

# **Experimental Test of Diversity Effects in Marine Metacommunities**

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## Summary

Increasing global species extinction have prompted ecologists to study the consequences of species loss for various ecosystem processes. A large number of ecological experiments recently showed that the loss of species diversity can cause decreased ecosystem functions such as biomass production. Most of these experiments, however, have been conducted in experimental communities which were locally restricted and closed for spatial dynamics of species and consisted of only one trophic level. Because the effects of species diversity have so far been studied without looking at the causes of diversity, it can be deemed questionable to extrapolate these results to the ecological consequences of species extinctions in real ecosystems.

Dispersal of species is a well-known factor which maintains species coexistence over time. Therefore, the metacommunity concept provides an unifying framework to assess the consequences of species extinction by including not only local community interactions but also spatial dynamics of species such as dispersal.

To address the regulating effects of spatial dynamics such as dispersal of species for the relationship between biodiversity and community biomass production I conducted three studies with experimental metacommunities.

In chapter I, I tested the role of initial local diversity and dispersal frequency of random propagule rains from the regional species pool into the local community patches. I used a microcosm system with marine benthic microalgae where local communities of algae were embedded in a large regional species pool. I was able to show that final local diversity and biomass production showed a unimodal pattern with increasing dispersal frequency. Initial local diversity had no effect on final diversity and biomass production. A positive correlation between final local species richness and biomass production revealed that the general relationship between diversity and ecosystem functioning remains valid in open systems, but that the maintenance of ecosystem processes depends on dispersal-mediating effects on local diversity.

Because in chapter I the actual mechanism for local species coexistence remained unclear, a second experiment using this microcosm system was conducted (chapter II). I manipulated the dispersal frequency of random propagule rains into local community patches, which were differentially disturbed. Together these two treatments created a mosaic of local patches in different successional stages. I was able to show that local biomass production was controlled by the number of local species which coexisted by a colonization-competition trade-off.

In Chapter III, I tested the effects of local grazer species richness and composition on grazing and microalgal biomass production in closed compared to open grazer communities

## Summary

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in artificial rock pools. The artificial rockpools were embedded in large tanks mimicking the oceanic region from where species and propagules could enter the local pools. Using this experimental system, I first showed that grazer species richness had a significant net biodiversity effect on microalgal biomass production in the closed but not in the open rock pools. The positive net diversity effect, however, depended on the presence of two effective grazers in the system which were able to compensate for less efficient grazers in species mixtures, hence it ensured the function of grazing. In the open rock pools the significant effect of grazer composition on algal biomass production persisted for the first half of the experiment and depended on the initial presence of one of the two efficient grazers. The efficiency of local top-down control of algal biomass in open systems thus depends on which particular species are lost.

Overall, the results of this work suggest that the impact of species diversity on ecosystem functioning cannot be predicted without considering factors such as dispersal or migration regulating stable coexistence of species. Moreover, for predicting ecological consequences of species loss the particular mechanism of species coexistence as a regulating factor the relationship between realized diversity and ecosystem functioning should be included.

Because species extinction is not a local event, for future research I suggest to switch the focus towards consequences of diversity loss in a whole region of connected habitats. I hypothesize that regional diversity and dispersal interactively regulate ecosystem functioning in a region of connected heterogeneous local habitat patches. For conservation management in highly fragmented landscapes it is largely important to know the regulating factors for stable coexistence of species maintaining ecosystem functions.

## Zusammenfassung

Aufgrund des zunehmenden globalen Artenaussterbens haben Ökologen begonnen, die Folgen des Artenverlustes für verschiedene Ökosystemprozesse zu untersuchen. Eine Reihe von experimentellen Studien haben unlängst gezeigt, dass der Verlust von Artendiversität eine Beeinträchtigung von wichtigen Ökosystemfunktionen wie z.B. verminderte Biomasseproduktion zur Folge haben kann. Allerdings wurden die meisten dieser Studien in lokal begrenzten experimentellen Gemeinschaften durchgeführt, die zum einen für räumliche Dynamiken geschlossen waren und zum anderen aus nur einer trophischen Ebene bestanden. Es ist somit fraglich, die bisher gewonnenen Ergebnisse über die ökologischen Konsequenzen von Artensterben auf natürliche Systeme zu übertragen, da nicht gleichzeitig die Voraussetzungen für das Bestehen von Artendiversität berücksichtigt wurden.

Räumliche Ausbreitung von Arten durch z.B. Ein- und Auswandern in und aus lokalen Habitaten ist ein bekannter Prozess, welcher die längerfristige Koexistenz von Arten ermöglicht. Das Metagemeinschaftskonzept (metacommunity concept) stellt daher einen guten Rahmen dar, welcher erlaubt, die Konsequenzen von Diversitätsverlust zu untersuchen, indem nicht nur lokale Gemeinschaftsinteraktionen, sondern auch räumliche Dynamiken wie die Ausbreitung von Arten berücksichtigt werden können.

Um die Rolle von räumlichen Dynamiken von Organismen für die Beziehung zwischen Artendiversität und Biomasseproduktion einer Gemeinschaft zu untersuchen, habe ich drei kontrollierte Studien in experimentellen Metagemeinschaften durchgeführt.

In Kapitel I habe ich zum einen die Rolle von initialer Diversität in offenen lokalen Gemeinschaften und zum anderen die Frequenz zufälligen Hineinkommens von Ausbreitungseinheiten in diese lokalen Gemeinschaften untersucht. Dazu habe ich ein Mikrokosmossystem mit marinen benthischen Mikroalgen benutzt, in welchem die lokalen Algengemeinschaften permanent mit einem großen regionalen Artenpool verbunden waren.

Mit ansteigender Häufigkeit hineinsinkender Ausbreitungseinheiten der Algen zeigten die am Ende des Experiments gemessene lokale Diversität und Biomasseproduktion einen unimodalen Verlauf mit einem Maximum bei mittlerer Häufigkeit hineinkommender Algen. Die initiale lokale Diversität hatte keinen Effekt auf die am Ende gemessene Diversität und Biomasseproduktion. Die positive Korrelation zwischen finaler lokaler Diversität und Biomasseproduktion zeigt, dass die bereits in geschlossenen Systemen gezeigte positive Beziehung zwischen Diversität und Ökosystemfunktionen auch in offenen Systemen zutrifft. Allerdings hängt die Aufrechterhaltung der betrachteten Ökosystemfunktion vom regelmäßigen Hinzukommen von Arten ab, was wiederum die lokale Koexistenz und Diversität erst ermöglicht.



Weil aus den Ergebnissen in Kapitel I zunächst nicht deutlich wurde, welcher Koexistenzmechanismus für den unimodalen Verlauf der lokalen Diversität verantwortlich war, habe ich eine zweite Studie mit demselben Mikroalgensystem durchgeführt. Wiederholt habe ich die Frequenz hineinkommender Mikroalgen manipuliert. Außerdem wurden die lokalen Gemeinschaften in verschiedenen Häufigkeiten gestört. Zusammen erzeugten diese beiden Manipulationen ein Mosaik von lokalen Gemeinschaften in unterschiedlichen Sukzessionsstadien. In Kapitel II konnte ich zeigen, dass die Biomasseproduktion in lokalen Gemeinschaften von der Anzahl der Arten abhängt, die aufgrund eines Colonization-Competition Trade-Offs koexistieren.

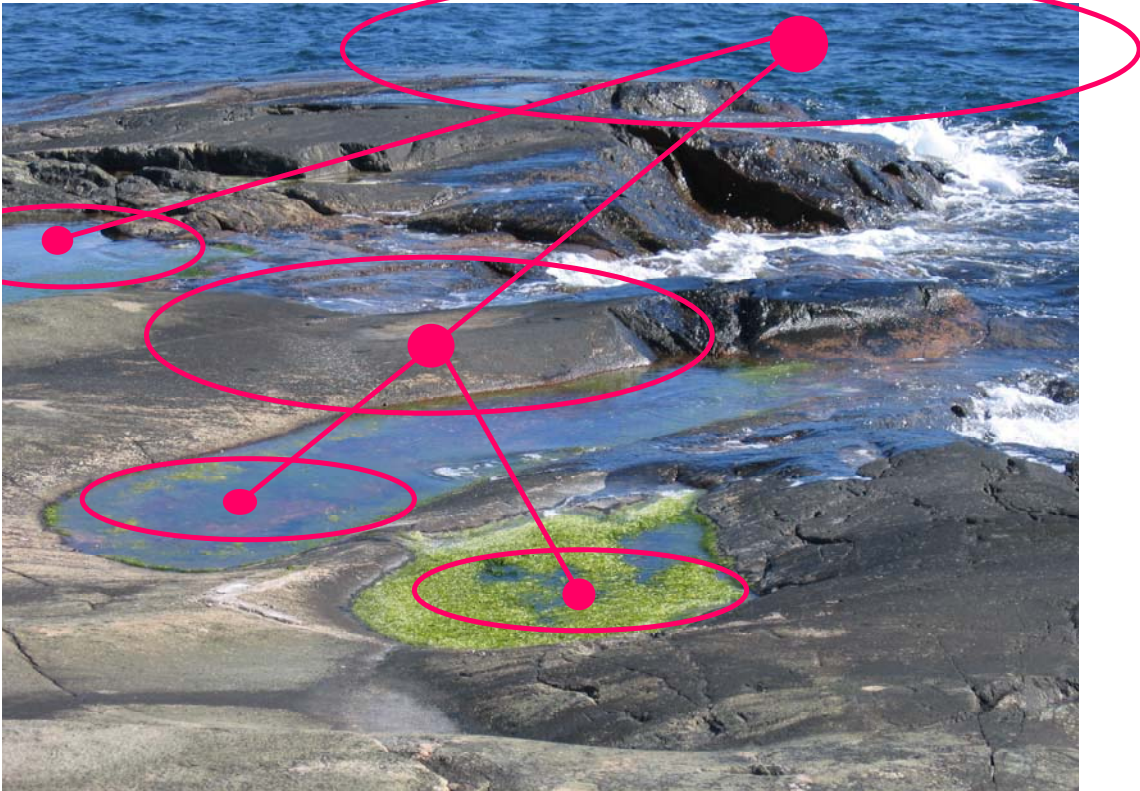
In Kapitel III habe ich die Rolle von Diversität und Artenzusammensetzung lokaler Herbivorengemeinschaften auf Algenkonsumtion und Algenbiomasseproduktion in je einem geschlossenen und einem offenen System von artifiziellen Rockpool-Metagemeinschaften getestet. Die einzelnen artifiziellen Rockpools waren in großen Tanks untergebracht, welche die Region (Ozean) darstellten und von wo aus die verschiedenen Arten und Ausbreitungseinheiten in die Rockpools gelangen konnten. Mit Hilfe dieses experimentellen Systems konnte ich zeigen, dass die Herbivorendiversität einen signifikanten Diversitätseffekt (net diversity effect) auf Algenbiomasseproduktion in den geschlossenen aber nicht in den offenen Rockpools hatte. Dieser positive Effekt beruhte allerdings auf der Anwesenheit von zwei sehr effizienten Konsumenten, welche für weniger effiziente Arten kompensierten und somit die Ökosystemfunktion ‚Algenkonsumtion‘ sichern konnten. In den offenen Rockpools zeigte die anfangs anwesende Artenzusammensetzung einen signifikanten Effekt auf Algenkonsumtion und blieb sogar bestehen, obwohl sich die lokalen Gemeinschaften miteinander vermischten. Auch dieser Effekt hing von der anfänglichen Präsenz einer der zwei effektiven Arten ab. Die Effizienz der lokalen Top-Down Kontrolle in offenen lokalen Gemeinschaften hängt also davon ab, welche, aber nicht wie viele Arten aus der Gemeinschaft verloren gehen.

Die Ergebnisse dieser Arbeit zeigen, dass der Einfluss von Artendiversität für die Funktionen von Ökosystemen nicht vorausgesagt werden kann, wenn nicht gleichzeitig Faktoren wie räumliche Dynamiken und Ausbreitung einbezogen werden, die eine stabile Koexistenz von Arten erst ermöglichen. Darüber hinaus können die ökologischen Konsequenzen von Artenverlusten auch nicht richtig abgeschätzt werden, wenn nicht zugleich der jeweilige Koexistenzmechanismus als regulierender Faktor für die Beziehung von Diversität auf Ökosystemfunktionen berücksichtigt wird.

Weil Artenaussterben kein lokales Ereignis ist, schlage ich für zukünftige Forschung an diesem Thema vor, die Konsequenzen von Artenaussterben in einer ganzen Region von miteinander verbundenen lokalen Habitaten zu untersuchen. Ich stelle daher die Hypothese auf, dass regionale Diversität zusammen mit der Schnelligkeit der Ausbreitung von Arten in

einer Region die lokalen und regionalen Funktionen von Ökosystemen regulieren. Gerade für Naturschutzmanagement in fragmentierten Landschaften ist es sehr wichtig die regulierenden Mechanismen für das stabile Koexistieren von Arten zu kennen, welche dann wiederum wichtige Ökosystemprozesse aufrechterhalten.

**Rock pools at the Swedish westcoast.**



Red lines explain how the communities in the rock pools can be connected to each other and to the ocean. Together the connected communities represent a metacommunity.

## Introduction

### ***Global biodiversity loss***

Over the past few hundred years, global rates of biodiversity loss have been accelerated to unprecedented levels. The impact of mankind has increased species extinction rates by as much as a thousand fold compared to background rates that were typical over Earth's history. Between 10% and 50% of well-studied higher taxonomic groups are currently threatened with extinction (Millennium Ecosystem Assessment 2005). Among these 12% of bird species, 23% of mammals, 25% of conifers, 32% of amphibians and 52% of cycad species are currently reported to be endangered. The most important direct drivers of biodiversity loss and change in ecosystem services are habitat change such as conversion of natural forests and grassland into cultivated systems, but also climate change, invasive alien species, overexploitation of species, and pollution (Millennium Ecosystem Assessment 2005).

Extinction rates of aquatic organisms (including both marine and freshwater) have not been studied to the same degree as terrestrial ones. However, reconstructed historical data for a world wide set of once diverse and productive coastal seas and estuaries show that habitat degradation and species extinction were correlated with human settlement (Lotze et al. 2006). Human impacts have depleted more than 90% of formerly important coastal species and destroyed more than 65% of coastal habitats such as seagrass beds or wetlands. Similarly, water quality has decreased and the rates of species invasions accelerated. For the open oceans a similar picture arises; diversity of large predators is reported to have declined between 10 – 50 % over the past 50 years, which correlates with increased fishing pressure (Worm et al. 2005).

### ***The role of biodiversity for ecosystem functions***

The accelerated rates of global diversity loss have prompted ecologists not only to identify the biotic and abiotic factors causing species coexistence and diversity, but also to study the consequences of biodiversity loss for various ecosystem functions such as biomass production, carbon storage, stability or pollination. During the past 15 years a large number of experimental and theoretical studies have shown that enhanced biodiversity can positively affect various ecosystem functions (summarized in Loreau et al. 2002b, Hooper et al. 2005). For example, net community biomass production increased with increasing numbers of species in grassland experiments across different sites in Europe and across several years in the United States (Hector et al. 1999, Tilman et al. 2001). Theoretical simulations (Bunker

et al. 2005) also predicted that above ground carbon storage in tropical forests depend on species richness of trees.

Whereas ecologists agreed on the positive effect of species diversity on community productivity, the effects of diversity on ecosystem stability were debated until recently. The insurance hypothesis predicts that diversity insures ecosystems against decline in their functions because a higher species richness provides higher probability that some species will maintain functioning even if others fail. For a long time the insurance hypothesis, however, could be shown only theoretically (Yachi and Loreau 1999, Loreau et al. 2003). Just recently, Tilman et al. (2006) were able to show that temporal stability of the experimental grassland communities increased with increasing number of species.

Biodiversity is not strictly defined as species diversity and can be also defined as genetic diversity within species or populations, or as functional diversity which combines different species according to their functional traits. Consequently, not only species diversity, but also genetic and functional diversity, can impact ecosystem functions. Enhanced functional pollinator diversity increased plant biomass by 50% (Fontaine et al. 2006), and functional diversity was the main factor explaining plant productivity in grasslands (Tilman et al. 2001). Addressing the role of genetic diversity, recovery rate after an extreme heat wave was enhanced by genotypic diversity in a monotypic seagrass community (Reusch et al. 2005).

The importance of biodiversity for maintaining various fundamental ecosystem functions can in turn have significant consequences for human society in terms of health and economic issues (Balmford and Bond 2005, Diaz et al. 2006): intact forests ensure the maintenance of drinking water for at least one third of the world large cities (Dudley and Stolton 2003). Preventing the collapse of the Newfoundland cod fisheries in the early 1990s would have saved tens of thousand jobs and at least \$2B in social costs for income support and re-training of unemployed people (Commission for Environmental Cooperation 2001).

### **Mechanisms for biodiversity effects**

The mechanisms for the described biodiversity effects can be partitioned into niche complementarity and selection effects. The complementarity effect means that more species or functional traits in an assemblage can lead to a more complete resource use, either by resource partitioning among species (Tilman et al. 1997b) or by facilitative species interactions (Eklöv and VanKooten 2001, Cardinale et al. 2002). In contrast, the selection effect (Tilman et al. 1997a, Loreau and Hector 2001) can lead to a diversity effect in the absence of resource use complementarity. Here, the probability of a community containing a species or a functional group with a particular trait statistically increases with increasing species or functional group richness. An example for a functional group with a particular trait are nitrogen-fixing cyanobacteria which are not dependent on soluble nitrogen-compounds

(such as ammonia and nitrate) compared to the rest of the phytoplankton community. These species and their particular attributes can become dominant and drive ecosystem functioning such as biomass production.

Both mechanisms have been controversially discussed (Wardle et al. 1997, Wardle 1999, Loreau 2000, Loreau and Hector 2001). Today, for the experimental local scale the most common consensus is that the extinction of species means loss of functional traits in a community which leads to lower resource use and hence to decreased ecosystem processes. Ecologists came to the conclusion that both selection and complementarity effects contribute to the relationship between diversity and ecosystem functioning (Ives et al. 2005). However, the relative contribution of either selection or complementarity effect is suggested to be largely scale-dependent. Even when species coexistence on the regional scale is mediated by resource partitioning, strong species sorting by competition can produce dominances and hence selection effects on the local scale. This in turn can be responsible for the bias towards selection effects in relatively short-termed experiments to test the effects of diversity on ecosystem functioning (Ives et al. 2005).

### ***The metacommunity perspective***

A major supposition of this work is that the consequences of biodiversity loss cannot be understood and predicted without considering mechanisms for the maintenance of species diversity. The conclusions concerning the ecological role of biodiversity hitherto have been made from artificially assembled and locally restricted communities (Loreau et al. 2001, Naeem 2001) where species were not able to coexist on short times scales. In most natural systems, however, local communities are connected to each other. Regional factors such as dispersal of propagules or disturbance which opens up new space for colonizers are well-known to mediate species coexistence by counteracting local competitive exclusion (Connell 1978, Flöder and Sommer 1999, Cadotte 2006a). Especially in marine environments the barriers for species dispersal are typically weak (Giller et al. 2004). Because experiments testing the effects of species diversity on ecosystem functioning have not allowed such factors to occur, fundamental processes of species coexistence have largely been omitted from our thinking in the debate about the functioning of biodiversity.

The metacommunity concept (recently summarized by Leibold et al. 2004, Holyoak et al. 2005) provides an appropriate framework to link mechanisms of species coexistence with the relationship between realized diversity and ecosystem-functioning. A metacommunity is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Gilpin and Hanski 1991, Wilson 1992). Four perspectives of species coexistence in metacommunities have been suggested (Leibold et al. 2004): the patch-dynamics, the mass-effect, the species-sorting and the neutral perspective. The four

perspectives of species coexistence as well as their theoretically predicted impacts on the relationship between biodiversity and ecosystem functioning are explained with further details in the introductions of chapters I and II. The metacommunity framework also allows consideration of ecological impacts of species diversity on different spatial scales. Diversity in a single local community within a metacommunity is defined as  $\alpha$ -diversity. Differences among local communities (such as species composition) within a metacommunity is defined as  $\beta$ -diversity. The overall diversity in a metacommunity is defined as  $\gamma$ -diversity (Whittaker 1960). It is predicted that diversity on the three spatial levels strongly depend on the connectivity between local community patches, and that the sum of  $\alpha$ - and  $\beta$ -diversity equals  $\gamma$ -diversity (Mouquet and Loreau 2003).  $\alpha$ -diversity is predicted to show a hump-shaped pattern with increasing dispersal among local patches with a maximum at intermediate dispersal rates.  $\beta$ -diversity is predicted to be maximized at low dispersal rates among local community patches. With increasing dispersal rates  $\beta$ -diversity is predicted to decrease because the local communities become more similar.  $\gamma$ -diversity is predicted to decrease at very high dispersal rates when the whole metacommunity is homogenized and functions as a large closed community. At very high dispersal rates competitive exclusion is predicted to take place on the regional metacommunity scale.

So far the effect of spatial scale on the relationship between biodiversity and ecosystem functioning has been addressed only conceptually (Bond and Chase 2002). It was also suggested that diversity at local sites mainly alters rates of ecosystem processes, whereas at regional scales diversity probably influences stability-related ecosystem functions (Bengtsson et al. 2002).

### ***The multitrophic perspective***

It was suggested that the loss of a low number of predator species often has impacts comparable in magnitude to those stemming from a large reduction in plant diversity (Duffy 2003). Dramatically global species loss is reported to be disproportionately high among consumer species (Worm et al. 2005). Therefore, another supposition of this work is that the loss of consumer species is expected to have profound ecological effects down the food web.

Parallel to the results about enhanced resource use complementarity and selection effects by increased plant diversity (Tilman et al. 1997b, Loreau 2000), theory predicts that more consumer species should be more effective in reducing prey biomass (Holt and Loreau 2001). Here, complementarity in resource use means that different consumer species have different food requirements in terms of prey species (Loreau 2000). Also facilitative

interactions among consumer species can increase consumer efficiency. A number of experimental studies manipulating consumer diversity support these predictions, but not all studies show evidence that higher consumer diversity means more efficient removal of prey biomass (summarized in Hillebrand and Shurin 2005). A positive effect of enhanced consumer diversity on top down-regulation of prey biomass can depend on the range of manipulated functional and species diversity. Whereas three species of grazers had no effect on epiphyte grazing or eelgrass biomass (Duffy et al. 2001), six species of grazers showed a significant decrease in algal biomass (Duffy et al. 2003). The top-down regulating effects of grazer diversity production becomes even more complex and produces different outcomes on plant biomass when specialist and generalist consumers are included (Thebault and Loreau 2003). However, predictions about such systems have been made so far only theoretically.

When a third trophic level comes into play, the presence of a predator can induce trophic cascades by indirect behavioural effects (Trussel et al. 2004). Duffy et al. (2005) showed that higher grazer diversity increased secondary production, epiphyte grazing, and seagrass biomass only at predator presence. Enhanced predator diversity can result in enhanced predation success by indirect facilitative effects if predators show spatial niche partitioning such as coexisting benthic and pelagic fish (Eklöv and VanKooten 2001). In this case, low predator diversity such as the presence of only one species left more refuges for the prey species and resulted in low predator consumption. In contrast, the presence of both predators, the pelagic and the benthic fish, reduced predation avoidance by prey and resulted in higher consumption of both predator species. In a tri-trophic food chain such an effect of predator diversity might also have cascading effects down to the lowest trophic level in terms of increased or decreased producer biomass. However, this largely remains to be experimentally tested.



## **Thesis outline**

This thesis is divided into four chapters. Each chapter represents an independent study addressing diversity effects in experimental marine metacommunities and/or multitrophic systems. This outline gives a short overview of the motivation for the single experimental studies. Resembling marine communities which are more or less connected to a large (oceanic) regional species pool, in all four chapters I used experimental metacommunities comprising homogeneous local community patches which were embedded in a large regional species pool.

### **Chapter I**

The first chapter describes a microcosm experiment with metacommunities of 15 species of marine benthic microalgae. The aim in this experiment was to test whether initial local diversity or the frequency of dispersal is more important for algal biomass production. I manipulated the initial species diversity and composition of local communities and the frequency of dispersal from the regional species pool into the local communities. To test whether this experimental system follows the well-known positive effect of dispersal on the number of coexisting species I first hypothesized that dispersal frequency affects local diversity. I also predicted that dispersal frequency affects local algal biomass production. Addressing the often shown positive effects of plant diversity on biomass production in closed experiments, I hypothesized that the positive effect of dispersal frequency on biomass production operated through changes of local diversity. This should be reflected in a positive correlation between realized local diversity and biomass production. Because local community interactions are expected to be stronger without dispersal or at low dispersal frequency I lastly hypothesized that the effect of initial local diversity on final diversity and biomass production decreases with increasing dispersal.

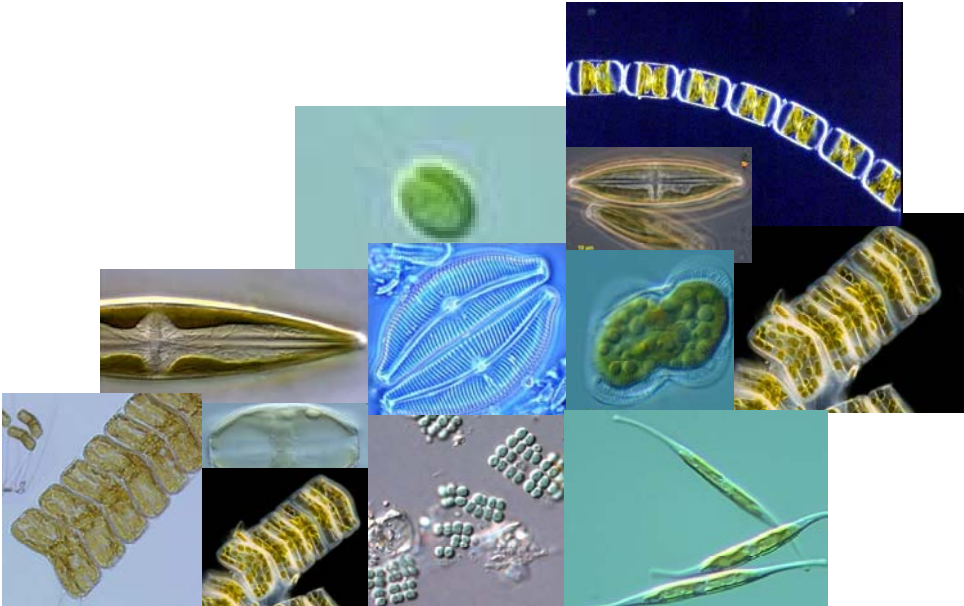
### **Chapter II**

In the first chapter I concluded that the non-linear hump-shaped pattern of local diversity with increasing dispersal frequency resulted from dispersal-mediated dynamics, which then was transferred into increased algal biomass production. I discussed that the dispersal effect on local diversity was a mix of alleviated dispersal limitation, a colonization-competition trade-off, and spatial niche separation. The colonization-competition trade-off is a widely cited mechanism of species coexistence in metacommunities with homogeneous local patches. However, the manipulation of dispersal in this experimental system could not finally proof whether enhanced local species richness resulting from a colonization-competition trade-off was translated into enhanced biomass production. To address this question I conducted a

second microcosm experiment with metacommunities of 11 species of marine benthic microalgae. This time, I factorially manipulated dispersal frequency as in chapter I and the frequency of local disturbance events which periodically opened up new space. Together, this created metacommunities representing a mosaic of local patches in different successional stages which were supposed to express species-specific traits in terms of colonizing abilities at early successional stages and competitive strength at late successional stages. By using this experimental design I predicted that dispersal and disturbance frequencies and the successional time of a local community affect local species richness and biomass production. I also predicted that enhanced realized local species richness translates into increased local biomass production. Because to my knowledge the effect of regional  $\beta$ -diversity for metacommunity biomass production remained to be experimentally tested I finally hypothesized that dispersal also affects  $\beta$ -diversity as known from theoretical models, and that  $\beta$ -diversity correlates negatively with mean metacommunity biomass production.

### **Chapter III**

In the third chapter my aim was to combine diversity effects of consumers on producer biomass production with system openness allowing for metacommunity dynamics. Together with my coworkers I conducted a mesocosm experiment with grazer communities in artificial local rock pools which were embedded in a large regional species pool containing six grazers. The initial local diversity and species composition of grazer species was manipulated in two subsets of the experiment. In one subset the local rock pools were closed for grazer migration, hence resembling 'classical' experiments about diversity and ecosystem-functioning. In the other subset the local rock pools were open for grazer migration. Because grazers can have large impacts on the top-down control of algal biomass in rock pools, I hypothesized that increased grazer species richness, identity and composition reduces algal biomass production in both open and closed rock pools. Addressing that migration of grazers might change local diversity – ecosystem functioning relationships I also hypothesized that migration of grazers in the open rock pools alters the effects of initial local grazer richness and composition on algal biomass over time.



Benthic marine microalgae

## CHAPTER I

**Dispersal frequency affects local biomass production by controlling local diversity*****Abstract***

Dispersal is a major factor regulating the number of coexisting species, but the relationship between species diversity and ecosystem processes has mainly been analysed for communities closed to dispersal. We experimentally investigated how initial local diversity and dispersal frequency affect local diversity and biomass production in open benthic microalgal metacommunities. Final local species richness and local biomass production were strongly influenced by dispersal frequency but not by initial local diversity. Both final local richness and final local biomass showed a hump-shaped pattern with increasing dispersal frequency, with a maximum at intermediate dispersal frequencies. Consequently, final local biomass increased linearly with increasing final richness. We conclude that the general relationship between richness and ecosystem functioning remains valid in open systems, but the maintenance of ecosystem processes significantly depends on the effects of dispersal on species richness and local interactions.

## ***Introduction***

Human activities are causing a global decline in biodiversity (Chapin III *et al.* 2000; Sala *et al.* 2000), which is often thought to lead to strong changes in ecosystem processes (Hooper *et al.* 2005). A large number of experiments have shown that several important ecosystem processes respond negatively to decreasing species richness (Loreau *et al.* 2001, Solan *et al.* 2004), functional richness (Tilman *et al.* 1997a), and genetic diversity (Reusch *et al.* 2005). The underlying mechanisms of complementarity and selection effects have been identified and controversially discussed (Wardle 1999; Loreau & Hector 2001; Loreau *et al.* 2001, 2002; Fox 2005).

Most of these experiments, however, have been performed with artificial species assemblages closed to immigration and propagule supply, and containing a single trophic level (Giller *et al.* 2004). There is an increasing effort to evaluate the functional role of biodiversity in a more natural setting by including multitrophic interactions (Worm and Duffy 2003, Hillebrand and Cardinale 2004, Duffy *et al.* 2005, Gamfeldt *et al.* 2005, Ives *et al.* 2005) and also--but to a much lesser extent--dispersal in open metacommunity systems (Kinzig and Pacala 2001, Bond and Chase 2002, Loreau *et al.* 2003, Cardinale *et al.* 2004). Experimentally, the biodiversity-ecosystem functioning question has so far been viewed independently from processes maintaining diversity. Local diversity is influenced not only by local species interactions, but also by regional processes such as dispersal (Ricklefs 1987, Palmer *et al.* 1996, Hillebrand and Blenckner 2002). Without dispersal, experimental systems lack a key process counteracting competitive exclusion. Losing species in local patches may have different consequences for ecosystem processes in isolated habitats compared to habitats connected to a regional species pool.

The metacommunity concept focuses on mechanisms of species coexistence by considering both local and regional community dynamics (Leibold *et al.* 2004) and therefore, can provide an appropriate framework to evaluate how naturally assembled communities of different biodiversity levels affect ecosystem functioning (here: biomass production) in open systems. Leibold *et al.* (2004) suggested different perspectives explaining species coexistence in metacommunities. First, the patch-dynamic perspective assumes identical local patches connected by dispersal where species coexist by means of a competition-colonization trade-off (Tilman 1994, Yu and Wilson 2001). In this perspective dispersal and colonization counteract the competitive exclusion of species. Second, the mass-effect perspective assumes heterogeneous patches where local diversity is quantitatively affected by dispersal. From the mass-effect perspective immigration quantitatively supplements local growth rates and the system follows source-sink dynamics (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, Mouquet and Loreau 2003). Third, the species sorting perspective assumes

heterogeneous patches where local abiotic factors determine local species interactions and community structure (niche-separation, Chase & Leibold 2003; Shurin *et al.* 2004). From this perspective, dispersal allows for colonization of best-adapted species to each local set of conditions. In addition, marine ecology has considered a regional (oceanic) influence on local interactions (Menge and Sutherland 1976, Moore *et al.* 2004).

The importance of metacommunity dynamics for the relationship between biodiversity and ecosystem functioning has recently been analyzed in a series of models. Based on a colonization-competition trade-off in homogeneous local patches, Mouquet *et al.* (2002) predicted a hump-shaped pattern of local plant species richness with increasing fecundity (the probability that a species reaches a site) and a positive relationship between fecundity and community productivity. The results of a patch-dynamic model (Cardinale *et al.* 2004) suggest that--at early successional stages in the local patches--the diversity-productivity relationship is amplified by including regional processes because the local ecosystem processes become a function of the regional diversity. A third conceptual model which additionally assumes local habitat heterogeneity combines local niche complementarity and regional source-sink dynamics. This model also suggests a hump-shaped pattern for local ecosystem functioning with increasing local diversity (Bond and Chase 2002). Correspondingly, Loreau *et al.* (2003) predicted that in heterogeneous landscapes increasing dispersal produces a hump-shaped pattern of local diversity, which then translates into a hump-shaped pattern of plant productivity with increasing dispersal frequencies.

Realistically not all species interactions in a given set of metacommunities will strictly follow either one or the other perspective (Leibold *et al.* 2004). At the same time, Mouquet *et al.* (2002) point out that the relationship between species richness and productivity depends on both the mechanism of coexistence and the cause of the species-richness gradient. However, these theoretical predictions regarding the consequences of biodiversity loss in a metacommunity framework largely remain to be experimentally tested. In particular, the role of how many and which species initially reach a local patch remains unknown across a gradient of dispersal strength in open systems. Fukami & Morin (2003) showed that the productivity-biodiversity relationship depends on assembly sequence. Theoretical models reveal that highly connected metacommunities homogenize and tend to behave like a large closed system (Loreau *et al.* 2003, Mouquet and Loreau 2003). Therefore, local community processes are probably more affected by initial species assemblages at low connectivity, but less at high connectivity. To our knowledge no experimental studies of ecosystem functioning have included both the manipulation of initial local species richness and the dispersal rate between these patches.

In this paper, we report an experiment in which we simulated initial reduction in local diversity in communities receiving different frequencies of random propagule rains from the

surrounding regional species pool. We measured the effects of initial species richness and dispersal frequency on local algal species richness and biomass production. Our experimental system represents highly connected metacommunities of local benthic and benthic-pelagic microalgae assemblages embedded within a large regional species pool.

With this experimental system we tested three hypotheses. First, the frequency of dispersal will affect local species richness. Based on theoretical studies (Bond and Chase 2002, Mouquet et al. 2002, Loreau et al. 2003), we predict local species richness to be highest at intermediate dispersal frequency. Second, dispersal will affect final local biomass (Mouquet et al. 2002). This effect of dispersal on biomass is expected to operate through changes in local species richness (Wardle et al. 1997, Loreau 2000). Third, initial diversity will influence final local species richness and biomass at low dispersal frequency (Fukami and Morin 2003). This effect is expected to decline with increasing dispersal frequency (Mouquet and Loreau 2003).

## **Methods**

### **Experiment**

The experiment consisted of 12 metacommunities of marine benthic and benthic-pelagic microalgae established in 10 l plastic aquaria. All metacommunities consisted of a regional species pool with a constant number of 15 species (for a detailed species list see Appendix A). Algal species were collected from biofilms from Kiel Fjord, Western Baltic Sea. The species varied in size and in attachment strength, since 12 species are considered to be exclusively benthic and three are considered benthic-pelagic (see Appendix A).

Each metacommunity was comprised of 16 local communities with varying species numbers (see below). The 15 species of the regional species pool were established in the aquaria and colonized the bottom outside the local communities. The patches for the local communities consisted of single homogeneous plastic tubes (surface area: 5.5 cm<sup>2</sup>, volume: 42.5 ml, height: 7.7 cm), which were closed at the bottom, but open at the top. These local communities were constantly connected to the regional species pool since the plastic tubes were permanently submerged.

The duration of the experiment was 28 days corresponding to 14 to 28 generations of the microalgae. The aquaria were filled with sterile filtered seawater (0.2 µm pore size) with added nutrients. The algae grew under nitrogen-limited conditions with a molar ratio of dissolved N to dissolved P of 9.3 : 1 at the beginning and 1 : 2.5 at the end of the experiment. At the onset of the experiment, the plastic tubes serving as local communities

were placed in each aquarium and the regional species pool was inoculated outside the local communities before experimental manipulations started.

In our experimental setup, we factorially manipulated the initial diversity of the local communities and the dispersal frequency of random propagule rains from the regional species pool into the local communities.

The diversity treatments in the local communities comprised three levels with two, four, or eight species. We used different species combinations in all diversity levels to avoid sampling effects: the two species level comprised six randomly chosen species combinations, whereas the four and eight species levels comprised five different combinations each (16 combinations in total, see Appendix B for a list of species combinations). These 16 different local species combinations (across 3 richness levels) were present in each of the 12 metacommunities (aquaria). Initially, all diversity levels were inoculated with equal total algal biovolumes (of  $8^6 \mu\text{m}^3$  per  $5.5 \text{ cm}^2$ ), which were calculated following Hillebrand *et al.* (1999).

The propagule rains (dispersal) from the regional species pool into the local communities were created by scraping the aquarium bottom between the local pools. This scraping effectively detached the algae from the bottom of the regional species pool and initiated stochastic propagule input into the local pools. The frequencies of propagule rains were manipulated in 6 levels in a logarithmic series (0, 1, 2, 4, 14, and 28 propagule rains in 28 days), which created a range from connected communities without enhanced dispersal up to a frequency of daily propagule rains during the experimental duration. It should be noted that the zero-dispersal treatment did not represent a closed treatment, but one without enhanced dispersal. Each frequency of propagule rains was replicated twice ( $2 \times 6 = 12$  aquaria). This design resulted in duplicate replication of each dispersal x species combination treatment and in 10 to 12 fold replication of each dispersal x local richness treatment.

### **Sampling and Measurements**

After 28 days all local communities were harvested. The plastic tubes (local communities) were carefully taken out of the aquaria and the algae were scraped off the bottom. The total content of algae and water of each local plastic tube were sampled. From each of these samples, we determined measures of local species richness, diversity and algal biomass. Species richness was represented by the number of species recorded in the sample, but we also used Chao 1 (Chao 2005) as a bias-corrected measure of species richness. The final algal biomass was measured microscopically as biovolume after Hillebrand *et al.* (1999). As a second measure of biomass chlorophyll a was extracted in 90% acetone (Strickland and Parsons 1972) and then measured photospectrometrically. The biovolume proportions were



used to calculate the Shannon- and Simpson-indices as measures of diversity (Hillebrand and Sommer 2000).

Two calculations were performed for the regional scale: Regional species richness (raw regional richness, Chao 1) in each aquarium was calculated as the summed number of species over all local pools. The mean dissimilarity between all local communities in one aquarium ( $\beta$ -diversity) was given by the Bray-Curtis index of dissimilarity (Bray and Curtis 1957) which reflects changes in the relative proportions of species.

### **Statistical analysis**

We analysed the experiment using a three-factor ANOVA, with the two fixed factors dispersal frequency and initial local diversity, plus species combination as random factor nested under diversity (Table 1). These analyses were performed for the final local species richness, Chao 1, Shannon- and Simpson-index, and for the final local biomass measured as biovolumes and chl a-content. The data for diversity and biovolumes were log-transformed to achieve homogeneous variances.

With a general linear model comprising linear and squared dispersal rates as continuous independent factors we addressed the predicted non-linear response of final local and regional richness, diversity and biomass to dispersal frequency.

To determine if a hump-shaped relationship between a response variable and dispersal frequency reaches a maximum within the range of dispersal frequencies we applied the test developed by Mitchell-Olds and Shaw [hereafter as MOS test (Mitchell-Olds and Shaw 1987, Mittelbach et al. 2001, Fukami and Morin 2003)] when the quadratic term of the regression was significant.

Pearson's correlation was used to address the relationship between final local species richness and local biomass production. We used Spearman's rank correlation to analyse  $\beta$ -diversity and species-specific significant trends of relative final biomass to dispersal frequency. We observed significant effects of species combinations on final diversity in the local assemblages. We tested for the identity of the species altering diversity by using presence and absence of each species (0; 1) as an independent variable in a stepwise multiple regression approach. We confined the set of independent variables to the 6 species contributing at least 1% to total biomass in at least one local assemblage (STA; MER; ISO; MEL; ENT; AMP, for species' abbreviations see Appendix A). We confined the dependent variables to those where we found a significant species combination effect. By using this approach, we were able to test for the effects of the initial presence of any of these species on final diversity.

## Results

### Algal biomass and diversity

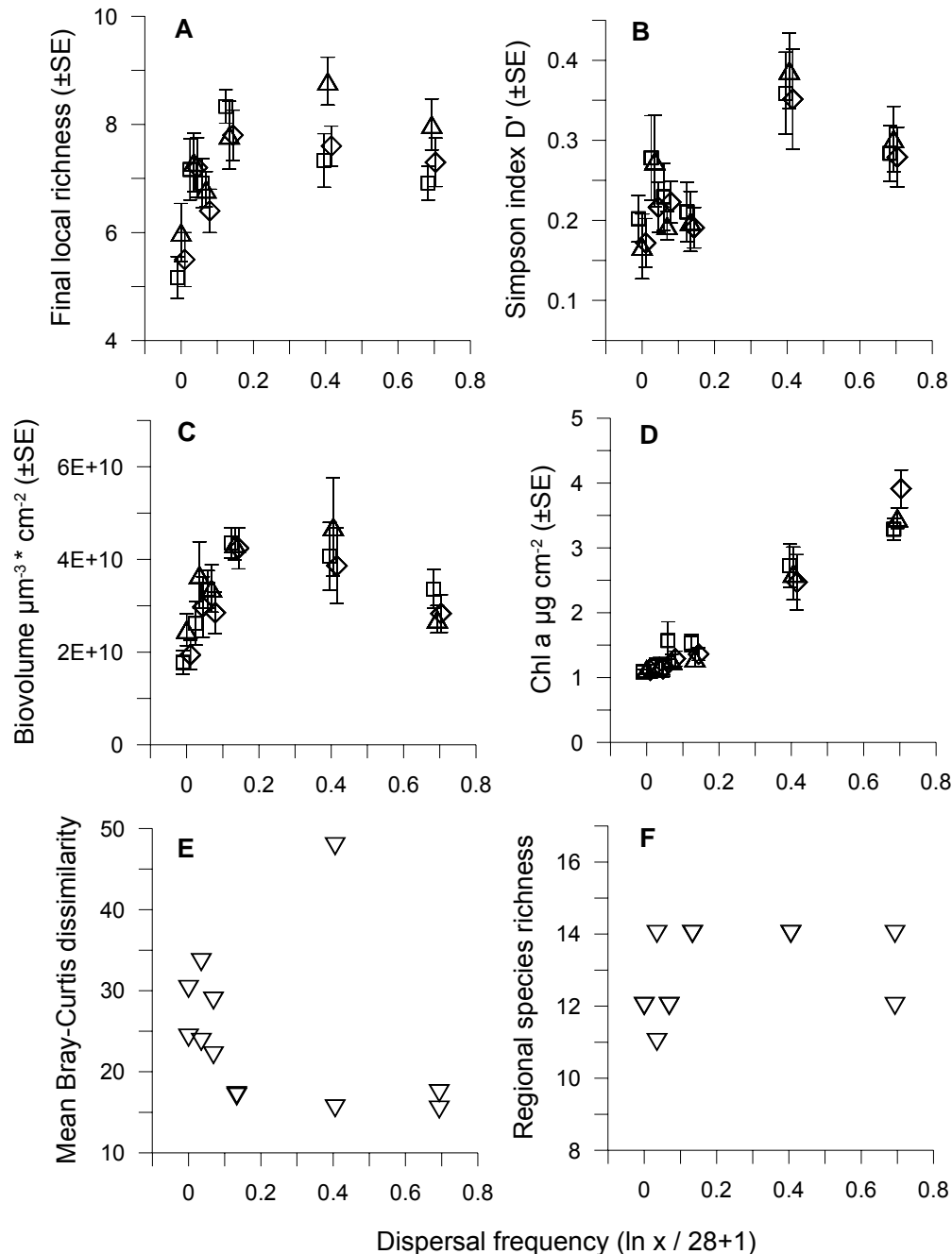
Dispersal frequency significantly influenced final local species richness (richness and Chao 1), diversity (Shannon- and Simpson-indices) and biomass production (biovolume, chlorophyll) in the local assemblages (Table 1, Fig.1). None of the response variables was affected by initial local diversity, and we found no significant interaction between initial diversity and dispersal frequency. Initial species combination affected final local diversity but not final local biomass production (Table 1, see below for details).

**Table I-1:** Summary of the three-factor ANOVA analyzing the effects of dispersal frequency, initial local diversity and species combination on final local species richness, Chao S Shannon-diversity H', Simpson-diversity D', and productivity measured as biovolume and chlorophyll a content. Dispersal frequency and initial diversity were used as two fixed factors, and species combinations as a random factor nested under diversity. The table provides information on the error term, and for each response variable F-ratio and significance level p.

Factor (df)	Error Term (df)	Local richness		Local Chao 1		H' (log-transf.)		D' (log-transf.)		Biovolume (log-transf.)		Chloroph a	
		F	P	F	P	F	P	F	P	F	P	F	P
Div (2)	Comb[Div] (13)	1.26	0.32	1.28	0.31	0.009	0.99	0.08	0.92	1.91	0.19	0.18	0.84
Comb[Div] (13)	Residual (96)	1.64	0.09	2.07	0.03	2.79	0.002	4.1	<0.001	0.26	1	0.79	0.67
Disp (5)	Comb[Div] X Disp (65)	13.33	<0.001	7.53	<0.001	12.42	<0.001	13.59	<0.001	11.74	<0.001	172.76	<0.001
Div X Disp (10)	Comb[Div] X Disp (65)	0.83	0.54	1.38	0.21	0.23	0.99	0.5	0.88	0.51	0.88	1.86	0.07
Comb[Div] X Disp (65)	Residual (96)	0.85	0.76	1.13	0.28	0.65	0.97	0.67	0.69	0.36	1	0.27	1

Final local species richness showed a significant non-linear hump-shaped pattern with increasing dispersal frequency (Table 2, Fig. 1 A). In the non-enhanced dispersal treatment species richness was lowest. Local coexistence was limited to a mean species richness of 5.5 without enhanced dispersal. With increasing dispersal frequency, final species richness increased and peaked at intermediate dispersal frequencies with a mean richness of 8 species and a maximum of 12 species. At highest dispersal frequency final species richness significantly decreased to a mean number of 7 species and a minimum of five species. None of the final local communities comprised all 15 species initially introduced. The Chao estimator of species richness showed an equivalent response (Table 2). Both diversity indices showed highest diversity at intermediate dispersal frequency (Table 2, Fig. 1B for Simpson's D'). The non-linear GLM was significant for Simpson's D', but only marginally significant for Shannon's H'.

Corresponding to the richness pattern, local biomass production measured as total biovolume showed a significant hump-shaped pattern with increasing dispersal frequency (Table 2, Fig 1 C). In contrast, local chlorophyll a content increased linearly with increasing dispersal frequency (Table 2, Fig. 1 D).



**Figure I-1:** Final local species richness (A), final local Simpson-diversity (B), local biovolume (C) and local chlorophyll a content (D), mean  $\beta$ -diversity (Bray-Curtis dissimilarity) (E), mean regional species richness (F) vs. dispersal frequency. Squares display the initial diversity of two species, triangles the initial diversity of four species and diamonds the initial diversity of eight species.

$\beta$ -diversity between local assemblages within each aquarium decreased with increasing dispersal frequency ( $r = -0.57$ ,  $N = 12$ ,  $p = 0.06$ ; Fig. 1 E). With the exception of one aquarium,  $\beta$ -diversity decreased exponentially with increasing dispersal frequency, where the assemblages became more similar up to a frequency of four propagule rains in 28 days ( $0.13 \text{ d}^{-1}$ ) and then remained constant with further increasing dispersal frequency. Mean regional species richness in each aquarium was not significantly affected by the dispersal treatments. (Table 2, Fig. 1 F).

Local biomass production (biovolume) significantly increased with final local species richness ( $r = 0.4$ ;  $N = 192$ ;  $p < 0.0001$ ; Fig. 2 A). Local biomass was lowest at the minimum final richness of four species and more than duplicated with increasing final richness. Biomass measured as chlorophyll a did not show a significant correlation with increasing final species richness ( $r = 0.11$ ;  $N = 192$ ;  $p = 0.1$ ; Fig. 2B).

**Table I-2:** Summary of the general linear model for non-linear effects of dispersal frequency on continuous dependent factors. The table gives variable names, the overall model explained variance ( $R^2$ ), F-ratio, and significance level, as well as the estimate, standard error (SE) and significance level for the linear and quadratic term. The last column gives the probability for non-internal maximum of the hump-shaped relationship according to the Mitchell-Olds and Shaw test.

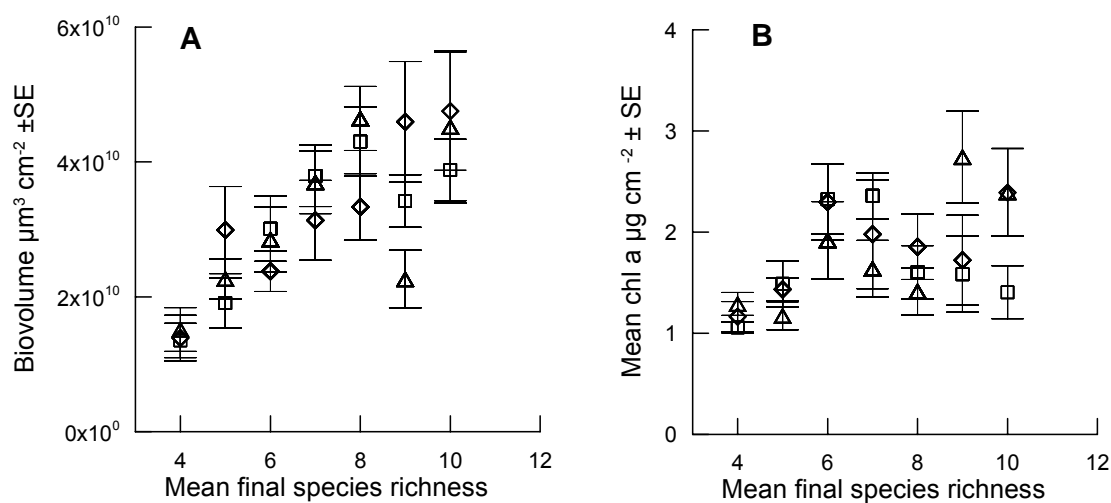
Variable	$R^2$	F	p	Factor	Estimate	SE	p	MOS p
Local richness	14 %	16.58	<0.001	Log disp	10.23	1.92	<0.001	
				Log disp <sup>2</sup>	-12.69	2.73	<0.001	<0.001
Local Chao 1	13 %	15.29	<0.001	Log disp	12.87	2.51	<0.001	
				Log disp <sup>2</sup>	-16	3.57	<0.001	<0.001
Local log H'	13 %	15.22	:0.001	Log disp	1.53	0.5	0.002	
				Log disp <sup>2</sup>	-1.34	0.7	0.058	0.02
Local log D'	13 %	15.48	<0.001	Log disp	2.75	0.69	<0.001	
				Log disp <sup>2</sup>	-2.88	0.98	0.004	0.001
Local log biovol	6 %	7.6	<0.001	Log disp	2.97	0.77	<0.001	
				Log disp <sup>2</sup>	-3.95	1.09	<0.001	<0.001
Local Chl a	63 %	165.07	<0.001	Log disp	3.69	0.83	<0.001	
				Log disp <sup>2</sup>	-0.13	1.18	0.91	
Regional richness	28 %	3.16	0.09	Log disp	11.46	4.79	0.04	
				Log disp <sup>2</sup>	-14.55	6.81	0.06	
Regional Chao 1	27 %	3.02	0.1	Log disp	11.2	4.89	0.05	
				Log disp <sup>2</sup>	-14	6.95	0.07	

## Community composition

Among the 15 species in the experiment only six species (AMP, ENT, MEL, STA, MER, ISO) contributed more than one percent to total final biomass in at least one local assemblage. With respect to absolute biomass production (biovolume) these species show species-specific differences along the dispersal gradient (Fig. 3). The benthic species (Fig 3. A-D)

showed lowest biomass production without enhanced dispersal and total biomass increased with increasing dispersal. For MEL total biomass was highest at two and four dispersal events in 28 days (low to intermediate dispersal frequencies). STA showed an optimum at 14 dispersal events in 28 days (intermediate dispersal; Fig. 3 B), and biomass of AMP and ENT linearly increased with dispersal and was highest at daily dispersal events (Fig. 3 C, D). The two benthic-pelagic species showed contrasting patterns in total biomass production. Whereas MER showed a hump-shaped pattern with the highest biomass at four dispersal events in 28 days, ISO showed a U-shaped pattern with increased total biomass production without enhanced dispersal and at high dispersal frequencies (Fig. 3 E, F).

With respect to relative contribution to total biovolume, the microalgal community was dominated by one very small benthic-pelagic species (MER; for visual presentation of relative biovolume see Appendix C). With nearly 90% of total biovolume the dominance of MER was highest in the treatments without enhanced and at low dispersal frequencies. In contrast, the benthic species contributed only 6% to the overall biomass without enhanced dispersal. At low dispersal frequency the relative biomass of the benthic species increased to 12 %. With increasing dispersal frequency, however, the relative contribution of MER significantly decreased to 66 % and the relative biomass of benthic species increased to 31 %. At high dispersal the relative contribution of MER increased again to 83 % and the contribution of benthic species decreased to 13 %. The increasing importance of benthic species compared to MER was reflected by significant positive correlations between the relative biomass of 7 benthic species and dispersal frequency (AMP, CYL, CYM, NAV, NITZ I, NITZ II, STA) as opposed to a negative correlation between MER and dispersal frequency (Table 3).



**Figure I-2:** The mean local biomass vs. the mean final local species richness. Biomass measured as biovolumes (A) and as chlorophyll a content (B). Squares display the initial diversity of two species, triangles the initial diversity of four species and diamonds the initial diversity of eight species.

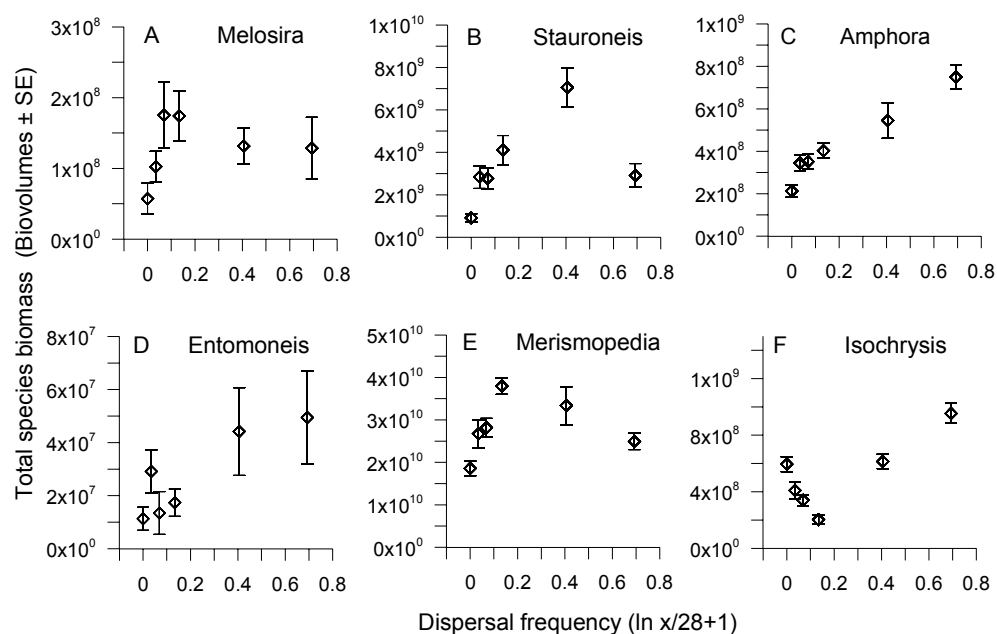
**Table I-3:** Summary of Spearman rank correlation of dispersal frequency (disp) vs. relative final biomass (biovolume) for each species (see appendix A for species codes).

Variables	N	Spearman	p
Disp & ACH	192	-0.04	0.58
Disp & AMP	192	0.26	<0.001
Disp & COC	192	0.11	0.11
Disp & CYL	192	0.30	<0.001
Disp & CYM	192	0.19	0.01
Disp & ENT	192	0.07	0.31
Disp & MEL	192	0.1	0.16
Disp & NAV	192	0.22	0.002
Disp & NITZ I	192	0.16	0.02
Disp & NITZ II	192	0.5	<0.001
Disp & NITZ III	192	0.05	0.45
Disp & STA	192	0.3	<0.001
Disp & THA	192	-0.02	0.76
Disp & MER	192	-0.29	<0.001
Disp & ISO	192	0.03	0.68

### Effects of species combinations

Whereas no effect of initial diversity or species combination on final algal biomass was detected, initial species combinations left a significant imprint on final diversity. The Chao estimator of richness and especially both diversity indices,  $H'$  and  $D'$  (Table 2) were affected by initial species combination. By using multiple regression we were able to identify STA as the most important species for final community structure. Initial presence of STA increased both  $H'$  and  $D'$  significantly (see Appendix D for full statistical results and graphical display).  $D'$  was also higher when ENT was initially present but lower when MER or

AMP were present (results only marginally significant).  $H'$  was reduced in communities with initial presence of MER or ISO. These species explained 19.1 and 10.1 of the variation in  $D'$  and  $H'$ , respectively, and both models were highly significant. For Chao 1, we observed only a decrease when STA was initially present, but the explanatory power of this model was low (< 5%).



**Figure I-3:** Biomass production measured as biovolumes of six species (AMP; ENT; MEL; STA; MER; ISO) vs. dispersal frequency. The biomass of the displayed species contributed at least 1% to total biomass in at least one local assemblage.

## ***Discussion***

In our experiment species coexistence and biomass production in the local communities strongly depended on dispersal at the metacommunity scale. Dispersal frequency affected species-specific colonization success from the regional pool into the local patches and thus altered the local community structure and biomass production. In this highly connected metacommunity system, dispersal strongly controlled final local species richness and diversity (accepting hypothesis 1). With increasing dispersal frequency, all measures of diversity first increased and then decreased, resulting in a hump-shaped pattern of final diversity in relation to dispersal frequency. The final local biomass was also affected by dispersal frequency and showed a corresponding hump-shaped curve with highest biomass at intermediate dispersal where local diversity was maximized. Final local biomass production correlated positively with final local species richness (accepting hypothesis 2). By contrast, initial local diversity did not influence final local species richness or diversity and there was no interaction between dispersal frequency and initial local diversity (refuting hypothesis 3). Our experimental results are mainly characterized by two important patterns: A single species (MER) was highly dominant in all treatments, but despite this dominance, dispersal frequency regulated the diversity of the local assemblages and its production of biomass.

The dominance of a single species is related to differential habitat use (niche separation). Our regional species pool comprised species collected from the same benthic location, but three species (MER, ISO, THA) are known to be benthopelagic. Of these species, the two dominant ones, MER and ISO, showed opposite responses along the dispersal gradient, suggesting that these two species interact in the pelagic of the local pools with low overlap in space and resource use with the benthic species.

The observed hump-shaped pattern of species richness and biomass production, however, cannot be explained by this dominance effect and by the largely independent species-interaction of MER and ISO in the pelagic. Despite increasing biomass of MER at low to intermediate dispersal frequencies, the number of coexisting species increased as well. Thus, dispersal-mediated dynamics on the metacommunity scale led to changes in the number of coexisting species and diversity, which then transfers into increasing biomass production. Whereas our experimental results closely resemble model predictions (Loreau et al. 2003) of a hump-shaped diversity and biomass pattern across a dispersal gradient, we emphasize that this resemblance is superficial since several model assumptions (equal intrinsic dispersal ability of species, environmental heterogeneity) are not coherent with our experimental setup. Our experimental metacommunity combines elements from at least two different metacommunity concepts (Leibold et al. 2004): As in the patch-dynamics concept,

our local patches were initially identical in spatial structure and total biomass (but not assemblage composition). As in the mass-effect concept, our regional pool represented a large source for propagules input into the local communities. However, the similarity of our results to model predictions suggests that different mechanisms may lead to maximized diversity and biomass production at intermediate dispersal frequencies, which indicates a strong generality of this pattern across metacommunity-types.

In the following, we discuss potential mechanisms for the effects of dispersal on local diversity, beta-diversity and biomass production.

### **Effects on local diversity and species composition**

We propose that dispersal effects on species composition and diversity depend on interacting process of 1) alleviating dispersal limitation, 2) a colonization-competition trade-off and 3) niche separation. The treatments without enhanced dispersal resulted in communities strongly dominated by one species. Due to its small size and benthic-pelagic life form, only MER successfully colonized the local patches, whereas the strictly benthic species were not able to colonize. Thus, local species richness without enhanced dispersal was low. The high dominance of MER was—at least partially—based on its ability to colonize the water column (niche separation).

With increasing dispersal frequency, more benthic species were able to colonize the local patches, increasing local species richness and diversity. Species-specific traits such as cell size (see Appendix A) and attachment strength caused different abilities to colonize new patches and resulted in species-specific patterns of biomass production along the dispersal gradient (Fig. 3).

Assuming a colonization-competition trade-off, better competitors should enter the local pools at high dispersal enhancement and exclude the good colonizers. In accordance with this proposition, several benthic species entered the local pools with increasing dispersal frequency and contributed significantly to the total biomass, whereas species contributing significantly to total biomass production at low dispersal were reduced at high dispersal (Fig. 3). Due to the destructive sampling protocol, we have no direct evidence to what extent these results rely directly on competition on the local and on the metacommunity scale (Tilman 1994, Yu and Wilson 2001, Mouquet and Loreau 2002). We can infer resource competition, however, from the strong depletion of the dissolved nitrogen pool (final N:P 1:2.5) and the increased chlorophyll per unit biovolume ratio at highest dispersal frequencies, reflecting increased light limitation. The latter pattern also led to the differential dispersal effects on biovolume and chlorophyll.

Due to niche separation within local pools (in contrast to niche separation across local pools in the species sorting paradigm, Leibold et al. 2004), however, we did not see a complete



shift in the assemblage composition. The benthic-pelagic life-style of MER allowed for persistent high biomass production (Fig. 3E), which was only reduced when a second benthic-pelagic species, ISO (Fig. 3F), was able to enter the local pools at highest dispersal frequencies.

The persistent effect of species combination on 3 out of 4 diversity measures allows for another potential mechanism affecting local coexistence, which is a facilitation- inhibition trade-off. We were able to identify species, whose presence in the initial assemblage enhanced or decreased final diversity. Especially strong positive effects were connected to the initial presence of STA and negative effects to initial presence of MER (Appendix D). These results suggest that the sequence of species entering the local community, matters for assemblage structure (Fukami and Morin 2003). In contrast to Fukami & Morin (2003) we did not consider different assembly sequences, but different initial local species compositions and diversity levels. We show that final local diversity is not affected by how many, but by which species were initially present in a local patch and that this effect was independent from the dispersal gradient.

### **Effects on beta-diversity and regional diversity**

Dispersal frequency had no significant effect on regional richness, but decreased  $\beta$ -diversity. Although all local communities at low dispersal were dominated by MER, the  $\beta$ -diversity remained high, since the identities and relative abundances of the subdominant species remained different between the local communities. With increasing dispersal frequency,  $\beta$ -diversity rapidly decreased since more species from the regional pool were able to colonize, and remained low from medium to high dispersal frequencies. We thus observed homogenization of the metacommunity at highest dispersal rates as predicted in many metacommunity models (Loreau et al. 2003, Mouquet and Loreau 2003).

The effects of dispersal on both local and  $\beta$ -diversity presumably has a strong temporal component, which we could not address in our experiment. In a long-term microcosm experiment Cadotte (2006b) showed that the decline in local species richness was significantly delayed when local communities and metacommunities were connected by dispersal, but this effect disappeared over time.

### **Effects on biomass production**

Biomass production followed the same hump-shaped pattern as species richness and diversity, leading to a significant linear correlation between biomass production and final local species richness. Two principal mechanisms can cause this pattern: 1) more passive input of biomass with increasing dispersal frequency, and 2) more complete resource use by the more diverse species assemblages.

Even without direct quantification of the biomass sinking into the local pools, we have good evidence that simple biomass transfer from the region into the local pool alone cannot explain the dispersal effect on biomass. First, total and species-specific biovolume production was reduced at highest dispersal frequency. These declines and differentiated species-specific biomass maxima point toward competitive displacement (Sommer 1996). Second, final biomass of the algal assemblage was 3 to 4 orders of magnitude higher than the biomass of the inoculum, indicating substantial growth within the local pools.

Instead, we propose that more species-rich assemblages have a higher biomass production because of more efficient resource use. Higher biomass production may reflect higher importance of single species traits (selection for the most productive species or higher complementarity in resource use). The microalgal assemblage was most efficient when the number and evenness of benthic-pelagic species as well as benthic species was maximized, allowing for efficient resource use in both the benthic and pelagic parts of the local habitat.

At non-enhanced dispersal, the biomass production in the local assemblages was low, which could be explained by both inefficient resource use of the good colonizer (colonization-competition trade-off sensu Mouquet *et al.* 2002) or by weak benthic production because low-dispersal treatments lacked substantial colonization by benthic species (recruitment limitation sensu Mouquet *et al.* 2002). At intermediate dispersal frequencies, the dominance of MER remained, but the presence of benthic species was enhanced and led to high biomass production. At high dispersal, assemblage structure shifted again to higher importance of benthic-pelagic species, with especially ISO increasing. Benthic-pelagic production might have shaded the benthic biofilm substantially, reducing benthic and total biomass production (Hansson 1992).

Several theoretical models predict changes in biomass with dispersal, but the direction and strength of the effects varies, depending on the metacommunity structure and the mechanisms for coexistence. Loreau *et al.* (2003) predicted a hump-shaped pattern of productivity across a dispersal gradient. In contrast to our experiment, the model employs different mechanisms leading to coexistence and proposes complementarity in resource use as the main factor leading to higher biomass production. Bond & Chase (2002) combine local niche complementarity and source-sink dynamics and conceptually explain the increasing part of the hump-shaped pattern of diversity and biomass production by local niche complementarity until the number of species equals the number of functional roles in the local community. Contrary to our findings a model assuming homogeneous local patches (Mouquet *et al.* 2002) predicts a positive relationship between increasing probability of a species reaching a site (fecundity) and community productivity. This model predicts that at highest species richness (intermediate dispersal) the productivity was relatively low since poor competitors used resources inefficiently (identical to an early successional stage) but at

high immigration rate the good competitor occupied the patch and used resources efficiently. The results of a patch-dynamic model (Cardinale et al. 2004) suggest that at local early successional stages (e.g., via high disturbance frequency) the diversity-productivity relationship is amplified by including regional processes since the local ecosystem processes become a function of the regional diversity. In this model open communities at late successional stages equaled closed communities where the local ecosystem functioning is driven mainly by local community interactions.

### **Conclusions and outlook**

Despite the simplicity of our experimental system, the results have important implications for potential effects of diversity on ecosystem functioning. Metacommunity dynamics strongly affect coexistence, shifting the question of how diversity affects ecosystem functioning to a larger spatial scale. Since dispersal is crucial to maintain high local species richness, it may be the regional and the dispersal-mediated beta-diversity across the entire metacommunity maintaining ecosystem functioning over long time scales, rather than local diversity having instantaneous effects on ecosystem processes. Thus, our results support the argument that dispersal and other metacommunity aspects need to be considered in order to understand the functional role of diversity. Our results suggest that we do not observe a new relationship between diversity and production when we consider realized richness in open communities. An important task for enhancing our understanding of consequences of diversity change is the consideration of time. Cadotte (2006b) presented evidence for the temporal dynamics of metacommunities at two different spatial scales, whereas Cardinale *et al.* (2004) provided evidence that the frequency and timing of disturbance is important for regional richness effects on ecosystem functions. Both studies suggest that dispersal effects on the maintenance of species vary over time, which leads to the question at which temporal scales (or in what kind of successional stages) we should expect a greater functional role for diversity.

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## CHAPTER II

**Biodiversity Effects in Metacommunities Depend on Dispersal and Disturbance Rates*****Abstract***

Biodiversity can play a major role for the maintenance of various ecosystem functions. However, the relationship between biodiversity and ecosystem functioning has been widely considered irrespective of the mechanisms allowing for species coexistence. By manipulating the rates of dispersal and disturbance in experimental metacommunities comprising marine benthic microalgae, we provide the first experimental evidence that enhanced species richness derived from a colonization-competition trade-off was translated into enhanced biomass production.

We were able to show that both local species richness and biomass production showed a non-linear hump-shaped pattern with an increasing ratio between dispersal and disturbance rates (successional time). Local biomass was positively correlated with increasing local species richness. For the regional scale, among-patch  $\beta$ -diversity showed a non-linear U-shaped pattern with increasing dispersal and metacommunity biomass production was negatively correlated with increasing  $\beta$ -diversity. Our data suggest that dispersal limitation regulated species coexistence and biomass production at early successional time, whereas local competitive interaction was the regulating factor at late successional time.

Especially in highly fragmented human dominated habitats the knowledge of the regulating factors for the maintenance of diversity and ecosystem processes (such as biomass production) can have important implications for conservation management.

## ***Introduction***

The rapidly accelerating rates of global species extinction (Lotze et al. 2006) have encouraged ecologists to study the ecological consequences of diversity loss. To date the majority of a large number of experimental studies suggests that species extinction can decrease important ecosystem processes such as biomass production (Hooper et al. 2005) or stability (Tilman et al. 2006). The findings have been mechanistically explained by locally operating effects of species complementarity and selection effects (Wardle 1999, Loreau and Hector 2001, Loreau et al. 2002b, Fox 2005). These studies made important arguments for the conservation of biodiversity, however, the vast majority of this reasoning derived from experiments conducted at a relative small (i.e. local) scale and in closed systems where competitive exclusion would prevent any diversity effects in the long term. Therefore, regional processes such as dispersal, allowing for species coexistence and the maintenance of biodiversity, should be taken into account. Diversity and its effects on ecosystem processes cannot be understood without knowing the mechanisms regulating species diversity. To make more realistic predictions about the consequences of species loss in real ecosystems, there is a strong need to place local processes into a broader spatial and temporal context such as the metacommunity perspective (Leibold et al. 2004, Holyoak et al. 2005) where factors such as dispersal and disturbance can mediate locally acting processes. The metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005) explains different perspectives for the coexistence of species by considering both local and regional processes, which in turn can be used to interpret the relationship between diversity and ecosystem functioning (here: biomass production). Two widely cited perspectives for species coexistence are the patch-dynamic and the mass-effect perspective. From the patch-dynamic perspective, dispersal and the colonization of new patches mediate local dominance effects in a set of identical homogeneous patches, and thereby prevent local competitive exclusion (competition-colonization trade-off) (Tilman 1994, Yu and Wilson 2001, Calcagno et al. 2006). From the mass-effect perspective, a set of heterogeneous local patches allows for different species to coexist regionally. Here, dispersal and colonization of patches can positively affect local coexistence by following source-sink dynamics, and local diversity is quantitatively affected by dispersal (Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). Because it is likely that elements of both mechanisms operate similarly in natural communities, recent models combined the two perspectives, trying to identify conditions under which elements of both mechanisms operate (Amarasekare et al. 2004, Mouquet et al. 2005).

For the local scale diversity in metacommunities we can observe consistent pattern in experimental and modelling results. Experimentally, local diversity shows a non-linear hump-

shaped pattern with increasing dispersal (Kneitel and Miller 2003, Cadotte 2006a, Matthiessen and Hillebrand 2006) which is also predicted by theoretical models (Mouquet et al. 2002, Mouquet and Loreau 2003). The importance of the actual mechanism of species coexistence for the relationship between diversity and community biomass production was underlined by a theoretical model (Mouquet et al. 2002) which predicted different outcomes between species richness and community productivity in metacommunities with and without any trade-off between reproductive and competitive abilities. A conceptual model (Bond and Chase 2002) combined species complementarity and source-sink dynamics and predicted a hump-shaped pattern for local ecosystem processes with increasing local diversity.

The role of community's successional time (i.e. the ratio between dispersal and disturbance) has so far not been considered as a regulating factor for the relationship between local species richness and biomass production. To our knowledge, only one patch dynamics-model (Cardinale et al. 2004) combined successional time with system openness. The model predicted that at early successional stages, local processes alone cannot generate a positive relationship between species richness and patch biomass production. By the time regional processes (dispersal) were included to the model, local patch biomass of highly disturbed patches in relation to colonization rates (early successional stages) become a function of regional species richness. In contrast, local communities at late successional stages (low disturbance rate in relation to colonization) produced the same positive relationship between species richness and biomass as in closed communities at late successional stages because here biomass production was primarily determined by local species interactions. Although this model did not simulate the rate of dispersal in relation to disturbance, it might point to the direction that the regulation of diversity and community biomass production can depend on successional time.

For the regional scale, theoretical models (Mouquet and Loreau 2003) and experimental data (Cadotte 2006b) predict that metacommunities homogenize with increasing dispersal which results in decreasing among patch-diversity ( $\beta$ -diversity). Due to regional competition at high dispersal rates, also regional metacommunity-diversity ( $\gamma$ -diversity) is predicted to decrease. Only one conceptual model (Bond and Chase 2002) predicts a (positive) relationship between regional diversity and ecosystem functioning by regional species complementarity. However, there is no evidence, neither theoretical nor experimental, how ecosystem processes such as biomass production on the metacommunity scale respond to increased or decreased  $\beta$ -diversity. Following the predictions above, the  $\beta$ -diversity is predicted to decrease when local richness increases. There is some evidence that an increased local diversity can cause increased local biomass production (Loreau et al. 2002b, Hooper et al.

2005), but an increased  $\beta$ -diversity need not to be positively correlated with biomass production.

To combine the partly known relationship between dispersal and diversity in a metacommunity with the prediction that enhanced species richness causes enhanced biomass production, we report a metacommunity study in which we experimentally simulated different rates of dispersal of random propagule rains from a surrounding regional species pool into physically equal local patches of benthic marine microalgae. The local patches were differentially disturbed to simulate different stages of succession (Cardinale et al. 2004). This experimental design created metacommunities representing a heterogeneous mosaic of local patches in different successional stages, allowing to test the following predictions:

First, dispersal and disturbance affect local species richness and biomass production.

Second, local species richness and biomass production both depend on the successional time of the local community.

Third, enhanced realized local species richness translates into increased local biomass production

Fourth, dispersal affects  $\beta$ -diversity and mean biomass production on the metacommunity scale.  $\beta$ -diversity correlates negatively with mean metacommunity biomass production.

## **Methods**

### **Experiment**

The experiment was conducted with 18 metacommunities of marine benthic diatoms.

All metacommunities consisted of 11 species which were collected from biofilms from Kiel Fjord, Western Baltic Sea. The species varied in size and in attachment strength to the bottom (for a detailed species list see Appendix A, Table A1).

Each metacommunity was located in a 10 L aquarium and comprised 16 local patches (with local communities) and a large surrounding region (Matthiessen and Hillebrand 2006). 12 of the 16 local communities were destined for final sampling, and four local patches were assigned to measure the increase in algal biomass during the experiment (see below). The local communities consisted of plastic tubes (surface area: 5.5 cm<sup>2</sup>, volume: 4.2 ml, height: 7.7 cm) which were vertically placed into the aquaria (region). The plastic tubes were permanently submerged, and thus constantly connected to the water of the surrounding region. While closed at the bottom and open on the top the tubes represented a barrier between the surrounding region and the local patches for the benthic algae.

The experimental duration was 56 days corresponding to 28-56 generations of microalgae. Before the experimental manipulations started the aquaria were filled with 7 L of sterile seawater (0.2  $\mu\text{m}$  pore size) with added nutrients (80  $\mu\text{mol}$  silicon, 90  $\mu\text{mol}$  nitrogen, and 6  $\mu\text{mol}$  phosphorus per L). The molar ratio of dissolved N to dissolved P was 32.9 : 1 at the beginning and 3.7 : 1 at the end of the experiment. During the experiment 250 mL of water from each aquarium was replaced with original medium three times a week. The 11 diatom species were established in the surrounding region and colonized the bottom outside the local patches. Each species contributed an equal amount of biovolume to the total initial inoculum of  $4.3^6 \mu\text{m}^3 \cdot \text{cm}^{-2}$  calculated following (Hillebrand et al. 1999).

In this experiment we factorially manipulated (1) dispersal rate of random propagule rains from the regional pool into the local patches and (2) disturbance of the communities in the local patches.

The propagule rains (dispersal) from the regional species pool into the local communities were created by scraping the aquarium bottom and afterwards cautiously stirring the water between the local pools. The scraping effectively detached the algae from the bottom of the regional species pool and the stirring initiated stochastic propagule input into the local pools. The rates of propagule rains were manipulated in 6 levels in a logarithmic series (0, 3, 7, 14, 28, 56 propagule rains in 56 days), which created a range from simple connected communities without enhanced dispersal up to a rate of daily propagule rains during the entire experiment. It should be noted that the zero-dispersal treatment did not represent a closed treatment, but one without enhanced dispersal. Each rate of propagule rains was replicated three times ( $3 \times 6 = 18$  aquaria).

Disturbance in the local communities was created by eliminating the algal biofilm. The method was simultaneously scraping and clearing off the algae from the bottom of the plastic tubes by suction using a 10 mL pipette. Disturbance was manipulated in three levels (non-, infrequently, and frequently disturbed). Infrequently disturbed was defined as one disturbance event per week, and frequently disturbed was defined as three disturbance events per week. The elimination of the algal biofilm opened up new space in the local communities. The walls of the plastic tubes comprising the local communities prevented the induction of dispersal in the regional pool while disturbing the local communities.

Each level of disturbance was replicated four times in each of the 16 metacommunities ( $3 \times 4 = 12$  local communities per metacommunity which were destined for final sampling). This design resulted in a three-fold replication of each dispersal x disturbance treatment.

Due to fungal contamination, one aquarium was omitted from the consecutive sampling and analyses.



## **Sampling and Measurements**

Termination of the experiment was predetermined to the time when local algal biomass growth reached a plateau. Therefore, every second week the algae of one of the four remaining (of the 16) local communities in each aquarium were sampled to measure the increase of local biomass over time (methods see below) and to decide upon the appropriate termination day of the experiment.

After 56 days the 12 local communities in each aquarium destined for the final sampling were sampled. The plastic tubes (local communities) were carefully taken out of the aquaria and the algae were scraped off the bottom. The total content of algae and water of each local plastic tube were collected. From each of these samples, we determined measures of local species richness and algal biomass. Local species richness was represented by the number of species recorded in the sample. The final algal biomass was measured microscopically as biovolume (Hillebrand et al. 1999). For the regional scale regional species richness in each aquarium was determined as raw species richness from qualitative sampling in the regional pools at the termination of the experiment. A second measure of regional richness was calculated as the summed number of species over all local pools. The among-patch diversity in one aquarium ( $\beta$ -diversity) was calculated using Whittaker-index which reflects changes in presence and absence of species (Whittaker 1960). Occupancy for each species was calculated as % local patches occupied by this species. Mean occupancy in any metacommunity was calculated as the arithmetic mean across all species. The metacommunity biomass production was calculated as the summed local biomass production in one metacommunity.

## **Statistical analysis**

Prior to these analyses, by using a block design ANOVA data were checked for differences between the three aquaria within the factor dispersal rate. No such block effect could be detected (ANOVA,  $P > 0.1$  for all response variables) and consequently the aquarium block factor was omitted from subsequent analyses. The data for local and regional biovolumes were LN-transformed to achieve homogeneous variances.

To test for hypothesis 1, the effects of dispersal and disturbance on local species richness and local biomass (measured as biovolumes) were analysed by using a two-way full factorial ANOVA. Non-linear responses of local richness and biomass to dispersal rate were tested with a general linear model (GLM) comprising linear and squared dispersal rates as continuous independent factors. Student-Neuman-Keuls (SNK) tests were used to test for differences among the three levels within the disturbance treatment.

Addressing hypothesis 2, the successional stage of a local community was defined as the time between dispersal and local disturbance and therefore expressed as the ratio between dispersal and disturbance rates ( $\text{LN}(\text{dispersal} + 1) - \text{LN}(\text{disturbance} + 1)$ ). Non-linear responses of local richness and biomass with increasing successional time were tested with a GLM using the linear and the quadratic successional time as continuous independent factors.

Addressing hypothesis 4, the effect of dispersal rate on the variables measured on the regional scale ( $\beta$ -diversity, mean metacommunity biomass, occupancy) were tested by using a GLM with the factor dispersal rate. Dispersal rate as the continuous factor in the linear and quadratic term addressed non-linear responses of  $\beta$ -diversity, mean metacommunity biomass, and mean occupancy to dispersal rates.

Pearson's correlation was used to test for the relationships between local species richness and biomass production, and between beta-diversity and mean metacommunity biomass production (hypotheses 3 and 4).

To determine if a hump-shaped or U-shaped relationship between a response variable and dispersal rate or successional time reaches a maximum or minimum within the range of dispersal rates or successional time, we applied the test developed by Mitchell-Olds and Shaw [hereafter MOS test (Mitchell-Olds and Shaw 1987, Mittelbach et al. 2001, Fukami and Morin 2003)] when the quadratic term of the regression was significant.

We used linear and non-linear (polynomial) regression to analyse species-specific significant trends of relative final biomass with increasing successional time.

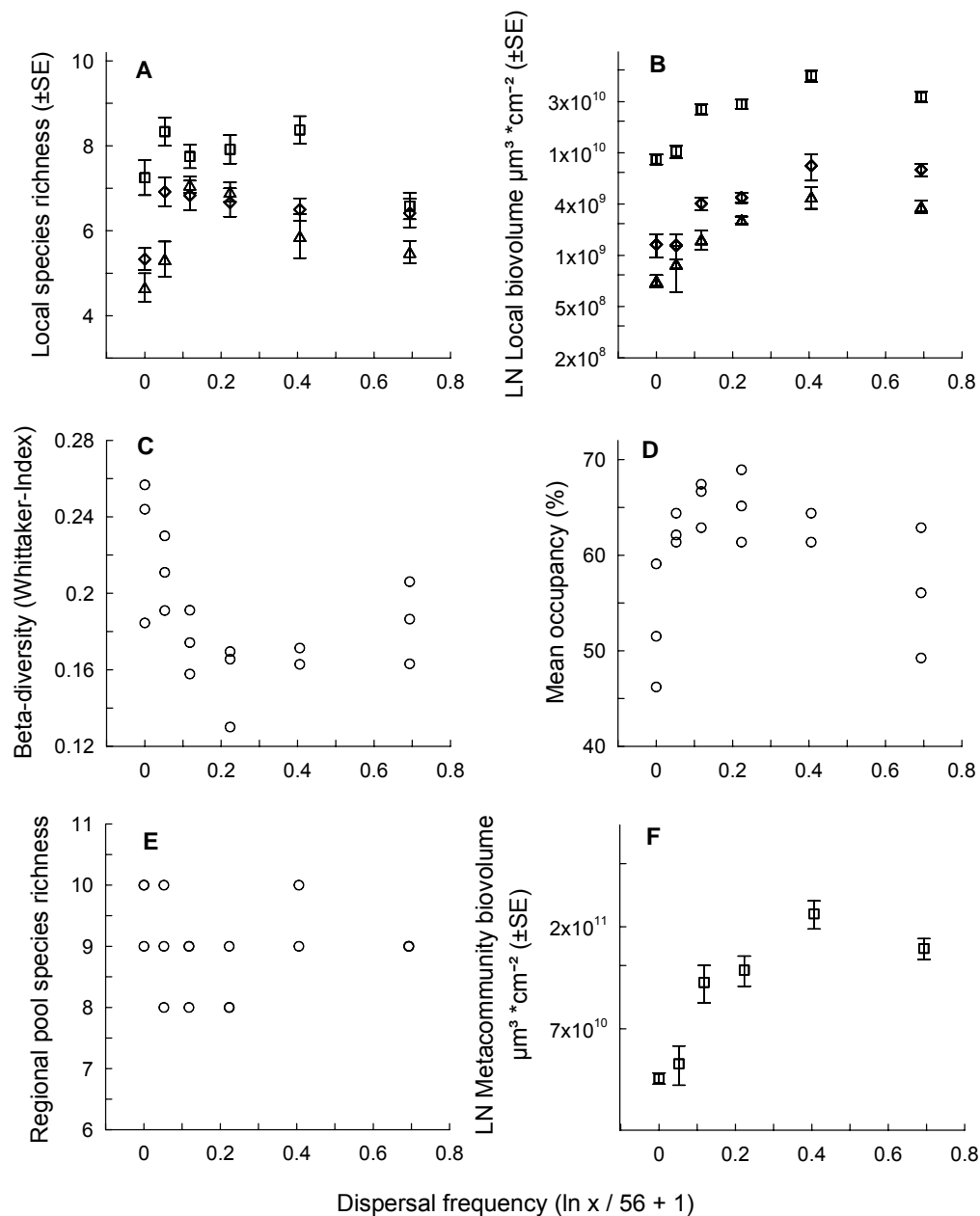
## **Results**

### **Local species richness**

On the local community scale, species richness was significantly affected by the rates of dispersal and disturbance (Table 1, Fig.1A). With increasing dispersal rate the overall local species richness showed a significant non-linear hump-shaped pattern with a maximum at intermediate dispersal rate (Table 2, Fig.1A).

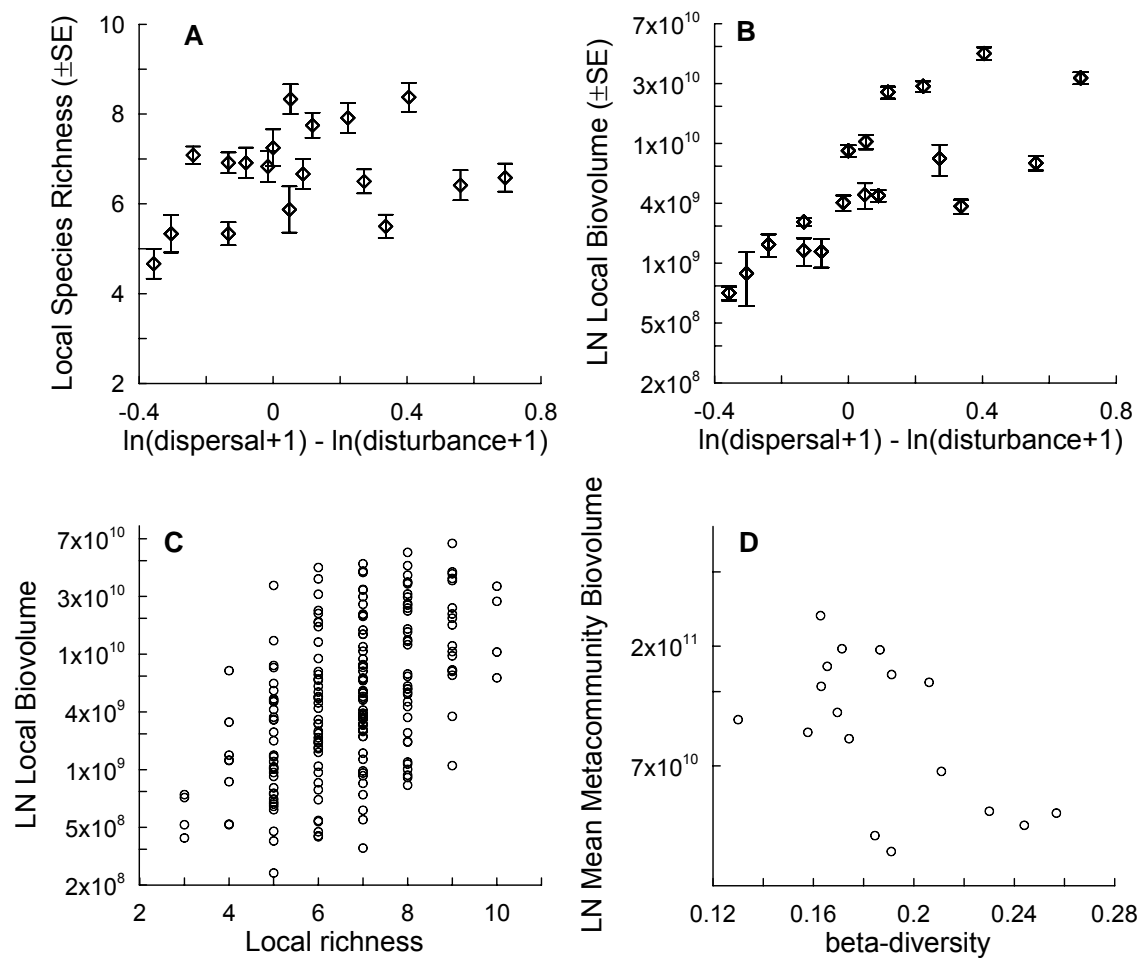
Differences in local species richness among the three disturbance treatments (non-, infrequently, frequently disturbed) along the dispersal gradient resulted in a significant interaction between dispersal and disturbance rate (Table 1, Fig. 1A). Without enhanced dispersal, local species richness was significantly lower in the disturbed patches compared to the non-disturbed patches (SNK test,  $p < 0.003$ , Fig. 1A). With increasing dispersal rates local species richness in all three disturbance treatments increased, and did not show any significant differences from each other at intermediate dispersal rates (SNK tests,  $p > 0.1$ , Fig.1A). From intermediate to high dispersal rates local species richness in the frequently

disturbed patches decreased, whereas species richness in the infrequently disturbed patches remained constant (Fig. 1A). Species richness in the non-disturbed patches first slightly increased (in the second highest rate of dispersal), and then decreased at highest dispersal (Fig. 1A). At highest dispersal rate there was no significant difference in species richness between the differential disturbed patches (SNK test,  $p < 0.1$ , Fig. 1A).



**Fig. II-1:** Effects of dispersal and disturbance rates on local species richness (A), local biovolume (B),  $\beta$ -diversity (Whittaker-index) (C), mean occupancy (D), regional pool species richness (E), mean metacommunity biovolume (F). Squares display the undisturbed patches, diamonds display infrequently disturbed patches, and triangles display frequently disturbed patches.

Local species richness was also significantly affected by the ratio between dispersal and disturbance rates (successional time). A significant non-linear hump-shaped pattern of local species richness could be observed with increasing successional time (Table 2, Fig. 2A). At early successional stages, where the rate of dispersal in relation to disturbance was low, local species richness was lowest and increased with increasing successional time. At intermediate successional time local richness was maximized. With further increasing successional time, where dispersal rates in relation to disturbance increased, local species richness decreased (Table 2, Fig. 2A).



**Fig. II-2:** Effects of the ratio between dispersal and disturbance rates (i.e. successional time) on local species richness (A) and local biomass productions (measured as biovolume) (B). Correlations between local species richness vs. local biomass production (C), and  $\beta$ -diversity vs. mean metacommunity biomass production (D).

**Table II-1:** Summary of the full factorial ANOVA analysing the effects of dispersal and disturbance rates on local species richness and local biomass production measured as biovolume. Dispersal and disturbance rates were used as two fixed factors. The table provides information on the degrees of freedom (d.f.), and for each response variable F-ratio and significance level P-value.

Factor	(d.f.)	Local species richness		Local Biovolume (ln-transf.)	
		F	P	F	P
Disp	(5)	10.21	< 0.001	61.8	< 0.001
Dist	(2)	46.71	< 0.001	417.07	< 0.001
Disp x Dist	(10)	3.06	0.001	0.69	0.73

test,  $p < 0.001$ , Fig. 1B), and within the same order of magnitude, significantly higher in the infrequently disturbed patches compared to the frequently disturbed patches (SNK test,  $p < 0.001$ , Fig. 1B).

A significant non-linear pattern of local biomass production could be also observed with increasing successional time (Table 2, Fig. 2B). At early successional stages, where the rate of dispersal in relation to disturbance was low, local patches biomass production was lowest and increased with increasing successional time. At late successional time, where rates of dispersal in relation to disturbance were high, local biomass production decreased (Table 2, Fig. 2B).

### **$\beta$ -diversity, occupancy and regional biomass production**

On the regional scale,  $\beta$ -diversity was significantly affected by dispersal rate, and showed a significant U-shaped pattern with increasing dispersal (Table 2, Fig. 1C). Without enhanced dispersal  $\beta$ -diversity was maximized and decreased with increasing dispersal rate.  $\beta$ -diversity was lowest at intermediate dispersal rate and increased with further increasing dispersal.

Mean occupancy of local patches in the metacommunities was also significantly affected by dispersal rate. Mean occupancy showed a significant hump-shaped pattern with increasing dispersal, and was maximized from low to intermediate dispersal rates (Table 2, Fig. 1D).

The overall regional species richness (summed richness over local pools and regional pool richness) was not affected by dispersal rate (Table 2, Fig. 1E).

Corresponding to local biomass production the mean metacommunity biomass production was affected by dispersal, and showed a significant hump-shaped pattern with increasing dispersal rate (Table 2 Fig. 1F).

### **Local biomass production**

Local algal biomass production was significantly affected by dispersal and by disturbance rate (Table 1). With increasing dispersal rate, overall local biomass production showed a significant non-linear hump-shaped pattern (Table 2, Fig. 1B). Local biomass was significantly one order of magnitude higher in the non-disturbed patches compared to the disturbed patches (SNK

## Correlations between local species richness, $\beta$ -diversity and algal biomass production

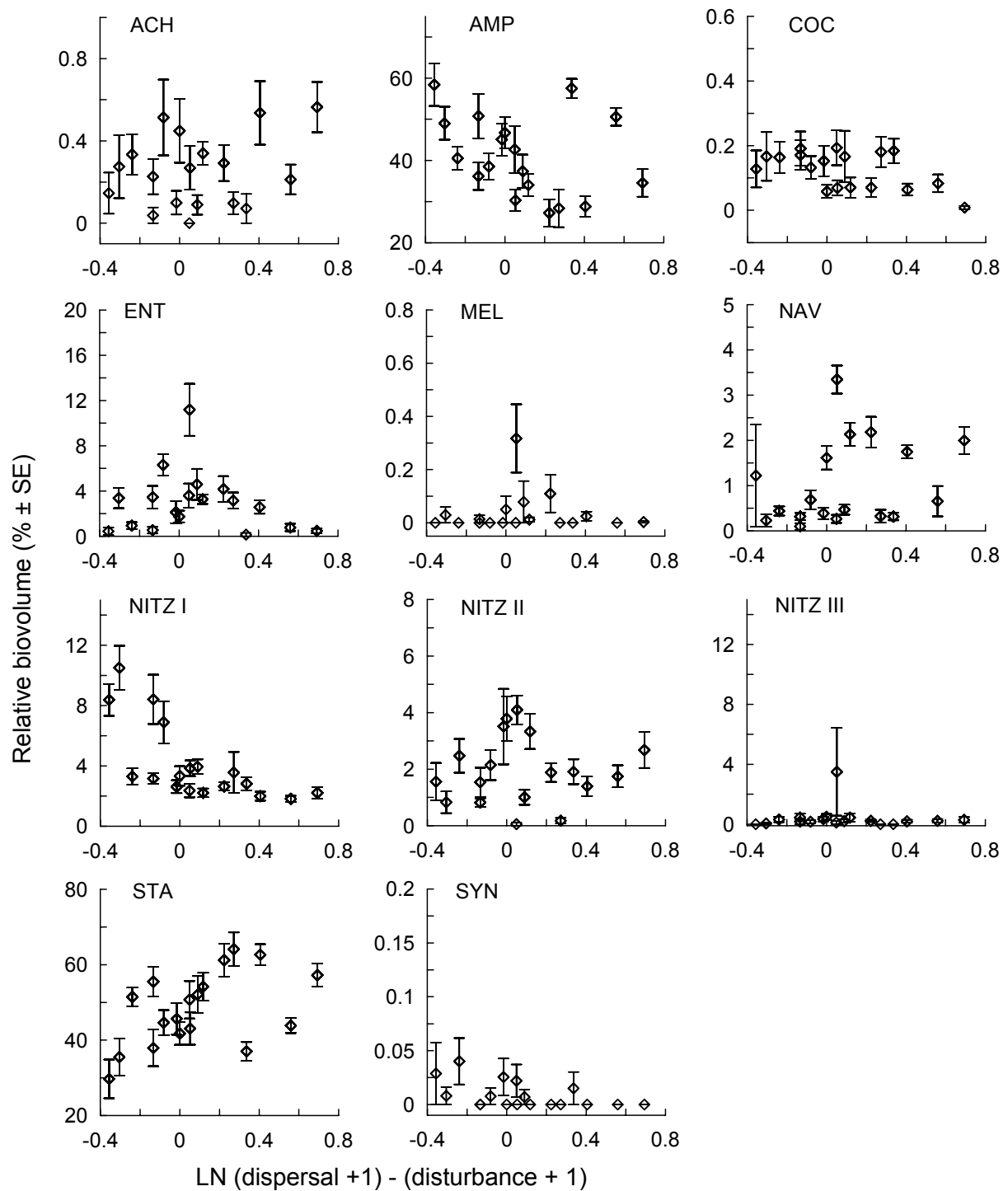
The mean local biomass production increased with increasing realized local species richness, and showed a significantly positive correlation with increasing local species richness ( $r = 0.41$ ,  $N = 204$ ,  $p < 0.001$ ; Fig. 2C). Mean metacommunity biomass production decreased with increasing realized  $\beta$ -diversity, and showed a significantly negative correlation with increasing  $\beta$ -diversity ( $r = -0.5$ ,  $N = 17$ ,  $p = 0.04$ ; Fig. 2D).

## Community structure

Species showed different species-specific contributions of relative biomass in patches of different stages in successional time (Fig.3). For the statistical results of all linear and polynomial regressions we are referring to in the following text see Appendix B, Table B1. Two species (NAV, STA) showed a significant increase in relative biomass production with increasing successional time (Fig.3). Three other species (AMP, COC, NITZ I) showed a significant decrease of relative biomass with increasing successional time (Fig. 3). One species (ENT) showed highest contribution of relative biomass in patches of intermediate successional stage (Fig. 3, for regression see Appendix B, Table B1).

**Table II-2:** Summary of the general linear model for non-linear effects of dispersal rate and the ratio between dispersal and disturbance rates on dependent variables. The table gives variable names, the overall model explained variance ( $R^2$ ),  $F$ -ratio, and significance level, as well as the estimate, standard error (SE) and significance level for the linear and quadratic term. The last column gives the probability for non-internal maximum or minimum of the hump- or U-shaped relationship according to the Mitchell-Olds and Shaw test.

Variable	$R^2$	$F$	$P$	Factor	Estimate	SE	$P$	MOS $P$ -value
Local richness	9%	10.76	<0.001	LN disp	6.74	1.58	<0.001	<0.001
				LN disp <sup>2</sup>	-9.98	2.18	<0.001	
LN local biomass	21%	27.53	<0.001	LN disp	3.11	0.57	<0.001	<0.001
				LN disp <sup>2</sup>	-3.14	0.78	<0.001	
Local richness	16%	20	<0.001	LN(disp/dist)	2.77	0.46	<0.001	0.02
				LN(disp/dist) <sup>2</sup>	-5.61	1.03	<0.001	
LN local biomass	56%	129.22	<0.001	LN(disp/dist)	4.3	0.29	<0.001	<0.001
				LN(disp/dist) <sup>2</sup>	-3.52	0.66	<0.001	
Beta-diversity	49%	8.81	0.003	LN disp	-0.37	0.09	0.001	0.002
				LN disp <sup>2</sup>	0.47	0.13	0.002	
LN metacomm biomass	82%	38.65	<0.001	LN disp	7.03	1.01	<0.001	<0.001
				LN disp <sup>2</sup>	-7.41	1.4	<0.001	
Mean occupancy	36%	5.5	0.02	LN disp	60.87	20.07	0.009	0.009
				LN disp <sup>2</sup>	-90.37	27.6	0.006	
Regional pool richness	12%	2.07	0.16					
Regional richness qual	3%	0.77	0.48					



**Fig. II-3:** Relative biomass contribution for each species in the local patches measured as biovolumes vs. the ratio between dispersal and disturbance rates.

## ***Discussion***

On the local scale in our experimental metacommunities, coexistence and community biomass production strongly depended on both the rate of propagule input from the regional pool and the frequency of local disturbance events (hypothesis one). Whereas dispersal rate alone can alter the species-specific dispersal success from the regional pool into the local patches, the ratio between dispersal and disturbance rates also determines the time for arrived species to grow. The non-linear hump-shaped pattern of local species richness and biomass production with increasing successional time shows that local species richness and also local biomass production significantly depend on the successional time (hypothesis two). Due to significant specific-specific differences in biomass production with increasing successional time, the maximized local richness at intermediate successional time can be explained by a colonization-competition trade-off. The corresponding non-linear pattern of local biomass production (with a significant quadratic term at late successional stages) strongly suggests that in our system enhanced realized local species richness was translated into increased local biomass production, which is also reflected by the significantly positive correlation of increasing biomass with local species richness (hypothesis three).

On the regional scale,  $\beta$ -diversity and mean metacommunity biomass production were significantly affected by dispersal rate, and mean metacommunity biomass production correlated negatively with increasing  $\beta$ -diversity (hypothesis four). The decreasing part of  $\beta$ -diversity with increasing dispersal rate can be explained by homogenisation of the whole metacommunity and the increasing part at late successional time can be attributed to a shift of subdominant species.

### **Effects of successional time on local species richness and biomass production**

Dispersal limitation was the major regulating factor for local species richness at early successional stages, whereas local richness depended more on local competitive interactions at late successional stages. The successional time of a local patch in our system determined both, the number of species that were able to colonize a local patch, and the time for species to grow after colonization, which indirectly changed the strength of local competitive interactions. Besides local species richness, also local biomass production showed a non-linear pattern with increasing successional time and declined at late successional stages. This implies that enhanced species richness was translated into enhanced biomass production.

At early successional stages only a limited number of species was able to (re)colonize the patches after frequent disturbance events and with only low average dispersal rate. Only three species in the algal community showed enhanced relative biomass at early



successional time (AMP, NITZ I, COC). With increasing successional time species richness increased. More species were able to colonize and to grow in the local patches. The enhanced number of species at intermediate successional stages can be explained by the co-occurrence of species which either decreased (i.e. good colonizers; AMP, NITZ I, COC) or increased (i.e. good competitors; STA, NAV) in relative biomass production with increasing successional time. Although we do not know species-specific competitive strength, this pattern strongly suggests that the increased number of coexisting species resulted from a colonization-competition trade-off at intermediate successional time (Tilman 1994, Yu and Wilson 2001). Both the permanent recolonization of species in intermediate dispersal rates but also the infrequent removal of biomass at intermediate successional time weakened local competition and allowed for the coexistence of more species.

With further increasing successional time high rates of propagule input in relation to disturbance frequency led to increasing local competition which resulted in decreasing species richness. Only two species (STA, NAV) showed increased biomass with increasing successional time.

The finding of a maximum in local species richness at intermediate dispersal rates reflects a general pattern in experimental metacommunities (Cadotte 2006a, Matthiessen and Hillebrand 2006) and also corresponds to modelling results (Loreau et al. 2003, Mouquet and Loreau 2003). Regarding the benthic microalgal species used in this system, it has been shown that dispersal rate altered species-specific dispersal in a similar metacommunity system (Matthiessen and Hillebrand 2006). Due to size and life-form, the algal species varied in their intrinsic dispersal abilities, and the colonization success of algal species depended on the frequency of induced dispersal (for cell-sizes of algae used in this study, see Appendix, Table A1).

We conclude that in this system enhanced species richness was translated into enhanced biomass production. At late successional time the biomass input from the regional species pools into the local patches was highest while the frequency of biomass removal by disturbance was relatively low. Thus, if only regional processes such as dispersal would have regulated local community biomass production in this system, we would have expected a linear increase of algal biomass with increasing successional time.

Diversity effects have been shown in many kinds of experimental systems, terrestrial (Hector et al. 1999), aquatic (Giller et al. 2004) as well as in multitrophic approaches (Duffy et al. 2005, Gamfeldt et al. 2005). A biodiversity effect per definition means that a species mixture show enhanced functioning (e.g. biomass production) compared to what can be expected from the species alone (Loreau and Hector 2001). A net diversity effect can be the result from species complementarity (Tilman et al. 1997b) and from species selection-effects (Wardle 1999). Whereas for closed systems there is consensus about the existence of a

diversity effect, research stands at the very beginning including the causes for diversity with the consequences for community or ecosystem functioning. So far, the importance of knowing the actual mechanism of species coexistence for the outcome of community productivity was suggested only theoretical (Mouquet et al. 2002): A competition-colonization trade-off model with homogeneous patches predicted a hump-shaped pattern of species richness with increasing fecundity (the probability that a species reaches a site), and an either positive or negative relationship between richness and productivity. The alternative model without a colonization-competition trade-off assuming heterogeneous local patches predicted increasing species richness with increasing fecundity and a positive relationship between richness and community productivity (Mouquet et al. 2002). Different to theoretical models about colonization-competition trade-offs (Calcagno et al. 2006), the species in the experiment could not be attributed to a clear hierarchy of competitive strength. Further, we could not clear-cut separate between how much biomass derived from local community production or from regional input. However, the decrease in local richness and biomass production at late successional stages strongly suggest that local interactions become more important with increasing succession. Further, both ends of the non-linear pattern of local biomass production can be explained by lower species richness, however, regulated by different processes.

To our knowledge only three experimental studies addressed system openness and the relationship of diversity and ecosystem functioning. In a similar microalgal system (Matthiessen and Hillebrand 2006) it has been shown that local diversity and biomass production were maximized at intermediate dispersal. However, compared to this study all patches were in late successional stages, so it was not possible to distinguish between regionally and locally driven processes. For actively migrating grazers (Matthiessen et al. 2006) it has been shown that in an open system of connected rock pools, it is rather initial grazer identity than grazer diversity which sustains grazing over time. Further, it has been shown that both, grazer diversity in a metacommunity and dispersal, interactively affect the predictability of ecosystem functioning in an eelgrass system (France and Duffy 2006).

### **Effects of dispersal rate on $\beta$ -diversity and regional biomass production**

Dispersal limitation led to high  $\beta$ -diversity without enhanced dispersal which is also reflected by the low mean occupancy of patches. Except for AMP, NITZ I and STA which were present in all local communities, not all subdominant species were able to colonize patches and to grow without enhanced dispersal, which led to high dissimilarity among local communities. As discussed above, with increasing dispersal more species were able to colonize and to grow which led to homogenisation of the metacommunities and to a decrease in  $\beta$ -diversity as predicted by theoretical models (Mouquet and Loreau 2003). Similarly, mean occupancy

increased because more species were able to disperse. Not predicted by any model was the increase in  $\beta$ -diversity at very high dispersal, which was also reflected in a decrease of mean occupancy. The shift from rather regional processes at early successional stages towards the regulation of local community processes by local community interactions at late successional stages might be reflected in the different subdominant species occurring at early and late successional stages, and thus, might have led to the increased  $\beta$ -diversity at high dispersal. Among the subdominant species SYN and COC were increased at early successional stages, whereas ACH and NAV were more present at late stages. The negative correlation of  $\beta$ -diversity with mean metacommunity biomass production is not surprising, since on both sides of the hump-shaped curves where local species richness and also biomass production was lowest,  $\beta$ -diversity was enhanced. However, this underlines that the relationship between diversity and ecosystem productivity strongly depends on the spatial scale. Further it shows how predictable local richness,  $\beta$ -diversity and biomass production interact in a metacommunity, even with rather uncontrolled random propagule input and biomass removal by disturbance.

### **Conclusions and outlook**

Our experimental results clearly show that increased local species richness resulting from a colonization-competition trade-off was translated into enhanced local biomass production. Overall metacommunity biomass production was negatively correlated with  $\beta$ -diversity since subdominant species in local patches were more different when local richness was low. The pattern of diversity and community biomass production on different spatial scales in the metacommunity was highly predictable. At early succession and with low dispersal, local species richness,  $\beta$ -diversity and (meta)community biomass production were regulated by regional processes such as dispersal limitation. At late successional time and with high dispersal rates local community interactions become more important as regulating factors for the relationship between diversity and biomass production.

To achieve generality between realized species richness and biomass production in metacommunities it remains to be experimentally tested whether increased species richness resulting from other mechanisms (such as source-sink dynamics) are also translated into enhanced ecosystem processes. This can also have consequences for the relationship between  $\beta$ -diversity and biomass production.

Furthermore the negative correlation between  $\beta$ -diversity and metacommunity biomass production as demonstrated here, must not be true for other ecosystem functions such as resilience. Here, one might hypothesize that after a metacommunity undergoes perturbation, a system of higher among patch-diversity might have a higher potential to recover.

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Rock pools with naturally co-occurring grazers used in the experiment in chapter III.  
Left to right: *Palaemon elegans*, *Littorina littorea*, *L. saxatilis*, *Idotea granulosa*, *L. fabalis*,  
*Gammarus duebenii*.

## CHAPTER III

### Effects of grazer richness and composition on algal biomass in a closed and open marine system

#### *Abstract*

Most natural local systems exchange organisms with a regional pool of species through migration and dispersal. Such metacommunity processes of interconnected multi-species assemblages are likely to affect local dynamics of both species and processes. We present results from an artificial marine outdoor rock pool system in which we investigated the factors of (1) local grazer richness and composition, and (2) connectivity of local patches to a regional species pool, and their effects on algal biomass. Local species richness of six grazers was manipulated in both open and closed pools, which were embedded in a regional species pool containing all six grazers. Grazer richness showed significant net biodiversity effects on grazing in the closed but not in the open system. Grazer composition, on the other hand, showed significant effects on grazing in both open and closed systems, depending on which species were initially present. The two most efficient grazers were able to compensate for less efficient grazers in species mixtures, hence ensuring the function of grazing. The efficiency of top-down control of algal biomass in open systems thus depends on which particular species are lost. Further, differences in grazing between the open and closed system changed over time due to temporal dynamics in grazer composition. The results emphasize the importance of including system connectivity in experimental designs to allow an extrapolation of biodiversity ecosystem-functioning relationships to natural systems.

## ***Introduction***

Global declines in biodiversity and the probability of ecosystem collapses have directed extensive research on the importance of species and functional group diversity on various ecosystem processes (Loreau et al. 2002a, Hooper et al. 2005). To date, the main focus of experimental studies has been on closed systems which are not open to input of propagules or adults from a surrounding regional environment (Naeem and Li 1997, Downing and Leibold 2002, Duffy et al. 2003). Most natural local systems, however, have some connection to a regional pool of species, to (and from) which organisms can migrate and disperse. This is especially true in marine environments where barriers to dispersal are typically weak (Giller et al. 2004). Therefore, it is unlikely that experimental and modelling results limited to closed local communities adequately predict the relationship of realized diversity and ecosystem processes in natural ecosystems. Consequently, to assess a more realistic relationship between biodiversity and ecosystem processes, it is important to consider system connectivity as a factor that influences diversity on different spatial scales (Cadotte and Fukami 2005).

Local communities consisting of multispecies assemblages that are linked by dispersal can be defined as a metacommunity (Wilson 1992, Leibold et al. 2004). In this framework, patches of local species assemblages interact with regional biota, resulting in spatial dynamics that affect local species diversity and hence also local ecosystem processes. Recent theoretical and experimental evidence has shown that immigration and dispersal are the main determinants of local species diversity and community functioning (Mouquet et al. 2002, Loreau et al. 2003, Matthiessen and Hillebrand 2006). To our knowledge, there are no experimental data that examine the effects of immigration and dispersal (i.e. "openness") on grazer richness and producer biomass.

In marine systems, grazing invertebrates and vertebrates can be important factors regulating ecosystem structure and functioning on coral reefs (Hughes and Connell 1999, Diaz-Pulido and McCook 2003) and rocky shores (Worm et al. 1999, Paine 2002). In the absence of grazers, ecosystems shift to alternate states with higher macroalgal standing biomass. Both theoretical (Holt and Loreau 2001, Thebault and Loreau 2003) and empirical work (Duffy et al. 2003, Gamfeldt et al. 2005) suggest that the diversity of grazers is an important factor regulating producer biomass. Higher species richness of consumers leads to more efficient use of the available resource space, reducing total producer biomass. Species also appear to be lost more frequently from higher than from lower trophic levels (Petchey et al. 2004). The loss of a few consumer species can have more profound long-term effects on ecosystem functioning compared to the consequences following the species loss of primary producers (Duffy 2003).

We used a system of naturally co-occurring invertebrates in Swedish west-coast rock pools to examine the effects of grazer richness and composition in open and closed systems. In several studies, it has been shown that grazers can have large impact on the algal community in rock pools through both direct and indirect effects (Metaxas et al. 1994, Trussel et al. 2004, O'Connor and Crowe 2005). Migration rates of grazers within any given pool depend on the connectivity to other pools and the ocean, and since grazer species differ in grazing efficiency (O'Connor and Crowe 2005), migration of such species may change local diversity – function relationships as often observed in closed systems. Depending on migration patterns (i.e. which species migrate where), local functioning may increase or decrease. We explored three hypotheses concerning the effects of grazer composition, richness and system openness on algal biomass. First, increasing local grazer richness reduces algal biomass in both closed and open communities. Second, local grazer identity and composition affect algal biomass in both closed and open communities. Third, migration of grazers in open systems alters the effects of initial local grazer richness and composition on local algal biomass over time.

## **Methods**

### **Experimental design**

We manipulated initial local grazer richness and composition of six marine invertebrate species in 96 outdoor plastic aquaria (40 × 30 × 20 cm), equally distributed in four large tanks (6 × 1.2 m). Each aquarium represented an artificial rock pool (local patch) situated within a larger tank (the regional pool). The six grazers all are common on local rocky shores and in rock pools, and include the snails *Littorina littorea* Linnaeus, *L. saxatilis* Olivi and *L. fabalis* Turton, and the crustaceans *Gammarus duebenii* Liljeborg, *Idotea granulosa* Rathke and *Palaemon elegans* Rathke (Ganning 1971, Berglund and Bengtsson 1981). Pre-assessments in the laboratory showed that all of these species grazed on benthic microalgae. Three richness levels were used (1, 3, 6) with four randomly assigned three-grazer compositions as well as a grazer-free control. We included all species in monoculture (*P. elegans* [A]; *L. littorea* [B]; *I. granulosa* [C]; *L. saxatilis* [D]; *G. duebenii* [E]; *L. fabalis* [F]; letters A – F describe species abbreviations used in the figures) to allow tests for net biodiversity effects (Loreau and Hector 2001). The twelve different treatments were replicated four times in each of the two connectivity treatments (see below). Following a substitutive design, grazer biomass (rather than abundance) was standardized across all treatments. Snail biomass was standardized equivalent to 100 individuals of *L. littorea* m<sup>-2</sup> (4.3 mg dry weight) and crustacean biomass equivalent to 50 *L. littorea* m<sup>-2</sup> (2.2 mg dry



weight, crustaceans are much less abundant in the field, in terms of biomass). 50 to 100 individuals per square meter lies within the natural abundance of *L. littorea* in the field. The initial numbers of individuals of each species, for all treatments, are shown in Appendix A.

In addition to grazer richness, we also manipulated connectivity between the local patches and the regional pool. In the two “closed system” tanks, each aquarium was covered with mesh (white fabric 0.039 g cm<sup>-2</sup> with 1-mm holes that allow light penetration of more than 90%, which is sufficient light for algal growth) to prevent migration of grazers. In the other two “open system” tanks, aquaria were also covered with mesh to create similar light conditions, but here, each mesh was elevated to allow migration between each aquarium and the surrounding water. When grazers left an aquarium (local patch) in the open system, they first entered the regional pool (space between the aquaria in a larger tank). Coming from the regional pool they could immigrate into each of the other local patches. Each of the four tanks (two for the open and two for the closed system) contained 24 aquaria which represented two randomly distributed replicates of each grazer richness × species composition treatment. Tanks and aquaria were normally supplied with continuously flowing seawater from the local bay (Tjärnö; 58°54' N, 11°7' W) to a depth of 15 cm. Equal water level in the tanks and aquaria was maintained by four drilled 1 mm holes at 15 cm height in the aquaria. Because they can move on dry surfaces, snails were able to migrate continuously, but to facilitate migration of all species we created high-water events every three days. For each such event the water level in all tanks was increased so that the tops of the aquaria were 5 cm under the surface for three hours. This also greatly increased exchange of seawater between the local and regional pools. On the Swedish west coast, intertidal rock pools receive water both from the ocean (through waves, splash and occasional floodings) and from rain. In this part of the world, the tidal range is approximately 0.3 m, and the main causes of water-level fluctuations are irregular changes in air pressure and wind direction (Johannesson 1989). Our choice of regular floodings every three days was a compromise between natural conditions (irregular but sometimes frequent floodings unrelated to tidal cycles) and an easy to follow schedule. This interval is thus as relevant as a cycle of, e.g., four or five days.

The total duration of the experiment was five weeks. At the start of the experiment, we placed four 5 × 5 cm bare unglazed ceramic tiles in each aquarium to measure algal biomass in the different grazer treatments. The tiles were sampled and scraped off at the termination of the experiment for analyses of chlorophyll (chl *a*), which we used as an estimate of algal biomass. To measure grazing rates, we added two pre-grown ceramic tiles in each aquarium twice (start and mid-experiment) during the experiment and sampled them after 24 hours for chl *a* analyses. The tiles had been pre-grown with algae for around four weeks in tanks with seawater from the bay. The periphyton on these tiles consisted mainly of diatoms with some

additional filamentous algae (*Ulva* spp.). Three pre-grown tiles not put in the aquaria were sampled, scraped and used as baselines for calculating the amount of grazed algae on the tiles in the aquaria. After sampling the tiles, the periphyton from all tiles was carefully scraped off, poured into a beaker (100 ml), and filled to a standard volume with filtered seawater. Due to differences in the amount of algal biomass, the volumes differed among the different response variables, but were similar for all samples within each variable (e.g. 50 ml for initial grazing rate). The algal biomass was evenly suspended by cautious stirring, and standardized volumes of subsamples (e.g. 5 ml for initial grazing rate) were filtered on glassfibre filters (Whatman GF/F) and immediately deep frozen at -20° C. Subsequently, chl *a* was extracted in 90% acetone (Strickland and Parsons 1972) after homogenizing the sample with glass sand on a vortex mixer and then measured spectrophotometrically. The two grazing rates are hereafter referred to as initial grazing rate (start) and mid-experiment grazing rate (mid-experiment).

### Statistical analysis

Prior to analysis, data were checked (using a block design ANOVA) for differences between the four tanks within the open and closed treatments. No such block effect could be detected (ANOVA,  $P > 0.1$  for all response variables), and consequently the tank block factor was omitted from subsequent analyses. To test for overall effects of grazer composition and system openness the experiment was analysed using a full-factorial two-way ANOVA with the fixed factors Grazer Composition and Connectivity (i.e. open and closed rock pools) and their interaction (using STATISTICA 6.1; StatSoft Inc., Tulsa, USA). To test for grazer richness effects between the single-grazer levels and the three- and six-grazer levels in the two subsets of the experiment, four planned contrast comparisons were conducted in this ANOVA. First, for the closed systems the single-grazer treatments (A, B, C, D, E, F) were tested versus the three grazer-levels (ABC, ABD, CEF, DEF), and second the single-grazer levels were tested versus the six-grazer level (ABCDEF). The same two planned comparisons were calculated for the initial grazer richness levels in the open systems. This ANOVA was calculated for all response variables (initial grazing rate, mid-experiment grazing rate, final yield of algal biomass). The data for the final yield of algal biomass were log-transformed to achieve homogeneous variances.

To test for grazer identity and specific composition effects in the open and closed treatments separately, two one-way ANOVAS with the fixed factor Composition were conducted. The zero-grazer level was excluded from this analysis, since we were interested in the effect of grazer identity and composition on algal biomass, but not in the effect of grazer presence. Student-Neuman-Keuls (SNK) tests were used to test for differences in grazing effects among the six species, as well as among the species mixture compositions. In order to

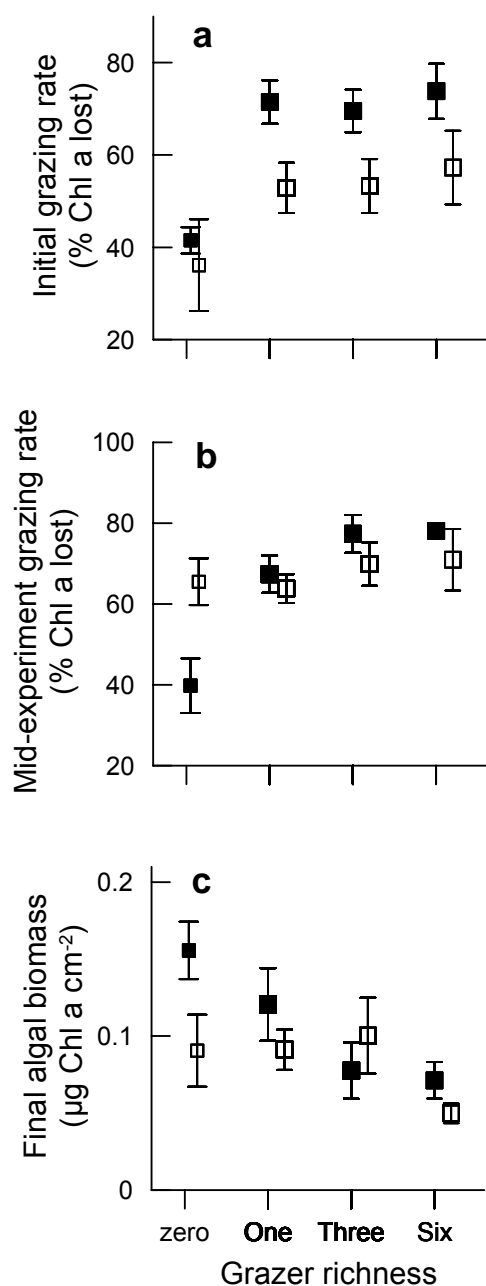
control for Type 1 errors in the multiple SNK-tests for three response variables (initial grazing rate, mid-experiment grazing rate, final yield of algal biomass), Dunn-Sidak's test was used to adjust p-values ( $p'=0.017$ ).

We calculated net biodiversity effects ( $\Delta Y$ ) of grazer richness on grazing rates and on the final yield of microalgal biomass, according to Loreau and Hector (2001). These calculations were separated for the closed and the open set of the communities. A significant net biodiversity effect means that grazer mixtures have higher effects on algae than is expected based upon their effects in the single-species grazer level (Loreau 1998). To calculate the expected contribution of each species in the three- and six-grazer mixtures (ABC, ABD, CEF, DEF, ABCDEF), we used the mean value of the respective single-grazer replicates ( $n = 4$ ). To test whether the net biodiversity effect was significantly different from the expected values based upon the monocultures, the  $\Delta Y$ -values of all mixed grazer levels (three and six species levels) were pooled and tested against zero with a two-tailed t-test. To test for a difference in net biodiversity effects between the three- and the six-grazer levels, the two groups were compared with a t-test. In order to quantify the turnover of species composition in closed versus open communities during the experiment, we calculated Bray-Curtis dissimilarities between the species compositions and species abundances of the grazer assemblages at the onset and at the end of the experiment. Bray-Curtis dissimilarities vary between 0 (complete similarity) and 1 (no similarity, Krebs 1989). We present for each of the initial compositions the mean dissimilarity ( $\pm$  SE) of the final assemblage to start conditions (Table 2). High dissimilarity between the start and the end composition of grazers in the open systems could be due to both migration and mortality, whereas in the closed systems only mortality could change local dynamics. Differences between the open and closed communities in Bray-Curtis dissimilarities were tested by a non-parametric sign-test.

## **Results**

### **Grazer richness effects**

Final yields of algal biomass were highest in the closed zero-grazer level and decreased in the presence of grazers (Fig. 1). Grazer richness and diversity showed a significant effect on grazing in the closed but not in the open systems (Table 1, Fig. 1, 2). In the closed systems, the three-grazer level (but not the six-grazer level) showed significantly higher grazing compared to the single-grazer level on the mid-experiment grazing rate and final algal yield (see contrasts Table 1, Fig. 1b, c). A significant net biodiversity effect of grazer richness was

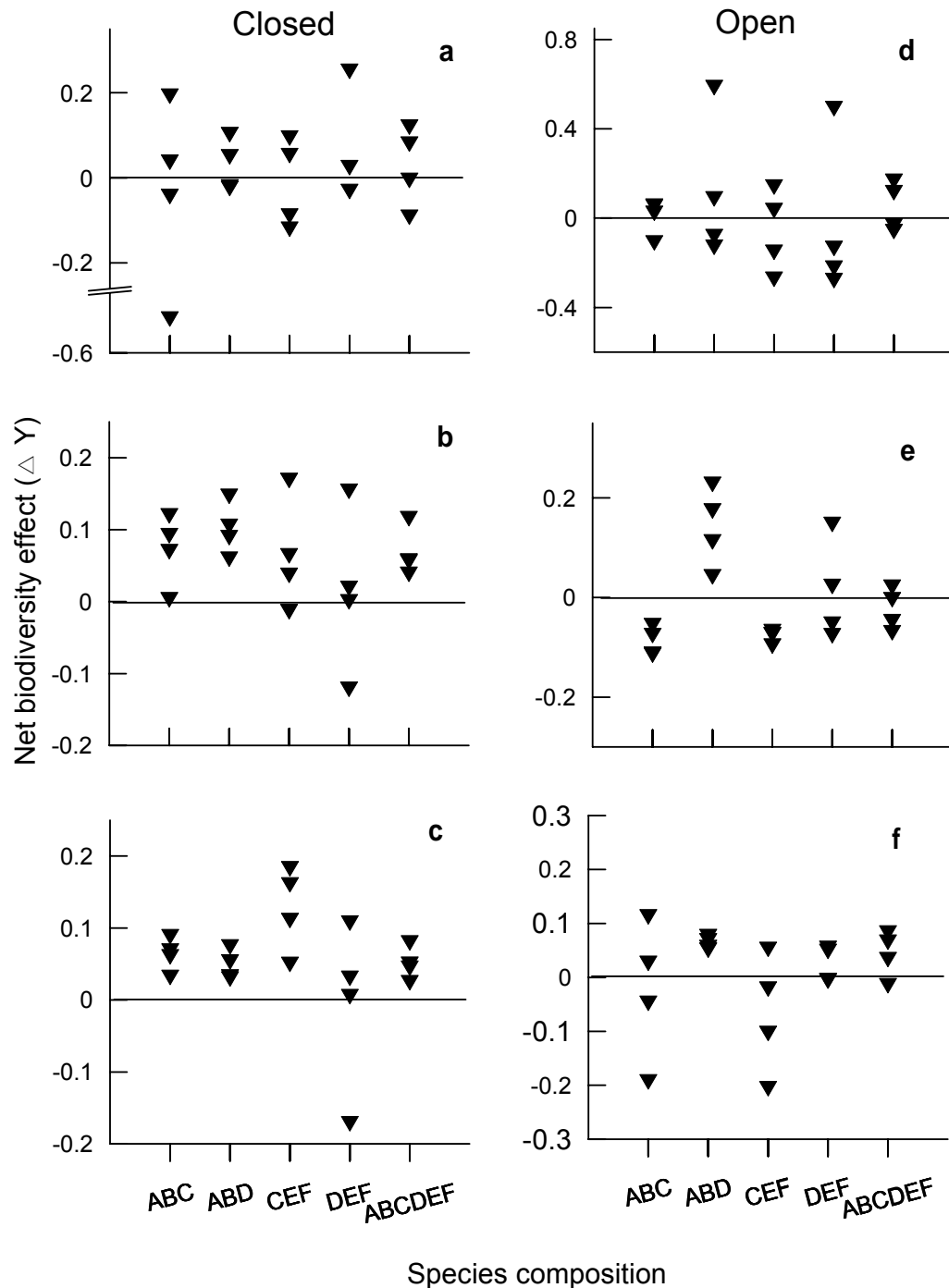


**Figure III-1:** Influences of grazer richness on grazing rates and final algal biomass in closed (filled squares) and open (open squares) rock pool mesocosms. Values are means ( $\pm$  SEs) of (a) initial grazing rate (% Chl a lost), (b) mid-experiment grazing rate (% Chl a lost), (c) final algal biomass ( $\mu\text{g Chl a cm}^{-2}$ ).

observed on mid-experiment grazing rate ( $t = -4.15$ ;  $P < 0.001$ ) and the final yield of algal biomass ( $t = 3.53$ ;  $P < 0.01$ , Fig. 2).

Mid-experiment grazing rates (Fig. 2b) were significantly higher in the mixtures (3 and 6 species), and final algal biomass (Fig. 2c) was significantly lower than could be expected from the performance of the respective species in the single-grazer level.

No increase in net biodiversity effect for any of these two response variables could be observed from the three-grazer level to the six-grazer level ( $t \leq -0.12$ ,  $P \geq 0.6$ ). For the initial grazing rate, the net biodiversity effect was non-significant ( $t = -0.3$ ;  $P = 0.75$ , Fig. 2a). In the open communities, planned contrasts showed a trend for the three-grazer level to be higher in grazing for the mid-experiment grazing rate (Table 1, Fig. 1b). This effect of initial grazer richness, however, did not persist to the end of the experiment. There was no (significant) lower yield in final algal biomass in the three-grazer compared to the single-grazer level (Table 1). Similar to the closed pools, there was no significant grazing effect of initially six grazers present compared to the initial single-grazer level (Table 1) at the mid-experiment grazing rate. No significant net biodiversity effects ( $\Delta Y$ ) for initial grazer richness could be observed ( $P \geq 0.68$  for all response variables, Fig. 2d, e, f).



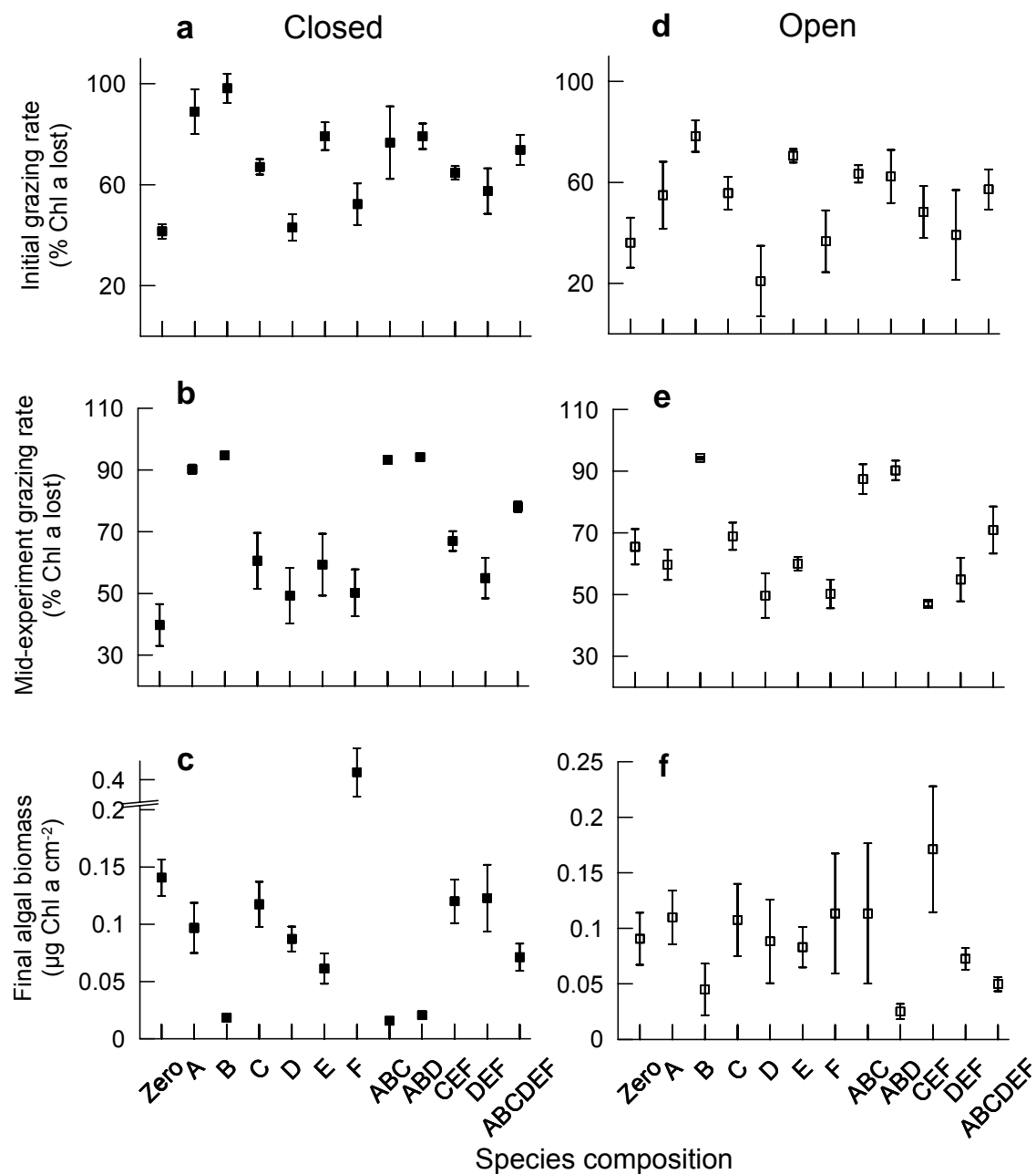
**Figure III-2:** Net biodiversity effect ( $\Delta Y$ ) on (a) initial grazing rate, (b) mid-experiment grazing rate, (c) final algal biomass in the closed communities; and on (d) initial grazing rate, (e) mid-experiment grazing rate, (f) final algal biomass in the open communities. Capital letters on the x-axis refer to different grazer species in the treatments: (A) *Palaemon elegans*, (B) *Littorina littorea*, (C) *Idotea granulosa*, (D) *Littorina saxatilis*, (E) *Gammarus dubenii*, (F) *Littorina fabalis*.  $\Delta Y = 0$  means that there is no difference between the expected grazing from the respective single-grazer levels and the observed grazing in the grazer mixtures.

**Table III-1:** Effects of connectivity (Conn), grazer composition (Comp) and grazer species richness (Contrasts) on initial grazing rate (% Chl a lost), mid-experiment grazing rate (% Chl a lost) and final algal biomass ( $\log \mu\text{g Chl a cm}^{-2}$ ). The results for the effects of grazer richness were calculated from planned contrasts for the three- and the six grazer richness levels vs. the single-grazer level. Contrasts were calculated separately for the closed and open systems. Significant ( $p < 0.05$ ) results are shown in boldface.

Overall analysis		Initial grazing			Mid-experiment grazing			Final algal biomass		
Factor	(df)	MS	F	P	MS	F	P	MS	F	P
Conn	(1)	<b>0.72</b>	<b>20.46</b>	<b>&lt;0.001</b>	<b>0.01</b>	1.49	0.23	0.02	0.29	0.59
Comp	(11)	<b>0.24</b>	<b>6.88</b>	<b>&lt;0.001</b>	<b>0.09</b>	<b>18.98</b>	<b>&lt;0.001</b>	0.63	<b>9.75</b>	<b>&lt;0.001</b>
Conn × Comp	(11)	0.01	0.33	0.98	0.01	<b>3.13</b>	<b>0.002</b>	0.21	<b>3.22</b>	<b>0.001</b>
Species richness										
Contrasts (df)		Initial grazing			Mid-experiment grazing			Final algal biomass		
<b>CLOSED</b>										
		MS	F	P	MS	F	P	MS	F	P
1 vs. 3	(1)	0.004	0.11	0.74	<b>0.04</b>	<b>7.89</b>	<b>0.006</b>	<b>0.51</b>	<b>7.89</b>	<b>0.006</b>
1 vs. 6	(1)	0.002	0.06	0.81	0.02	3.25	0.08	0.02	0.3	0.58
<b>OPEN</b>										
1 vs. 3	(1)	<0.001	0.01	0.94	0.01	2.94	0.09	0.01	0.14	0.71
1 vs. 6	(1)	0.007	0.21	0.65	0.007	1.45	0.23	0.08	1.17	0.28

### Grazer identity and composition

Grazer composition showed a significant effect on grazing rates and on final algal yield in closed and open communities (Table 1, Fig. 3). The mean grazing efficiency among species was highly variable (Fig. 3). The results from the Student-Neuman-Keuls tests (Appendix B) indicated a strong effect of species identity for the different grazer compositions on grazing rates and final algal biomass for both the open and closed system (Fig. 3). Despite temporal dynamics towards homogenisation of the whole metacommunity (see below), the separate ANOVA for the open system shows that initial grazer compositions had significant effects on grazing rates during the course of the experiment ( $F = 2.43$ ,  $P = 0.03$  for initial grazing,  $F = 12.37$ ,  $P < 0.001$ , Fig. 3d, e). Nonetheless, there was no significant effect of initial grazer composition on the final yield of algal biomass ( $F = 1.71$ ,  $P = 0.12$ , Fig. 3f). Among the single-grazer treatments in the closed system, both *P. elegans* (A) and *L. littorea* (B) showed high grazing for initial and mid-experiment grazing rates (Fig. 3a, b, for SNK tests see Appendix B). *L. littorea* (B) single-grazer treatments also showed the highest grazing for final algal yield (Fig. 3c).



**Figure III-3:** Grazing rates and final yield of algal biomass (chlorophyll a) for all grazer compositions in open and closed pools. Values are means ( $\pm$  SEs) of (a) initial grazing rate (% Chl a lost), (b) mid-experiment grazing rate (% Chl a lost), (c) final algal biomass ( $\mu\text{g Chl a cm}^{-2}$ ) in the closed communities; and of (d) initial grazing rate (% Chl a lost), (e) mid-experiment grazing rate (% Chl a lost), (f) final algal biomass ( $\mu\text{g Chl a cm}^{-2}$ ) in the open communities. Capital letters on the x-axis refer to different grazer species in the treatments: (A) *Palaemon elegans*, (B) *Littorina littorea*, (C) *Idotea granulosa*, (D) *Littorina saxatilis*, (E) *Gammarus dubenii*, (F) *Littorina fabalis*.

Initial and mid-experiment grazing rates for *P. elegans* (A) and *L. littorea* (B) and final algal yield for *L. littorea* (B) did not differ from the three-species mixtures including these species in the closed system (ABC, ABD, Fig. 3a, b, c, SNK tests Appendix B). In the open communities *L. littorea* (B) showed the highest grazing for mid-experiment grazing rate (Fig. 3e, SNK tests Appendix B). Grazing of these *L. littorea* (B) single-grazer treatments did not

differ from the three-species mixtures including these species (ABC, ABD, Fig. 3e, SNK tests Appendix B). *L. fabalis* (F) showed the lowest grazing for final algal yield in the closed communities (Fig. 3c, SNK test Appendix B). Final yield of algal biomass was even higher with *L. fabalis* (F) present than in the zero-grazer controls (Fig. 3c).

Among the three-grazer treatments in the closed communities, the compositions ABC and ABD (both containing *L. littorea* and *P. elegans*) showed significantly highest grazing for mid-experiment grazing rate (Fig. 3b) and final algal biomass (Fig. 3c). ABC and ABD were also most efficient for mid-experiment grazing rates in the open communities (Fig. 3e, SNK tests Appendix B).

**Table III-2:** Mean ( $\pm$  standard error) Bray-Curtis dissimilarity between start and final species composition for each species composition treatments. For species codes, see methods.

Initial grazer composition	Closed	Open
no	0 ( $\pm$ 0)	0.75 ( $\pm$ 0.25)
A	0.328 ( $\pm$ 0.033)	0.940 ( $\pm$ 0.06)
B	0 ( $\pm$ 0)	0.679 ( $\pm$ 0.05)
C	0.281 ( $\pm$ 0.053)	0.725 ( $\pm$ 0.035)
D	0.049 ( $\pm$ 0.017)	0.764 ( $\pm$ 0.01)
E	0.199 ( $\pm$ 0.037)	0.966 ( $\pm$ 0.021)
F	0.704 ( $\pm$ 0.043)	0.922 ( $\pm$ 0.063)
ABC	0.260 ( $\pm$ 0.019)	0.627 ( $\pm$ 0.032)
ABD	0.016 ( $\pm$ 0.001)	0.645 ( $\pm$ 0.074)
CEF	0.263 ( $\pm$ 0.032)	0.726 ( $\pm$ 0.058)
DEF	0.583 ( $\pm$ 0.241)	0.907 ( $\pm$ 0.072)
ABCDEF	0.254 ( $\pm$ 0.05)	0.612 ( $\pm$ 0.081)

### Connectivity

The grazers in the closed communities showed significantly stronger grazing compared to the open communities for initial grazing rate (significant effect of connectivity, Table 1, Fig.1a). A significant interaction between connectivity and grazer composition was observed for mid-experiment grazing rate and the final yield of algal biomass (Table 1). The difference between open and closed systems, and the interaction between connectivity and grazer composition, indicate temporal changes of grazer composition by migration in the open communities. These dynamics are shown by means of Bray-

Curtis dissimilarities of local grazer compositions between the start and final assemblages (Table 2). Irrespective of the starting assemblage, open grazer communities showed higher dissimilarity compared to closed ones (average dissimilarity of open treatments was 3-4 times higher than that of closed treatments; non-parametric sign test,  $Z = 6.65$ ,  $P < 0.001$ ).



## **Discussion**

### **Richness and composition effects**

Our findings of a significant net biodiversity effect in the closed system seem to be consistent with other studies that found positive net biodiversity effects in closed multitrophic systems. Using an eelgrass system, (Duffy et al. 2003) showed that increasing grazer richness decreased algal biomass. The positive effect of consumer richness on consumption rates has also been shown in a microbial food web (Gamfeldt et al. 2005) and in stream-shredder communities (Jonsson et al. 2002). Although our results seem to resemble those studies, we suggest that the positive net biodiversity effect does not result from a more complete resource use (Tilman et al. 1997b) in the mixed-grazer treatments, but from a compensatory effect of the most efficient grazers in those mixtures (compare Fig. 2 and Fig. 3). The grazer community that was used in this rock pool system contained two efficient (*L. littorea*, *P. elegans*) and one weak-grazing species (*L. fabalis*), which suffered high mortality during the course of the experiment. The other three grazers *I. granulosa*, *L. saxatilis*, and *G. dubenii* showed intermediate grazing (Fig. 3, Appendix B). Only the three-grazer mixtures in the closed system showed significantly higher grazing compared to single-grazer treatments, and none of the mixtures showed higher grazing rates or lower algal biomass than the two most effective monocultures, i.e. there was no transgressive over-yielding (Fridley 2001, compare Fig. 3). Further, the three-grazer mixtures that contained the two effective species showed significantly higher grazing efficiency compared to mixtures lacking these species (Fig. 3b, c, Appendix B). This effect was probably even stronger due to the presence of *L. fabalis* in the mixtures without the two efficient species. This means that grazing was not sustained by grazer richness per se but by two efficient species, which compensate for the less efficient species. The underlying mechanisms for positive effects of species richness on ecosystem processes are often separated into a selection effect (dominance by few species) and a complementarity effect (niche differentiation among species, Loreau and Hector 2001, Cardinale et al. 2002, Fox 2005). Although we could not test for these mechanisms we suggest that the observed grazing patterns mainly resulted from a selection effect of the two most efficient species.

Our study differs from those of more classical biodiversity-ecosystem function experiments performed in microbial- and plant systems (McGrady-Steed et al. 1997, Hector et al. 1999). In grazer mixtures, species cannot expand and grow at the expense of other species on a short temporal scale such as in this experiment, and hence the relative abundance among species (at least in closed systems) will not change (except for when mortality occurs). When mixtures show the same grazing efficiency as certain single-grazer treatments, this means

that efficient grazers can compensate for the presence of less efficient species. Even though an efficient grazer is present in lower abundance as compared to when in monoculture, it is still able to control algal biomass. In a way, the high efficiency and dominance of *L. littorea* even when it is not dominant in terms of abundance (as in the three-species mixtures) is the classical concept of a keystone species (sensu Paine 1966). The strong effect of species identity and composition in our results are consistent with the findings of Norberg (2000), Duffy et al. (2001), Emmerson et al. (2001), O'Connor and Crowe (2005), which showed idiosyncratic effects of different species in different species richness levels on algal biomass. Our results also suggest that the effects of grazer identity and richness can be strongly density dependent (Benedetti-Cecchi 2004) as the densities of individuals of one species (e.g. *L. littorea*) were higher in the three-grazer species levels compared to the six-grazer level. However, our experimental design does not allow for explicitly testing density dependent effects. As in natural rock pools (Ganning 1971), *L. littorea* was an important part of our-rock pool system, and wherever it was present grazing was ensured (compare Fig. 3b, c). A possible explanation for a 40% grazing rate in the grazer-free controls could be attributed to the presence of micrograzers (which we did not control for in our experiment). Even though not originally considered in the experimental setup, it is clear that predation affected the results of this study. Large-sized *P. elegans* were observed to consume on both *Idotea* and *Gammarus* (occasionally even on *L. fabalis*) on several occasions during the experiment, which was also reflected in the final total number of grazers (data not shown). These prey species were all less abundant at the termination of the experiment. It is plausible that this enhanced the dominating effect of *L. littorea* by reducing the number of grazing crustaceans (lethal direct effect). Further, even when crustaceans survived, *P. elegans* could have affected grazing by triggering local escape behaviour in its prey populations (non-lethal indirect effect, Trussel et al. 2004).

### **The role of connectivity**

The important role of grazer composition and identity for regulating algal biomass is apparent also in the open system. Effects of initial species composition were present until the mid-term of the experiment but vanished at the end. We suggest that this is an effect of metacommunity dynamics, where grazers migrated between the regional and local pools. As seen in Fig. 3f, variances for final algal biomass for the different initial compositions were large in comparison to variances for the grazing rates. This indicates that initial species composition may say little about the total final impact on algal biomass in open systems. However, an imprint of the initial presence of a compensating species was reflected in the significantly higher mid-experiment grazing rate of local communities with *L. littorea* initially

present (Fig. 3d). The local top-down regulation of algal biomass can thus to some extent depend on initial local grazer species composition.

A recent model suggests that both selection and complementarity effects can be produced by the same biological process operating at different scales (Cardinale et al. 2004), where a complementarity effect on the regional scale is the pre-condition to produce a selection effect at local scales (Mouquet et al. 2002, Cardinale et al. 2004, Loreau 2004). Ives et al. (2005) showed that in models with two trophic levels, both selection and complementarity effects are responsible for lower resource densities at higher consumer diversity. Because closed experiments are often too small to produce resource partitioning, Ives et al. (2005) concluded that most experiments tend towards detecting selection effects rather than complementarity effects. Such a dominance of selection effects is presumably also realized in our experiment due to the strong effects of two species (*L. littorea*, *P. elegans*) and the weak effect of one species (*L. fabalis*). On a small spatial and temporal scale, we suggest that the loss of local consumer diversity, or the loss of certain consumer species, will have a stronger effect on local ecosystem processes when metacommunity dynamics (immigration and emigration) play a minor role.

The open system of connected pools represented an assemblage of discrete, permanent habitat patches like rock pools and oceanic islands. Hence, it represents a case within the patch-dynamic paradigm, which is one of the theoretical definitions of a metacommunity according to Leibold et al. (2004). Theoretically, in such a patch-dynamic paradigm local coexistence derives from a competition-colonization trade-off (Tilman 1994), where dispersal and colonization counteract the competitive exclusion of species. Mouquet et al. (2002) pointed out that the relationship between species richness and productivity in open systems depends on the mechanism of coexistence. We could not take into account the causes of local species richness due to long generation times of grazers and the short experimental duration. Rather, we addressed short-term seasonal effects of the number and identity of grazer species that enter a rock pool in spring when algae start to grow. At first, our findings seem to contradict predictions of a recent model stating that regional processes like dispersal can amplify the biodiversity - ecosystem functioning relationship (Cardinale et al. 2004). This model predicts that when dispersal rates are high, the coupling of local communities and the regional pool produces positive local diversity-functioning relationships because local ecosystem processes become a function of the regional diversity (Cardinale et al. 2004). The assumptions for these results are, however, that the regional species pool has to be large and that there is a differentiation in resource availability among local patches. Neither of these assumptions was valid in our study. The richness of the regional pool was similar to the highest richness level in the local communities in our experiment (six grazers), and the

resource availability was similar in all local communities. Therefore, the experimental environment did not allow for different species to be better adapted to some pools than others, hence not mitigating regional coexistence (Leibold et al. 2004).

The differences between closed and open systems in our experiment are probably related to the high degree of connectivity in the open system. Theoretical model results suggest that a metacommunity tends to behave like a single large community at high connectivity (Loreau et al. 2003). Both the model (Loreau et al. 2003) and empirical data from laboratory experiments (Matthiessen and Hillebrand 2006) show that local richness is highest at intermediate dispersal rates. Because we did not actively transplant individuals in the open system, we manipulated connectivity in a way that reflects the natural stochasticity of dispersal. Therefore, we do not know where our system is located on the scale between low and high dispersal as defined by the model (Loreau et al. 2003).

Since most natural systems are more or less connected to a surrounding species pool, analyzing the effects of biodiversity on ecosystem functions in the absence of regional processes may be highly misleading (Bengtsson et al. 2002). Our study shows that migration can alter local processes by changing the composition of local species assemblages. Openness and habitat connectivity are hence important factors to consider when examining both biodiversity – ecosystem function relationships as well as other ecological questions.

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## Conclusions and outlook

Overall, the results of this work suggest that predicting the impacts of diversity on ecosystem functions requires shifting the focus towards regional processes influencing species coexistence. Dispersal is a well known factor controlling local species richness (Cadotte 2006a), and hence also influences ecosystem functioning such as producer biomass production within and across trophic levels (Chapters I-III). Moreover, the results suggest that impacts of realized diversity on ecosystem processes cannot be studied without acknowledging the particular mechanisms allowing for stable species coexistence (Chapters I-II). By including both spatial dynamics and local community interactions, the metacommunity concept (Leibold et al. 2004, Holyoak et al. 2005) provides an excellent theoretical framework to test the ecological impacts of diversity by allowing species to coexist over time. For future work the metacommunity concept also allows to switch the focus from diversity effects on the small (i.e. local) scale to larger spatial (i.e. regional) scales.

This thesis contains results of novel experimental approaches testing new hypotheses concerning the relationship between local diversity and community functioning after communities assembled by propagule and species dispersal (chapter I-III). Hitherto no experimental study considered if such realized diversity has regulating impacts on community functioning. First, I could show that the frequency of dispersal in the experimental metacommunities showed a general and well known non-linear effect on local community diversity (Cadotte 2006a, Chapter I-II). Second, I was able to demonstrate that this increased realized diversity was translated into enhanced biomass production (chapter I-II) and thus corroborated the often described positive effects of enhanced diversity on community biomass production in closed systems (Hooper and Vitousek 1997, Tilman et al. 2001, Loreau et al. 2002b). The importance of including regional factors such as dispersal for the maintenance of ecosystem functioning was also emphasized by the result that initial local diversity had no effect on final community biomass production (chapter I), not even without enhanced dispersal which most resembled closed systems and where local interactions were expected to be strong.

However, the unimodal relationship of algal species diversity with increasing dispersal frequency in chapter I, gave no evidence which particular mechanism of species coexistence (sensu Leibold et al. 2004) led to enhanced algal diversity. Therefore, in chapter I it remained to be discussed whether enhanced biomass production resulted from enhanced local species diversity or (partly) from quantitative input of propagules from the regional pool. In chapter II, I was able to provide the first experimental evidence linking stable species coexistence by a colonization-competition trade-off (one of the four coexistence perspectives, summarized in Leibold 2004) to a positive relationship between diversity and ecosystem functioning.

Previously, regulating effects of particular mechanisms of species coexistence for the diversity-ecosystem functions relationship have been addressed only in theoretical modeling approaches (Mouquet and Loreau 2002). The experimental metacommunities followed the patch-dynamics perspective (explained in Chapter I; Introduction) and the experimental design involving a mosaic of homogeneous community patches in different successional stages (*sensu* Cardinale et al. 2004) allowed me to show that species locally coexisted by the trade-off between colonizing and competitive abilities (Tilman 1994, Yu and Wilson 2001). Enhanced realized local species richness then translated into increased biomass production by diversity effects such as species complementarity or selection effects (Wardle 1999, Loreau 2000). Involving other mechanisms of species coexistence might result in alternative diversity-functioning relationships. Therefore, future diversity-ecosystem functioning studies should explicitly consider the particular mechanism of species coexistence. The regulating impact of the remaining three perspectives of species coexistence in metacommunities (mass-effect, species sorting, neutral perspective) largely remain to be experimentally tested.

Species diversity effects across trophic levels in chapter III confirm results of other studies which manipulated consumer diversity in closed systems (Duffy 2002, Duffy et al. 2003). I suggested, however, that the grazer richness effect on algal biomass production in the closed rock pool system depended on the presence of two effective grazer species (*Littorina littorea*, *Palaemon elegans*). These strong species identity effects confirm theoretical predictions that diversity effects in locally restricted and short-termed experiments are biased towards selection effects (Ives et al. 2005). In the open rock pool system which allowed grazers to migrate I showed that the strong identity effect by one of the two effective grazer species (*Littorina littorea*) remained over time. For local biomass production such as in rock pools this might imply that it can be critical which grazer species but not how many initially immigrate or settle when the summer season starts. Whereas local extinction of such an important consumer in an open system might not have any strong effects on local primary production because new individuals can immigrate, the extinction in the whole region of a metacommunity might have important ecological consequences in terms of consumer top down control.

Species diversity in natural communities is not locally restricted. Local communities differ from each other in terms of composition and diversity, and the totalized local and among habitat diversity determines the diversity of the overall species pool in a region. Therefore, for future research on the importance of diversity I suggest to test the impacts of realized  $\beta$ - and  $\gamma$ -diversity for ecosystem productivity and also for ecosystem stability.

Theoretical models predict that environmental heterogeneity among local patches is the precondition for enhanced  $\beta$ -diversity because without dispersal different species can

dominate different patch types varying in resource availability (mass-effect perspective, Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). With increasing dispersal  $\beta$ -diversity is predicted to decrease because source-sink effects between heterogeneous local communities quantitatively allow more species to coexist locally which leads to a homogenization of the metacommunity (Mouquet and Loreau 2003). Although the experimental designs in this work did not involve environmental heterogeneity, decreasing  $\beta$ -diversity with increasing dispersal (chapter I and II) suggest that this prediction might be also valid for other coexistence mechanisms than the mass-effect perspective.

Showing that  $\beta$ -diversity was negatively correlated with metacommunity biomass production (chapter II) provided a first step to evaluate the ecological role of  $\beta$ -diversity for community productivity on the regional metacommunity scale. However, because local habitat patches in the experimental patch-dynamics systems did not vary in resource availability (see above) the negative relationship between  $\beta$ -diversity and metacommunity biomass production only reflected the positive diversity-biomass production relationship from the local scale. The impact of  $\beta$ -diversity on community productivity yet largely remains to be tested in source-sink metacommunities where varying resource availabilities among local patches allow different species dominating local communities. One could hypothesize that the relationship between  $\beta$ -diversity and biomass production will be positive because the regional coexistences of the most productive species also means regional complementarity in resource use. This in turn would imply that local diversity (which is maintained by source-sink dynamics) negatively impacts local productivity because less productive species are maintained by rescue effects and thus will distract resources from the most effect one. However, in real ecosystems neither colonization-competition trade-offs nor source-sink dynamics alone allow for species coexistence (Mouquet et al. 2005). Thus, after disentangling the regulating impacts of coexistence mechanisms, the direction and aim must be to detect general patterns for the impact of diversity on ecosystem functioning.

I also want to highlight the potential role of  $\beta$ -diversity for ecosystem stability. Theoretical models (Yachi and Loreau 1999, Loreau et al. 2003) and few experimental results (Tilman et al. 2006) showed that with increasing species diversity the temporal stability of communities can increase which is regarded as an community insurance effect. However, the importance of  $\beta$ -diversity for ecosystem recovery after perturbations remains to be tested. One could hypothesize that  $\beta$ -diversity can be important for the maintenance of ecosystem functions after a perturbation event which affected a whole region such as an extreme climate event. More differences among local communities (i.e. less homogenization) might represent an insurance because some local communities might inhabit more resistant species than others which can recolonize the region and hence maintain ecosystem functions.



Finally, because species extinction is a regional event I also suggest that independently from the mechanism for species coexistence it is important to experimentally test the ecological impact of metacommunity regional species pool diversity. I suggest to test that ecosystem functions are interactively regulated by regional pool size and by dispersal rates among local community patches which in turn will influence realized diversity on the different spatial scales. This approach would enable ecologists to test for the relationships between realized  $\alpha$ ,  $\beta$ -, and  $\gamma$ -diversity and respective ecosystem functions under different scenarios of regional species extinctions and dispersal between habitat patches.

Especially for conservation management in highly fragmented landscapes it is essential to know how coexistence mechanisms are linked to the maintenance of ecosystem functions across spatial scales and under different scenarios of regional species extinctions .

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## Appendix

### Chapter I

**Appendix I-A:** Table listing the species, cell sizes and life-forms of microalgae included in our experiment.

Total species pool	Abbreviation	Mean biovolume/cell ( $\mu\text{m}^3$ )	Life form
Achnanthes brevipes	(ACH)	1615	benthic
Cylindrotheka closterium	(CYL)	127	benthic
Stauroneis constricta	(STA)	5150	benthic
Cocconeis sp.	(COC)	431	benthic
Amphora coffaeiformes	(AMP)	55	benthic
Thalassiosira weissflogii	(THA)	16028	benthic-pelagic
Melosira nummuloides	(MEL)	2233	benthic
Nitzschia sp. (I)	(NITZ I)	1630	benthic
Navicula ramosissima	(NAV)	1745	benthic
Nitzschia oblongella	(NITZ III)	5100	benthic
Merismopedia punctata	(MER)	58	benthic-pelagic
Isochrysis sp.	(ISO)	95	benthic-pelagic
Nitzschia sp. (II)	(NITZ II)	40	benthic
Entomoneis paludosa	(ENT)	2950	benthic
Cymbella sp.	(CYM)	1161	benthic

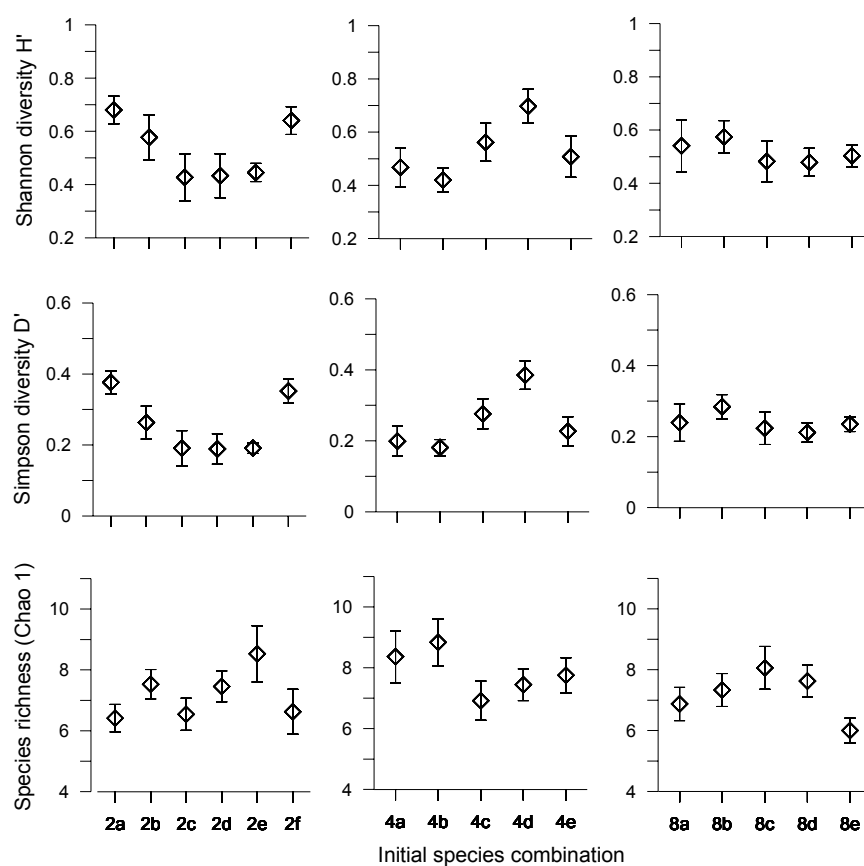
**Appendix I-B:** Table with species combinations used in our experiment.

Initial diversity level	Initial species combination	Species in the treatment
2	a	STA, ENT
2	b	MEL, NITZ III
2	c	ISO, Nitz II
2	d	NAV, MER
2	e	ACH, CYM
2	f	STA, COC
4	a	COC, NITZ I, ISO, NITZ II
4	b	ACH, MER, ISO, CYM
4	c	CYL, STA, AMP, ISO
4	d	STA, NITZ I, NITZ III, ENT
4	e	ACH, MEL, NITZ I, ENT
8	a	CYL, AMP, THA, MEL, NAV, NITZ III, ISO, NITZ II
8	b	ACH, STA, COC, MEL, NITZ III, MER, NITZ II, CYMB
8	c	ACH, CYL, COC, AMP, ISO, NITZ II, ENT, CYMB
8	d	CYL, COC, THA, NAV, NITZ III, ISO, NITZ II, CYM
8	e	ACH, CYL, STA, COC, AMP, THA, NITZ I, MER



**Appendix I-D:** Table with results of stepwise forward multiple regressions to identify species altering community diversity. Stepwise forward multiple regression testing the effect of species presence or absence on diversity measured as D, Chao 1 or H', respectively. The table gives dependent variables, the overall model explained variance ( $R^2$ ), F-ratio, and significance level, as well as the estimate, standard error (SE) and significance level for the included terms.

Dependent	Model $R^2$	Model F	Model p	Included	Estimate	SE	p
D	19.1%	11.58	<0.001	Intercept	0.21	0.02	<0.001
				STA	0.12	0.02	<0.001
				MER	-0.04	0.02	0.097
				AMP	-0.05	0.02	0.045
				ENT	0.04	0.02	0.074
Chao	4.9%	10.29	0.002	Intercept	7.85	0.21	<0.001
				STA	-1.06	0.33	0.002
H'	10.1 %	7.67	<0.001	Intercept	0.52	0.03	<0.001
				STA	0.13	0.04	<0.001
				MER	-0.09	0.04	0.023
				ISO	-0.05	0.04	0.148



**Appendix I-E:** Graphical display of final diversity in local assemblages for different initial species combinations

## Chapter II

**Appendix II-A:** The table gives species used in the experimental communities, abbreviations of species names in the text and mean cell sizes.

Total species pool	Abbreviation	Mean biovolume/cell ( $\mu\text{m}^3$ )
Achnanthes brevipes	(ACH)	1712
Amphora coffaeiformes	(AMP)	173
Cocconeis sp.	(COC)	357
Entomoneis paludosa	(ENT)	4293
Melosira varians	(MEL)	304
Navicula ramosissima	(NAV)	979
Nitzschia sp. (I)	(NITZ I)	62
Nitzschia oblongella (II)	(NITZ II)	2175
Nitzschia sigma	(NITZ III)	3597
Stauroneis constricta	(STA)	3387
Synedra sp.	(SYN)	532

**Appendix II-B:** Results of linear and polynomial regressions testing the effect of the ratio between dispersal and disturbance (i.e.  $\ln(\text{dispersal}+1) - \ln(\text{disturbance}+1)$ ) on relative contribution to total biomass of each species. The table gives dependent variables, the overall model explained variance ( $R^2$ ), F-ratio, and significance level, as well as the estimate, standard error (SE) and significance level for the included terms.

Dependent	$R^2$	$F$	$P$	Factor	Estimate	SE	$P$
Rel biomass	(%)						
ACH	0.7	2.51	0.11	LN (disp/dist)	0.15	0.09	0.11
AMP	3	7.02	<0.01	LN (disp/dist)	-9.83	3.71	<0.01
COC	3	7.58	<0.01	LN (disp/dist)	-1.1	0.04	<0.01
ENT	9	11.85	<0.001	LN (disp/dist)	2.85	1.3	0.03
				LN (disp/dist) <sup>2</sup>	-13.64	2.92	<0.01
MEL	2	2.5	0.08	LN (disp/dist)	0.08	0.05	0.13
				LN (disp/dist) <sup>2</sup>	-2.8	0.12	0.03
NAV	3	7.07	<0.01	LN (disp/dist)	0.94	0.35	<0.01
NITZ I	22	58.28	<0.001	LN (disp/dist)	-6.15	0.81	<0.001
NITZ II	0.3	0.35	0.55	LN (disp/dist)	0.33	0.55	0.55
NITZ III	0.4	0.003	0.96	LN (disp/dist)	-0.03	0.63	0.96
STA	7	18.07	<0.001	LN (disp/dist)	16.02	3.77	<0.01
SYN	2	4.69	0.03	LN (disp/dist)	-0.02	0.01	0.03

### Chapter III

**Appendix III-A1:** The number of animals from each species that were included in each of the 12 species compositions used in the experiment, for both the closed and open treatments, for one local pool (0.14 m<sup>2</sup>). The biomass of snails in each local pool was standardized to an equivalent of 100 individuals of *L. littorea*/m<sup>2</sup> and the biomass of crustaceans was standardized to an equivalent of 50 *L. littorea*/m<sup>2</sup>. The biomass was held constant across treatments so that biomasses for each species were divided by three (in the three-species mixtures) and six (in the six-species mixture).

Closed/open	Composition	<i>Palaemon</i>	<i>L. littorea</i>	<i>Idotea</i>	<i>L. saxatilis</i>	<i>Gammarus</i>	<i>L. fabalis</i>
closed	A	6	0	0	0	0	0
closed	B	0	21	0	0	0	0
closed	C	0	0	25	0	0	0
closed	D	0	0	0	22	0	0
closed	E	0	0	0	0	32	0
closed	F	0	0	0	0	0	30
closed	ABC	2	7	8	0	0	0
closed	DEF	0	0	0	7	11	10
closed	ABD	2	7	0	7	0	0
closed	CEF	0	0	8	0	11	10
closed	ABCDF	1	3	4	4	5	5
closed	Zero	0	0	0	0	0	0
open	A	6	0	0	0	0	0
open	B	0	21	0	0	0	0
open	C	0	0	25	0	0	0
open	D	0	0	0	22	0	0
open	E	0	0	0	0	32	0
open	F	0	0	0	0	0	30
open	ABC	2	7	8	0	0	0
open	DEF	0	0	0	7	11	10
open	ABD	2	7	0	7	0	0
open	CEF	0	0	8	0	11	10
open	ABCDF	1	3	4	4	5	5
open	Zero	0	0	0	0	0	0
regional pools (per tub)	ABCDF	12	38	46	40	59	55

**Appendix III-A2:** Mean dry weights (g) for one specimen of each species. These dry weights were based on measurements of 10 specimens for each species.

Species	Dry weight (g)
<i>Gammarus</i>	0.01365
<i>Idotea</i>	0.017585
<i>L. fabalis</i>	0.02905
<i>L. saxatilis</i>	0.0409
<i>L. littorea</i>	0.04278
<i>Palaemon</i>	0.069185



**Appendix III-B:** This appendix includes seven tables. Table B1 shows the results of the one-way ANOVAs with the factor species composition that were calculated separately for the closed and the open system. Results are considered to be significant when  $p < 0.05$ . Table B2-7 show the results of the Newman-Keuls Posthoc-Tests between all grazer treatments for all response variables (initial grazing rate, mid-experiment grazing rate and final yield of algal biomass) in the closed (tables 2-4) and in the open communities (tables 5-7). Significant results ( $< 0.017$ ) are shown in boldface.

Capital letters in the tables refer to different grazer species in the treatments: (A) *Palaemon elegans*, (B) *Littorina littorea*, (C) *Idotea granulosa*, (D) *Littorina saxatilis*, (E) *Gammarus dubenii*, (F) *Littorina fabalis*.

#### Appendix III-B1: Results of ANOVAs for the closed and open system

CLOSED		Initial grazing			Mid-experiment grazing			Final algal biomass		
Factor	(df)	MS	F	P	MS	F	P	MS	F	P
Comp	(10)	<b>0.11</b>	<b>4.76</b>	<b>&lt;0.001</b>	<b>0.05</b>	<b>9.87</b>	<b>&lt;0.001</b>	<b>0.69</b>	<b>27.2</b>	<b>&lt;0.001</b>
OPEN										
Comp	(10)	<b>0.11</b>	<b>2.43</b>	<b>0.03</b>	<b>0.05</b>	<b>12.37</b>	<b>&lt;0.001</b>	0.19	1.71	0.12

#### Appendix III-B2: Initial Grazing Rate (closed communities)

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		0.383	0.318	<b>0.004</b>	0.627	0.032	0.651	0.361	0.266	0.084	0.606
<b>B</b>	0.383		0.073	<b>0.001</b>	0.286	<b>0.004</b>	0.265	0.181	0.054	<b>0.012</b>	0.212
<b>C</b>	0.318	0.073		0.172	0.655	0.503	0.631	0.773	0.819	0.634	0.523
<b>D</b>	<b>0.004</b>	<b>0.001</b>	0.172		0.029	0.382	0.042	0.036	0.186	0.363	0.060
<b>E</b>	0.627	0.286	0.655	0.029		0.168	0.812	1.000	0.638	0.324	0.865
<b>F</b>	0.032	<b>0.004</b>	0.503	0.382	0.168		0.211	0.203	0.474	0.625	0.263
<b>ABC</b>	0.651	0.265	0.631	0.042	0.812	0.211		0.969	0.661	0.371	0.786
<b>ABD</b>	0.361	0.181	0.773	0.036	1.000	0.203	0.969		0.732	0.389	0.955
<b>CEF</b>	0.266	0.054	0.819	0.186	0.638	0.474	0.661	0.732		0.498	0.659
<b>DEF</b>	0.084	0.012	0.634	0.363	0.324	0.625	0.371	0.389	0.498		0.414
<b>ABCDEF</b>	0.606	0.212	0.523	0.060	0.865	0.263	0.786	0.955	0.659	0.414	

## Appendix III-B3: Mid- Experiment Grazing Rate (closed communities)

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		0.949	<b>0.006</b>	<b>0.001</b>	<b>0.007</b>	<b>0.001</b>	0.719	0.884	0.023	<b>0.002</b>	0.155
<b>B</b>	0.949		<b>0.004</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	0.984	0.951	<b>0.024</b>	<b>0.001</b>	0.291
<b>C</b>	<b>0.006</b>	<b>0.004</b>		0.658	0.881	0.603	<b>0.004</b>	<b>0.004</b>	0.448	0.779	0.106
<b>D</b>	<b>0.001</b>	<b>0.000</b>	0.658		0.627	0.912	<b>0.000</b>	<b>0.000</b>	0.300	0.776	0.023
<b>E</b>	<b>0.007</b>	<b>0.004</b>	0.881	0.627		0.524	<b>0.004</b>	<b>0.004</b>	0.633	0.603	0.131
<b>F</b>	<b>0.001</b>	<b>0.000</b>	0.603	0.912	0.524		<b>0.000</b>	<b>0.000</b>	0.282	0.573	0.023
<b>ABC</b>	0.719	0.984	<b>0.004</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>		0.912	<b>0.017</b>	<b>0.001</b>	0.179
<b>ABD</b>	0.884	0.951	<b>0.004</b>	<b>0.000</b>	<b>0.004</b>	<b>0.000</b>	0.912		0.020	<b>0.001</b>	0.235
<b>CEF</b>	0.023	0.024	0.448	0.300	0.633	0.282	<b>0.017</b>	0.020		0.482	0.192
<b>DEF</b>	<b>0.002</b>	<b>0.001</b>	0.779	0.776	0.603	0.573	<b>0.001</b>	<b>0.001</b>	0.482		0.064
<b>ABCDEF</b>	0.155	0.291	0.106	0.023	0.131	0.023	0.179	0.235	0.192	0.064	

## Appendix III-B4: Final Yield of Algal Biomass (closed communities)

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		<b>0.000</b>	0.387	0.871	0.316	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.599	0.314	0.551
<b>B</b>	<b>0.000</b>		<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.654	0.571	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>C</b>	0.387	<b>0.000</b>		0.556	0.089	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>	0.925	0.660	0.236
<b>D</b>	0.871	<b>0.000</b>	0.556		0.266	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.670	0.329	0.382
<b>E</b>	0.316	<b>0.000</b>	0.089	0.266		<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.098	0.021	0.490
<b>F</b>	<b>0.000</b>	<b>0.000</b>	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>		<b>0.000</b>	<b>0.000</b>	<b>0.001</b>	<b>0.003</b>	<b>0.000</b>
<b>ABC</b>	<b>0.000</b>	0.654	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>		0.566	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>ABD</b>	<b>0.000</b>	0.571	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.566		<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>CEF</b>	0.599	<b>0.000</b>	0.925	0.670	0.098	<b>0.001</b>	<b>0.000</b>	<b>0.000</b>		0.441	0.278
<b>DEF</b>	0.314	<b>0.000</b>	0.660	0.329	0.021	<b>0.003</b>	<b>0.000</b>	<b>0.000</b>	0.441		0.082
<b>ABCDEF</b>	0.551	<b>0.000</b>	0.236	0.382	0.490	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.278	0.082	

## Appendix III-B5: Initial Grazing Rate (open communities)

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		0.698	0.958	0.174	0.898	0.614	0.979	0.959	0.656	0.545	0.987
<b>B</b>	0.698		0.653	0.018	0.602	0.177	0.577	0.705	0.481	0.211	0.620
<b>C</b>	0.958	0.653		0.207	0.856	0.704	0.955	0.898	0.870	0.684	0.919
<b>D</b>	0.174	0.018	0.207		0.056	0.297	0.137	0.134	0.274	0.445	0.213
<b>E</b>	0.898	0.602	0.856	0.056		0.384	0.634	0.846	0.744	0.430	0.809
<b>F</b>	0.614	0.177	0.704	0.297	0.384		0.627	0.605	0.719	0.868	0.736
<b>ABC</b>	0.979	0.577	0.955	0.137	0.634	0.627		0.944	0.909	0.666	0.911
<b>ABD</b>	0.959	0.705	0.898	0.134	0.846	0.605	0.944		0.877	0.631	0.736
<b>CEF</b>	0.656	0.481	0.870	0.274	0.744	0.719	0.909	0.877		0.546	0.929
<b>DEF</b>	0.545	0.211	0.684	0.445	0.430	0.868	0.666	0.631	0.546		0.742
<b>ABCDEF</b>	0.987	0.620	0.919	0.213	0.809	0.736	0.911	0.736	0.929	0.742	

**Appendix III-B6: Mid-Experiment Grazing Rate (open communities)**

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		<b>0.000</b>	0.383	0.485	0.956	0.373	<b>0.003</b>	<b>0.001</b>	0.374	0.494	0.374
<b>B</b>	<b>0.000</b>		<b>0.007</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.580	0.558	<b>0.000</b>	<b>0.000</b>	<b>0.010</b>
<b>C</b>	0.383	0.007		0.086	0.208	0.075	0.030	0.020	0.046	0.197	0.771
<b>D</b>	0.485	0.000	0.086		0.573	0.938	<b>0.000</b>	<b>0.000</b>	0.699	0.738	0.058
<b>E</b>	0.956	0.000	0.208	0.573		0.498	<b>0.002</b>	<b>0.001</b>	0.429	0.737	0.269
<b>F</b>	0.373	0.000	0.075	0.938	0.498		<b>0.000</b>	<b>0.000</b>	0.886	0.508	0.053
<b>ABC</b>	<b>0.003</b>	0.580	0.030	<b>0.000</b>	<b>0.002</b>	<b>0.000</b>		0.683	<b>0.000</b>	<b>0.001</b>	0.023
<b>ABD</b>	<b>0.001</b>	0.558	0.020	<b>0.000</b>	<b>0.001</b>	<b>0.000</b>	0.683		<b>0.000</b>	<b>0.000</b>	0.023
<b>CEF</b>	0.374	<b>0.000</b>	0.046	0.699	0.429	0.886	<b>0.000</b>	<b>0.000</b>		0.669	0.029
<b>DEF</b>	0.494	<b>0.000</b>	0.197	0.738	0.737	0.508	<b>0.001</b>	<b>0.000</b>	0.669		0.162
<b>ABCDEF</b>	0.374	<b>0.010</b>	0.771	0.058	0.269	0.053	0.023	0.023	0.029	0.162	

**Appendix III-B7: Final Yield of Algal Biomass (open communities)**

	A	B	C	D	E	D	ABC	ABD	CEF	DEF	ABCDEF
<b>A</b>		0.417	0.693	0.981	0.848	0.920	0.990	0.190	0.511	0.957	0.861
<b>B</b>	0.417		0.610	0.434	0.638	0.613	0.308	0.588	0.151	0.552	0.404
<b>C</b>	0.693	0.610		0.998	0.882	0.970	0.999	0.334	0.544	0.991	0.955
<b>D</b>	0.981	0.434	0.998		0.999	0.998	0.973	0.256	0.819	0.998	0.776
<b>E</b>	0.848	0.638	0.882	0.999		0.932	1.000	0.367	0.623	0.989	0.960
<b>F</b>	0.920	0.613	0.970	0.998	0.932		1.000	0.358	0.694	0.955	0.945
<b>ABC</b>	0.990	0.308	0.999	0.973	1.000	1.000		0.195	0.854	0.999	0.522
<b>ABD</b>	0.190	0.588	0.334	0.256	0.367	0.358	0.195		0.053	0.325	0.357
<b>CEF</b>	0.511	0.151	0.544	0.819	0.623	0.694	0.854	0.053		0.752	0.529
<b>DEF</b>	0.957	0.552	0.991	0.998	0.989	0.955	0.999	0.325	0.752		0.903
<b>ABCDEF</b>	0.861	0.404	0.955	0.776	0.960	0.945	0.522	0.357	0.529	0.903	

## CURRICULUM VITAE

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### Publikationen

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Matthiessen, B., Gamfeldt, L., Hillebrand, H., Jonsson, P. (2006)  
Grazer richness and composition effects on algal biomass in a  
closed and open marine system. Ecology: in press

Matthiessen, B., Hillebrand, H. (2006) Dispersal frequency  
affects local biomass production by controlling local diversity.  
Ecology Letters. 9: 252 – 662

Matthiessen, B., Fock H. O. (2004) A null model for the analysis of dietary overlap in *Macroramphosus spp.* at the Great Meteor Seamount (NE Atlantik). *Archive for Fisheries Research*. 51(1-3): 291-302.

Matthiessen, B., Fock, H. O., von Westerhagen, H. (2003) Evidence for two sympatric species of snipefishes *Macroramphosus spp.* (Syngnathiformes, Centriscidae) on Great Meteor Seamount. *Helgoland Marine Research* 57: 63 – 72.

Fock, H. O., Matthiessen, B. et al., (2002) Diel and habitat dependent resource utilisation of deep-sea fishes at the Great Meteor seamount (subtropical NE Atlantic): niche overlap and support for the sound scattering layer-interception hypothesis. *Marine Ecology Progress Series* 244: 219 – 233

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## **Description of the individual scientific contribution to the multiple-author papers**

The chapters of this thesis are partly published (chapters I and II) or submitted (chapter III) to scientific journals with multiple authorship. This list serves as a clarification of my personal contributions on each publication.

### **Chapter I:**

#### **Dispersal frequency affects local biomass production by controlling local diversity**

Authors: Birte Matthiessen, Helmut Hillebrand;

Published in *Ecology Letters* (2006) 9: 652-662

Contributions: BM and HH developed the ideas for this study, BM conducted the experiment, BM conducted data analyses; BM and HH discussed the results, BM wrote the manuscript.

### **Chapter II:**

#### **Biodiversity effects in metacommunities depend on dispersal and disturbance rates**

Authors: Birte Matthiessen, Helmut Hillebrand

Submitted

Contributions: BM and HH discussed the ideas for this study, BM conducted the experiment, BM conducted data analyses, BM and HH discussed the results, BM wrote the manuscript.

### **Chapter III:**

#### **Effects of grazer richness and composition on algal biomass in a closed and open marine system**

Authors: Birte Matthiessen, Lars Gamfeldt, Per Jonsson, Helmut Hillebrand

Published in *Ecology*, in press.

Contributions: BM, LG, PJ and HH developed the ideas for this study, BM and LG conducted the experiment, BM and LG conducted data analyses; BM, LG, PJ and HH discussed data analysis and results, BM and LG wrote the manuscript.

BM and LG equally contributed to this manuscript.



## **Erklärung**

Hiermit erkläre ich, dass die vorliegende Dissertation, abgesehen von der Beratung meiner Betreuer, selbstständig von mir angefertigt wurde und dass sie nach Form und Inhalt meine eigene Arbeit ist. Sie wurde keiner anderen Stelle im Rahmen eines Prüfungsverfahrens vorgelegt. Dies ist mein einziges und bisher erstes Promotionsverfahren. Die Promotion soll im Fach Biologische Meereskunde erfolgen. Des weiteren erkläre ich, dass ich Zuhörer bei der Disputation zulasse.