GLOBAL DIVERSITY PATTERNS IN MARINE FOULING COMMUNITIES

Exploring latitudinal effects and the local-regional richness relationship

Dissertation
zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultät
der Christian-Albrechts-Universität zu Kiel

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Der Dekan

Para a minha mulher Valentyna

e para o meu filho Diniz

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Summary

Fouling communities are distributed worldwide, particularly in shallow and exposed marine systems. Due to their fast growth and their capacity to settle on artificial surfaces, these assemblages represent a suitable study system for ecologists and are therefore often used to investigate ecological models. Investigating broad scale ecological models has been of key interest since the time of the famous naturalist Charles Darwin. Two examples of well recognized macro-ecological patterns are i) the ‘latitudinal gradient of species richness’ and ii) the ‘relationship between local and regional diversity’. The first is the oldest paradigm about a large-scale ecological pattern and simply states that the tropical regions are richer in species than temperate and polar regions at higher latitudes. However, when exploring global diversity patterns, it is essential to comprehend not only the importance of differences in spatial scale for the observed patterns, but also how diversity at one scale may relate to diversity at a different scale. Indeed, several studies have shown that the number of species within small localities may increase either linearly or asymptotically with regional species richness (relationship between local and regional diversity).

Exploring global diversity patterns still constitutes an important challenge for ecologists because it reflects the need to determine the current status of biodiversity. With the knowledge of today’s biodiversity, we can predict its future status and, as a consequence, be able to provide new answers to its probable response to phenomena such as climate change. In the present work, I investigate global diversity patterns in marine fouling communities, mainly by examining the previously mentioned macro-ecological patterns, i.e. the latitudinal gradient of species richness and the relationship between local and regional diversity. Previous studies investigating the local-regional diversity relationship have often assessed the number of species in a region by consulting available species lists. However, regional species pools based on such inventories may include species not susceptible to recruit into the community considered because they are restricted to different habitats and seasons. With the purpose of dealing with these difficulties, a few investigations have estimated regional richness based on local samples but confirmed a strong bias in relation to sampling effort. In order to optimize the quality of regional richness estimations, the current study develops a new statistical tool for estimating regional richness based on a limited number of replicates. Using three data-sets with a large number of replicates from different temperate shallow water habitats, I compare common richness estimators against the asymptote of the species accumulation curve, which was used as a reference for true regional richness. Subsequently and more importantly, the mis-estimation was quantified as a function of sampling effort.

To complete this work, the relationship between local and regional diversity was expanded by integrating two categories of diversity (taxonomic and functional) and different successional stages at two different scales: European and global. At the European scale, the shape of the pattern was compared for different methods in assessing regional richness: species colonizing during a given period (transient regional richness) versus species colonizing during any phase of the experiment (total regional richness). At the global scale, I further examine whether the diversity of local communities is affected by parameters other than regional richness, such as number of functional groups or availability of resources.

The results of this investigation support a clear influence of latitude on local species richness in marine fouling communities. In Chapter I, I show that tropical regions hold more marine fouling species when compared to areas at higher latitudes. In what concerns the regional richness assessment, I conclude that regional richness can be estimated based on a limited number of samples and that the quality of the estimation increases with sample effort. Moreover, the strength of the inevitable mis-estimation can be quantified (Chapter II). In addition, at the European scale (Chapter III), it was found that the shape of the relationship between local and regional diversity is sensitive to successional stage, the way regional richness is estimated and the dimension of diversity considered. The relevant regional richness, i.e. the regionally available colonizers, seems to vary in time and is larger when pooling all sampling events. As a consequence, the relationship between local and regional diversity is also influenced by the method in which regional richness is estimated. At a global scale (Chapter IV), the relationship between local and regional diversity in fouling assemblages is also affected by the succession process, if either taxonomic or functional diversity are considered. Local taxonomic diversity exhibits saturation at early stages of succession while saturation of local functional richness occurs later. In addition, functional groups were reported as the most influential predictor for local species richness.

Zusammenfassung

Aufwuchsgemeinschaften sind weltweit verbreitet und kommen vor allem im Flachwasser exponierter mariner Standorte vor. Aufgrund ihres schnellen Wachstums und ihrer Fähigkeit künstliche Oberflächen zu besiedeln stellen diese Gemeinschaften ein geeignetes Studienobjekt für Ökologen dar und werden daher häufig bei der Untersuchung ökologischer Modelle eingesetzt. Zwei bekannte Beispiele makro-ökologischer Modelle sind i) der Latitudinalgradient des Artenreichtums und ii) das Verhältnis zwischen lokaler und regionaler Diversität. Bei dem erstgenannten handelt es sich um das älteste, schon seit Darwin's Zeiten diskutierte, Paradigma über umfassende ökologische Muster dessen einfache Aussage lautet, dass tropische Regionen artenreicher sind als gemäßigte oder polare Regionen. Bei der Erforschung globaler Diversitätsmodelle ist es jedoch essentiell nicht nur das Maß der Unterschiede in räumlichen Einheiten für das beobachtete Muster zu verstehen, sondern auch in wie weit eine Diversitätskala in Relation zu einer anderen Diversitätskala steht. In der Tat haben mehrere Studien gezeigt, dass die Anzahl der Arten innerhalb kleiner Gebiete meist entweder linear oder asymptotisch mit der regionalen Artenzahl (Beziehung zwischen lokaler und regionaler Diversität) ansteigt.

Die Erforschung globaler Diversitätsmuster stellt immer noch eine wichtige Herausforderung für Ökologen dar, weil sie die Notwenigkeit reflektiert den derzeitigen Stand der Biodiversität zu bestimmen. Mit dem Wissen über die heutige Biodiversität ist es möglich ihren zukünftigen Status zu prognostizieren, und in der Folge daraus sind wir in der Lage, neue Aussagen über etwaige Reaktionen auf Phänomene wie den Klimawandel machen zu können. In der vorliegenden Arbeit habe ich globale Diversitätsmuster in marinen Aufwuchsgemeinschaften analysiert, in erster Linie durch Untersuchung der bereits angesprochenen makro-ökologischen Muster, d.h. anhand des Latitudinalgradienten der Artenvielfalt und der Beziehung zwischen lokaler und regionaler Diversität. In vorausgegangenen Studien des Verhältnisses zwischen lokaler und regionaler Diversität wurde die Artenzahl innerhalb einer Region meist durch Heranziehen bereits vorhandener Artenlisten bestimmt. Auf Basis solcher Listen erstellte regionale Artengemeinschaften können jedoch Arten enthalten, die aufgrund ihrer Beschränkung auf bestimmte Habitate oder Jahreszeiten nicht in den untersuchten Gemeinschaften anzutreffen sind. Um diesen Schwierigkeiten Rechung zu tragen wurde in anderen wenigen Untersuchungen die regionale Artenvielfalt aus lokalen Probennahmen bestimmt, wobei eine starke Abhängigkeit vom Probenumfang festgestellt wurde. Um die Qualität bei der Bestimmung der regionalen Artenvielfalt zu optimieren, entwickelt die vorliegende Arbeit eine neue statistische Methode zur Bestimmung der regionalen Artenvielfalt auf Basis einer begrenzten Replikatzahl. Unter Verwendung von drei Datensätzen mit einer hohen Anzahl an Replikaten aus unterschiedlichen

Flachwasserhabitaten der gemäßigten Breiten wurden in dieser Arbeit allgemein gebräuchliche Berechnungsmethoden zur Kalkulation der Artenvielfalt gegen die Asymptote der Arten-Akkumulationskurve getestet, welche als Referenzwert für die real vorhandene regionale Artenvielfalt diente. Anschließend und in Konsequenz daraus wurde die Fehleinschätzung als Funktion des Probenumfangs quantifiziert.

Um die Untersuchung zu vervollständigen wurde das Verhältnis zwischen lokaler und regionaler Diversität durch die Integration von zwei weiteren Diversitätskategorien (taxonomische und funktionale Diversität) sowie um verschiedene aufeinanderfolgende Sukzessionsstadien in zwei räumlichen Skalen erweitert: europäisch und global. Auf europäischer Ebene (Kapitel III) wurde die Form des Musters verschiedener Berechnungsmethoden der regionalen Artenvielfalt verglichen: Arten, die während eines bestimmten Zeitraums siedeln (vorübergehender, regionaler Artenreichtum) gegenüber Arten, die während jeglicher Phase des Versuchs siedeln (gesamter, regionaler Artenreichtum). Auf globaler Ebene wurde untersucht, ob die Diversität lokaler Gemeinschaften durch andere Parameter als durch regionale Artenvielfalt beeinflusst wird, wie etwa die Anzahl der funktionalen Gruppen oder die Ressourcenverfügbarkeit.

Die Ergebnisse dieser Arbeit weisen darauf hin, dass es einen deutlichen Einfluss des Breitengrades auf die lokale Artenvielfalt mariner Aufwuchsgemeinschaften gibt. In Kapitel I wird gezeigt, dass in Aufwuchsgemeinschaften tropischer Regionen mehr Arten vorkommen als in Gebieten der höheren Breitengrade. Bezüglich der Berechnung der regionalen Artenvielfalt komme ich zu dem Schluss, dass es möglich ist diese anhand einer begrenzten Anzahl von Proben zu bestimmen, wobei die Qualität der Aussage mit dem Probenumfang steigt. Des Weiteren kann die Stärke der unvermeidlichen Fehleinschätzung quantifiziert werden (Kapitel II). Außerdem zeigte sich, dass die Form der Beziehung zwischen lokaler und regionaler Diversität unter dem Einfluss des Sukzessionsstadiums, der Berechnungsmethode der regionalen Artenvielfalt sowie der betrachteten Diversitätkategorie steht. Die relevante regionale Artenvielfalt, (d.h. die regional vorhandenen Besiedler), variiert in Abhängigkeit von der Zeit und ist dadurch größer wenn alle Probennahmen zusammengefasst werden. Daraus folgt, dass die Beziehung zwischen lokaler und regionaler Diversität durch die Methode beeinflusst wird, welche zur Berechnung der regionalen Artenvielfalt eingesetzt wird (Kapitel III). Auf globaler Ebene (Kapitel IV) wird die Beziehung zwischen lokaler und regionaler Diversität in Aufwuchsgemeinschaften außerdem durch den Sukzessionsprozess beeinflusst, unabhängig davon ob taxonomische oder funktionale Diversität betrachtet werden. Bei lokalen Aufwuchsgemeinschaften ist unter Berücksichtigung der taxonomischen Diversität bereits in frühen Sukzessionsstadien eine Sättigung der Diversität festzustellen, während diese bei Betrachtung der funktionalen Artenvielfalt erst später eintritt.

Funktionale Gruppen gelten abgesehen davon auch als einflussreichste Vorhersagevariablen für die lokale Artenvielfalt.

General Introduction

Marine fouling communities

Every hard-substratum in the marine environment is subjected to the accumulation of microorganisms and propagules of sessile macroorganisms in a process recognized as ‘biofouling’ (Wahl 1989; Railkin 2004). This process has been viewed as a sequence that starts with biochemical conditioning, followed by bacterial colonization and ending in unicellular and multicellular eukaryotic fouling (Clare et al. 1992; Wahl 1997). This four-step process involves i) adsorption of dissolved organic molecules to a newly submerged surface, ii) bacterial colonization of the surface, iii) colonization by microscopic eukaryotes (e.g. diatoms, fungi) and iv) settlement and development of invertebrate larvae and algal spores (Dobretsov et al. 2005). Typical macrofoulers include sponges, hydroids, corals, sessile polychates, barnacles, mussels, bryozoans, sea cucumbers, ascidians and macroalgae, while microorganisms are represented by sessile bacteria, diatoms, microscopic fungi, heterotrophic flagellates, sarcodines and sessile ciliates (Railkin 2004). The actual species composition of the fouling community will depend upon both its spatial location and the temporal period within which is observed.

Due to their fast growing and their easiness to settle on artificial substrates, biofouling assemblages represent an opportune study system for ecologists (Sutherland and Karlson 1977) and are therefore often used to investigate ecological models (Lin and Shao 2002).

Fouling communities are distributed worldwide, especially in shallow and exposed marine environments. They are among the most diverse and productive assemblages of macroorganisms. Their ecological importance and the fact, that their abundance and distribution are currently affected by human activities (aquaculture, artificial reefs, ship hull transport) and climate change, make them suitable for the study of global patterns.

Seeking global diversity patterns

Understanding global patterns of biodiversity is a useful goal for ecologists because it has the capacity to provide insights on phenomena such as the spread of invasive species, the control of diseases and the effects of climate change (Gaston 2000). A number of hypotheses which seek to clarify spatial variation in biodiversity have been explored including comparisons between biogeographical regions, variation with spatial scale and along gradients across space (Gaston 2000, 2003; Mora et al. 2003; Turner 2004). However, in the marine realm there is still a relative lack of global studies as compared to terrestrial studies (Kuklinski et al. 2006). While in the last few decades, large scale patterns have been acknowledged for some marine taxonomic groups (Stehli and Wells 1971; Holmes et al. 1997; Roy et al. 1998; Giangrande and Licciano 2004; Gobin and Warwick 2006) broader patterns of marine biodiversity are still poorly recognised (Clarke 1992; Clarke and Crame 1997; Gray 2001).

The almost paradigmatic 'latitudinal gradient of species richness' (Figure 1), which states that the tropics hold more species than higher latitudes, is considered the oldest and the most reliable concept of a large-scale ecological pattern (Rosenzweig 1995; Willig et al. 2003; Hillebrand 2004a). However, this pattern appears less consistent in the marine than in the terrestrial environment (Clarke and Crame 1997; Rivadeneira et al. 2002; Gobin and Warwick 2006). Clear gradients of decreasing diversity towards the poles have been found, e.g. for molluscs in the western Atlantic and eastern Pacific Oceans (Roy et al. 1994; Roy et al. 1998; Roy et al. 2000), bryozoans in the North Atlantic (Clarke and Lidgard 2000), deep-sea isopods, gastropods and bivalves in the North Atlantic (Rex et al. 2000), and in intertidal sessile communities along the North-western Pacific coast of Japan (Okuda et al. 2004). In contrast, studies on polychaetes and nematodes (Boucher 1990; Mackie et al. 2005; Gobin and Warwick 2006), macroalgae (Santelices and Marquet 1998) and in marine soft sediments (Ellingsen and Gray 2002; Gray 2002) did not find evidence of a latitudinal trend in species richness.

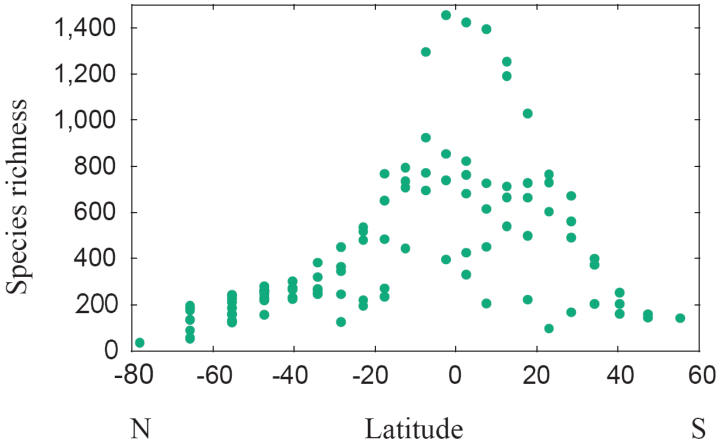


Figure 1. The latitudinal gradient of species richness: birds in grid cells (~ 611,000 km^2) across the New World. Modified after Gaston (2000).

Recently, in a meta-analytical comparison from approximately 600 published articles, Hillebrand (2004b) concluded that marine organisms generally display a decline in species richness towards the poles, but the strength and slope of the gradient depends on regional factors, as well as habitat and organism characteristics. The same study demonstrated that the strength of the gradient is sensitive to the life form at regional and local scales. Sessile organisms (a dominant component of marine fouling communities) and infauna revealed the weakest relationship to latitude at both spatial scales, while nekton, plankton and mobile epifauna showed stronger gradients (Hillebrand 2004b).

The determinant of biodiversity is, clearly, not latitude by itself, but the environmental variables linked with latitude. Currently, more than 30 hypotheses have been suggested for generating latitudinal diversity gradients, but after decades of study, no consensus has been reached so far (Gaston 2000; Willig et al. 2003; Mittelbach et al. 2007).

One of the proposed hypotheses to understand the causes of the gradient is the area of the climatic zones. Terborgh (1973) and later Rosenzweig (1992; 1995) pointed that tropical diversity could be explained, to some extent, by the larger area of the tropical belt when compared to other latitude belts. First, because the north and south tropical belts are joined at the equator while other latitude belts are separated by the tropics. Second, because the planet is wider at the equator than at the poles (Terborgh 1973; Rosenzweig 1992; Rosenzweig 1995). Moreover, greater diversity in the tropics today may be a consequence of historical evolutionary processes, since most of the land masses of the planet were tropical or subtropical during the Tertiary period (Ricklefs 2004).

On the other hand, the high levels of solar radiation in the tropics increase productivity which in turn may increase biodiversity through the increased availability of resources (Blackburn and Gaston 1996). Furthermore, higher temperatures in the tropics may lead to reduced generation times and greater mutation rates, accelerating speciation in tropical areas (Rohde 1992).

More recently, as a consequence of the rising accessibility of phylogenetic, molecular and biogeographical information, evolutionary and historical explanations for the latitudinal gradient of species richness have received more attention. A recent review (Mittelbach et al. 2007) discussed the recent developments and concluded: the tropical diversity maximum is considered very old in terms of the geological time period; speciation rates are higher in the tropics because molecular evolution rates in ectotherms are higher in warmer climates; speciation rates are higher in the tropics since larger biome areas increase the probability for geological or ecological isolation of sub-populations and because more biotic interactions force specialization and speciation. As a consequence, tropical diversification rates are higher due to faster speciation and slower extinction. Species originating in the tropics tend to disperse to higher latitudes but retain their presence in the tropics (Mittelbach et al. 2007).

The number of species in one location has been reported to depend on two categories of processes: local and regional (Caley and Schluter 1997; Ricklefs 2004; Shurin and Srivastava 2005). The terms ‘local’ and ‘regional’ are related to the spatial scale at which ecological and biogeographic processes, respectively, prevail. Local processes include predation, parasitism, competition and disturbance while long-distance dispersal, speciation and extinction are considered regional processes (Cornell and Lawton 1992).

As a further well-known macroecological pattern, the analysis of the 'relationship between local and regional diversity' has been used to compare the influence of local (e.g. disturbance, competition) and regional processes (e.g. speciation, migration) on local assemblages (e.g. Cornell and Lawton 1992; Hillebrand and Blenckner 2002; Witman et al. 2004; Freestone and Harrison 2006; Russell et al. 2006; Cornell et al. 2008). Theoretically, if regional species richness is driving local species richness, a positive and linear relationship is expected, and we would expect more species coexisting in a given area or volume in more species-rich regions than in species-poorer regions. In this case, communities are referred to as "unsaturated" or "type I" (Figure 2). In contrast, if local species richness finds a ceiling at high levels of regional richness local communities are referred to as "saturated" or "type II" (Cornell 1985; Cornell and Lawton 1992). "Type I" communities were reported more frequently which has been interpreted as regional species richness driving local species richness with few richness limitations imposed by local processes (for reviews see Lawton 1999; Srivastava 1999; Shurin and Srivastava 2005).

In recent years, however, different views on the use of the local-regional richness plots to examine species saturation have emerged and other techniques have been proposed. These aspects are discussed in chapters III and IV.

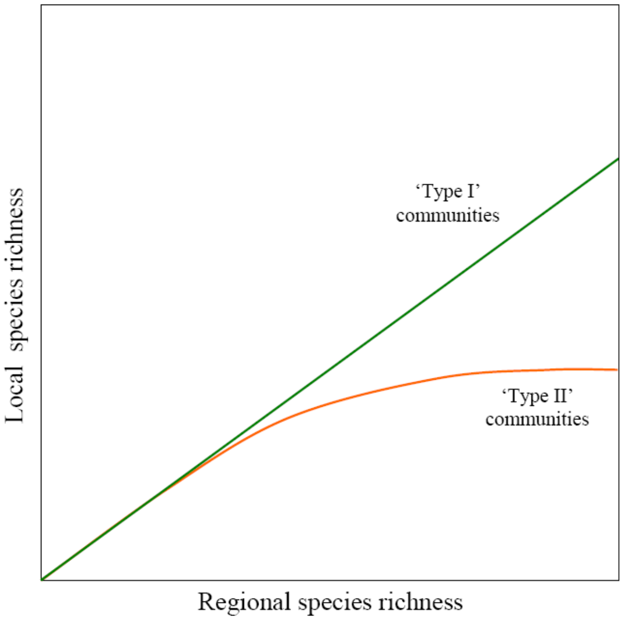


Figure 2. The relationship between local and regional diversity: if local assemblages are unsaturated or 'Type I', local richness will increase with regional diversity in a linear relationship (green line). In contrast, if saturated with species, local communities will reach a ceiling of maximum species richness ('Type II communities - orange line).

Regional species richness: from the known to the unknown

Estimating global biodiversity has challenged ecologists since the time of the renowned naturalist Linnaeus. Linnaeus initially catalogued 20.000 species (Dobson et al. 2008) and since then, numerous studies have attempted to estimate how many species exist on our planet (e.g. May 1988; 1990; 1992; Erwin 2004). The best and most recent 'guess' concludes that there are approximately 6 million species existing on Earth of which 1.4 million have been described (Dobson et al. 2008). Most ecosystems are experiencing a rapid loss of biodiversity which can be observed at both local and regional scales (Hooper et al. 2005; Sala and Knowlton 2006). It is therefore crucial for future estimates to quantify present day species richness at both spatial scales.

The question whether community richness is ecologically limited or relates directly to regional richness is not only essential for our understanding of an ecosystem but also for evaluating at which point of the process the richness and functionality of local communities will be affected.

In numerous studies that investigate the relationship between local and regional diversity, regional richness has been determined by questioning experts or consulting available species inventories (e.g. Rivadeneira et al. 2002; Witman et al. 2004). This approach can both under- and overestimate the regional number of relevant species, i.e. the majority of potential species colonizing local communities. Thus, complete inventories of the fauna and flora of a region are often hard to obtain and in many areas, the 'true' species richness of a region is unknown. Moreover, it is difficult to appreciate the completeness of such inventories (Soberon and Llorente 1993) and comparisons between published species lists are frequently unreliable due to different sampling methods, terminology or data handling systems (Dennis and Ruggiero 1996). On the other hand, many listed species may never colonize the habitat of interest because they have been registered in different areas or seasons. For this reason, the statistical assessment of regional richness based on a limited number of replicates, constitutes an important alternative (Colwell and Coddington 1994; Gotelli and Colwell 2001)

In order to extrapolate from the known to the unknown, i.e. from a reasonable number of properly inventoried samples to the 'true' number of relevant species in a certain area, several estimation techniques have been developed (Colwell and Coddington 1994). These techniques can be grouped into three classes: (i) parametric models (ii) non-parametric estimators and (iii) extrapolations of species accumulation curves (Magurran 2004). When species fit a log normal distribution, i.e. in the case of a parametric model to estimate species richness, it is possible to estimate the theoretical number of species in the community by extrapolating the shape of the curve. Most of the parametric methods are, however, reported to perform improperly and have not been used in recent years (Melo and Froehlich 2001). Non-parametric estimators were originally developed to estimate population size based on capture-recapture data and adapted to extrapolate total species richness (Williams et al. 2002). With this technique, richness is estimated from the predominance of rare species in each sample. The higher the proportional abundance of infrequent species, the greater the probability of encountering additional new species with increasing sampling effort (Williams et al. 2007). However, non-parametric estimators do not extrapolate beyond the last sample to estimate richness at an asymptote. Instead, they predict richness, including species not found in the sample, from the proportional abundances of species within the total sample (Soberon and Llorente 1993). Finally, the third approach to estimate species richness from samples is through the extrapolation of species accumulation curves. In such curves, the cumulative number of species is plotted against a cumulative measure of sampling effort, e.g. the number of individuals observed, samples or traps (Moreno and Halffter 2000; Gotelli and Colwell 2001). The species richness can then be estimated by fitting an equation to the curve and estimating its asymptote. Theoretically, the asymptote's location represents the 'true' richness, i.e. the total number of species that would be observed with a hypothetical infinite sampling effort (Soberon and Llorente 1993; Colwell and Coddington 1994; O'hara 2005; Jimenez-Valverde et al. 2006). Among these different methods for estimating total species richness from samples, the non-parametric estimators have been suggested to perform best (Baltanas 1992; Colwell and Coddington 1994; Walther and Morand 1998; Walther and Martin 2001; Chiarucci et al. 2003; Hortal et al. 2006).

Which factors affect the richness of local assemblages?

Recent studies have emphasized that local-regional richness plots alone are an inadequate tool to make inferences on the influence of local and regional processes in local communities (Russell et al. 2006; Cornell et al. 2008). In view of the fact that the number of species coexisting in a limited area or volume of habitat may be affected by parameters other than competition or predation, the shape of the relationship between local and regional richness may, on theoretical grounds, be expected to change during the succession of a community (community assembly time, Mouquet et al. 2003) and possibly with functional diversity.

One central aspect ignored in most previous studies is that the drivers of the relationship, and as a consequence the resulting relationship, may change during community assembly (Morton and Law 1997). Only a few theoretical and observational studies have postulated a successional shift of the local-regional richness relationship (Mouquet et al. 2003; Fukami 2004; Munguia 2004;

Starzomski et al. 2008). Mouquet et al. (2003) predicted, in a theoretical model, saturation at early stages of the assembly process, and emphasized that this may be due to only a subset of the regional species pool being available to colonize a local habitat. At intermediate successional stages, an unsaturated relationship is expected because competitive exclusion of species takes time. At last, when communities reach an equilibrium, competitive exclusion should produce a saturated relationship (Mouquet et al. 2003).

Additionally, if communities exhibit species saturation as a consequence of competitive exclusion this process should be more intense and saturation reached faster when species functionally overlap with regard to the limiting resource(s). How many functional groups may coexist in a community and how this relates to regional species richness has never been explored before. The degree to which different species show similar functional qualities may result in different relationships between taxonomic and functional diversity (Micheli and Halpern 2005; Halpern and Floeter 2008). One possible scenario is a positive linear relationship between taxonomic and functional diversity (slope = 1) when each species constitutes a unique functional group. If species exhibit overlap with regard to functions or requirements, the relationship may result in a linear plot with a lower slope or in a curvilinear, i.e. a saturated relationship. Thus, at high levels of species richness the probability that recruiting species overlap functionally may be higher leading to an asymptotic increase in functional richness with increasing regional species diversity (Micheli and Halpern 2005).

Objectives

This study investigates global biodiversity patterns in marine fouling communities. In particular, the latitudinal gradient of species richness and the relationship between local and regional diversity are examined. Previous studies focusing the analysis of the local-regional diversity relationship in the marine environment have often assessed regional species richness by questioning experts or consulting available species lists. However, the degree of completeness of such inventories varies between regions and may include species not likely to recruit in a given habitat or a given time. As a consequence, the statistical estimation of regional richness based on a limited number of replicates, constitutes an important alternative. In this work, a new methodology was developed to estimate regional species richness. The analysis of the relationship between local and regional diversity in marine fouling assemblages was then expanded by incorporating two categories of diversity (taxonomic and functional richness) and different successional stages at two different scales: European and global.

This thesis is divided in four chapters of which each represents a separate study. The aim of Chapter I was to examine a possible trend in the distribution of biofouling assemblages at a global scale. For this purpose, various case studies were selected, to provide an overview in plausible interpretations of the spatial variation of biofouling diversity. In particular, the latidudinal gradient of species richness was examined in a study comprising 16 biogeographic regions.

The study scope was then extended to the estimation of regional species richness, crucial in the analysis of the local-regional diversity relationship. Chapter II reports a novel methodology, with the purpose of optimizing the quality of regional richness estimations. First, we extrapolate to the asymptote of the species accumulation curves for three data sets, each with a large number of replicates and from three different types of marine benthic communities. Second, we use the asymptote's location as a reference for 'true' regional richness and then compare the performances of six different richness estimators. Finally, we quantify the mis-estimation as a function of replication.

Chapter III investigates the local-regional relationship in marine fouling assemblages using an expanded approach. The percent cover of all sessile species present in our experimental units has been recorded in four different biogeographic regions at a European scale. Both taxonomic and functional richness measured at three different successional ages have been taken into consideration. Thus, the shape of the pattern for differently calculated regional richness was compared.

Chapter IV accounts on a large-scale experiment in marine fouling assemblages growing on artificial substratum highly replicated at a global scale. At four different successional ages the percent cover of all sessile species present in our experimental units, the availability of resources (measured as percentage cover of unoccupied substratum) and functional richness has been inventoried. In particular, we analyse if the relationship between local and regional species diversity in fouling assemblages displays a linear or curvilinear shape and if the relationship is sensitive to community assembly time. Thus, we investigate if the nature of the local-regional richness relationship changes when only functional diversity is taken into consideration. Finally, we further examine whether the diversity of local communities is affected by other parameters than regional richness, such as number of functional groups or availability of resources.

The work is finalized with a closing chapter ('Synthesis and Conclusions') where the major findings and conclusions of this investigation are summarised. Further insights and recommendations for future studies on global diversity patterns are also given.

Chapter I

Patterns of fouling on a global scale

Abstract

The aim of this chapter is to seek and explain a possible trend in the distribution of biofouling assemblages at a global scale. For this, we have selected various case studies, one of them new, to provide an overview in plausible interpretations of the spatial variation of biofouling diversity. What types of biofoulers would settle on artificial panels deployed close to the tropics and those in higher latitudes? How fast is biomass accrual in these different locations? How do biofouling communities differ between regions with regard to taxonomic and functional properties? In an attempt to answer these questions, here we review the present understanding of diversity in biofouling communities at a global scale with special emphasis on the latitudinal gradient and on the relationship between region and local diversity in these assemblages.

Background

Global-scale patterns in biodiversity have challenged biologists since the 18th and 19th centuries (Ricklefs 2004). In fact, large-scale patterns are one of the most studied trends in ecology (Gaston 2000). The observation that the tropics hold more species than higher latitudes is the oldest paradigm about a large-scale ecological pattern (Willig et al. 2003; Hillebrand 2004a). Although not as well investigated as the latitudinal gradient, longitudinal gradients can also be recognised in some marine and terrestrial environments (Jetz and Rahbek 2001; Roberts et al. 2002; Callisto and Goulart 2005).

A congregation of theories that aim to explain the spatial variation in biodiversity has been investigated (Gaston 2000). For example, the *species-area hypothesis* is a relationship recognised since the beginning of the 20th century in ecology (Arrhenius 1921; Rosenzweig 1995). It proposes that larger areas hold more species, since their larger populations and more stable conditions reduce the risk of extinction and because they contain more barriers and heterogeneous habitat which promote speciation (Rosenzweig 1995; Chown and Gaston 2000). The *relationship between local and regional richness* can be illustrated by plotting local species diversity against regional species diversity (Caley and Schluter 1997; Krebs 2001). A linear relationship between local and regional diversity is expected if communities are unsaturated, and a curvilinear relationship if communities are saturated (Hillebrand and Blenckner 2002; Hillebrand 2004b) (Figure 1). Other patterns of spatial variation in species richness were explored along environmental gradients (depth, exposure, emersion, pollution, peninsulas, bays, isolation, productivity/energy) (Gaston 2000). Nonetheless, in the marine environment there is still a lack of global studies as compared to the terrestrial environment (Kuklinski et al. 2006). While in recent decades patterns on a large scale have been acknowledged for some marine taxonomic groups (Stehli and Wells 1971; Holmes et al. 1997; Roy et al. 1998; Giangrande and Licciano 2004; Gobin and Warwick 2006), major trends in marine biodiversity are still poorly understood (Clarke 1992; Clarke and Crame 1997; Gray 2001).

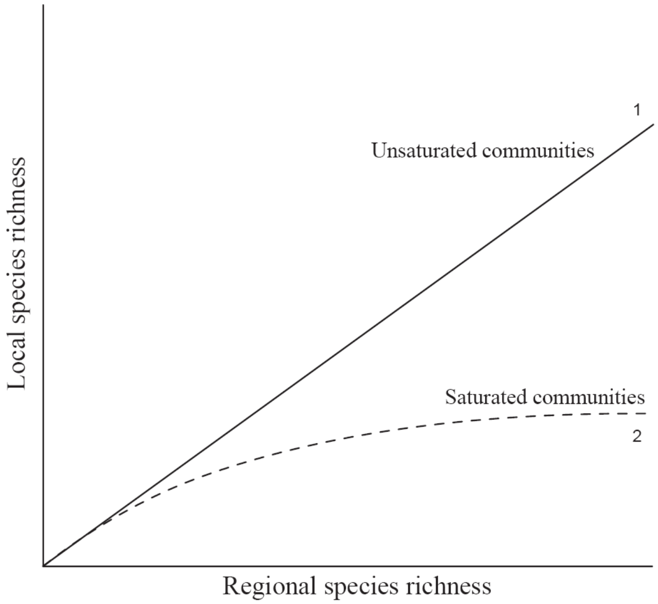


Figure 1. The local and regional diversity relationship. If local assemblages are unsaturated, community diversity will continue to rise with regional diversity in a linear way (line 1). If saturated with species, local communities will reach a plateau or maximum species richness (line 2).

Biofouling communities are distributed worldwide, especially in shallow and exposed marine environments. They are among the most diverse and productive assemblages of macroorganisms. Their ecological importance and the fact, that their abundance and distribution are currently affected by human activities (aquaculture, artificial reefs, ship hull transport) and climate change, make them suitable for the study of global patterns.

Is there a latitudinal cline in fouling organisms?

Among the spatial patterns of biological diversity, the *latitudinal gradient of species richness*, which states that maximum species richness occurs in the tropics and decreases toward higher latitudes, is considered one of the most reliable patterns in ecology (Rosenzweig 1995). When compared to the terrestrial realm, however, this pattern appears to be less consistent in the sea (Clarke and Crame 1997; Rivadeneira et al. 2002; Gobin and Warwick 2006). Clear gradients have been reported, e.g. in bryozoans in the North Atlantic (Clarke and Lidgard 2000), molluscs in the Western Atlantic and Eastern Pacific Oceans (Roy et al. 1994; Roy et al. 1998; Roy et al. 2000), deep-sea isopods, gastropods and bivalves in the North Atlantic (Rex et al. 2000), and in the intertidal sessile assemblages along the North-western Pacific coast (Okuda et al. 2004). In contrast, studies on polychaetes and nematodes (Boucher 1990; Mackie et al. 2005; Gobin and Warwick 2006), macroalgae (Santelices and Marquet 1998) and on marine soft sediments (Ellingsen and Gray 2002; Gray 2002) did not find evidence of a latitudinal gradient in diversity.

Hillebrand (2004b) performed a meta-analysis on approximately 600 published articles and concluded that generally marine organisms demonstrate a decrease in species richness towards the poles but the strength and slope of the gradient depend on regional, habitat and organism characteristics. Sessile organisms, i.e. the major constituents of biofouling communities, showed a weak relationship to latitude at both local and regional scales (Hillebrand 2004b).

In a recent comparison of benthic marine algae, Kerswell (2006) performed a meta-analysis based on 191 species lists from primary literature. Data were compiled at the genus-level for the classes Rhodophyceae, Phaeophyceae and Chlorophyceae and at species-level for all algae belonging to the order Bryopsidales. This latter order was treated with higher resolution because it is a group well studied and taxonomically stable. The author concluded that algal genera display an inverse latitudinal gradient with highest diversity in temperate regions. In contrast, number of species of the order Bryopsidales was maximum in the tropics and decreases towards the poles (Kerswell 2006). The genus richness was highest in southern Australia and Japan and moderate in the Indo-Australian Archipelago and Southern Indian Ocean. Algal richness in the Atlantic Ocean was higher in the eastern coastline with a hotspot situated at the European coast. Lowest diversity in algal genera was described for the polar regions (Kerswell 2006). We cannot exclude that some research bias contributes to certain features of this distributional pattern (high diversity on European shores, low diversity in Polar regions). A common explanation for a decrease in algal richness in the tropics is its competition with corals and elevated herbivore pressure at low latitudes. According to Kerswell, global patterns of algal richness can partially be explained by the species-area hypothesis. Bryopsidalean species richness is closely related to corals and reef fish diversity, implying a common regulatory mechanism. The meso-scale location of algal-richness hotspots may be determined by major ocean currents through propagule dispersal and changes in oceanic conditions (Kerswell 2006).

A recent review (Mittelbach et al. 2007) discussed the different hypotheses around the commonly observed latitudinal diversity pattern. They conclude (i) that the tropical diversity maximum is geological very old, (ii) speciation rates are higher in the tropics because (iia) molecular evolution rates in ectotherms is higher in warmer climates, (iib) larger biome areas enhance the chance for geological or ecological isolation of sub-populations and (iic) more biotic interactions – in a positive feedback – drive specialisation and speciation. As a result, tropical diversification rates are higher due to faster speciation and slower extinction. Species originating in the tropics tend to disperse to higher latitudes while retaining their presence in the tropics (Mittelbach et al. 2007).

Recently, Witman et al. (2004), conducted an investigation on epifaunal invertebrate communities encrusting subtidal vertical rock wall habitats using high resolution photos. The authors compared 12 biogeographic regions from 62 ºS to 63 ºN latitude to test the effects of latitude and richness of the regional species pool on local species richness. In their study, local diversity at each site was estimated as the asymptote of the species accumulation curve, using both the number of species observed (S_{obs}) and Chao2 (Colwell and Coddington 1994) as a local species richness estimator. Regional diversity was assembled from published species lists and by consulting taxonomic experts in each of the 12 different biogeographic regions. They reported that the sessile communities were from 10 different invertebrate phyla, where sponges, cnidarians and ascidians were the dominant groups (Witman et al. 2004). They also found a clear latitudinal pattern with maximum species richness at low latitudes at both regional and local scales (Figure 2). However, this pattern was more robust at a regional scale (Witman et al. 2004).

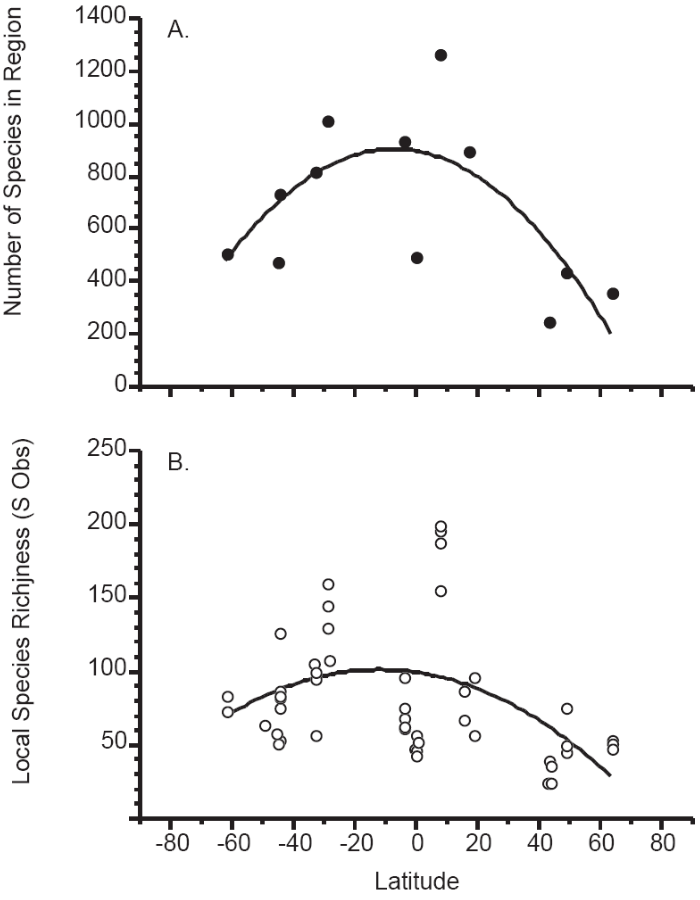


Figure 2. Species richness as a function of latitude. (A) Regional species richness; (B) Local species richness as number of species observed (S_{obs}). Lines represent significant, best fits to second-order polynomial equations. Reprinted from Witman et al. (2004). Copyright (2007) National Academy of Sciences, U.S.A.

The pattern revealed by a global modular fouling experiment

The core of a Global Approach by Modular Experiment project (GAME, 2000) conducted by our group was to achieve a broad knowledge in community ecology by conducting identical experiments in different coastal shallow water hard-bottom ecosystems of both hemispheres. Identical experimental designs allow consistent comparisons and global interpretations. Here we analyse 23 GAME studies performed between 2003 and 2007 in 16 biogeographic regions from 42 ºS to 59 ºN latitude (Table 1). All studies were focused on a benthic ecology topic, e.g. the intermediate disturbance hypothesis in biofouling communities (Miethe 2005; Spindler 2005; Valdivia et al. 2005; Jara et al. 2006; Svensson et al. 2007; Canning-Clode et al. 2008; Sugden et al. 2008; Valdivia et al. 2008), temporal variability of disturbances (Herbon 2005; Rich 2005; Schröder 2006; Atalah et al. 2007; Cifuentes et al. 2007; Sugden et al. 2007) and diversity and stability of marine communities (Keller 2006; Wiesmann 2006; Wunderer 2006; Jochimsen 2007; Krüger 2007; Lauterbach 2007; Link 2007; Stockhausen 2007; Weseloh 2007). In all regions, 15 x 15 cm polyvinylchloride (PVC) panels were submerged for colonisation at approximately 0.5 m depth during a period between 5 to 8 months. For the purpose of this analysis, only common sessile species (mean abundance > 1 % cover) on untreated control panels (n = 6) were taken into consideration.

Table 1. Dominant biofoulers on the PVC panels recorded from the 23 studies analysed from the GAME project between 2003 and 2007. Site coordinates are indicated. Total species refer to the total number of species observed during the course of the study in each location.

Location	Lat.	Long.	Total species	Dominant Algae	Dominant Invertebrates	References
Finland	59 ºN	23 ºE	9	*Cladophora rupestris*, *Ectocarpus siliculosus*	*Balanus improvisus*, *Electra crustulenta*	(Stockhausen 2007)
Sweden	58 ºN	11 ºE	39	*Ceramium rubrum*, *Polysiphonia fucoides*	*Ciona intestinalis*, *Ascidiella aspersa*, *Laomedea flexuosa*	(Svensson et al. 2007)
England	54 ºN	1 ºW	13	---	*Ascidiella aspersa*	(Sugden et al. 2008)
			12	*Ectocarpus siliculosus*	*Ascidiella aspersa*, *Botrylloides leachi*	(Sugden et al. 2007)
			25	*Ectocarpus siliculosus*	*Ascidiella aspersa*, *Didemnum spp.*	(Lauterbach 2007)
Poland	54 ºN	18 ºE	11	*Enteromorpha ahlneriana*, *Cladophora rupestris*	*Mytilus edulis*, *Balanus improvisus*	(Schröder 2006)
Italy	43 ºN	10 ºE	21	*Cladophora* sp., *Ceramium* sp.	*Mytilus edulis*, *Serpula vermicularis*	(Spindler 2005)
Japan	38 ºN	141 ºE	51	*Ceramium kondoi*, *Ulva arasakii*, *Sargassum horneri*	*Tricellaria occidentalis*, *Watersipora subovoidea*, *Mytilus galloprovincialis*	(Miethe 2005)

Table 1. (Continuation)

Location	Lat.	Long.	Total species	Dominant Algae	Dominant Invertebrates	References
	35 ºN	139 ºE	48	*Enteromorpha intestinalis*	*Molgula manhattensis, Balanus amphitrite, Mytilus galloprovincialis*	(Link 2007)
Portugal	32 ºN	16 ºW	36	*Lithophyllum incrustans; Polysiphonia* sp.	*Diplosoma* sp., *Serpula vermicularis*	(Canning-Clode et al. 2008)
			32	*Cladophora coelothrix, Ceramium virgatum*	Family Serpuliadae	(Jochimsen 2007)
Malaysia	5 ºN	102 ºE	23	*Padina australis, Lobophora variegata*	*Balanus amphitrite*	(Weseloh 2007)
			21	Rodophyta	*Balanus* sp.	(Herbon 2005)
Brazil	22 ºS	43 ºW	25	*Bryopsis pennata, Codium taylorii*	*Bugula neritina, Schizoporella errata*	(Jara et al. 2006)
			32	*Enteromorpha* sp., *Ulva* sp.	*Bugula neritina, Styela* sp.	(Wunderer 2006)
	23 ºS	42 ºW	27	Phaeophyceae	*Balanus trigonus, Megabalanus* sp.	(Jara et al. 2006)
Chile	29 ºS	71 ºW	32	*Ulva* sp. *Polysiphonia* sp.	*Pyura chilensis, Diplosoma* sp.	(Valdivia et al. 2005)
			40	*Ulva* sp.	*Austromegabalanus psittacus, Pyura chilensis*	(Cifuentes et al. 2007)
			25	*Ectocarpus* sp., *Polysiphonia* sp.	*Pyura chilensis, Diplosoma* sp., *Bugula neritina*	(Krüger 2007)
Australia	34 ºS	150 ºE	25	---	*Hydroides elegans, Botrylloides leachi, Pyura stolonifera*	(Rich 2005)
	35 ºS	138 ºE	30	Encrusting coralline algae, *Ulva* sp., *Mychodea* sp.	*Galeolaria* sp.	(Valdivia et al. 2008)
New Zealand	36 ºS	174 ºE	33	brown filamentous algae; *Ulvella sp.*, *Acrochaetium* sp.	*Balanus trigonus, Elminius modestus*	(Atalah et al. 2007)
			28	*Ralfsia* sp., *Ulvella* sp.	*Balanus trigonus, Elminius modestus*	(Wiesmann 2006)
Tasmania, Australia	42 ºS	147 ºE	26	*Scytosiphon lomentaria, Asperococcus bullosus*	*Elminius modestus, Watersipora subtorquata, Cryptosula pallasiana*	(Keller 2006)

According to the GAME results, the most common biofoulers worldwide were ascidians, bryozoans, barnacles and mussels. High abundances of the ascidians *Ascidella aspersa* and *Ciona intestinales* were observed in several sites in the northern hemisphere. In contrast, the presence of the genera *Styela* and *Pyura* were more frequent in the southern hemisphere. Furthermore, species like *Botrylloides leachi* and *Diplosoma* sp. were present in both hemispheres (Table 1). In what is concerned to bryozoans, the genus *Watersipora* was dominant in two sites from different hemispheres (Tasmania and Japan). Considerable abundances of *Bugula neritina* were verified in Brazil and Chile. Barnacles belonging to the genus *Balanus* had a very broad distribution. The species *Balanus improvisus* and *Balanus amphitrite* were more common in the north (e.g. Finland, Poland, Japan and Malaysia) while *Balanus trigonus* was regularly seen on panels deployed in the southern hemisphere (e.g. Brazil, New Zealand). The mussels *Mytilus edulis* and *Mytilus galloprovincialis* were also prevailing in various locations above 32 ºN. In addition, macroalgae had a vast distribution with the genera *Ulva*, *Ceramium* and *Polysiphonia* being common in several sites from both hemispheres (Table 1). A latitudinal diversity cline was found. Species diversity was significantly greater in tropical areas than at higher latitudes ($R^2 = 0.52$; $p = 0.0003$; Figure 3A). Within this general pattern, regional differences are evident. High species richness was found on Malaysia (5 ºN) and Madeira Island, Portugal (32 ºN), while minimum species richness was registered in Poland and Tasmania. Since the biofouling communities on the 5 to 8 months old panels in many cases cannot be considered ‘mature’, these results represent more a sampling of the diversity of the different coloniser pools.

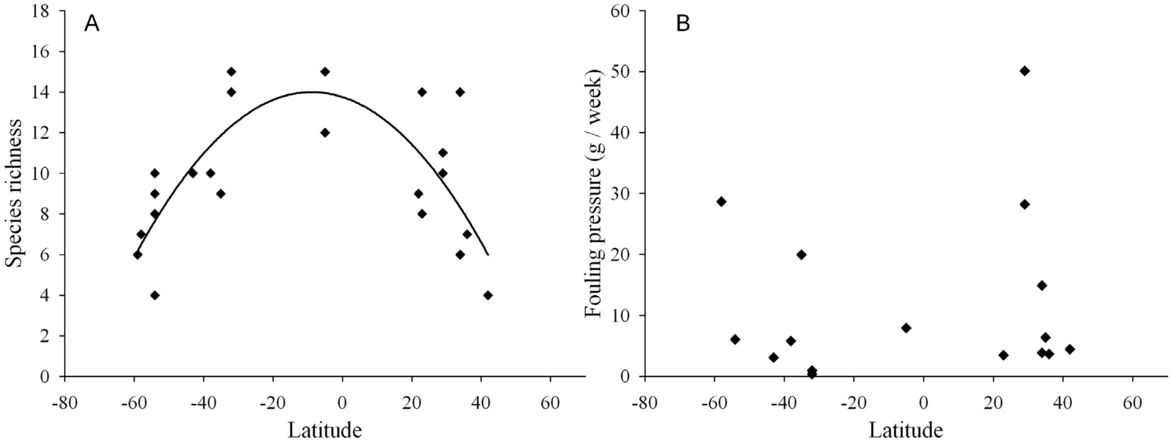


Figure 3. The GAME analysis: relationship between macrofouling species richness and latitude (A) and fouling pressure across latitude assessed as wet weight (g) accrual per time (weeks) (B).

The speed of community assemblage is likely to differ between regions. In order to investigate this, we calculated the biofouling pressure in 16 of the 23 GAME studies, as the quantity of biomass (wet weight) accrual (representing recruitment plus growth) per week and panel (Figure 3B). Fouling pressure varied from 3 to 50 g week^{-1} wet weight of biomass. Latitude does not explain this large variability. Therefore, other factors than those linked to the sum parameter ‘latitude’ (as a surrogate for warm temperature, environmental constancy and high diversity) like regional salinity, productivity, or species identity may override any global scale trend. Fouling pressure was highest in Sweden and Chile where ascidians were the dominant organisms.

Are biofouling communities saturated? The relationship between local and regional diversity

Diversity in local communities is regulated by local and regional processes. Local processes include predation, competition, and disturbance while migration, speciation, extinction and historical events are regional processes (Hillebrand and Blenckner 2002; He et al. 2005). Moreover, local and regional richness are differentiated by spatial scale. Local diversity is measured on a scale in which all the species in the community potentially interact with each other in some unit of ecological time, typically a generation (Krebs 2001). In contrast, regional diversity refers to a larger spatial scale like the biogeographic distribution of colonists in a location (Srivastava 1999).

One manner to separate evolutionary and ecological patterns consists in testing which proportion of regionally available species is represented in a local community. Ecological limitation (i.e. saturation) means that with increasing number of available species in the regional pool (i.e. along the latitudinal gradient) or with invasion events, local richness does not increase beyond an intrinsically determined maximum (Srivastava 1999). Therefore, based on ecological models that rely on species interactions, a saturation pattern is predicted when species are interacting and not expected when species are not or only weakly interacting (Loreau 2000; Shurin and Allen 2001). The relationship between regional and local richness can be demonstrated by plotting local species diversity against regional species diversity. Here, communities in which local diversity is linearly dependent on regional diversity over the entire range of regional diversities are referred to as “unsaturated” or “Type I” communities (Cornell 1985; Cornell and Lawton 1992), i.e. the number of coexisting species does not seem limited – at least during the period of observation. Alternatively, as regional richness increases, local diversity might reach a ceiling above which it does note rise despite further increases in regional diversity. In this case local communities are said to be “saturated” with species and are referred to as “Type II” communities (Cornell 1985; Cornell and Lawton 1992).

In the previously mentioned study conducted by Witman et al.(2004), the exploration of the relationship between regional and local diversity in epifaunal invertebrate communities was another objective. To test saturation in epifaunal communities, they used the slopes in a log-log analysis. A steady rise of local species richness with increasing regional species richness is represented by a slope of 1 in a log-log plot, while local saturation (an asymptote) is represented by a slope significantly smaller than 1 (Witman et al. 2004). They found that the slopes did not differ from 1 for both S_{obs} and Chao2. This indicates that the number of species coexisting in local communities is not limited within the size of the regional species pool (“Type I” communities, Figure 4). Witman et al. (2004) further emphasised that the strong effect of regional diversity on local communities involves that patterns of local diversity in marine benthic assemblages at a global scale are influenced by processes of speciation, migration, extinction and geologic events.

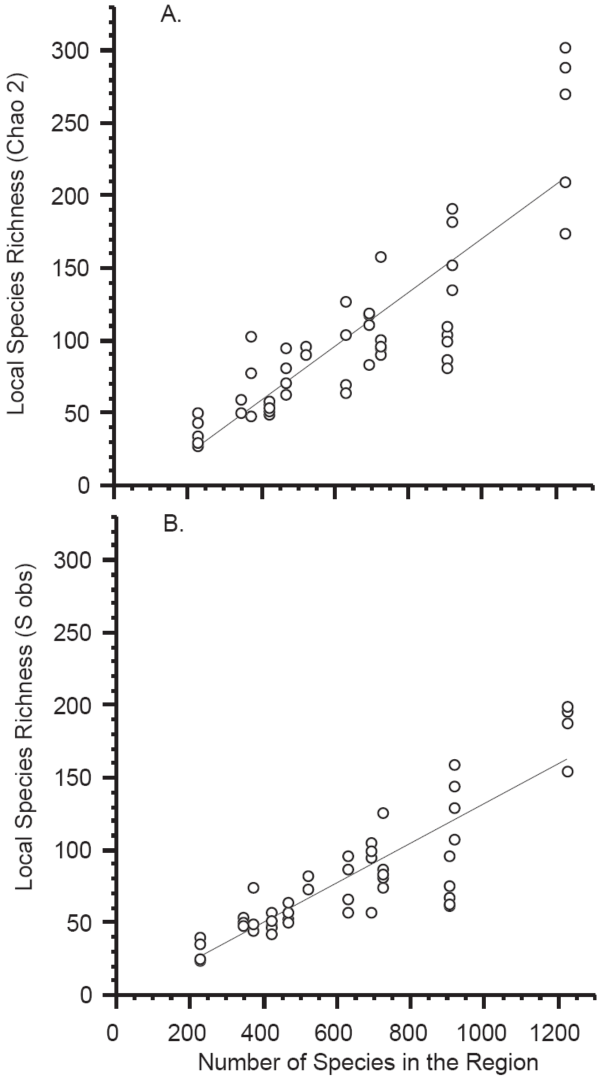


Figure 4. Plots of regional versus local species richness based on the Chao2 (Colwell and Coddington 1994) (A) and S_{obs} (B) estimates of species richness. Lines represent significant, best fits by least-squares linear regression. Reprinted from Witman et al. (2004). Copyright (2007) National Academy of Sciences, U.S.A.

Discussion and future perspectives

The examples presented in this overview have shown a clear relationship between latitude and biofouling species richness. The study performed by Witman et al. (2004) as well as the analysis we presented here with the GAME data both demonstrated that the tropical regions hold more biofouling species when compared to areas at higher latitudes. Our findings are, therefore, in accordance to Hillebrand’s meta-analysis (2004b) where from 600 published gradients, the author found a significant average tendency of decreasing marine biodiversity with increasing latitude. This global diversity pattern reflects that the regions closer to the tropics are richer in biofouling species than at higher latitudes, and highlights the need of protection for certain species in these areas. Factors such as predation, age, competition, climate, productivity and regional species pool have been proposed as possible explanations for the latitudinal gradient (Rosenzweig 1995; Willig et al. 2003; Ricklefs 2004). More recently, interest in evolutionary and historical explanations for the gradient is increasing with the availability of molecular, phylogenetic and palaeontological data (Mittelbach et al. 2007). Furthermore, in their interpretation of the relationship between local and regional diversity, Witman et al. (2004) found a “Type I” curve which indicates that the number of coexisting species is unsaturated.

The most striking outcome of this review is that, while large scale patterns have been recognised for some taxonomic groups (Stehli and Wells 1971; Holmes et al. 1997; Roy et al. 1998; Giangrande and Licciano 2004; Gobin and Warwick 2006; Kerswell 2006) and habitats, (e.g. intertidal, Leonard 2000; Okuda et al. 2004; Kuklinski et al. 2006) in the past, there is not a satisfying understanding about global patterns and their causes in biofouling communities. The relative simplicity by which such assemblages can be studied and manipulated on artificial substrata should facilitate further latitudinal and regional comparisons.

The two investigations described here have found the latitudinal pattern at different depths, community age and substrata. In contrast to the GAME investigation, Witman et al. (2004) reported that sponges were dominant organisms in their survey which might have been influenced by depth (see Cowie in press, for the influence of depth in biofouling patterns). To avoid this heterogeneity, standardisation in the methodology of future biofouling studies with regard to depth, age and substrata would facilitate global comparisons.

In the GAME analysis, only one study was carried out in the tropics proper (Malaysia) leaving a sampling gap. More knowledge in biofouling assemblages in areas between 30 ºN and 20 ºS latitude might have created a different pattern than the one we found. Additionally and in contrast to the study conducted by Witman et al. (2004), our analysis did not include a study site in the Antarctic region. Although little is known concerning biofouling assemblages in Antarctica (but see e.g. Bowden et al. 2006; Waller 2008), for a more adequate and accurate global perspective on biofouling organisms this area should be included in future surveys.

A relevant fact that requires further investigation is the presence of non-native biofouling species in regional diversity and its influence in the global diversity pattern. The introduction of non-native species in the marine realm is considered a relevant threat for the biodiversity of the marine system (Hewitt and Campbell 2007). Recent studies have revealed ship traffic as the main vector for marine non-native species. Species transported in the ballast water of vessels as well as sessile and sedentary organisms growing on ship hulls are considered a major source of invaders (Minchin and Gollasch 2003). Common biofoulers like barnacles, bryozoans and mussels present life forms that make possible their survival on ship hulls (see Lewis and Coutts in press). Moreover, the availability of open space has been demonstrated as a limiting resource in marine hard-bottom assemblages, (e.g. Stachowicz and Byrnes 2006). In a study to assess the effects of diversity on the invasion of sea squirts in a subtidal epifaunal community, Stachowicz et al. (2002) observed that space availability decreased and was more consistent over time, in more diverse communities. In their study, they have demonstrated that the survival and percent cover of the invaders was reduced with diversity (Stachowicz et al. 2002). This may indicate that locations close to the tropics, i.e. that hold more different species, are more resistant to the invasion process.

Finally, the question whether community richness is ecologically limited or relates directly to regional richness is not only essential for our understanding of an ecosystem. In addition, in the context of the dramatic decrease of species numbers on both global and regional scales we must be able to evaluate at which point of the process the richness and functionality of local communities will be affected. Furthermore, the relationship between local and regional richness may be affected by other parameters such as facilitation and abiotic stress (Russell et al. 2006). It is certainly of importance which section of the regional richness gradient is examined.

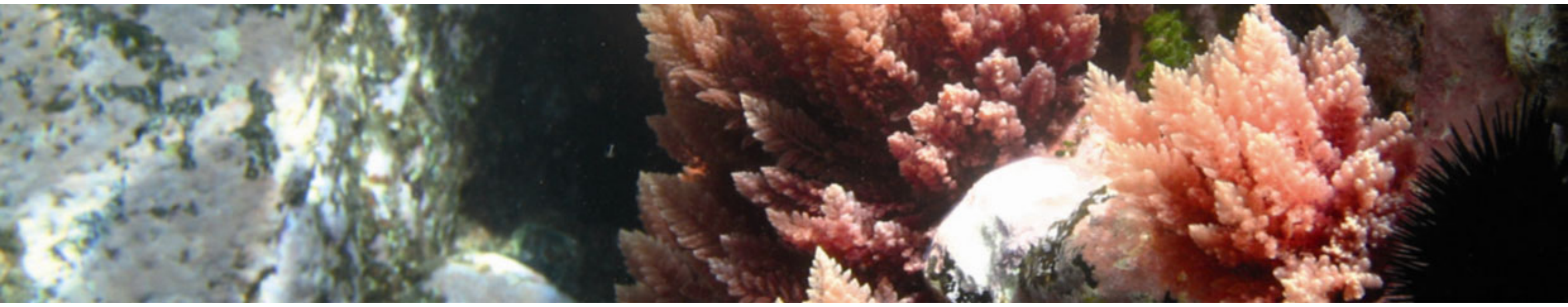
Conclusions

The latitudinal gradient and the relationship between local and regional species richness are common spatial patterns that seek to explain biological diversity.

A clear relationship between latitude and biofouling diversity was reported in two different investigations. Moreover, one of the studies showed that local diversity was dependent on regional diversity in a linear way.

A poor understanding in biofouling global trends still persists. This fact highlights the need for additional large-scale studies focusing on these assemblages.

Chapter II



Estimation of regional richness in marine benthic communities: quantifying the error

Abstract

Species richness is the most widely used measure of biodiversity. It is considered crucial for testing numerous ecological theories. While local species richness is easily determined by sampling, the quantification of regional richness relies on more or less complete species inventories, expert estimation or on the mathematical extrapolation from a number of replicated local samplings. However the accuracy of such extrapolations is rarely known. In this study we compare the common estimators MM (Michaelis-Menten), Chao1, Chao2, ACE (Abundance-based Coverage Estimator) and the first and second order Jackknifes against the asymptote of the species accumulation curve, which we use as a baseline for true regional richness. Subsequently we quantified the role of sample size, i.e. number of replicates, for precision, accuracy and bias of the estimation. These replicates were sub-sets of three large data-sets of benthic assemblages from the NE Atlantic: (i) soft-bottom sediment communities in the Western Baltic (n = 70); (ii) hard-bottom communities from emergent rock on the Island of Helgoland, North Sea (n = 52) and (iii) hard-bottom assemblages grown on artificial substrata in Madeira Island, Portugal (n = 56). For all community types, Jack2 showed a better performance in terms of bias and accuracy while MM exhibited the highest precision. However, in virtually all cases and across all sampling efforts, the estimators underestimated the regional species richness, regardless of habitat type, or selected estimator. Generally, the amount of underestimation decreased with sampling effort. A logarithmic function was applied to quantify the bias caused by low replication using the best estimator, Jack2. The bias was more obvious in the soft-bottom environment, followed by the natural hard-bottom and the artificial hard-bottom habitats, respectively. If a weaker estimator in terms of performance is chosen for this quantification, more replicates are required to obtain a reliable estimation of regional richness.

Introduction

Species richness is the simplest and most commonly accepted measure of biodiversity (Whittaker 1972; Magurran 1988; Gaston 1996) and is crucial for testing ecological models such as the saturation of local communities colonized from regional species pools (Cornell 1999). Ecological limitation (i.e. saturation) means that with increasing number of available species in the regional pool or with invasion events, local richness does not increase beyond an intrinsically determined maximum (Srivastava 1999). Thus, if only regional richness is driving local richness, a positive linear relationship is often predicted (Cornell and Lawton 1992; Srivastava 1999). Conversely, while concerns have been expressed (Loreau 2000; Hillebrand and Blenckner 2002; Ricklefs 2004) it has been widely accepted that if local assemblages are saturated with species due to ecological interactions and niche overlap, an asymptotic relationship is expected (Cornell and Lawton 1992; Cornell and Karlson 1997; Srivastava 1999).

Several studies that seek to explain and/or test the relationship between local and regional diversity have assessed the regional species pool based on published species lists and by consulting taxonomic experts (e.g. Hugueny and Paugy 1995; Lawes et al. 2000; Rivadeneira et al. 2002; Chalcraft et al. 2004; Witman et al. 2004; Harrison et al. 2006). However, complete inventories of the fauna and flora of a region are exceptionally hard to obtain and will probably remain unavailable for most regions for the next few centuries (Petersen and Meier 2003; Hortal et al. 2006). This problem is more delicate in the marine environment where there is a large phyletic diversity in certain groups and limited information about others, e.g. Porifera (Foggo et al. 2003). Moreover, it is difficult to appreciate to what degree such inventories are complete or incomplete (Soberon and Llorente 1993) and comparisons between published species lists are frequently unreliable due to different sampling methods, terminology or data handling systems (Dennis and Ruggiero 1996). In addition, when saturation in certain assemblages is to be investigated, the species capable to recruit into this habitat type (the *relevant* richness) are only a subset of the entire regional richness.

To deal with these difficulties a number of estimation techniques have been developed to extrapolate from the known to the unknown, i.e. from a reasonable number of properly inventoried samples to the true number of relevant species in a certain area (Colwell and Coddington 1994). These techniques can be grouped into three classes: (i) parametric models (ii) non-parametric estimators and (iii) extrapolations of SAC (species accumulation curves) (Magurran 2004). When species fit a log normal distribution i.e., a case of a parametric model to estimate species richness, it is possible to estimate the theoretical number of species in the community by extrapolating the shape of the curve. Most of the parametric methods are, however, reported to perform improperly and have not been used in recent years (Melo and Froehlich 2001).

In contrast, the non-parametric estimators have been suggested to perform better than SAC and parametric methods (Baltanas 1992; Colwell and Coddington 1994; Walther and Morand 1998; Walther and Martin 2001; Hortal et al. 2006). These non-parametric estimators were originally developed to estimate population size based on capture-recapture data and adapted to extrapolate total species richness (Williams et al. 2002). With this technique, species richness is estimated from the prevalence of rare species in each sample but does not extrapolate beyond the last sample to an asymptote. In its place, they predict richness, including species not found in the sample, from the proportional abundances of species within the total sample (Soberon and Llorente 1993). To date, several evaluations on the performance of different estimators have been carried out (see review from Walther and Moore 2005). In most cases, the estimators Chao1 (Chao 1984), Chao2 (Chao 1984, 1987; Colwell 2005), first order Jackknife (Jack1 - Burnham and Overton 1979; Heltshe and Forrester 1983) and second order Jackknife (Jack2 - Smith and Van Belle 1984) perform better in terms of bias, precision and accuracy than other estimators (Walther and Moore 2005). In a recent study, Hortal et al. (2006) compared 15 species richness estimators using arthropods abundances data and concluded that Chao1 and ACE (Abundance-based Coverage Estimator, Chao and Lee 1992; Chazdon et al. 1998; Chao et al. 2000) have shown the best performance among all estimators. For the marine system, Foggo et al. (2003) performed an evaluation on the performance of six estimators using simulations. They concluded that the estimator's performance was affected by sampling effort and no particular estimator performed best in all cases. Nevertheless, Foggo et al. (2003) suggested Chao1 as the most appropriate choice for a limited number of samples although acknowledging that its performance may vary significantly in cases of larger spatial scales and species richness. In these circumstances, the frequency of rare species could deteriorate the performance of Chao1 (Foggo et al. 2003). This was later confirmed by Ugland and Gray (2004) in benthic assemblages of the Norwegian continental shelf where Chao1 provided a large underestimation of true richness.

Finally, the third category of assessing inventory completeness is through the extrapolation of SAC. In such curves, the cumulative number of species is plotted against a cumulative measure of sampling effort, e.g. the number of individuals observed, samples or traps (Moreno and Halffter 2000; Gotelli and Colwell 2001). The species richness can then be estimated by fitting an equation to the curve and estimating its asymptote. While many functions have been proposed for this task (see Tjorve 2003 for a review in possible model candidates), the negative exponential function, the Clench equation, the Weibull function and the Morgan-Mercer-Flodin (MMF) model have been frequently used (Soberon and Llorente 1993; Colwell and Coddington 1994; Flather 1996; Lambshead and Boucher 2003; Jimenez-Valverde et al. 2006; Mundo-Ocampo et al. 2007). In theory, the asymptote's location represents the 'true richness', i.e. the total number of species that would be observed with a hypothetical infinite sampling effort (Soberon and Llorente 1993; Colwell and Coddington 1994; O'hara 2005; Jimenez-Valverde et al. 2006). The quality of the fitting of the equation to the curve and, thus, the reliability of the plateau should relate directly to the number of replicates.

Thus, previous studies have compared the performance of richness estimators and others have explored the extrapolation of SAC. The current study addresses the estimation of regional richness using a novel approach. First, we extrapolate to the asymptote of the SAC for three data sets, each with a large number of replicates and from three different types of marine benthic communities. Second, using the asymptote's location as a reference for true regional richness, we then compare precision, bias and accuracy of the regional richness produced by six different estimators - Michaelis-Menten (MM), ACE, Chao1, Chao2, Jack1 and Jack2. Finally, we quantify the mis-estimation as a function of sampling effort.

Materials and Procedures

For this study we explored three sets of benthic communities: (i) soft-bottom: In Kiel Bay, Western Baltic, (54º 38.3' N, 10º 39.6' E) 70 replicates of macrofaunal samples were collected to investigate the performance of species richness estimation techniques. The 70 samples were collected in sequence from the same site in the early autumn of 1995 at the Station "Millionenviertel 14" using a 1000 cm^2 van Veen grab at a depth of 24m (covering a total of 7 m^2 of sea bed). Samples were preserved in 4% formaldehyde and later identified to species level (Rumohr 1999; Rumohr et al. 2001). (ii) In spring 2006, in Helgoland Island, North Sea (54º 11.4' N, 07º 55.2' E) one of us (NV) sampled sessile hard-bottom communities and identified them to species level in 52 replicate quadrates of 400 cm^2 in intertidal rocky abrasion platforms. The study site "Nordostwatt", located in the north-east part of the island, covers approximately 450 m^2 and was extensively studied and inventoried by Janke (1986). Janke (1986) described horizontal belts in the intertidal as the *Enteromorpha*, *Mytilus*, *Fucus serratus* and *Laminaria* zones. The data we use in this report is from 7 sub-habitats distributed in the *F. serratus* habitat. (iii) In early summer 2004, young hard-bottom communities were collected by immersing 56 replicate polyvinylchloride (PVC) panels (225 cm^2) for 5 months at Madeira Island, Portugal, NE Atlantic (32º 38.7' N, 16º 53.2' W). The panels were distributed in 12 PVC rings (60 cm diameter, 25 cm height) hung from a buoy at approximately 0.5 m depth. Minimum distance between rings was 5 m. The original study focused on the influence of disturbance and nutrient enrichment in hard-bottom assemblages (Canning-Clode et al. 2008). For the purpose of this analysis, only sessile species on untreated control panels were taken into consideration. Hereafter, these data-sets are referred to as soft-bottom, natural hard-bottom and artificial hard-bottom, respectively.

Predicting the asymptote of the SAC

Species accumulation curves (SAC) were used (PRIMER 6, Clarke and Gorley 2006) to calculate the total number of species observed ("S_{obs} Curve") in the maximum sample size. Here, we used 52 replicates as maximum sampling size for all habitats since this was the maximum replicate number found in all habitat samples. Replicates were permuted randomly 999 times. The analytical form of the mean value of the accumulation curve over all permutations was given by the UGE Index (Ugland et al. 2003). Ugland et al. (2003) developed a total species curve (T-S curve) from SAC obtained from single subareas. This curve can then be extrapolated to estimate the probable total number of species in a given area (Ugland et al. 2003). They showed for the Norwegian continental shelf that the conventional SAC gave a large underestimation compared with the T-S curve. In order to estimate the asymptote of the SAC (represented as true regional richness in this analysis) for all habitats, the non-linear Morgan-Mercer-Flodin (MMF) growth model (Morgan et al. 1975) was chosen. The MMF model was selected by the curve fitting software *CurveExpert* (Hyams 2005) because of its superior fit regarding coefficient of correlation (r) and standard error of the estimate (SE) in all three data sets. The MMF model takes the form:

$$y = (ab + cx^d) / (b + x^d)$$

where y is species richness and x represents the number of replicates. The parameters a, b, c and d have the following interpretation: a is the calculated ordinate intercept of the replicates-species richness curve; c represents the maximum species richness, i.e. asymptote of the curve, as the number of replicates (x) approaches infinity; b and d are model parameters that describe the shape of the curve between the two extremes (Morgan et al. 1975). This model was previously used in two studies that performed a regional estimation of deep sea and littoral nematodes (Lambshead and Boucher 2003; Mundo-Ocampo et al. 2007). However they extrapolated from a SAC based on number of individuals rather than number of samples based on the UGE index as we do here.

Species richness estimations using variable replicate numbers

To investigate the effect of sample size (number of sampling units representing the replicates of 'local richness') in estimating regional richness, we employed the frequently used software *'EstimateS'* (version 7.5, Colwell 2005). This program computes sample-based rarefaction curves for a variety of species richness estimators, presenting the mean number of random samples re-orderings. Rarefaction and SAC were computed ten times (using 10 randomly drawn sub-sets of replicates from the entire data-set) for the replication levels 2, 4, 8, 16, 32 and 52 for each habitat.

It should be noted that due to the fact that there were 70, 52 and 56 available replicates for the soft-bottom, natural hard-bottom and artificial hard-bottom data-sets, respectively, there was a higher chance of samples overlap when selecting the 32 and 52 samples sets. The rarefaction curve was based on 100 randomizations of the number of replicates sampled. We focussed our investigation on five non-parametric estimators as well as on the asymptotic Michaelis-Menten (MM) richness estimator (Raaijmakers 1987) (Table 1). These six estimators were previously used in several evaluations and were reported to perform well (Walther and Moore 2005, see their table 3). Rosenzweig et al. (2003) theoretically differentiated these two varieties of estimators. Non-parametric estimators intend to overcome sample-size insufficiencies and to report the number of species present in sampled habitats. They operate only on the results obtained from a subset of the total data set and do not represent an extrapolation. In contrast, MM extrapolates species number to the asymptote of the SAC (Rosenzweig et al. 2003). *'EstimateS'* calculates the MM estimator in two ways: (i) for each of the 100 randomizations which is then averaged (MMRuns) or (ii) the mean accumulation curve is calculated by averaging over 100 accumulation curves derived from 100 runs (MMMeans). Due to its less erratic estimation (Colwell 2005; Walther and Moore 2005), we used the latter in this analysis.

Table 1. Summary of the species richness estimators used for this analysis. NP: non-parametric estimator; P: parametric estimator.

Richness estimators	Type	Description	References
ACE	NP	Abundance-based Coverage Estimator. It is a modification of the Chao & Lee (1992) estimators based on the ratio between rare (less than 10) and common species.	Chao and Lee 1992; Chazdon et al. 1998; Chao et al. 2000
Chao1	NP	Abundance-based estimator based on the number of rare species in a sample, i.e. represented by less than 3 individuals.	Chao 1984
Chao2	NP	Incidence-based estimator. Takes into account the distribution of species amongst samples, i.e. the number of species that occur in only 1 sample ('rare species') and the number of species that occur in exactly 2 samples.	Chao 1984, 1987
Jack1	NP	First-order Jackknife. Is based on the species occurring only in a single sample.	Burnham and Overton 1979; Heltshe and Forrester 1983
Jack2	NP	Second-order Jackknife. Is based on the species occurring in only 1 sample as well as in the number that occur in exactly 2 samples.	Smith and Van Belle 1984
MMMean	P	Michaelis-Menten Mean richness estimator. Computes the mean accumulation curve. Is calculated by averaging over all accumulation curves derived from the selected runs.	Raaijmakers 1987

Estimator performance evaluation

Following Walther and Moore (2005), we calculated three different quality indicators that are commonly used to describe the performance of the chosen estimators: bias, precision and accuracy. Bias quantifies the mean difference between an estimated richness and the true species richness. For measuring bias we used the scaled mean error:

$$\text{Bias} = \frac{1}{\text{An}} \sum_{\text{j}=1}^{\text{n}} (\text{E}_\text{j} - \text{A}),$$

where A is the asymptote of the SAC, E_j is the estimated species richness for the $_j{}^{\text{th}}$ replicate, and n is the number of replicates. Positive and negative bias indicates overestimation and underestimation, respectively.

Precision measures the variability of estimates among repeated estimation runs for a given sample. For measuring precision we used the complement of the coefficient of variation, the latter being the ratio of deviation (SD) and mean ($\bar{\text{E}}$):

$$\text{Precision} = 1 - (\text{SD} / \bar{\text{E}})$$

Accuracy measures the closeness of an estimated value to the true richness (Brose and Martinez 2004). It is often measured using the mean squared error, combining bias and precision (Hellmann and Fowler 1999). Here we applied the scaled mean square error according to the formula:

$$\text{Accuracy} = 1 - (\frac{1}{\text{A}^2\text{n}} \sum_{\text{j}=1}^{\text{n}} (\text{E}_\text{j} - \text{A})^2),$$

where A is the asymptote of the SAC, E_j is the estimated species richness for the j^{th} sample, and n is the number of replicates.

Quantifying the relation between estimation error and number of replicates

The relative estimation error of the six estimators was expressed using the following formula:

$$y = (\text{E} / \text{A})\ 100,$$

where y is the estimation error (in percent), E represents the estimated species richness given by an elected estimator, and A is the asymptote of the SAC in a given habitat. The mis-estimation was then plotted against the number of replicates using a logarithmic model. This model takes the form:

$$y = a + b \ln(x)$$

where y represents the underestimation of a given estimator when compared to the asymptote of the SAC of a given habitat, x is the number of replicates and a and b are model parameters. Here too, the model was selected by the curve fitting software *CurveExpert* based on a high value of r and low estimate *SE*.

Assessment

Predicting the location of the asymptote

In all three habitats, species richness increased as a function of sampling effort (Figure 1). The total number of species observed in maximum sample size, i.e. 52 replicates, was 55 species in the soft-bottom habitat, 43 species for the natural hard-bottom assemblages and 32 species for the artificial hard-bottom habitat (Figure 1).

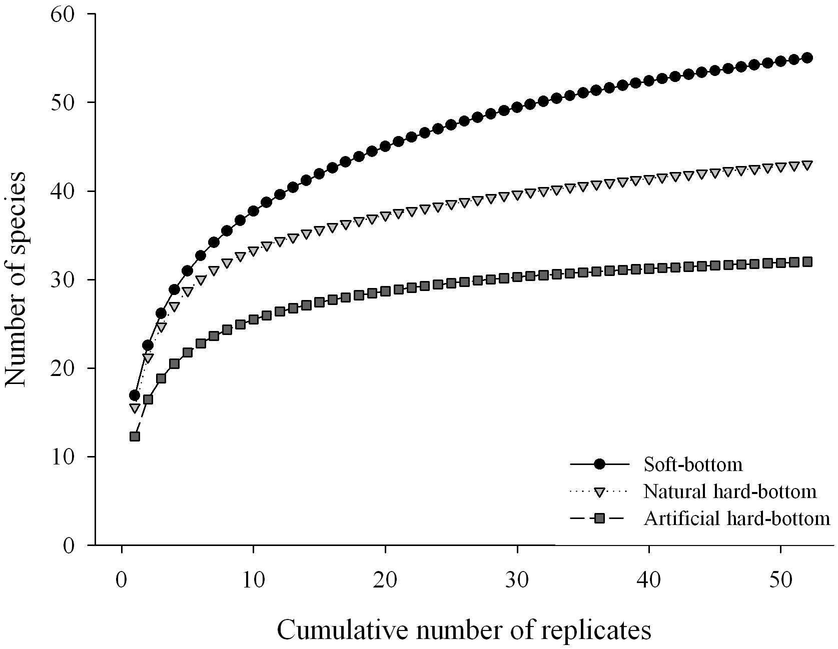


Figure 1. Species accumulation curves (SAC) for the three community types. These curves were plotted using the UGE index calculated in PRIMER 6.0.

The MMF model was chosen to extrapolate and predict the location of the asymptote. This model described the data of the SAC for the three habitats very well, with $r \approx 1$ for all curves (Table 2). Nevertheless, the model performed less well for the natural hard-bottom assemblages as indicated by a greater standard error of the estimate. The asymptote of species richness (parameter c) was located at 103 species for soft-bottom, 65 for natural hard-bottom and 38 for the artificial hard-bottom habitat (Table 2).

Table 2. Coefficients of correlation (*r*), standard error of the estimate (*SE*) and parameter values of the MMF model used for the extrapolation of the asymptote of the SAC for all habitats.

	Parameters					
Habitat	*a*	*b*	*c*	*d*	*r*	*SE*
Soft-bottom	-8.12	3.41	102.67	0.38	0.999	0.074
Hard-bottom	-63.05	0.63	65.48	0.27	0.999	0.205
Artificial hard-bottom	-3.62	1.60	37.90	0.58	0.999	0.023

Estimator's performance

In general, Jack2 performed better (with respect to bias and accuracy) at all replicate levels (low sampling effort: < 8 replicates; intermediate sampling effort: 8 - 16 replicates; high sampling effort: > 16 replicates) in the three habitats (Figure 2). The estimator MM also had a satisfactory performance at low replication for all habitats, but with increasing sampling effort its performance in terms of bias and accuracy improved less steeply as for the other estimators. In most cases, at low and intermediate sampling effort, Chao1, Chao2 and ACE performed worse. Bias decreased with rising sampling effort and was consistently negative (i.e., underestimation) for all estimators in the soft-bottom and natural hard-bottom habitats (Figure 2A - B). In the artificial hard-bottom habitat, too, all six estimators underestimated the asymptote of the SAC with the single exception that at replicate level 52, Jack2 produced the only overestimation ever observed (Figure 2C). Generally, the underestimation was more pronounced for the soft-bottom communities.

Accuracy improved steadily with increasing replication, with a similar slope in all community types, but generally more smooth in the soft-bottom communities (Figure 2D - F). Jack2 was the most accurate estimator in all habitats when replication exceeded 2. At low and intermediate sampling effort, MM was as accurate as Jack2 for the natural and artificial hard-bottom habitats (Figure 2E – F). In contrast, MM was the least accurate estimator for the soft-bottom community (Figure 2D) and at high sampling effort for the other two habitats.

Precision of the estimation increased rapidly in the first 10 replicates and more slowly after that (Figure 2G - I). This pattern was similar in all communities, probably because it is a statistical property (i.e. it approximates to the standard deviation). Nevertheless, in the natural hard-bottom assemblages, Jack2 showed a high imprecision at intermediate sampling effort due to a large variability of species richness within replicates (Figure 2H). In this habitat both of the Chao estimators showed weak precision at low sampling effort. Precision was 1 at maximum sampling effort for the natural hard-bottom habitat as there was only one possible combination of the 52 replicates (Figure 2H). MM showed high precision in almost all levels of replication and all community types. While the shapes of all curves are comparable for the 3 community types, for a similar quality of estimation less replicates are required for the artificial hard-bottom community than for the soft-bottom community.

In summary, Jack2 seems to be the most appropriate choice at all levels of sampling effort for all habitats. MM constitutes an alternative solution at low sampling effort for the natural and artificial hard-bottom habitats.

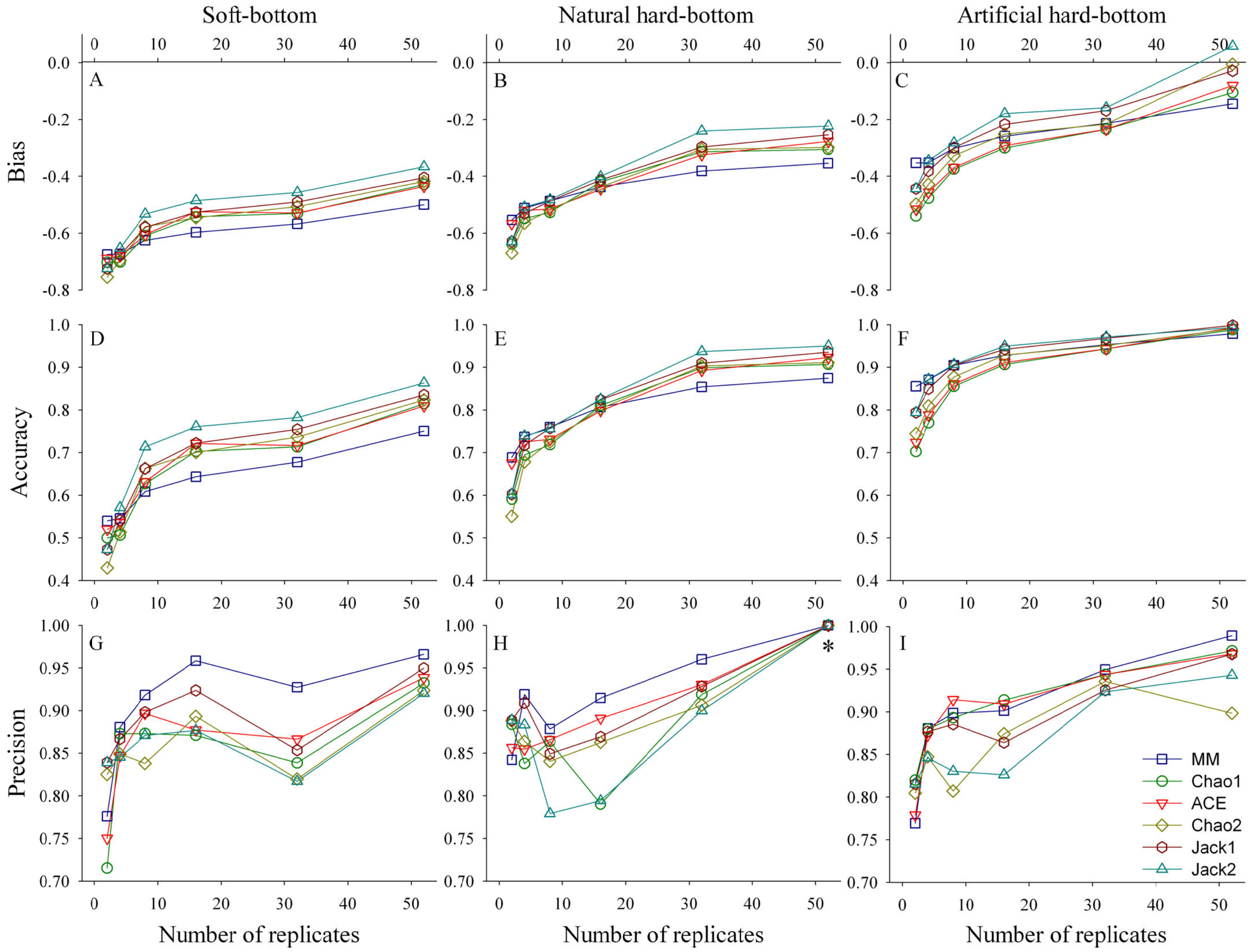


Figure 2. Bias (panels A - C), accuracy (D - F) and precision (G - I) of the selected estimators (MM, Chao1, ACE, Chao2, Jack1 and Jack2) for the three habitats using variable replicate numbers. * In panel H precision was 1 at replicate level 52 as there was only one set of 52 replicates.

For all community types and all estimators, the relative mis-estimation and its error decreased with increasing replication (Figure 3). It should be noted, however, that the decrease in error, especially at replication levels 32 and 52, might be an artefact caused by the statistically increased probability of re-sampling of the same replicates.

In the soft-bottom data-set, underestimation was never lower than 35%, even at maximum sampling size (Figure 3A). In the natural hard-bottom communities, it was always larger than 20% (Figure 3B).The underestimation was lowest for the artificial hard-bottom habitat (Figure 3C). At low sampling effort, which probably is the most common case in ecological studies, MM and Jack2 yield a substantially better estimation of regional richness than the other four estimators for all assemblages. At maximum sampling size for the artificial hard-bottom habitat, average mis-estimation was below 20% for MM, ACE, Jack1, Chao1 and Chao2, while Jack2 overestimated the asymptote of the SAC (Figure 3C).

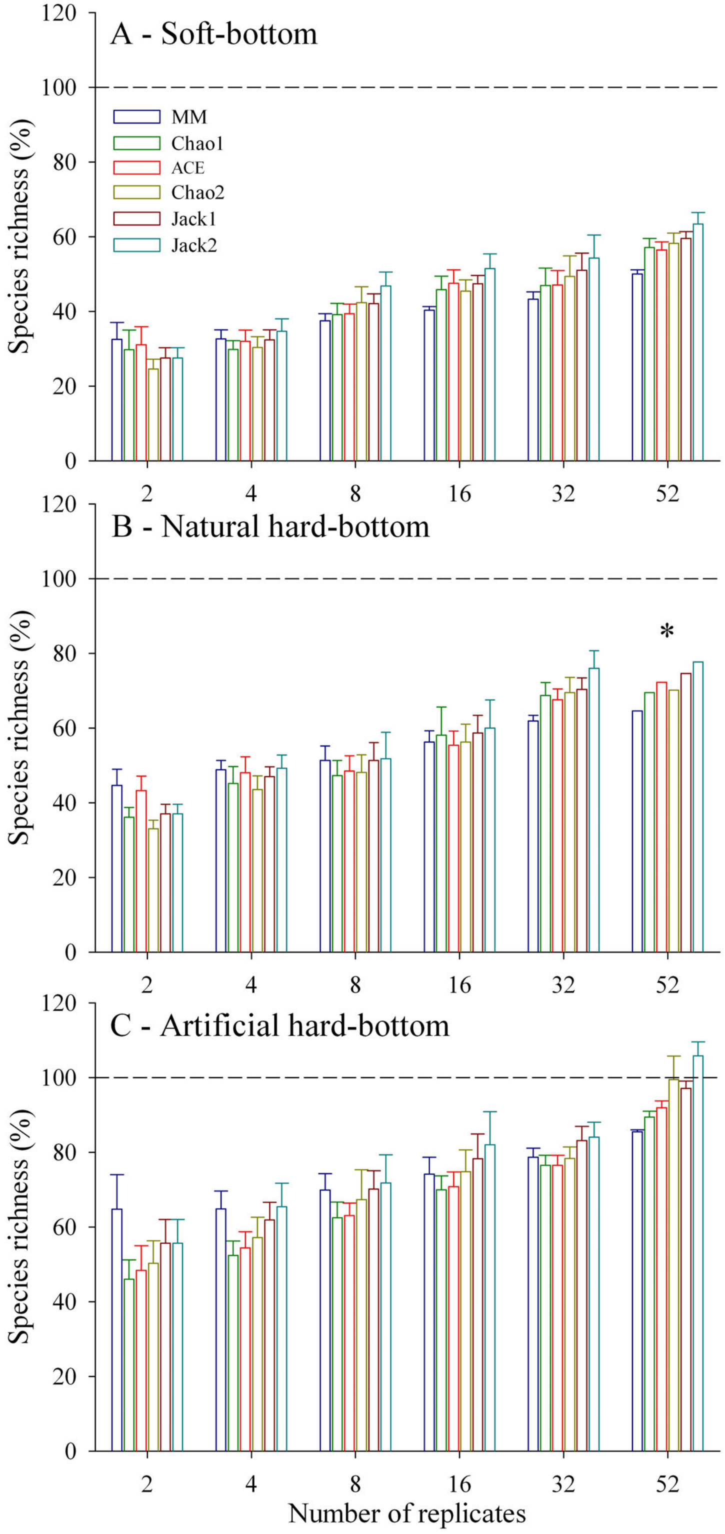


Figure 3. Percentages of asymptotic species richness estimated by MM, Chao1, ACE, Chao2, Jack1 and Jack2 using variable replicate numbers for the (A) soft-bottom, (B) natural hard-bottom and (C) artificial hard-bottom habitats. Means and 95 % confidence intervals are indicated (n = 10). Dashed line indicates the asymptote of the SAC given by the UGE index. * In panel B at replicate level 52 confidence intervals are zero as there was only one set of 52 replicates.

To investigate in more detail the mis-estimation in all habitats, we have selected a logarithmic model and the Jack2 estimator due to its best overall performance. The logarithmic model properly described the data for all habitats (Figure 4; soft-bottom: r = 0.98, SE = 2.67; natural hard-bottom: r = 0.98, SE = 3.39; artificial hard-bottom: r = 0.96, SE = 5.51). The mis-estimation is decreasing with replication. Based on this model, we quantified the bias caused by low replication for all habitats (Table 3). With each doubling of replication number the mis-estimation by Jack2 decreases in average by 6.6% for the soft-bottom habitat, 8.4% for the natural hard-bottom habitat and 8.5% for the artificial hard-bottom habitat (Figure 4, Table 3).

Overall, we have demonstrated that Jack2 performed best in all habitats. Using the logarithmic model, we predict that one would need 1865 samples to equal the asymptote of the SAC in the soft-bottom habitat (Table 3). For the natural and artificial hard-bottom habitats, a considerably less sampling effort would be required to reach the asymptote of the SAC.

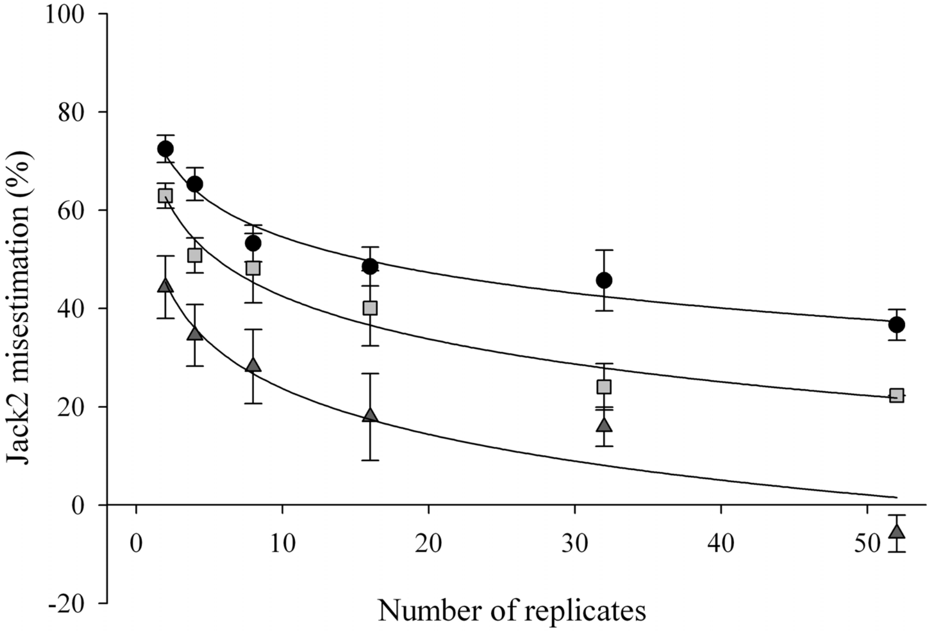


Figure 4. Mis-estimation by Jack2 using variable replicate numbers for the soft-bottom (●), natural hard-bottom (■) and artificial hard-bottom (▲) habitats using the logarithmic model $y = a + b \ln(x)$. Means and 95 % confidence intervals are indicated (n = 10).

Table 3. Quantification of the mis-estimation by Jack2. Based on the logarithmic model we calculated the approximate mis-estimation by Jack2 (%) to compensate the bias caused by low replication. With the same model we also calculated for each habitat, the required sampling effort for the Jack2 estimator to be unbiased ($y(0)$).

	Number of replicates						
Habitat	2	4	8	16	32	52	$y(0)$
Soft-bottom	71.37	64.14	56.9	49.67	42.43	37.37	1865.43
Natural hard-bottom	62.74	54.02	45.31	36.60	27.88	21.78	294.13
Artificial hard-bottom	45.36	36.07	26.71	17.39	8.07	1.54	58.31

Discussion

Studies that are searching for a clear understanding of the local vs. regional diversity pattern in the marine environment, have often defined the number of species in a region by questioning experts or consulting available species inventories (e.g. Rivadeneira et al. 2002; Witman et al. 2004). In many poorly studied areas, however, true regional species numbers are unknown. Therefore the statistical estimation of regional richness based on a limited number of replicates, constitutes an important alternative for the marine realm. In the present study we have evaluated the potential and limitations of such an approach. Fort this purpose we selected three data-sets with a large number of replicates from different temperate shallow water habitats. We compared the performance of six different estimators of regional richness against the asymptote of the species accumulation curve (SAC) using randomly selected replicates for a range of sample sizes.

The most conspicuous outcome of this analysis is that as a general rule the estimation of regional species richness based on local assemblages underestimates the asymptote of the SAC, regardless of habitat type, number of replicates, or selected estimator. The only exception was when a single estimator, Jack 2, using 52 replicates overestimated the asymptote of the SAC in the artificial hard-bottom habitat. For all estimators, the amount of underestimation gradually decreased with increasing sample size.

The mis-estimation was strongest in the soft-bottom environment, followed by the natural hard-bottom and the artificial hard-bottom habitats. Nevertheless, the similarity of the mis-estimation patterns between the three data sets is surprising in view of the (intentional) differences between the selected samples regarding community type, community age, diversity and method of sampling. For instance, the size of a single sampling unit was 1000, 400 and 225 cm^2, in the soft-bottom, natural and artificial hard-bottom samples, respectively. Thus, at comparable species density, a single replicate for the soft-bottom habitat possibly contained a larger proportion of the regional species pool than in the other samples. Also, the suspended PVC panels used for the Madeira data-set can be considered island communities on patchy substrata, with diversity possibly constrained by habitat (panel) size, while the samples from the other two data-sets were sub-areas from much larger contiguous habitats. Sample unit size and patchiness of habitat may affect the similarity between replicates and, thus, the initial slope of the curve. Moreover, the slow accumulation and consequently, the larger number of replicates required to reach the plateau in the soft bottom sample may be linked to the number of rare species present, as well as to the sensitivity of the sampling method.

Despite the extensive differences between the samples chosen with regard to size of sampling area, patchiness of habitat or age of community, the performance of the estimators applied to the described data-sets was comparable. This may be indicative of a remarkable robustness of the observed pattern. The fact that the six estimators underestimated the true richness (in this study assessed as the asymptote of the SAC) is consistent with other studies that use the same and other estimators (e.g. Petersen and Meier 2003; Brose and Martinez 2004; Cao et al. 2004). Beyond the general similarity among estimator's performances, Jack2 was more accurate and less biased for all habitats in almost all replication levels. In contrast, MM exhibited a high precision in all habitats. At low sampling effort, MM and Jack2 performed best in terms of bias, accuracy and precision for the natural and artificial hard-bottom communities. For the soft-bottom community, Jack2 was clearly the least biased and the most accurate estimator at all levels of replication. For estimations based on larger samples both Chao1 and ACE seem to perform slightly better than MM but worse than Chao2 and both Jackknifes. These findings are comparable to some previously reported results. For instance, the study by Walther and Moore (2005) revealed prime performance by Chao2 (Chao 1987) while, Jack2, Jack1 and Chao1 ranked 2nd, 3rd and 4th, respectively. The MMMean and ACE estimators were reported to perform worse (Walther and Moore 2005). Although they did not evaluate the performances of ACE, MM and Jack2, Foggo et al. (2003) concluded that amongst 6 different techniques to estimate marine benthos species richness, Chao1 represented the best non-parametric alternative for a limited number of survey units. In contrast, Ugland and Gray (2004) argue that Chao1 severely underestimates the true richness in benthic assemblages of the Norwegian continental shelf. In their study, Chao1 predicted approximately 1100 species from a data-set with 809 species. Nevertheless, when surveying larger areas of the shelf than the ones they use in their analysis (see their Table 1), over 2500 species were found (Ugland and Gray 2004). The large underestimation by Chao1 is caused by infrequent species (Ugland and Gray 2004). In a recent evaluation of 15 different estimators using arthropods abundances, Hortal et al. (2006) concluded that the performance of 10 estimators were highly dependent on the level of replication. In that study, Chao1 and ACE showed a higher precision at low replication but the superiority of these two estimators over the rest decreases with increasing sample size. Conversely, in a study using Monte Carlo simulations, Brose and Martinez (2004) showed that ACE, Chao1, Chao2 and Jack2 were positively biased under high replication. However, in some of the previously mentioned studies, 'true richness' was calculated based on inventories, experts, simulated landscape models or museum collection data (Brose et al. 2003; Petersen and Meier 2003; Brose and Martinez 2004; Cao et al. 2004; Hortal et al. 2006) and not on real and numerous community sub-units, as done in this study. If incomplete lists suggest a lower-than-real regional richness, apparent overestimations may result. Only one of the previously mentioned studies has estimated true richness based on the asymptote of the species accumulation curve (Foggo et al. 2003).

In this study, we used as a baseline for true regional richness the extrapolation of the SAC given by the UGE index using the non-linear Morgan-Mercer-Flodin (MMF) growth model (Morgan et al. 1975). The MMF model was previously employed in two surveys on the diversity of deep sea and littoral nematodes (Lambshead and Boucher 2003; Mundo-Ocampo et al. 2007). Lambshead and Boucher (2003) estimated the marine nematode species richness in 16 locations. They have compared the estimations given by the MMF model with the non-parametric incidence-based coverage estimator (ICE - Lee and Chao 1994; Chazdon et al. 1998; Chao et al. 2000). In 88% of the cases the estimation given by the extrapolation was higher than the estimation provided by ICE. In one instance both methods provided identical estimates of nematodes species, in another one ICE produced higher numbers (Lambshead and Boucher 2003). Mundo-Ocampo et al. (2007) used the same approach to compare nematode biodiversity in two shallow, littoral locations of the Gulf of California. In both locations, the MMF extrapolation gave a higher estimation of nematode richness than ICE (Mundo-Ocampo et al. 2007). Both studies did not attempt to quantify the relationship between mis-estimation and low replication, as we do here. In opposition to these investigations where SAC were plotted as a function of the accumulated number of *individuals*, our study uses SAC plotted against the accumulated number of *samples*. The decision which type of curves to use depends on the nature of the data available (Gotelli and Colwell 2001). If sample-based data are available, a SAC based on samples is preferable, as it can account for natural levels of sample patchiness (i.e. heterogeneity between replicates) in the data (Gotelli and Colwell 2001). A further distinction of the present study from the investigations by Lambshead and Boucher (2003) and Mundo-Ocampo et al. (2007) is the use of the T-S curve (given by the UGE index) developed by Ugland et al. (2003) followed by the MMF model fitting to it. The resulting extrapolation of the asymptotic richness is a more realistic estimation than the usual SAC (Ugland et al. 2003).

We demonstrate that the minimum sampling effort to reach a realistic estimation of true regional richness is variable among communities or sampling methodology. Below this threshold sampling effort estimation is negatively biased. The unavoidable mis-estimation caused by low replication can, however, be quantified as shown in this paper. In addition, the logarithmic function used to quantify the mis-estimation also informs at which sampling effort the estimation approaches the asymptote of the SAC. Consequently, we predict that if a weaker estimator in terms of performance is chosen, the logarithmic function will approach the x- axis far later, i.e. a greater amount of replicates would be required to equal the asymptote of the SAC.

The extrapolation of the SAC is a computation and the shape of the curve is affected by the presence/absence of rare species in the samples as well as the amount of samples used in the model. In order to assess how well the plateau reflects the "real" regional richness we compared the plateau values obtained by our approach to the numbers provided by existing comprehensive inventories in the three systems. (i) A 30-year-long survey of the soft-bottom macrofauna in the Kiel Bay, Western Baltic Sea lists 184 species at the Station “Millionenviertel 14” (Rumohr, pers com). (ii) On Helgoland island, three extensive studies in the same sub-habitats we used here, reported 53 sessile animal species (Janke 1986; Reichert 2003) and 39 species of macroalgae (Inka Bartsch, unpublished data). (iii) Finally, studies on the diversity of hard-bottom communities growing on artificial substrata conducted during three consecutive years in the south coast of Madeira Island (Jochimsen 2007; Canning-Clode et al. 2008, Manfred Kaufmann, unpublished data) reported a total of 44 species growing on the same type of substrata, depth and study site as the artificial hard-bottom data-set in this analysis. Compared to these values our extrapolation still underestimates the “real” richness of the investigated habitats by 44% for the soft-bottom, 29% for the natural hard-bottom and 14% for the artificial hard-bottom habitats. However, it should be noted that the reference lists include species from several seasons, years and successional stages which, in contrast to our data set, do not necessarily co-exist at the local scale. Regional species pools based on such inventories may include species not susceptible to recruit into the community considered because they are restricted to different habitats and seasons.

We conclude that regional richness can be estimated from sub-samples, that the quality of the estimation increases with sample size, and that the magnitude of the unavoidable mis-estimation can be quantified and, thus, corrected to some extent. We encourage further studies to include data from more locations and then provide more robust correction values to compensate the bias caused by low replication.

Chapter III

Local-regional richness relationship in fouling assemblages – effects of succession and regional richness assessments

Abstract

The number of species in a local habitat depends on local and regional processes. One common approach to explore ecological saturation of local richness has been to plot local versus regional richness. We expand this approach by incorporating two dimensions of diversity - taxonomic and functional - and different successional ages of marine fouling communities. In four different biogeographic regions (Mediterranean Sea, NE Atlantic, Western Baltic Sea and North Sea) 60 experimental units made from artificial substratum were deployed for colonization. Local richness was assessed as the average number of species and functional groups (FG) per unit area while regional richness was estimated using the non-parametric richness estimator Jack2 for both species and FG based on local panel communities. We also investigated the influence of two measures of regional richness: one-time listing of species (transient RR) versus species cumulated over repeated assessments (total RR). Our findings indicate that the nature of the relationship between local and regional diversity is sensitive to successional stage, the dimension of diversity considered and the way regional richness is estimated. However, as a general pattern, for taxonomic and functional richness, the slope of the local-regional relationship increased in the course of succession. We discuss how this pattern could have been produced by a combination of early recruiting species limitation and the progression of competitive exclusion during succession.

Introduction

The number of species in one location has been reported to depend on two categories of processes: local and regional (Caley and Schluter 1997; Ricklefs 2004; Shurin and Srivastava 2005). The terms ‘local’ and ‘regional’ are related to the spatial scale at which ecological and biogeographic processes, respectively, prevail. Local processes include predation, parasitism, competition or disturbance while long-distance dispersal, speciation or extinction are considered regional processes (Cornell and Lawton 1992). A widely used approach for evaluating the relative influence of local versus regional processes on local assemblages has been to plot local versus regional richness, a method originally employed by Terborgh & Faaborg (1980). Since their publication in 1980, the local-regional relationship has been investigated in more than a hundred studies for different taxonomic groups, spatial scales and habitats (Russell et al. 2006). In most studies, the plotted relationships were positive and linear which has been interpreted as regional species richness driving local species richness with little richness limitations imposed by local processes (for reviews, see Lawton 1999; Srivastava 1999; Shurin and Srivastava 2005). For such relationship, local communities are referred to as “unsaturated” or “type I”. Conversely, if the plot shows a relationship where local species richness reaches an asymptote at high levels of regional richness, local communities are referred to as “saturated” or “type II” and local limiting processes seem important (Cornell 1985; Cornell and Lawton 1992).

In recent years, however, the use of the local-regional richness plots to examine species saturation has been criticized on a number of different grounds (for reviews see e.g. Hillebrand and Blenckner 2002; Hillebrand 2005; Shurin and Srivastava 2005). Thus, Hillebrand & Blenckner (2002) pertain that the local-regional richness relationship is sensitive to the definition of local and regional scales, i.e. a linear relationship could be caused by autocorrelation when the local area is relatively large as compared to the regional area considered. This problem can be avoided using independent data-sets to measure local and regional richness (Srivastava 1999) as well as by selecting scales for sampling local richness that are sufficiently small, to reduce internal environmental heterogeneity (Harrison and Cornell 2008). Drawbacks can also emerge by inappropriate statistical analysis. For example, if local diversity is underestimated and/or regional diversity overestimated, a phenomenon recognized as *pseudosaturation* may occur (Cornell 1993; Srivastava 1999). However, suggestions have been made recently to circumvent this setback: underestimation of true local richness can be corrected using indices that take into account the presence/absence of rare species (e.g. non-parametric estimators), while regional overestimation can be avoided by including in the regional richness only those species capable to recruit into the local habitat (Harrison and Cornell 2008).

One central aspect ignored in most previous studies is that the drivers of the relationship, and as a consequence the resulting relationship, may change during community assembly (Morton and Law 1997). Only a few theoretical and observational studies have postulated a successional shift of the local-regional richness relationship (Mouquet et al. 2003; Fukami 2004; Munguia 2004; Starzomski et al. 2008). Mouquet et al. (2003) predicted, in a theoretical model, saturation at early stages of the assembly process since only a subset of the regional species pool may be available to colonize a local habitat. At an intermediate successional stage, an unsaturated relationship is expected because competitive exclusion of species takes time. At last, when communities reach an equilibrium, competition should induce a saturated relationship (Mouquet et al. 2003).

Assuming that saturation of local assemblages is induced by local processes such as competition, we predict that this process should be more intense and saturation reached faster when species functionally overlap considering the limiting resource(s). A recent study on the number of functional groups that may coexist in a community and its relationship with regional species richness (Canning-Clode and Wahl Submitted) suggests that the local-regional relationship is sensitive to succession as well as to the dimension of diversity (taxonomic versus functional) considered. Species richness and functional richness shifted from unsaturated to saturated during succession, but species richness reached saturation faster than functional richness (Canning-Clode and Wahl Submitted).

In addition, the size of the regional species pool, which is influenced by regional processes, logically affects local diversity patterns (Karlson et al. 2004). Therefore, if different methodologies in assessing regional richness are used, the shape of the local-regional diversity pattern is expected to change.

Here, we investigate the local-regional richness relationship in marine fouling assemblages using an expanded approach. The percent cover of all sessile species present in our experimental units has been recorded in four different biogeographic regions located in the northern hemisphere. Both taxonomic and functional richness measured at three different successional ages (3, 6 and 12 months) have been taken into consideration. Further, we compare the shape of the pattern for differently calculated regional richness: “transient regional richness” (i.e. species colonizing during a given period) versus “total regional richness” (i.e. species colonizing during any phase of the experiment). In particular we hypothesize that the relationship between local and regional richness in fouling assemblages is affected by the size of the regional species pool considered, the dimension of diversity used, and by the successional stage of a community as predicted by Mouquet et al. (2003).

Materials and methods

Study system and functional richness

The experiment lasted 12 months and was conducted, simultaneously, in four different regions located in the northern hemisphere: Athens, Greece, Mediterranean Sea (37º 53’ 32’’N, 23º 43’ 04’’ E), Madeira Island, NE Atlantic (32º 44’ 30’’N, 16º 42’ 40’’ W), Kiel Bight, Germany, Baltic Sea (54º 21’ 57’’N, 10º 08’ 54’’ E) and Helgoland Island, North Sea (54º 10’ 49’’N, 07º 53’ 20’’ E). Hereafter, these regions are referred to as Mediterranean, NE Atlantic, Baltic Sea and North Sea regions, respectively.

At the staggered beginning of the experiment (March – May 2006), 60 polyvinylchloride (PVC) panels (15 x 15 x 0.3 cm) distributed in 6 PVC rings (60 cm diameter, 25 cm height) hung from a buoy at approximately 0.5 m depth, were exposed for colonization at each region. The minimum distance between rings was 2 meters. Communities colonizing the experimental units over the next 12 months were structurally analyzed by measuring percent cover of all sessile species larger than 1 mm at three different successional ages: 3 months (July – August 2006), 6 months (September – November 2006) and 12 months (March – May 2007). Three month old communities comprise early recruits that only settled in spring and early summer. Six month old communities encompass species that settled during spring and summer while twelve month old panels represent all year's settlers, excluding species that disappeared in the course of succession. Total percent cover could exceed 100% in case of multi-strata growth. Prior to the experiment we randomly determined 20 panels for each survey. Each panel was only used once to avoid carry-over effects between surveys.

Functional groups are either defined by their ecosystem services (Halpern and Floeter 2008) or by the way in which they use various resources (Arenas et al. 2006). With regard to their small scale co-existence the latter classification is more informative and was employed in this study. More competition among species within functional groups is expected since those species display overlapping requirements. In this work, functional groups (FG) were determined according to five ecological dimensions: body size, growth form, trophic type, modularity and motility (Wahl in press, Table 1). Each ecological dimension can be expressed in 2-5 qualities. For each species, the functional group was defined as the set of ecological qualities realized at the adult stage. We did not consider ontogenetic shifts of functionalities since larvae and juveniles constituted a relatively small portion of the individuals. Since our study focuses only on sessile hard-bottom assemblages, within the category 'motility', only the 'attached' type was considered.

Table 1. The five ecological dimensions used to determine the functional groups in this study (modified from Wahl in press).

Body size	Growth form	Trophic type	Modularity	Motility
S - <1mm	B – bushy	A – autotroph	C – colonial	A – attached
M -1mm - <10mm	E – encrusting	D - deposit feeder	S – solitary	B – burrowing
L - 10mm - <100mm	F – filamentous	G – grazers		C – crawling
X - 100 – 1000mm	M – massive	P – predators		D – drifting
XX - >1000mm		S - suspension feeder		S – swimming

Spatial scales and data analysis

In each region, local species richness was calculated as the average species number present on five randomly selected panels (from the 20 panels designed for a given survey). Correspondingly, local functional richness was defined as the average number of FG colonizing the same five panels.

In numerous studies the regional richness has been determined by questioning experts or consulting available species inventories (e.g. Rivadeneira et al. 2002; Witman et al. 2004). This approach can both under- and overestimate the regional number of relevant species. Thus, complete inventories of the fauna and flora of a region are often hard to obtain and in many areas, the true species richness of a region is unknown. On the other hand, many listed species may never colonize the habitat of interest because they have been registered in different areas or seasons. For that reason, the statistical assessment of regional richness based on a limited number of replicates, constitutes an important alternative (Colwell and Coddington 1994; Gotelli and Colwell 2001). In the present study, regional diversity (taxonomic and functional) was estimated as the asymptote of the species and FG accumulation curves using the second-order Jackknife estimator (Jack2 - Smith and Van Belle 1984).

This non-parametric estimator takes into account the distribution of species amongst samples, i.e. considers both the number of species found in one sample only (‘infrequent species’) and in exactly two samples. Species accumulation curves were built from 999 permutations of the panels reserved for this estimation in each region using the PRIMER software (Clarke and Gorley 2006). In a recent evaluation on the performance of six different estimators at different habitats, Jack2 was reported to perform best for a large range of sampling effort. In particular, Jack2 had prime performance in an almost identical study system as we use here, i.e., using the same substratum, size of experimental units and depth (Canning-Clode et al. Submitted). In this analysis, we calculated taxonomic and functional regional richness at two temporal scales: by restricting the estimation to the panels of single sampling events we estimated the number of regionally available species which in fact settled at the given depth, on the given substrata during the period considered (n = 15; ‘transient’ regional richness); basing the estimation on the panels designated for the evaluation of regional richness of all sampling events we produced the number of regional species colonizing the given substrata at the given depth at any time during the experimental duration (n= 45; ‘total’ regional richness). Both are relevant sub-sets of species inventories listing all observed species regardless of season, year, depth or substratum. To avoid autocorrelation between spatial scales, panels used for local diversity assessment were not considered for the regional pool.

Space has frequently been confirmed as a limiting resource (Stachowicz et al. 2002). In order to assess the potential for competition for space in local assemblages, we have calculated the average total percent cover of fouling species colonizing local panels (n = 5) through time presuming that the intensity of competition relates inversely with the availability of this resource.

The relation between local and regional richness was determined at different stages of succession for both transient regional richness (transient RR) and total regional richness (total RR). This was done to test whether this relation is affected by the size of the regional species pool considered.

We used linear regression between log local diversity ('independent') and log regional diversity ('dependent') (for both dimensions of diversity) to distinguish between 'type I' and 'type II' curves. In this double log analysis, a slope of 1 indicates a continuous rise of local diversity with increasing regional diversity, while a slope significantly smaller than 1 represents local saturation (Griffiths 1997). This method was reported advantageous when compared to the common linear and nonlinear regressions since estimates of the slope are not influenced by the errors present in the independent variable and thus the slope can be used for more consistent meta-analytical comparisons (Hillebrand and Blenckner 2002).

Results

Taxonomic total RR (all seasons pooled) was the highest in the North Sea region, followed by the Mediterranean, NE Atlantic and Baltic Sea regions (Figure 1A). Functional total RR ranked in a slightly different order: North Sea, NE Atlantic, Mediterranean and Baltic Sea (Figure 1B). Total species and functional groups accumulation curves for the Mediterranean region were constructed only based on 35 replicates because 10 panels were lost during the second sampling. Using almost identical conditions as we use here (substratum, panel size and depth), Canning-Clode et al. (Submitted) quantified the error by Jack2 in estimating regional richness. At this level of sampling effort (n = 35), Jack2 underestimated true richness by 6.8% only (Canning-Clode et al. Submitted). Therefore, we do not expect severe implications in the local-regional richness analysis. Throughout the succession process of fouling assemblages, the transient RR displayed a different pattern than total RR (Table 2). Here too, accumulation curves for the Mediterranean region after 6 months, were constructed only based on 5 replicates (instead of 15) due to the loss of experimental units. However, at these circumstances, differences in the estimation may be expected since according to the analysis by Canning-Clode et al. (Submitted) an underestimation of 33.04% and 18.25%, for 5 and 15 samples, respectively, is predicted. Among the four regions, values for both taxonomic and functional regional richness were higher for the North Sea region after 3 and 6 months of colonization, while the NE Atlantic region was the most diverse region after 12 months. Low levels of transient regional diversity were recorded at all succession ages in the Baltic Sea region (Table 2).

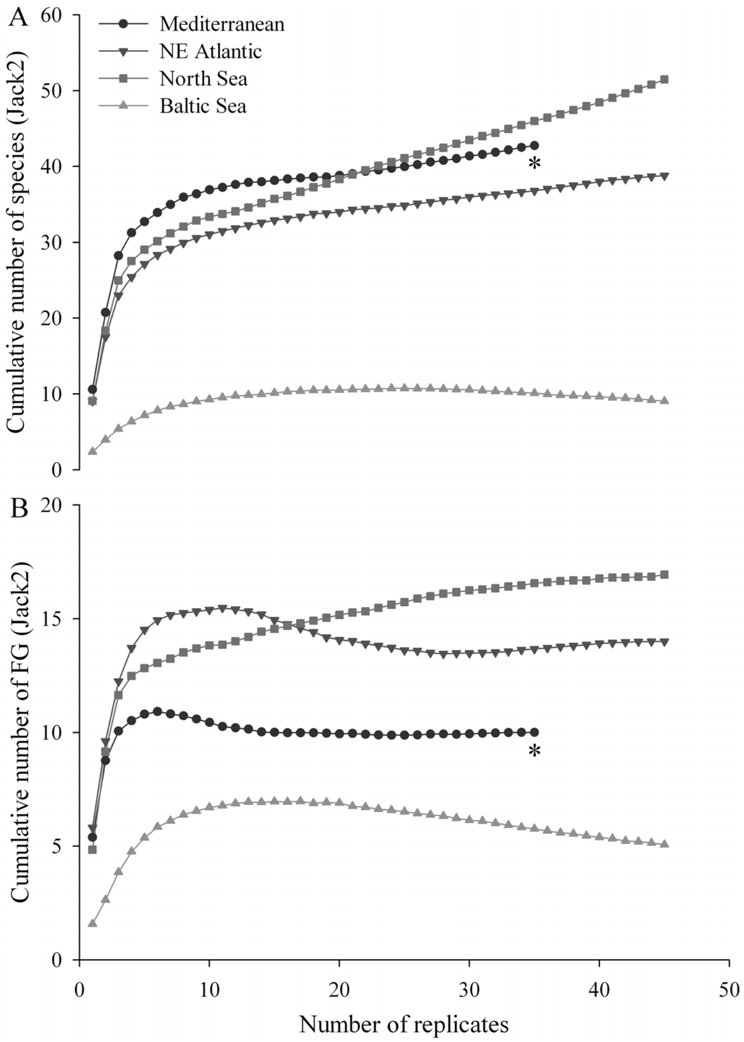


Figure 1. Species (A) and functional groups (B) accumulation curves for 4 regions as a function of number of panels by using the Jack2 estimator of species richness. The endpoint of each curve was used as total regional richness in the log-log regression of local-regional richness. * Jack2 estimation at the Mediterranean region is based on 35 replicates due to the lost of replicates after 6 months of succession.

Table 2. Transient regional richness for both taxonomic and functional diversity. Transient regional richness was estimated as the asymptote of the species accumulation curve using the non-parametric estimator Jack2 based on 15 replicates per each sampling event (* for the Mediterranean region only based on 5 replicates).

	Taxonomic transient RR			Functional transient RR		
Region	3 months	6 months	12 months	3 months	6 months	12 months
Baltic Sea	4.00	6.00	6.00	2.00	5.00	5.00
Mediterranean	9.00	19.30*	36.20	6.00	8.40*	9.00
NE Atlantic	10.00	23.40	32.59	7.00	12.80	14.80
North Sea	18.80	29.99	32.40	12.80	13.79	12.00

With the exception of the Mediterranean region after 3 months and North Sea after 6 months, average percent cover of local fouling species always exceeded 100% (Figure 2) suggesting a large potential for competition for space even at early stages of succession.

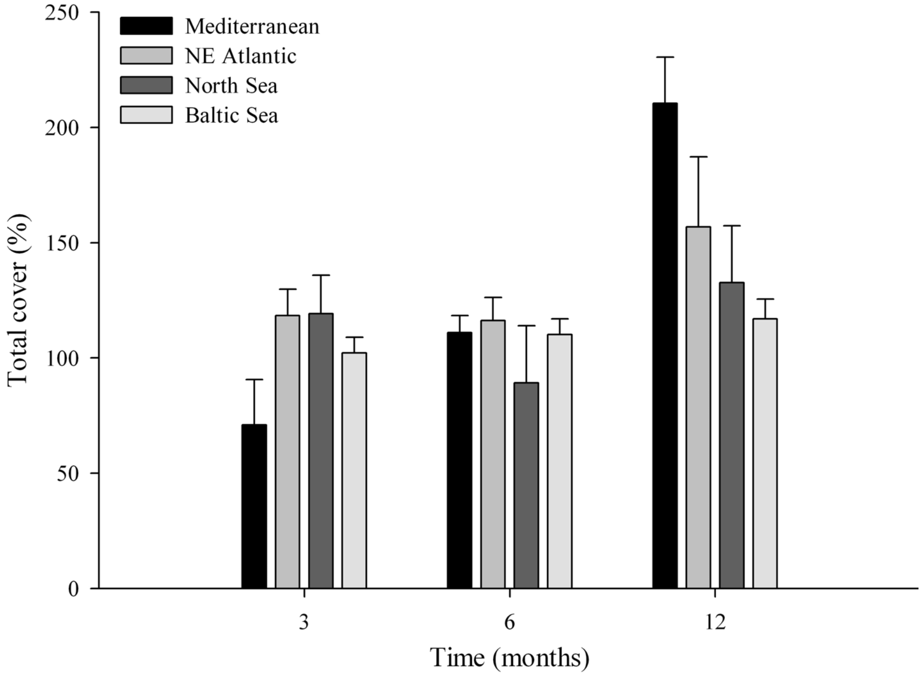


Figure 2. Total percent cover of fouling species colonizing local panels (n = 5) at all regions throughout succession. Means and 95% confidence intervals are indicated.

Taxonomic and functional diversity in the course of succession related similarly in all regions regarding total as well as transient RR (Figure 3). For both dimensions of diversity, the portion of total RR species coexisting at the local scale increased during succession (Figure 3A-B). However, for taxonomic diversity all ratios along succession were below 0.4 which indicate that the regional pool of species colonizing these substrata at this depth was at least 2 times higher than the average number of species found on a given panel (Figure 3A). In general, the number of locally found FG was closer to the regionally available functional richness, particularly after 12 months were ratios exceeded 0.5 in the Mediterranean and Baltic Sea regions (Figure 3B). In contrast, an almost opposite pattern was found when for transient RR, i.e. the local/regional richness ratios decrease with time (Figure 3C-D). At the first successional age, Mediterranean, NE Atlantic and Baltic Sea regions showed very high ratios in both dimensions of diversity, indicating that regional richness was not much higher than local richness. This might be explained by high initial homogeneity among samples leading to a lower estimate of transient RR. Additional infrequent species and more heterogeneity among samples may have caused a decrease in local/regional richness ratios in the subsequent surveys. High levels of transient RR in the North Sea region at the first two successional ages (Table 2) contributed to the lowest local/regional richness ratios in that region (Figure 3C-D).

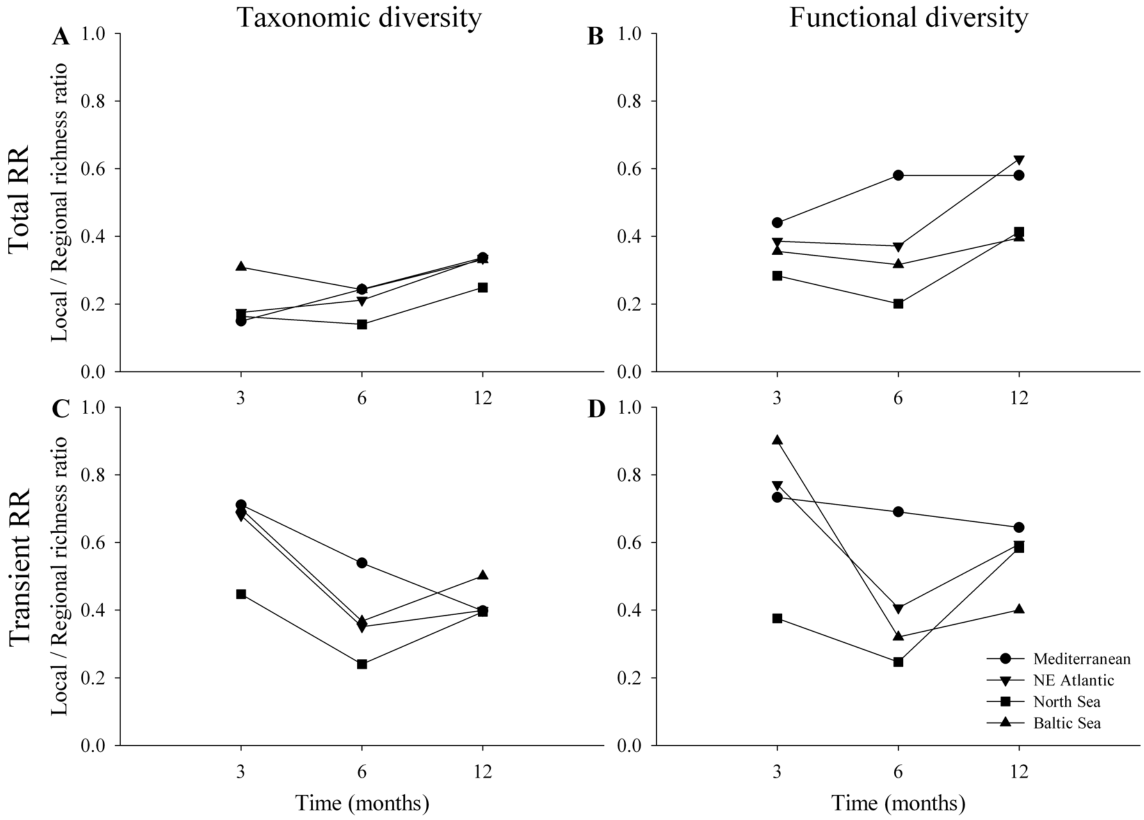


Figure 3. Local / regional richness ratios at all stages of succession for taxonomic diversity and total RR (A); functional diversity and total RR (B); taxonomic diversity and transient RR (C); functional diversity and transient RR (D).

Whether considering total or transient RR, the slope of the log-log regression tends to increase with time for taxonomic richness (Figure 4A, C) indicating that a larger portion of the RR species coexists in more mature communities. Independently of the general trend, saturation is significant after 3 months relative to total RR (Figure 4A), and after 12 months relative to transient RR (Figure 4C). For functional diversity, the slope was not significantly different from 1 (due to large variance) at all stages of succession and for both methods of regional richness assessment (Figure 4B, D). Here, the slope of the log-log regression tends to increase during succession only for transient RR (Figure 4D).

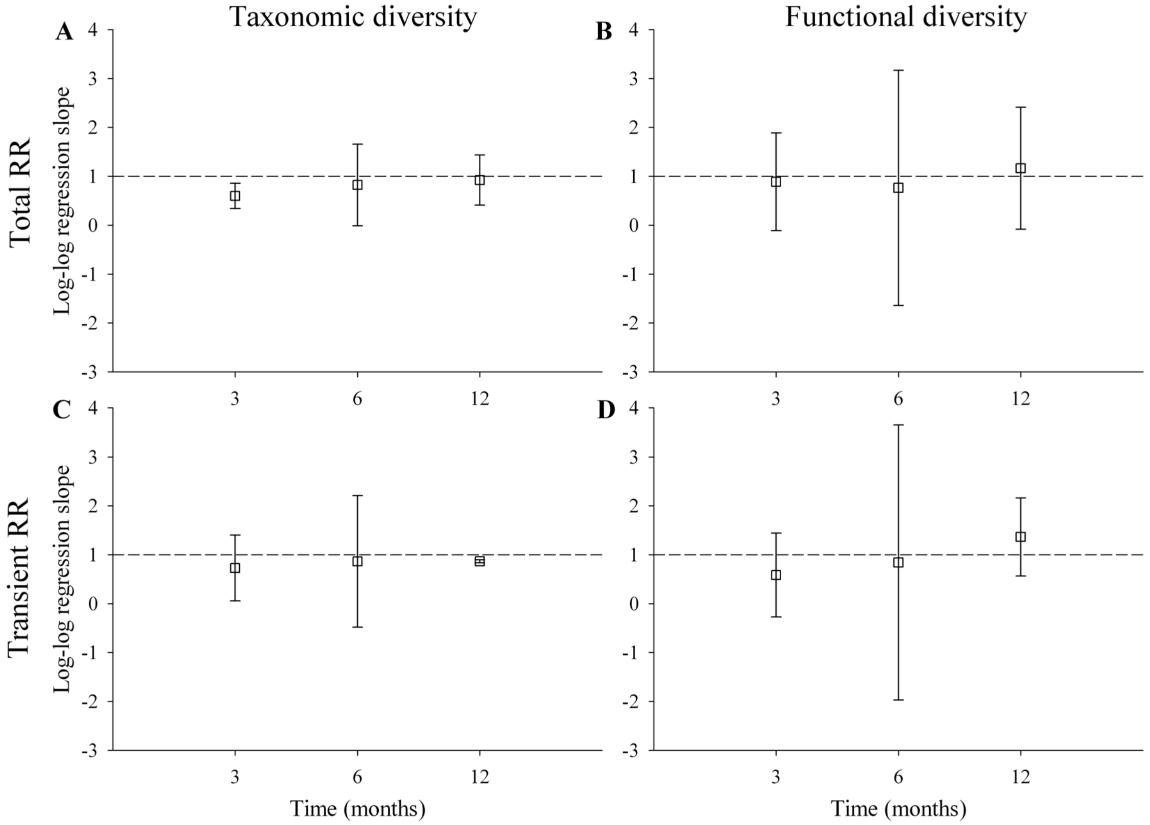


Figure 4. Slopes of the double log regression analysis over time for taxonomic diversity and total RR (A); functional diversity and total RR (B); taxonomic diversity and transient RR (C); functional diversity and transient RR (D). Slopes and 95% confidence intervals are indicated. Dashed line indicates a slope = 1. A slope that does not differ from 1 is indicative of unsaturation while local saturation is represented by a slope significantly smaller than 1.

Discussion

In recent years, for a variety of statistical and theoretical issues, regressions of local against regional richness have been criticised (e.g. Hillebrand 2005; Shurin and Srivastava 2005).

In this study we avoided a number of these drawbacks by following several recommendations (Hillebrand and Blenckner 2002; Harrison and Cornell 2008). First, we employed an independent characterization of both spatial scales to avoid circularity between local and regional scales. Second, *pseudosaturation* caused by overestimation of regional richness was avoided by using for the estimation of the regional species or functional pool only those species or FG capable of occupying the local habitat at the given depth and time. Third, a possible underestimation of true regional richness was corrected by using the non-parametric estimator Jack2 which is based on the presence/absence of infrequent species. Moreover, Jack2 was found to have prime performance among five other estimators in a study performed at almost identical circumstances as we use here (Canning-Clode et al. Submitted). Finally, we used the double-log regression to distinguish between 'type I' and 'type II' curves.

To the best of our knowledge, this is the first contribution on the local-regional richness relationship that incorporates simultaneously different successional stages, two dimensions of diversity, and different methods of assessing regional richness. We demonstrate that the relevant regional richness, i.e. the regionally available colonizers, varies in time, and is larger when pooling all sampling events. In contrast to the common use of species inventories, our method of estimating the relevant regional pool of species or functional groups avoids the danger of including species which were not available during the assembly of a community or which for ecological reasons would not establish in the particular habitat under consideration.

Independently of the method used to calculate taxonomic regional richness, the 'degree of unsaturation', the mean slope of the log-log relationship, tend to increase in the course of succession. However, saturation is significant at the first and last successional stages when considering total and transient RR, respectively. In contrast, local communities with regard to functional diversity displayed an unsaturated pattern at all successional ages for both methods in assessing regional richness.

For taxonomic diversity and considering total RR, our findings partially corroborate the theoretical approach developed by Mouquet et al. (2003). According to their model we would have expected to find (pseudo-)saturation early in succession, followed by transient unsaturation and possibly merging into saturation at a more mature stage of community assemblage. Indeed, in our study 3 month old communities were saturated changing to unsaturated in the 2 subsequent surveys. We can not exclude that the second saturated pattern was not obtained because communities were still immature. However, space was limited from a community age of 3 months onward and competitive exclusion should have had sufficient time to produce saturation. Only with regard to transient RR did taxonomic local communities display a 'type II' curve after 12 months of colonization. Disturbances can limit competitive exclusion and, consequently, the appearance of a saturated relationship. However, our method of suspending fouling panels from floats limited benthic predation or mechanical damage and, indeed, disturbance marks were rarely observed.

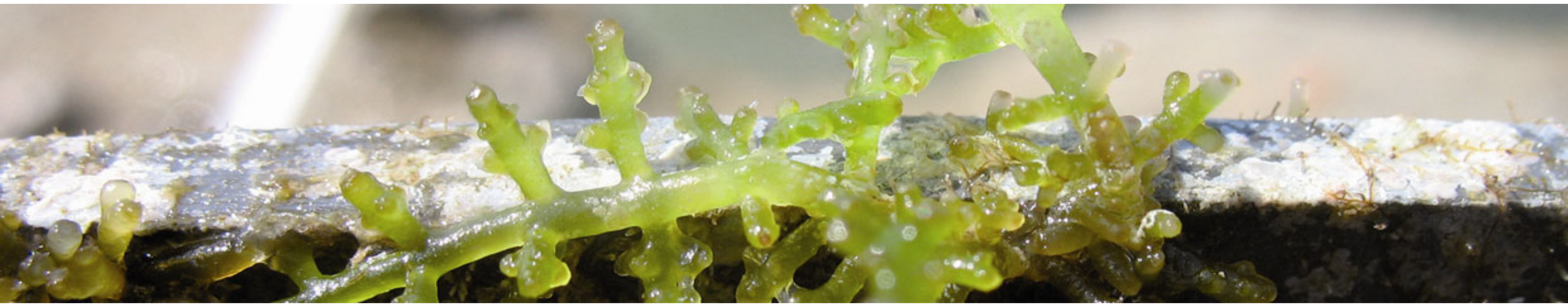
The model by Mouquet et al. (2003) should be used just as a general qualitative trend since the time scales depend on the dynamics of colonization and the competition mode of the communities under investigation. There was no prediction in Mouquet's model for the development of the local–regional relationship regarding functional diversity. However, in a recent global study on the local-regional richness pattern in fouling assemblages, Canning-Clode & Wahl (Submitted) incorporated functional richness. In their study, the mean slope of the log-log relationship for functional richness, tended to decrease in the course of succession, becoming saturated with time, which may indicate that the community is ‘filling up’ functionally (Canning-Clode and Wahl Submitted).

Interestingly, in displaying the same unidirectional trend towards unsaturation for taxonomic diversity, both methods of assessing regional richness seem to have their individual advantages. By estimating regional richness based on pooled samples from 3 different successional ages during 12 months and the corresponding seasons (total RR), we assure that the most species capable of recruiting under the given conditions (i.e. the relevant richness) are incorporated in the regional pool. On the other hand, by estimating regional richness based on single successional phases (transient RR), we make sure to consider the interaction between the available pool and the species recruiting locally. However, in the latter case, the assessment might lose power due to lower sampling effort (underestimation).

Finally, the present study on the local-regional richness relationship may also be influenced by the number of regions and the range of regional richness values. While more regions and a wider richness range are undoubtedly advantageous, some previous studies used even fewer regions (e.g. Hugueny et al. 2007). We consider that there are no simple rules concerning the number of regions one needs to examine the pattern as long as it is more than two and employs appropriate spatial scales and theoretical interpretations.

The core conclusion of this study is that the shape of the relationship between local versus regional diversity in fouling communities is sensitive to succession. Here we show that the mean slope of the log-log relationship, tend to increase in the course of succession. Therefore, we emphasize the need to incorporate this aspect in futures analysis of the pattern. In addition, we also demonstrate that the relevant regional richness varies in time and is larger when pooling all sampling events. As a consequence, the relationship between local and regional diversity is also affected by the way regional richness is estimated.

Chapter IV



Gradual saturation during succession of both taxonomic and functional local richness in fouling assemblages – a large-scale perspective

Abstract

The shape of the relationship between local and regional diversity has repeatedly been used to examine the contribution of regional processes on local assemblages for different habitats, taxonomic groups or spatial scales. We investigate this relationship using a new concept. This expanded approach incorporated both taxonomic and functional richness, different successional stages of marine fouling communities, and 8 different biogeographic regions. The shape of the relationship between local and regional diversity depended on successional stage, and the dimension of diversity considered, i.e. taxonomic versus functional richness. Both species richness and functional richness shifted from unsaturated to saturated during succession, but species richness reached saturation faster (4 months) than functional richness (8 months). Younger and unsaturated communities were not constrained by the availability of substratum while older and saturated assemblages were. Moreover, multivariate analysis determined that regional richness was not a primary factor affecting local fouling assemblages during succession.

Introduction

Understanding large-scale gradients in biodiversity has been of interest to ecologists since the time of the naturalist Charles Darwin (Leonard 2000). A congregation of theories that seek to explain the spatial variation in biodiversity has been examined including the *species-area relationship*, *latitudinal gradients in species richness* and the *relationship between local and regional richness* (reviewed in Gaston 2000). The number of species in one location has been reported to depend on both local and regional processes (Ricklefs 1987; Caley and Schluter 1997; Ricklefs 2004; Shurin and Srivastava 2005). Plots of local species richness against regional species richness have been used to compare the influence of local processes (e.g. disturbance, competition) and regional factors (e.g. speciation, migration) on local assemblages (e.g. Cornell and Lawton 1992; Hillebrand and Blenckner 2002; Witman et al. 2004; Freestone and Harrison 2006; Russell et al. 2006; Cornell et al. 2008). Theoretically, if regional species richness is driving local species richness, a positive and linear relationship is expected, and we would expect more species coexisting in a given area or volume in more species-rich regions. In this case, communities are referred to as “unsaturated” or “type I”. In contrast, if local species richness finds a ceiling at high levels of regional richness local communities are referred to as “saturated” or “type II” (Cornell 1985; Cornell and Lawton 1992). “Type I” communities were reported more frequently suggesting that the regional availability determines the number of species in local communities (see reviews by Lawton 1999; Srivastava 1999; Shurin and Srivastava 2005).

In recent years, the use of the local-regional richness plots to examine species saturation has been criticized for different reasons: statistical concerns, the definition of the employed spatial scales and theoretical problems with its interpretation (Srivastava 1999; Hillebrand and Blenckner 2002; He et al. 2005; Hillebrand 2005; Shurin and Srivastava 2005). As a consequence, several of these pitfalls have been addressed and suggestions in improving the analysis of the local-regional richness relationship have been made (Harrison and Cornell 2008). One of the statistical problems arises when local diversity is underestimated and/or regional diversity overestimated, a phenomenon identified as *pseudosaturation* (Cornell 1993; Srivastava 1999). While the underestimation of true local richness can be corrected using indices that take into account the presence/absence of infrequent species (e.g. non-parametric estimators), regional overestimation can be avoided by including in the regional richness only those species capable to recruit into the local habitat (Harrison and Cornell 2008). Moreover, the relationship between local and regional species richness was recognized to be sensitive to the definition of the two spatial scales (Hillebrand and Blenckner 2002). If the area of the local habitat is large when compared with the area of the regional habitat the majority of species in the regional pool would be present in the local community, producing linear relationships caused by autocorrelation between the two scales (Hillebrand and Blenckner 2002). This problem can be avoided using independent data-sets to measure local and regional richness (Srivastava 1999) as well as by selecting scales for sampling local richness that are sufficiently small, to reduce internal environmental heterogeneity (Harrison and Cornell 2008).

In view of the fact that the number of species coexisting in a limited area or volume of habitat may be affected by other parameters than competition or predation and that the relationship may, on theoretical grounds, be expected to change during succession of a community (community assembly time, Mouquet et al. 2003) and likely with functional diversity, several authors (Russell et al. 2006; Cornell et al. 2008) have recently cautioned to view the plotted relationship alone more as a starting point for more thorough investigations.

To date, numerous studies have addressed the relationship between local and regional richness in different habitats, taxonomic groups and spatial scales (see Srivastava 1999; Hillebrand and Blenckner 2002). However, only a limited number of theoretical and observational studies have explored whether this pattern changes during succession of a community assembly (Mouquet et al. 2003; Fukami 2004; Munguia 2004; Starzomski et al. 2008). In their theoretical model, Mouquet et al. (2003) predicted saturation at early stages of the assembly process since only a subset of the regional species pool may colonize a local habitat. At intermediate stages of assembly time, a positive linear relationship is expected because competitive exclusion of species takes time. Finally, when communities are at equilibrium, competition induces a curvilinear relationship (Mouquet et al. 2003). In a succession survey of marine benthic communities on pen shells at independent regions of St Joe Bay in Florida, Munguia (2004) showed that both motile and sessile species richness increased over time. In addition, the author found different shapes in the local-regional species richness plots through time: motile species exhibited saturation while sessile species showed an unsaturated pattern. Munguia (2004) further suggests that the level of species saturation will depend on the successional stage of a community.

If communities exhibit species saturation as a consequence of competitive exclusion this process should be more intense and saturation reached faster when species functionally overlap with regard to the limiting resource(s). How many functional groups may coexist in a community and how this relates to regional species richness has never been explored before. The degree to which different species show similar functional qualities may result in different relationships between taxonomic and functional diversity (Micheli and Halpern 2005). One possible scenario is a positive linear relationship between taxonomic and functional diversity (slope = 1) when each species constitutes a unique functional group. If species execute overlap with regard to functions or requirements, the relationship may result in a linear plot with a lower slope or in a curvilinear, i.e. saturated, relationship. Thus, at high levels of species richness the probability that recruiting species overlap functionally may be higher leading to an asymptotic increase in functional richness with increasing regional species diversity (Micheli and Halpern 2005, see their Figure 1).

In the present study, we report a large-scale experiment in marine hard-bottom assemblages growing on artificial substratum highly replicated at eight different bio-geographic regions. At four different successional ages we have inventoried the percent cover of all sessile species present in our experimental units, the availability of resources (measured as percentage cover of unoccupied substratum) and functional richness. In particular, we ask the following questions: (1) does the relationship between local and regional species diversity in fouling assemblages display a linear or curvilinear shape at a global scale? (2) Is this relationship sensitive to community assembly time? (3) Does local functional richness relate to regional functional richness in a similar way as local species richness relate to regional species richness? (4) Is the diversity of local communities affected by parameters other than regional richness, such as number of functional groups or availability of resources?

Methods

Study system and definition of spatial scales

For the analysis of the relationship between local and regional diversity during the succession process of fouling assemblages we use the data-sets of eight field experiments from a modular global experiment - Global Approach by Modular Experiments (GAME, 2000) - performed during 2003 and 2005 in eight different biogeographic regions (more detailed methods in e.g. Canning-Clode et al. 2008; Sugden et al. 2008): Australia (35° 36'S, 138° 35'E), Brazil (43° 08'W, 22° 02'S), Chile (29° 58'S, 71° 22'W), England (54°41'N, 001°12'W), Italy (43° 30'N, 10° 20'E), Japan (38° 20'N, 141° 05'E), Portugal (32°38'N, 16°53'W) and Sweden (58°52'N, 11°08'E). In each region, 120 polyvinylchloride (PVC) panels (15 x 15 x 0.3 cm) distributed in 12 PVC rings (60 cm diameter) were submerged for colonization at approximately 0.5 m depth during an 8 month period. The minimum distance between rings was 5 meters. Panels were mechanically disturbed (removal of biomass from randomly selected 20% panel area) at 7 different frequencies: non-disturbed (control) and disturbed every 2nd, 4th, 6th, 8th, 10th and 12th week. This was intended to span the typical range of locally occurring natural disturbances and to allow new species to recruit at all times. Communities colonizing the experimental units were structurally analyzed by measuring percent cover of all sessile species > 1 mm at four different successional ages: 2, 4, 6 and 8 months. In addition, the percentage cover of unoccupied substratum ('availability of resources') was recorded. Local species richness in a given region was assessed as the average species number on the non-disturbed panels (n = 8) at each successional age. Following the definition by Krebs (2001) that the number of species in a region is the number of species that can disperse to a locality in one unit of ecological time, i.e. generation, and is able to survive in that physical realm, we assessed regional species richness in a given region as the total number of species observed on any panel, disturbed and non-disturbed (n = 112), during any of the four surveys within each of the 8 regions. This approach is probably one of the most accurate assessments of the relevant regional species richness since it accounts for all or nearly all species available to recruit into the system under consideration, i.e. on a specific substratum, at a given depth during a defined portion of the year in a particular locality. Using available species lists would distort regional richness since the probability is high that they do not include all potential colonizers (as defined above) and at the same time include species which would never colonize into the system considered. To avoid autocorrelation between local and regional scales, panels used for taxonomic local richness assessment were not considered for the regional species pool.

Functional richness description

Functional groups comprise all species of a community which share a certain number of qualities linked to ecological functions (Raghukumar and Anil 2003) and are normally defined according to the way in which they use and compete for any kind of resources (Arenas et al. 2006). In this study, functional groups (FG) were determined according to five dimensions: body size, growth form, trophic type, modularity and motility (Wahl in press, Table 1). Each ecological dimension is subdivided into 2-5 qualities. For each species, the functional group was defined as the set of ecological qualities realized at the adult stage. Since our study focuses sessile hard-bottom assemblages, within the category ‘motility’, only the ‘attached’ type was considered. We expect more competition among species within FG because those species exhibit similar requirements, for example space, light or nutrients/food. Functional local richness was defined as the average number of FG colonizing the control panels (n = 8), and functional regional richness as the total number of FG observed in the disturbed and non-disturbed panels (n = 112) during any of the 4 successional ages of experimental duration. Panels utilized for functional local richness assessment were not considered for the functional regional pool.

Table 1. Dimensions used for the determination of the functional local richness and functional regional richness

Body size	Growth form	Trophic type	Modularity	Motility
S (<1mm)	E (encrusting)	A (autotroph)	S (solitary)	A (attached)
M (1mm-<10mm)	M (massive)	P (predators)	C (colonial)	C (crawling)
L (10mm - <100mm)	B (bushy)	S (suspension feeder)		S (swimming)
X (100 - 1000mm)	F (filamentous)	D (deposit feeder)		D (drifting)
XX (>1000mm)		G (grazers)		B (burrowing)

Statistical analysis

The differentiation between ‘type I’ and ‘type II’ curves was examined by regressing log local diversity on log regional diversity (in terms of both taxonomic and functional diversity). In this double log analysis, a continuous rise of local diversity with increasing regional diversity is represented by a slope of 1, while local saturation is represented by a slope significantly smaller than 1 (Griffiths 1997). This method was reported advantageous when compared to the common linear and nonlinear regressions since estimates of the slope are not influenced by the errors present in the independent variable and thus the slope can be used for more consistent meta-analytical comparisons (Hillebrand and Blenckner 2002).

To test whether local fouling assemblages are influenced by other parameters than regional enrichment, we ran a multiple regression for each of the 4 successional ages between local richness (dependent variable) and four predictors: regional species richness, regional functional richness, open space, and local FG or local species (local FG when dependent variable is taxonomic local diversity; local species when dependent variable is functional local diversity). The general fit of all models is given as adjusted R^2 to consider the inclusion of multiple predictors. We used absolute standardized parameter estimates (β-values) as indicative of the individual contribution of each predictor to the model due to its independency on the units of measurement of the variables. To verify the degree of multicollinearity among predictors, we calculated the variance inflation factor (VIF) which indicates if a predictor has a strong linear relationship with other predictors (Field 2005). VIF values higher than 4 have been used as a criteria indicating serious multicollinearity (O'brien 2007). All data analysis were performed using SPSS version 15 (SPSS Inc., Chicago IL).

Results

During the 4 surveys in 8 months of experimentation, taxonomic regional richness was highest in Australia and Japan (58 species each) followed by Chile (37 species), Portugal (36 species), Brazil (33 species), Sweden (25 species), Italy (23 species) and England (15 species). In contrast, functional regional richness ranked in a slightly different order with Portugal containing most FG (17) followed by Chile and Australia (15 FG), Japan (14 FG), Brazil (13 FG), Italy (12 FG), Sweden (9 FG) and England (8 FG). Thus, regional functional diversity does not increase at the same rate as regional species richness corroborating the expectation that additional species may be functionally similar to species already present (Micheli and Halpern 2005). As usual, average portion of unoccupied substratum in local communities of the 8 regions declined with time (mean open space: 2 months = 27.3; 4 months = 21.7; 6 months = 18.6; 8 months = 16.9) suggesting that space is becoming increasingly limiting over time.

In order to distinguish between unsaturated and saturated communities we used the slope of a double log regression for both taxonomic and functional diversity. The slope of the log-log regression increases with time for taxonomic richness while the opposite occurs when functional richness is considered (Figure 1). For taxonomic diversity, the slope is not significantly different from 1 at the first successional age (due to large variance) while it is significantly smaller than 1 in the subsequent surveys (Figure 1A). The unexpected tendency of an increasing slope over time suggests that in the course of succession, regional processes tend to become more important relative to local processes. Low dispersal rates at early stages of succession may also contributed to the unsaturated pattern observed after 2 months. The opposite tendency is observed for functional richness (Figure 1B).

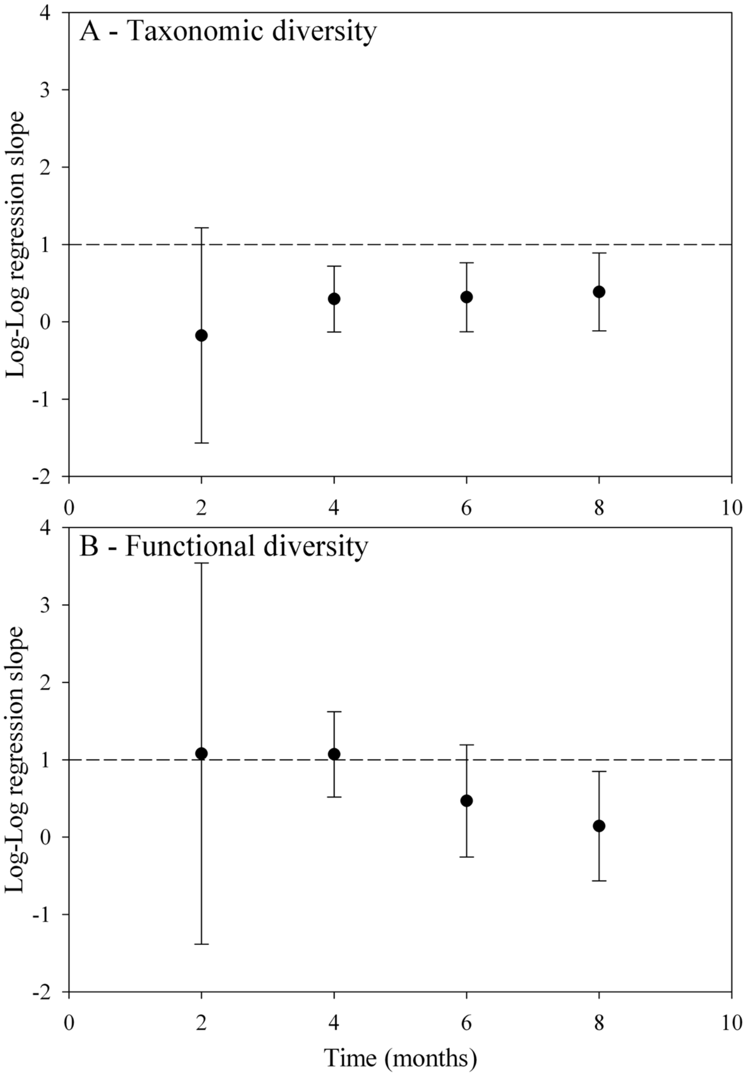


Figure 1. Slopes of the double log regression analysis over time for taxonomic diversity (A) and functional diversity (B). Slopes and 95% confidence intervals are indicated. Dashed line indicates a slope = 1. A slope that does not differ from 1 is indicative of unsaturation while local saturation is represented by a slope significantly smaller than 1.

No serious multicollinearity among predictors was detected in the multiple regression analysis as maximum VIF was 3.01 (Table 2). The multivariate models of taxonomic local richness identified local 'FG' as the best predictor at each of the four successional stages, with its contribution (β-values) slightly decreasing with time (Table 2a). 'Open space' was the second best predictor in 2 and 4 month old communities but not in older assemblages. The standardized parameter estimates for 'open space' were negative which indicates that local species richness increases when more of the available space is occupied. This probably just reflects the filling of available space by new species from the pool – instead of by species already present in the community. Regional enrichment was not a key parameter affecting local diversity: the influence of ‘regional species richness’ was significant only after 8 months of colonization while ‘regional functional richness’ did not affect local species assemblages at any time during succession. On the other hand, the number of local species had the strongest positive influence on functional local richness (Table 2b) and, ‘regional functional richness’ was the second most significant predictor in assemblages after 2 months, followed by ‘regional species richness’ and ‘open space’. At this age of succession, opposing signals of β-values in both categories of regional diversity indicate that the number of local FG decreases with increasing regional species richness but rises with increasing regional functional richness. After 4 months of colonization, ‘regional functional richness’ and ‘open space’ ranked 2^{nd} and 3^{rd}, respectively, as the most influent predictors. Local functional communities with 6 and 8 months were only affected by local species richness.

Table 2. Results of multiple regressions for each of the four succeccional ages between local diversity (dependent variable: a) taxonomic local richness or b) functional local richness) and four predictors: regional species richness, regional functional richness, open space, and number of FG (when taxonomic local richness as dependent variable) or number of species (when functional local richness as dependent variable).

Time	Predictors	a) Taxonomic local richness			b) Functional local richness		
		β	*P*-value	VIF	*β*	*P*-value	VIF
2 months							
	(Intercept)	1.11	0.275		-0.76	0.163	
	Reg. species richness	0.15	0.070	2.34	-0.24	0.001	2.08
	Reg. functional richness	-0.12	0.194	2.94	0.29	<0.001	2.46
	FG[a] / species[b]	0.96	<0.001	1.58	0.81	<0.001	1.33
	Open space	-0.22	<0.001	1.15	0.19	0.001	1.20
4 months							
	(Intercept)	2.18	0.012		-1.14	0.064	
	Reg. species richness	0.11	0.348	2.19	-0.20	0.054	2.09
	Reg. functional richness	0.11	0.406	3.01	0.37	0.002	2.59
	FG[a] / species[b]	0.72	<0.001	1.91	0.61	<0.001	1.63
	Open space	-0.37	<0.001	1.26	0.33	<0.001	1.29
6 months							
	(Intercept)	0.91	0.384		1.17	0.091	
	Reg. species richness	0.11	0.309	2.04	0.09	0.432	2.05
	Reg. functional richness	0.01	0.921	2.12	0.04	0.721	2.12
	FG[a] / species[b]	0.72	<0.001	1.25	0.75	<0.001	1.29
	Open space	0.10	0.241	1.24	-0.11	0.228	1.23
8 months							
	(Intercept)	-0.71	0.573		2.74	<0.001	
	Reg. species richness	0.40	<0.001	1.97	-0.17	0.210	2.39
	Reg. functional richness	0.00	0.998	1.95	-0.01	0.930	1.95
	FG[a] / species[b]	0.62	<0.001	1.17	0.81	<0.001	1.55
	Open space	-0.06	0.428	1.17	-0.09	0.326	1.16

$N = 64$ and $P < 0.001$ for each successional age and for both dependent variables. a) 2 months: $R^2_{adj} = 0.82$, $F = 70.5$; 4 months: $R^2_{adj} = 0.63$, $F = 28.2$; 6 months: $R^2_{adj} = 0.62$, $F = 26.9$; 8 months: $R^2_{adj} = 0.65$, $F = 30.7$. b) 2 months: $R^2_{adj} = 0.84$, $F = 86.4$; 4 months: $R^2_{adj} = 0.69$, $F = 35.6$; 6 months: $R^2_{adj} = 0.61$, $F = 25.4$; 8 months: $R^2_{adj} = 0.54$, $F = 19.7$.

Discussion

Regressing local diversity against regional diversity to examine the consequences of regional processes on local assemblages, has been frequently used for different habitats, taxonomic groups or spatial scales (e.g. Valone and Hoffman 2002; Witman et al. 2004; Freestone and Harrison 2006; Cornell et al. 2008). Some studies have even used these plots to test its dependency on the type of metacommunity structure (Hugueny et al. 2007) whilst others have incorporated spatial turnover in the analysis (Koleff and Gaston 2002; Belmaker et al. 2008). However, for a range of statistical and theoretical concerns, local-regional richness plots have been recently criticised (e.g. Hillebrand 2005; Shurin and Srivastava 2005). We avoided the major acknowledged pitfalls by following updated recommendations such as: (i) a proportional characterization of local and regional scales to avoid circularity between scales; (ii) we avoided *pseudosaturation* caused by overestimation of regional richness by including in the regional species/functional pool only those species/FG capable to occupy the local habitat; (iii) the use of the double-log regression to distinguish between 'type I' and 'type II' curves; (iv) and by employing multiple regression analysis of local and regional influences on local diversity for improved interpretations (Hillebrand and Blenckner 2002; Witman et al. 2004; Freestone and Harrison 2006; Harrison and Cornell 2008). Furthermore, we consider that our regional richness assessment did not underestimate the regional species pool in our specific system. By surveying 112 disturbed and undisturbed experimental units at four different successional ages during 8 months, at the same depth and colonizing identical substratum, we assure that the most part of potential foulers colonizing local communities (i.e. the relevant richness) is present in the regional pool.

As another improvement, this is the first study to simultaneously incorporate two further aspects of the local-regional diversity pattern: time and functional richness.

We have demonstrated that 2 month old local communities with regard to species richness are unsaturated or 'type I' while 'type II' communities established in the subsequent stages of succession. This apparent difference between successional stages was, however, entirely due to an initially very high variance. Indeed, the 'degree of unsaturation', the mean slope of the log-log relationship, tended to increase in the course of succession. An almost inverse pattern was observed for functional richness which became more saturated with time.

In a model using simulations originally developed for plant communities, Mouquet et al. (2003) predicted saturation at early stages of succession, unsaturation at intermediate stages and once again saturation when communities reach an equilibrium at later stages of succession. The authors argue that local communities appear saturated at early stages of community assembly time as only a portion of the regional species pool can colonize a locality. It is difficult to decide whether our findings correspond to Mouquet's prediction. Although neither the species richness nor functional richness per panel increased after month 6, we are undoubtedly dealing with early to mid successional communities which may not have reached late-successional status yet. So, according to the model we should have observed initial (pseudo-)saturation followed by transitory un-saturation and possibly blending into mature saturation. Instead, for both species richness and functional richness we found a unidirectional development, towards unsaturation for the former and towards saturation for the latter. The evolution of the local-regional relationship of species richness could correspond to the pattern described by Mouquet's model for the first half of succession. There was no prediction for the development of the regional-local functional richness relationship. The observation that functional richness becomes more saturated during succession may indicate that the community is 'filling up' functionally. However, it should be noted that the time scales of successional dynamics are not defined in the theoretical model by Mouquet et al. (2003) and may have differed among the biogeographical regions investigated herein.

The theoretical model developed by Mouquet et al. (2003) was previously tested in the marine and terrestrial realms (Munguia 2004; Starzomski et al. 2008). In a 4 month old study of motile and sessile marine organisms colonizing natural substratum (pen shells) in Florida, Munguia (2004) confirmed the assumption that the local-regional richness relationship is sensitive to the successional stage of a community. In his investigation, Munguia (2004) defined local communities as each individual shell and regions as 5 x 5 m plots separated by at least 60 m. The author observed that due to their high dispersal rates, motile species displayed a saturation pattern while sessile species established gradually and showed a positive linear relationship at all sampling events (Munguia 2004). Recently, Starzomski et al. (2008) tested the effects of alterations in the regional species richness using micro-arthropods communities in moss ecosystems during 16 months. Local species richness was not dependent on regional richness at all sampling dates, potentially due to *pseudosaturation*. Nonetheless, the authors found evidence that complex interactions between community assembly time, seasonality and regional species pool determine the structuring of local communities (Starzomski et al. 2008).

Recent studies have highlighted that local-regional richness plots should be used only as a starting point for interpreting the influence of local and regional processes in local communities (Russell et al. 2006; Cornell et al. 2008). By employing a multiple regression analysis we were able to test the sensitivity of other parameters on species and functional richness at the local scale. The number of functional groups was the most influential predictor for local species richness. This was not caused by a correlation between functional richness and species richness since collinearity was low. Rather, more functional diversification could permit more species to coexist in a restricted space. Unoccupied space too, was reported as the second best predictor for local species richness, but only in early successional communities (2 and 4 months). More open space corresponded to lower species richness (indicated by a negative slope of the relationship) which is typical for early succession where species recruit gradually. Interestingly, the relationship between open space and local functional richness at these 2 stages is positive which might be explained by a lack of competition for space at early stages of succession allowing more functional groups to coexist. Competition for space is paramount in fouling assemblages and has been demonstrated as a limiting resource (Stachowicz et al. 2002). In this analysis, we illustrate a tendency where space is not limiting young unsaturated communities and is constraining more developed and saturated fouling assemblages. This tendency suggests that primary species interactions are limiting diversity.

In addition, the use of the variance inflation factor (VIF) seems to constitute a useful tool to detect multicolinearity among studies parameters. In this report, maximum VIF was well bellow 4, which confirms that collinearity among predictors does not constitute motive for alarm (O'brien 2007).

Whether taxonomic or functional diversity are considered, we conclude that the relationship between local and regional diversity in fouling assemblages is affected by the succession process. Local taxonomic fouling diversity exhibits saturation at early stages of succession while saturation of local functional richness occurs later. We also confirmed that a higher local functional diversity affects local species communities at all stages of succession. Regional enrichment is not the most important factor in determining local diversity.

Synthesis and conclusions

Synthesis

One of the key goals for community ecology is to comprehend why certain areas are home to more species than others. Understanding global patterns in biodiversity has been of interest to ecologists since the time of the naturalist Charles Darwin (Leonard 2000). Since then, several hypotheses that seek to explain the spatial variation in biodiversity have been examined. The oldest paradigm about a large-scale ecological pattern is the observation that tropical regions are richer in species than temperate and polar regions at higher latitudes (Willig et al. 2003; Hillebrand 2004a). However, when exploring global patterns in biodiversity, it is crucial to understand the importance of dissimilarities in spatial scale for the patterns that are observed, as well as how diversity at one scale relates to diversity at other scale (Gaston 2000). In fact, numerous studies have shown that local species richness may increase either linearly or asymptotically with regional species richness. This pattern, recognized as the relationship between local and regional diversity, has been explored in recent years towards a better knowledge in the spatial variation of biodiversity (e.g. Cornell and Lawton 1992; Hillebrand and Blenckner 2002; Witman et al. 2004; Freestone and Harrison 2006; Russell et al. 2006; Cornell et al. 2008).

The present work has contributed substantially to a better understanding of global diversity patterns in fouling communities, and additionally, in the marine environment. The case studies reported in Chapter I have shown a clear relationship between latitude and biofouling diversity. The study performed by Witman et al. (2004) in epifaunal invertebrate communities encrusting subtidal vertical rock walls, as well as the new analysis performed with the GAME data, have demonstrated that tropical regions hold more biofouling species when compared to areas at higher latitudes.

Studies investigating the local-regional diversity relationship in the marine environment, have often defined the number of species in a region by questioning experts or consulting available species inventories (e.g. Rivadeneira et al. 2002; Witman et al. 2004). However, regional species pools based on such lists may include species not susceptible to recruit into the community considered since they are restricted to different habitats and seasons. With the purpose of dealing with these difficulties, other studies have estimated regional richness based on local samples but confirmed strong bias in relation to replication. In order to improve the quality of regional richness estimations, Chapter II develops a new statistical tool for estimating regional richness based on a limited number of samples. Using three data-sets with a large number of replicates from different temperate shallow water habitats, I compare the performance of six common species richness estimators (ACE, Chao1, Chao2, Jack1, Jack2 and MM) against the asymptote of the species accumulation curve given by the UGE index, which was used as a baseline for true regional richness. More importantly, the mis-estimation was subsequently quantified as a function of sampling effort. The results of Chapter II demonstrate that, in general, the estimation of regional species richness based on local assemblages underestimates the true richness, regardless of habitat type or the selected estimator. The performance of the estimators applied to the three independent data-sets was comparable, independently of the size of sampling area considered, patchiness of habitat or age of community. This may indicate a notable robustness of the observed pattern, i.e. the underestimation. Despite the general similarity among estimator's performances, Jack2 was more accurate and less biased for all habitats in almost all replication levels. In contrast, MM exhibited a high precision in all habitats. As an outcome from this analysis, we now have a quantifiable idea concerning the strengths and limitations of the elected estimators. Thus, appropriate corrections can be used in futures studies which may substantially improve this technique.

After developing this new tool, the study was then extended to the analysis of the local-regional relationship at two different scales: European (Chapter III) and global (Chapter IV). In both studies, the local-regional relationship was investigated during succession of a community assembly, an aspect commonly ignored in most previous studies focusing on the pattern. In fact, only a few theoretical and observational studies have postulated a successional shift of the local-regional richness relationship (Mouquet et al. 2003; Fukami 2004; Munguia 2004; Starzomski et al. 2008). After extensive literature searches, Chapters III and IV appear to be the first studies that incorporate both dimensions of diversity: taxonomic and functional, which by itself constitute a further improvement on the analysis of the pattern.

When considering four different biogeographic regions in the northern hemisphere (Chapter III), it was found that the shape of the relationship between local and regional diversity is sensitive to successional stage, the way regional richness is estimated and the dimension of diversity considered. As a general trend, the slope of the local-regional relationship increased in the course of succession for both dimensions of diversity. The method of assessing regional richness influenced the outcome: one-time listing of species (transient RR) produced saturation earlier in succession than when local species richness was calculated as the number of species cumulating over repeated assessments (total RR). In contrast, local functional diversity displayed an unsaturated pattern at all successional ages and for both methods of assessing regional richness.

Finally, chapter IV reports a large-scale experiment in marine fouling assemblages growing on artificial substratum highly replicated at eight different bio-geographic regions from both hemispheres. At four different successional ages, the percent cover of all sessile species present in the experimental units was inventoried, as well as the availability of resources (measured as percentage of unoccupied substratum) and functional richness. At a global scale, I have confirmed that 2 month old local communities with regard to species richness are unsaturated or 'type I' while 'type II' communities established in the subsequent stages of succession (4, 6 and 8 months). However, the 'degree of unsaturation', the mean slope of the log-log relationship, tended to increase in the course of succession. An almost inverse pattern was observed for functional richness which became more saturated with time. In addition, I employed a multiple regression analysis to test for the sensitivity of other parameters on species and functional richness at the local scale. The results indicate functional groups as the most influential predictor for local species richness. More functional diversity could consent a higher number of species coexisting in a limited space. In addition, unoccupied space seems to constitute an important predictor for local species richness, but only at early stages of succession. As a consequence of more open space, species richness decreases, which is a common scenario in early succession where species recruit gradually. Also, the number of functional groups increased with open space at early stages of succession, which may be indicative of modest competition taking place, allowing more functional groups to coexist.

Conclusions

This thesis gives new insights on global diversity patterns in marine fouling communities. There is an evident influence of latitude on local species richness in marine fouling communities.

Furthermore, when investigating the local-regional diversity relationship, I conclude that regional richness can be estimated based on a limited number of samples. For all community types considered, Jack2 showed a better overall performance. Thus, the quality of the estimation increases with sample size, and that the magnitude of the unavoidable mis-estimation can be quantified and, consequently, corrected to some degree. Studies including data from more locations within the same habitat type are highly encouraged since it may provide more robust correction values to compensate the bias caused by low replication.

In addition, the relevant regional richness, i.e. the regionally available colonizers, seems to vary in time. Thus, this relevant regional richness is larger when pooling all sampling events. As a consequence, the relationship between local and regional diversity is also influenced by the method in which regional richness is assessed.

Whether taxonomic or functional diversity are considered, the relationship between local and regional diversity in fouling assemblages is affected by the succession process. At a global scale I showed that both species and functional richness shifted from unsaturated to saturated during succession, but species richness reached saturation faster than functional richness. Therefore, I emphasize the need to incorporate this aspect in futures analysis of the pattern.

Finally, the local-regional richness relationship may also be influenced by the number of regions and the range of regional richness values. While more regions and a wider richness range are undoubtedly advantageous, some previous studies used even fewer regions (e.g. Hugueny et al. 2007). There are no simple rules concerning the number of regions one needs to examine the pattern as long as it is more than two and employs appropriate spatial scales and theoretical interpretations.

Looking ahead

In addition to the global-scale surveys, the effects of latitude on the diversity of marine fouling communities have been assessed at smaller scales (e.g. within countries), in particular, in rocky intertidal sessile assemblages (Gaines and Lubchenco 1982; Leonard 2000; Okuda et al. 2004; Schoch et al. 2006). However, at smaller scales the outcome is not always consistent. For example, Okuda et al. (2004) observed a clear latitudinal gradient for regional species richness of rocky intertidal sessile assemblages along the North-western Pacific coast of Japan. In contrast, in a study covering fifteen degrees of latitude in the California Current region, Schoch et al. (2006) concluded that diversity declined with decreasing latitude in the low intertidal zone at different scales. This inconsistency at lower resolution scales emphasizes the need for large-scale assessments in marine fouling assemblages to acquire a more complete understanding about global patterns and their causes in these communities. Furthermore, longitude has been relatively unexplored when compared to latitude, but longitudinal gradients were also recognised in both marine and terrestrial environments (Jetz and Rahbek 2001; Hughes et al. 2002; Roberts et al. 2002; Kerswell 2006). The relative ease by which marine fouling communities can be observed and manipulated could facilitate more comprehensive comparisons at a global scale. Therefore, studies only focusing on latitude may be insufficient and thus, longitude should be incorporated in future large-scale surveys.

Finally, Mouquet et al. (2003) predicted in their theoretical model local-regional relationships for different combinations of community assembly times and disturbance rates. At low and high disturbances intensities, Mouquet et al. (2003) do not expect a relationship between local and regional diversity since the community is saturated at equilibrium or because disturbance is so harsh that just a few species can survive. However, at intermediate disturbance rates, saturation is expected if the community assembly is short. Disturbance may also play a greater role at later stages of community assembly, resulting in an unsaturated pattern (Mouquet et al. 2003). In order to better comprehend the interplay between both community assembly and disturbance, these aspects should be incorporated in future observational studies on the local-regional richness relationship.

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Origin of pictures:

Canning-Clode, João: all pictures

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Education

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International research projects

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2004 - 2005	International student training and research programme GAME (Global Approach by Modular Experiments). IFM-GEOMAR

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Erklärung

Hiermit erkläre ich, dass ich die vorliegende Dissertation selbstständig verfasst und keine anderen als die angegebenen Hilfsmittel und Quellen verwendet ha-be. Ich habe bisher ke inen anderen Promotionsversuch unternommen, und diese Arbeit hat weder ganz noch teilweise im Rahmen eines anderen Prü-fungsverfahrens vorgelegen. Bei der Erstellung dieser Abhandlung habe ich mich an die Regeln guter wissenschaftlicher Praxis gehalten.

Teile dieser Arbeit wurden bereits wie folgt veröffentlicht bzw. eingereicht:

Canning-Clode J, Wahl M (2008). Patterns of Fouling on a Global Scale. In: Biofouling, (eds Dürr S, Thomason J). Wiley-Blackwell. Oxford. *In press*.

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