig. 4.4c).

*Sieve Treatments.*—Assemblage-level drilling frequencies are not significantly different when larger sieve mesh sizes are used in the Paris Basin. In contrast, use of larger sieves in the Korneuburg Basin result in significantly higher

drill frequencies than those derived from samples processed with smaller sieves (Table 4.2, Fig. 4.5a).

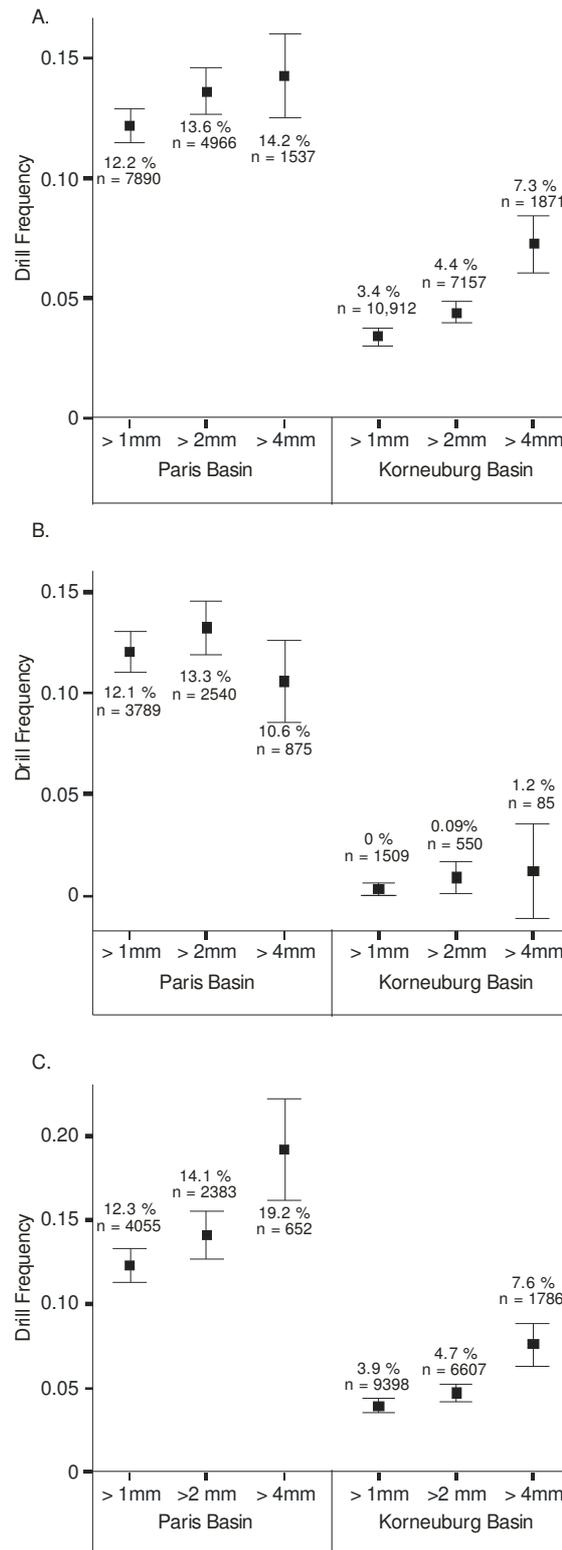


**Fig. 4.4.** Drilling frequencies of common families calculated from each size fraction within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Upper Burdigalian, Miocene) Basins. A, Ostreidae; B, Venereidae; C, Potamididae; D, Turritellidae; E, Naticidae; F, Turridae. Error bars represent 95 % confidence intervals.

**Table 4.2.** Summary of drill frequency data calculated for the total assemblage, bivalves, gastropods and abundant families for each sieve treatment in the Eocene Paris Basin and the Miocene Korneuburg Basin

Classes	Eocene Paris Basin			Miocene Korneuburg Basin		
	>1 mm n DF (%)	>2 mm n DF (%)	>4 mm n DF (%)	>1 mm n DF (%)	>2 mm n DF (%)	>4 mm n DF (%)
Total Assemblage	7890	4966	1537	10912	7157	1871
Bivalvia	3789	2540	875	1509	550	85
Gastropoda	4055	2383	652	9398	6607	1786
Bivalve Families						
Arcidae	232	164	31			
Noetidae	421	239	2	96	57	6
Glycymeriidae	192	134	63			
Ostreidae	413	232	103	136	126	59
Lucinidae	111	52	17	666	153	11
Cardiidae	1169	867	374			
Veneridae	526	381	99	401	98	9
Corbulidae	227	112	47	398	103	3
Gastropod Families						
Neritidae				4014	3026	187
Hydrobiidae				373	1	0
Rissoiidae				214	1	0
Cerithiidae	260	28	0	306	35	24
Batillariidae	318	135	24			
Potamidiidae	812	541	60	2940	2300	931
Turritellidae	200	132	39	500	329	178
Naticidae	871	581	234	161	141	73
Nassariidae	167	121	61	1408	1214	550
Turridae	76	36	9	77	71	38

n = number of shells, DF (%) = drill frequency.



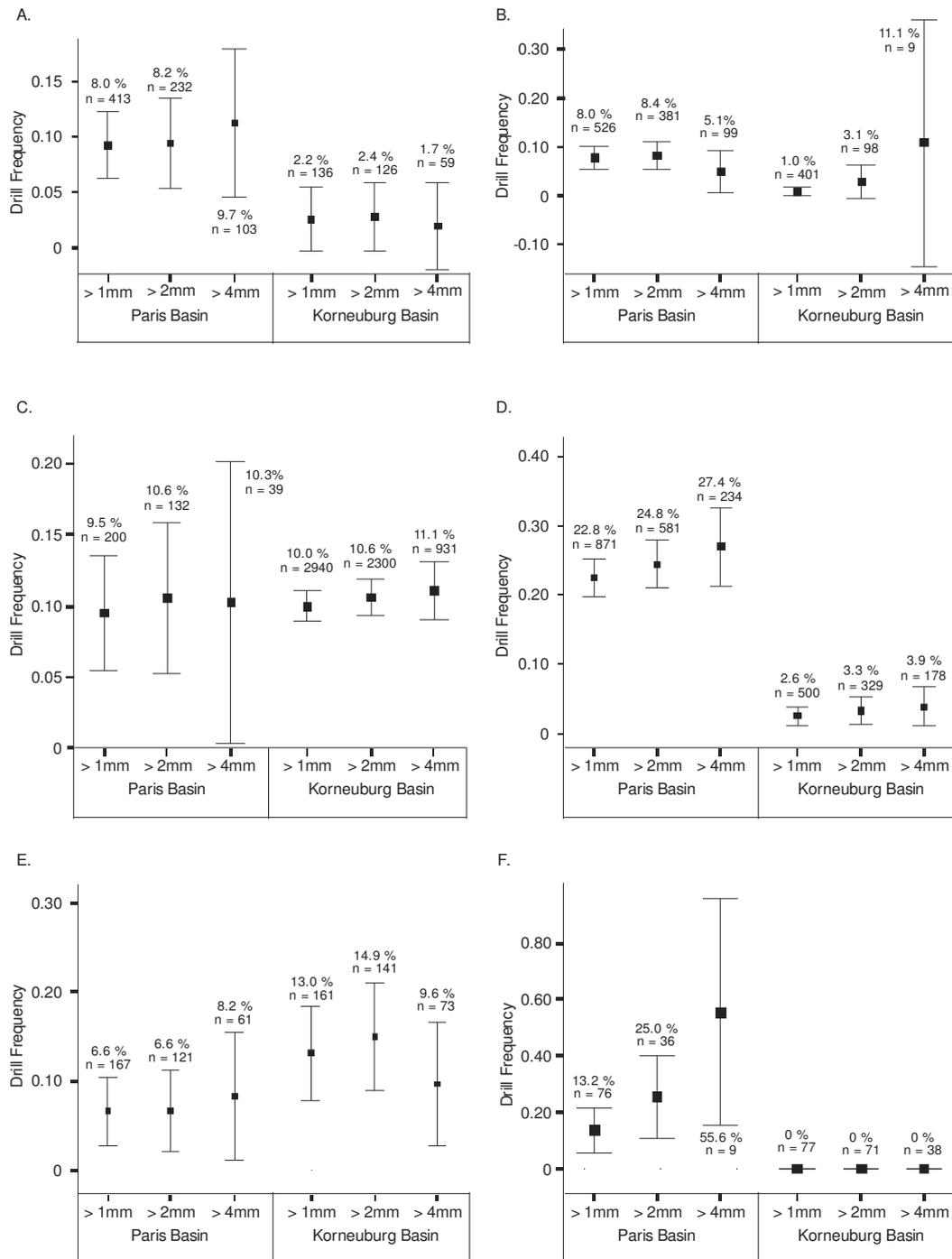
**Fig. 4.5.** Molluscan drilling frequencies derived from using different sieve sizes to process samples within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Burdigalian, Miocene) Basins. A, total assemblage; B, Bivalvia; C, Gastropoda. Error bars represent 95 % confidence intervals.

The patterns of drilling frequencies found by sample processing with various sieve sizes are not consistent between bivalves and gastropods in either basin. Bivalves from both the Paris and Korneuburg basins have similar drilling frequencies regardless of the sieve size used (Fig. 4.5b). In contrast, gastropods in both basins appear to be drilled significantly more frequently when the 4 mm sieve is employed, but not so when the 1 mm and 2 mm sieves are used (Fig. 4.5c). At the family-level, no differences were observed between sieve-size treatments in either basin (Fig. 4.6).

At the assemblage and class levels, drilling frequencies are always significantly higher in the Paris Basin than in the Korneuburg Basin, regardless of the sieve used to process samples. At the family level, no differences were found in drilling frequencies between basins for the Potamididae (Fig. 4.6c) or the Naticidae (Fig. 4.6e), and the Turritellidae (Fig. 4.6d) were always drilled more frequently in the Paris Basin, independent of the sieve treatment. However, use of a 1 mm sieve (all shells >1 mm examined) resulted in significantly different drill frequencies in both the Ostreidae (Fig. 4.6a) and Veneridae (Fig. 4.6b) between the Paris and Korneuburg Basins that were missed by the 2 mm (all shells >2 mm examined) and 4 mm (all shells > 4 mm examined) sieves.

#### **4.6. Discussion**

Examination of the affects of size filtering is important not only because sieving is so widely employed, but also because different protocols are frequently used by researchers, even when goals or targeted taxa are similar (Kidwell et al., 2001—Table 4.1; Kowalewski and Hoffmeister, 2003—Figure 1). Many workers



**Fig. 4.6.** Drilling frequencies of common families derived from using different sieve sizes to process samples within the Paris (Lutetian and Lower Bartonian, Eocene) and Korneuburg (Burdigalian, Miocene) Basins. A, Ostreidae; B, Veneridae; C, Potamididae; D, Turritellidae; E, Naticidae; F, Turridae. Error bars represent 95 % confidence intervals.

have assumed that as long as comparative analyses use the same methodology, any biases would be equivalent and therefore negligible (Gage et al., 2002; Hannisdal, 2004; Battle et al., 2007; Sawyer and Zuschin, in review), but this may not always be the case (Kowalewski and Hoffmeister, 2003). In the fossil record, taphonomy and time averaging would also alter diversities. Sieve retention is affected by the size frequency distribution of taxa, the tendency of those taxa to fragment during sampling and the vigor applied when washing samples (Rodrigues et al., 2007). Diversity measures are likely to be dependent upon a rather complex combination of the area sampled, the size distribution of organisms present, and the sieve mesh size used (Warwick and Clark, 1996).

Kowalewski and Hoffmeister (2003) and Bush et al. (2007) used a large dataset of virtually sieved mollusks from the Miocene Paratethys and Boreal provinces of Europe to examine size-filtering effects on a variety of paleoecological data. In contrast to physical sieving, which divides elements by their minimum dimensions; they assigned shells to bins based on their maximum dimensions. They tested their results using both the largest and smallest dimensions for bivalves, which showed nearly identical results. They did not, however, address this effect on gastropods, which would have been more likely to be assigned to different size fractions had their minimum dimensions been used. Because our data was physically sieved using mesh sizes that are quite typical for studies on Cenozoic mollusks, our results may reveal important additional insights into the effects of physical sieving at the assemblage level.

Kidwell (2001) reported that using coarse mesh sizes increases fidelity between live and dead assemblages in modern deposits because use of finer mesh sizes results in assemblages that are dominated by larvae and newly settled

juveniles. Settlement occurs in pulses and most juveniles do not survive to adulthood; therefore, censuses of live data are sensitive to the timing of sampling. In addition, many small taxa are opportunistic species that may not be a part of the normal community. As such, use of small sieves results in abundances dominated by transient individuals instead of adult and late-stage juveniles that dominate by biomass. Kidwell (2001) further argued that small shells (< 1 mm) are more likely to be transported out of their natural habitats, and are also more susceptible to chemical dissolution than larger shells. As such, she suggested that fossil deposits would best represent living communities if 2 mm to 4 mm sieves were used. Most modern ecologists, however, recommend using either 0.5 mm or 1 mm sieves to study macrofauna (e.g. Birkett and McIntyre, 1971; Lewis and Stoner, 1981; James et al., 1995; Crewe et al., 2001). In fact, many caution that 1 mm sieves tend to under-sample the benthos due to loss of juveniles and small taxa. For example, Tanaka and Leite (1998) found that 93.1 % of gastropods from living algal communities were retained on a 0.5 mm sieve, but only 68.2 % on a 1 mm sieve. Even so, sometimes the use of larger sieves may be warranted, either because a particular species and/or size class is desired (Biss et al., 1996), or because increasing mesh size, reduces sample-processing time sufficiently to allow many more additional samples to be included in analyses (Warwick, 1993; James et al., 1995; Crewe et al., 2001). James et al. (1995) found that increasing mesh size to 1 mm and identifying taxa to family- instead of to species-level, decreased sample processing time by two-thirds. Still, others contend that the loss of smaller individuals is not worth the decreased effort because results are less precise and inadequate assessments of community composition are inevitable (Schlacher and Woolridges, 1996; Tanaka and Leite, 1998). Furthermore, the

ability to distinguish groups using the non-parametric multivariate techniques (e.g. ANOSIM) common in the ecological (and increasingly so in the palaeoecological) literature appears to be dependent upon the smallest macro-organisms; if the smaller size classes are filtered out, then their importance to community structure would remain unknown (McKindsey and Bourget, 2001). Interestingly, the loss of small species and juveniles is exactly what Kidwell et al. (2001) credit with increasing fidelity between live/dead assemblages when coarser size fractions are examined. Modern ecologists wishing to use the rock record to obtain baseline community data would then be advised to use larger size fractions (Kidwell 2001). Without greater agreement between ecologists and paleoecologists in terms of sampling methods, comparisons between Recent and Fossil ecosystems will remain difficult.

Modern ecologists have noted that the abundance of intermediate-sized organisms is greater than that of small and large organisms (Warwick and Clark, 1996). Based on the size-fraction data presented here (Table 4.1), molluscs from the Paris and Korneuburg Basins follow a similar pattern, with the highest abundances observed in the intermediate size fraction. It is interesting that intermediate-sized shells also likely suffer from greater levels of taphonomic degradation (Kowalewski and Hoffmeister, 2003). Our data suggest that species richness and diversity may be highly dependent upon the sieve size examined. For example, in the Paris Basin, the 2 mm sieve recovered 77 % of the species richness found by the 1 mm sieve, but the 4 mm sieve only recorded 42.5 %. That equates to 115 species lost using the 2 mm sieve, and 287 using the 4 mm sieve. In the Korneuburg Basin, the 2 mm sieve also recovered 77 % of the species found by the 1 mm sieve, and the 4 mm sieve recorded only 51 %. That equates to

28 species lost by the 2 mm sieve compared to those recovered with the 1 mm sieve, and 60 lost using the 4 mm sieve. These losses, while smaller than in the Paris Basin, are still significant. This is in contrast to Kowalewski and Hoffmeister (2003), who found relatively stable species richness until very large sieves (9-10 mm) were used, and relatively small changes in evenness from 2 mm to 10mm sieve sizes.

The effects of size filtering on metrics of predation intensities have received little attention. This is discouraging considering that many predators are known to attack a preferred size of prey (Allmon et al, 1990; Kingsley-Smith et al, 2003a, b). Some studies have reported increases in drilling frequencies in larger size fractions (e.g. Kowalewski and Hoffmeister, 2003), while others find increasing values in smaller fractions (e.g. Sawyer and Zuschin, 2010). Kowalewski (2002) and Kowalewski and Hoffmeister (2003) report an increase of ~ 50 % in drilling frequency (from ~ 15% to ~ 23%) from 2 mm to 10 mm sieves in assemblages from the Miocene of Europe. In the Korneuburg Basin, which is a small sub-system of the Paratethys province studied by Kowalewski and Hoffmeister (2003), differences in assemblage level drilling frequencies between sieve treatments can be even more severe, despite that the range in sieve sizes studied there is much smaller. Interestingly, significant differences are not observed between sieve size treatments in bivalves in either the Paris Basin or the Korneuburg dataset. This opens the possibility that bivalve drilling frequencies are not severely affected by the mesh size in either Eocene or Miocene deposits. Gastropod drilling frequencies, on the other hand, were significantly affected by sieve size treatments in both basins. The effects of sieve size on comparative analyses of the Paratethys and Boreal provinces were stronger (Hoffmeister and

Kowalewski, 2003) than those observed between the Paris and Korneuburg Basins. While all sieve sizes in both studies consistently assigned higher values to the same temporal/geographic area, the differences in the absolute values reported were greater in Kowalewski and Hoffmeister's (2003—Figure 4) study than those determined here (Fig. 4.3).

It is heartening that none of the most common families showed significantly different drilling frequencies based on the sieve size used in either the Paris or Korneuburg Basins. This suggests that at finer taxonomic resolution, the choice of sieve mesh size might not be critical to interpretations of drilling intensities, although admittedly, some families, or combinations of families must drive the assemblage-level patterns. This also suggests that the differences in drilling frequencies observed at the assemblage and class levels are probably more dependent upon differences in the presence and abundance of constituent taxa from one region to another, than preferences of particular predators for prey at specific size classes.

#### **4.6.1. Previous and New Suggestions for Sieving Approaches**

Kidwell (2001) and Kidwell et al. (2001) suggest using 2-4 mm sieves in order to increase live/dead fidelity between assemblages, and that researchers should collect data independently from several size fractions when evaluating taphonomic signatures. Bush et al. (2007) largely agree, but add that smaller mesh sizes could be used if juveniles were assigned to ecological groups appropriately (Bush et al., 2007). Kowalewski and Hoffmeister (2003) suggest using fine mesh sizes (maximum 1 mm) and measuring every specimen whenever possible. Alternatively, separate fractions could be analyzed independently and data

presented accordingly, as suggested by Kidwell et al. (2001) and Peeters et al. (1999).

Bush et al. (2007) stressed that averaging heterogeneously collected data may remove some of the effects of size filtering. In other words, while comparisons of ecological composition of individual samples may be overly sensitive to the mesh sizes, comparisons of regional or global faunas are likely to be more robust. This suggests that differential size filtering may not be an obstacle to large-scale secular comparisons.

The severity of mesh-size biases depends, in part, on the size frequency distribution of individual samples (Bush et al., 2007). Therefore, samples dominated by small species would be the most sensitive to sieve effects. Considering that tropical samples typically consist of many small species (e.g. Bouchet et al., 2002; Zuschin & Oliver 2005) environments such as that represented by the Paris Basin in which nearly every clast is a shell may not be adequately sampled using coarse sieves. Therefore, simply using the same mesh size may not result in meaningful comparisons between terrigenous temperate and carbonate tropical environments.

Kowalewski and Hoffmeister (2003) also suggest that ensuring that standard mesh sizes are used in comparative analyses is insufficient because results may depend on the choice of the mesh size used. Several ecologists have used pilot studies in which two or more mesh sizes were used on a small set of samples for a given ecosystem in order to determine the largest sized mesh that adequately captures a community's taxonomic composition (e.g. Tanaka and Leite, 1998; Gage et al., 2002). Such pilot studies could also be employed by paleoecologists. Based on the results of other researchers summarized above, as

well as our own, it may not be as important to analyze samples collected using the same sieve size as it is to adequately capture the entire community. Therefore, we suggest that such pilot studies should be conducted for large-scale community-based studies. We concur with Kowalewski and Hoffmeister's (2003) suggestion that initial sieving should be done with a very fine mesh, and then shells either measured or separated by size fractions (using coarser sieves) to aid in overall understanding of the size frequency distribution of the community, and to aid in future comparative analyses.

#### **4.7. Conclusions**

Our results are encouraging for comparative analyses between basins that are expected to be different in terms of diversity or predation frequencies. No single protocol is optimal or sufficient for all ecosystems, habitats, times or objectives. Therefore, we suggest that pilot studies similar to those performed by modern ecologists could be conducted to determine which sieves are appropriate for characterizing individual fossil communities. Even if coarser sieves are found to be sufficient, initial sieving should be done with a finer mesh and smaller fractions stored for future use if necessary. As it will not always be possible to measure every single specimen in all datasets, we suggest that size fractions be maintained and comparisons restricted accordingly. Such size-fraction analyses may be especially meaningful for taphonomic and predation studies.

#### 4.8. References

- Allmon, W.D., Nieh, J.C., Norris, R.D., 1990. Drilling and peeling of turritelline gastropods since the Late Cretaceous. *Palaeontology* 33, 595-611.
- Baumiller, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeography, Palaeoclimatology, Palaeoecology* 123, 434-351.
- Battle, J.M., Jackson, J.K., Sweeney, B.W., 2007. mesh size affects macroinvertebrate descriptions in large rivers: examples from the Savannah and Mississippi Rivers. *Hydrobiologia* 592, 329-343.
- Biss, J., III; Laruelle, F.H., and Molloy, D.P., 1996. Use of sieves for the rapid size selection of *Dreissena polymorpha* samples. *Journal of Shellfish Research* 15, 747-750.
- Berry, A.J., 1982. Predation by *Natica maculosa* Lamarck (Naticidae: Gastropoda) upon the trochacean gastropod *Umbonium bestiarum* (L.) on a Malaysian shore. *Journal of Experimental Marine Biology and Ecology* 64, 71-89.
- Birkett, L., and McIntyre, A.D., 1971. Treatment and sorting of samples. *In*: Holme, N.A. and McIntyre, A.D. (eds.) *Methods for the study of marine benthos*. I.B.P. Handbook No. 16. Blackwell Scientific Publications, Oxford.
- Bouchet, P., Lozouet, P., Maestrati, P., Heros, V., 2002. Assessing the magnitude of species richness in tropical marine environments: exceptionally high numbers of molluscs at a Caledonia site. *Biological Journal of the Linnean Society* 75, 421-436.

- Bush, A.M., Kowalewski, M., Hoffmeister, A.P., Bambach, R.K., and Daley, G. 2007. Potential paleoecologic biases from size-filtering of fossils: strategies for sieving. *Palaios* 22, 612-622.
- Carriker, M.R., and Yochelson, E.L., 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *Contributions to Palaeontology: Geological Survey Professional Paper 593(B)*, B1-B26.
- Colwell, R.K., 2009. EstimateS: Statistical estimation of species richness and hared species from samples. Version 8.2. User's Guide and application published at: <http://purl.oclc.org/estimates>.
- Cossmann, M., and Pissarro, G., 1904-1906. *Iconographie Complète des Coquilles Fossiles de L'Éocène des Environs de Paris. Pélécypodes, Tome 1*. Hermann, Paris, 45 pls.
- Cossmann, M., and Pissarro, G., 1910-1913. *Iconographie Complète des Coquilles Fossiles de L'Éocène des Environs de Paris. Scaphopodes, Gastropodes, Brachiopodes, Céphaloüpodes & Supplément, Tome 2*. Hermann, Paris, 65 pls.
- Crewe, T.L., Hamilton, D.J., and Diamond, A.W., 2001. Effects of mesh size on sieved samples of *Corophium volutator*. *Estuarine, Coastal and Shelf Science* 53, 151-154.
- Čtyroký, P., 2002. Marine und brachyhaline Bivalven aus dem Karpatium des Korneuburger Beckens (Untermiozän; Österreich). *Beiträge zur Paläontologie* 27, 215-257, 1 pls., Vienna.
- Edwards, D.G., and Huebner, J.D., 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbour, Massachusetts, USA. *Ecology* 58, 1218-1236.

- Gage, J.D., Hughes, D.J., Gonzalez Vecino, J.L., 2002. Sieve size influence in estimating biomass, abundance and diversity in samples of deep-sea macrobenthos. *Marine Ecology Progress Series* 225, 97-107.
- Gely J.P. & Lorenz C. 1991. Analyse séquentielle de l'Eocène et de l'Oligocène du bassin Parisien (France) Sequence Analysis of the Eocene-Oligocene Paris Basin, France. *Oil & Gas Science and Technology - Rev. IVP* 46, 713-747.
- Gobalet, K.W., 2005. Comment on „Size matters: 3-mm sieves do not increase richness in a fishbone assemblage from Arrawarra I, an Aboriginal shell midden in the mid-north coast of New South Wales, Australia“ by Vale and Gargett. *Journal of Archaeological Science* 32, 643-645.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2001. PAST: Palaeontological statistics software package for education and data analysis: *Palaeontologia Electronica* 4, 1-9, [https://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](https://palaeo-electronica.org/2001_1/past/issue1_01.htm). Checked February 2010.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D., 2004. PAST: Palaeontological Statistics, ver 1.99, 194 p. <http://folk.uio.no/ohammer/past>. Checked February 2010.
- Hannisdal, B., 2004. Clams and brachiopods: chips that pass out of sight. *Palaios* 19, 507-513.
- Harzhauser, M., 2002. Marine und brachyhaline Gastropoden aus dem Karpatium des Korneuburger Beckens und der Kreuzstettener Bucht (Österreich, Untermiozän). *Beträge zur Paläontologie* 27, 61-159, 12 pls., Vienna.
- Harzhauser, M., Böhme, M., Mandic, O., and Hofmann, Ch.-Ch., 2002. The Karpatian (Late Burdigalian) of the Korneuburg Basin—a

- palaeoecological and biostratigraphical synthesis. *Beträge zur Paläontologie* 27, 441-456.
- Jablonski, D., 1996. Body size and macroevolution: *In*: Jablonski, D., Erwin, D., and Lipps, J.H., (eds.), *Evolutionary Paleobiology*: University of Chicago Press, Chicago p. 256-289.
- James, R.J., Lincoln Smith, M.P., and Fairweather, P.G., 1995. Sieve mesh-size and taxonomic resolution needed to describe natural spatial variation of marine macrofauna. *Marine Ecology Progress Series* 118, 187-198.
- Kaplan, P., and Baumiller, T.K., 2000. Taphonomic inferences on boring habit in the Richmondian *Onniella meeki* Epibole. *Palaios* 15, 499-510.
- Kidwell, S.M. 2001. Preservation of species abundance in marine death assemblages. *Science* 294, 1091-1094.
- Kidwell, S.M., Rothfus, T.A., and Best, M.M.R., 2001. Sensitivity of taphonomic signatures to sample size, sieve size, damage scoring system and target taxa. *Palaios* 16, 26-52.
- Kingsley-Smith, P.R., Mann, R., Harding, J., 2003a. A predation signature-based key to attribute predation upon bivalves to native versus invasive gastropods. *Proceedings of the Third International Conference on Marine Bioinvasions*, La Jolla, California, p. 72.
- Kingsley-Smith, P.R., Richardson, C.A., Seed, R., 2003b. Stereotypic and size-selective predation in *Polinices pulchellus* (Gastropods: Naticidae) Risso 1826. *Journal of Experimental Marine Biology and Ecology* 295, 173-190.
- Kitchell, J.A., 1986. The Evolution of Predator-Prey Behavior: Naticid Gastropods and Their Molluscan Prey. *In*: Nitecki, M., Kitchell, J.A.

- (eds.), *Evolution of Animal Behavior: Paleontological and Field Approaches*. Oxford University Press, Oxford, pp. 88-110.
- Kowalewski, M., 2002. The fossil record of predation: an overview of analytical methods. *In: Kowalewski, M., Kelley, P.H., (eds.) The Fossil Record of Predation*. Paleontological Society Papers, vol. 8. Yale University, New Haven, pp. 3-42.
- Kowalewski, M., and Hoffmeister, A.P., 2003. Sieves and fossils: effects of mesh size on paleontological patterns. *Palaios* 18, 460-469.
- LaBarbara, M., 1986. The evolution and ecology of body size. *In: Raup, D., and Jablonski, D., (eds.), Patterns and Processes in the History of Life: Life Sciences Research Reports*, v. 36, Springer, Berlin, p. 69-98.
- Leighton, L.R., 2001. Evaluating the accuracy of drilling frequency as an estimate of prey preference and predation intensity. *PaleoBios* 21, 83 Supplement to number 2.
- Lewis, G.F. III and Stoner, A.W., 1981. An examination of methods for sampling macrobenthos in seagrass meadows. *Bulletin of Marine Science* 31, 116-124.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell, pp. 256.
- Martin, R.E., 1999. *Taphonomy: A Process Approach*: Cambridge, Cambridge University Press, 508 p.
- McKindsey, C.W., and Bourget, E., 2001. Body size and spatial variation of community structure in subarctic intertidal boulder fields. *Marine Ecology Progress Series* 216, 17-30.

- Peeters, F.J.C., Ivanova, E.M., Conan, S.M.H., Brummer, G.J., Ganssen, G.M., Troelstra, S.R., and Van Hinte, J., 1999. A size analysis of planktic Foraminifera from the Arabian Sea. *Marine Micropaleontology* 36, 31-63.
- Rodrigues, A.M., Meireles, S., Pereira, T., and Quintino, V., 2007. Spatial heterogeneity recognition in estuarine intertidal benthic macrofaunal communities: influence of sieve mesh-size and sampling depth. *Hydrobiologia* 587, 37-50.
- Rohr, D.M., 1991. Borings in the shell of an Ordovician (Whiterockian) gastropod. *Journal of Paleontology* 65, 687-688.
- Sawyer, J.A., and Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeography, Palaeoclimatology, Palaeoecology* 285, 152-173.
- Sawyer, J.A., and Zuschin, M., *In Review*. Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the Early and Middle Miocene marine fossil record of the Central Paratethys. *Palaios*.
- Schlacher, T.A., and Wooldridge, T.H., 1996. How sieve mesh size affects sample estimates of estuarine benthic macrofauna. *Journal of Experimental Marine Biology and Ecology* 201, 159-171.
- Tanaka, M.O., and Leite, F. P. P., 1998. The effect of sieve mesh size on the abundance and composition of macrophyte-associated macrofaunal assemblages. *Hydrobiologia* 389, 21-28.
- Vale, D., and Gargett, R.H., 2002. Size matters: 3-mm sieves do not increase richness in a fishbone assemblage from Arrawarra I, an Aboriginal

- Australian shell midden on the mid-north coast of New South Wales, Australia. *Journal of Archaeological Science* 29, 57-63.
- Warwick, R.M., 1993. Environmental impact studies on marine communities: pragmatical considerations. *Australian Journal of Ecology* 18, 63-80.
- Warwick, R.M., and Clarke, K.R., 1996. Relationships between body-size, species abundance and diversity in marine benthic assemblages: facts or artefacts? *Journal of Experimental Marine Biology and Ecology* 202, 63-71.
- Zohar, I., and Belmaker, M., 2005. Size does matter: methodological comments on sieve size and species richness in fishbone assemblages. *Journal of Archaeological Science* 32, 635-641.
- Zuschin, M., Oliver, P.G., 2005. Diversity patterns of bivalves in a coral dominated shallow-water bay in the northern Red Sea – high species richness on a local scale. *Marine Biology Research* 1, 396-410.



## **Appendix A**



**Appendix A Table 1.** Summary of living and dead molluscs pooled across all samples

	Family	Species	Dead (n)	Live (n)	Live (%)
Bivalvia	Nuculanidae	<i>Nuculana pella</i>	193	0	0.0
		<i>Nuculana illirica</i>	1	0	0.0
	Nuculidae	<i>Nucula</i> cf. <i>nucleus</i>	228	8	3.4
	Arcidae	<i>Arca noae</i>	100	0	0.0
		<i>Barbatia barbata</i>	51	0	0.0
		<i>Anadara</i> sp.	4	0	0.0
	Noetinae	<i>Striarca lactea</i>	56	0	0.0
	Glycymerididae	<i>Glycymeris</i> sp. juv	1	0	0.0
	Crenellinae	<i>Musculus subpictus</i>	53	1	1.9
	Mytilinae	<i>Mytilus galloprovincialis</i>	298	0	0.0
		<i>Lithophaga</i> sp.	1	2	66.7
	Modiolinae	<i>Modiolus</i> cf. <i>barbatus</i>	122	1	0.8
		<i>Modiolula phaseolina</i>	1	0	0.0
	Pectinidae	<i>Aviculopecten opercularis</i>	47	0	0.0
		<i>Flexopecten glaber</i>	105	0	0.0
		<i>Menachlamys varia</i>	53	1	1.9
	Spondylidae	<i>Spondylus</i> sp.	3	0	0.0
	Anomiidae	<i>Anomia ephippium</i>	233	0	0.0
	Limidae	<i>Lima lima</i>	1	0	0.0
		<i>Lima</i> cf. <i>hians</i>	1	0	0.0
	Ostreidae	<i>Ostrea edulis</i>	193	0	0.0
	Chamidae	<i>Chama gryphoides</i>	179	0	0.0
	Lucinidae	<i>Anodontia fragilis</i>	45	3	6.3
		<i>Lucinella divaricata</i>	152	0	0.0
		<b><i>Loripes lacteus</i></b>	303	40	11.7
		<i>Ctena decussata</i>	26	1	3.7
		<i>Thyasira flexuosa</i>	1	0	0.0
	Galeommatidae	<i>Mysella bidentata</i>	2001	1	0.0
		<i>Galeomma turtoni</i>	12	0	0.0
		<i>Bornia sebetia</i>	3	0	0.0
		<i>Galeommatidae</i> sp. 1	1	0	0.0
		<i>Galeommatidae</i> sp. 2	1	0	0.0
		<i>Galeommatidae</i> sp. 3	88	0	0.0
		<i>Galeommatidae</i> sp.4	7	0	0.0
		<i>Cyamioidea</i> indet.	1	0	0.0
	Cardiidae	<i>Acanthocardia echinata</i>	103	0	0.0
		<i>Parvicardium papillosum</i>	933	0	0.0
		<i>Cerastoderma glaucum</i>	491	9	1.8
	Mactridae	<i>Lutraria</i> sp.	52	0	0.0
		<i>Spisula subtruncata</i>	152	1	0.7
	Solenidae	<i>Solen marginatus</i>	7	0	0.0
	Pharellidae	<i>Phaxas adriaticus</i>	5	1	16.7
	Semelidae	<i>Abra alba</i>	59	0	0.0
		<i>Scrobicularia plana</i>	335	8	2.3
	Tellinidae	<i>Tellina serrata</i>	2	1	33.3
		<i>Tellina fabula</i>	4	0	0.0
		<i>Tellina</i> cf. <i>pulchella</i>	126	0	0.0
		<i>Tellina tenuis</i>	236	26	9.9
		<i>Tellina nitida</i>	2	0	0.0
		<i>Gastrana fragilis</i>	8	1	11.1

**Appendix A Table 1 (continued).** Summary of living and dead molluscs pooled across all samples

	<b>Family</b>	<b>Species</b>	<b>Dead (n)</b>	<b>Live (n)</b>	<b>Live (%)</b>	
	Psammobiidae	<i>Psammobia fervensis</i>	1	0	0.0	
	Solecurtidae	<i>Azorinus chamasolen</i>	13	0	0.0	
		<i>Pharus legumen</i>	0	3	100.0	
	Donacidae	<i>Donax trunculus</i>	5	0	0.0	
		<i>Donax</i> sp.	8	0	0.0	
	Petricolidae	<i>Mysia undata</i>	1	0	0.0	
		<i>Petricola</i> sp.	2	0	0.0	
	Veneridae	<i>Callista chione</i>	95	7	6.9	
		<i>Gouldia minima</i>	522	1	0.2	
		<i>Pitar rudis</i>	8	0	0.0	
		<i>Venerupis</i> cf. <i>rhomboides</i>	352	34	8.8	
		<i>Venerupis aurea</i>	75	0	0.0	
		<i>Chamelea gallina</i>	711	2	0.3	
		<b><i>Tapes decussatus</i></b>	25	11	30.6	
		<i>Dosinia lupinus</i>	13	1	7.1	
		<i>Irus irus</i>	23	0	0.0	
		<i>Venus</i> cf. <i>verrucosa</i> juv.	57	0	0.0	
		<i>Timoclea ovata</i>	3	0	0.0	
		<i>Veneroidea</i> indet.	2	0	0.0	
		Corbulidae	<i>Corbula gibba</i>	1878	72	3.7
			<i>Lentidium mediterraneum</i>	2019	0	0.0
	Gastrochaenidae	<i>Gastrochaena dubia</i>	3	0	0.0	
	Hiatellidae	<i>Hiatella artica</i>	238	2	0.8	
		<i>Hiatella</i> sp.	2	0	0.0	
	Pholadidae	<i>Pholas dactylus</i>	0	1	100.0	
	Pandoridae	<i>Pandora inaequalis</i>	11	0	0.0	
	Cuspidariidae	<i>Cuspidaria cuspidata</i>	4	0	0.0	
	Thraciidae	<i>Thracia</i> sp. juv.	2	1	33.3	
	Indetermined	<i>Bivalvia</i> indet.	2	0	0.0	
Gastropoda	Patellidae	<i>Patella</i> sp.	9	0	0.0	
	Fissurellidae	<i>Diodora graeca</i>	89	0	0.0	
		<i>Emarginula</i> sp.	2	0	0.0	
	Scissurellidae	<i>Scissurella costata</i>	21	0	0.0	
	Haliotidae	<i>Haliotis lamellosa</i>	3	0	0.0	
	Phasianellidae	<i>Tricolia pulla</i>	238	0	0.0	
	Trochidae	<i>Calliostoma laugierii</i>	17	0	0.0	
		<i>Calliostoma</i> sp. 1	819	0	0.0	
		<i>Calliostoma</i> sp. 2	2	0	0.0	
		<i>Gibbula adansonii</i>	1122	1	0.1	
		<i>Gibbula magus</i>	100	1	1.0	
		<i>Gibbula</i> sp. 1	118	0	0.0	
		<i>Gibbula</i> sp. 2	62	0	0.0	
		<i>Gibbula</i> sp. 3	65	0	0.0	
		<i>Gibbula</i> sp. 4	81	0	0.0	
		<i>Jujubinus</i> cf. <i>exasperatus</i>	72	0	0.0	
		<i>Clanculus</i> sp.	39	0	0.0	
	Iravadiidae	<i>Hyala</i> sp.	156	0	0.0	
	Rissoidae	<i>Alvania</i> sp. 1	430	0	0.0	
		<i>Alvania</i> sp. 2	1605	0	0.0	
		<i>Alvania</i> sp. 3	56	0	0.0	
		<i>Alvania</i> sp. 4	33	0	0.0	

**Appendix A Table 1 (continued).** Summary of living and dead molluscs pooled across all samples

Family	Species	Dead (n)	Live (n)	Live (%)
	<i>Alvania</i> sp. 5	59	0	0.0
	<i>Alvania</i> sp. 6	344	0	0.0
	<i>Alvania</i> sp. 7	21	0	0.0
	<i>Pusillina</i> cf. <i>marginata</i>	984	0	0.0
	<i>Rissoa labiosa</i>	1780	0	0.0
	<i>Rissoa</i> sp.	104	0	0.0
	<i>Rissoidae</i> sp. 1	1542	0	0.0
	<i>Rissoidae</i> sp. 2	95	0	0.0
	<i>Rissoidae</i> sp. 3	558	0	0.0
	<i>Rissoidae</i> sp. 4	40	0	0.0
	<i>Rissoidae</i> sp. 5	42	0	0.0
	<i>Rissoidae</i> sp. 6	39	0	0.0
	<i>Rissoidae</i> sp. 7	669	0	0.0
	<i>Rissoina bruguieri</i>	87	0	0.0
	<i>Rissoina</i> sp.	21	0	0.0
	<i>Cingula</i> sp.	209	0	0.0
	<i>Manzonia</i> sp.	259	0	0.0
Hydrobiidae	<i>Hydrobia ulvae</i>	2754	0	0.0
	? <i>Hydrobia</i> sp. 1	16	0	0.0
	? <i>Hydrobia</i> sp. 2	6	0	0.0
Truncatellidae	<i>Truncatella subcylindrica</i>	14	0	0.0
	<i>Truncatella</i> sp.	7	0	0.0
Cerithiidae	<i>Bittium reticulatum</i>	2296	0	0.0
	<i>Bittium latreilli</i>	8934	1	0.0
	<i>Cerithium vulgatum</i>	202	1	0.5
	<i>Littorina</i> sp.	50	0	0.0
Turritellidae	<i>Turritella communis</i>	2209	0	0.0
Aporrhaidae	<i>Aporrhais pespelecani</i>	412	0	0.0
Calyptraeidae	<i>Calyptraea chinensis</i>	299	0	0.0
Naticidae	<i>Euspira macilenta</i>	384	0	0.0
Tonnoidea	<i>Tonna galea</i>	13	0	0.0
Muricidae	<i>Murex (Bolinus) brandaris</i>	48	1	2.0
	<i>Hexaplex trunculus</i> juv.	2	0	0.0
	<i>Ocinebrina</i> sp.	18	0	0.0
	<i>Muricopsis</i> sp.1	67	0	0.0
	<i>Muricopsis</i> sp. 2	46	0	0.0
Buccinidae	<i>Cantharus</i> sp.	4	0	0.0
	<i>Chauvetia</i> sp.	64	0	0.0
Nassariidae	<i>Nassarius</i> cf. <i>pygmaeus</i>	2387	21	0.9
	<b><i>Nassarius incrassatus</i></b>	187	22	10.5
	<i>Nassarius mutabilis</i>	57	2	3.4
	<b><i>Nassarius reticulatus</i></b>	23	9	28.1
	<i>Nassarius corniculus</i> juv.	52	0	0.0
	<b><i>Cyclope neritea</i></b>	39	15	27.8
Marginellidae	<i>Granulina clandestina</i>	76	0	0.0
Mitridae	<i>Mitra</i> cf. <i>cornicula</i> juv.	1	0	0.0
Costellariidae	<i>Vexillum</i> sp.	27	0	0.0
Conidae	<i>Conus mediterraneus</i>	36	0	0.0
Turridae	<i>Bela</i> spp.	78	0	0.0
	<i>Mangelia</i> spp.	377	0	0.0
	<i>Raphitoma</i> spp.	13	0	0.0
	? <i>Mitrolumna</i> spp.	30	0	0.0

**Appendix A Table 1 (continued).** Summary of living and dead molluscs pooled across all samples

Family	Species	Dead (n)	Live (n)	Live (%)
Cerithiopsidae	<i>Cerithiopsis tubercularis</i>	8	0	0.0
	<i>Cerithiopsis</i> sp.	27	0	0.0
Triphoridae	<i>Monophora</i> sp. 1	79	0	0.0
	<i>Monophora</i> sp. 2	87	0	0.0
	<i>Metaxia metaxa</i>	15	0	0.0
Epitoniidae	<i>Epitonium celesti</i>	51	0	0.0
	<i>Epitonium</i> sp.	31	0	0.0
Aclididae	<i>Aclis</i> sp.	1	0	0.0
Eulimidae	<i>Eulima</i> spp.	36	0	0.0
	<i>Melanella</i> spp.	23	0	0.0
	<i>Vitreolina curva</i>	4	0	0.0
	<i>Haliella stenostoma</i>	1	0	0.0
Pyramidellidae	<i>Odostomia</i> spp.	119	0	0.0
	<i>Turbonilla</i> spp.	127	0	0.0
	<i>Eulimella</i> sp.	3	0	0.0
	<i>Folinella excavata</i>	11	0	0.0
	<i>Chrysallida</i> spp.	70	0	0.0
Acteonidae	<i>Acteon tornatilis</i>	11	0	0.0
Haminoeidae	<b><i>Haminoea navicula</i></b>	54	34	38.6
	<i>Atys jeffreysi</i>	8	0	0.0
Philineidae	<i>Philine aperta</i>	1	0	0.0
	<i>Philine scabra</i>	3	0	0.0
	<i>Laona pruinosa</i>	1	0	0.0
Scaphandridae	<i>Cylichna cylindracea</i>	47	0	0.0
Retusidae	<i>Retusa semiculcata</i>	92	0	0.0
	<i>Rhizorus acuminatus</i>	3	0	0.0
Ellobiidae	<i>Ovatella myosotis</i>	1	0	0.0
Scaphopoda				
Dentaliidae	<i>Dentalium</i> sp. 1	1572	58	3.6

Columns 'Dead' and 'Live' list counted individuals (bivalves adjusted to account for disarticulated valves) and '% Live' lists the percentage recovered alive. The 6 species of which n > 10 and at least 10 % were living are in bold font.

**Appendix A Table 2.** Summary of drill hole data for ecological categories across environments

Category	Environment	n	D	ID	DF (%)	IDF (%)	PE (%)
<b>Bivalve Diet:</b>							
<b>Chemosymbiotic</b>							
	Tidal Flat	300	2	0	0.7	0.0	0.0
	Sublittoral	231	119	4	51.5	1.7	3.3
	Delta	11	6	0	54.5	0.0	0.0
	Mud	2	0	0	0.0	0.0	.
	Sand	218	113	4	51.8	1.8	3.4
<b>Carnivore</b>							
	Tidal Flat	0	0	0	0.0	0.0	0.0
	Sublittoral	4	2	0	50.0	0.0	0.0
	Delta	0	0	0	0.0	0.0	0.0
	Mud	4	2	0	50.0	0.0	0.0
	Sand	0	0	0	0.0	0.0	0.0
<b>Deposit-feeder</b>							
	Tidal Flat	572	9	0	1.6	0.0	0.0
	Sublittoral	634	180	2	28.4	0.3	1.1
	Delta	50	8	1	16.0	2.0	11.1
	Mud	447	126	1	28.2	0.2	0.8
	Sand	137	46	0	33.6	0.0	0.0
<b>Suspension-feeder</b>							
	Tidal Flat	2563	5	2	0.2	0.1	28.6
	Sublittoral	8845	2763	344	31.2	3.9	11.1
	Delta	672	128	12	19.0	1.8	8.6
	Mud	4714	1631	272	34.6	5.8	14.3
	Sand	3459	1004	60	29.0	1.7	5.6
<b>Gastropod Diet</b>							
<b>Browsing carnivore</b>							
	Tidal Flat	75	0	0	0.0	0.0	.
	Sublittoral	838	164	3	19.6	0.4	1.8
	Delta	1	0	0	0.0	0.0	.
	Mud	2	0	0	0.0	0.0	.
	Sand	835	164	3	19.6	0.4	1.8
<b>Detritivore</b>							
	Tidal Flat	1	0	0	0.0	0.0	.
	Sublittoral	568	71	2	12.5	0.4	2.7
	Delta	8	0	0	0.0	0.0	.
	Mud	344	28	0	8.1	0.0	0.0
	Sand	216	43	2	19.9	0.9	4.4
<b>Herbivore</b>							
	Tidal Flat	9108	158	0	1.7	0.0	0.0
	Sublittoral	16143	4764	33	29.5	0.2	0.7
	Delta	202	49	0	24.3	0.0	0.0
	Mud	124	26	0	21.0	0.0	0.0
	Sand	15817	4689	33	29.6	0.2	0.7

**Appendix A Table 2 (continued).** Summary of drill hole data for ecological categories across environments

Category	Environment	n	D	ID	DF (%)	IDF (%)	PE (%)
<b>Parasite</b>							
	Tidal Flat	11	0	0	0.0	0.0	.
	Sublittoral	683	141	19	20.6	2.8	11.9
	Delta	11	2	0	18.2	0.0	0.0
	Mud	143	34	0	23.8	0.0	0.0
	Sand	529	105	19	19.8	3.6	15.3
<b>Predator</b>							
	Tidal Flat	138	1	0	0.7	0.0	0.0
	Sublittoral	4084	681	56	16.7	1.4	7.6
	Delta	250	26	0	10.4	0.0	
	Mud	2001	222	50	11.1	2.5	18.4
	Sand	1833	433	6	23.6	0.3	1.4
<b>Suspension-feeder</b>							
	Tidal Flat	0	0	0	0.0	0.0	0.0
	Sublittoral	2508	981	1	39.1	0.0	0.1
	Delta	14	2	0	14.3	0.0	0.0
	Mud	2319	928	1	40.0	0.0	0.1
	Sand	175	51	0	29.1	0.0	0.0
<b>Scaphopod Diet</b>							
<b>Predator</b>							
	Tidal Flat	0	0	0	0.0	0.0	0.0
	Sublittoral	1573	41	4	2.6	0.3	8.9
	Delta	5	0	0	0.0	0.0	0.0
	Mud	1489	38	2	2.6	0.1	5.0
	Sand	79	3	2	3.8	2.5	40.0
<b>Bivalve Substrate Relationship</b>							
<b>Borer</b>							
	Tidal Flat	1	0	1	0.0	100.0	100.0
	Sublittoral	8	0	0	0.0	0.0	.
	Delta				0.0	0.0	.
	Mud	4	0	0	0.0	0.0	.
	Sand	4	0	0	0.0	0.0	.
<b>Commensal</b>							
	Tidal Flat	4	0	0	0.0	0.0	.
	Sublittoral	2153	876	2	40.7	0.1	0.2
	Delta	47	8	0	17.0	0.0	0.0
	Mud	1927	825	2	42.8	0.1	0.2
	Sand	179	43	0	24.0	0.0	0.0
<b>Infaunal</b>							
	Tidal Flat	3414	16	1	0.5	0.0	5.9
	Sublittoral	5848	1638	309	28.0	5.3	15.9
	Delta	658	133	11	20.2	1.7	7.6
	Mud	2653	828	266	31.2	10.0	24.3
	Sand	2537	677	32	26.7	1.3	4.5

**Appendix A Table 2 (continued).** Summary of drill hole data for ecological categories across environments

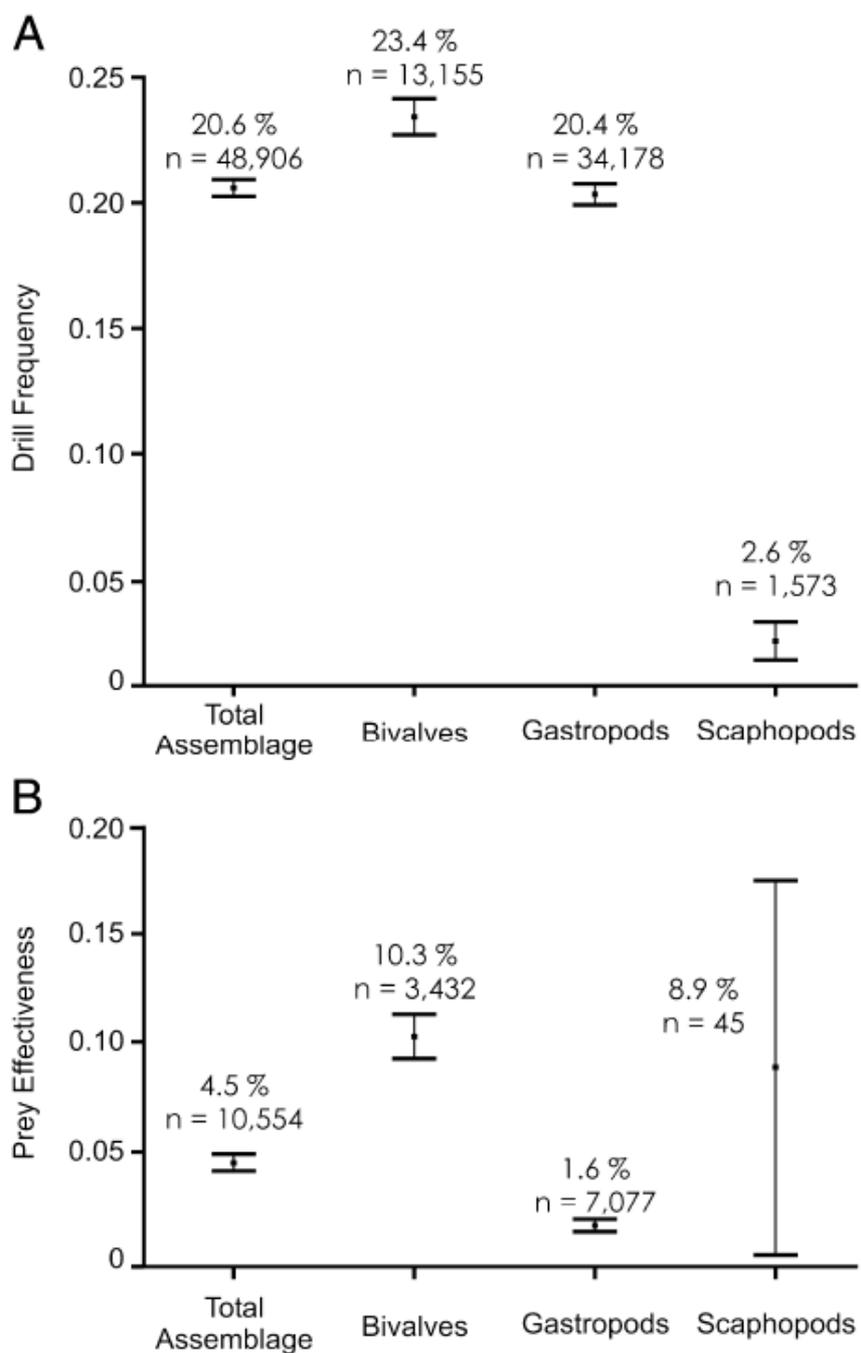
Category	Environment	n	D	ID	DF (%)	IDF (%)	PE (%)
<b>Nestler</b>							
	Tidal Flat	3	0	0	0.0	0.0	.
	Sublittoral	267	87	4	32.6	1.5	4.4
	Delta	2	0	0	0.0	0.0	.
	Mud	113	16	3	14.2	2.7	15.8
	Sand	152	71	1	46.7	0.7	1.4
<b>Epifaunal</b>							
	Tidal Flat	13	0	0	0.0	0.0	.
	Sublittoral	1433	462	35	32.2	2.4	7.0
	Delta	22	1	2	4.5	9.1	66.7
	Mud	469	89	2	19.0	0.4	2.2
	Sand	942	372	31	39.5	3.3	7.7
<b>Epifaunal Bivalve Attachment</b>							
<b>Bysally</b>							
	Tidal Flat	10	0	0	0.0	0.0	0.0
	Sublittoral	672	184	4	27.4	0.6	2.1
	Delta	7	0	0	0.0	0.0	0.0
	Mud	43	6	0	14.0	0.0	0.0
	Sand	622	178	4	28.6	0.6	2.2
<b>Cemented</b>							
	Tidal Flat	2	0	0	0.0	0.0	0.0
	Sublittoral	610	263	31	43.1	5.1	10.5
	Delta	12	1	2	8.3	16.7	66.7
	Mud	304	72	2	23.7	0.7	2.7
	Sand	294	190	27	64.6	9.2	12.4
<b>Recliner</b>							
	Tidal Flat	1	0	0	0.0	0.0	0.0
	Sublittoral	151	15	0	9.9	0.0	0.0
	Delta	3	0	0	0.0	0.0	0.0
	Mud	122	11	0	9.0	0.0	0.0
	Sand	26	4	0	15.4	0.0	0.0

*n* = abundance (corrected to account for disarticulated bivalves), *D* = number of complete drill holes, *ID* = number of incomplete drill holes, *DF* = drill frequency, *IDF* = incomplete drill frequency, *PE* = prey effectiveness.

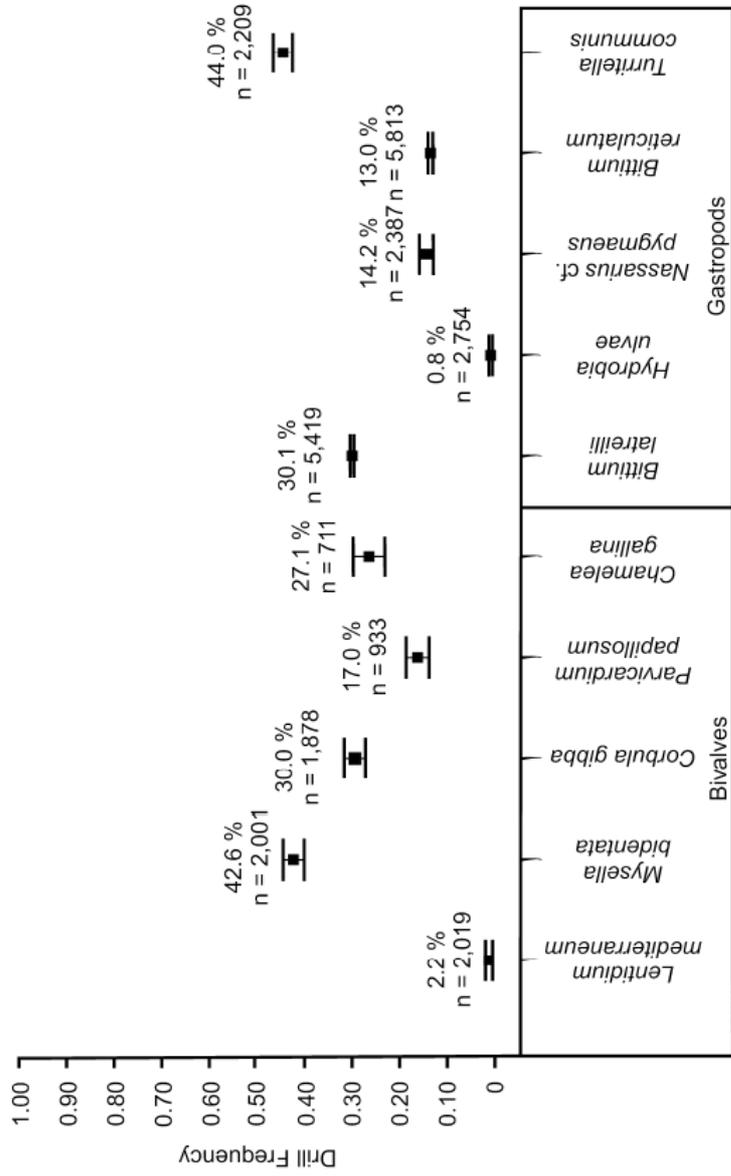


## **Appendix B**

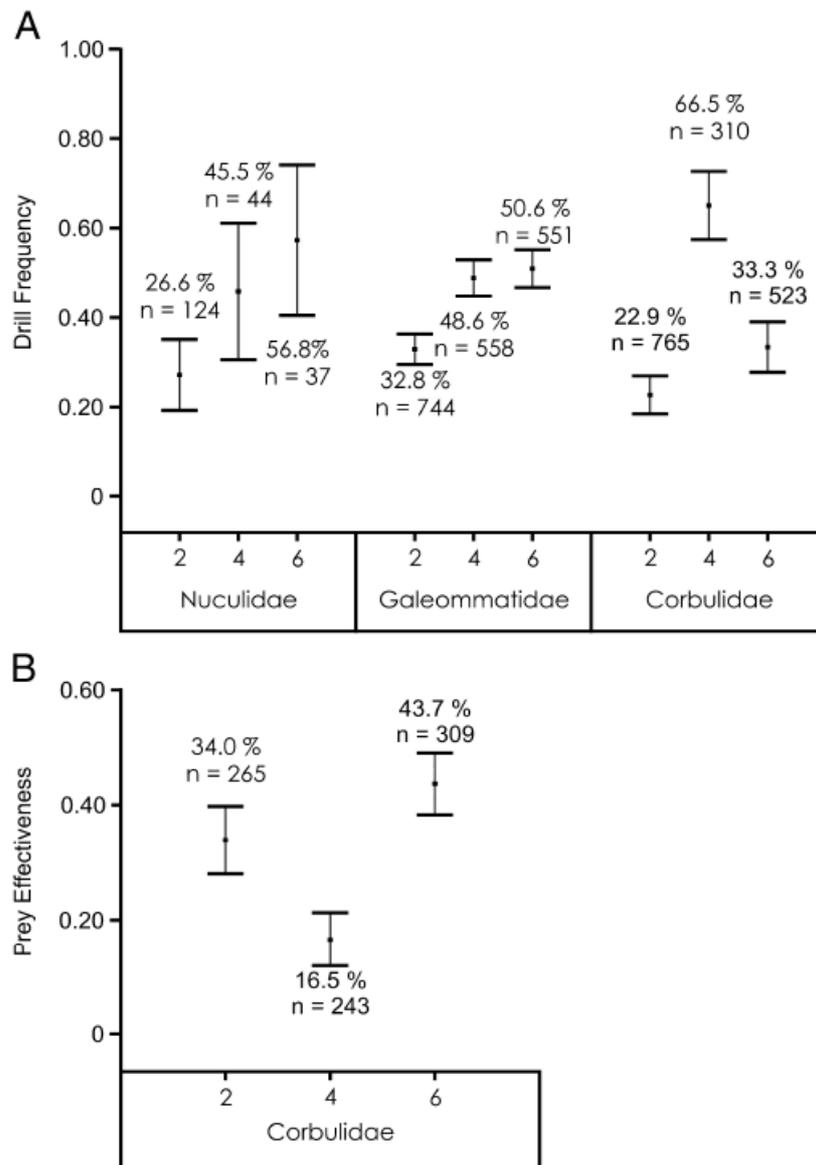




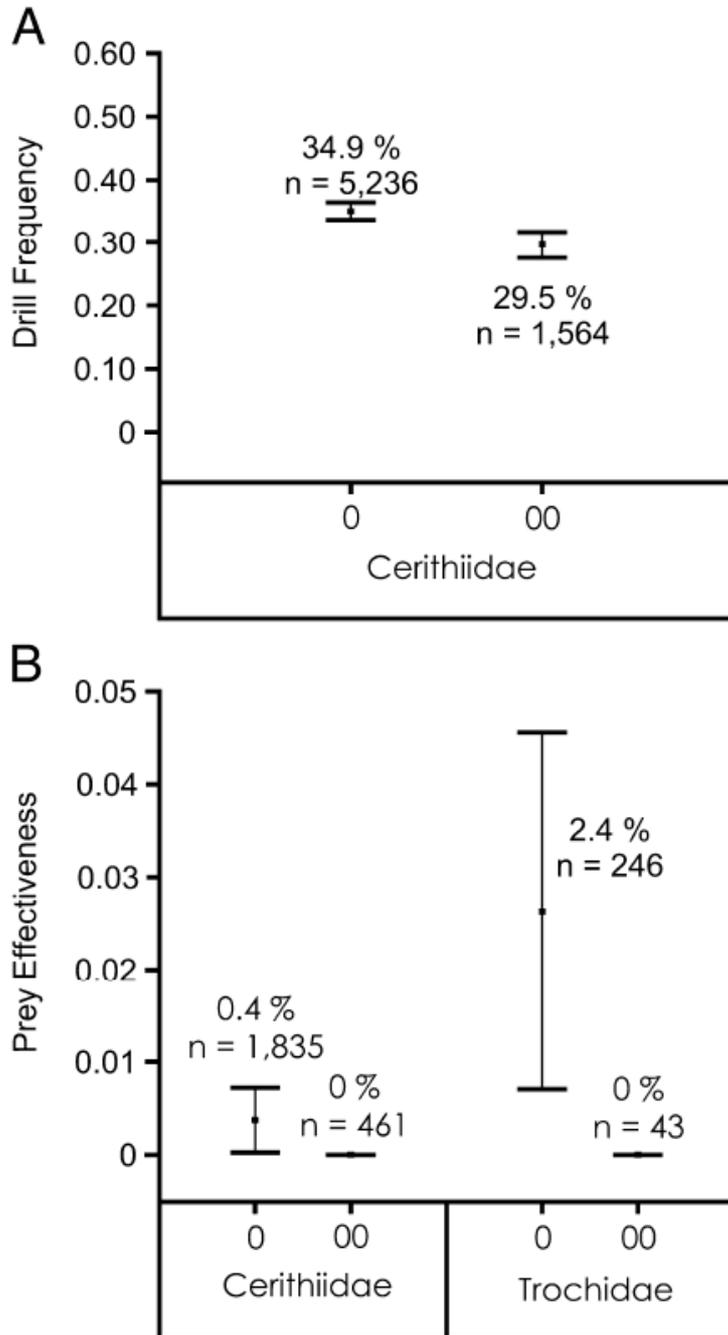
**Appendix B Fig. 1.** A) Mean drill frequencies of the total assemblage and among classes pooled across all samples. B) Prey effectiveness of the total assemblage and among classes pooled across all samples. In a) 'n' is the total number of individuals in the assemblage. In b) 'n' is the total number of predatory attempts (complete plus incomplete drill holes). Error bars are 95 % confidence intervals.



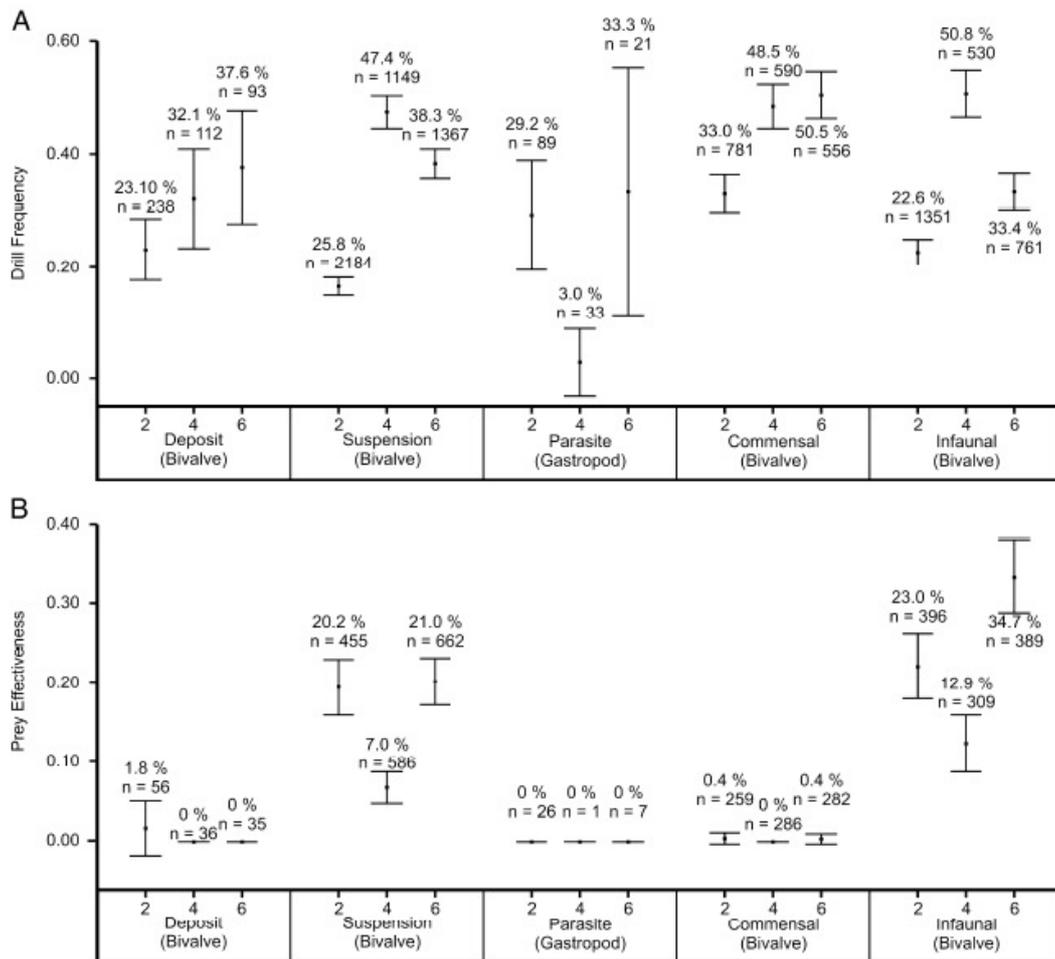
**Appendix B Fig. 2.** Mean drilling frequencies of the five most abundant bivalve and gastropod species pooled across all samples. Error bars are 95 % confidence intervals.



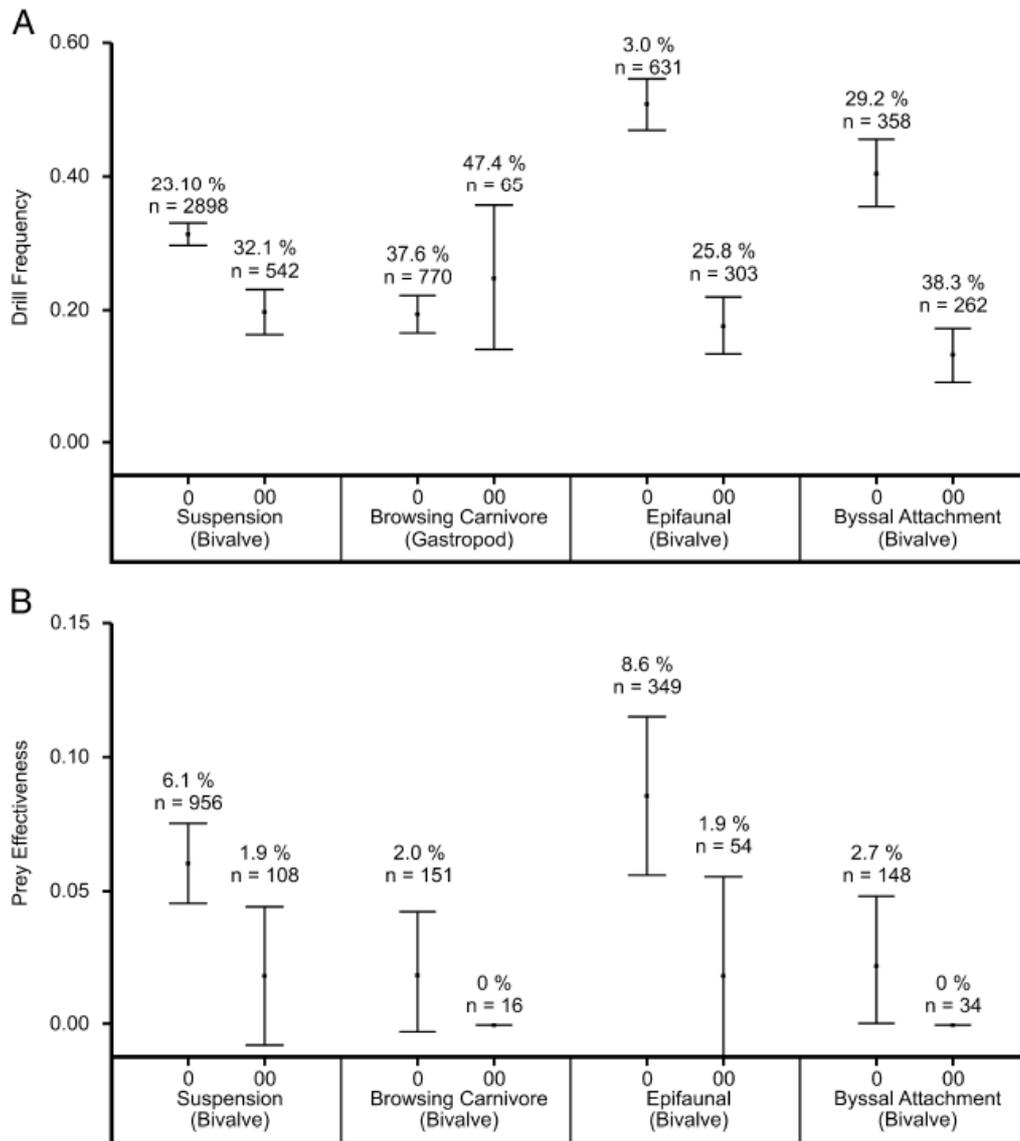
**Appendix B Fig. 3.** A) Significantly different intra-environmental drill frequencies for families ( $n > 20$ ) from level bottom mud samples. B) Intra-environmental prey effectiveness for Corbulidae, the only family ( $n > 20$ ) from level bottom mud samples showing significantly different prey effectiveness ( $n$  = complete plus incomplete drill holes). Error bars are 95 % confidence intervals.



**Appendix B Fig. 4.** A) Intra-environmental drill frequencies for the family Cerithiidae, the only family ( $n > 20$ ) from level bottom sand samples with significantly different drill frequencies. B) Intra-environmental prey effectiveness for families ( $n > 20$ ) in both level bottom sand samples. 'n' = complete plus incomplete drill holes. Error bars are 95 % confidence intervals.



**Appendix B Fig. 5.** A) Intra-environmental comparison of drill frequencies for ecological categories with significant differences among level bottom mud samples. 'n' = number of molluscs (adjusted to account for disarticulated bivalves). B) Intra-environmental comparison of prey effectiveness for ecological categories with significant differences in drill frequency among level bottom mud samples. 'n' = incomplete plus complete drill holes. Error bars are 95 % confidence intervals.



**Appendix B Fig. 6.** A) Intra-environmental comparison of drill frequencies for ecological categories with significant differences between level bottom sand samples. 'n' = number of molluscs (adjusted to account for disarticulated bivalves). B) Intra-environmental comparison of prey effectiveness for ecological categories with significant differences in drill frequency between level bottom sand samples. 'n' = incomplete plus complete drill holes. Error bars are 95 % confidence intervals.

CURRICULUM VITA  
**Jennifer A. Sawyer, MSc**

CONTACT

Full Name: Sawyer, Jennifer Ashley  
Address: Wiedner Hauptstraße 142/1/7  
1050 Vienna, Austria  
Phone (Mobile): +43 664 778 851 0629  
E-mail: jennifer.sawyer@univie.ac.at

PERSONAL DETAILS

Date of Birth: 27 April, 1983, Sanford, North Carolina  
Nationality: USA

EDUCATION

- Since 02/2007 Ph.D., Title: "Quantitative studies of drilling predation on Cenozoic and Recent marine molluscs from Europe", University of Vienna, Austria. Supervisor: Ao. Prof. Dr. M. Zuschin
- 08/2004-05/2007 MSc. Geological Sciences, Title: "Effects of predation on the morphology of bellerophonid gastropods: a community analysis of gastropods from Late Pennsylvanian shales of North-Central Texas", San Diego State University, California, USA. Supervisor: Prof. Dr. Lindsey R. Leighton
- 05/2001-08/2004 B.Sc. Geology, Title: "Phenotypic variation in the bryozoan *Leioclema punctatum* (Hall, 1858) from Mississippian ephemeral host substrates", Appalachian State University, North Carolina, USA. Supervisor: Prof. Dr. Steve J. Hageman  
Departmental Honors

PUBLICATIONS

- Hageman, S.J. & **Sawyer, J.A.**, 2006. Phenotypic variation in the bryozoan *Leioclema punctatum* (Hall, 1858) from Mississippian ephemeral host microcommunities. *Journal of Paleontology*, 80, 1047-1057.
- Sawyer, J.A.**, Zuschin, M., Riedel, B., & Stachowitsch, M., 2009. Predator-prey interactions from in situ time-lapse observations of a sublittoral mussel bed in the Gulf of Trieste (Northern Adriatic). *Journal of Experimental Marine Biology and Ecology*, 371, 10-19.
- Sawyer, J.A.** & Zuschin, M., 2010. Intensities of drilling predation of molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285, 152-173.
- Sawyer, J.A.** & Zuschin, M., In Review. Spatial variation in drilling predation from intertidal, shallow sublittoral and shelf environments from the early and middle Miocene marine fossil record of the Central Paratethys. *Palaios*.

## CONFERENCE ABSTRACTS

\*\* indicates the presenter of the talk associated with the abstract.

\* indicates the presenter of the poster associated with the abstract.

- Sawyer, J.A.\*\*** & Zuschin, M. 2009. Comparison of Eocene to Recent patterns of drilling predation from molluscan assemblages of Central Europe: preliminary results. 9<sup>th</sup> North American Paleontological Convention Abstracts, Cincinnati Museum Center Scientific Contributions 3, p. 18.
- Sawyer, J.A.\*** & Zuschin, M. 2009. Intensities of drilling predation from molluscan assemblages along a subtidal transect through the northern Gulf of Trieste (Adriatic Sea). 9<sup>th</sup> North American Paleontological Convention Abstracts, Cincinnati Museum Center Scientific Contributions 3, 324-325.
- Sawyer, J.A.\*\*** & Zuschin, M. 2008. Predatory drilling frequencies in Burdigalian and Badenian molluscan assemblages from the Central Paratethys. Erlanger geologische Abhandlungen 6, p. 55.
- Sawyer, J.A.\*** & Zuschin, M. 2008. Intensities of drilling predation from molluscan assemblages along a transect through the northern Gulf of Trieste (Adriatic Sea). Erlanger geologische Abhandlungen 6, p. 110.
- Sawyer, J.A.\*** & Zuschin, M. 2008. Modern molluscan drilling frequencies in the Gulf of Trieste. Journal of Alpine Geology (Mitt. Ges. Geol. Bergbaustud. Österr.) 49, p. 92.
- Sawyer, J.A.\*** & Zuschin, M. 2008. Predatory drilling intensities of Karpatian and Badenian molluscan assemblages from the Central Paratethys. Journal of Alpine Geology (Mitt. Ges. Bergbaustud. Österr.) 49, p. 92-93.
- Sawyer, J.A.**, Zuschin, M., Riedel, B.\* & Stachowitsch, M. 2008. Predator-prey interactions between *Hexaplex trunculus* (Gastropoda: Muricidae) and the black mussel *Mytilus galloprovincialis* (Bivalvia: Mytilidae) in the Gulf of Trieste. In: Abstracts of the 43<sup>rd</sup> European Marine Biology Symposium (EMBS); Ponta Delgada, Azores; 2008 Sept 08-12; Abstracts p.3.36, p. 113.
- Sawyer, J.A.** & Leighton, L.R.\*\* 2007. Sampling the predator's buffet: a multiple-prey study of predation on Late-Pennsylvanian gastropods from Texas. Geological Society of America, Abstracts with Programs. 39, p. 14.
- Sawyer, J.A.\*\*** & Zuschin, M. 2007. Predatory drilling frequencies in lower Miocene (Karpatian) near-shore molluscan assemblages from the locality Laa (Lower Austria). Joannea Geol. Paläont. 9, p. 92.
- Sawyer, J.A.\*** & Zuschin, M., 2007. Patchiness of predatory drilling frequencies of Lower and Middle Miocene molluscan assemblages from the Central Paratethys. Wiss. Mitt. Inst. Geol. 36, p. 120.
- Sawyer, J.A.\*\*** & Zuschin, M., 2007. Modern intensities of drilling predation in the Northern Adriatic Sea: a poor Paleozoic and Cretaceous analogue. Geological Society of America, Abstracts with Programs, 39, p. 532.
- Sawyer, J.A.\*\*** & Leighton, L.R. 2006. Morphological response to predation in an upper-Pennsylvanian bellerophonid gastropod. Geological Society of America, Abstracts with Programs. 38, p. 538.

### CONFERENCE ABSTRACTS (Continued)

Tyler, C.L. \*\*, Leighton, L.R., Redman, C.M., Landau, E. & **Sawyer, J.A.** 2006. Community paleoecology of the Bird Spring Group, Arrow Canyon, NV. Geological Society of America, Abstracts with Programs. 38, p. 404.

Leighton, L.R.\*\* & **Sawyer, J.A.**, 2005. Predator-prey dynamics of Late Paleozoic ecosystems: A case-study on the role of molluscs. American Malacological Society & Western Malacological Society Joint Meeting.

**Sawyer, J.A.** \*\* 2005. Timing of morphological change in gastropods during the mid-Paleozoic precursor to the Mesozoic Marine Revolution. Geological Society of America, Abstracts with Programs. 37, p. 3.

**Sawyer, J.A.**\*\* & Leighton, L.R. 2005. Predator-prey dynamics in Pennsylvanian nearshore shales: Effects of molluscan invasion into "normal" marine habitats. Geological Society of America, Abstracts with Programs. 37, p. 13.

**Sawyer, J.A.**\* & Hageman, S.J. 2003. Phenotypic variation in an epibiotic bryozoan (*Leioclema* sp.) from Chesterian ephemeral host substrates. Geological Society of America, Abstracts with Programs. 35, p. 163.

### TEACHING EXPERIENCE (as Teaching Assistant)

Fall 2004	GEOL 537 Geobiology Laboratory
Spring 2004	GEOL 101 Dynamics of the Earth Laboratory
	GEOL 105 Historical Geology Laboratory
Fall 2003	GLY 1101 Introduction to General Geology laboratory

### EMPLOYMENT (Geosciences)

03/2007-02/2010	Research Assistant, Institut für Paläontologie, Geowissenschaften, Geographie und Astronomie, Universität Wien
08/2005-07/2006	Research Assistant, Department of Geological Sciences, San Diego State University
01/2005-07/2005	Graduate Teaching Assistant, San Diego State University
08/2004-12/2004	Graduate Teaching Assistant Coordinator, San Diego State University
03/2003-07/2004	Undergraduate Research Assistant, Appalachian State University

### HONORS AND AWARDS

2004	Departmental Honors, Department of Geology Appalachian State University
2006	GSA Student Research Grant \$2300 with Outstanding Mention
2006	Paleontological Society Student Research Grant \$500

### PROFESSIONAL MEMBERSHIPS:

Palaeontological Association; Paleontological Society; Society for Sedimentary Geology; Geological Society of America.