ECOLOGICAL INTERACTIONS AND COMMUNITY STRUCTURE IN LIVING AND SUBFOSSIL MOLLUSC ASSEMBLAGES FROM THE SOUTHERN GREAT BARRIER REEF



One Tree Island, photo credit: Darrel Kaufman

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Esta tesis, fruto de mucho amor y esfuerzo, va dedicada a mis papás;

gracias por enseñarme a ser curiosa y perseverante, y por apoyarme en nuevos desafíos.

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STATEMENT OF CANDIDATE

I certify that the work in this thesis entitled "*Ecological interactions and community structure in living and subfossil molluscan assemblages from the southern Great Barrier Reef*" has not previously been submitted for a degree nor has it been submitted as part or requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself have been appropriately acknowledged. In addition, I certify that all information sources and literature used are indicated in thesis.

Julieta Martinelli

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SUMMARY

Understanding the processes that affect diversity and community structure in environments with little anthropogenic impact is key to validating conservation palaeobiological studies. This thesis investigates how much of the ecology of living molluscan communities can be inferred from dead molluscan assemblages. Ecological and subfossil molluscan assemblages were collected from the One Tree Reef (OTR) lagoon, southern Great Barrier Reef. One Tree Reef has been subject to minimal anthropogenic disturbance, making it well suited to studies linking ecology and palaeobiology. An examination of the living species' spatial distribution and diversity indicated that neither aggregation nor diversity were different from a random community (Chapter 1). I analysed dead assemblage fidelity and showed that these accurately preserve the living molluscan community (Chapter 2). Observed compositional differences were mainly due to the low probability of sampling rare species, but some taphonomic effects were found (20% of the species). In the last two chapters I provide an in-depth analysis of drilling predation in the OTR lagoon. I initially examined the relation between predator/prey encounter frequencies and predation frequencies (Chapter 3). Then, I examined the effectiveness of individual-level morphological traits previously used in Optimal Foraging experiments as effective defences against drilling predators (Chapter 4). I showed that while shell size and thickness have a strong explanatory power, species-level differences better predict predation frequency. Therefore, traits typically used to explain predation frequency do not hold their explanatory power at the community level. Overall, by retrieving information from living communities and preserved shell assemblages, I provide new insights into the most studied interaction by palaeobiologists, and show that shell assemblages from a protected reef lagoon are reliable records of past living communities. Confirming dead assemblage fidelity enables us to determine an essential baseline to quantify and remediate changes that marine communities may be subject to in the near future.

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INTRODUCTION

One of the greatest challenges faced by ecologists is understanding how natural systems work, while simultaneously documenting how they are changing. Given the impacts of humans on marine ecosystems (Jackson et al. 2001, Jackson 2008, 2010, Hughes et al. 2003, Halpern et al. 2008), it is fundamental to comprehend how ecological systems operate in the least human-modified conditions possible. Of equal importance are historical studies that add 'another layer' to the modern communities ecologists study. For example, studies that utilise data from the recent past (decades to hundreds of years) as a baseline for comparison with extant communities and ecosystems (e.g. Kowalewski et al. 2000, Jackson et al. 2001, Kidwell 2001, Kowalewski et al. 2014).

The last few decades have seen the emergence of Conservation Palaeobiology, an applied sub-discipline of Palaeobiology. The main objective of Conservation Palaeobiology is to use information from fossil assemblages to inform management - among other applications - about recent communities and ecosystems (Dietl & Flessa 2011, Kidwell 2013). The foundational studies of this discipline have shown that valuable ecological information can be retrieved from past assemblages (e.g. Kowalewski et al. 2000, Jackson et al. 2001, Kidwell 2001, Kowalewski et al. 2014). However, rising above ecologists' resistance to use data from non-living organisms (i.e. no manipulative experiments) to draw ecological conclusions still remains one of the greatest challenges of Conservation Palaeobiology (Kidwell 2013).

In order to provide reliable quantitative ecological information from observational studies, very large numbers of individuals are needed. This is due to several reasons. First, in order to determine species diversity, rank abundances and other metrics of community structure, multiple organisms need to be collected - ideally across all seasons - as natural populations have temporal fluctuations that can affect these metrics (Gaines & Roughgarden 1985; Powell et al. 1986). Second, large numbers of individuals are necessary to quantify diversity given the very high proportion of rare species, particularly in coral reef areas

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(Bouchet et al. 2002; Zuschin & Oliver 2005). Other informative patterns such as species' spatial distributions, as well as biotic interactions cannot be accurately determined with small sample sizes or limited time-series. Third, there are numerous biases associated with the preservation of living organisms in dead assemblages (i.e. taphonomic biases) that - even if unavoidable - can be reduced by collecting large sample sizes. For example, the chances of finding unbroken specimens of fragile shells are higher if the sample size is large. Likewise, rare species with specialised life habits are also more likely to be present in large samples due to sampling probability. Taking large samples will help to ensure a 'representative' sample, giving an accurate estimate of community structure and composition.

Marine molluscs are a frequent focus of ecological, taphonomic and palaeobiological studies (e.g. Kowalewski et al. 2000, Kidwell 2001), mainly because they allow for large sample sizes both in living and in dead communities. Molluscs are very abundant in environments that range from estuaries to coral reefs (Kowalewski et al. 2000, Bouchet et al. 2002, Zuschin & Oliver 2005); they have calcium carbonate shells that confer high preservation potential; and biotic interactions such as predation by drilling gastropods can be readily quantified from traces in their shells. Consequently, molluscs make a suitable group to study - and confirm - the usefulness and applicability of the Conservation Palaeobiology framework.

For this thesis, I use ecological and sub-fossil data from a species-rich mollusc community from carbonate lagoons from One Tree Reef, in the Capricorn group, southern Great Barrier Reef (23°20' S, 152°06' E). One Tree Reef (OTR) is well-suited to studies at the interface between Ecology and Palaeobiology for several reasons. First, OTR has minimal human impact, as it is a Scientific Research Zone part of the Great Barrier Reef Marine Park. Second, mollusc shells from sediments adjacent to the reef have been dated, and they show a

chronostratigraphical order (Kosnik et al. 2015), indicating OTR is a reliable system to study temporal changes. This is relevant because this stratigraphic order has not been found in other reefs from the Great Barrier Reef (Kosnik et al. 2007, Kosnik et al. 2009). Finally, a previous study of the soft sediment mollusc community from OTR carried out 30 years ago (Jones et al. 1990) provides a valuable opportunity to compare, contrast and corroborate some of the results obtained in some of the chapters of this thesis.

This dissertation encompasses four independent manuscripts that are united under the theme of community structure and ecological interactions in living and dead mollusc assemblages. As such, there is an overlap between ecological and palaeobiological questions and methodologies. My thesis aims to investigate how much of the ecology of the living communities can be inferred from dead mollusc assemblages; and my over-arching hypothesis is that in this protected system, dead mollusc assemblages provide a reliable and informative record of the living communities and (some) of the processes that shape them. In order to test this, I investigated different aspects of community structure, together with organisms' spatial distribution, compositional agreement between living communities and dead assemblages, and an in-depth analysis of drilling predation.

I start by exploring the diversity and spatial distribution of the living mollusc community (Chapter 1). By looking at spatial aggregation metrics and quantifying alpha and beta diversities at two spatial scales, I found evidence that species' spatial distribution and diversity are not significantly different from a random community. This suggests that local interactions such as competition for space or food do not have a strong impact on this community. This manuscript is aimed at a general ecological audience, and it underwent one round of reviews. Suggestions from previous reviewers have been incorporated, and the manuscript has been prepared for submission to *Marine Ecology*.

Introduction

In Chapter 2, I investigated the agreement in composition between the living mollusc community and dead mollusc assemblage. I determined the community composition of both assemblages, and established comparisons between them, and the assemblage collected 30 years ago by Jones et al. (1990). Results suggest that dead assemblages explain 80% of the living assemblage rank abundance order, and that compositional differences are due to sampling probabilities of rare species. Taphonomic factors account for less than 20% of the variability. This manuscript is aimed at both an ecological and a palaeobiological audience, so it will be submitted to *Coral Reefs*.

In the last two data chapters I shifted the focus to drilling predation in order to further understand the role of biotic interactions in this ecosystem. In Chapter 3, I analyse a community-level aspect of drilling predation, namely prey encounter frequency. I used species relative abundances as a measure of encounter frequency with predators to test the hypothesis that high encounter frequencies lead to high predation frequencies. Results suggest this is not the case, as predators tend to forage randomly instead of showing preference for the most abundant prey. This manuscript is primarily aimed at a palaeobiological audience, and it was submitted to *PALAIOS* in 2014. This manuscript has recently returned from first review, and these comments have been incorporated in the manuscript. It will be resubmitted following the submission of my thesis.

To further explore predation, in Chapter 4, I examined individual-level morphological defensive traits that have been used in Optimal Foraging experiments and models. I measured these defensive traits in all the individuals from the five species that make up 80% of the drilling predators' diet. I show that while shell size and thickness have a strong explanatory power, species-level differences better predict predation frequencies. This manuscript is aimed both at an ecological and a palaeobiological audience interested in predation, and it has been prepared for submission to *Marine Ecology Progress Series*.

Finally, I conclude with a synthesis of my results and argue that observational studies of the living mollusc communities do not show evidence of diversity and spatial distribution being different from random. Further, traits typically used by ecologists and palaeobiologists to explain predation do not hold their explanatory power at the community level, as defensive strategies are species-specific. Overall, by retrieving information from living communities and preserved shell assemblages, I provide novel insights into arguably the most well-studied biotic interaction by palaeobiologists, and show that preserved assemblages from a protected coral reef lagoon are reliable records of the living molluscan communities. The corroboration that these assemblages retain fidelity provides a fundamental baseline for conservation studies aimed at quantifying and remediating changes that communities from the Great Barrier Reef may be subject to in the coming years.

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ESTIMATED PROPORTION OF CONTRIBUTION TO ARTICLES

Co-authored and submitted	Extent of intellectual input by the candidate (%)				
chapters	Study concept and design	Acquisition of data *	Analysis and interpretation of data	Drafting of manuscript	Critical revision
Chapter 1: 'Mollusc spatial distribution and diversity are not different from random in a reef lagoon community'	80%	80%	90%	90%	80%
Chapter 2: 'Dead shell assemblages from One Tree Reef lagoon are a faithful record of the living communities'	80%	80%	70%	90%	80%
Chapter 3: 'Encounter frequency does not predict predation frequency in tropical dead- shell assemblages'	50%	80%	70%	90%	80%
Chapter 4: 'Species-specific variations in defensive traits explain predation in tropical molluscs'	60%	70%	70%	90%	80%

* I received help from fellow divers for sample collection, and from volunteers and/or research assistants for sample processing and measurement of specimens. All these people acknowledged in the corresponding Chapters.

OTHER RELEVANT PUBLICATIONS DURING CANDIDATURE

1) **Martinelli JC**, Gordillo S, Archuby FM (2013) Muricid drilling predation at high latitudes: Insights from the southernmost Atlantic. Palaios 28:33-41

Relevance to my thesis: In this paper I quantified drilling predation across a latitudinal gradient in a climatically harsh environment. I had processed all the data prior moving to Australia but the entirety of the analyses and the writing of the manuscript were carried out during the first year of my PhD, with guidance from Matthew Kosnik. This helped me get familiarised with the drilling predation literature, statistical analyses and scientific writing.

2) Madin JS, Kuo CY, **Martinelli JC**, Mizerek T, Baird AH (2014) Very high coral cover at 36° S on the east coast of Australia. Coral Reefs 1-1

Relevance to my thesis: *This contribution was put together after a sampling trip with my cosupervisor (Joshua Madin) to the south coast of New South Wales. This allowed me to learn about temperate coral reef systems in Australia.*

3) Archuby FM, Adami M, **Martinelli JC**, Gordillo S, Boretto GM, Malvé ME (2015) Regional-scale compositional and size fidelity of rocky intertidal communities from the Patagonian Atlantic coast. Palaios (accepted)

Relevance to my thesis: This paper is a contribution with collaborators from Argentina that was written during my last year of candidature. Given that it is a comparison between the composition of living and dead assemblages in Patagonia, it helped me get acquainted with the literature, and become aware of the contrasts in agreement between different environments (coral reefs vs the coast of Patagonia). CHAPTER 1

Mollusc spatial distribution and diversity are not different from random in a reef lagoon community

Submitted to Marine Ecology Progress Series as: Martinelli JC, Kosnik MA, Madin JS. Molluscan coexistence is not regulated by competition in coral reef lagoons (comments by reviewers incorporated to thesis version)

1.1 Abstract

Spatial aggregation is an important factor mediating species coexistence and diversity. In marine soft sediments, where burrowing organisms utilize a third dimension (depth), the role of aggregation in regulating coexistence and diversity is not well understood. Here, we test if spatial aggregation is related to molluscan diversity in soft sediment communities from the Great Barrier Reef. The most abundant species in these communities coexist and share the same feeding habit, suggesting they could be competing. We show that molluscs (n = 2888, 49 species) tend to be randomly distributed in space and exhibit low levels of intraspecific and interspecific aggregation. Local diversity (within quadrats) was lower, and beta diversity (among quadrats) was higher than expected by chance. This statistical significance is, however, unlikely biologically meaningful as it represents a 1 to 3 species difference in a 49 species community. Neither alpha or beta diversity were correlated with intraspecific or interspecific aggregation indices. These results suggest that these indistinguishable levels of aggregation could be caused by depth, which increases spatial partitioning. Since species spatial distribution does not appear to be strongly affecting diversity, we propose that predation or dispersal could instead play more important roles regulating molluscan coexistence in this soft sediment reef lagoon community.

1.2 INTRODUCTION

Understanding the processes that regulate species coexistence and spatial distribution is central to ecology (Connell 1963, Chesson 2000). These processes are suggested to range from biotic interactions and niche differentiation (niche-based theories) through to stochastic and demographic mechanisms (neutral-based theories) (Leibold & McPeek 2006). Generally, in patchy (or heterogeneous) habitats, coexistence is hypothesized to be mediated by competition for resources that are spatially or temporally distinct (Amarasekare 2003). Field studies over the past decade have refined and supported this hypothesis (e.g. Krijger & Sevenster 2001, Veech et al. 2003, and Veech 2005). One idea that has received empirical support is that competition, measured as spatial aggregation, influences patterns of diversity. For example, in patchy environments, individuals from the same species or guild tend to aggregate around resources (e.g. Krijger & Sevenster 2001, Belmaker et al. 2008), such that the number of species within patches (alpha diversity) is lower, and turnover of species between patches (beta diversity) is higher (Krijger & Sevenster 2001). Less is known however about the importance of spatial aggregation in determining coexistence and diversity in less spatially structured (or homogeneous) habitats.

In marine systems, biotic interactions such as competition and predation are also some of the mechanisms suggested to affect coexistence and spatial distribution (Connell 1961, Paine 1966, Woodin 1974). Classic studies of rocky intertidal communities, where competition for two-dimensional substratum is intense, provided particularly strong support to this idea (Connell 1961, Connell 1972, Menge & Sutherland 1976). This important role for competition maintaining coexistence and species diversity was also found in other communities, such as coral reefs, where high aggregation between conspecific fishes using the same resource led to decreased local diversity (Belmaker et al. 2008). Despite advances in understanding how spatial distribution can affect species diversity in rocky and reef systems, comparatively less is known about these patterns and the processes that rule them in neighbouring soft sediments.

Soft sediments represent the largest type of environment on Earth (Wilson 1991, Snelgrove 1999), making them a relevant system to understand. They provide important services such as nutrient cycling, and nursery grounds for commercially valuable species (Snelgrove 1998, 1999). 'Soft' habitats also offer an interesting contrast to 'hard' habitats as some species use space differently, i.e. by burrowing into the sediment they use a third dimension, depth. This difference in habitat dimensionality leads to differences in the role of competition determining species aggregation and diversity. Such differences have been illustrated by several classic experimental studies in soft sediment organisms. For example, Connell looked at the spatial distribution of clams (1956) and amphipods (1963) in regards to the behaviour of conspecifics and found aggregated and overdispersed distributions respectively. Similarly, other studies looking at the distribution of polychaetes in soft sediments found that the presence of conspecifics and heterospecifics also had an effect on spatial patterns (Woodin 1974). Although these and several other contributions have provided very valuable insights into distribution patterns in regard to conspecifics (Connell 1956, 1963, 1983, Gurevitch et al. 1992), it is still unclear how spatial aggregation and coexistence are associated in natural communities with multiple species, and whether spatial aggregation has an effect on diversity at that scale.

Observational studies carried out at a community scale can provide insight into other regional drivers for coexistence and diversity (Loreau & Mouquet 1999). Previous research at local scales has focused on biotic interactions, whereas inquiry at regional scales has focused on dispersal (e.g. Cadotte & Fukami 2005, Cadotte 2006). Given that these scales are interrelated, an integrated approach of local and regional paradigms (e.g. Ricklefs 2004, Harrison & Cornell 2008) at a community level can be useful. Similarly, questions about

species coexistence and spatial distribution need to be addressed with a ubiquitous group of organisms. In this regard, molluscs are well suited for community-level observational studies because they are species rich, widely distributed and easy to quantify (e.g. Bouchet et al. 2002).

Here, we examined the relationship between spatial aggregation and diversity of soft sediment marine molluscs at different spatial scales at One Tree Reef (Great Barrier Reef, Australia). In this community, the most abundant species coexist and share the same feeding mode, suggesting they should be competing for space and/or other resources. If this were the case, their distribution in space would not be random, and this would affect diversity patterns. To test this, we partitioned diversity into alpha (informative of local processes) and beta (informative of regional processes) components (Loreau 2000), and quantified intra- and inter-specific spatial aggregation (Krijger & Sevenster 2001). We considered three possible scenarios. First, if resources are uniformly distributed, and conspecifics highly competitive, individuals should avoid each other and their spatial distribution should be uniform. For this 'overdispersion scenario', local diversity (alpha) would be lower than expected by chance, and diversity between patches (beta) would be higher as patches would contain different species (Figures 1.1A & D). Second, if resources are patchy and conspecifics highly competitive, individuals should aggregate around resource patches (be it suitable space or food). For this 'aggregated scenario', alpha diversity would be significantly lower and beta diversity significantly higher than expected by chance (Figures 1.1B & E). Third, as an alternative to the first two scenarios, organisms are randomly distributed in space, possibly governed by stochastic factors, such as dispersal (Figures 1.1C & F). For this 'random scenario', alpha and beta diversity would not be significantly different from what is expected by chance. These three scenarios would remain unchanged for intraspecific and interspecific interactions, as long as the species share a same life habit and feeding mode.

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UNIFC	ORM α = 1,	β=3	AGGREGAT	ΈD α = 0.5	55, β = 5.45	RANDON	1 α = 1.44,	β = 2.08
•		• A	• • •		В		•	с
•	•	•	•	. • •				•
•		•				• •	• "	
1	1	D 1	1	1	E 0	3	2	F 0
1	1	1	1	1	0	0	1	1
1	1	1	1	0	0	2	2	2

Figure 1.1. The three scenarios considered for the relationship between spatial distribution and diversity. Panels (A-C) illustrate spatial distributions for three different species (squares, triangles and circles), and panels (D-F) indicate how many numbers of species would be present per plot. (A, D) Uniform distribution of organisms in space would lead to lower alpha diversity than random, and higher beta diversity than random. (B, E) Aggregated distribution in space would lead to lower alpha diversity and higher beta diversity than random (and uniform). (C, F) Random spatial distribution.

1.3 MATERIALS AND METHODS

1.3.1 Study area and collection of organisms

Soft sediment molluscan communities were sampled at One Tree Reef, southern Great Barrier Reef (23°20'S, 152°06' E). One Tree Reef comprises three lagoons (roughly 10 - 13 km² in extension, Davies et al. 1976) each containing coral patches interspersed with sand

(Ludington 1979). Molluscs were collected four times in 2012 (February, May, September and November) in three plots in each of the three lagoons (Figure 1.2). The plots that yielded a good number of live individuals (typically more than 20) were resampled in subsequent trips. The plots that did not yield sufficient live individuals were replaced by new plots on subsequent trips. Thus the different number of plots per lagoon (Figure 1.2). In total we collected sediment from 36 plots (nine for each trip).



Figure 1.2. Map of One Tree Reef, southern Great Barrier Reef showing sampling plots. The reef outline is the shaded grey area, the three lagoons are in white, and One Tree Island in black. Reef and lagoon outline were traced from Google Earth imagery.

Given that spatial aggregation is scale-dependent (Veech et al. 2003), we used two base-units for our analysis: 0.25 m^2 quadrats and 1 m^2 plots, each plot consisting of four pooled quadrats collected at close proximity (less than 2 m apart). We consistently sampled fine-grained (sand to mud) sediments with as little coral rubble as possible. Water depth ranged from 4.3 - 6.1 m (ponded), and samples were collected with an 80 mm diameter air-lift and 1 mm mesh bags. In each quadrat, we removed the top ten centimetres of sediment, as previous work found that living molluscs are not typically found below this depth (Kosnik et al. 2007, 2009, 2015). Samples were wet sieved after collection and the live-collected molluscs from the > 4 mm fraction were counted and identified using published literature (Lamprell & Whitehead 1992, Lamprell & Healey 1998), the Australian Museums' Malacology collection and the help of molluscan taxonomists. In order to know which species belonged to the same guild, we also determined feeding modes and life habits from the literature (Lamprell & Whitehead 1992, Beesley et al. 1998, Lamprell & Healey 1998, Table 1.1).

Table 1.1. Absolute abundance, life habit and feeding mode of all the gastropod and bivalve species collected at One Tree Reef lagoons.

GASTROPODA	Abundance	Life habit	Feeding mode
Acteonidae			
Pupa nitidula	21	Epifaunal	Carnivore
Pupa sulcata	4	Epifaunal	Carnivore
Architectonicidae			
Architectonicidae indet.	1	Epifaunal	Carnivore
Cerithiidae			
Rhinoclavis fasciata	1	Epifaunal	Microalgae/detritus
Cerithium indet. 2	1	Epifaunal	Microalgae/detritus
Columbellidae			
Mitrella ligula	30	Epifaunal	Grazer
Costellariidae			
Costellariidae indet.	2	Epifaunal	Carnivore
Epitoniidae			
Epitonium philippinarum	1	Epifaunal	Carnivore
Haminoeidae			
Atys cylindricum	6	Epifaunal	Herbivore
Atys hyalina	80	Epifaunal	Herbivore
Atys naucum	9	Epifaunal	Herbivore
16			

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Nassaridae			1
Nassarius (Niotha) albescens	2	Epifaunal	Scavenger
Nassarius (Zeuxis) bicallosus	86	Epifaunal	Scavenger
Nassarius cf. estilbus	15	Epifaunal	Scavenger
Naticidae			
Natica (Naticarius) onca	1	Semi-infaunal	Carnivore
Notocochlis gualtieriana	37	Semi-infaunal	Carnivore
Polinices mammilla	10	Semi-infaunal	Carnivore
Tectonatica bougei	5	Semi-infaunal	Carnivore
Strombidae			
Strombus gibberulus	7	Epifaunal	Herbivore
Terebridae			
Duplicaria evoluta	1	Epifaunal	Carnivore
Trochidae			
Ethalia guamensis	4	Epifaunal	Herbivore
Turridae			
Lophiotoma acuta	11	Epifaunal	Carnivore
Gastropoda indet. 1	1	-	-

BIVALVIA	Abundance	Life habit	Feeding mode
Cardiidae			
Fragum fragum	28	Infaunal	Suspension feeders
Fulvia indet.	1	Infaunal	Suspension feeders
Microfragum festivum	3	Infaunal	Suspension feeders
Nemocardium indet.	2	Infaunal	Suspension feeders
Cardiidae indet.	1	Infaunal	Suspension feeders
Galeommatidae			
Ambuscintilla praemium	7	Infaunal	Detritus feeders
Lucinidae			
Cavatidens omissa	2	Infaunal	Chemosymbionts
Ctena bella	4	Infaunal	Chemosymbionts
Wallucina fijiensis	2	Infaunal	Chemosymbionts
Pinnidae			
Pinnidae indet.	1	Semi-infaunal	Filter feeders
Solemyidae			
Solemya indet.	4	Infaunal	Deposit/Chemosymbionts

Abranda jeanae	1126	Infaunal	Deposit/suspension
Cadella semen	1	Infaunal	Deposit/suspension
Loxoglypta clathrata	550	Infaunal	Deposit/suspension
Loxoglypta virgulata	12	Infaunal	Deposit/suspension
Pharaonella perna	3	Infaunal	Deposit/suspension
Pharaonella rostrata	1	Infaunal	Deposit/suspension
Pinguitellina robusta	653	Infaunal	Deposit/suspension
Scissulina dispar	89	Infaunal	Deposit/suspension
Tellina (Quadrans) gargadia	1	Infaunal	Deposit/suspension
Tellina indet. 1	1	Infaunal	Deposit/suspension
Tellina indet. 2	4	Infaunal	Deposit/suspension
Tellina virgata	43	Infaunal	Deposit/suspension
Veneridae			
Callista (Striacallista) phasianella	11	Infaunal	Filter feeders
Dosinia amphidesmoides	1	Infaunal	Filter feeders
Veneridae indet. 1	1	Infaunal	Filter feeders

1.3.2 Calculation of alpha and beta diversities

We used multiplicative partitioning of diversity ($\beta = \gamma / \alpha$) to calculate alpha and beta diversities at the quadrat and plot scales (Whittaker 1972). Multiplicative partitioning is the only way in which beta can be methodologically independent of gamma and alpha diversities (Baselga 2010). This is relevant because if these metrics are not independent, the observed pattern is not biologically meaningful (Jost 2010), and the mechanisms behind it cannot be properly understood (Baselga 2010).

At the quadrat scale, alpha diversity was calculated as the mean richness of the four quadrats, and gamma diversity was the total richness found in those four quadrats. For the plot scale, alpha was calculated as the mean richness of 36 plots, while gamma diversity was the total richness found in all 36 plots. Given that sampling was carried out every three months, the same 0.25 m² of sediment were never resampled. Therefore, the benthic sediment

Tellinidae
samples from each trip were considered to be independent. We further tested for this independence by running separate analyses at the plot scale for each of the four sampling months. We did not find any effects of seasonality but to make this visually clear to the reader, we show the results obtained for plots from each month with a different symbol.

Observed and expected alpha and beta diversity values for a random community were computed using multiplicative partitioning in PARTITION 3.0 (Veech et al. 2003). The randomization routine maintains the total number of individuals per sample, as well as the number of individuals per species (for details see Veech et al. 2003). A mean, minimum and maximum value for multiplicative alpha and beta were returned for 10,000 randomizations, and the observed alpha and beta values were compared to these modelled distributions to assess significance. For PARTITION 3.0, if *p* value < 0.05, the observed value is significantly larger than the expected value, and if *p* value > 0.95, the observed diversity value is significantly smaller than the expected one (Veech et al. 2003, Veech 2005). If molluscs are distributed randomly, then the expected: observed diversity ratio will not be significantly different from 1 (e.g., dotted line, Figure 1.3, Veech 2005). We also used Welch two-sample t-tests to determine if the group means for observed vs. expected alpha, and observed vs. beta were significantly different at the quadrat and site scales.

1.3.3 Calculation of intraspecific and interspecific aggregation indices

We employed two widely used indices to quantify intraspecific (within members of the same species) and interspecific (between species) aggregation. Intraspecific aggregation for all non-singleton species was calculated using a standardized version of Morisita's Index of dispersion 'I_{δ}' (Morisita 1962, Smith-Gill 1975). This index is a reliable metric (Krebs 1999), and has been previously used to quantify intraspecific aggregation for a range of taxa (i.e. terrestrial insects Veech 2005, and reef fishes Belmaker et al. 2008). I_{δ} was calculated as:

$$I_{\delta} = IMS = \frac{p \cdot \sum_{i=1}^{p} [n_i(n_i - 1)]}{N \cdot (N - 1)}$$

where p is the number of patches (in our case, quadrats or plots), n_i the number of individuals in the ith patch, and N is the total number of individuals in all patches (Smith-Gill 1975). I_{δ} was rescaled according to Smith-Gill (1975), so that it ranged from -1 to 1, and this rescaledI_{δ} was renamed standardized Morisita Index (IMS). IMS values between -0.5 and 0.5 indicate a random distribution in space (i.e. Poisson), IMS smaller than -0.5 indicate a uniform distribution (overdispersion), and IMS greater than 0.5 indicate aggregation. An Exact binomial test was used to determine if the probability of aggregation for a species (at the quadrat and plot scales) was significantly different from the probability of a random distribution (i.e. what is the probability that out of 32 species, 'X' number of species present an aggregated distribution). A mean IMS was calculated for each patch by calculating an average between all the species present in that patch (be it a quadrat or a plot). Spearman correlations were used to assess the association between IMS and observed: expected alpha and beta diversity ratios. A significant association would provide support for the prediction that intraspecific aggregation has an effect on the diversity of the sampled communities.

Interspecific aggregation was quantified using the C index (Ives 1988), which has been previously shown to be a reliable metric to quantify interspecific competition (e.g. Krijger & Sevenster 2001, Veech et al. 2003, Presa Abos et al. 2006). This pairwise metric measures interspecific aggregation between a pair of species by the following equation:

$$C_{(i,j)} = \frac{\left\lfloor 1/(x_i \cdot p) \cdot \sum_{i=1}^{p} n_i \cdot n_j \right\rfloor - x_j}{x_j}$$

where x_i and x_j are the mean number of individuals of species i and j per patch, p the total number of patches, n_i and n_j the individuals of species i and j per patch. For each pair of species, C measures the relative change in the mean number of heterospecifics with which individuals from species i must compete (Ives 1988). The index ranges from -1 to positive infinity, and equals zero when heterospecifics are randomly associated (Ives 1988, Krijger & Sevenster 2001). Negative values indicate partitioning of species between patches (uniform distribution or overdispersion) and positive values indicate a tendency for species to coexist (Krijger & Sevenster 2001). The C index was calculated for all the possible species pairs in our samples, and a mean C value was computed for each quadrat and plot. We chose not to remove any species from the analyses a priori because, even if some species do not share a feeding mode (Table 1.1), they may be aggregated in a suitable patch for other reasons. For example, predators could be present in a patch due to prey aggregations rather than competition. In this case, a mean C was calculated with and without predatory species. These mean C values (with and without predators) were then used in a Spearman correlation with observed: expected alpha and beta diversity ratios. A significant association would indicate that aggregation between species affects diversity in this molluscan community.

Analyses were done using the 'vegan' package (version 2.0-7, Oksanen et al. 2013) in the R statistical software (version 3.0.0, R Development Core Team 2013). The data and the R codes used to calculate C and other analyses are provided as supplementary online material.

1.4 **Results**

1.4.1 Alpha and beta diversities at the quadrat and plot scales

We sampled 2888 live-collected individuals belonging to 49 bivalve and gastropod species (Table 1.1). Results obtained from PARTITION 3.0 indicated that the observed mean quadrat alpha diversity (5.6) was significantly lower than the expected mean value (7.2, p value > 0.99, Figure 1.3A), and the observed mean quadrat beta diversity (1.9) was significantly higher than the expected mean value (1.8, p value < 0.05, Figure 1.3A). Results were similar for the plot scale, where observed plot alpha diversity (10.1) was significantly lower than the expected value (11.8, p value > 0.99, Figure 1.3B) while observed plot beta diversity (4.8) was significantly higher than the expected value (4.1, p value < 0.05, Figure 1.3B). Seasonality had no effect, as alpha was lower and beta higher than expected at the plot scale for each of the four months (p value > 0.99 for alpha, all months; p value < 0.05 for beta, all months). Observed gamma diversity at the quadrat scale was 10.8 species whereas the random expectation was 13.4 species.



Figure 1.3. Boxplots showing ratio of observed:expected alpha and beta diversity for (A) quadrats and (B) plots. Horizontal notches indicate the median values, boxes enclose the 25^{th} to 75^{th} percentiles, and whiskers indicate the most extreme data points. Black line indicates a ratio of 1, where observed diversity equals expected random diversity.

These results were supported by Welch t-tests that indicated that observed alpha was significantly lower than the expected alpha at the quadrat (Welch two sample t-test, t = -14.05, df = 143, *p* value < 2.2^{-16}) and plot (t = -4.10, df = 35, *p* value = 2.3^{-6}) scales. Similarly, observed beta was significantly higher than expected at the quadrat (t = 3.94, df = 143, *p* value < 1.2^{-8}) and plot (t = 3.83, df = 35, *p* value = 0.5^{-4}) scales. Even if these results are supported by two tests, the actual values of the expected alpha and beta from the modelled communities fall within the confidence intervals of the observed alpha and beta at both scales (Figure 1.4).



Figure 1.4. Barplot showing observed values of alpha and beta diversity at the quadrat and plot scales. Confidence intervals (95%) are indicated by vertical grey lines. Horizontal black lines indicate the mean modeled values. Notice that the modeled values always fall within the confidence intervals of the observed values.

1.4.2 Intraspecific aggregation index

The standardized version of the Morisita index (IMS) (Morisita 1962, Smith-Gill 1975), showed substantial variation for most non-singleton species (32 of 49) at both the quadrat and the plot scales (Table 1.2). At the quadrat scale, IMS ranged from -0.16 to 0.62, with 56% of species showing random distributions, 44% of species showing intraspecific aggregation, and no species showing overdispersion. The number of species with aggregated distributions (Exact binomial test, n = 32, *p* value = 0.59). At the plot scale, IMS ranged from -0.31 to 0.57, and the number of species with random distributions (63%) was also not significantly different than the number of species (37%) (Exact binomial test, n = 30, *p* value = 0.20). No species showed overdispersion at the plot scale either.

Table 1.2. Intraspecific aggregation values for IMS at the quadrat and plot scales. Values > 0.5 indicate aggregation, values < -0.5 indicate overdispersion, and values in between indicate a random distribution in space.

GASTROPODA	IMS (quadrat)	IMS (plot)
Acteonidae		
Pupa nitidula	0.52	0.57
Pupa sulcata	0.54	0.41
Collumbellidae		
Mitrella ligula	0.51	0.53
Costellaridae		
Costellariidae indet.	-0.01	-
Haminoeidae		
Atys cylindricum	0.50	0.54
Atys hyalina	0.50	0.40
Atys naucum	0.51	0.51
Nassaridae		
Nassarius (Zeuxis) bicallosus	0.50	0.51
Nassarius cf. estilbus	0.07	0.01
Naticidae		
Tectonatica bougei	-0.06	-0.14
Polinices mammilla	-0.14	-0.31
Notocochlis gualtieriana	0.48	0.51
Strombidae		
Strombus gibberulus	-0.11	-0.21
Trochidae		
Ethalia guamensis	-0.05	-0.10
Turridae		
Lophiotoma acuta	0.50	0.53
BIVALVIA		
Cardiidae		

Galeommatidae		
Ambuscintilla praemium	0.50	0.12
Lucinidae		
Cavatidens omissa	-0.02	-0.03
Ctena bella	-0.05	-0.10
Wallucina fijiensis	-0.01	-0.03
Solemyidae		
Solemya sp. indet	-0.06	0.41
Tellinidae		
Abranda jeanae	0.50	0.52
Loxoglypta clathrata	0.50	0.51
Loxoglypta virgulata	0.18	0.53
Pharaonella perna	0.62	-
Pinguitellina robusta	0.50	0.51
Scissulina dispar	0.52	0.57
Tellina virgata	0.35	0.50
Tellina indet. 2	-0.05	-0.10
Veneridae		
Callista (Striacallista) phasianella	-0.16	0.26

Mean intraspecific aggregation calculated at the plot scale ranged from 0.24 to 0.52, with 86% of the plots falling in the random range, and 14% in the aggregated range (Figure 1.5A). Spearman correlations between observed: expected ratios for alpha and beta with mean IMS plot values were not significant (p value > 0.05; Figures 1.5A & C).



Figure 1.5. Histograms showing (A) mean intraspecific aggregation per plot and (B) mean interspecific aggregation per plot.

1.4.3 Interspecific aggregation index

Mean interspecific aggregation varied greatly at the quadrat scale (C ranged from -0.89 to 4.66), however, in 70% of the quadrats species were randomly distributed (as indicated by C values in the 0 - 0.5 range). In 24% of the quadrats species showed a tendency to share patches (as indicated by C values higher than 0.5), while in the remaining 6% of the quadrats species showed a tendency to partition patches or be overdispersed (as indicated by negative C values). Mean interspecific aggregation exhibited less variation at the plot scale (C ranged from -0.19 to 1.36). Again, species were randomly distributed in 67% of the plots, whereas aggregation between heterospecifics was found in 30% of the plots, and overdispersion in 3% (Figure 1.5B).

Values for mean C index did not change when predator species were excluded from the analyses (Supplementary Tables 1 & 2). The low incidence of interspecific aggregation was confirmed by Spearman correlation between observed: expected ratios for alpha and beta with mean C values (for quadrats and plots). No significant associations were found between the variables at either spatial scale (p value > 0.05; Figures 1.6B & D), and no differences were found by month (see the different symbols indicating the different months in Figures 1.6B & D).

1.5 DISCUSSION

Results from this observational study encompassing over 2800 live-collected individuals suggest that spatial distribution is not significantly different from random and it does not affect diversity. Alpha and beta diversities were significantly lower and higher than expected by chance, and this significant difference between observed and modelled diversity could be interpreted as supporting the aggregation scenario. However, there were no significant differences in the number of individuals or species showing aggregated or random distributions, and no species showed an overdispersed pattern. This statistical significance is also unlikely to have a strong biological meaning (e.g. mean observed quadrat alpha of 5.6 relative to the mean modelled alpha of 7.2), as expected values fall within the confidence intervals of observed values (Figure 1.4). Mean aggregation between conspecifics and heterospecifics was also found to be random in most plots, and these values were not significantly correlated with diversity (Figure 1.6). We discuss methodological caveats that could affect the interpretation of our results (i.e. quadrat size vs individual size, depth sampled, and the presence of other benthic fauna). Despite these caveats, our findings strongly suggest that neither spatial aggregation nor diversity are significantly different from random in this soft sediment reef community.

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Figure 1.6. Scatter plots showing the relationship between (A) observed:expected ratio for alpha diversity and Morisita intraspecific Index, (B) observed:expected ratio for alpha diversity and mean interspecific C Index; (C) observed:expected ratio for beta diversity and Morisita Index, and (D) observed:expected ratio for beta diversity and mean interspecific C Index. No correlation was significant (Spearman p value > 0.05). Circles, squares, diamonds and triangles represent plots from February, May, September, and November respectively.

1.5.1 Interspecific aggregation index

The values for alpha and beta diversity in the samples were significantly higher and lower than the values predicted for a random community. Regardless of this statistical significance, the differences between observed and predicted diversities ranged between 1 and 3 species. For example, the observed alpha diversity at the plot scale was 10.1 while the modelled value was 11.8. Arguably, a difference of less than two species is unlikely to have any important effect in a biological assemblage or community of 49 sampled species. The same applies to beta diversity, where there was a 0.7 difference between the observed beta diversity (4.8) and the modelled (4.1). Despite the statistical significance, the expected values fall within the confidence intervals of the observed values (Figure 1.4), therefore, the compositional differences between the modelled and the observed communities are minor and not different from random for biological purposes.

1.5.2 Spatial aggregation and diversity in different environments

Previous studies using randomizations to compare observed and expected diversity at a community or assemblage scale found evidence for lower alpha and higher beta diversities than expected (e.g. Veech et al. 2003, Veech 2005, Belmaker et al. 2008). Those studies, however, focused on patchy systems, such as terrestrial insect communities and corals reefs. In those environments, intraspecific aggregation was found to be a suitable explanation for decreased alpha and increased beta diversities (Veech et al. 2003, Veech 2005, Belmaker et al. 2008). Similarly, Krijger & Sevenster (2001) found that aggregation not only explained coexistence for *Drosphila* communities, but also showed a clear association with local diversity. Potential differences between the heterogeneous nature of those environments, and the more homogeneous environment we examined, may explain why spatial aggregation was not high in our case. Similarly, in terrestrial insect communities and marine hard substrates competitors are interacting in a two-dimensional space, whereas in this benthic soft sediment system individuals live buried in the sediment using a three-dimensional space. Overall, this suggests that the relative importance of aggregation as a driver for diversity is highly contingent on the nature of environment under study.

1.5.3 Spatial distribution and caveats of the sampling design

A few variables in our observational study could affect our interpretation of spatial distribution and coexistence. Namely, the size of the smallest sampling unit (0.5 m x 0.5 m quadrat) relative to the size of the species, and the depth of the sediment layer collected could be important (e.g. Pielou 1960, Woodin 1974).

Given that distribution patterns are scale dependent, and dependent on the size of the organism (Pielou 1960), we tried to control the relationship between sampling scale and organism size by working with individuals larger than 4 mm. This size fraction ensured that all the smaller organisms and juveniles were not included in our analyses. There were however size differences between the adults of the numerically dominant species (Table 1.3) that could be relevant to our conclusions. Previous research (Pielou 1960) has found that negative interactions (overdispersion) were masked as random distributions due to size differences between species. Therefore, the fact that we found no evidence for intraspecific overdispersion does not necessarily mean that it is the case for all species, as some negative interactions between species may be present and we have been unable to detect them.

Species	Family	Relative abundance	Size (mm)	Measured individuals
Abranda jeanae	Tellinidae	39%	254	196
Loxoglypta clathrata	Tellinidae	19%	49	115
Pinguitellina robusta	Tellinidae	23%	138	153

Tellinidae

Scissulina dispar

Table 1.3. Family, relative abundance, and median geometric size for the four most abundant species.

Another variable that could affect the interpretation of our results is the depth of sediment that was collected. It is possible that individuals or species are aggregating or

3%

101

191

overdispersing at smaller scales. Previous studies have subsampled layers of 2 cm of depth (Woodin 1974) to look at distribution in a third dimension. A way to control for this would have been to subset these samples into 0-5 cm and 5-10 cm depth bins during sediment collection. However, given the size of our adult individuals (Table 1.3), it is unlikely that a 5 cm difference would be ecologically meaningful as these organisms also move around in the sediment. Another bias related to our sampling is that molluscs could retreat deeper into the sediment if disturbed by an air-lift. While possible, we suspect this did not have a major impact given the high densities of individuals collected (mean abundance per quadrat = 20 individuals).

1.5.4 Biases related to species life history and other benthic fauna

Besides methodological biases, there are biological caveats such as pooling together taxa with different feeding habits, and the presence of other potential competitors that we did not take into account. The feeding habits of infauna have been used to explain their spatial distributions (e.g. Connell 1963). For example, deposit feeders and grazers are typically found uniformly distributed in space - overdispersed (e.g. *Tellina tenuis*, Holme 1950). In contrast, suspension feeders have been found aggregated in suitable habitat patches (see Connell 1963 for a summary). In soft sediments from reef lagoons, deposit-feeding tellinids represented 86% of the mollusc fauna (Table 1.2), suggesting that differences in life and feeding habit with minor constituents of the fauna were not important at a community scale. Moreover, the results for aggregation did not change when analyses were re-run without predator species that could be 'artificially' aggregated around prey (see Supplementary Online Material).

Other potential competitors for resources (space and food) such as crabs and polychaetes were also present in our samples. These were not included in the analyses because molluscs were the most abundant group. Crabs are more active than molluscs, suggesting they do not necessarily coexist for long periods of time. Polychaetes were present in most of our samples but their biomass was very low relative to molluscs (author's personal observations).

1.5.5 Other community level and regional level drivers for diversity

Other biotic interactions such as predation, or regional scale processes like dispersal might also offer insights into the diversity drivers in this three-dimensional ecosystem. Predation and competition are known to both affect community structure, and to also interact between them (Chesson & Kuang 2009). For instance, the seemingly low spatial aggregation observed in this system could be an artefact of high predation that leads to a reduction in competitive interactions (Gurevitch et al. 2000, Chase et al. 2002). If this were the case, predation would then be promoting coexistence (Chase et al. 2002). The fact that we did not quantify predation, or account for possible interactions between predation and spatial competition could be leading us to dismiss the role of local factors without sufficient evidence. Previous studies looking at fish predation on soft sediment molluscs from One Tree reef have shown that these predators do not have a significant effect on the population dynamics of their mollusc prey (Jones et al. 1992). However, other predators like drilling gastropods could have an impact on the diversity of this system. Extensive work by Vermeij (1980, 2002) and many others (e.g. Kelley & Hansen 1993, 1996, Huntley & Kowalewski 2007, Sawyer & Zuschin 2010, Martinelli et al. 2013) has shown that drilling gastropods play significant roles in their communities. Therefore, a better understanding of the role of predators in this system is necessary in order to have a more accurate picture of the relative importance of biotic interactions.

Besides biotic interactions, regional and stochastic mechanisms can also be important. For instance, a model for sessile organisms with a dispersal phase showed that migrants from

a neighbouring community were enough to control local coexistence and diversity (immigration intensity > 0.001, see Loreau & Mouquet 1999 for details). Following from this conclusion, it is possible that for a certain level of dispersal, patches that are less productive support fewer individuals on average, leading to a decrease in local diversity by stochastic extinction, and thus, an increase in beta diversity (Loreau 2000). This mechanism would be a feasible explanation for the observed lower and higher alpha and beta diversities, without the need to invoke interactions. If stochastic processes are important, the Lottery hypothesis (Sale 1977) could shed light on our results. This hypothesis puts forward that during the larval dispersal stage, a random element (or lottery) determines the settlement of larvae in space. This stochasticity is intrinsic to the community (Fagerstrom 1988), and it leads to variability, promoting coexistence and diversity (Sale 1977, Fagerstrom 1988). Interestingly, Peterson (1979) suggested that this process could be operating in molluscs, and suggested that after a disturbance, the species that could colonize an empty patch would be the ones that by chance had larvae in the plankton, and that this random process could lead to patchiness in species distributions that would depend on the scale of the disturbance. Therefore, there is room for larval dispersal and other stochastic processes to have a stronger effect than local interactions on species' spatial distribution.

These results from observational data in a natural community indicate that the spatial distribution of molluscs in reef associated soft sediments is mostly random, suggesting that local processes such as spatial competition are not strongly driving diversity patterns. Assuming the methodological biases we discuss would not significantly change the interpretation of our results, we partly attribute this lack of aggregation to 3D spatial structure that likely favours spatial partitioning (Wilson 1991). In addition to this 3D nature of soft sediments, the role of other local interactions such as predation, and regional mechanisms such as dispersal needs to be addressed. In the meantime, our results provide support to

Lawtons' (1999) proposition that the main controls for species diversity are at the regional to the local scale. If this were the case, the role of immigration and dispersal from neighbouring areas would be the dominant drivers of diversity and species composition (Tilman 1994, Vellend 2010), making the system highly contingent on stochastic processes and the regional species pool.

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CHAPTER 2

Dead shell assemblages from One Tree Reef lagoon are a faithful record of the living mollusc communities

2.1 Abstract

Reef-associated sediments accumulate over time, recording the history of biological communities. The agreement between living communities and dead assemblages has been extensively studied because discrepancies between the two can reveal taphonomic bias and/or anthropogenic impact. Given the potential of sedimentary assemblages to provide preanthropogenic perspectives on modern communities, assessments of live-dead agreement in mollusk community composition are necessary and timely. One Tree Reef 'OTR' (southern Great Barrier Reef, Australia) has had very little direct anthropogenic influence allowing a focus on taphonomic patterns. Living (n = 1507) and dead (n = 6417) molluscan assemblages were collected from OTR's three soft sediment lagoons. Diversity and evenness metrics indicate no significant difference between the live community and dead assemblage, and dead assemblage rank order abundance explains 73% of that of the living assemblage. Differences in composition were largely due to sample size and the probability of sampling rare species. Taphonomic factors are only responsible for 20% of the differences in species composition between living mollusk communities and dead shell assemblages. The live molluscan community we collected in 2012 is also very similar to the live molluscan community collected 30 years ago at OTR, suggesting that the composition of this community has remained largely unchanged. These findings indicate that dead assemblages preserved in fully carbonate environments primarily reflect the composition of the live communities; making them useful data for conservation baselines and identifying changes in community composition over time in areas where anthropogenic impacts are present.

2.2 INTRODUCTION

Given the long history of human-mediated changes to tropical reef communities (Jackson 1997, Jackson et al. 2001, Pandolfi et al. 2003), it may be not be possible to find a natural baseline against which to measure historical as well as future changes (Jackson et al. 2001, Kidwell 2013). Ecological, historical, archaeological and paleoecological records have shown evidence of strong changes to coral reef ecosystem structure caused by even very low human population densities (Jackson et al. 2001, Sandin et al. 2008). While data obtained by community ecologists provide quantitative information with more precision than archaeological or paleoecological records, they are restricted to the anthropogenic period. Therefore, in order to quantify and understand anthropogenic impacts on living marine communities, community ecologists must make use of other sources of quantitative temporal information such as can be extracted from dead assemblages (Kidwell & Tomašových 2013).

Comparing living communities and dead assemblages requires accounting for the biological, geological and chemical processes that affect variability in live communities and the preservation of death assemblages. Firstly, biological processes such as recruitment pulses result in variable species composition (e.g. Powell et al. 1986) and morphological traits result in variable preservation probabilities (Kosnik et al. 2009). When organisms die, biological processes such as bioturbation or bioerosion also affect preservation (Roy et al. 1994). Physical processes such as sedimentation rate, wave energy, abrasion and fragmentation, chemical dissolution and cementation can also impact the formation of dead shell and fossil assemblages (Fürsich & Aberhan 1990, Kidwell & Bosence 1991, Pandolfi 1992). The importance of these factors varies depending on environment and the species composition, as there are certain traits, or a combination of traits that may convey higher durability in the sediment (e.g., Kosnik et al. 2009).

The fidelity of coral reef-associated sedimentary death assemblages was an important

point of contention following Walbran et al.'s (1989) historical analysis of *Acanthaster planci* outbreaks on the Great Barrier Reef (Fabricius & Fabricius 1992, Keesing et al. 1992, Pandolfi 1992). Looking at the sedimentary record of population outbreaks of crown-of-thorns, Keesing et al. (1992) and Pandolfi (1992) discuss the importance of physical and biological processes that take place when sediments are accumulating, and how this complicates the patterns found by Walbran et al. (1989). Only by directly comparing living communities and dead assemblages at a timescale appropriate to the time averaging in the death assemblage, can the relevant biases be quantified.

Mollusks are often used in paleobiological studies and they have been the subject of many studies comparing living communities and dead assemblages (e.g. Kidwell 2001 and references therein, Zuschin & Oliver 2003, Lockwood & Chastant 2006, Zuschin & Stachowitsch 2007, Albano & Sabelli 2011, Feser & Miller 2014). These invertebrates are an integral part of reef ecosystems because they carry out important ecosystem functions such as nutrient cycling, particle filtering that contributes to water clarity, and prey for benthic and larger pelagic predators (Wilson 1991, Snelgrove 1999, Przesławski et al. 2008). Given the relevance of these components of the soft sediment fauna, they can be indicative of future, broader implications for the overall functioning of reef ecosystems (Przesławski et al. 2008).

An informative approach to look at and monitor temporal changes in molluscan faunas is to use mollusk dead shell assemblages or 'DAs' (Kidwell 2001, 2007, 2013). These assemblages can be defined as 'taxonomically identifiable empty shells that are collected from a standardized area or volume of seabed' (Kidwell 2013). Extensive research by paleontologists in different marine environments has shown that the live-dead agreement between molluscan faunas has implications for conservation (Kidwell 2001, 2007, 2013, Kidwell & Tomašových 2013). In particular, Kidwell (2007) found that DAs from areas with high anthropogenic impact (i.e. eutrophication) showed a higher disagreement with their living community relative to DAs from less impacted areas. Examples of similar studies in reef communities are limited (but see Zuschin et al. 2000, Zuschin & Oliver 2003, Zuschin & Stachowitsch 2007) and there is none for the Great Barrier Reef.

Here, we quantify the agreement between dead shell assemblages and living communities in tropical reef sediments from One Tree Reef (OTR), southern Great Barrier Reef. One Tree Reef is a useful study system given that it is a relatively isolated outermost reef with local anthropogenic impacts limited to researchers at One Tree Island Research Station. Therefore, differences between the living and dead mollusk assemblages should be primarily driven by taphonomic rather than human factors. This live-dead study is the first of its kind for the Great Barrier Reef as well as for a relatively intact fully carbonate lagoon.

2.3 MATERIALS AND METHODS

2.3.1 Study area and sample processing

Sampling was carried out at One Tree Reef, southern Great Barrier Reef, Australia ($23^{\circ}20^{\circ}$ S, $152^{\circ}06^{\circ}$ E, Figure 2.1). The reef crest surrounds three soft sediment lagoons, of roughly 10 - 13 km² in area (Davies et al. 1976). Infauna were collected at three sites in each of the three lagoons. Sampling was carried out four times in 2012, totaling 36 samples. Some sites were re-sampled during subsequent sampling (see Table 2.1), but the same sediment was not recollected, so samples were considered to be independent. Sites with low abundance of living molluscs were replaced by different ones during subsequent sampling trips (indicated by the different site numbers in Figure 2.1). All sites ranged between 4.3 to 6.1 m ponded depth. For each sample, divers used an 80 mm diameter air-lift and 1 mm mesh bags to collect the top 0.1 m of sediment of four 0.25 m² quadrats.

Some previous studies (e.g. Kidwell 2001) have found 2 mm sieves to be suitable for

mollusk live-dead comparisons, but we used the molluscan material retained by a 4 mm sieves because we observed juvenile recruitment pulses in the 2 mm sieve fractions. Sampling juveniles makes identification more difficult, as transitory settlement events distract from our focus on the live-dead agreement between samples, and the comparability with the fossil record (Kidwell 2001). Since living faunal abundance is the limiting factor for live-dead comparisons, samples with less than 20 living individuals were not included in the analyses. The abundance of living mollusks was variable between samples, so we processed between one and four replicate quadrats to meet the minimum of 20 live-collected individuals per sample (replicate quadrats for each sample, and did the same with the dead shells from the matching quadrats and samples. The total number of samples analyzed was 27 (Table 2.1).



Figure 2.1. Schematic map of One Tree Reef, southern Great Barrier Reef. The reef outline is the shaded grey area, the three lagoons are in white, and One Tree Island in black. Site numbers inside each lagoon agree with the collection samples listed in Table 2.1. Reef and lagoon outline were traced from Google Earth imagery.

Sample	Month	Site name	Quadrats processed	Abur	ndance	Richness		ess Diversity		Evenness	
				L	D	L	D	L	D	L	D
1	Feb	3rd Lagoon 1	842, 844, 846, 848	95	264	9	5	1.24	0.86	0.56	0.53
2	Feb	3rd Lagoon 2	850, 852,854,856	58	384	8	18	1.35	1.29	0.65	0.45
3	Feb	3rd Lagoon 3	858,860,862	34	104	13	10	1.53	1.03	0.6	0.45
4	Feb	1st Lagoon 1	794,796,798	78	290	13	27	1.74	1.97	0.68	0.6
5	Feb	1st Lagoon 3	810,812,814,816	54	327	10	14	1.72	1.34	0.75	0.51
6	Feb	2nd Lagoon 2	826,830,832	67	243	18	22	2.26	2.05	0.78	0.66
7	Feb	2nd Lagoon 3	834,836,838,840	66	166	9	10	1.56	1.39	0.71	0.6
8	May	3rd Lagoon 2	948,952,954	43	724	7	21	1.67	1.21	0.86	0.4
9	May	1st Lagoon 1	916,918	82	210	7	22	0.78	2.08	0.4	0.67
10	May	2nd Lagoon 2	900,904	41	233	6	15	1.55	1.56	0.87	0.58
11	May	2nd Lagoon 3	932,934,936	82	323	12	9	1.77	0.92	0.71	0.42
12	May	1st Lagoon 4	908,912	36	64	9	16	1.53	2.25	0.7	0.81
13	Sep	3rd Lagoon 1	1002	29	35	5	5	1.27	1.57	0.79	0.98

Table 2.1. Details of samples used for analyses. Site names coincide with those mentioned in Figure 2.1. The absolute abundance of living (L) and dead (D) individuals per site is present, as well as species richness, Shannon diversity index and Pielous' evenness index for both assemblages.

14	Sep	2nd Lagoon 2	982,984	21	188	7	10	1.79	1.51	0.92	0.66
15	Sep	2nd Lagoon 3	1024,1026	36	218	6	8	1.23	1.29	0.69	0.62
16	Sep	1st Lagoon 5	956,960,962	55	180	9	9	1.01	1.66	0.46	0.76
17	Sep	1st Lagoon 6	968,970	47	125	8	10	0.91	1.16	0.44	0.5
18	Sep	1st Lagoon 7	974,976	95	100	6	11	0.7	1.49	0.39	0.62
19	Sep	2nd Lagoon 5	988,990	64	223	10	14	1.69	1.48	0.73	0.56
20	Nov	3rd Lagoon 1	1126,1130	63	401	10	22	1.51	1.39	0.66	0.45
21	Nov	3rd Lagoon 3	1142,1146	48	483	9	14	1.62	1.48	0.74	0.56
22	Nov	1st Lagoon 1	1100,1104	37	109	4	13	0.54	1.74	0.39	0.68
23	Nov	1st Lagoon 2	1108,1110,1114	76	175	13	19	1.35	1.72	0.53	0.58
24	Nov	2nd Lagoon 2	1156,1162	39	220	10	8	1.54	1.33	0.67	0.64
25	Nov	2nd Lagoon 3	1148,1152	48	183	11	8	1.7	1.26	0.71	0.61
26	Nov	1st Lagoon 5	1116,1118,1120	56	129	3	8	0.5	1.49	0.46	0.72
27	Nov	2nd Lagoon 5	1168,1170	34	237	7	16	1.15	1.22	0.59	0.44

We used published literature (Lamprell & Whitehead 1992, Lamprell & Healey 1998), the Australian Museums' Malacology collections, and help from mollusc taxonomists to identify individual shells to the species level. Once species were identified, only non-fragmented individuals from bivalve and gastropod species were counted. For bivalves, the minimum number of individuals was estimated as the number of articulated valves plus the total number of right valves.

2.3.3 Abundances and diversity metrics

Species relative abundances per sample were calculated for living assemblages (LAs) and dead shell assemblages (DAs) to test for a live-dead agreement. High live-dead agreement is indicated by species plotting along a 1:1 line in a bivariate plot of live versus dead relative abundance (e.g. Kidwell 2007, Tomašových & Kidwell 2011, see Figure 2.2). We run linear regression models with a) the total relative abundance, b) the relative abundance of bivalves, and c) the relative abundance of gastropods in the living and dead assemblages. To test if the slopes of those regressions were significantly different from 1 we calculated the upper and lower confidence intervals. If a slope of 1 fell within the confidence intervals we assumed that differences were not significant. The residuals for the regression with the total relative abundances in the living assemblage. For those species, we looked further into the morphology, size and life habits to determine if the differences in abundance could be attributed to: insufficient sampling of the live community; our inability to identify living individuals while sieving; or a genuine absence of the species from the living assemblage.

Different diversity indices were used to determine live-dead agreement. We calculated Shannon's diversity index (Shannon & Weaver 1963), Pielou's evenness index (Pielou 1966), and Chao's Jaccard similarity index (Chao et al. 2005). Chao's Jaccard index includes the effect of species that are shared but unseen (either because they are rare or because the samples that are being compared have substantial differences in size like these live-dead assemblages). By accounting for unseen species, this estimator is less biased than the classic Jaccard index that is only based on presence-absence data (Chao et al. 2005). Lastly, we used Spearman rank order correlation of species relative abundance as an indicator of similarity between LAs and DAs (e.g. Kidwell 2001). Chao's Jaccard similarity index and Spearman's rank order correlation are typically plotted on bivariate plots to represent compositional and abundance similarity in the living and dead assemblages. In this plot, sites located in the upper right hand quadrant have the highest live-dead agreement and sites in the lower left hand quadrant have the lowest live-dead agreement (Kidwell 2007). Samples with less than five living individuals or less than two species were excluded from these analyses (Zuschin & Ebner 2015). Indices were calculated with the 'diversity' and 'chao.jaccard' functions, in the 'vegan' and 'fossil' packages in the statistical programming language R (Version 3.1.2, R Core Team 2014).

Species rank abundance plots are also good descriptors of communities (McGill et al. 2007). Several theories and models have been proposed to explain the different shape of rank abundance plots in communities (see McGill et al. 2007 for a review). Here we fit five of these models (Broken stick, Pre-emption, log-Normal, Zipf and Zipf-Mandelbrot) to the rank abundance orders of the living and dead assemblages to determine the best fit model for each dataset. The best model was chosen based on at least a two-point difference in Akaike Information Criterion (AIC). We carried out these analyses with the 'radfit' function in the

'vegan' package in the statistical programming language R (Version 3.1.2, R Core Team 2014).



Figure 2.2. Species relative abundance in dead shell assemblages (DAs) as a function of relative abundances in living assemblages (LAs). Dark gray circles represent bivalve species and light grey diamonds represent gastropod species. The dashed line indicates a 1:1 relationship between DAs and LAs relative abundance.

2.3.4 Live-dead agreement and temporal autocorrelation

Given that the median age of DAs from OTR is ~20 years (Kosnik et al. 2015), it is highly likely that LAs and DAs are temporally autocorrelated. Therefore, we complement univariate metrics with a method developed by Tomašových & Kidwell (2011) that accounts for temporal autocorrelation in live-dead assemblages. By accounting for temporal autocorrelation, this method allows for the deconstruction of live-dead variation into premortem and post-mortem components. Examples of pre-mortem processes (inherent to living communities) are biological and sampling biases such as demographic stochasticity, migration rates, and sampling effects (Powell et al. 1986, Lande 1993, Moore et al. 2007). Examples of post-mortem processes are differences in population turnover and preservation rates between species.

The approach developed by Tomašových & Kidwell (2011) is based on a modification of HMD (homogeneity of multivariate dispersions), a non-parametric method that looks for differences in the multivariate dispersions among groups (Anderson 2006). The method assumes that the sampled LAs are equivalent to the source living communities (at larger spatial scales), and that the dispersion based on replicate LAs accounts for biological stochasticity. This dispersion delimits the bounds for the compositional variation that can be expected among DAs if there are no post-mortem effects. The total live-dead variation is thus the average distance among individual DAs and the centroid of LAs. The post-mortem variation not explained by variation among LAs is the average distance between LAs and their centroid (the pre-mortem variation) minus the average distance among DAs and the centroid of LAs. The average distance among DAs and the centroid of LAs measures over- or under-dispersion of DAs relative to the composition of LAs. Under-dispersion of DAs indicates a loss of variation compared with that of LAs. Over-dispersion of DAs indicates that DAs occupy portions of multivariate space outside those occupied by LAs (Tomašových & Kidwell 2011). The significance of this over- and under-dispersions is evaluated by a p value that determines if DAs are significantly more or less dispersed relative to the centroid of LAs than are LAs.

We carried out these live-dead agreement analyses with different grouping possibilities for our samples to make sure over- and under-dispersion patterns were consistent at different spatial scales. For example, we conducted the analyses using 27 independent samples but we also grouped the samples from each lagoon together (three larger samples) to

validate our results at different spatial scales. All analyses were carried out using the 'vegan' and 'ade4' packages in the statistical programming language R (Version 3.1.2, R Core Team 2014). The distance metric used was Horn-Morisita following Tomašových & Kidwell (2011), the code for the analyses was provided by Adam Tomašových.

2.4 Results

2.4.1 Abundance and diversity metrics

The 27 samples analyzed yielded LAs comprised of 1507 live-collected individuals representing 38 species, and DAs comprised of 6417 shells without live mollusks representing 58 species (Table 2.1). There was a combined richness of 71 species, of which 25 were found both in living and dead assemblages.

Univariate diversity metrics were not significantly different between LAs and DAs (Table 2.1). Species richness was not significantly different (Kruskal-Wallis rank sum test, $\chi^2 = 16.19$, p = 0.30), neither were Shannon's or Pielou's diversity indices (Kruskal-Wallis rank sum test, $\chi^2 = 28$, p = 0.46 for both tests). In addition, species relative abundances in living and dead assemblages showed a significant positive correlation (Spearman rank correlation, rho = 0.73, p < 0.001, Figure 2.2). Linear models also indicated that living assemblages were significant predictors of the species relative abundance in dead assemblages for the total assemblage (adjusted R² = 0.63, F = 42.76, p < 0.001), bivalves (adjusted R² = 0.44, F = 0.78, p = 0.01), and gastropods (adjusted R² = 0.78, F = 46.4, p < 0.001). Confidence intervals also indicated that slopes were not significantly different from 1 for the total assemblage (lower CI = 0.69, upper CI = 1.34), bivalves (lower CI = 0.19, upper CI = 1.41), and gastropods (lower CI = 0.62, upper CI = 1.20). Chao's Jaccard index for median compositional similarity

between living and dead shell assemblages was 0.86 for the total assemblage (n sites = 27), 0.90 for bivalves (n sites = 27), 0.63 for gastropods (n sites = 16). The range of values for this index is from 0 to 1, 1 being the highest compositional similarity. Moreover, a visual inspection of the bivariate plot with Chao's Jaccard similarity index and Spearman's rho shows that 89% of the sites fall in the upper right hand side quadrant, indicating that live-dead agreement is high (Kidwell 2007, Figure 2.3, Table 2.2). Significance for Spearman rank correlations for total individuals, bivalves and gastropods per site are shown in Table 2.2.

Table 2.2. Spearman rho for rank order correlations and Chao's Jaccard similarity index for total assemblages, bivalves and gastropods respectively. Values in bold indicate significant correlations.

Sample	Total assem	blage	Bivalve	S	Gastropods			
	Spearman's rho	Chao's J	Spearman's rho	Chao's J	Spearman's rho	Chao's J		
1	0.52	0.62	0.50	0.63	-	-		
2	0.26	0.86	0.36	0.91	-	-		
3	0.25	0.97	0.41	0.97	-	-		
4	0.32	0.89	0.31	0.89	0.33	0.67		
5	0.59	0.91	0.39	0.93	0.88	0.82		
6	0.26	0.83	0.44	0.94	0.22	0.44		
7	0.54	0.92	0.54	0.95	-	-		
8	0.24	0.89	0.26	0.93	-	-		
9	0.34	0.86	0.28	0.78	0.40	0.56		
10	0.28	0.80	0.36	0.89	-	-		
11	0.39	0.99	0.53	1.00	0.18	0.31		
12	0.15	0.51	0.03	0.42	-	-		
13	0.34	0.33	0.33	0.35	-	-		
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0.53	0.70	0.77	0.81	0.37	0.43			
0.50	0.93	0.67	0.98	-	-			
0.46	0.74	0.61	0.72	0.33	0.61			
0.37	0.92	0.47	0.91	0.31	0.65			
0.56	0.78	0.50	0.53	0.63	0.86			
0.37	0.88	0.50	0.91	0.36	0.54			
0.38	1.00	0.34	0.95	0.42	0.92			
0.55	0.95	0.40	0.92	0.81	0.72			
0.5	0.49	0.36	0.45	0.61	0.71			
0.38	1.00	0.27	0.90	0.48	0.95			
0.31	0.77	0.45	0.79	0.13	0.42			
0.68	1.00	0.56	1.00	-	-			
0.63	0.45	0.48	0.43	0.81	0.62			
0.13	0.79	0.23	0.87	-	-			
	0.53 0.50 0.46 0.37 0.56 0.37 0.38 0.55 0.5 0.5 0.38 0.31 0.68 0.63 0.13	0.530.700.500.930.460.740.370.920.560.780.370.880.381.000.550.950.50.490.381.000.310.770.681.000.630.450.130.79	0.530.700.770.500.930.670.460.740.610.370.920.470.560.780.500.370.880.500.381.000.340.550.950.400.550.490.360.381.000.270.310.770.450.630.450.480.130.790.23	0.530.700.770.810.500.930.670.980.460.740.610.720.370.920.470.910.560.780.500.530.370.880.500.910.381.000.340.950.550.950.400.920.50.490.360.450.381.000.270.900.310.770.450.790.630.450.480.430.130.790.230.87	0.53 0.70 0.77 0.81 0.37 0.50 0.93 0.67 0.98 - 0.46 0.74 0.61 0.72 0.33 0.37 0.92 0.47 0.91 0.31 0.56 0.78 0.50 0.53 0.63 0.37 0.88 0.50 0.91 0.36 0.38 1.00 0.34 0.95 0.42 0.55 0.95 0.40 0.92 0.81 0.5 0.49 0.36 0.45 0.61 0.38 1.00 0.27 0.90 0.48 0.31 0.77 0.45 0.79 0.13 0.63 0.45 0.48 0.43 0.81 0.13 0.79 0.23 0.87 -			

Species rank abundance distributions for both LAs and DAs were best explained by Zipf-Mandelbrot models, as indicated by AIC (Tables 2.2A, B, Figures 2.4A, B). The main difference between the three model parameters between LAs and DAs was observed for parameter 1, which represents the fitted abundance of the most abundant species (Wilson 1991). This parameter had a higher value for LAs (compare the position of the three dominant species from Figure 2.4A to those in Figure 2.4B, Table 2.4A). The other two model parameters are β and γ (Wilson 1991). β represents the potential niche diversity of the environment, and a positive β results in greater evenness amongst the most abundant species (Frontier 1985 in Wilson 1991). The parameter γ represent the average probability of the appearance of a species, with values close to 1 indicate greater evenness (Frontier 1985 in Wilson 1991). The differences in these parameters between the living community and the

dead assemblage indicate that the dead assemblage has greater evenness because γ is closer to 1 (1.21 dead vs. 3.73 living, Table 2.4A and B), and β is less negative than for the living community (-2.56 dead vs. -3.39 living, Table 2.4A and B).



Figure 2.3. Bivariate plot of taxonomic similarity (Chao's Jaccard) and rank-order correlation of relative abundances (Spearmans' rho) for live and dead assemblages from One Tree Reef, southern Great Barrier Reef. Sites located in the upper right hand quadrant have the highest live-dead agreement and sites in the lower left hand quadrant have the lowest live-dead agreement.

Table 2.3. Species composition and relative abundances in living and dead shell assemblages from One Tree Reef. Species also present in the Jones et al. (1990) dataset are indicated with an 'X'.

GASTROPODA	Dead	Living	Present in Jones et al.
			(1990)
Acteonidae			
Pupa nitidula	69	18	Х
Pupa sulcata	2	1	Х
Architectonicidae			
Architectonicidae indet.	0	1	
Cerithiidae			
Rhinoclavis fasciata	0	1	Х
Cerithium indet. 1	1	0	
Cerithium indet. 2	0	1	
Cerithiidae indet. 1	50	0	
Cerithiidae indet. 2	15	0	
Columbellidae			
Mitrella ligula	21	19	Х
Costellariidae			
Costellariidae indet.	1	1	
Eucyclidae			
Herpetopoma atrata	3	0	
Herpetotoma aspersa	4	0	
Epitoniidae			
Epitonium philippinarum	1	1	
Fissurellidae			
Emarginula indet.	15	0	
Fissurellidae indet.	16	0	
Haliotidae			
Haliotis indet.	4	0	
Haminoeidae			
Atys cylindricum	0	5	Х
Atys hyalina	96	49	
Atys naucum	5	3	
Liloa indet.	1	0	
Nassaridae			

Nassarius (Niotha) albescens	1	0	Х
Nassarius (Zeuxis) bicallosus	27	39	
Nassarius cf. estilbus	12	6	Х
Naticidae			
Natica (Naticarius) onca	2	0	Х
Notocochlis gualtieriana	15	23	Х
Polinices mammilla	3	6	Х
Ranellidae			
Gyrineum lacunatum	3	0	
Strombidae			
Strombus gibberulus	1	3	Х
Terebridae			
Terebridae indet.	1	0	
Turbinidae			
Astralium indet.	1	0	
Triviidae			
Trivia (Trivirostra) oryza	4	0	
Trochidae			
Ethalia guamensis	6	2	Х
Stomatella indet.	1	0	
Trochidae indet.	1	0	
Turridae			
Lophiotoma acuta	8	5	Х
Gastropoda indet. 1	0	1	
Gastropoda indet. 2	1	0	
Gastropoda indet. 3	2	0	

BIVALVIA	Dead	Living	Present in Jones et al.
			(1990)
Arcidae			
Barbatia indet.	2	0	
Cardiidae			
Fragum fragum	169	19	Х
Fulvia indet.	0	1	Х
Microfragum festivum	27	3	

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Nemocardium indet.	5	0	
Galeommatidae	10		
Ambuscintilla praemium	10	4	
Marikellia indet.	4	0	
Lucinidae		_	
Cavatidens omissa	0	1	X
Ctena bella	169	2	
Wallucina fijiensis	11	0	
Mytilidae			
Brachidontes indet.	3	0	
Pinnidae			
Pinnidae indet.	0	1	
Solemyidae			
Solemya indet.	0	1	Х
Tellinidae			
Abranda jeanae	655	540	Х
Cadella semen	0	1	Х
Loxoglypta clathrata	711	357	Х
Loxoglypta virgulata	7	9	Х
Pinguitellina robusta	3328	302	Х
Scissulina dispar	855	46	Х
Tellina (Quadrans) gargadia	18	0	Х
Tellina fijiensis	22	0	
Tellina indet. 1	2	0	
Tellina indet. 2	1	0	
Tellina virgata	4	23	
Tellinidae indet. 1	0	1	
Tellinidae indet. 2	0	3	
Veneridae			
Callista (Striacallista) phasianella	13	7	Х
Dosinia amphidesmoides	1	0	Х
Pitar (Pitarina) indet.	1	0	
Veneridae indet. 1	1	0	
Veneridae indet. 2	0	1	
Veneridae indet. 3	3	0	
Bivalvia indet.	2	2	



Figure 2.4. Rank abundance distribution for (A) dead assemblages, and (B) living assemblages. Black lines indicated best fit abundance distribution model (Zipf-Mandelbrot, see Table 2.4 for model parameters).

Table 2.4. Model fit results from the 'radfit' function for the (A) living and (B) dead assemblages. The parameters for the five different fitted models are shown. Decreasing AIC values provide support to the Zipf-Mandelbrot model.

A) Living

Model	Parameter 1	Parameter 2	Parameter 3	AIC
Null	-	-	-	2073.19
Pre-emption	0.295	-	-	544.30
Lognormal	1.558	2.234	-	440.80
Zipf	0.479	-1.609	-	487.88
Zipf-Mandelbrot	78.244	-3.398	3.734	298.09

B) Dead

Model	Parameter 1	Parameter 2	Parameter 3	AIC
Null	-	-	-	13631.51
Pre-emption	0.325	-	-	2809.57
Lognormal	1.401	2.829	-	748.40
Zipf	0.554	-1.823	-	841.77
Zipf-Mandelbrot	3.819	-2.560	1.213	632.86

2.4.2 Species composition of LAs and DAs

Two thirds of the species found living were also present in DAs (Table 2.3). Of the missing taxa, 85% were singletons in the live community (yielding an expectation of approximately four individuals in the dead assemblage: 1507 living / 6417 dead = 0.23), and the other 15% had less than five live individuals (yielding an expectation of less than 17 individuals in the dead assemblage). It is worth pointing out that some of the live singletons missing from the dead assemblage had particularly fragile shells (e.g. Pinnid indet.) or fragile shells and chemoautotrophic life habit (*Solemya* indet.). The other two non-singleton taxa missing from the DAs were a tellinid bivalve that could have been misidentified, and *Atys cylindricum* (Haminoeidae), a very thin-shelled bubble snail. Despite these particular cases, our results suggest that sampling probability of rare species is the main reason for these disagreements between living and dead assemblages (Table 2.3).

Approximately 40% of the species from the dead assemblages were found alive. Of the dead species missing from living assemblages, 36% were singletons meaning that even in the dead assemblage they each had a sampling probability of 1 in 6417, so we only expect to sample 0.23 of an individual from a live collected sample of 1507 individuals. An additional 43% had less than five individuals (an expectation of sampling approximately one live individual), and only 21% had an expectation of sampling as many as 10 live individuals (still

expected to be fewer than 1% of the live fauna). Despite their low abundance, taphonomic factors could explain the live-dead disagreement for the species for which we did not find those 10 live individuals (gastropods *Emarginula* sp., Fissurellidae sp., Cerithiidae indet. 1, Cerithiidae indet. 2; and bivalves Tellina fijiensis, Tellina (Quadrans) gargadia and Wallucina fijiensis). For example, two of the gastropods are fissurelids, which are typically epifaunal taxa that could have been transported from coral rubble and be allochthonous to the dead assemblage; while the two cerithid gastropods appear to be juveniles that were still captured by the 4 mm sieve, and unless we sampled at the time of recruitment we would not had found them alive. The three bivalve species are small, explaining why we may have missed them in the living community. The largest three individuals of each of T. fijiensis, T. (Q.) gargadia and W. fijiensis from our dead assemblages had a respective mean size of 4.09 mm, 4.03 mm, and 5.16 mm, suggesting we may have missed the living individuals in the 4 mm fraction, or may have been unable to tell they were alive. There were no differences in life habit or feeding mode between these taxa, with the exception of W. fijiensis (Lucinidae), which is chemosymbiotic and may be found living in sediments deeper than 10 cm. Despite these potential taphonomic differences, all of these missing species can be considered rare. Using the proportion of sum definition of rarity (abundances less than x% of the summed abundances of all species in the assemblage, Gaston 1994), none of the species missing from the living community had a proportional abundance in the dead assemblage higher than 0.8%. This finding is not surprising given that very high numbers of rare taxa have also been found in DAs from other tropical molluscan communities (e.g. Bouchet et al. 2002, Zuschin & Oliver 2007).

Only two species that were present in both living and dead assemblages were found to be outliers in the regression models. These species had notably different relative abundances, and this was the case both for the pooled assemblage and for the assemblage from each individual lagoon. The first species, *Abranda jeanae* was more abundant than expected in the living community (Table 2.3), particularly in First Lagoon. We found three times more live individuals than expected based on their abundance in the death assemblage (154 predicted live based on dead vs. 540 found live). The second species, *Ctena bella* was more abundant in the dead assemblage than in the living community (Table 2.3), particularly in Second Lagoon. We found less than 5% of the expected number of living *Ctena bella* based on their abundance in the death assemblage (40 predicted live based on dead vs. 2 found live).

2.4.3 Live-dead variation

Species composition in the 27 living and dead assemblages analyzed was not significantly different (Test of homogeneity of multivariate dispersions, p = 0.24). The homogeneity of dispersions test takes into account the temporal autocorrelation between LAs and DAs instead of assuming (like the previous metrics do) they are independent. To compare species composition, the mean composition of the source LAs (or centroid in a multivariate space) is considered to be the same as the one of the LAs that gave rise to the dead assemblages (Tomašových & Kidwell 2011). A non-significant *p* value indicates that the variation among DAs and the LAs centroid is not significantly different from variation among LAs and their centroid. Thus, neither pre-mortem nor post-mortem processes dominate.

The magnitude of total live-dead variation (mean distance between each DA and the LAs centroid) in the 27 assemblages was 0.39 (Figure 2.5A). From this total, the magnitude of pre-mortem variation (mean distance between each LA to the LAs centroid) was 0.34 (Figure 2.5B), and the magnitude of total post-mortem variation (Pre-mortem variation - Total variation) was 0.05 (Figure 2.5C). So while the variation amongst the LAs and DAs were not significantly different, variability in LAs contributes more to the total live-dead variation than

the variability in the DAs. Analyses using data pooled at the lagoon level yielded no notable difference to those conducted at the sample level.



Figure 2.5. Results from the homogeneity of multivariate dispersions test. (A) total live-dead variation for the 27 samples, (B) the contribution of pre-mortem processes to the total live-dead variation, (C) the contribution of post-mortem processes to the total live-dead variation. The dashed line in each panel represents the mean value for each variation among the 27 samples. Total live-dead variation and the pre-mortem variation can only have positive values, while the post-mortem variation can have negative values (pre-mortem variation minus total live-dead variation).

2.5 DISCUSSION

Species richness, diversity, evenness were not significantly different between LAs and DAs, and compositional similarity was high (as indicated by Chao's Jaccard index). Similarly, there was a positive significant relationship between species relative abundances in LAs and DAs; and living and dead shell assemblages both had the same best-fit curve for rank abundances (Zipf-Mandelbrot, Tables 2.2A and B). The observed differences in composition are attributable to sample sizes and sampling probability of rare species. Species present in both assemblages had very similar live and dead abundances with the exception of two taxa that were identified as outliers in the residuals of the linear regression models. Similarly, analyses accounting for temporal autocorrelation indicated non-significant differences in species composition of living and dead assemblages. These findings are consistent with other contributions and meta-analysis from non-reef soft sediment areas (Kidwell 2001, 2013); and they also strengthen previously documented contrasts with rocky reefs (Zuschin et al. 2000, Zuschin & Oliver 2003, Zuschin & Stachowitsch 2007), and silicilastic (Albano & Sabelli 2011) and carbonate seagrass environments (Feser & Miller 2014). This first study from a low-impacted, fully carbonate lagoon shows that these environments preserve with high fidelity the composition of soft sediment molluscan communities.

2.5.1 Compositional differences between living and dead assemblages

Species that were found both in LAs and DAs showed agreement in relative abundance with the exception of *Abranda jeanae* and *Ctena bella*. For these species, the differences in abundances between LAs and DAs are likely due to morphological traits that affect their preservation potential (e.g. Kosnik et al. 2009). One of these traits is thickness, as thicker shells need more force to break (Zuschin & Stanton 2001). *Abranda jeanae* (overly represented in LAs relative to its dead abundance) has a median size of 235.84 mm and a median thickness of 0.17 mm (n = 196), suggesting a low preservation potential. On the contrary, *C. bella* (poorly represented in LAs relative to its dead abundance) has a median size of 38.43 mm and a median thickness of 0.48 mm (n = 127), suggesting a higher preservation potential. Despite being smaller, *C. bella* shells are much thicker possibly conferring greater durability relative to translucently thin *A. jeanae* shells; supporting the idea

that morphological traits are important predictors of preservation potential in reef sediments (Kosnik et al. 2009).

These results suggest that rarity in conjunction with sample size and species-specific morphological traits related to shell durability are the main reasons for the observed live-dead disagreement. Biological processes such as variations in recruitment pulses were accounted for – at least the pulses previous to the sampling months – as we avoided the juvenile size fraction. Similarly, a stratigraphically ordered sediment at OTR (Kosnik et al. 2015), together with our personal observations of the underwater environment indicate that bioturbation by callianasid shrimp is low. Differential preservation due to bioerosion was also accounted for. Bioeroders like clionid sponges were not observed in shells from the dead assemblage. Other bioerosion traces that could affect preservation i.e. drill holes (Roy et al. 1994, but see Zuschin & Stanton 2001, Kelley 2008) are unlikely to have a major influence given that the percentage of shells with drill holes in our samples was small (mean predation rate = 9.6%).

2.5.2 Sediment age and taphonomic inertia in One Tree Reef

The degree of temporal autocorrelation between DAs and LAs is dependent on timeaveraging (Tomašových & Kidwell 2011). Given that DAs continuously receive newly dead individuals from LAs, the length of time in which those shells are in the taphonomically active zone will also affect the live-dead agreement (Olszewski 1999, 2004). Feser & Miller (2014) recently showed that changes in LAs, sometimes even seasonal variations, get incorporated to DAs in less than a decade. Therefore, good agreement between LAs and DAs does not necessarily mean that the environment has not changed, but rather that DAs are rapidly incorporating these changes (Feser & Miller 2014). This phenomenon is particularly relevant to OTR sediments given the young age of shells in the taphonomically active zone (19 years, Kosnik et al. 2015). We know however that the stratigraphic record of OTR is ordered (Kosnik et al. 2015), so even if changes are recorded 'fast' by the first 20 cm of the sediment, the record below 20 cm can still be used for paleontological studies.

Examination of the species list from OTR mollusk fauna collected in 1985 (Jones et al. 1990) supports the conclusion that the sediments from the top 20 cm are not just 'rapidly absorbing changes'. Sampling carried out by Jones et al. (1990) found the same dominant species as found in the DAs and LAs sampled in 2012. Most of the species found in the 1985 dataset were sampled in 2012, or are co-generic (see Table 2.3). Because there are no voucher specimens or abundance data available for the 1985 dataset (Doug Ferrell pers. comm.), critical analyses of taxonomic differences or changes in taxon abundance are not possible. The only major difference in composition is the presence of the gastropods Atys hyalina and Nassarius (Zeuxis) bicallosus in the 2012 samples, but not in the 1985 samples. Without being able to compare specimens we cannot be certain if these species were missing from the Jones et al. (1990) samples or if the taxa were given them different names. Minor differences in taxonomic composition could be due to several factors. First, it is possible that there are differences between identifications and taxonomies. For example, the differences between Atys hyalina and Atys cylindricum are very subtle and this may explain the different identifications between Jones et al. (1990) and this work. Second, the two studies sampled different areas of the OTR lagoon. Their sampling was carried out in different areas of First Lagoon (see Jones et al. 1900, Figure 1), whereas we focused on the northern edge of First Lagoon and sampled Second and Third Lagoons (see Figure 2.1). Third, there are likely to be biannual or multi-annual changes in community composition and/or abundance. Fourth, there may have been slight, but genuine directional changes in minor constituents of the community

that could explain the minor disagreements between datasets. Regardless, the overall agreement between the 2012 and 1985 datasets is particularly important given that the Jones et al. (1990) samples are outside the window of time averaging (i.e. the sediments they sampled are buried below the ones we sampled), suggesting that the live community has not changed considerably in at least three decades.

2.5.3 Accounting for differences in substrates and spatial heterogeneity

Paleontologists have a very good understanding of how the nature of the environment (e.g., soft sediments vs. hard substrates), its heterogeneity (e.g., homogeneous sandy/muddy bottoms vs. patchy seagrass or rocky reefs), the degree of human impact (e.g., proximity to coasts and other sources of eutrophication), and the size of the shells studied (e.g., sieve mesh size) can affect the fidelity of dead shell assemblages relative to living communities (see reviews and meta-analysis by Kidwell 2001, 2007, 2013, and numerous references therein). In this regard, one of the most important predictors of fidelity is soft sediments versus hard substrates. The extensive literature from sandy and muddy benthic environments consistently reports high live-dead fidelity such as that observed here. Meta-analysis of 85 molluscan datasets has shown that DAs from soft-sediment environments provide a reliable estimate of species abundances (Kidwell 2001). There were however no fully carbonate soft-sediment assemblages included as part of that meta-analysis, and the few available studies carried out in reefs environments are from hardgrounds (see Zuschin et al. 2000, Zuschin & Oliver 2003, Zuschin & Stachowitsch 2007). Rocky reefs in the Red Sea yielded live-dead agreement in species abundances as low as 6%, and rarely above 50% (Zuschin et al. 2000). Hardgrounds from the Seychelles showed an overlap in species composition and rank order correlations between LAs and DAs, but this similarity was not found in coral-associated (instead of

hardground-associated) molluscan assemblages (Zuschin & Oliver 2003). The poor live-dead agreement found in reef hardgrounds was suggested to be due to dead specimens being overgrown by living organisms, which made dead shells hard to sample (Zuschin et al. 2000, Zuschin & Stachowitsch 2007). Other benthic ecosystems with high environmental heterogeneity such as seagrass and coralligenous algae assemblages also have shown lower live-dead agreement than soft-sediment (e.g. Albano & Sabelli 2011, Feser & Miller 2014). For example, a three-decade analysis of seagrass mollusks from St Croix (Virgin Is.) revealed that the composition of LAs and DAs varied significantly, mainly due to shifts in rank orders of the key species through time (Feser & Miller 2014).

2.5.4 Using a live-dead approach to monitor reef ecosystems

Ecologists and conservation planners are increasingly aware of the importance of long-term temporal perspectives to understand changes to communities and ecosystems (e.g. Jackson et al. 2001, Kidwell 2001). Nevertheless, the information available about pre-anthropogenic impact composition of natural communities is still scarce. Pre-anthropogenic ecological baselines are thus urgently needed to support management decisions (Kidwell 2007). The mismatch between living communities and dead assemblages can be powerful tools for environmental assessment (Kidwell 2007), and as such they can also provide valuable information to assess reef health.

Previous studies have suggested that the status of a reef should be determined by using taxa in addition to corals and fish, given that the presence and abundance of other invertebrates is strongly linked to the healthy functioning of reefs (Zuschin & Stachowitsch 2007, Przeslawski et al. 2008). Therefore, the fact that mollusks have been one of the main taxonomic groups used in taphonomic studies (but see Pandolfi & Minchin 1995, Greenstein

& Pandolfi 1997, Edinger et al. 2001) provides an added benefit. Since the abundance and diversity of mollusks in tropical areas is very high (Bouchet et al. 2002), they are informative and useful for rapid assessments of coral reef diversity and health (Wells 2000).

Here, we present the first live-dead agreement study for soft sediment molluscan communities from a fully carbonate reef lagoon and for the Great Barrier Reef, Australia. Results from species richness, evenness, relative abundance, rank order correlations, among other analyses, show that the live-dead agreement is high. Differences in composition and abundance seem to be driven by rare species. Some species-specific morphological traits could also be conferring greater preservation potential. Our results are further supported by compositional agreement with a 30-year-old mollusk dataset from OTR, indicating temporal stability in composition outside the window of time averaging. Thus, together with previous research at OTR, our data show that soft sediments from low-impacted fully carbonate systems have a high potential for conservation paleobiology studies, which are much needed to yield baseline ecological information about coral reef health in changing oceans.

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CHAPTER 3

Encounter frequency does not predict predation frequency in

tropical dead-shell assemblages

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3.1 Abstract

Predation is frequently suggested to be a key biotic process that can shape ecological communities and drive coevolution. The premise behind these hypotheses is that predators select prey to ensure maximum gain per unit effort; for example, by selecting species that are more abundant or accessible. In this study, we tested for predator selectivity in a tropical molluscan assemblage by quantifying the influence of relative abundance (encounter frequency) on predation frequencies. We collected macromolluscs from 15 sites in three softsediment reef lagoons at One Tree Reef (southern Great Barrier Reef, Australia). Dead molluscs were counted and identified to species level (61 species, n = 7395), and species predation frequencies were calculated as the proportion of dead shells with drill holes. We found that in this infauna-dominated community levels of drilling predation were low (9.6% on average), and there was no evidence that predators selected prey based on encounter frequency. This result was consistent across prey species and lagoons. Overall, drilling predators do not specialize on more accessible prey species and are not a major cause of mortality in this molluscan assemblage. These findings from a soft-sediment carbonate reef suggest that the variability in predation intensity is contingent on the species composition of a given assemblage.

3.2 INTRODUCTION

Predation is a key biotic process that shapes communities and the evolution of interacting species (e.g. Vermeij 1993, Leighton 1999). Predation contributes to the flow of energy and resources through communities and ecosystems (Vermeij 1993, Chapin et al. 1997) and can alter the relative abundances of species in lower trophic groups. Changes in relative dominance of trophic groups can impact community structure and function (Paine 1966, Chapin et al. 1997, Duffy 2002, Meyer & Byers 2005). Over generational time scales, improvements in predator effectiveness can also lead to changes in prey defences (Vermeij 1993). For example, epifaunal tropical gastropods subject to intense predation by crabs have developed thicker shells, smaller apertures and stronger sculpture (Zipser & Vermeij 1978, Bertness & Cunningham 1981). Thus, predators can be important drivers of the evolution of species and communities over time.

Predators have more pronounced effects on community structure and natural selection when predation frequencies are high and predators are selective. For instance, Navarrete and Castilla (2003) showed that gastropod and sea-star predation had a large controlling effect on community structure in Chilean intertidal communities. By removing large numbers of their preferred prey, these predators controlled the population of a bivalve that would otherwise dominate the community. On the other hand, Jones et al. (1992) show that fish predation on molluscs, while omnipresent in tropical reef communities, had very little influence on the molluscan community structure at One Tree Reef. In order to determine what drives predation frequencies, it is important to understand if predators select prey based on community-level or individual-level characteristics. Community characteristics such as prey abundance and life habit primarily determine the accessibility or probability of encountering prey (Vermeij 1983, Leighton 2002, Leonard-Pingel & Jackson 2013). Whereas, individual traits such as prey size, shape and mechanical properties largely determine the cost of handling or eating the prey (e.g. Kelley 1988, Kelley & Hansen 1996, Dietl & Alexander 2000, Chiba & Sato 2012, Chattopadhyay et al. 2014). Studies of predation in palaeontology have tended to focus on individual-level traits (but see Kelley & Hansen 2006), because community-level data are difficult to collect and can be biased by taphonomic processes. Therefore, focusing on a community-level attribute such as relative abundance can provide new insights into predation.

Given that predation is high in tropical environments (Dudley & Vermeij 1978, Allmon et al. 1990, Schemske et al. 2009, among others), predator selectivity, which leads to more efficient predation, should be more important at low latitudes. Previous research has shown that there is a diversity hotspot for molluscs in Southeast Asian and Australian tropical seas (Crame 2000, Bouchet et al. 2002). One mechanism suggested to maintain this high diversity is higher predation intensities in the tropics relative to other locations (Schemske et al. 2009). Preferential predation on the most abundant species can lead to competitive release that can explain this higher diversity (Menge 1995, Duffy 2002). Predation frequencies are high for tropical marine snails that are preyed upon by crabs (Zipser & Vermeij 1978) and palaeontological studies have also found evidence for high predation at low latitudes (Vermeij 1980, 1993, Alexander & Dietl 2001). Therefore, tropical communities are an ideal study system in which to study predator selectivity given that molluscan are diverse in these environments, accessible to sample in large numbers, and predation frequencies can be easily quantified from traces in prey shells.

Predator selectivity must be evaluated relative to the prey community, and prey encounter frequencies can be accounted for by using relative abundances of individuals in dead shell assemblages. Prey abundance is a surrogate for the frequency that a foraging predator potentially encounters a prey species (Leighton 2002). The probability of

interspecific encounter has a long history; perhaps most familiar to palaeontologists is the discussion by Hurlbert in his 1971 paper most commonly referenced for its contributions to rarefaction. A non-selective predator model assumes that all prey are equally available to a predator. So the probability of a predator encountering a particular prey is the preys' relative abundance. Prey abundance can be obtained from dead-shell assemblages (DA) given that extensive research on DA indicates that they are good sources of community-level information (Kelley & Hansen 2006, Kidwell & Tomašových 2013). Indeed, shell assemblages from the Cretaceous to Pleistocene have been used to show that prey relative abundance was not correlated to drilling frequencies in several bivalve families (Kelley & Hansen 2006). Thus, since it is easier to collect DA than to sample living communities, DA have been widely used as surrogates for living communities.

In this study, we tested for drilling predator selectivity in a tropical molluscan community from One Tree Reef (southern Great Barrier Reef, Australia) by quantifying the effects of relative abundance and life habit (infaunal or epifaunal) on species predation frequencies. We test for predator selectivity using prey abundances in the dead assemblage as a proxy for the preys' encounter rate. We discuss our results in the context of predation in tropical communities and prey life habits given that these are the most relevant to better understand the role of predators in extant and extinct environments.

3.3 MATERIALS AND METHODS

3.3.1 Study site and material

Sampling was carried out at One Tree Reef, southern Great Barrier Reef, Australia (23°20' S, 152°06' E, Figure 3.1). The reef crest surrounds three lagoons (roughly 10 - 13 km² in extension, Davies et al. 1976) that have coral patch reefs interspersed with sand (Ludington

1979). Sediment containing dead shells was collected at 15 sites spanning three lagoons. Sites ranged in depth from 4.3 to 6.1 m (ponded depth). At each collection site, four 0.25 m^2 replicate quadrats of 1 m² of sediment were sampled by divers using an 80 mm diameter airlift and 1 mm mesh bags. Only the top 0.1 m of sediment was removed. Sampling was carried out four times in 2012 therefore each site has 16 replicate quadrats.



Figure 3.1. Schematic map of One Tree Reef, southern Great Barrier Reef. The reef outline is the shaded grey area, the three lagoons are in white, and One Tree Island in black. Site numbers inside each lagoon agree with the collection sites listed in Table 3.1. Reef and lagoon outline were traced from Google Earth imagery.

After collection, samples were wet sieved using a 4 mm sieve. Previous studies (e.g. Kidwell 2001) have found 2 mm sieves to be suitable for molluscs, but we observed these sieves were still capturing juveniles. Since smaller shells have a lower probability of being preserved relative to larger shells (Kosnik et al. 2007), we used 4 mm sieves to ensure comparability with the fossil record (Kidwell 2001). The death assemblage from one quadrat

from each site was sorted, where necessary to achieve sufficient sample size additional replicate quadrats were sorted (Table 3.1). Individuals were identified to the species level with the aid of published literature (Lamprell & Whitehead 1992, Lamprell & Healey 1998), the Australian Museums' Malacology collections, and mollusc taxonomists. The number of bivalve and gastropod individuals per species were counted. For bivalves, the minimum number of individuals was the number of articulated valves plus the total number of unfragmented right valves.

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Table 3.1. Total abundance, richness, and sampled area for dead assemblages from different sites. Latitude, longitude and depth are also provided for each site. Depth is ponded depth in meters determined by diver depth gauge and lagoon specific tidal corrections sourced from the Great Barrier Reef Ocean Observing System, * indicates an estimated ponded depth.

Site	Abundance	Richness	Area (m ²)	Latitude	Longitude	Depth
1st Lagoon, Site 1	528	14	1.75	-23.49159°	152.07444°	4.7m
1st Lagoon, Site 2	160	8	0.5	-23.49461°	152.06969°	4.9m
1st Lagoon, Site 3	293	8	1	-23.49399°	152.06875°	4.9m*
1st Lagoon, Site 4	37	5	0.5	-23.48585°	152.08090°	5.1m
1st Lagoon, Site 5	187	5	1	-23.49677°	152.06587°	4.5m
1st Lagoon, Site 6	82	4	0.5	-23.49406°	152.07054°	5.3m
1st Lagoon, Site 7	82	5	0.5	-23.49214°	152.07440°	4.3m
2nd Lagoon, Site 2	822	14	2.25	-23.50030°	152.06017°	4.9m
2nd Lagoon, Site 3	861	6	2.25	-23.50170°	152.05995°	4.6m
2nd Lagoon, Site 4	72	4	0.5	-23.50043°	152.06168°	5.0m
2nd Lagoon, Site 5	364	5	1	-23.49871°	152.05949°	5.0m
3rd Lagoon, Site 1	921	8	2	-23.49729°	152.05243°	5.3m
3rd Lagoon, Site 2	1171	8	2	-23.49631°	152.05169°	6.0m
3rd Lagoon, Site 3	686	8	1.5	-23.49468°	152.05145°	6.1m
3rd Lagoon, Site 4	284	6	0.5	-23.49849°	152.05316°	5.7m

Given the abundance of dead shell material, encounter rates were calculated for each species using between 2 to 9 replicate quadrats per site (Table 3.1). Overall, a total of 7395 dead bivalve and gastropod individuals were included in these analyses, representing 61 species from 26 different families (Table 3.2). These were all the identifiable species present in the dead shell assemblage. Species were separated into life habits using published literature (Lamprell & Whitehead 1992, Beesley et al. 1998, Lamprell & Healey 1998, Table 3.2). Tellinidae, Lucinidae, Veneridae, Cardiidae, and Galeonmatidae bivalves were classified as infaunal (Table 3.2). Gastropods and the rest of the bivalves were classified as epifaunal given that some of them are mobile predators (e.g. Naticidae), others are scavengers and/or deposit feeders (e.g. Nassaridae), and others are grazers (e.g. Haminoeidae), suggesting that they are not solely restricted to the infauna. The most abundant taxa were infaunal tellinid bivalves (95%), followed by non-tellinid bivalves (3%), and gastropods (2%) (Table 3.3).

Table 3.2. Life habit, total number of individuals, number of individuals with drill holes, and drilling frequency (median value between sites) for bivalve and gastropod species from One Tree Reef.

	Life habit	Total abundance	Drilled	Drilling
		(drilled + undrilled)	individuals	frequency
GASIKOFODA				
Acteonidae				
Pupa nitidula	Epifaunal	77	45	0.5
Pupa sulcata	Epifaunal	2	2	1
Cerithiidae				
Cerithium indet. 1	Epifaunal	1	1	1
Cerithiidae indet. 1	Epifaunal	54	19	0.4
Cerithiidae indet. 2	Epifaunal	15	5	0.38
Columbellidae				
Mitrella ligula	Epifaunal	22	7	0.12

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Costellariidae				
Costellariidae indet.	Epifaunal	1	0	0
Eucyclidae				
Herpetopoma atrata	Epifaunal	3	0	0
Herpetotoma aspersa	Epifaunal	4	0	0
Epitoniidae				
Epitonium philippinarum	Epifaunal	1	1	1
Fissurellidae				
Emarginula indet.	Epifaunal	17	2	0.06
Fissurellidae indet.	Epifaunal	16	0	0
Haliotidae				
Haliotis indet.	Epifaunal	4	0	0
Haminoeidae				
Atys hyalina	Epifaunal	108	1	0
Atys naucum	Epifaunal	5	1	0.12
Liloa indet	Epifaunal	1	0	0
Nassaridae				
Nassarius (Niotha) albescens	Epifaunal	1	0	0
Nassarius (Zeuxis) bicallosus	Epifaunal	30	10	0
Nassarius cf. estilbus	Epifaunal	12	7	0.67
Naticidae				
Natica (Naticarius) onca	Epifaunal	2	0	0
Notocochlis gualtieriana	Epifaunal	15	1	0
Polinices mammilla	Epifaunal	5	0	0
Ranellidae				
Gyrineum lacunatum	Epifaunal	3	0	0
Strombidae				
Strombus gibberulus	Epifaunal	1	0	0
Terebridae				
Terebridae indet.	Epifaunal	1	0	0
Turbinidae				
Astralium indet.	Epifaunal	1	0	0
Triviidae				
Trivia (Trivirostra) oryza	Epifaunal	5	0	0
Trochidae	•			
Ethalia guamensis	Epifaunal	6	1	0
Stomatella indet.	Epifaunal	1	0	0
Trochidae indet.	Epifaunal	2	0	0
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Turridaa				Chapter 3
	Eniformal	0	0	0
Сортогота асша	Ерпациан	9	0	0
Gastropoda indet. 1	Epifaunal	1	0	0
Gastropoda indet. 2	Epifaunal	2	1	0.5
BIVALVIA				
Arcidae				
Barbatia indet.	Epifaunal	2	0	0
Cardiidae				
Fragum fragum	Infaunal	185	24	0.07
Microfragum festivum	Infaunal	28	3	0
Nemocardium indet.	Infaunal	5	1	0.2
Galeommatidae				
Ambuscintilla praemium	Infaunal	16	0	0
Marikellia indet.	Infaunal	4	0	0
Kelliidae				
Kellia rotunda	Infaunal	1	0	0
Lucinidae				
Ctena bella	Infaunal	216	16	0
Wallucina fijiensis	Infaunal	11	0	0
Mytilidae				
Brachidontes indet.	Epifaunal	3	0	0
Tellinidae				
Abranda jeanae	Infaunal	701	85	0.10
Loxoglypta clathrata	Infaunal	892	107	0.10
Loxoglypta virgulata	Infaunal	8	1	0.25
Pinguitellina robusta	Infaunal	3858	275	0.07
Scissulina dispar	Infaunal	953	54	0.006
Tellina (Quadrans) gargadia	Infaunal	23	6	0.08
Tellina fijiensis	Infaunal	24	0	0
Tellina indet. 1	Infaunal	2	0	0
Tellina indet. 2	Infaunal	1	0	0
Tellina virgata	Infaunal	7	1	0
Tellinidae indet. 1	Infaunal	1	0	0
Veneridae				
Callista (Striacallista)	Infaunal	15	1	0

				Chapter 3
phasianella				Ĩ
Dosinia amphidesmoides	Infaunal	1	1	1
Pitar (Pitarina) indet.	Infaunal	1	0	0
Veneridae indet. 1	Infaunal	1	0	0
Veneridae indet. 2	Infaunal	5	1	0
Veneridae indet. 3	Infaunal	1	0	0
Bivalvia indet.	Infaunal	2	1	0.5

3.3.2 Calculation of predation frequencies

Predatory drill-holes in the DA were identified using the following criteria: (1) holes of a circular shape and regular outline; (2) holes perpendicular to the shell; and (3) in the case of articulated valves, holes that only go through one of the valves (Kelley & Hansen 2003, Yanes & Tyler 2009).

Predator selectivity can be readily quantified using drilling predation metrics and taking into account species relative abundances in assemblages or communities. Predation frequency is usually calculated as the number of individuals of a taxon with a predation trace, divided by the total number of individuals from that same taxon (Lower Taxon Frequency, Kowalewski 2002). This species-level metric can account for selectivity if it is considered relative to the species abundance in a sample. For example, if predators are non-selective, then predation frequency for a given species is constant (slope = 0) irrespective of the preys' relative abundance in the sample. Therefore, to differentiate between selective and nonselective predation the frequency at which predators encounter prey is required. Since we used all 61 species to calculate encounter frequency, drilling frequency was also calculated for all 61 species.

We found no significant differences between predation in right and left valves for tellinids ($\chi^2 = 0.95$, df = 3, *p* value = 0.81), and no shell had multiple drill holes. Thus, we 86

considered any unfragmented right valve with a drill-hole to be a drilled individual. The three naticid species present in the samples had a similar size range (Table 3.3), indicating they could attack the same prey. Therefore, we collectively treat these three naticid species as 'the predator', and assume they all have the same selective/non-selective behavior.

Table 3.3. Absolute abundance of drilling naticid predators per lagoon. Median size of predators and of the six most abundant species is also shown. More individuals were measured from other samples when needed (i.e., the number of naticid individuals measured exceeds the number used for analyses).

Species	1st Lagoon	2nd Lagoon	3rd Lagoon	Size (mm)	N measured
GASTROPODA					
Naticidae					
Natica (Naticarius) onca	2	0	0	92.71	6
Notocochlis gualtieriana	6	5	4	78.67	38
Polinices mammilla	3	0	2	101.51	17
BIVALVIA					
Cardiidae					
Fragum fragum	75	35	75	87.17	149
Lucinidae					
Ctena bella	62	26	128	38.43	135
Tellinidae					
Abranda jeanae	371	171	159	254.38	196
Loxoglypta clathrata	99	311	482	48.92	115
Pinguitellina robusta	751	1055	2052	138.52	153
Scissulina dispar	105	582	266	101.37	191

3.3.3 Model selection

A generalized linear mixed-effects model (GLMM) with a binomial response variable (drill hole = 1, no drill hole = 0) was used to determine which explanatory variable best predicted the per species frequency of drill holes. Relative abundance of species in samples (i.e., encounter frequency) and species life habit (infaunal or epifaunal) were included as fixed factors. Species identity and lagoon were included as random factors, and models were tested with and without an effect of relative abundance on species (i.e., random slope). We also included a variable for each replicate as a random factor, because the ratio of model residual deviances to residual degrees of freedom tended to be greater than one, indicating overdispersion. GLMM analyses were carried out using the 'glmer' function in the 'lme4' package in the statistical programming language R (Version 3.0.2, R Core Team 2013). We used the 'drop1' function with chi-squared test to determine which of the fixed factors and interactions to keep in the final model. We used the 'anova' function to determine which configuration of random factors to retain. R code and data files are provided in supplementary material.

3.4 Results

3.4.1 Species life habits

The overwhelming majority of the species found in the soft sediment assemblages from One Tree Reef were infaunal (93%, Table 2). As a consequence, and given that all potential prey (infaunal or epifaunal) were collected at the same depth (0 - 10 cm) and in the same volume of sediment, we considered the ecological differences between what we classified as infaunal and epifaunal species to be minimal. Other studies have found life habit to be an explanatory factor for predation (e.g. Leonard-Pingel & Jackson 2013) but since the absolute majority of taxa had the same life habit, it was excluded as a predictor for predation frequency from the models.

3.4.2 Predation frequencies

The most abundant prey species had median predation frequencies per site between 0 and 10% (*Pinguitellina robusta* (7%), *Scissulina dispar* (0.6%), *Loxoglypta clathrata* (10%), *Abranda jeanae* (10%), *Ctena bella* (0%), *Fragum fragum* (7%), Table 3.2). Median drilling frequencies for the 61 species ranged from 0% to 100% but this was strongly affected by singletons and species with less than 10 individuals (Table 3.2). The abundance of drilling predators was very low in all three lagoons; in First lagoon, the relative abundance of predators was 0.64%, in Second lagoon 0.21%, and in Third lagoon 0.18% (Table 3.3).

3.4.3 Model selection

Species relative abundance was not a significant predictor of drilling frequencies. Model selection based on AIC indicated that the model without relative abundance (AIC = 670.02) was better than the model with the fixed factor included (AIC = 708.89). These results indicate that the added parameter did not significantly improve the model fit, and therefore predation frequency is not related to prey accessibility.

The best model indicated a constant predation frequency of 9.6% (thick black line, Figure 3.2). Model selection did not find relative abundance or the intercept to be significant, and the best model included both species and lagoon as random effects (Table 3.4). The model without the slope term for individual species as a function of relative abundance had lower AIC and BIC than the model with the slope term for individual species (Table 3.5), suggesting little advantage of the additional parameter. Predation frequencies of abundant species tended to match the final model; whereas, species making up less than 2% of the death assemblage had more uncertain predation frequencies due to low sample sizes. In the most extreme case, a species represented in a sample by one individual must be either 0% or 100% preyed upon (Figure 3.2). Despite having the most drilling predators, the First lagoon assemblages had the lowest predation frequencies, approximately 4.9% lower than the model

average; and despite having fewer predators, the Third lagoon assemblages had the highest rate, approximately 5.1% higher (Tables 3.3 & 3.4). Overall, the results suggest that drilling predators are not selective for prey abundance across lagoons, and that the most abundant species in the assemblage have drilling frequencies below 13%.



Figure 3.2. Scatterplot of predation frequency and encounter frequency for dead molluscan assemblages. Each symbol represents a species at a site. Circles indicate species in sites from First lagoon, squares indicate species in sites from Second lagoon, and triangles indicate species in sites from Third lagoon. (A) The thick dark line is the overall model fit (intercept), and it indicates that the overall value for drilling predation is 9.6%. The thinner lines are the random effects for each species. (B) Idem previous but incorporating a random slope.
Table 3.4. Summary of generalized linear mixed model statistics for the likelihood of a shell being drilled relative to its encounter frequency. Final best-fit model showing random effects for the slope term for each lagoon and for the different species as a function of relative abundance.

Random effects		
Lagoon	Intercept	
First	-0.189	
Second	0.078	
Third	0.222	
Species	Intercept	Relative abundance
GASTROPODA		
Acteonidae		
Pupa nitidula	0.195	-0.424
Pupa sulcata	-0.329	-0.532
Cerithiidae		
Cerithium indet. 1	-0.242	-0.377
Cerithiidae indet. 1	0.072	-0.217
Cerithiidae indet. 2	-0.178	-0.272
Columbellidae		
Mitrella ligula	-0.225	-0.271
Costellariidae		
Costellariidae indet.	0.042	0.062
Eucyclidae		
Herpetopoma atrata	0.085	0.137
Herpetotoma aspersa	0.097	0.156
Epitoniidae		
Epitonium philippinarum	-0.155	-0.323
Fissurellidae		
Emarginula indet.	0.045	0.045
Fissurellidae indet.	0.173	0.332
Haliotidae		
Haliotis indet.	0.101	0.152

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Haminoeidae		
Atys hyalina	0.157	0.588
Atys naucum	-0.035	-0.087
Liloa indet	0.033	0.053
Nassaridae		
Nassarius (Niotha) albescens	0.024	0.051
Nassarius (Zeuxis) bicallosus	0.126	-0.182
Nassarius cf. estilbus	-0.198	-0.414
Naticidae		
Natica (Naticarius) onca	0.055	0.088
Notocochlis gualtieriana	0.078	0.106
Polinices mammilla	0.105	0.182
Ranellidae		
Gyrineum lacunatum	0.082	0.125
Strombidae		
Strombus gibberulus	0.046	0.067
Terebridae		
Terebridae indet.	0.034	0.052
Turbinidae		
Astralium indet.	0.031	0.053
Triviidae		
Trivia (Trivirostra) oryza	0.113	0.175
Trochidae		
Ethalia guamensis	-0.088	-0.097
Stomatella indet.	0.042	0.062
Trochidae indet.	0.072	0.111
Turridae		
Lophiotoma acuta	0.145	0.254
Gastropoda indet. 1	0.046	0.067
Gastropoda indet. 2	-0.147	-0.241

BIVALVIA

Arcidae			
Barbatia indet.	0.055	0.088	
Cardiidae			
Fragum fragum	-0.156	-0.258	

Microfragum festivum	-0.267	-0.279
Nemocardium indet.	-0.230	-0.325
Galeommatidae		
Ambuscintilla praemium	0.122	0.198
Marikellia indet.	0.098	0.153
Kelliidae		
Kellia rotunda	0.046	0.067
Lucinidae		
Ctena bella	-0.069	-0.032
Wallucina fijiensis	0.088	0.156
Mytilidae		
Brachidontes indet.	0.093	0.139
Tellinidae		
Abranda jeanae	-0.136	-0.291
Loxoglypta clathrata	0.195	-0.048
Loxoglypta virgulata	-0.130	-0.169
Pinguitellina robusta	-1.161	-1.051
Scissulina dispar	-0.477	0.041
Tellina (Quadrans) gargadia	-0.125	-0.343
Tellina fijiensis	0.206	0.413
Tellina indet. 1	0.067	0.102
Tellina indet. 2	0.034	0.052
Tellina virgata	-0.020	-0.027
Tellinidae indet. 1	0.046	0.067
Veneridae		
Callista (Striacallista) phasianella	0.036	-0.058
Dosinia amphidesmoides	-0.329	-0.489
Pitar (Pitarina) indet.	0.033	0.053
Veneridae indet. 1	0.024	0.051
Veneridae indet. 2	-0.034	-0.079
Veneridae indet. 3	0.044	0.071
Bivalvia indet.	-0.178	-0.264

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Model	d.f.	AIC	BIC	logLik	Deviance	χ^2	χ^2 d.f.	$\Pr(\chi^2)$
Without slope	4	670.02	684.65	-331.01	662.02			
With slope	5	707.27	725.55	-348.63	697.27	0	1	1

Table 3.5. Analysis of variance results for comparison between final models with and without a random slope for species.

3.5 DISCUSSION

We found no evidence that drilling gastropods were actively selecting more abundant prey in this tropical dead shell assemblage. This result was consistent across the 61 species and all three of One Tree Reef's lagoons (Figure 3.2). Differences in predation intensity between lagoons do not reflect differences in the number of predators. Species-level differences in predation frequency only became pronounced for rare species (< 2% of sample, Table 3.2), suggesting that sampling probabilities were driving these differences. Nonetheless, species- or individual-level predator selectivity (e.g., based on morphological traits) are not evaluated here and cannot be ruled out. These results suggest that drilling predators are randomly selecting prey at very low levels relative to other mortality agents, and therefore unlikely to be playing a major role in structuring this tropical molluscan assemblage.

Previous contributions have shown that by affecting the abundance of their prey, predators can have an effect on prey populations and ultimately, on community structure (Menge 1995, Duffy 2002). Changes to community structure can in turn affect community function (Chapin et al. 1997), especially if changes in population size affect species with high abundance or biomass. For instance, if predators selectively target prey that are carrying out a specific function in the community i.e. filter feeding particular nutrients from the water column, predators can potentially affect the nutrient cycling of said community. The 94

magnitude of predatory interactions has also been suggested to be dependent on temperature, where higher temperatures lead to increases in metabolic and consumption rates (Sanford 2002, Dell et al. 2014). The data at hand, however, indicate that regardless the tropical nature of the environment these predators do not have a strong effect on reef lagoon communities, as the overall predation rate was 9.6% and predators were not selective for accessible prey. Before drilling predators are assumed to have an important role regulating populations of these infaunal species and communities, it is first necessary to demonstrate predator selectivity. Only after non-random predation is demonstrated does it need to be explained.

All the predators found in the samples were naticids, and in most cases the drill-holes had the typical naticid bevelled morphology. It is possible however, that by assuming that all drilling predators leave a quantifiable trace we are underestimating predation intensity. Some naticid gastropods consume prey by suffocation without leaving a drill-hole, thus the drilling gastropods in our samples may have consumed prey this way. Experiments carried out in Fiji and Guam on the reef-dwelling naticid Polinices tumidus found that this predator killed 15-55% of the prey without leaving a borehole (Vermeij 1980, Ansell & Morton 1987). It is thus possible that *P. mamilla* from One Tree Reef exhibits similar behaviour as its cogeneric *P.* tumidus. However, given that N. gualteriana, and not P. mamilla was the most abundant predator in this assemblage (Table 3.3), and that killing by suffocation has not been documented for this species (boreholes produced in 100% of the attacks, n = 14, Ansell & Morton 1987), it is unlikely that we are significantly underestimating predation frequencies. Moreover, other experiments testing for alternative modes of predation in naticids found very little evidence to suggest that suffocation is a pervasive feeding behaviour (Visaggi et al. 2013). There are, however, other prey-specific behaviours we may be missing, such as the case of Atys hyalina, a seasonally very abundant gastropod that was never found drilled

(Table 3.2). Since *Atys* has a big shell aperture, predators could be killing this prey by suffocation instead of drilling its shell.

Another biological factor that could be affecting the interpretation of our results is the potential role of hermit crabs 'sequestering' naticid shells. Hermit crabs have been suggested to create anomalies in the abundance of certain shells they occupy (Walker 1989). If this were the case, we would find less naticid predators in the dead shells assemblages than there really are. The samples from One Tree Reef had several live hermit crabs in them (one or two per 0.25 m^2 quadrat) but the great majority of them were occupying highly coiled shells (almost exclusively cerithids) and we never found a living hermit crab using a naticid shell. Thus, even if we cannot discard the role of hermit crabs creating an anomaly in the abundance of naticid shells, the data at hand suggest it is unlikely.

In addition to the drilling predators quantified in this analysis, there are other predators in these soft-sediment communities that can be important causes of mortality. We only have access to records of drilling predation in the dead assemblage but in Recent marine communities, ecologists have carried out research on mollusc predators such as teleost fish, cartilaginous fish, and crabs (e.g. Williams 1982, Jones et al. 1992, Jacobsen & Bennett 2011). More specifically, research also undertaken in the One Tree Reef lagoon showed that predation by three teleost fish did not have a significant impact on the demography or size structure of the benthic mollusc populations (Jones et al. 1992). The authors found that even if these fish were consuming molluscs, it was not sufficient to alter the population dynamics of eight out of ten molluscan prey. Similarly, a study of the stomach contents from over 170 whiptail rays, *Himantura astra*, found molluscs in only 2.2% of this potential predators' stomachs (Jacobsen & Bennett 2011). Among the invertebrates, shell-crushing predators such

as crabs are known to be important mollusc consumers (Vermeij 1976, Zipser & Vermeij 1978, Bertness 1981). In the samples collected for this study, we found decapods belonging to the Portunidae, Calappidae and Parenthropidae, and some species from these families are known to prey on molluscs (Williams 1982, Lestang et al. 2000). However, given their small size relative to the size of the bivalves, no crab or crab claw found in our same samples would have been capable of crushing a shell retained by the 4 mm sieve (authors' personal observations). We cannot discard however that decapod predators influence the population structure of these soft sediments molluscs. Even if there are some techniques that have been developed to quantify crushing predation in relation to drilling predation (e.g. Vermeij Crushing Analysis, Stafford & Leighton 2011); given the low drilling frequencies in this system, telling apart crushing predation from other sources of breakage (i.e. the collection process) could be ambiguous, and it exceeded the goals of this study. Still, if crushing predation were important, it would lead to fewer intact shells, and the drilling frequencies here calculated would be inflated. Thus, drilling could be even less important than indicated by these results. Together with evidence from other predation studies in soft-sediment from the Great Barrier Reef, our findings do not support high predation frequencies in these reeflagoon communities. Instead, these results are consistent with Jones et al. (1992) statement that predation does not seem to be structuring the molluscan community at One Tree Reef.

In addition to finding lack of selectivity for abundant species, we also found an overwhelming dominance of infaunal taxa in this soft sediment environment. Tellinids were the most abundant taxa in the studied assemblages, and the predation frequencies observed agree with previous studies that report drilling predation on this family (e.g. Vermeij et al. 1980, Sawyer & Zuschin 2010). Predation frequencies for tellinids from Guam were between 1 and 27% (Vermeij et al. 1980), and 11.6% for tellinids from Bay of Panzano, Italy (Sawyer

& Zuschin 2010). The interesting nature of the mollusc community at One Tree Reef, which is dominated by infauna and has low numbers of drilling predators, could be interpreted as a 'special system' or as a system that is not representative of what is expected from a tropical environment. However, little research has been carried out on soft sediment mollusc communities from Australia and the Indo Pacific (but see Vermeij 1980, Jones et al. 1990, Bouchet et al. 2002) suggesting there is little evidence to substantiate a claim that One Tree Reef is particular in any way. Moreover, One Tree Reef is a Scientific Research Zone in the Great Barrier Reef Marine Park and therefore has been subject to minimal anthropogenic impact. This system thus provides an informative analogue to carbonate soft sediments environments preserved in the fossil record.

Using a species-rich dead shell assemblage with taxa that span three orders of magnitude in abundance, we show that drilling predators do not display selectivity for prey species based on encounter frequency. Previous research on rocky hard substrates and intertidal systems has shown that keystone predators disproportionately consume the most abundant prey (Paine 1966, Navarrete & Castilla 2003, Navarrete & Manzur 2008), leading to substantial changes to the structure and functioning of those communities. This important role for predators has also been suggested to have an effect at larger time scales (Vermeij 1993), such as in the ecosystem-wide changes associated with the Mesozoic Marine Revolution (Vermeij 1977, Aberhan et al. 2006, Finnegan et al. 2011). In contrast, the evidence we present from a tropical community dominated by infaunal taxa suggests that drilling predators are unlikely to have important effects on prey populations, and therefore seem to have a limited role shaping the structure of this soft sediment system. Ultimately, articulating this selectivity approach with individual-level traits used in Optimal Foraging studies, and with

detailed analysis of other durophagous predators, can lead to a better understanding of the role of predation in the building and maintenance of this tropical infaunal community.

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Chapter 3

CHAPTER 4

Species-specific variations in defensive traits explain

predation in tropical molluscs

4.1 Abstract

Predation is a key biotic interaction shaping ecological communities. Defensive morphological traits are thought to improve prey survivorship, and knowing which traits are successful is key to understand predator-prey dynamics and its impact on community composition. Optimal foraging theory and single species experiments suggest that shell size and shell thickness are traits that affect mollusc drilling predation. We analyse the effectiveness of these morphological traits in the One Tree Reef lagoon (southern Great Barrier Reef, Australia), a tropical community where predation pressure was expected to be high. We measured shell mass, shape, thickness, and predation frequency in five bivalve species (n = 804) constituting 79% of the predators' diet. We used multiple regression to determine which morphological traits best predicted drilling predation and if these were consistent among species. Because mass and shape were highly correlated, where larger individuals tended to be heavier and more spherical, only mass and thickness were included in the analysis. We found both these traits and their interaction to be important for predation, where drilling was more likely in thinner and larger shelled individuals. However, support for the model that included species effects was markedly stronger, indicating that the morphological traits we measured are not general predictors of predation across prey species. Contrary to common belief, our results suggest that defensive morphologies are inconsistent among species, and that trait-only models are unlikely to adequately explain predator-prey dynamics at the community level.

4.2 INTRODUCTION

Predators can shape community structure, and on larger time scales, drive the evolution of species and ecosystems (Vermeij 1993, Aberhan et al. 2006, Finnegan et al. 2011). By affecting the fitness of their prey, predators can also lead to changes in prey population dynamics (Meyer & Byers, 2005). Over time, these changes can modify the relative proportion of different trophic groups in a community (Paine 1966, Duffy 2002). However, individual defensive morphologies that increase prey fitness modify how predators and prey interact. Therefore, understanding which morphological traits are successful for survival can help elucidate whether predation is an important selective pressure and how it can impact community structure.

Anti-predatory morphological traits that improve individual survivorship are more prevalent in the tropics, given that predation tends to be higher at low latitudes (Dudley & Vermeij 1978, Vermeij 1983, Schemske et al. 2009). Since species interactions are temperature dependent (Sanford 2002, Dell et al. 2014), consumption rates in the tropics increase because metabolic rates are higher (Allen et al. 2002). Morphological traits that help defend against predation should therefore be more prominent in these low-latitude environments. If these morphological traits are effective against a predator, or predator guild, then their effectiveness should span across individuals from different prey species (i.e., be 'universal' for drilling predators' prey [Vermeij 1993]). Thus, the best way to determine which morphologies are more successful against predators is by testing their effectiveness across individuals from different species in the prey community.

Molluscs are ideal candidates for predator-prey studies, because they are a key component of benthic marine communities worldwide. Various surveys and meta-analyses have established that molluscs are exceptionally abundant and diverse at low latitudes (Roy et al. 2000, Bouchet et al. 2002), and that this diversity can be both taxonomic and morphological (Roy & Foote 1997, Roy et al. 2001). Even if diversity and disparity are not

always coupled (Roy et al. 2001), molluscs are well suited to study anti-predatory defensive morphologies. The study of morphological traits is particularly tractable for gastropod predators that drill through the shell of their prey given that they leave quantifiable evidence of their attack. Also, since drilling predation is ubiquitous among molluscs (Kelley 1988, Kowalewski et al. 1998, Sawyer & Zuschin 2010, Leonard-Pingel & Jackson 2013, Martinelli et al. 2013), valuable insights on the relevance of morphological traits can be inferred from this particular predatory interaction. Extensive research under the optimal foraging theory framework (MacArthur & Pianka 1966) has shown that morphological traits such as shell size, shell shape and shell thickness can be anti-predatory for molluscs (Kitchell et al. 1981, Vermeij 1983, Kelley & Hansen 1993, Leonard-Pingel & Jackson 2013).

Size-limited predation, where larger prey individuals are able to escape predators, is a defensive strategy that influences the size-structure of communities (Osenberg & Mittelbach 1989, Persson et al. 1996, Urban 2007). Evidence for size refuges has been found in a wide array of organisms. For example, mouth gape is a major constraint in the ability of fish to capture prey (Osenberg & Mittelbach 1989, Persson et al. 1996, Ray & Corkum 1997, but see Scharf et al. 2000). Similarly, gape width is also important for fruit-eating birds, mammals, reptiles, and among the invertebrates, sea stars and gastropod predators (Paine 1976, Wheelwright 1985, Jaksic 1989, Karanth & Sunquist 1995, Rodriguez-Robles et al. 1999). For naticid gastropods in particular, predation can be size-limited because naticids use their foot or mesopodium to hold and wrap around their prey (Carriker 1981). If the prey is large, the gastropod cannot hold it properly and the risk of the prey escaping increases. In terms of optimal foraging, predators should prefer larger prey because this allows them to maximize the energy return per time unit of foraging (Kitchell et al. 1981). Drilling predators should therefore select larger individuals, but a size-refuge would be attained if larger individuals have a lower mortality relative to attack frequency.

Shell shape influences the ability of predators to seize their prey (Quensen & Woodruff 1997, DeWitt et al. 2000, Lakowitz et al. 2008). Bivalves and gastropods have a wide range of shapes (Raup 1961, 1966, Stanley 1970, 1975), and although it remains largely understudied, some of this morphological diversity can be high in the tropics (Roy et al. 2001). Evidence for changes in morphology and shape brought about by predators has been found in marine, freshwater and terrestrial molluscs (Seeley 1986, Quensen & Woodruff 1997, DeWitt et al. 2000, Lakowitz et al. 2008). Despite this, no study has explicitly hypothesized which shape makes prey easier to seize or capture by drilling predators. We propose that, for a given prey size, a spherical shell will be easier for the predator to grab and drill than an ellipsoidal shell because the gastropod foot could fully encompass a sphere, but only partly surround an ellipsoid. The previous proposition has an implicit confounding effect with size, but given that shape and size are highly correlated they cannot be fully disentangled.

Shell thickness is a biomechanical morphological trait that influences energetic costs of drilling for a predator (Kitchell et al. 1981, Boggs et al. 1984). In terms of optimal foraging, for a given prey size, individuals with thicker shells provide a lower energetic gain because the cost of drilling them is higher than the cost of drilling individuals with a thinner shell. Since drilling gastropods dissolve shells by secreting acids and enzymes and scraping shell tissue with their radula (Carriker 1981, Kabat 1990), thicker shells require more acid. Drilling thicker shells also demands more time (Boggs et al. 1984), and if gastropods are more vulnerable while drilling, they can be at risk of being attacked by predators themselves. It is unknown whether drilling gastropods can determine if some shells are thicker than others (Kabat 1990), but if they cannot, they will likely abandon a prey item that takes too long to drill. Even if avoiding an attack is better than fighting one, incomplete attacks also decrease prey mortality, suggesting that individuals with thicker shells will have higher fitness than

individuals with thinner shells.

The aim of this study was to determine which of these morphological traits are effective defenses against drilling predators in a tropical marine system. Models based on optimal foraging theory and single species experiments suggest that large and thin shells will experience higher predation whereas predators will avoid shells that are too large and too thick. Alternatively, the influence of morphological traits is not consistent among species or they are not important at all (i.e., predators attack the prey community randomly). Our analysis seeks to (1) determine which potentially anti-predatory morphological traits are effective in reducing prey mortality in tropical environments, and (2) establish if these defensive morphological traits are pervasive across the prey community or if there are species-specific variations. Our results will lead to a better understanding of the role of defensive morphologies, which is key in determining the role of predators in shaping community structure.

4.3 MATERIALS AND METHODS

4.3.1 Study site and materials

Sampling was carried out at One Tree Reef, southern Great Barrier Reef, Australia ($23^{\circ}20^{\circ}$ S, $152^{\circ}06^{\circ}$ E) in 2012. The reef crest surrounds three lagoons (roughly 10 - 13 km² in extension) that have coral patches interspersed with sand (Ludington 1979). Sedimentary infauna was collected at four to seven different sites in each of the three lagoons (Figure 4.1). Sites ranged in depth from 4.3 to 6.1 m (ponded depth). At each collection site divers sampled the top 0.1 m of 1 m² of sediment using an 80 mm diameter air-lift and 1 mm mesh bags. After collection, samples were wet sieved using a 4 mm sieve.

To quantify the effectiveness of potential defensive morphologies we selected a subset of species that contributed most to the diet of drilling predators (Table 4.1, Figure 4.2). The predators' diet was previously estimated as the proportion of each prey species to the total drilled assemblage (see Chapter 3), and we focus on the five bivalve species with sufficient sample size (> 100 individuals). Gastropods were either not a significant component of the predators' diet, or were not abundant enough to include in the analyses.



Figure 4.1. Schematic map of One Tree Reef, southern Great Barrier Reef. The reef outline (shaded grey area) surrounds the three lagoons (white), and One Tree Island (black). Numbers inside each lagoon indicate the sites were samples were collected. Reef and lagoon outline were traced from Google Earth imagery.

Table 4.1. Details about the five study species: family, relative abundance, contribution to the predators' diet, the number of individuals measured, median individual thickness (mm) and shell mass (mg).

Species	Family	Relative	Contribution to	Measured	Thickness	Mass
		abundance	predators' diet	individual	(mm)	(mg)
Abranda jeanae	Tellinidae	11%	13%	196	0.17	121.94
Loxoglypta clathrata	Tellinidae	13%	18%	115	0.19	30.30
Pinguitellina robusta	Tellinidae	58%	38%	153	0.38	89.44
Scissulina dispar	Tellinidae	13%	6%	191	0.18	76.44
Fragum fragum	Cardidae	2%	4%	149	0.41	61.00



Figure 4.2. Images of the taxa used in this study. All scale bars are 10 mm. (A) <u>Abranda jeanae</u>, (B) <u>Loxoglypta clathrata</u>, (C) <u>Pinguitellina robusta</u>, (D) <u>Scissulina</u> <u>dispar</u>, (E) <u>Fragum fragum</u>. (Photographed specimens will be vouchered at the Australian Museum).

4.3.2 Identification of predatory traces

Predation by drilling predators was assumed successful when the drill holes were complete i.e. the hole went through the shell. Holes had to have a regular circular outline and be perpendicular to the shell (Kelley & Hansen 2003, Yanes & Tyler 2009). There were no significant differences between predation on right and left valves ($\chi^2 = 0.95$, *p* value = 0.81, df = 3), and no shell had multiple drill-holes. Therefore, only unfragmented right valves were counted and measured. Any unfragmented right valve with a drill-hole was considered a drilled individual.

4.3.3 Measurement of anti-predatory traits

Shell mass was measured for each individual (804 right valves in total, Table 4.1). To determine the shell mass of the articulated bivalve at death, individual valve mass was multiplied by two.

Shell shape was measured as the sum of the absolute deviations of x, y and z relative to a sphere of the same geometric mean size, d: ([|d - x| + |d - y| + |d - z|] / d) to obtain a dimensionless shape metric (following Kosnik et al. 2009).

Shell thickness was measured at the centre of each right valve using a thickness gauge. All linear measurements were made to the nearest 0.01 mm and \log_2 transformed. All the correlation values presented correspond to \log_2 measurements.

4.3.4 Model selection

A generalized linear model (GLM) with a logit link function and binomial response variable (drill-hole=1, no drill-hole=0) was used to determine if any of the morphological traits, or an interaction between traits had a significant effect on the probability of an individual being drilled. Because mass and shape were strongly collinear (see Results), only mass and

thickness were included as predictor variables. To explore species effects, we ran a second GLM allowing for species-specific intercepts and mass and thickness slopes. We checked for overdispersion by calculating the ratio of model residual deviances to residual degrees of freedom. GLM analyses were carried out using the 'glm' function in the 'stats' package in the statistical programming language R (Version 3.0.2, R Core Team 2014). We used the 'drop1' function with chi-squared test to determine which of the fixed factors and interactions to keep for each of the two models. Code and data files are provided as supplementary material.

4.4 **RESULTS**

4.4.1 Correlations between measured variables: mass, shape and thickness

Shell shape and mass were highly correlated, and larger species tended to be more spherical than smaller species (Pearson correlation, r = 0.91, *p* value < 2.2^{-16} , df = 803, Figure 4.3). As a result, shape was not included in the GLM but results were interpreted taking into account that mass is representative of shape. Finally, shell thickness and mass were significantly correlated but the correlation coefficient was not high (Pearson correlation, r = 0.45, *p* value < 2.2^{-16} , df = 803, Figure 4.4), therefore thickness and mass were included in the GLM analyses (Zuur 2010).



Figure 4.3. Scatterplot showing the correlation between shell shape and mass.



Figure 4.4. Scatterplot showing the correlation between shell mass and thickness. Species symbols as in Figure 4.3.

4.4.2 Model selection

The best trait-only model shows that prey with thicker shells and lower mass tend to experience lower levels of mortality by drilling predators (AIC = 548.03, Figure 4.5, Table 4.2). However, when the data points for undrilled (solid grey) and drilled (open white) individuals are plotted over the model probabilities this trend is not visually obvious (Figure 4.5, and 4.6). Allowing for species effects improves the model (AIC = 536.16, Table 4.3). Interactions between species and mass, and a three-way interaction between species, mass and thickness were not significant. The best model indicates that only thickness explains predation frequency for three of the five species, suggesting that prey shell mass and thickness do not have a pervasive effect against drilling predators (Table 4.3).

We did not find evidence for overdispersion of residuals for either model as the ratio of model residual deviances to residual degrees of freedom was smaller than 1 in both cases.



Figure 4.5. Probabilities of predation based on the defensive morphologies model. Lighter shades of grey indicate higher predation probabilities and darker shades of grey lower predation probabilities. Small dots in darker grey represent non-drilled individuals from the five species. Larger light grey dots represent drilled individuals from the five species.

Table 4.2. Summary of generalized linear model statistics for the effects of mass and thickness on the likelihood of a bivalve shell being drilled. A) The effect of dropping the variables (an interaction) from the full model, with Akaike Information Criterion (AIC) and chi-square statistics. B) The final predictive model (showing estimates, standard errors and p values).

A) Variable			
	d.f.	AIC	$\Pr(\chi^2)$
Thickness: Mass	1	548.03	0.005 **
B)	Estimate	SE	p value
Intercept	-1.523	1.186	0.199
Thickness	0.091	0.174	0.602
Mass	-0.910	0.496	0.066
Thickness: Mass	0.254	0.084	0.002 **

Table 4.3. Summary of generalized linear model statistics for the effects of mass and thickness on the likelihood of a bivalve shell being drilled accounting for species effects. A) The effect of dropping variables (and interactions) from the full model, with Akaike Information Criterion (AIC) and chi-square statistics. B) The final predictive model (showing estimates, standard errors and p values).

A) vallaule			
	d.f.	AIC	$\Pr(\chi^2)$
Thickness: Species	5	536.16	3.188e-06 ***
B)	Estimate	SE	p value
Intercept	-0.730	0.912	0.423
Abranda jeanae	-6.927	2.219	0.002 **
Loxoglypta clathrata	-7.978	2.478	0.001 **
Pinguitellina robusta	-2.624	1.527	0.086
Scissulina dispar	-6.314	2.259	0.005 **

A) Variable

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Thickness: Abranda jeanae	-1.740	0.685	0.011 *
Thickness: Loxoglypta clathrata	-2.741	0.872	0.002 **
Thickness: Pinguitellina robusta	-1.479	0.838	0.077
Thickness: Scissulina dispar	-1.564	0.731	0.032 *
Thickness: Fragum fragum	0.976	0.737	0.185

4.5 DISCUSSION

Using over 800 individuals of key bivalve prey species in a tropical reef-lagoon community, we found that drilling predators tend to select individual prey based on shell thickness and mass, but that these patterns were not generalizable among species. Our results therefore suggest that conclusions from single-species studies about the effectiveness of morphological traits for decreasing predation risk do not necessarily apply at the community level.

4.5.1 Predator preference at an assemblage level: shell thickness and mass

Despite species-specific differences there was a tendency for predators to target individuals with thinner shells, a behavior which maximises net energetic return (Kitchell et al. 1981, Boggs et al. 1984). The production of the acids and enzymes that dissolve calcium carbonate has a metabolic cost (Person et al. 1967), and possibly a 'storage' cost given that boring gastropods have specialized organs to produce and store these chemicals (accessory boring organ or ABO, Carriker 1969, 1981). Histological studies looking at the secretory cells of the ABO have found significantly more mitochondria in the cells of snails that were drilling relative to other snails (Carriker et al. 1963).

Attacking individuals with thinner shells can reduce the time spent drilling a single prey. Consuming prey quickly enables the predator to consume more prey per time unit (Boggs et al. 1984), assuming drilling is the rate-limiting step (vs. searching). This is likely given the high density of living molluscs in these reef lagoons (median density: 152

individuals/m², see Chapter 3). Drilling prey quickly also reduces the time predators are exposed to their own predators, be it conspecifics or predators from a different guild. Given that, in general, selective pressures imposed by predators are stronger than selective pressures by prey (Vermeij 1993), consuming prey quickly would increase the fitness of the predator as it is less exposed to becoming a prey itself.

How did selectivity for thinner shells evolve? While cost-benefit analyses of drilling predator behavior have also found support for drilling prey with thinner shells (Kitchell et al. 1981, Kelley 1988, 1991, Chattopadhyay & Baumiller 2009), it is unlikely that predators are able to determine shell thickness prior to drilling them (Boggs et al. 1984, Kabat 1990). Boring gastropods use their osphradium - a sensory epithelium - to recognize prey chemical cues (Emery 1992). If a predator learns to associate particular chemical cues with a particular prey, this could be a mechanism through which predators could select thinner-shelled prey. If, however, gastropods are not able to consistently identify prey depending on their thickness or other cues, it is possible that thicker-shelled individuals have higher fitness than thinner-shelled ones. This higher success of thicker-shelled individuals could indirectly explain the higher predation on thinner shelled ones.

Along the same lines, is interesting to ask why selectivity for a trait varies between prey species. Bivalves with thinner shells are the ones for which thickness was a significant predictor of predation (see Tables 4.1 and 4.3). Also, and perhaps more important, the range of shell thickness variation is not the same for all the species (Figure 4.6, compare *Pinguitellina* and *Fragum* with the rest). Assuming that predators select thinner prey, they would not have much variation to choose from in *Pinguitellina* and *Fragum*. Why some traits are more variable than others among species is a question we cannot answer, but our findings suggest that for a trait to be informative at a community level, the range of variation in that trait should be similar between species.

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Figure 4.6. Scatterplots showing correlation between shell mass and thickness for each species. (A) <u>Fragum fragum</u>, (B) <u>Pinguitellina robusta</u>, (C) <u>Abranda jeanae</u>, (D) <u>Loxoglypta</u> <u>clathrata</u>, (E) <u>Scissulina dispar</u>.

Shell mass and shape are also important to drilling predators, but given that these morphological traits are highly correlated (Figure 4.3A), their relative importance cannot be disentangled by this analysis. We found that larger individuals had higher predation frequencies than smaller individuals, and that more spherical individuals had higher predation

frequencies than ellipsoidal individuals. There seems to be a trade-off between mass and shape throughout ontogeny (within species) as, in general, shells become more spherical with increasing mass (Figure 4.3). Since shell mass and shape were only significant for one species when random slopes were accounted for (Table 4.3), any further explanation on the relevance of these traits for predators would be highly speculative. The fact that our results do not provide strong support for a defensive role for these traits suggests that other selective pressures, such as an infaunal life habit, or even phylogenetic constraints could be having a stronger effect on shell mass and shape than drilling predators. It is also possible that there are traits that we have not explored, which would account for this species-specific variability.

4.5.2 Implications for experiments testing for optimal foraging

Prey preference has been extensively studied in an optimal foraging context (e.g. Kitchell et al. 1981, Kelley 1988, 1991, Leighton 2002, Chattopadhyay & Baumiller 2009, Chattopadhyay & Dutta 2013). According to this hypothesis, predators maximize net energy gain per time unit (MacArthur & Pianka 1966, Kitchell et al. 1981, Leighton 2002). For drilling predators, the most time and energy consuming activities are time spent searching and time and energy spent drilling prey. Search time should be negatively correlated to prey density, drilling time should be positively correlated with prey shell thickness (Kitchell 1981, Kelley 1988), and the amount of energy gained should be positively correlated with shell volume or biomass (Kitchell 1981, Stanton & Powell 1985). These three variables are however, measured at different levels. Prey density (search time) is a community-level attribute while mass and thickness are individual-level traits. In a previous study testing for selectivity by drilling gastropods in the same reef lagoon system, we looked at the effect of relative abundance (prey encounter rate) on drilling frequencies. Predation frequencies and prey relative abundance were found to be independent, as predators consumed prey at a constant rate (see Chapter 3). It is worth clarifying the difference between search time and prey encounter rate. Search time includes the time when the predator encounters no prey item, while encounter rate is the probability that the next prey item a predator encounters with be a particular prey item. In this system, search time (mean absolute abundance of *Pinguitellina* per m^2) is correlated with encounter rate (mean relative abundance of *Pinguitellina* per m^2) (Pearson correlation, r = 0.62, *p* value = 0.01, df = 13) (see Chapter 3). Given that these two values are positively correlated, prey encounter rate can be an informative (albeit not perfect) estimate of search time. Leaving aside encounter rate that is important at a community level, here we focused on the two individual-level traits, mass and thickness.

Both marine ecologists and palaeobiologists have used the optimal foraging theory to test hypothesis using experimental and observational data (e.g. Kitchell et al. 1981, Boggs et al. 1984, Kelley 1988, 1991, Anderson et al. 1991, Leighton 2002, Chattopadhyay & Baumiller 2009, Chattopadhyay & Dutta 2013). Experiments in aquaria have the benefit that variables can be controlled, but at the same time the simplified environment can lead to modified behaviors (Kabat 1990). The results we present here are from data collected in the natural system where the interaction plays out, and can help link observational and experimental studies. We found that model fits are better when species effects are included, and that defensive traits that appear to be significant at an assemblage level cease to be significant when species-specific variations are accounted for (Tables 4.2 and 4.3). Therefore, if experimentalists seek to obtain results that are informative of how interactions play out in nature, great care needs to be taken to select a natural prey population because species-specific preferences may not be reflective of assemblages or natural communities.

Overall, results from a tropical reef system where morphologies are expected to be anti-predatory show that these traits are not universally defensive, and that species exhibit different ranges of variation for these traits. This lack of generality in the explanatory power of defensive traits suggests that shell size, thickness and shape may be under selection by forces other than predators, or that we have not captured a more explanatory anti-predatory trait.

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Synthesis

SYNTHESIS

The high diversity in tropical environments has fascinated naturalists for centuries (e.g. Wallace 2002, Humboldt 2006). Ecologists and paleobiologists have focused on these systems to understand how this diversity came about, and how it is maintained (Roy et al. 1998, Crame 2000, Roy et al. 2000, Jablonski et al. 2006, Mittelbach et al. 2007, Kiessling et al. 2010, Leonard-Pingel et al. 2012). Being a key marine biodiversity hotspot in the planet (Crame 2000, Hughes et al. 2002), the Great Barrier Reef is no exception to this interest in recent and fossil tropical biotas (e.g. Pandolfi & Greenstein 1997, Roff et al. 2012). Corals and fish have been the cornerstones of ecological studies (e.g. Sale 1977, Hughes et al. 1999, Jones et al. 1999, Bellwood & Hughes 2001), while groups such as molluscs - typically studied by paleobiologists - are comparatively understudied in todays' reef ecosystems (but see Jones et al. 1990, Schlacher et al. 1998, Zuschin et al. 2001, Zuschin & Oliver 2003, 2005). Regardless, paleobiologists have shown that molluscs are invaluable tools to understand and explain local and regional-scale changes in past ecosystems (e.g. Vermeij 1977, 1987, Kelley & Hansen 1993, 1996, Kowalewski et al. 2000, Dietl et al. 2004, Aberhan et al. 2006, Martinez et al. 2013, among many others). For example, the process of escalation, or enemy-driven evolution (Vermeij 1987), was suggested as a driver for the increasing diversity and complexity in Mesozoic marine communities, and many examples supporting this hypothesis come from mollusc shell morphology (Vermeij 1977). More specifically, drilling gastropods and other durophagous predators evolved at that time (Sohl 1987, Kase & Ishikawa 2003), and their predatory action led to important changes in the structure and complexity of benthic marine communities (Aberhan et al. 2006, Finnegan et al. 2011).

Recent ecological studies are showing that molluscs are valuable study organisms to understand, quantify and predict consequences of human-mediated changes to marine ecosystems. Given the key functions that molluscs play in reef ecosystems (e.g. improving water clarity, nutrient cycling and bioturbation, Przeslawski et al. 2008), scientists can predict how reef communities will be affected by increasing water temperature and acidification (among other consequences of climate change), by using taxa other than corals and fish which are not necessarily informative of benthic processes. Such predictions about loss of ecosystem functions are supported by a suite of experimental studies on mollusc mortality and survival under different climate change scenarios. For example, gastropod embryos have shown increased mortality rates and altered development when exposed to different combinations of temperature and UV radiation (e.g. Przeslawski et al. 2005, Davis et al. 2013). Similarly, decreases in pH as a consequence of ocean acidification significantly decrease the ability of some molluscs to calcify shells (Miller et al. 2009, Byrne et al. 2011), and to repair damaged shells (Coleman et al. 2014). The consequences of these biological processes, i.e. increased mortality (leading to decreased populations size), inability to calcify thicker shells (leading to thinner, and likely more breakable shells), and inability to repair damaged shells (leading to higher breakage, lower fitness, and possibly decreased population size) can be measured in dead shell assemblages. By knowing the responses of living organisms to these changing environmental factors, and having temporal baselines to compare, very specific predictions can be made regarding differences in composition, abundance, fragmentation rates, etc. between subfossil (decadal or centurial) assemblages and living communities. These integrated approaches advocated by Conservation Paleobiology are the ones that will ultimately provide new insights into changes to communities that could not be observed by solely doing experiments, or by studying past communities in isolation from their living counterparts. Therefore, there is ample room for a much stronger articulation between ecological and paleobiological studies to understand, quantify and predict changes to marine ecosystems in the near future.

A central aspect of this dissertation was to determine how much of the ecology of living molluscan communities can be inferred from dead molluscan assemblages. This is because understanding the processes that affect diversity and community structure in environments with little anthropogenic impact is key to validating conservation paleobiological studies. Extensive work has been done in soft sediment environments from the Cenozoic to understand biotic interactions, and to describe how mollusc predators affected those communities (e.g. Kelley & Hansen 1993, 1996, Hoffmeister & Kowalewski 2001, Sawyer & Zuschin 2011, Chattopadhyay & Dutta 2013). Changes in mollusc assemblages have also been studied in fossil and recent Caribbean reef-associated communities (Leonard-Pingel et al. 2012), modern rocky reef environments (Zuschin et al. 2001, Zuschin & Oliver 2003), sea-grass environments (Albano & Sabelli 2011, Feser & Miller 2014), and siliciclastic and human-modified environments (Kidwell 2007, Korpanty & Kelley 2014). Here, I attempted to contribute to this rich body of literature, by using living and dead mollusc assemblages from a fully carbonate reef system. Carrying out these studies in a protected setting from the Great Barrier Reef provides information from a soft sediment environment analogous to what can be preserved in the Phanerozoic fossil record, but different and complementary to the aforementioned studies.

By combining different lines of evidence such as diversity, species spatial distribution, temporal changes in composition, and predation intensity based on individual- and community-level traits, I provide a general picture of some key ecological features of a tropical mollusc community. In particular, I present the first study of drilling predation for this tropical biodiversity hotspot, and a live-dead study - that coupled with time-averaging data - shows that there is high fidelity between the living community and the subfossil assemblages. This high fidelity enables future contributions to consider One Tree Reef sediments - along with similar Recent and fossil carbonate environments - a trustworthy baseline for temporal change. It is my hope that this dissertation will contribute to bridge some of the gaps between ecologists and paleobiologists, with the prospect of linking disciplines and encouraging the articulation of data from living and non-living organisms to generate predictions that will be fundamental to understand and protect rapidly changing marine ecosystems.

FUTURE DIRECTIONS

To achieve a better articulation between ecological and paleobiological studies, it would be useful to start using dead shell assemblages to serve conservation-related purposes. For example, some of the applications of dead shell assemblages can be as proxies for regional species pools, to determine the presence of rare species that are seldom sampled in ecological surveys, and to determine changes in species ranges and/or the presence of new potentially invasive species (Kidwell & Tomašových 2013). For One Tree Reef in particular, the age of shells in the sediments has already been estimated, allowing for a temporal comparison with living communities. If this system continued to be monitored in time, potential changes in species abundances and ranges can be determined, and the importance of rare species can also be quantified. Specific predictions based on experimental results could also be tested, e.g. are species with thinner shells less abundant now than they were in the recent past? Are fragmentation rates higher? These are a few of the questions that could be addressed by future studies.

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APPENDICES

CHAPTER 1: 'Mollusc spatial distribution and diversity are not different from random in a reef lagoon community'

Link to online material: http://marinescience.mq.edu.au/postgrad/martinelli/CHAPTER1.zip

There are two folders, one contains the R code and the other one contains the input data files (.txt) to create the plots and calculate the intraspecific and interspecific aggregation indices presented in the manuscript. A third folder contains the following documents:

-Supplementary Table 1: C index with and without predators for quadrats (.doc)

Supplementary Table 2: C index with and without predators for sites (.doc)

CHAPTER 2: 'Dead shell assemblages from One Tree Reef lagoon are a faithful record of the living communities'

Link to online material: http://marinescience.mq.edu.au/postgrad/martinelli/CHAPTER2.zip

There are two folders, one contains the R code and the other one contains the input data files (.txt) to create the plots and calculate the relative contribution of post-mortem and pre-mortem processes to dead shell assemblages. The first R code is used to create the object that is used in the analyses on the second R code file. This second R code file ('Code 2_C2.R') was written by Adam Tomašových, with the exception of the code for Figure 4.

CHAPTER 3: 'Encounter frequency does not predict predation frequency in tropical dead-shell assemblages'

Link to online material: http://marinescience.mq.edu.au/postgrad/martinelli/CHAPTER3.zip

There are two folders, one contains the R code and the other one contains the input data file (.txt) to run the models and create the plot presented in the manuscript.

CHAPTER 4: 'Species-specific variations in defensive traits explain predation in tropical molluscs'

Link to online material: http://marinescience.mq.edu.au/postgrad/martinelli/CHAPTER4.zip

There are two folders, one contains the R code and the other one contains the input data files (.txt) to run the models and create the plots presented in the manuscript.

Appendix 1 – Supplementary Table 1. Data used in Chapter 1.

Other papers I was involved in during my candidature:

Appendix 2 – **Martinelli JC**, Gordillo S, Archuby FM (2013) Muricid drilling predation at high latitudes: Insights from the southernmost Atlantic. Palaios 28:33-41

Appendix 3 – Madin JS, Kuo CY, **Martinelli JC**, Mizerek T, Baird AH (2014) Very high coral cover at 36° S on the east coast of Australia. Coral Reefs 1-1

Appendix 4 – Archuby FM, Adami M, **Martinelli JC**, Gordillo S, Boretto GM, Malvé ME (2015) Regional-scale compositional and size fidelity of rocky intertidal communities from the Patagonian Atlantic coast. Palaios (accepted)

Quadrat	Month	Lagoon	Site	Replicate	Fraction	Abundance	Richness	
1	Feb	Third	First	А	842	23	6	
2	Feb	Third	First	В	844	37	6	
3	Feb	Third	First	С	846	22	4	
4	Feb	Third	First	D	848	22	4	
5	May	Third	First	А	940	20	5	
6	May	Third	First	В	942	16	6	
7	May	Third	First	С	944	5	3	
8	May	Third	First	D	946	26	4	
9	Sep	Third	First	А	996	16	4	
10	Sep	Third	First	В	998	12	3	
11	Sep	Third	First	С	1000	24	4	
12	Sep	Third	First	D	1002	36	8	
13	Nov	Third	First	А	1124	29	7	
14	Nov	Third	First	В	1126	38	6	
15	Nov	Third	First	С	1128	18	7	
16	Nov	Third	First	D	1130	26	7	
17	Feb	Second	First	А	818	9	5	
18	Feb	Second	First	В	820	6	3	
19	Feb	Second	First	С	822	9	5	
20	Feb	Second	First	D	824	8	3	
21	Feb	Third	Second	А	850	12	6	

Supplementary table 1. Data used for analyses in Chapter 1. Absolute abundance and species richness per quadrat. Data are presented by collection month, lagoon, site number, replicate number (A-D) and fraction number.

22	Feb	Third	Second	В	852	11	4
23	Feb	Third	Second	С	854	15	4
24	Feb	Third	Second	D	856	23	5
25	May	Third	Second	А	948	11	5
26	May	Third	Second	В	950	4	3
27	May	Third	Second	С	952	16	5
28	May	Third	Second	D	954	21	5
29	Sep	Third	Second	А	1004	4	2
30	Sep	Third	Second	В	1006	4	3
31	Sep	Third	Second	С	1008	4	3
32	Sep	Third	Second	D	1010	5	3
33	Nov	Third	Second	А	1132	2	2
34	Nov	Third	Second	В	1134	12	4
35	Nov	Third	Second	С	1136	5	3
36	Nov	Third	Second	D	1138	2	2
37	Feb	Third	Third	А	858	17	6
38	Feb	Third	Third	В	860	5	5
39	Feb	Third	Third	С	862	13	4
40	Sep	Third	Third	А	1012	14	3
41	Sep	Third	Third	В	1014	10	3
42	Sep	Third	Third	С	1016	6	4
43	Sep	Third	Third	D	1018	10	6
44	Nov	Third	Third	А	1140	17	8
45	Nov	Third	Third	В	1142	24	4
46	Nov	Third	Third	С	1144	6	5

47	Nov	Third	Third	D	1146	24	8
48	Feb	First	First	А	794	28	8
49	Feb	First	First	В	796	28	8
50	Feb	First	First	С	798	19	6
51	Feb	First	First	D	800	27	5
52	May	First	First	А	916	31	3
53	May	First	First	В	918	59	7
54	May	First	First	С	920	57	5
55	May	First	First	D	922	80	7
56	Nov	First	First	А	1100	30	3
57	Nov	First	First	В	1102	26	7
58	Nov	First	First	С	1104	10	2
59	Nov	First	First	D	1106	38	6
60	Feb	First	Second	А	802	11	7
61	Feb	First	Second	В	804	23	7
62	Feb	First	Second	С	806	20	6
63	Feb	First	Second	D	808	12	4
64	May	First	Second	А	924	21	4
65	May	First	Second	В	926	46	5
66	May	First	Second	С	928	14	5
67	May	First	Second	D	930	37	5
68	Nov	First	Second	А	1108	34	5
69	Nov	First	Second	В	1110	27	4
70	Nov	First	Second	С	1112	9	2
71	Nov	First	Second	D	1114	19	9

72	Feb	First	Third	А	810	9	4
73	Feb	First	Third	В	812	14	8
74	Feb	First	Third	С	814	21	6
75	Feb	First	Third	D	816	8	4
76	Feb	Second	Second	А	826	17	8
77	Feb	Second	Second	В	828	13	8
78	Feb	Second	Second	С	830	23	9
79	Feb	Second	Second	D	832	14	7
80	May	Second	Second	А	900	24	6
81	May	Second	Second	В	902	33	5
82	May	Second	Second	С	904	23	6
83	May	Second	Second	D	906	24	6
84	Sep	Second	Second	А	980	25	5
85	Sep	Second	Second	В	982	13	5
86	Sep	Second	Second	С	984	8	7
87	Sep	Second	Second	D	986	12	5
88	Nov	Second	Second	А	1156	15	4
89	Nov	Second	Second	В	1158	16	7
90	Nov	Second	Second	С	1160	16	6
91	Nov	Second	Second	D	1162	24	8
92	Feb	Second	Third	А	834	16	6
93	Feb	Second	Third	В	836	18	7
94	Feb	Second	Third	С	838	18	5
95	Feb	Second	Third	D	840	14	4
96	May	Second	Third	А	932	33	9

97	May	Second	Third	В	934	21	7
98	May	Second	Third	С	936	35	7
99	May	Second	Third	D	938	25	5
100	Sep	Second	Third	А	1020	21	9
101	Sep	Second	Third	В	1022	6	4
102	Sep	Second	Third	С	1024	28	4
103	Sep	Second	Third	D	1026	14	4
104	Nov	Second	Third	А	1148	24	9
105	Nov	Second	Third	В	1150	20	4
106	Nov	Second	Third	С	1152	23	5
107	Nov	Second	Third	D	1154	22	6
108	May	Second	Fourth	А	884	5	4
109	May	Second	Fourth	В	886	8	4
110	May	Second	Fourth	С	888	6	5
111	May	Second	Fourth	D	890	10	5
112	May	Third	Fourth	А	892	20	6
113	May	Third	Fourth	В	894	10	7
114	May	Third	Fourth	С	896	11	7
115	May	Third	Fourth	D	898	5	2
116	May	First	Fourth	А	908	19	5
117	May	First	Fourth	В	910	14	3
118	May	First	Fourth	С	912	19	8
119	May	First	Fourth	D	914	9	5
120	Sep	First	Fifth	А	956	15	7
121	Sep	First	Fifth	В	958	28	5

122	Sep	First	Fifth	С	960	20	4
123	Sep	First	Fifth	D	962	21	4
124	Nov	First	Fifth	А	1116	17	3
125	Nov	First	Fifth	В	1118	18	2
126	Nov	First	Fifth	С	1120	24	2
127	Nov	First	Fifth	D	1122	21	3
128	Sep	First	Sixth	А	964	13	6
129	Sep	First	Sixth	В	966	19	3
130	Sep	First	Sixth	С	968	19	4
131	Sep	First	Sixth	D	970	27	5
132	Sep	First	Seventh	А	972	57	7
133	Sep	First	Seventh	В	974	48	5
134	Sep	First	Seventh	С	976	49	4
135	Sep	First	Seventh	D	978	84	8
136	Sep	Second	Fifth	А	988	35	6
137	Sep	Second	Fifth	В	990	29	8
138	Sep	Second	Fifth	С	992	17	4
139	Sep	Second	Fifth	D	994	8	4
140	Nov	Second	Fifth	А	1164	28	4
141	Nov	Second	Fifth	В	1166	22	3
142	Nov	Second	Fifth	С	1168	25	5
143	Nov	Second	Fifth	D	1170	13	4



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MURICID DRILLING PREDATION AT HIGH LATITUDES: INSIGHTS FROM THE SOUTHERNMOST ATLANTIC

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ABSTRACT

Drilling predation is frequently studied in the fossil record. Less information is available from recent environments, however. Previous studies have indicated that drilling predation is usually higher in the tropics but little research has been undertaken in high latitudes. To address this hypothesis, we examine muricid-drilling predation along a 1,000 km transect in southern South America. Drilling frequencies ranged between 3% and 36%, and they were not correlated with the abundance of the predator (Trophon geversianus) or the abundance of its preferred prey. The only locality with exceptionally high predation (36%) was a heavily anthropogenically impacted site. Trophon exhibited different drilling strategies on different prey, and edge drilling represented 27%-56% of the drill holes in mytilids. Drilling frequencies were not correlated with latitude or water temperature. Our results, however, show that drilling frequencies are indeed lower at high latitudes compared to the tropics, and these data provide a recent baseline to compare and interpret spatial variability in muricid drilling predation from past environments. The fact that dead-shell assemblages seem to be recording human-related impacts in this system strengthens their relevance as potentially valuable conservation tools.

INTRODUCTION

Predation is central to ecology as predators affect the distribution and abundance of their prey and this impacts community structure (Chapin et al., 1997; Meyer and Byers, 2005; Begon et al., 2006). In marine paleoenvironments, drilling gastropods from the families Naticidae and Muricidae are well studied (e.g., Dudley and Vermeij, 1978; Hansen and Kelley, 2003; Klompmaker, 2009) as they leave a drill hole (an excavation of a characteristic shape, Kabat, 1990) in the shell of their prey. Given that these traces are easy to recognize and quantify, they have been widely used to study predation on evolutionary and ecological scales (e.g., Sohl, 1969; Vermeij, 1980; Hansen and Kelley, 1995; Hoffmeister and Kowalewski, 2001; Kosnik, 2005), and latitudinal differences in predation intensity in recent and fossil environments have been suggested (Vermeij, 1993; Hansen and Kelley, 1995; Kelley and Hansen, 2007). For instance, drilling by naticids on recent Turritella from high latitudes-e.g., Canada, the Shetlands, and New Zealand-resulted in frequencies of 0% (sample n = 29), 2.9% (n = 34), and 2% (n = 50), respectively (Dudley and Vermeij, 1978). In contrast, low-latitude localities (Mexico and the Philippines) had drilling frequencies of 19% (n = 68) and 68% (n = 138), respectively (Dudley and Vermeij, 1978). For fossil Turritella from high latitudes, frequencies of predation by naticids were 20% (n = 519, Paris, Eocene) and 28% (n = 101, United States, Miocene). Low-latitude drilling frequencies on species from the same genus were higher, ranging between 27% (n = 263, Nigeria, Eocene) and 62% (n = 60, Panama, Miocene). Despite these differences, a clear relationship between

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drilling predation and latitude has been hard to establish (Schemske et al., 2009), possibly due to the fact that most of the available information comes from the Northern Hemisphere and a few tropical islands; and also because methodological differences between studies may hinder the interpretation of results. For example, naticid drilling frequencies for the Eocene in the United States were higher in Virginia than in the Gulf coast, potentially indicating an equator-ward decrease in predation intensity (Hansen and Kelley, 1995). The number of samples for each area was different (4 vs. 11 respectively), however, and so were the environments the samples came from (inner shelf vs. open ocean). European Miocene gastropods also showed a decrease in drilling frequencies from higher to lower latitudes, but this result was only found for some habitats (Hoffmeister and Kowalweski, 2001). Studying recent bivalves from the east coast of the United States, Alexander and Dietl (2001) found higher naticid drilling frequencies in Florida than in New Jersey when comparing two species. Another contribution looking at recent shell assemblages from Maine to Florida failed to find any clear monotonic trend as naticid drilling predation increased in the Carolinian Province and decreased both to the north and to the south (Kelley and Hansen, 2007). Overall, differences in drilling predation with latitude have been documented for past and recent environments, yet no clear conclusions can be drawn. Moreover, since efforts have not been equally distributed across regions and across drilling predators, more data is needed from high latitudes (Hansen and Kelley, 2003), and from muricid predators.

Despite an extensive coast with variability in water temperature and mollusk composition (Gordillo, 1998b; Balech and Ehrlich, 2008), very few studies concerning drilling predation have been conducted in the South Atlantic. In this regard, the Argentine coast provides an interesting study case given its extension to poleward latitudes and the presence of two distinct biogeographic provinces (Balech and Ehrlich, 2008). These are the Magellan (43°S to 55°S) and Argentine (30°S to 43°S) provinces. The boundary between these provinces has not been clearly established as it varies seasonally between 41°S and 43°S with northward fluctuations of the cold Malvinas current in the winter (Balech and Ehrlich, 2008). In order to be conservative, for this study we establish the southern limit of the Argentine Province to be 43°S. The dominance of different water masses in these two provinces causes water temperatures to be lower in the Magellan Province (3.5 °C to 11 °C, Boltovskoy, 1979) than in the Argentine Province (18 °C to 24 °C, Boltovskoy, 1979). These water temperature differences are one of the main determinants of the molluscan fauna composition of these two regions (Gordillo, 1998b; Pastorino, 2000). In this regard, differences in water temperature could have significant effects on predation rates of marine low-intertidal organisms. Local changes of 3° have been found to decrease predation rates in the Northern Hemisphere muricid Nucella (Sanford, 2002). Whether temperature affects predation rates in the South Atlantic remains an open question as the only available information on drilling predation comes from Tierra del Fuego (e.g., Gordillo, 1994, 1998a, 2001; Gordillo and Amuchástegui, 1998; Gordillo and Archuby, 2012a), a paper from

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Buenos Aires (Pastorino and Ivanov, 1996), and two from Patagonia (e.g., Borzone, 1988; Zaixso and Bala, 1995). Interestingly, a muricid (*Trophon geversianus*) seems to be the dominant drilling predator in this area (Gordillo, 1994, and references therein). This muricid dominance provides a novel setting as previous work on spatial variability in drilling predation has focused on naticid predators (e.g., Vermeij, 1980; Allmon et al., 1990; Hansen and Kelley, 1995; Alexander and Dietl, 2001; Kelley and Hansen, 2007).

The information available on water currents indicates that local water temperature decreases toward the south. On a regional scale, this would be observed as a monotonic decrease in water temperature from the Argentine to the Magellan Province. In this context, we put forward the hypothesis that drilling predation will be lower in the Magellan Province (high latitude) than in the southern part of the Argentine Province (intermediate latitude, Fig. 1). Regionally this would be observed as a decrease in drilling frequencies coupled with a decrease in temperature. To test this, we analyze this biotic interaction along a gradient that stretches for 1,000 km in the Patagonian coast. As predators are expected to have a stronger impact on species rather than on communities (Harper, 2003), questions were addressed at the assemblage and species levels. We investigated whether locality and species-specific drilling frequencies (DFs) differed for the Argentine and Magellan provinces. Four localities were sampled from the Argentine Province (Puerto Lobos, Puerto Pirámides, El Doradillo, Puerto Madryn) and seven localities were sampled from the Magellan Province (Playa Unión, Playa Elola, Bahía Bustamante, Rada Tilly, Caleta Olivia, Cabo Blanco, Puerto Deseado). In addition, to better characterize Trophon as a predator we also seek to answer the following questions. (1) Do locality and species drilling frequencies show a positive correlation with the abundance of the gastropod? (2) Is the percentage of preferred species in a locality a good proxy for the percentage of drilled fauna? Valve-specific predation and edge drilling were also analyzed in detail for three prey species. Preference for right or left valves was calculated for the bivalves Brachidontes purpuratus. Aulacomya atra, and Venus antiqua. Preference for either of the valves would be an indicator of the bivalves' life mode (i.e., if it rests on the right or left valve), and we expect this to be manifested by differential drilling frequencies on either valve. Other choices such as wall or edge drilling can help characterize the drilling strategies used by the muricid. Experiments have found that edge drilling reduces the drilling time to a third and that this mechanism is important where potential enemies are abundant (Dietl and Herbert, 2005). As this behavior has been previously recorded for T. geversianus (Gordillo and Archuby, 2012a), we quantified it for the mytilids B. purpuratus and A. atra. Additionally, incomplete and multiple drill holes were calculated for V. antiqua and Crepidula cf. onyx, two prey species that were very abundant in specific localities.

MATERIALS AND METHODS

Geographic Location and Sample Collection

In April 2010, molluscan dead-shell assemblages were sampled at 11 beaches in Argentina (42–48°S), spanning approximately 1,000 km in the Argentine and Magellan Provinces (Fig. 1, Table 1). The area is mostly dominated by hard substrates, and affected by a strong macrotidal regime (Balech and Ehrlich, 2008; Servicio de Hidrografia Naval, 2012) and southwestern winds (45–140 km/h, Camacho, 1979; Bertness et al., 2006). Water temperature values for the localities were obtained from Servicio de Hidrografia Naval (Table 1), and the mean minimum water temperature was correlated with drilling frequencies, as low temperatures have been suggested to decrease feeding rates in invertebrates (Sanford, 2002).

The molluscan death assemblage at each locality was characterized using a minimum of 200 unbroken individuals sampled from the high-



FIGURE 1-Location of studied sites along the coast of Argentina.

tide line. The reasoning behind this quota was to obtain a sample size that would be representative of the dead assemblage species composition and representative for statistical analyses. The high-water mark was sampled every 10 m using 0.5×0.5 m quadrats. Shells were collected from the sediment surface, and in some cases up to 10 cm deep if the beach was pebbly. Depending on density, shells from 10 to 20 quadrats were combined to obtain the 200-individual quota.

Identification of Drill Holes and Calculation of DFs

Samples were wet sieved using nested 10 mm and 1.0 mm sieves. Bivalves and gastropods were identified to the species level whenever possible using published literature (Pastorino, 1994; Núñez Cortés and Narosky, 1997; Aguirre and Farinati, 2000; Forcelli, 2000; Valdovinos and Rüth, 2005; de Aranzamendi et al., 2009; González Wevar et al., 2010). Each gastropod shell with at least a preserved apex was counted as one individual (fragmented or not). Left and right bivalve valves were independently counted and the larger of these plus the number of articulated valves was considered as the minimum number of individual bivalves. Any right or left valve with a drill hole was considered a drilled individual.

Predatory drill holes were identified using the following criteria: (1) holes of a circular shape and regular outline, (2) holes perpendicular to the shell, and (3) in the case of articulated valves, holes that go through only one of the valves (Kelley and Hansen, 2003; Yanes and Tyler, 2009; Sawyer and Zuschin, 2010). Since muricid holes can sometimes resemble naticid ones (Gordillo, 1998a), the identity of the driller was inferred from the presence and abundance of predators in the samples (Klompmaker, 2009). The large majority of drill holes observed, however, were cylindrical in shape (see Gordillo and Archuby, 2012a, and Gordillo and Archuby, 2012b), for a detailed examination of the morphology of drill holes produced by *T. geversianus* on different prey species).

Drilling frequencies were calculated using only unfragmented shells to avoid underestimating the number of drill holes (Yanes and Tyler, 2009). We estimated drilling frequencies for each locality, and each species in each locality using the formula from Kowalewski (2002). The drilling frequency is the number of individuals with at least one predation trace divided by the total number of individuals (excluding fragmentary shells). In the case of species-specific analyses, drill holes

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TABLE 1—Sampled localities with their abbreviation, latitude, characterization of substrate type and water temperature (mean annual minimum and maximum values). Data taken from different sources (Boltovskoy, 2010; Helbling et al., 2010; and personal observations. 2010).

Locality	Locality abbreviation	Latitude	Substrate characteristics	Water temperature (°C)
Argentine Province	· · · · · · · · · · · · · · · · · · ·			
Puerto Lobos	PL	41° 59' 54.2"	Hard substrates of conglomerate and tuff. Sectors with fine sand beaches.	9.7-17.9
Puerto Pirámides	PP	42° 34' 43.6"	Bottoms with sand and mud, some hard substrates. Sandy beaches. Cliffs.	9.6-16.9
El Doradillo	ED	42° 39' 27.7"	Bottoms with sand and mud, some hard substrates. Sandy beaches.	9.7-16.9
Puerto Madryn	PM	42° 46' 56.6"	Bottoms with sand and mud, some hard substrates. Sandy beaches.	9.8-16.9
Magellan Province				
Plava Unión	PU	43° 18' 31.5"	Beaches with pebbles. Gravel and sand in the inferior horizons. Limestone rockgrounds.	8-18
Playa Elola	PE	44° 50' 17.5"	Beaches with sandy gravel, hard substrates with basalt; some sandy and muddy.	6.4-16.1
Bahia Bustamante	BB	45° 07' 42.5"	Rockgrounds alternating with sandy beaches, pebbles, and gravel. Hard and soft bottoms	. 7.1-18
Rada Tilly	RT	45° 56' 37"	Beaches with fine sand, tuff rockgrounds. Infralittoral with muddy and sandy bottoms.	6.5-15.5
Caleta Olivia	CO	46° 29' 29.6"	Beaches with coarse sand and pebbles. Some rockgrounds in the midlittoral area.	5.2-14
Cabo Blanco	CB	47° 12' 09.8"	Beaches with gravel and pebbles. Areas with hardgrounds with tidal forests of macroalgae	4.2-12.9
Puerto Deseado	PD	47° 45' 24.2"	Gravel beaches, some cliffs with sandy beaches, and sectors with hardgrounds.	4.9-13.5

were recorded as present on either right or left valves, and the position in the valve (wall vs. edge) was also documented. We represent these drilling frequencies as percentage of drilled individuals.

Subsampling Methods

Given the variability in the sample sizes (n = 218 to n = 2117), localities were standardized to the smallest sample size (n = 218, excluding fragmented shells), and resampled 10,000 times without replacement (Efron and Gong, 1983) using the R statistical software (R Development Core Team, 2012). A mean value and 95% confidence intervals were calculated for the locality and *Brachidontes purpuratus* drilling frequencies.

RESULTS

Mollusc Diversity and Abundance

A total of 12,680 individuals were sampled from 11 localities in the Argentine Patagonia. In total, 41 mollusk species were recognized, 21 gastropods (13 families), and 20 bivalves (9 families) (Supplementary Data 1¹). Local species richness ranged from 10 to 23; Puerto Lobos, Puerto Pirámides, El Doradillo and Puerto Madryn were the localities with the highest values (Table 2). Gastropods were more abundant in the center of the sampled region, while bivalves (mytilids mainly) increased in abundance toward the northern and southern extremes.

TABLE 2—Richness, number of individuals found at each locality (N), and drilling frequencies per shell assemblage (DFs).

Locality	Richness	N	DFs (%)
Argentine Province			
Puerto Lobos	23	1,940	7
Puerto Pirámides	18	1,355	4
El Doradillo	20	1,053	5
Puerto Madryn	19	4,077	3
Magellan Province			
Playa Unión	11	834	36
Playa Elola	13	466	9
Bahia Bustamante	14	830	19
Rada Tilly	14	380	11
Caleta Olivia	11	669	10
Cabo Blanco	11	327	4
Puerto Deseado	10	751	3

1 www.palaios.ku.edu

The majority of the molluscs came from the 10 mm sieve fraction, therefore, the drilling predation results that we present are only representative of specimens larger than that size fraction.

Three drilling predators were found in our samples: two muricids and one naticid (Table 3). Single *T. geversianus* individuals were found drilled at two sites. The naticid *Notocochlis isabelleana* was present at two sites in very low abundance.

Spatial Variability in Muricid Predation along a Temperature Gradient

Locality Drilling Frequencies.—Drilling frequencies ranged from 3% at Puerto Madryn to 19% at Bahia Bustamante (Table 2). Playa Unión had an unusually high drilling frequency of 36%. The drilling frequencies for the Argentine and the Magellan groups did not differ significantly (Wilcoxon rank sum test, p = 0.185, W = 6.5, no. sites = 11, Fig. 2B). The locality drilling frequencies of the Magellan Province displayed a higher variance than the ones from the Argentine Province (Fig. 2B).

No significant correlation was found between mean low water temperature and locality drilling frequencies (Spearman rank order correlation, p = 0.906, r = -0.04). Drilling frequencies, however, were higher (DF: 20%–36%) at mid-temperatures ($\sim 7-8$ °C), and lower (DF: 3%–4%) at both higher (~ 10 °C) and lower (~ 4 °C) water temperatures (Fig. 3B).

Preferred Taxa and Predator Abundance.—The percentage of mytilids (B. purpuratus, A. atra, Mytilus edulis chilensis, and Mytilus edulis platensis) at each locality was not correlated with the percentage of drilled species at a site (Spearman rank order correlation, p = 0.529,

TABLE 3-Number of individuals of the potential drilling predators found at each locality.

Locality	Trophon geversianus	Trophon plicatus	Notocochlis isabelleana
Argentine Province	- 1		
Puerto Lobos	146		2
Puerto Pirámides	18		14
El Doradillo	17	1.4	-
Puerto Madryn	122		9
Magellan Province			
Playa Unión	9	3	
Playa Elola	18	10.0	- Q.,
Bahía Bustamante	20	4	
Rada Tilly	11	-	2.
Caleta Olivia	33	1.1	10
Cabo Blanco	7	3	191
Puerto Deseado	4		

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FIGURE 2—Boxplots showing A) *B. purpuratus* drilling frequencies (DFs expressed as %) for the Argentine and Magellan Provinces, B) locality drilling frequencies (DFs expressed as %) for the Argentine and Magellan Provinces. Horizontal bars represent median values, boxes enclose the 25th to 75th percentiles, and whiskers indicate the minimum and maximum values.

r = 0.242, Fig. 4). Additionally, no significant correlation was found between the relative abundance of *T. geversianus* and the drilling frequency at the site (Spearman rank order correlation, p = 0.257, r = 0.396).

Species Drilling Frequencies.—Across all localities 16 species were drilled. Puerto Madryn, with the largest sample size, had the highest number of drilled species (9), whereas Playa Unión and Cabo Blanco had the lowest (2) (Supplementary Data 2¹). In some localities drill holes were seen exclusively on mytilids (Cabo Blanco and Puerto Deseado), and the only site where mytilids were not found drilled was Playa Unión. The species that were drilled in most localities were: Brachidontes purpuratus (in 8 out of 11 sites); Aulacomya atra (7 sites); Crepidula dilatata (5 sites); Mytilus edulis chilensis and Tegula (A.) patagonica (4 sites); Mytilus edulis platensis, Brachidontes rodriguezii, Nacella magellanica, Venus antiqua, and Siphonaria lessoni (3 sites); Crepidula cf. onyx, Buccinanops globulosus, and Trophon geversianus





Water temperature (°C)

FIGURE 3—Scatter plot showing A) *B. purpuratus* drilling frequencies (DFs expressed as %) and mean minimum water temperature, B) locality drilling frequencies (DFs expressed as %) and mean minimum water temperature. Sites are organized from south (Magellan Province) to north (Argentine Province); locality abbreviations as in Table 1.

(2 sites). The remaining species were consumed only once: Nacella delicatissima, Fissurella spp. and Olivella tehuelcha.

As *B. purpuratus* was the most abundant prey species across all sites, drilling frequencies based on standardized resampling data were calculated. Predation intensities ranged between 0% (Cabo Blanco) and 12% (Playa Elola) (Table 4). Similarly to what was found for locality-level DFs, no significant differences were found for the Argentine and Magellan groups (Wilcoxon rank sum test, p = 1, W = 8.5, no. sites = 8), and the variance in DFs from the Magellan was higher than the one from the Argentine Province (Fig. 2A).

No significant correlation was found between mean low water temperature and *B. purpuratus* drilling frequencies (Spearman rank



FIGURE 4—Scatter plot showing drilled individuals per locality (DFs expressed as %) and mytilids per locality (%). Locality names as in Table 1.

correlation, p = 0.223, r = 0484). A similar tendency as the one observed for locality-level drilling frequencies was observed: drilling frequencies were higher (DF: 12%) at mid-temperatures (~6.5 °C), and lower (DF: 0%–5%) at both higher (~10 °C) and lower (~3 °C) water temperatures (Fig. 3A).

Drilling Strategies of the Predator on Specific Prey

Complete Drill Holes.—Four prey species were studied in more detail in order to better understand Trophons' drilling behavior. The predator exhibited no valve specific predation on the mytilid Brachidontes purpuratus (Wilcoxon rank sum test, p = 1, W = 31.5, no. sites = 8) or on Aulacomya atra (Wilcoxon rank sum test, p = 0.751, W = 14.5, no. sites = 6). Edge drilling accounted for 27% of the drill holes recorded in B. purpuratus. In contrast, for the mytilid A. atra, 56% of the drill holes were edge drilled (Fig. 5, Table 5). Valve-specific predation in Venus

TABLE 4—Drilling frequencies for *Brachidontes purpuratus*, and number of individuals found at each locality (N). 1 = Drilling frequency for *Tawera gayi* from Tierra del Fuego, shells collected using our same methodology (Gordillo, 1994). 2 = Drilling frequency for *Mytilus edulis chilensis* from Tierra del Fuego, shells collected using our same methodology (Gordillo and Archuby, 2012a). 3 = Drilling frequency for *Mytilus edulis chilensis* from Tierra del Fuego, shells were collected randomly by hand along the high-water mark (Gordillo, 1994, unpublished data).

Locality	N	DFs (%)	
Argentine Province			
Puerto Lobos	774	5	
Puerto Pirámides	473	4	
El Doradillo	81	6	
Puerto Madryn	358	7	
Magellan Province			
Playa Unión	3	0	
Playa Elola	170	14	
Bahía Bustamante	0	0	
Rada Tilly	29	17	
Caleta Olivia	191	8	
Cabo Blanco	58	0	
Puerto Deseado	344	3	
Canal Beagle ¹	543	22	
Bahia Golondrina ²	295	16	
Cabo San Pablo3	300	26	



Brachidontes Aulacomya

FIGURE 5-Boxplot showing edge drilling (%) for *B. purpuratus* and *A. atra*. Bars, boxes, and whiskers as in Figure 2.

antiqua, was not significant (p = 0.09, $\chi^2 = 2.9$), but right valves were drilled twice as often as left valves (9% left versus 19% right).

Incomplete and Multiple Drill Holes.—There was no significant difference between the distribution of incomplete drill holes on the valves of V. antiqua (p = 0.13, $\chi^2 = 2.3$, Table 5). For the gastropod Crepidula cf. onyx, incomplete drill holes represented 9% of the total drill holes, and multiple drill holes accounted for 10% of the total (Table 5).

DISCUSSION

Contrary to expectation, no difference in drilling frequencies was found between northern (Argentine Province) and southern (Magellan Province) localities. Locality drilling frequencies were usually <10% in the studied sites with the exception of Playa Unión (36%). Mytilids were the most abundant prey, and the drilling frequencies for *B. purpuratus* ranged from 0% to 12%. No difference in muricid predation between Argentine and Magellan Provinces was found for this species either. Neither predator abundance nor percentage of preferred prey species were verified as predictor variables of drilling frequencies. The predator used different strategies for the different prey species studied.

Muricid Predators

Comparing the abundance of the Naticidae and the Muricidae in our samples, muricids are clearly dominant in Patagonian shallow marine habitats. A recent review of naticids from Patagonia only mentions 13 species, and states that naticid diversity is not as high as it is in other regions (Pastorino, 2005a). In contrast, muricids from the genus Trophon are highly diverse (46 species reviewed by Aldea and Troncoso, 2010) and abundant in South America. T. geversianus is the most widespread species (Pastorino, 2005b), and the dominant predator in our samples (Table 3). T. geversianus and other species of this genus are important predators in Magellan and Antarctic systems based on experimental and field studies (Gordillo, 1994, 1998a; Zaixso and Bala, 1995; Gordillo and Amuchástegui, 1998; Harper and Peck, 2003; Andrade and Ríos, 2007; Andrade et al., 2009). In addition, muricids are expected to be better represented than naticids, which are typical of soft sediment habitats (Kabat, 1990), given that our samples were mostly dominated by epifaunal rocky-shore fauna (mytilids). These

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TABLE 5-Valve-specific predation, edge drilling, incomplete (incomplete drill holes/total drill holes) and multiple drilling for the most abundant prey species.

	Valve-specific predation		Edge drilling			Incomplete drilling			Multiple
Species	Selectivity?	No. sites	Mean (%)	Range (%)	No. sites	Mean (%)	Range (%)	No. sites	drilling (%)
Brachidontes purpuratus	No, $p = 1$	8	27	5-40	6	10	0-23	9	
Aulacomya atra	No, $p = 0.75$	5	56	7-100	6	6	0-19	6	
Venus antiqua	No, $p = 0.09$	1 (BB)	1.2	8.1	-	3		1 (BB)	-
Crepidula cf. onyx	- intani		-	1911	-	9		1 (PU)	10

observations led to the conclusion that most of the drill holes are likely the work of *T. geversianus*, the most abundant drilling predator in this part of South America.

Drilling Frequencies in High Latitudes

Drilling gastropod predation traces were found in all 11 localities, indicating that it is a generalized phenomenon in this area. The predation levels found in this study are similar to those found by Dudley and Vermeij (1978), in which naticid drilling frequencies were calculated from recent Turritella museum specimens for several highlatitude localities. Labrador Peninsula in Canada (DF: 0%-2.9%), Alaska (DF: 3.7%), and New Zealand (DF: 2%-19.3%) had predation values comparable to the ones found in this study. Kelley and Hansen (2007) calculated naticid-drilling frequencies of 0% to 3%, and 5% for samples from the Virginian and Nova Scotian Provinces respectively. Similarly, Alexander and Dietl (2001) obtained naticid drilling frequencies of 4% for New Jersey. Our results for drilling predation in Patagonia are also consistent with frequencies obtained for other prey attacked by Trophon in Tierra del Fuego (Table 5). These values suggest that muricid predation in the Southern Hemisphere is similar to what has been previously found for high-latitude predation by naticids from the Northern Hemisphere.

Scales of Variability along a Temperature Gradient

Our results show that drilling frequencies are lower at high latitudes (lower temperature) than at lower latitudes (higher temperature). The role of temperature at smaller scales (regional and local) is not clear, however, and local factors may have a stronger incidence in the activity of predators. Even if temperature decreased along the gradient, the expected regional monotonic decrease in drilling frequencies coupled with water temperature was not observed. Looking at each Province in detail, predation did not differ between the Argentine and Magellan Provinces (p = 0.122, Fig. 2). The variance in drilling frequencies was lower for the Argentine Province, yet this is not surprising as there were four sites (Puerto Lobos, Puerto Pirámides, El Doradillo and Puerto Madryn) versus seven sites from the Magellan Province (Playa Unión, Playa Elola, Bahía Bustamante, Rada Tilly, Caleta Olivia, Cabo Blanco, and Puerto Deseado). A tendency found both for locality-level and species-specific analyses (B. purpuratus) was that drilling frequencies were lower at the lowest and highest temperature values. At midtemperature, drilling frequencies were approximately three times higher $(p < 0.001, \chi^2 = 17.3, \text{ no. sites} = 10, \text{ Fig. 3})$. This is possibly not directly linked to temperature, as the dominant species at this locality (Bahía Bustamante, DF = 19%) was a semi-infaunal venerid (V. antiqua), which may be preferred over mytilids.

On a local level, environmental factors such as water temperature can affect drilling frequencies by altering the physiology and metabolism of marine benthic predators (Sanford, 2002). Within the tolerance limits of an organism, an increase of 4 °C in water temperature could cause biological rates to be 30%–55% higher (Sanford, 2002). Although this remains to be tested experimentally, local differences in temperature do not seem to affect the predatory activity of *Trophon*. Previous investigations in Tierra del Fuego, where water temperature is lower (average minimum temperature is 2.3 °C, Servicio de Hidrografía Naval, 2012) found drilling frequencies similar to the ones documented here (10%–26%, Gordillo et al., 2011; Gordillo and Archuby, 2012; Table 5). Given the southern origin of this genus (Pastorino, 2005b), this predator may have adapted to cold water temperatures and thus shows no decrease in predatory activity with changes in local temperature toward the south of its distribution. The lack of differences between provinces and of a decrease in DFs on a regional level could be a manifestation of this adaptation. Thus, at least for *Trophon*, the effect of water temperature on DFs at different scales (regional and local) is not as straightforward as predicted.

Is Anthropogenic Impact Recorded on Predation Rates?

The relevance of dead-shell assemblages as tools for conservation and prediction of anthropogenic-related changes in ecosystems has been previously established (e.g., Kidwell, 2007; Dietl and Flessa, 2011). In this regard, one of our most significant findings was that Playa Unión, a site with strong eutrophication (Esteves et al., 1997; Helbling et al., 2010), was an outlier that displayed the highest drilling frequency (36%, Table 2), almost twice as high as the second highest (19%), and more than ten times higher than the lowest (2.7%). The most abundant species at the site (92% of the total specimens found), Crepidula cf. onyx, has been found to be favored by eutrophic environments (Zhao et al., 2003), and was present in only one site other than Playa Unión. This would be suggesting that the dominance of Crepidula is a consequence of a eutrophic environment. The link between this high abundance and high predation is straightforward as the predator is eating what is most abundant. In addition, and despite the low abundance of Trophon in the area (2%), the high abundance and low mobility of the prey could explain the high drilling frequency. A possible scenario could be that the species is attacked in high proportion given that it is an easy target as individuals attach themselves one on top of the other forming distinctive chains as part of their mating behavior (Gallardo, 1977). Crepidula females also undergo periods of temporary or permanent immobility during the time they are brooding their young (Chaparro et al., 1998); this could also increase their chance of being preyed upon. Finally, whether eutrophication in nutrient-rich marine environments favors higher consumption rates in predators needs to be addressed in future research.

Drilling Strategies of the Predator on Specific Prey

Complete Drill Holes.—Experimental studies carried out by Gordillo and Archuby (2012a) in Tierra del Fuego showed that T. geversianus exhibits different drilling behavior when attacking different mytilid prey species. These experimental results are in agreement with what we found in dead-shell assemblages. For the mytilids B. purpuratus and A. atra, no preference for left or right valves was found (Table 5). Edge drilling was the predominant strategy used by the muricid to feed on these bivalves, accounting for 27% and 56% of the drill holes in B. purpuratus and A. atra respectively (Table 5, Fig. 5). Gordillo and Archuby (2012a) suggested that the ribs on the shells of these species

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may be the reason the gastropod chooses edge over wall drilling (especially for *A. atra*), as wall drilling would take longer due to the thick ribs. It is possible that the use of edge drilling reduces the time *Trophon* is exposed to potential predators, and it could also be a less energy-intensive strategy as well.

Two other prey species that were very abundant in only two sites were V. antiqua and C. cf. onyx. In V. antiqua drill holes always occurred on the walls, and not on the edges. Valve specificity analyses indicated no preference for right or left valves of the venerid (Table 5).

Incomplete and Multiple Drill Holes.—For Crepidula, incomplete drill holes represented 9% of the attacks and multiple drill holes 10% of the attacks. This pattern may reflect the lack of mobility in brooding females and the chain mating behavior previously mentioned (Gallardo, 1977; Chaparro et al., 1998).

Potential Biases in the Estimation of Drilling Frequencies

The Role of Other Consumers.—Drilling predation is only one of several types of predation in coastal marine systems. Sea stars, crustaceans, fish, and birds also consume mytilids and other molluses. Thus, the role of predatory snails could depend on the predatory pressure by local sea stars, crabs, and fish that may be reducing their efficiency by density-dependent regulation. The activity of durophagous crabs has been known to lead to overestimations of drilling frequencies as the crushed shells will be lost from the death-assemblage (Vermeij et al., 1989). Given that there is insufficient information on crushing predators in Patagonia, the magnitude of this predation or its potential impact on our drilling frequency calculations is difficult to determine. Techniques like the Vermeij Crushing Analysis (Stafford and Leighton, 2011) could be used in the future to assess the impact of crushing predators in these environments.

Taphonomic Biases .- Preservational biases could be important if drilled and undrilled shells have different probabilities of being preserved or sampled. Roy et al. (1994) found that drilled valves are significantly more likely to undergo fragmentation than undrilled valves. To account for this variation, Roy et al. (1994) suggested considering the degree of fragmentation of the shell assemblages. If fragmentation is high, then drilling frequencies will likely be underestimated. In our case, fragmentation at the different localities varied between 14% and 47%. The degree of fragmentation was not correlated with drilling frequencies (Spearman rank correlation, p 0.95, r = 0.8), so taphonomy is unlikely to be driving the observed pattern. Biased postmortem transportation can also affect the degree of representation of shells from different environments in the samples. As all of our samples come from different sites, the degree of preservation is expected to vary given varying local conditions; however, most of the species are found living on rocky shores, suggesting that these death assemblages are primarily representing the upper part of the intertidal community, and possibly there is an underrepresentation of the soft subtidal environments.

An added taphonomic bias is the presence of fossil assemblages along the coast of Patagonia, which could potentially mix with the samples we collected. Egidio Feruglio (1949) described most of these assemblages in a pioneering work on the molluscs from marine terraces in Patagonia. Several of the horizons he described were found during our sampling, therefore, we can be confident that the samples used in this study do not belong to fossil assemblages.

Implications for the Fossil Record of Drilling Predation

Drilling predation is the biotic interaction with the most well-known fossil record (Kowalewski et al., 1998). This is reflected by the fact that most contributions on this topic have been made by paleontologists or in a paleontological context (e.g., Allmon et al., 1990; Hansen and Kelley, 1995; Harper, 2003; Dietl et al., 2004; Klompmaker, 2009; among many others). Given that recent drilling predation is understudied, this

contribution offers a recent baseline that can be used to interpret patterns observed from high latitudes sites in the fossil record. The fact that the fossil record of drilling predation for muricids is less abundant than the one from naticids could limit the extrapolation of our results. Fossil muricids are abundant in Patagonia from the Oligocene onward, however (Griffin and Pastorino, 2005), and we think that rather than being a limitation, the study of muricid drilling predation in fossil and recent molluscs from Patagonia can provide novel insights that so far are not available from anywhere else in the world. Moreover, the fact that *Trophon* selected mytilid prey, and displayed different drilling strategies for the different species, sets a precedent for feeding preferences. Knowledge of this kind of behavior is lacking from the fossil record and it would be interesting to examine if it is limited to recent muricid genera or when it evolved.

CONCLUSIONS

1. We provide the first data on spatial variability for muricid predation in high latitudes of the Southern Hemisphere. Overall, drilling frequencies were generally lower than 10%, strengthening the idea that drilling frequencies for high-latitude environments are lower than those documented for low latitudes.

2. Our data also suggests that muricid predation varies spatially; however, this does not seem to be related to changes in water temperature along this gradient, as the Argentine and Magellan Provinces showed similar drilling predation values. Thus, there is not a clear relationship between water temperature and drilling predation at different scales.

3. A remarkably high drilling frequency in one site with high eutrophication may indicate that the impact of humans on recent marine environments can be recorded in dead-shell assemblages.

4. The drilling frequencies at locality or species level were not correlated with the abundance of the drilling gastropod, or with the abundance of the preferred prey.

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Very high coral cover at 36°S on the east coast of Australia

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Reef sites

Very high coral cover at 36°S on the east coast of Australia



There are very few data on the occurrence of scleractinian coral species in temperate regions. Here, we conducted a series of surveys along the New South Wales coastline to document their distribution and abundance. Interestingly, one species dominated the benthos at a number of these sites. For example, very high densities of the geographically widespread coral Plesiastrea versipora were found together with high densities of the sea urchin Centrostephanus rodgersii at Montague Island (36.2449°S, 150.2239°E), amongst a colony of Australian fur seals (Fig. 1a, b). At up to 80 % cover (mean 42 %, range 0-80 %), coral abundance equals or exceeds those on tropical reefs. However, due to cool water temperatures and low carbonate saturation state, P. versipora grows slowly (Burgess et al. 2009) and reef accretion does

Fig. 1 a Beneath the Australian fur seal colony at Montague Island, NSW, Australia. b High densities of *Plesiastrea versipora* sharing space with \mathbf{c} the sea urchin *Centrostephanus rodgersii*. d The sea urchin excavating a colony of *P. versipora*

not occur. Preliminary observations suggest that stable populations of herbivorous sea urchins at 5–15 m depth contribute to the success of this coral in sheltered temperate sites. However, living in close quarters with an algal-grazing urchin, which mechanically burrows into solid granite for protection from predators, resulted in a high number of instances in which the urchin burrowed into the softer corals themselves (Fig. 1c, d). More work on coral populations at high latitudes is required to establish the exact mechanisms that lead to their ecological success.

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REGIONAL-SCALE COMPOSITIONAL AND SIZE FIDELITY OF ROCKY INTERTIDAL COMMUNITIES FROM THE PATAGONIAN ATLANTIC COAST

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ABSTRACT

The use of rocky intertidal assemblages in paleoecology and conservation paleobiology studies is limited because those environments have low preservation potential. Here, we evaluate the fidelity between living intertidal mussel bed communities (life assemblages or LAs) and mollusk shell accumulations (death assemblages or DAs) from the environmentally-harsh Patagonian Atlantic Coast. Patagonian shores are characterized by a pronounced macrotidal regime and frequent strong winds, allowing us to explore live/dead agreement in environmentally and temporally variable conditions. Living assemblages (n = 6) were sampled from rocky mid-intertidal and mussel-dominated habitats. Since dead shells do not accumulate in rocky mid-intertidals, live-dead mismatch cannot be assessed at local scale at the same sites. Therefore, death assemblages (n = 10) were collected from the high water mark at beaches in close proximity to the living intertidal community to assess live-dead mismatch at regional scales. Shells from DAs in beach environments belonged to species inhabiting upper intertidal to subtidal habitats and hard- and soft-bottom habitats. To ensure comparability with LAs, we used the subset of species in the DAs that inhabit rocky intertidals. A total of 37,193 mollusk specimens from 15 intertidal species were included in the analysis. Ten species were present in LAs, 14 in DAs, and nine were shared by LAs and DAs. DAs showed higher diversity, less dominance and more rare species than LAs. Despite finding a good agreement in species composition between DAs and musseldominated LAs within the same region, smaller species are underrepresented, as shown by differences in intraspecific size-frequency distributions. Our findings indicate that the composition of DAs is a result of the combined effects of spatial and temporal averaging, size-related biases and biases related to low detectability of boring and vagile species in LAs. Thus, DAs do not accurately detect within-provincial latitudinal

gradients in composition. However, DAs clearly capture differences between the Argentine-Magellanic transition zone and the Magellanic Province, indicating that DAs are informative tools at regional scales despite the environmental harshness they are subjected to.

INTRODUCTION

The degree of fidelity between living communities and their fossil counterparts constrains the usefulness of the preserved assemblages to reconstruct past ecosystems. Determining how much of the biological signal reaches the shell beds after the influence of biological and physical agents and time averaging, and how this preservability varies in time and space remains one of the key steps in paleontological analysis (Fürsich, 1978, 1995; Kidwell, 1985, 1986, 2001; Kidwell et al., 1986; Fürsich and Aberhan, 1990; Kidwell and Flessa, 1995; Kowalewski et al., 2003; Tomašových et al., 2006). Previous contributions have found that there is a fairly good agreement between the species composition of living assemblages (LAs) and the co-occurring death assemblages (DAs) in marine environments (e.g., Fürsich and Flessa, 1987; Kidwell, 2001, 2002, 2013; see examples in Kidwell and Bosence, 1991) as well as in other settings and/or taxa, such as land snails (Yanes, et al., 2008; Yanes, 2011), fresh water mollusks (De Francesco et al., 2013; Erthal et al., 2011; Tietze and De Francesco, 2012), marine mammals (Liebig et al., 2003), ungulate mammals (Miller, 2011; 2012), nonvolant terrestrial mammals (Miller et al., 2014), small mammals (Terry, 2010; see other examples in Kidwell and Tomašových (2013)). However, the degree of similarity between living communities and the corresponding dead remains shows a large variation (Kidwell, 2001), particularly among marine benthic communities (Kidwell and Bosence, 1991; Zuschin et al., 2000; Zuschin and Oliver, 2003; Albano and Sabelli, 2011; Feser and Miller, 2014). The dissimilarities between LAs and DAs in marine soft-bottom environments can be largely explained by the effect of time averaging and probably less by taphonomic biases

(Tomašových and Kidwell, 2009, 2010, 2011; Kidwell and Tomašových, 2013). This finding has also been established in several other contributions both from terrestrial and marine ecosystems (Kidwell and Tomašových, 2013 and references therein). A conservative estimation of the effects of time averaging on DAs indicates that in a few decades to centuries, alpha diversity increases and beta diversity decreases at small spatial scales, species dominance is reduced and rare species become more common (i.e., rank abundance distributions become flatter) (Tomašových and Kidwell, 2010).

The composition of snapshot-like LAs (i.e., sampled at a single time) is not necessarily an accurate estimate of the composition of the source assemblages from which DAs originate (i.e. integrated over a longer time). Short-term changes in species composition in living communities can be substantial (Kidwell and Bosence, 1991) and compositional variations can also be enhanced by anthropogenic effects (Kidwell, 2007). In addition, sampling living marine communities can be costly and logistically complicated (Warwick and Light, 2002). An example of the changes that living communities experience over short time intervals that can strongly influence the results of discrete sampling (censuses) of LAs can be seen in the surf clam Mesodesma mactroides. This bivalve changed from being the dominant species in sandy beaches in Argentina to completely disappearing in less than a month due to a natural mass mortality event in 1995 (Fiori and Cazzaniga, 1999; Dadon, 2005). The populations recovered soon because only the benthic life stages were affected. If samples from the living communities had been taken before and after the mass mortality event, they would have been drastically different. The mass mortality of Mytilus edulis caused by high temperature on rocky shores represents another example (Tsuchiya, 1983) (see other examples documented in Fiori and Cazzaniga, 1999 and Dadon, 2005). In this regard, one of the benefits of DAs is that they average out these atypical short-term events, providing a more conservative overview of community composition at broader temporal and spatial scales (Fürsich, 1978; Fürsich and Aberhan, 1990; Kidwell and Bosence, 1991; Tomašových and Kidwell, 2010; Kidwell and
Tomašových, 2013). The inertia of DAs to short-term changes in species composition thus turns them into good proxies for long-term or regional-scale studies of benthic assemblages.

In the Southwestern Atlantic, one of the most conspicuous benthic assemblages are represented by rocky intertidal communities. These habitats invariably consist of dense and extended monocultures of small *Brachidontes* mussels, which are very important ecosystem engineers (Olivier et al., 1966a, b; Adami et al., 2013, 2008; Bertness et al., 2006). Other larger mytilids (e.g., Mytilus spp., Aulacomya atra) are also present along the rocky shores, but at low population densities (López Gappa et al., 1990; Adami et al., 2004). Intertidal mussels frequently occur as multilayered beds (Guiñez and Castilla, 1999) of considerable structural complexity (Commito and Rusignuolo, 2000). These mussel beds buffer other species against biotic and abiotic fluctuations, and produce an array of microhabitats that facilitates persistence of associated organisms (Silliman et al., 2011). Studies conducted in Patagonia have shown that the extreme desiccation is an important and unique feature of these intertidal mussel-dominated beds (Bertness et al. 2006). The strong dry winds, combined with low rainfall probably make these shores one of the most physically demanding rocky intertidal systems in the world. These mussel beds thus offer an exceptional opportunity to assess the preservability of rocky intertidal communities by quantifying fidelity between LAs and DAs. In addition, most live-dead studies in marine environments have focused on soft or mixed sediment habitats (but see Zuschin et al., 2000; Zuschin and Oliver, 2003; Zuschin and Stachowitsch, 2007) while compositional fidelity in rocky-bottom intertidal environments still remains poorly known.

Here, we evaluate the correspondence between mollusk DAs from Patagonian beaches that represent natural sediment traps for inhabitants of rocky intertidal communities (Martinelli et al., 2013, and additional previously unpublished data), and a database of intertidal mussel bed communities from the same area (Adami et al., 2013). We seek to establish the degree of fidelity with which compositional and ecological information from living communities is

represented by DAs in this climatically harsh environment. To do this, we (1) compare LAs and DAs within two biogeographic provinces and (2) assess the regional variability of fidelity in species composition across the boundary between two biogeographic provinces (i.e. Argentine and Magellanic). Rocky shores are dominated by erosion and do not tend to accumulate any sediment, consequently dead shells are destroyed or quickly transported away to other habitats. Therefore, the nature of live-dead comparison is based on LAs and DAs sampled at different sites within the same regions, allowing regional-scale inferences on the preservability of ecological signals within and between biogeographic provinces. We hypothesize that DAs maintain the species composition from the communities from which they derive, even after suffering the biases brought about by various taphonomic agents, and the effects of time-averaging. In particular, we predict that the DAs will share roughly the same species composition and abundances with the LAs. In agreement with previous studies, we also anticipate that DAs will be enriched in larger specimens (Fürsich and Oschmann, 1993; Valentine et al., 2006), and will show higher taxonomic richness and eveness than LAs (Fürsich and Aberhan, 1990; Olszewski and Kidwell, 2007; Kidwell and Tomašových, 2013).

MATERIALS AND METHODS

The Study System

The study region encompasses 1,500 km along the south Argentine Atlantic coastline (41 - 48° S, Figure 1), including the transition zone between the Argentine and Magellanic Biogeographic Provinces (41°S and 43°S, Balech and Ehrlich, 2008), and the northern part of the Magellanic Province (43-48°S). Both LAs and DAs from this area are exposed to high-energy flows during high tides (mean tidal amplitude ranges from 1.76 to 6.74 m, while maximum tidal amplitude varies between 2.46 and 9.57 m, Balech and Ehrlich, 2008; Servicio de Hidrografía Naval, 2012). Temperatures are usually low (min SST ranges between 4.2 and 10.8° C, max SST ranges between 12.9 and 20.1° C, Table 1) and winds are 164

frequent and strong (45 - 140 km/h, Camacho, 1979; Bertness et al., 2006). The geographical spread and the characteristics of rocky shores in our study area are shown in Table 1.

Figure 1.

Table 1.

The configuration of the Argentinean Patagonian coastal margin is the result of several factors mainly related to sea level variations associated with glacioeustatic-climate changes, geotectonic and isostatic compensation processes (Clapperton, 1993; Rostami et. al 2000; Schellmann et al., 2000, 2010; Pedoja et al., 2011). The geographical spread and the characteristic of rocky shores of our study area are shown in Table 1.

Mussel beds in rocky intertidal shores. — Several mytilid species are found in intertidal mussel beds along the coasts of the southwestern Atlantic (Scarabino et al., 2006; Ríos, 2009; Adami et al., 2013; Trovant et al., 2013). Our study area is dominated by two small-sized *Brachidontes* species that form dense beds along with other species in minor proportions (i.e., *Mytilus* spp.) (Olivier et al., 1966a, b; Adami et al., 2004, 2008; Bertness et al., 2006; López Gappa et al., 1990). *Brachidontes rodriguezii* dominates rocky intertidals from Buenos Aires to north Patagonia (Penchaszadeh, 1973; López Gappa et al., 1990; Adami et al., 2004; Adami, 2013), and *Brachidontes* (= *Perumytilus*) *purpuratus* is most abundant from northern Patagonian over to the Pacific Ocean coast up to Ecuador (Bernard, 1983). Both species coexist in the transition zone between the Argentine and Magellanic Biogeographic provinces (41°S - 43°S) and, although both species are morphological and biological very similar, the structure of their mussel beds and their accompanying fauna differ significantly (Arribas et al., 2013).

METHODS

Two databases were used for the live-dead comparisons. The first one has exhaustive counts of living mollusks (LAs) from the middle rocky intertidal from six localities along the Atlantic coast of Patagonia (Figure 1, Table 1). The second database contains counts of intertidal mollusks from death assemblages sampled at ten localities within same region (Figure 1, Table 1) because rocky-bottom habitats are dominated by erosional processes, and hence do not accumulate shells. Therefore, DAs were collected at beaches where depositional settings accumulated shells from intertidal and subtidal habitats, and locations of LAs thus do not precisely coincide with locations of DAs. The selection of sites where DAs were sampled was designed to capture the spatial variation in species composition of shell accumulations in the study area. However, out of 16 localities, three localities with DAs are located close to localities with LAs (localities 3 and 4 at Playas Doradas, localities 10 and 11 at Playa Elola/Camarones, and localities 13 and 14 at Caleta Olivia), thus forming three pairs of LAs and DAs that can be also compared at smaller spatial scales (see Table 1 for latitude details). To make the samples of DAs comparable with those from LAs, we selected the subset of species that occur in rocky intertidal habits on the basis of evidence independent from LA composition (i.e. from published literature and/or field observation) (Table 2).

Sampling. — Living communities were sampled at six localities between 2004 and 2008 (Table 1) (Adami, 2005). In every locality five or six replicates of 14 x 14 cm (200 cm²) were taken and all living specimens counted. The replicates were randomly spread at each sampling site. Samples were always obtained from the mid-intertidal zone, aiming at the centroid of patches with 100% mussel cover developed over gently sloping surfaces (Figure 2A and B). Samples were sieved using a 0.5 mm mesh, and mussels and other macrofaunal organisms were retrieved. DAs were collected in April of 2010 at ten localities along the Atlantic coast

of Patagonia (Table 1). The high-water mark was sampled every 10 m using a 0.5 m x 0.5 m quadrat (Figure 2C and D). Shells were carefully collected from the sediment surface and in some cases up to 10 cm deep if the beach was pebbly. Depending on density, shells from 10 to 20 quadrats were combined to obtain at least 200 complete shells. Bivalves were counted as one specimen per articulated shell plus the amount of left or right valves (the most numerous of them).

Figure 2.

Univariate and multivariate analyses. — Species richness (S) and an evenness index (Pielou's J or equitability index) (Hammer and Harper, 2006) were calculated for all LAs and DAs using PAST (Hammer et al., 2001). Owing to the different sample sizes we also estimated species richness with rarefaction for n = 301 with PAST (Hammer et al., 2001). Differences in abundances of the most common species between LAs and DAs were graphically compared with bar-plots (Figure 3). These plots were constructed for Playas Doradas (localities 3 and 4), Playa Elola/Camarones (localities 10 and 11) and Caleta Olivia (localities 13 and 14). Similar graphical representations were used to compare LAs and DAs at provincial level. For analyses at the provincial scale we calculated the average percentage of each species across all localities in the corresponding biogeographic unit and type of sample (DA or LA).

A non-metric multidimensional scaling (NMDS) was used to assess the similarity in species composition among LAs and DAs. A matrix was built with all the mollusk species from both databases (15 species; n = 37,193 individuals). Absolute abundances were standardized to percentages, and then transformed with (a) square root and (b) presence/absence. The Bray-Curtis distance was used for abundance data (Clarke, 1993; Clarke and Warwick, 2001; Clarke et al., 2006) and Sorensen coefficient for binary data (Hammer et al., 2001). Plots were rotated in order to arrange samples latitudinally. Differences in species composition on the basis of percentages between LAs and DAs were assessed with a one-way PERMANOVA

test (non-parametric multivariate analysis of variance) using Bray-Curtis as a distance index, using PAST (Hammer et al., 2001). This analysis was done for the whole matrix and by biogeographical province, with 9999 permutations. The same procedure was used to compare species composition between biogeographic provinces for DAs and LAs.

In order to test the hypothesis that size-selective biostratinomic factors (tides, waves and wind) affect the preservation of shells in DAs, we compared the size-frequency distributions of living and dead specimens of *B. purpuratus* and *B. rodriguezii*. We predicted that physical agents eliminate small specimens from the DAs increasing the average specimen size and/or causing the displacement of size-frequency distribution (SFDs) of DAs to larger sizes. For *B. rodriguezii*, we compared the size-frequency distribution for Playas Doradas (LA and DA), and El Doradillo (DA) vs. Punta Ninfas (LA). For *B. purpuratus* we compared the size-frequency distribution for Playa Elola (DA) vs. Camarones (LA) and Caleta Olivia (LA and DA). We measured the maximum linear dimension of the shell (length) in mm to construct size-frequency distributions. Digital calipers were used for larger mussels, and a microscope micrometer for the smaller ones. A Kolmogorov-Smirnov test was performed to detect overall differences in the distribution of the two samples. Analyses were run with PAST (Hammer et al., 2001).

RESULTS

COMPOSITION OF DEATH ASSEMBLAGES

Death assemblages consist of a mix of intertidal and subtidal species inhabiting soft and hard substrates, caused by the mosaic distribution of rocky, muddy and sandy substrates along the sampling area. Out of the 11,339 specimens from 34 species sampled in the DAs, 86.4% (9,797 specimens, 14 species) inhabit the rocky intertidal belt and were included in the

analysis (Figures 3A–B). From the remaining 13.6%, 3.4% (360 individuals, 10 species) belong to subtidal mollusks and 10.2% correspond to soft-bottom intertidal species (1,152 specimens, 10 species). Therefore, intertidal species accounted for 96.6% of the specimens in DAs.

Figure 3.

COMPOSITIONAL FIDELITY

A total of 37,193 specimens from 15 species were included in the analysis (LA: 27,396; DA: 9,797, Table 3). From the 15 species, ten were found in the LAs, 14 in DAs, and nine species in both assemblage types. One species found in the LAs was thus absent in samples from dead shell accumulations (*Lasaea* sp., see below, Table 3). Conversely, five species detected in DAs were not found in living communities. These dead-only species were one lithophagid mytilid (*Lithophaga patagonica*), two Calyptraeidae (*Crepidula aculeata* and *C. dilatata*), the limpet *Nacella magellanica* and the snail *Tegula patagonica* (Table 3). Large mytilids (*Aulacomya atra, Mytilus edulis chilensis* and *M. edulis platensis*) are scarce in living middle intertidal communities, but present or even abundant in DAs (Table 3).

Table 3.

Table 4.

Diversity was consistently higher in DAs than in LAs (Table 4). Species richness was highly variable in the DAs, and consistently low in the LAs (Figure 4A). Pielou's evenness index was higher in DAs (Figure 4B). Rarefaction of species richness to n = 301 individuals confirms the higher species richness in DAs (Figure 4C)

Figure 4.

The NMDS showed that both latitude (that correlates with biogeographic affinity of localities) - and assemblage type (LA versus DA) discriminate assemblages in a multivariate space (Figures 5A and B). DAs belonging to the Argentine-Magellanic transition zone (localities 4 to 8) cluster together, and are separated from southern Magellanic localities (localities 10, 12 and 14 to 16). When using presence/absence (Figure 5B), the dissimilarity between the two zones is less pronounced compared to the results obtained with abundances (Figure 5A). Living communities show a latitudinal arrangement all along the y-axis of the NMDS plot (with equatorward localities on the top, Figures 5A and B). Although DAs do not show the latitudinal signature within the two biogeographical provinces, they still clearly segregate the transitional and Magellanic Province. PERMANOVA tests confirm this observation: DAs from the transition zone differ significantly from those sampled in the Magellanic Province (F = 5.47; p = 0.009). The composition of LAs did not significantly differ between the transition zone and the Magellanic Province (F = 2.75; p = 0.133). However, this result could be an artifact of a small number of samples, with only two LAs in the Magellanic Province.

Species composition and abundance was significantly different between LAs and DAs for the full matrix (F = 4.38; p = 0.002) and for the samples from the transition zone between provinces (F = 4.50; p = 0.013). Within the Magellanic Province species composition was not significantly different (F = 4.20; p = 0.096), although, this result could be related to the small number of LAs in the Magellanic Province (n = 2). Comparison of species abundances between LAs and DAs within closely spaced localities show for Playas Doradas (placed within the transition zone), overrepresentation of *Tegula patagonica* and underrepresentation of *Lasaea* sp. in DAs (Figure 6). In the case of Camarones/Playa Elola and Caleta Olvia (placed in the Magellanic Province), *Aulacomya atra* and *Nacella magellanica* are overrepresented and in both cases *Lasaea* sp. is underrepresented in DAs (Figure 6). In turn, comparisons within provinces show that *Tegula patagonica* being highly over-represented in DAs in the transition zone while *Lasaea* sp. is underrepresented (Figure 7). Within the 170

Figure 5

Figure 6

Figure 7

Size fidelity

Dead shells of *B. purpuratus* and *B. rodriguezii* are larger than shells from living communities (p < 0.0001 in all five comparisons; Figures 8A–E, Table 5). Size frequency distributions of living mussels show a bimodal or multimodal distribution (frequently with high abundance of specimens smaller than 5 mm), while dead shells show a unimodal distribution with modes at ~ 15-20 mm (Figures 8A–E). In addition, measurements from DAs have consistently lower variation than those taken from living communities because the confidence limits of the coefficients of variation that do not overlap in any of the comparisons (Table 5).

Figure 8.

Table 5.

DISCUSSION

The results of our analyses show a general agreement with previous studies restricted to single habitats, mainly performed in subtidal and soft-bottom environments: 90% of the living species are found dead in the same study area, and 64% of the dead species are found alive in the same area. Summarizing these live/dead indices from various marine environments, Kidwell and Bosence (1991) showed that the live species represented in DAs range from 83%

(intertidal) to 95% (coastal subtidal), while dead species found in living communities range from 33% (coastal subtidal) to 54% (intertidal).

One of the factors affecting the magnitude of live-dead indices observed in our study can be the variability in the proportion of soft and hard substrates among localities and in the detectability of some species in LAs due to their vagile life habits. For instance, Puerto Madryn is dominated by sandy and muddy soft substrates (Table 1), which correlates with the high abundance of *Tegula patagonica* in DAs (that is absent in LAs). Similarly, the muricid Trophon geversianus is normally found in the lower intertidal to subtidal, and in our study it is more abundant in DAs than in LAs. Both species are vagile and are thus able to escape subaerial exposure during low tides, decreasing their probability of being sampled in the LAs. Another species with particular life habits is Lithophaga patagonica, a rock borer that inhabits bottle-shaped bioerosions. This species is present in DAs but absent in living communities, most likely due to a low detectability caused by its cryptic life habit (a similar factor also affects a low detectability of cryptic species in LAs in hard-bottom habitats in coral reefs in Zuschin et al. (2000) and in off-shore reefs dominated by coralline algae and Posidonia oceanica in Albano and Sabelli (2011)). Also, DAs were not sieved and this fact could have added an artificial bias against small specimens, even when sampling design was developed to reduce the drawback. Finally, the possible effect of anthropic impact on communities (Kidwell, 2013) was not considered. These factors should be assessed in future studies.

ORIGIN OF INTERTIDAL DEATH ASSEMBLAGES

Death assemblages, accumulated above the intertidal belt in Patagonian rocky shores, include a mix of shallow subtidal to upper intertidal species, inhabiting hard or soft substrates. However, most specimens belong to species living in the intertidal belt (96.6%), and more than three quarters of them are hard-substrate dwellers (86.4%) (Figure 3). These proportions

suggest that, the supratidal high-water mark is a good area to obtain samples from intertidal species in Patagonian shores and, at the same time, our results indicate that the bathymetric mixing of faunas from intertidal and subtidal is minor, affecting only 3.4% of the specimens. The formation of intertidal DAs can be explained as strandings caused by storms and high tides that move shells and live specimens from sublittoral bottoms to the swash zone and beyond (López et al., 2008). In our case, both storms and high tides can explain the genesis of DAs. We also observed *Mytilus* shells rolling in the beach due to strong winds, suggesting that winds can also aggregate shells into DAs.

SIZE-ASSOCIATED TAPHONOMIC BIASES

Despite the general agreement between LAs and LAs, multivariate analyses show that DAs and LAs are compositionally segregated at all latitudes. Species that are underrepresented in DAs tend to be smaller. The absence of Lasaea sp. in DAs is one of the most striking examples. Lasaea sp. represents 7% of the abundance of the pooled samples from living communities, reaching as much as 21.5% in Puerto Madryn (Table 3). However, this species is completely absent from all DAs (Table 3). It is likely that individuals from this species could have been destroyed or transported away because they are 3 mm long and very thin and live attached to mussels by byssus (Forcelli, 2000, and observations of the authors). Transportation by water is possible because minute valves are washed away during high tides, kept in suspension and finally deposited in deeper, calmer bottoms (Valentine et al., 2006; Fürsich, 1990; and observations of the authors). The strong winds in Patagonia are also able to remove these shells, and cause the small sized mussels (< 5 mm) to be transported by the wind. This interference is consistent with the observation that body size is one of the main factors explaining the absence of living species in the fossil record (Valentine et al., 2006). All size-frequency comparisons for *Brachidontes* species show that DAs are enriched in shells larger than 7 mm with respect to LAs (Figure 8A–E), whereas juvenile individuals are present in all size-frequency distributions in LAs (Figure 8). Also, histograms indicate that the

rather complicated bimodal to multimodal distribution in LAs becomes simplified in unimodal (Figure 8A–D) or platykurtic distributions in DAs (Figure 8E). Therefore, the main bias between the LAs and DAs is probably size-related. All samples come from communities living in the middle intertidal, and are thus subject to high water flows during high tides, which could be regulating the transport process towards the upper intertidal, at least for the small sized shells. In the absence of burial in rocky intertidal habitats and under reduced burial rates in mixed-bottom intertidal environments, juvenile specimens are also more likely destroyed than large-sized and thicker adults (Tomašových, 2004).

The interpretation of a size-related bias is also supported by the observation that *Brachidontes* species are less frequent in DAs than in LAs. Mean per-sample percentages show that these small-sized mytilids represent almost 93% of the LAs and only 44% of the DAs. This underrepresentation of small-sized mytilids in DAs is consistent within each biogeographic unit. Therefore, the decrease in dominance of *Brachidontes* species could be explained by the effect of destruction and transportation out of the habitat. Also, this decrease could alternatively be explained by the effect of time coarsening: DAs may combine the abundance structure of communities that changed dominant species through time (Tomašových and Kidwell, 2010). Methodological differences in sampling collection between LAs and DAs might have partly contributed to the differences.

EFFECTS OF TEMPORAL AND SPATIAL AVERAGING ON SPECIES DIVERSITY

The DAs studied here are inferred to be time-averaged, i.e., shells were added many times during at least decades and most probably thousands of years (Kidwell and Tomašových, 2013), although the effective scale of time averaging in the studied habitats remains unknown. A consequence of this process is the mixing of several generations in the same environment (Fürsich and Aberhan, 1990; Tomašových and Kidwell, 2009; Kidwell and Tomašových, 2013). Higher levels of species richness and evenness coincide with the prediction of

increased diversity in DAs (Fürsich and Aberhan, 1990; Tomašových and Kidwell, 2010; Kidwell and Tomašových, 2013). The reduction in dominance and enrichment in rare species has also been identified as a likely result of time averaging because as the time during which a DA receives hard parts increases, the probability of incorporation of new species by immigration of nearby locations and/or the occurrences of changes in habitat conditions (e.g., varying proportions of soft- and hard-bottom patches in intertidal environments) also increases (Tomašových and Kidwell, 2010; Kidwell and Tomašových, 2013), although similar effects can be produced by spatial mixing.

Calyptraeid species, true limpets and large mytilids, that are absent or scarce in LAs but present and in some cases abundant in DAs, are typical of lower intertidal to subtidal environments and rarely occur alive in middle intertidal rocky habitats (Olivier et al., 1966b; Zaixso and Pastor, 1977; Bertness et al., 2006; Silliman et al., 2011). Similarly, the mismatch in abundance of the snail *Tegula patagonica*, that reaches high abundances in DAs (1885 individuals in Puerto Madryn) but does not occur in LAs (and is considered a rare inhabitant of the mid-intertidal rocky habitat -Sánchez and Zaixso, 1995; Wieter et al., 2012), gives another example of a species that is rare in the LAs and becomes common in the DAs. All these species that are absent or rare in LAs, but present and sometimes abundant in DAs correspond to rare inhabitants of the middle intertidal that were incorporated in disproportionately higher abundances due to the temporal coarsening or spatial mixing of these samples.

SPATIAL VARIATION IN COMPOSITION AT BIOGEOGRAPHIC SCALES

The species composition and abundances of LAs vary in a latitudinal gradient (Figure 5), following a poleward decrease in seawater temperature. On one hand, this latitudinal pattern is not present among DAs within the same biogeographic unit. On the other hand, compositional differences between the transitional zone and Magellanic provinces are still

clearly captured by DAs. The latitudinal gradient captured by LAs coincides with a gradual replacement of *Brachidontes rodriguezii* (species characteristic of the Argentine Biogeographic Province) by *B. purpuratus* (typical of the Magellanic Biogeographic Province) (Figure 9). In contrast, DAs in the transition zone are characterized by a relatively stable percentage of both *Brachidontes* species (sites 5 to 8), with the exception of Playas Doradas that has a small proportion of *B. purpuratus* (Figure 9). Mussel beds placed in the transition zone show a high heterogeneity (patchy distribution) with respect to the proportion of both *Brachidontes* species (Arribas et al., 2013), a pattern that does not help in explaining the lack of gradual replacement in DAs. However, the increase in *Brachidontes rodriguezii* from the Magellanic towards the transition zones contributes to the between-province separation in the DAs. The temporal changes in community structures of DAs at the contact between the Magellanic and Argentine Biogeographic Provinces likely produced a mix of shells from both provinces with variable proportions, but did not lead to the homogenization of the two biogeographic zones.

Boretto et al. (2013) detected temporal changes in the molluscan species composition during the Quaternary along the Puerto Lobos coastal area. These authors compared the Pleistocene, Holocene and Modern fauna. The presence of *Tegula atra* and *Mactra patagonica* in the Pleistocene sediments indicated a greater proportion of taxa typical from the cold-water Magellanic Province, however during the Holocene the most typical element in the area was *Glycymeris longior*, characteristic of the Argentinean Province. During the late Holocene, this study area also recorded a faunal shift in which species belonging to the Magellanic Province displaced the fauna of the Argentinean Province to the north, probably in coincidence with the Little Ice Age.

The presence of *B. rodriguezii* in the same region can be traced back to the Miocene Formations Paraná and Madryn of Argentina and Uruguay (del Río and Martínez, 1998). *B.*

purpuratus, in turn, seems to be a more recent immigrant from the south eastern Pacific (during Plio-Pleistocene transition) based on genetic, morphological and geological evidence (Trovant et al., 2013; 2015). Trovant et al. (2015) suggest that the distribution of *B. purpuratus* is related to latitudinal gradients in the SST – occurring at median SST below 13°-, although its expansion northward is probably blocked by the high densities of *B. rodriguezii*. In this way, climatic fluctuations in the last few hundreds or thousands or years may have pushed the transition zone northward or southward and then blurred the pattern of gradual replacement between species in the DAs. Possible temporal changes in the distribution of these species may also help explain the low association in rank abundances between adjacent localities observed in this study (Figure 6, upper part). This observation is reflected in the statistical significant differences between LAs and DAs in the transition zone (see PERMANOVA in Results).

This result coincides with those of Tomašových and Kidwell (2009) where the variability in species composition among DAs is lower than among LAs both for abundance and presence/absence data. It is possible that the time involved in the formation of DAs caused mixing in the species composition of the communities due to ecological succession, immigration, extinction, or due to stochastic and environmental changes (Fürsich and Aberhan, 1990; Bennington, 2003; Tomašových and Kidwell, 2009), leading to the lack of latitudinal gradient in composition of DAs within provinces. However, the possible homogenization generated by those mechanisms was not sufficient to reduce differences between the Argentine-Magellanic transition zone and the Magellanic Province.

Figure 9.

CONCLUSIONS

 Death assemblages from intertidal rocky shores in the Atlantic coast of Patagonia show a moderate agreement in species composition and abundances between DAs sampled in mixed-bottom intertidal environments and living mussel communities inhabiting nondepositional rocky bottoms in the same region. Even when spatial variation within the two provinces seems to be homogenized (probably due to the averaging of successive communities affected by fluctuating temporal changes in the biota), differences between the transition Argentine-Magellanic zone and the Magellanic Province are clearly detected by DAs. Our results reinforce the usefulness of death assemblages as proxies of living communities at regional spatial scale (Kidwell and Tomašových, 2013) and justify the reliability of studies based on them (e.g., Gordillo and Archuby, 2012, 2014; Martinelli et al., 2013).

2. Death assemblages have higher diversity than living assemblages, probably due to their time-averaged nature (and spatial mixing).

3. The main taphonomic distortion between LAs and DAs is the smaller abundance of small-sized species and the underrepresentation of smallest specimens (less than 8 mm). This bias is probably caused by differential transport and destruction by waves, currents and wind. Another source of live-dead mismatch seems to be related to reduced detectability of vagile epifaunal species and boring species in LAs.

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Figure captions

FIGURE 1—Map of the study area with the sampled localities. Triangles and circles represent living assemblages or LA and death assemblages or DA respectively. For more details see Table 1.

FIGURE 2—A) View of a mussel bed in Bahía Camarones (CA-L). B) Detail of a mussel bed. C) Panoramic view of high tide line accumulation of dead shells. D) Sampling of death assemblages.

FIGURE 3—Pie charts with details of the distribution of abundance and species richness of death assemblages for data pooled across samples. A) Absolute abundance. B) Species richness. Plots on the left side of the figure differentiate between intertidal and subtidal species while on the right side indicate distribution of species and specimens between hard and soft substrates of the intertidal belt.

FIGURE 4—Boxplots show that diversity indices are higher in DAs than LAs. A) Species richness (S). B) Evenness index (J). C) Species richness estimated by rarefaction technique. Boxes range from first to third quartile. Whiskers represent minimum and maximum values. LA: life assemblages. DA: death assemblages.

FIGURE 5— Bidimentional NMDS plots show segregation between two provinces for both living and death assemblages but also a consistent segregation between living and death assemblages. A) Square root transformation after standardization to percentages. B) Presence/absence data. Axes were rotated to place samples in a latitudinal order. Triangles: living assemblages. Circles: death assemblages. Filled symbols: Argentine-Magellanic transition zone. Empty symbols: Magellanic Biogeographic Province. **FIGURE 6**— Bar-plots with species-level composition of the living and death assemblages. Dissimilarities between LAs and DAs are reflected in differences in rank order and abundance of the taxa.

FIGURE 7— Bar-plots with species-level composition of the living and death assemblages for data pooled across samples per biogeographic region. Dissimilarities between LAs and DAs are reflected in differences in rank order and abundance of the taxa.

FIGURE 8—Size-frequency distributions of death assemblages are characterized by higher proportions of large-sized specimens with respect to specimens from living communities for *Brachidontes rodriguezii* and *B. purpuratus* in different localities. A) *Brachidontes rodriguezii*, Playas Doradas (LA vs. DA). B) *B. rodriguezii*, El Doradillo (DA) vs. Punta Ninfas (LA). C) *B. purpuratus*, El Doradillo (DA) vs. Punta Ninfas (LA). D) *B. purpuratus*, Playa Elola (DA) vs. Camarones (LA). E) *B. purpuratus*, Caleta Olivia (LA vs. DA). Black: specimens from death assemblages. Grey: specimens from life assemblages.

FIGURE 9—Proportions of *Brachidontes rodriguezii* (light grey) and *B. purpuratus* (dark grey) across the studied area show that both living and death assemblages capture the latitudinal gradients in their abundance. Circles: death assemblages); triangles: living assemblages.

Table captions

TABLE 1—Detail of the localities included in this study.

TABLE 2— Summary of species found in the death assemblages. Zonation (subtidal, intertidal), substrate type (H: hard, S: soft), life habit (Ep: epifaunal, In: infaunal) and species documented for intertidal rocky-bottom substrates (DRI*).

TABLE 3— Database with species counts per sample.

TABLE 4—Information of samples of living and death assemblages used in the analysis.

TABLE 5—Descriptive statistics of the sizes of *Brachidontes rodriguezii* y *B. purpuratus*, separated by locality and type of sample.


















Number and Name of Localities	Abbreviations	Southern Latitude	Sampling Date	Sample type	Substrate characteristics	Biogeographic region	Sea water temperature (°C)
Las Grutas (1)	LG_L	40° 50' 02"	Jan 2004, 08	Live	Friable epiclastic sedimentites, marine deposits (Tertiary)	Arg-Mag. Provinces transition zone	10.8-20.1
Punta Mejillón (2)	PM_L	41° 00´ 51"	Jan 2004, 08	Live	Friable epiclastic sedimentites, marine deposits (Tertiary)	Arg-Mag. Provinces transition zone	10.1-18.9
Playas Doradas (3)	PD_L	41° 36' 41"	Jan 2004, 08	Live	Limestone, calcareous sandstone and coquina (Paleocene)	Arg-Mag. Provinces transition zone	10.1-18.9
Playas Doradas (4)	PD_D	41° 36' 41"	April 2010	Dead	Limestone, calcareous sandstone and coquina	Arg-Mag. Provinces transition zone	10.1-18.9
Puerto Lobos (5)	PL_D	41° 59' 54"	April 2010	Dead	Hard substrates of conglomerate and tuff. Sectors with fine sand beaches.	Arg-Mag. Provinces transition zone	9.7 - 17.9
Puerto Pirámides (6)	PP_D	42° 34' 43"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches. Cliffs.	Arg-Mag. Provinces transition zone	9.6 - 16.9
El Doradillo (7)	ED_D	42°39′27"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches.	Arg-Mag. Provinces transition zone	9.7 - 16.9
Puerto Madryn (8)	PM_D	42° 46' 56"	April 2010	Dead	Bottoms with sand and mud, some hard substrates. Sandy beaches.	Arg-Mag. Provinces transition zone	9.8 - 16.9
Punta Ninfas (9)	PN_L	42° 58´ 02"	Jan 2004, 06	Live	Limestone. Marine deposits	Arg-Mag. Provinces transition zone	9.4 - 16.8
Playa Elola (10)	PE_D	44°50′17"	April 2010	Dead	Beaches with sandy gravel, hard substrates with basalt; some sandy and muddy.	Magellanic Province	6.4 - 16.1
Camarones (11)	CA_L	44° 54´ 34"	Jan 2004	Live	Consolidate limestone. Shores of basaltic rock.	Magellanic Province	7.3 -16.2
Rada Tilly (12)	RT_D	45° 56' 37"	April 2010	Dead	Limestone. Marine deposits	Magellanic Province	6.5 - 15.5
Caleta Olivia (13)	CO_L	46° 20´ 06"	Jan 2004	Live	Limestone. Marine deposits	Magellanic Province	5.2 - 14
Caleta Olivia (14)	CO_D	46° 29´ 29"	April 2010	Dead	Beaches with coarse sand and pebbles. Some rockgrounds in the midlittoral area.	Magellanic Province	5.2 - 14
Cabo Blanco (15)	CB_D	47°12' 09"	April 2010	Dead	Beaches with gravel and pebbles. Areas with hardgrounds with tidal forests of macroalgae.	Magellanic Province	4.2 - 12.9
Puerto Deseado (16)	PuD_D	47°45' 24"	April 2010	Dead	Gravel beaches, some cliffs with sandy beaches, and sectors with hardgrounds.	Magellanic Province	4.9 - 13.5

				Life	
Family	Species	Zonation	Substrate	Habit	DRI *
Gastropoda	^				
Nacellidae	Nacella (P.) magellanica (Gmelin)	Intertidal-subtidal	Н	Ep	*
Nacellidae	Nacella (N.) mytilina (Helbling)	Subtidal	Н	Ep	
Fissurellidae	Fissurella spp.	Intertidal-subtidal	Н	Ep	*
Trochidae	Tegula (A.) patagonica d'Orbigny	Intertidal-subtidal	Н	Ep	*
Calyptraeidae	Crepidula aculeata (Gmelin)	Intertidal-subtidal	Н	Ep	*
Calyptraeidae	Crepidula dilatata Lamarck	Intertidal-subtidal	Н	Ep	*
Naticidae	Notocochlis isabelleana (d'Orbigny)	Intertidal-subtidal	S	In	
Epitoniidae	Epitonium georgettina (Kiener)	Intertidal-subtidal	S	Ep	
Muricidae	Trophon geversianus (Pallas)	Intertidal-subtidal	H-S	Ep	*
Buccinidae	Buccinanops globulosum (Kiener)	Intertidal-subtidal	S	Ep	
Buccinidae	Buccinanops sp.	Intertidal-subtidal	S	Ep	
Buccinulidae	Pareuthria plumbea (Philippi)	Intertidal-subtidal	Н	Ep	*
Olividae	Olivancillaria carcellesi Klappenbach	Intertidal-subtidal	S	Ep	
Olivellidae	Olivella tehuelcha (Duclos)	Subtidal	S	Ep	
Volutidae	Odontocymbiola magellanica (Gmelin)	Subtidal	S	Ep	
Siphonariidae	Siphonaria lessonii (Blainville)	Intertidal	Н	Ep	*
Bivalvia					
Pectinidae	Aequipecten tehuelchus (d'Orbigny)	Subtidal	Н	Ep	
Mytilidae	Lithophaga patagonica (d'Orbigny)	Intertidal-subtidal	Н	Ep	*
Mytilidae	Aulacomya atra (Molina)	Intertidal-subtidal	Н	Ep	*
Mytilidae	Brachidontes purpuratus (Lamarck)	Intertidal-subtidal	Н	Ep	*
Mytilidae	Brachidontes rodriguezi d'Orbigny	Intertidal-subtidal	Н	Ep	*
Mytilidae	Mytilus edulis chilensis Hupé	Intertidal-subtidal	Н	Ep	*
Mytilidae	Mytilus edulis platensis d'Orbigny	Intertidal-subtidal	Н	Ep	*

Solenidae	Ensis macha (Molina)	Intertidal-subtidal	S	In
Mactridae	Mactra isabelleana d'Orbigny	Subtidal	S	In
Tellinidae	Macoma sp.	Subtidal	S	In
Tellinidae	Tellina petitiana d'Orbigny	Subtidal	S	In
Veneridae	Amiantis purpurata (Lamarck)	Intertidal-Subtidal	S	In
Veneridae	Retrotapes exalbidus (Dillwyn)	Subtidal	S	In
Veneridae	Tawera gayi (Hupé)	Subtidal	S	In
Veneridae	Venus antiqua King & Broderip	Subtidal	S	In
Petricolidae	Petricola (P.) pholadiformis Lamarck	Intertidal-subtidal	S	In
Semelidae	Semele proficua (Pulteney)	Intertidal-subtidal	S	In
Hiatellidae	Panopea abbreviata Valenciennes	Subtidal	S	In

References: Charo et al., 2013, 2014; Rechimont et al., 2013; Scarabino et al., 2006; Gonzalez et al., 2011; Rosemberg, 2009; Marquez and Van der Molen, 2011; Pastorino, 1994; Gordillo, 2006; Bertness et al., 2006; Cuevas et al., 2006; Adami et al., 2004, 2008, 2013; Signorelli and Pastorino, 2011; Signorelli et al., 2012; Lomovasky et al., 2002, 2005; Teso et al., 2011; Wieters et al., 2012; Bigatti et al., 2008; Aldea and Troncoso, 2010; Morsan et al., 2007

Sample number	Locality	Abbreviation	Sample type	N (Individuals number)	Species Richness (S)	Rarefaction S(n=301)	Equitability J
1	Las Grutas	LG_L	Live	3903	4	2,80	0.16
2	Punta Mejillón	PM_L	Live	5573	6	5,00	0.36
3	Playas Doradas	PD_L	Live	3564	6	4,27	0.43
4	Playas Doradas	PD_D	Dead	634	11	10,65	0.57
5	Puerto Lobos	PL_D	Dead	1778	11	10,11	0.72
6	Puerto Pirámides	PP_D	Dead	1094	11	8,86	0.58
7	El Doradillo	ED_D	Dead	913	10	9,32	0.75
8	Puerto Madryn	PM_D	Dead	3013	11	8,41	0.53
9	Punta Ninfas	PN_L	Live	2772	7	3,88	0.27
10	Playa Elola	PE_D	Dead	401	8	8,00	0.74
11	Camarones	CA_L	Live	6255	4	2,89	0.40
12	Rada Tilly	RT_D	Dead	341	8	7,87	0.55
13	Caleta Olivia	CO_L	Live	5329	7	3,08	0.07
14	Caleta Olivia	CO_D	Dead	602	7	6,86	0.70
15	Cabo Blanco	CB_D	Dead	295	8	8,00	0.55
16	Puerto Deseado	PuD_D	Dead	726	6	5,84	0.67

Species	LG_L	PM_L	PD_L	PD_D	PL_D	PP_D	ED_D	PM_D	PN_L	PE_D	CA_L	RT_D	CO_L	CO_D	CB_D	PuD_D
Aulacomya atra (Molina)	0	0	0	18	68	3	215	38	0	65	1	23	1	142	9	110
Brachidontes purpuratus (Lamarck)	196	373	2436	2	885	543	103	438	2358	192	4873	38	5187	227	68	384
Brachidontes rodriguezii d'Orbigny	3694	4617	982	69	179	231	25	244	314	0	0	0	0	0	0	0
Crepidula aculeata (Gmelin)	0	0	0	4	1	0	0	1	0	0	0	0	0	0	0	0
Crepidula dilatata Lamarck	0	0	0	17	15	1	41	71	0	12	0	28	0	8	13	0
Fissurella sp.	0	0	0	26	50	5	13	1	1	0	0	0	0	0	1	0
Lithophaga patagonica (d'Orbigny)	0	0	0	0	0	1	1	3	0	0	0	0	0	0	0	0
Mytilus edulis chilensis Hupé	0	0	0	0	0	7	0	0	1	5	0	229	1	7	184	184
Mytilus edulis platensis d'Orbigny	5	106	4	10	93	25	17	30	0	0	0	0	0	0	0	0
Nacella (P.) magellanica (Gmelin)	0	0	0	11	67	0	0	0	0	48	0	9	0	182	10	38
Pareuthria plumbea (Philippi)	0	0	0	0	0	0	0	0	0	8	0	0	1	3	3	6
Siphonaria lessonii (Blainville)	8	52	116	21	145	191	174	180	1	53	37	2	112	0	0	0
Tegula patagonica d'Orbigny	0	0	0	406	129	69	307	1885	0	0	0	1	0	0	0	0
Trophon geversianus (Pallas)	0	1	1	50	146	18	17	122	7	18	0	11	3	33	7	4
Lasaea sp.	0	424	25	0	0	0	0	0	90	0	1344	0	24	0	0	0

Brachidonte	s rodriguezii					
	PD_D	Lower conf.	Upper conf.	PD_L	Lower conf.	Upper conf.
Ν	65	I		58	1	
Mean	14.02	13.33	14.67	9.27	7.88	10.60
Variance	7.75	5.55	9.99	28.24	22.95	34.23
Median	14.02	13.38	14.58	8.05	3.50	10.12
25 percentil	12.19	11.15	13.72	4.60	3.28	6.08
75 percentil	15.77	14.26	16.82	14.05	12.32	15.41
Coeff. var	19.86	17.25	22.94	57.32	48.61	66.68
	ED/PN_D	Lower conf.	Upper conf.	ED/PN_L	Lower conf.	Upper conf.
N	28			39		
Mean	18.42	16.73	20.01	10.23	8.75	11.72
Variance	20.32	10.50	30.16	23.62	17.67	30.55
Median	17.87	15.55	20.69	8.36	3.56	9.68
25 percentil	14.47	12.10	14.81	6.23	5.01	7.58
75 percentil	21.11	17.86	23.99	14.57	12.86	17.96
Coeff. var	24.47	19.95	30.60	47.49	40.51	55.44
Brachidonte	s purpuratus					
	ED/PN D	Lower conf	Upper conf	ED/PN L	Lower conf	Upper conf
N	77		orrection.	114		opper com
Mean	15.20	14.51	15.83	11.31	10.29	12.35
Variance	8.65	4.99	11.59	31.84	25.95	37.98
Median	14.91	14.12	15.65	11.55	9.79	12.94
25 percentil	13.09	12.19	13.94	6.93	4.95	8.86
75 percentil	16.64	14.76	17.35	15.50	13.36	16.73
Coeff. var	19.36	16.02	22.76	49.88	43.03	56.77
NT.	PE/C_D	Lower conf.	Upper conf.	PE/C_L	Lower conf.	Upper conf.
N	250	16.22	17.10	230	(51	0.00
Variance	16.73	16.33	17.12	1.32	0.51	8.08
Madian	9.91	/./0	11.88	5 26	31.51	43.09
25 percentil	14.52	14.03	17.22	2.20	2.03	2.60
75 percentil	18.65	18.05	19.20	10.74	8.45	12.80
Coeff var	18.82	16.05	20.76	84.48	78.28	90.84
	10.02	10177	20.70	0.1.10	, 0.20	20101
	CO_D	Lower conf.	Upper conf.	CO_L	Lower conf.	Upper conf.
N	150			170		
Mean	20.39	19.62	21.15	7.00	5.82	8.11
Variance	23.01	18.69	27.32	58.36	45.22	72.10
Median	20.35	19.09	21.39	2.91	1.62	3.39
25 percentil	16.71	15.66	17.62	1.62	1.49	1.90
75 percentil	24.34	23.71	25.51	12.56	9.10	18.83
Coeff. var	23.53	21.18	26.00	109.11	99.16	119.31



Julieta Martinelli <julieta.martinelli@mq.edu.au>

Fwd: 14-054R1 Decision Letter

Fernando Archuby <farchuby@unrn.edu.ar> To: Julieta Martinelli <julieta.martinelli@mq.edu.au> Thu, Feb 19, 2015 at 2:40 AM

-----Forwarded message ------From: <palaios.editor@gmail.com> Date: 2014-12-29 19:41 GMT-03:00 Subject: 14-054R1 Decision Letter To: farchuby@unrn.edu.ar

Dear Dr. Archuby:

I am pleased to inform you that you may consider your manuscript "REGIONAL-SCALE COMPOSITIONAL AND SIZE FIDELITY OF ROCKY INTERTIDAL COMMUNITIES FROM THE PATAGONIAN ATLANTIC COAST" accepted for publication in PALAIOS, pending your revisions. This will be an excellent contribution to the journal.

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Please see reviewer comments below. Associate Editor (Comments for the Authors):

I think the authors did a very good job in revising the paper and addressing the comments of reviewers and my comments. The figures are also greatly improved. The manuscript now clarifies the role of several factors in

affecting fidelity in their study system (body size effect, mechanical mixing, detectability), well explains the sampling design, and the emphasis on regional scales and on the preservation of biogeographic gradients as summarized by Figure 5 should be revealing and consequential. I have added several tracked-changes in the text to improve the structure of text and its readability, and with few final comments below, I suggest that that paper can be accepted pending these minor comments.

1. In Introduction, it can be useful to add some references from terrestrial live-dead studies when authors talk about live-dead mismatch in general. It should be useful to replace "assemblages" by shortcuts LAs and DAs in most of the text - I did this in some parts. Also, I would replace "equitability" with "evenness". Starting sentences with "This * * is consistent...." without the subject, i.e., without specifying what is "this" is sometimes difficult to follow and should be fixed - I have suggested some changes in the text.

Explain the selection of pairs of LAs and DAs in the last paragraph of methods about SFD analyses - see my yellow highlight - e.g., these pairs correspond to regions with ?relatively closely located LAs and DAs
When describing differences between DAs and LAs in "Compositional fidelity" in Results, when referring to

figures 6 and 7, add actual (but short) statements what species are over (or underrepresented) - see my addition at the end of the paragraph in Results.

4. Into Abstract and Conclusions, I have added "biases related to low detectability of boring and vagile epifaunal species in living assemblages" - this issue with differential detectability seems to be one part of finding that seems to be implied in Discussion, I think the reasoning makes sense, and this should be highlighted as another source of live-dead mismatch (a similar issue for hard-bottom habitats was highlighted by Zuschin in one of his papers). I think over-representation of Tegula applies to this.

5. Final tweaks for figure and table captions - it will be useful to add simple statements what do the plots/tables actually imply - see my suggestions: e.g., FIGURE 9-Proportions of Brachidontes rodriguezii (light grey) and B. purpuratus (dark grey) across the studied area *show that both living and death assemblages capture the latitudinal gradients in their abundance.*

6. In Figure 5, even when the symbols for two provinces are in the caption, I would add a more or less horizontal (or zigzag) dashed line showing the separation of the samples belonging to two zones (adding "Transition zone" in the upper quadrant and "Magellanic zone" in the lower part) thus quickly showing biogeographic separation.

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