DISPERSAL AND METACOMMUNITY DYNAMICS IN A SOFT-SEDIMENT BENTHIC SYSTEM

– how well is the seafloor connected?

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"The direct measurement of dispersal is for most organisms and systems a logistical nightmare."

– **KNEITEL & CHASE 2004**

ABSTRACT

Connectivity depends on rates of dispersal between communities. For marine soft-sediment communities dispersal involves more than just initial colonization (recruitment) of substrate by pelagic larvae. Continued small-scale dispersal as post-larvae and as adults can be equally important in maintaining community composition. Our knowledge of post-larval dispersal potential of marine organisms in general is, however, very limited. This is particularly true for non-tidal benthic systems, such as the Baltic Sea, where dispersal has not previously been quantified. Having an understanding of how and when individuals are dispersing relative to underlying environmental heterogeneity within a given region is key to interpreting scale-dependent patterns of diversity (α-, β-, γ-diversity). Nevertheless, in nature a difficulty has been to actually measure dispersal directly, which has caused empirical work to fall far behind theoretical developments; in both metacommunity and metapopulation ecology.

In this thesis, a variety of direct and indirect measures of dispersal were used to investigate connectivity in marine soft-sediment communities. Post-larval (juveniles and adults) dispersal was quantified using a variety of trap types, along with ambient community composition, at different sampling intervals across sites that varied in local environmental conditions (e.g. sediment grain size, exposure to wind-waves). Taxa dispersed in relative proportion that was distinctly different from resident community composition and a significant proportion (40%) of taxa were found to lack a planktonic larval life-stage. Several system and species–specific dispersal-related strategies were demonstrated, as well as underlying mechanisms by which communities are connected. Local community composition was found to change predictably under varying rates of dispersal and physical connectivity (waves and currents). This response was, however, dependent on dispersal related traits of taxa. Actively dispersing taxa will be relatively better at maintaining their position, as they are not as dependent on hydrodynamic conditions for dispersal and will be less prone to be passively transported by currents and deposited back down onto the sediment.

Community assembly was also re-started in a large-scale manipulative field experiment across several sites, which revealed how patterns of community composition (α-, β- and λ-diversity) change depending on rates of dispersal. Dispersal can become limiting for some species and/or life-stages (patch dynamic) at early assembly or if a newly created disturbance (empty patch) is large relative to the scale of underlying environmental heterogeneity. In response to small-scale disturbances, however, findings suggest that initial dispersal and recruitment will be by nearby-dominant species after which species will arrive from successively further away. If rates of dispersal remain high the number of

coexisting species will increase beyond what would be expected purely by local niche requirements (species sorting), thus transferring regional differences in community composition (β-diversity) to the local scale (α-diversity, mass effect).

In contrast to initial larval recruitment, frequent small-scale dispersal as post-larvae can significantly extend the dispersal period and thus contribute to resilience of benthic communities when faced with disturbance. *In situ* findings of this thesis complement several theoretical and laboratory-based studies in demonstrating how both dispersal and environmental heterogeneity contribute to the assembly and maintenance of spatio-temporal patterns of community composition.

CONTENTS

LIST OF ORIGINAL PAPERS

This thesis is based on the following papers, which are referred to in the text by their respective numbers:

Paper 1
Valanko S., Norkko A. & Norkko J. (2010) Strategies of post-larval dispersal in non-tidal soft-sediment communities. *Journal of Experimental Marine Biology and Ecology* 384: 51–60.

Paper 2
Valanko S., Norkko A. & Norkko J. (2010) Rates of post-larval bedload dispersal in a non-tidal soft-sediment system. *Marine Ecology Progress Series* 413: 253–266.

Paper 3
Valanko S., Norkko J. & Norkko A. (2012) Trait mediated change in community composition under varying strength of connectivity and dispersal. *Manuscript.*

Paper 4
Valanko S., Norkko J., Whitlatch R.B., Cottenie K. & Norkko A. (2012) Patterns of diversity and metacommunity structure over assembly time: an empirical field study. *Manuscript.*

1. INTRODUCTION AND BACKGROUND

Marine soft-sediments are the most common habitats on earth (Snelgrove 1999) and cover approximately 70% of the planet. Community composition of benthic invertebrates vary predictably depending on niche requirements of member species and dominant local environmental conditions, which include (but is not limited to) grain size characteristics (Gray 1974, Snelgrove & Butman 1994, Anderson 2008) and food supply (Pearson & Rosenberg 1978). In addition to local environmental filtering, it has been recognized that the flux of individuals to and from regional dispersal pools and their residence time also profoundly impact local communities (Palmer et al. 1996). Thus, dispersal between localities has the potential to influence species distribution across multiple temporal and spatial scales. For example, episodic larval supply and post-settlement survival may be important in maintaining large-scale patterns of community composition (i.e. during peak recruitment, usually in spring/summer). However, it has also been recognized that continued small-scale dispersal as post-larvae and as adults can be equally important in maintaining spatio-temporal patterns (especially in heterogeneous near-shore environments). Thus, key to interpreting scale-dependent patterns of diversity (α-, β-, γ-diversity) is having an understanding of how and when individuals are dispersing relative to underlying environmental heterogeneity within a given region (i.e. metacommunity dynamics, Leibold et al. 2004).

Even though metacommunity and metapopulation ecology are well established, a difficulty has been to actually measure dispersal directly in nature, which has caused empirical work to fall far behind theoretical developments (Agrawal et al. 2007, Jacobson & Peres-Neto 2010). In an effort to simplify, many theoretical studies in ecology have also overlooked environmental heterogeneity, and dispersal is often assumed to be constant across scales and between species (e.g. Hanski 1999). However, in ecological reality we know that the landscape is more often spatially heterogeneous, and that dispersal operates over disparate spatial and temporal scales depending on species and life-history dispersal strategies (papers 1–3). Being able to translate such information on dispersal into knowledge of how communities are connected (paper 3 and 4) is of fundamental importance in conservation, when, for example, predicting responses to disturbances or in the design of effective networks of MPAs (marine protected areas). This is evident for regions such as the Baltic Sea, where increasingly larger and more frequent benthic disturbances are occurring in both coastal and offshore areas due to hypoxia (Norkko & Bonsdorff 1996, Diaz & Rosenberg 2008, Conley et al. 2009, Conley et al. 2011). Hence a shift towards manipulative, large-scale field experiments is all the more appropriate, as they provide the relevant context within which both validation and application of ecological theory is most urgently needed in conservation.

1.1 Outline and aims of thesis

The overarching aim of this thesis is to provide a better understanding of how benthic communities are connected, with specific reference to post-larval dispersal processes in shallow non-tidal soft-sediment habitats (see Fig. 1). To do this specific themes have been addressed in four complementary field studies (paper 1–4). The thesis combines manipulative field experiments, as well as several indirect and direct measures of benthic invertebrate dispersal. The thesis not only addresses study system-specific knowledge gaps, but provides an increased understanding of how benthic communities are connected by applying ideas from metacommunity ecology.
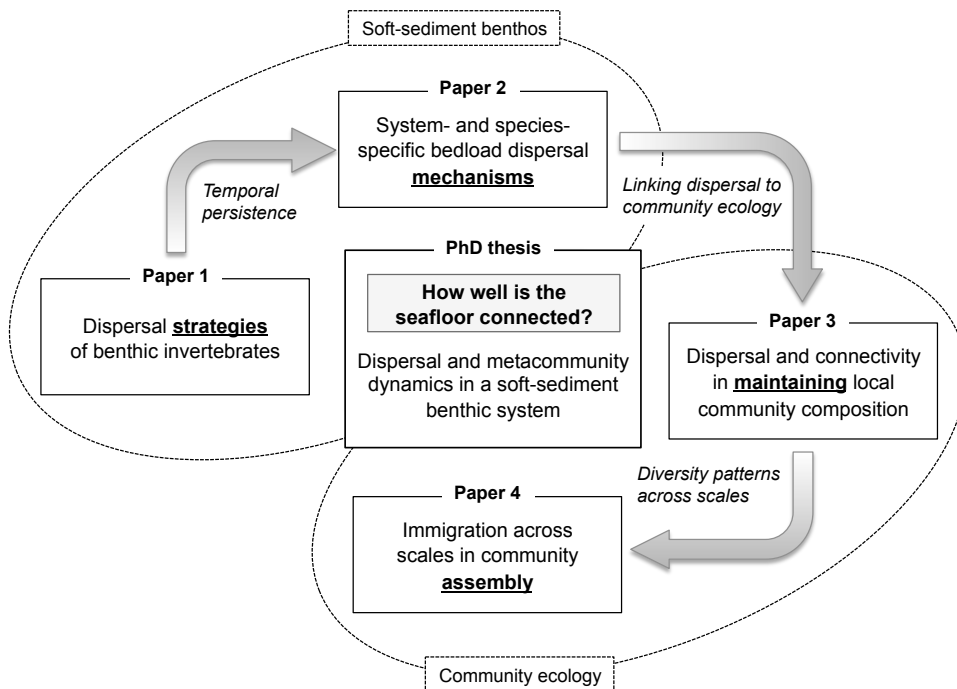
Figure 1. Conceptual diagram showing how the field studies in papers 1–4 build upon each other and contribute to the central question of the PhD thesis as a whole. Papers 1 and 2 investigate study system-specific dispersal strategies and mechanisms, while paper 3 links changes in local community composition to direct measures of dispersal and connectivity. Paper 4 investigates how patterns of diversity are assembled by applying metacommunity ecology at a scale relevant to management.

Paper 1: **Dispersal <u>strategies</u> of benthic invertebrates**
Our knowledge of post-larval dispersal potential of marine organisms in general is very limited. This is particularly true for non-tidal benthic systems, such as the Baltic Sea, where dispersal has not previously been quantified. Therefore an initial aim of this thesis (paper 1) was to determine whether benthic invertebrates disperse as post-settlers, and if so, how?

Paper 2: **System- and species- specific bedload dispersal <u>mechanisms</u>**
In paper 2, a study was designed to gain further insight into the general mechanisms of bedload dispersal (identified in paper 1 as an important mode of dispersal). Understanding connectivity in soft-sediment benthic communities requires an appreciation of how sediment transport and associated dispersal of invertebrates can vary predictably depending on energy and grain size characteristics, as well as species-specific traits.

Paper 3: **Dispersal and connectivity in <u>maintaining</u> local community composition**
Building on study system-specific understanding of post-larval dispersal (papers 1 and 2), paper 3 investigated whether dispersal can quantitatively affect community composition. This is a pertinent question in ecology, as temporal field studies testing theoretical predictions under varying rates of dispersal are rare (but see: Adler 2004, Chase 2007, Hubbell 2009). This is largely due to the fact that measuring dispersal of multiple species across an appropriate temporal scale is still rarely done, as it is logistically and methodologically challenging (Jacobson & Peres-Neto 2010). The study in paper 3 was therefore designed to test whether variation in rates of dispersal and physical connectivity (i.e. waves and currents) predictably affect the temporal stability of local community composition. Several different direct measures of dispersal (i.e. trap types) were used, which increased the likelihood of also capturing dispersing rare species by accounting for different dispersal strategies of taxa. The study was thus also able to test whether maintained community composition was associated to dispersal related traits of species.

Paper 4: **Immigration across scales in community <u>assembly</u>**
In dynamic systems such as benthic soft-sediment communities, rates of dispersal are key in maintaining patterns of diversity (Cadotte 2006). Building on findings from papers 1–3, a manipulative field experiment was conducted in which community assembly was re-started (recolonization experiment) at several localities simultaneously. This allowed investigation of how patterns of diversity change depending on immigration history (α- versus β-diversity), as well as evaluation of the relative importance of different metacommunity processes over time. Paper 4 provides an empirical example of how increasing rates of dispersal across a heterogeneous landscape can influence the assembly of scale-dependent patterns of diversity (α-, β-, γ-diversity) over time (e.g. Mouquet & Loreau 2002). Paper 4 was also conducted at a relevant scale for management and conservation, thus providing practical understanding of connectivity across benthic communities.

1.2 Dispersal of marine soft-sediment invertebrates

Connectivity can be defined as the rate of dispersal between communities (see review by Tischendorf & Fahrig 2000). For benthic marine invertebrates dispersal involves spatial extents ranging from a few centimeters to thousands of kilometers, and temporal frequencies ranging from seconds to seasons (see reviews by Palmer 1988, Armonies

1994, Palmer et al. 1996). It is a process by which the spatial distribution of individuals changes by movement in the water column, on top or within the sediment (see glossary for definition). Propensity to disperse depends on species-specific characteristics, as well as life-history strategy (Thorson 1950, Grantham et al. 2003, Pedersen et al. 2008); whether its larval, post-larval or adult phase is being considered (Fig. 2). It has been recognized that dispersal involves more than just initial colonization (recruitment) of substrate and that it can regularly modify local processes such as competition and predation (Palmer et al. 1996).
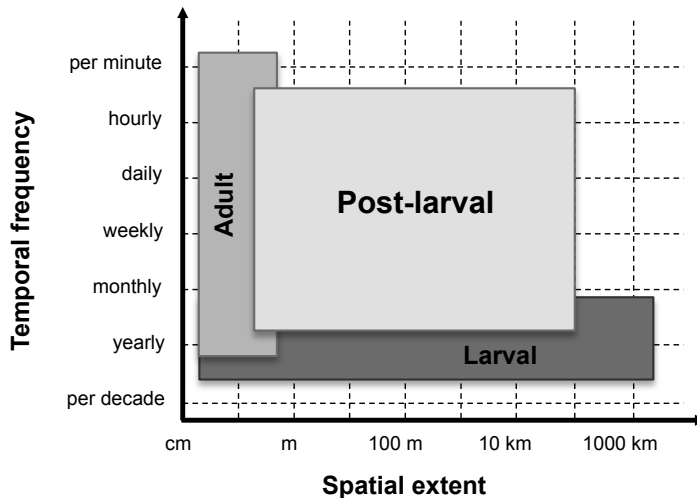
Figure 2. Dispersal of marine soft-sediment benthic invertebrates can vary in spatial extent and temporal frequency, depending on whether their larval, post-larval or adult phases are being considered. The net sum of frequent-small scale dispersal may therefore be equally as important as episodic long-distance dispersal events (adapted from Hewitt et al. 2010).

Much of our present insight into the dispersal dynamics of benthic invertebrates comes indirectly from studies on recolonization after disturbance (e.g. Bonsdorff 1989, Norkko & Bonsdorff 1996, Thrush & Whitlatch 2001). While large-scale recruitment events are mostly driven by seasonal larval recruitment, many soft-sediment species continue to disperse after settlement throughout the year (Günther 1992, Grantham et al. 2003). For example, as adults some benthic invertebrates are able to actively burrow or crawl in or on the sediment surface. Bedload transport of sediment and subsequent post-larval dispersal can also provide the opportunity for repeated small-scale dispersal, particularly when individuals are small juveniles (Emerson & Grant 1991). In tidal systems many post-larval benthic invertebrates, even ones lacking a planktonic larval stage, have been observed to be passively transported and/or actively swim higher up in the water column (e.g. Martel & Chia 1991, Beukema 1993). It is now widely recognized that post-larval dispersal plays a significant role in the spatial patterns of distribution and abundance of benthic communities, especially for soft-sediments where species are not permanently

attached to their substrate (e.g. Palmer 1988, Armonies 1994, Hewitt et al. 1997, Norkko et al. 2001).

In the past, however, an over-emphasis on supply-side ecology (*sensu* Gaines & Roughgarden 1985) has led to a very static picture of the benthos, in which dispersal was considered to be limited to episodic long-distance dispersal by larvae (Lundquist et al. 2006, Pineda et al. 2009, Cowen & Sponaugle 2009). Viewed as purely a physical process, larvae from a well-mixed larval pool disperse and will settle into local populations (i.e. demographically open, over >1000 km). This has been an attractive view due to its conceptual simplicity. Studies have been conducted, for example, by deploying passive tracers or modeling oceanic currents (e.g. Palumbi 2003). However, in contrast to passive particles, it has been demonstrated that upon release larvae can be retained within very close proximity (Osman & Whitlatch 1998). With distance and time larval density may rapidly diminish owing to advective and diffusive properties of the mixing and stirring of currents (e.g. 20–30 km, Becker et al. 2007). Larval dispersal can also be very costly, incurring high rates of mortality (e.g. 85.2–97.6%, Pedersen et al. 2008). In contrast, dispersal at the post-larval stage can involve higher survival rates and prolonged periods of dispersal, and thus its net importance can be more significant than initial larval recruitment for the mature adult population (Pedersen et al. 2008, Pineda et al. 2009). Furthermore, 40–60% of benthic invertebrates do not even have a larval phase (Grantham et al. 2003, paper 1), relying instead, for example, on brooded larval release. Marine populations are thus now considered much less open demographically (see Levin 2006, Becker et al. 2007, Cowen & Sponaugle 2009).

Understanding post-larval dispersal processes in marine coastal environments is especially important as they represent critical habitats for many invertebrates, linking the sea with land and freshwater habitats (Levin et al. 2001, Cowen & Sponaugle 2009). However these environments are exceedingly complex to work in for physical oceanographers. Close to the coast, wind-induced waves and long-shore currents can be transformed, creating complex near-bottom current regimes. Thus many physical drivers converge and interact depending on, for example, depth, coastal configuration and exposure to wind-waves. The distribution of hydrodynamic forcing can also affect sediment erosion, transport and deposition rates, and thus sediment grain size characteristics at a locality. Other material, such as seasonal drift algae that is transported along the seafloor can provide a means of dispersal by rafting for species associated with algae (e.g. Highsmith 1985, Norkko et al. 2000). Bedload transport of sediment, the movement of particles in continuous or near-continuous contact with the bed, is greatest at times when bottom shear stress (BSS) is sufficient to cause erosion (Le Hir 2007). When species are not permanently attached to their substrate, erosion and transport of post-larvae in the bedload is an especially important process (Emerson & Grant 1991). It has been shown that juvenile benthic invertebrates living closer to the sediment surface will be more susceptible to erosion by waves and currents. With increasing size, however, many species will be able to burrow deeper or actively emerge, thus regulating their erosion rates and subsequent transport along the bottom as bedload (Armonies 1988, Hewitt et al. 1997, Lundquist et al. 2004). In tidal systems, fluxes in post-larval bedload dispersal have been

associated with wind-wave activity and sediment resuspension (e.g. Commito et al. 1995, Lundquist et al. 2006). However, we do not know whether dispersal as post-larvae is relatively more restricted by the lack of regular tidal energy (i.e. the Baltic Sea).

1.3 Spatial ecology in coastal benthic environments

In nature species rarely exist in homogenous environments (e.g. Ricklefs 2008, Hewitt et al. 2010). Indeed, environmental heterogeneity has been recognized as one of the most important properties of ecological systems when moving from local to regional scales (Levin 1992). Environmental gradients across the seafloor includes: amount of interstitial space, sediment surface roughness, sediment mud content, organic material (POM, DOM), oxygen concentration, depth, light, exposure to waves and wind, above ground vegetation or the presence of other structures. Furthermore these can interact or change in nature depending on temporal scales, such as: seasonality (temperature, ice-cover, peaks in primary-productivity) or inter-annual changes (oxygen, salinity). The seafloor can thus be considered a continuum of overlapping environmental gradients operating across different spatial and temporal scales (i.e. heterogeneity).

A benthic community will consist of those species whose distributions include a particular point in space and time, with specific environmental conditions and dispersal history. The community can thus be viewed as being embedded within a larger metacommunity that it forms part of (Alonso et al. 2006, Hu et al. 2007). How well this community is connected to its metacommunity depends on the temporal frequency and spatial extent of dispersal in the region (Hu et al. 2007, Matias et al. 2012). This is mainly governed by dominant hydrodynamic forcing, which is regular but variable in strength depending on wind-generated waves and currents in the region (Soomere et al. 2008). Local diversity can thus be considered the result of a sum of processes operating over spatial scales that greatly exceed the generally accepted extent of a local community (Palmer et al. 1996, Ricklefs 2008). Regional niche differentiation between species in benthic communities can explain local coexistence in its metacommunity through immigration and emigration process (e.g. source-sink dynamics, Mouquet & Loreau 2002).

In contrast to many other systems, an important property for soft-sediment communities is that species do not become permanently attached once they have colonized, but are subject to continued emigration and immigration – with high rates of turnover of individuals. For example in tidal-systems, residence times of 1–2 days have been recorded for *Hydrobia ulvae, Cerastoderma edule*, *Macoma balthica,* and *Macomona liliana* (Armonies 1994, Norkko et al. 2001). In these dynamic systems, waves can approach the coast from different directions, with longshore currents in either direction along the shoreline. For beaches and their sub-littoral habitats this back and forth transport will result in large fluxes of sediment over a locality, but the net transport will be low. While high rates of passive dispersal of animals associated with sediment transport can promote turnover of individuals for a community, it does not necessarily mean that there has been a net transport of individuals (e.g. Norkko et al. 2001), or for that matter a gain or loss of

species from one locality to another. Benthic studies have noted that the continuous movement of individuals by transport events that are highly variable in space, time and intensity can have a dramatic impact on local population and community dynamics (Hewitt et al. 1997, Commito & Tita 2002). In ecology, the empirical validation of how varying rates of dispersal affect patterns of community composition is of fundamental interest (e.g. Cadotte 2006, Heino 2011). *In situ* testing of theory may, however, be logistically more feasible in model systems such as marine soft-sediment communities, given the relatively faster temporal scale over which spatial processes operate (paper 3 and 4).

1.4 Patterns of diversity and metacommunity ecology

Interpreting patterns of multiple species' distributions, their relative abundances and interactions is fundamental to community ecology (e.g. Whittaker 1960, MacArthur & Wilson 1967, Levins 1969). Continued losses in diversity have also highlighted the pressing need to better understand how species coexist in both space and time (Butchart et al. 2010, Chase & Myers 2011, Weiher et al. 2011). While local niche-based processes (i.e. deterministic, see glossary) are important in determining community composition, an underlying prerequisite is that dispersal has been sufficient for species to establish in the first place. Rates of dispersal between communities, or connectivity, have also been recognized as critical when studying responses to ecological change (Brown & Kodric-Brown 1977, Thrush et al. 2008). As rates of dispersal increase, communities become more open, so that immigration and emigration will quantitatively affect local population dynamics and thus community composition (Mouquet & Loreau 2002). These effects are twofold; immigration of individuals can act to supplement local birth rates while emigration can also act to increase loss rates of individuals (Leibold et al. 2004).

Metacommunity ecology recognizes local communities as interacting assemblages connected by dispersal (Leibold et al. 2004, paper 3 and 4). Hence, both local and regional processes can be at work in producing spatio-temporal patterns in community composition. "Regional" relates to dispersal and landscape features or space, while "local" relates to environmental conditions and niche requirements of species. To date, empirical field studies have mainly involved describing patterns by determining the relative importance of spatial versus environmental factors in creating site-to-site variability in community composition (β-diversity; Cottenie 2005, Laliberté et al. 2009). Depending on the relative significance of local and regional processes, four different metacommunity models have been proposed (Cottenie 2005; see glossary for: neutral, species-sorting, mass effect, patch dynamic models). However, empirical studies often only consider equilibrium communities that are limited to a single snapshot in time (Cottenie 2005, Jacobson & Peres-Neto 2010, Logue et al. 2011). Due to the challenge of quantifying dispersal, studies also often accept space (a constant) as a "good proxy" of dispersal, although dispersal is known to be highly variable between species (Jacobson & Peres-Neto 2010).

To advance empirical research, studies will need to address more explicitly how the underlying mechanisms of dispersal and environmental heterogeneity are operating,

rather than merely describing patterns (Logue et al. 2011, Winegardner et al. 2012). For example, an initial question to ask is whether variation in rates of dispersal (i.e. connectivity) can quantitatively affect temporal stability in local community composition (paper 3)? Similarly, insight can also be gained by investigating how the relative importance of different metacommunity models can shift *in situ* over assembly time with increasing dispersal (e.g. Mouquet et al. 2003, paper 4). Temporal changes in community structure, let alone the history of species immigration, are scarcely considered, simply because such data is rarely available (Fukami 2010). However, *in situ* recolonization experiments conducted in soft-sediment benthic communities have the potential to provide such insight (Thrush et al. 2008, paper 4). In the benthos disturbance is seldom the cause of dispersal (Günther 1992), but it provides the prerequisite for community assembly to be started (i.e. recovery), a process in which dispersal is central. Assembly is a time-dependent process, defined by Fukami (2010) as "construction and maintenance of local communities through sequential arrival of potential colonists from an external source pool". Following a disturbance, a given sub-set of the regional species pool (γ-diversity) will be assembled to coexist at that specific point in space if local environmental conditions are favorable and/or dispersal has been sufficient to the locality (Weiher et al. 2011). It can be expected that in this process, communities do not come about by simultaneous arrival of a set of species (e.g. Morton & Law 1997). Recruitment depends on rates of dispersal, which is per definition a space and time dependent process (i.e. distance over time). Therefore as assembly history is restarted, it can be expected that the cumulative number of immigration events, as well as the spatial scale from where additional colonist arrive will gradually increase with time.

Rates of immigration will depend on the size and timing of disturbance, so that a combination of larval, post-larval and adult dispersal will be important in the recovery process (Whitlatch et al. 1998). If disturbances are small, nearby dominant species sharing the same niche-environment relationship will be able to disperse and recruit as larvae, juvenile post-larvae or as adults (Osman & Whitlatch 1998, Lundquist et al. 2006, Norkko et al. 2010). However, if a disturbance is large enough relative to the scale of underlying environmental heterogeneity, dispersal may become limiting for some species and/or life-stages (Tilman 1994, Whitlatch et al. 1998, Petraitis & Latham 1999). Dispersal over larger scales can also be more costly than small-scale dispersal due to, for example, risk of predation (Osman & Whitlatch 1998, Pedersen et al. 2008). If connectivity between localities is high within a region, continued rates of dispersal will increase the number of coexisting species beyond what would be expected purely by local niche requirements (mass effects, Winegardner et al. 2012). Species that continue to migrate into an area can be found there even if the habitat is a sink (e.g. Mouquet & Loreau 2002). Thus, it has been shown that local species richness (α-diversity) will typically be higher in metacommunities where dispersal among localities is more frequent relative to those with less-frequent dispersal (Cadotte 2006). Similarly, Mouquet & Loreau (2003) suggest that increased rates of dispersal will transfer regional differences in community composition (β-diversity) to the local scale (α-diversity). Dispersal is thus central in both the assembly (paper 4) and maintenance of community composition (paper 3), but will vary depending

on species identity and life-history strategies, as well as source area abundances that can also vary between species and/or community location (paper 1 and 2).

2. MATERIALS AND METHODS

2.1 Study area and organisms

The studies for papers 1–4 of this thesis were conducted on a total of 15 different sandy sub-littoral sites with a mean depth of 5.2 m (SE ± 0.2 m) across an area of approximately 50 km^2 (see map, Fig. 3). Study sites were located along the Hanko peninsula in south-western Finland, within close proximity to Tvärminne Zoological Station (59°50'N: 23°15'E). This region of the Baltic Sea has no regular tides (Soomere et al. 2008); hence passive dispersal of benthic invertebrates requires wind-induced currents and waves. Weather conditions in the region vary on a synoptic-scale of about 5–10 days (Soomere et al. 2008). In addition the region has an irregular coastline and extensive archipelago, which means that wave-energy propagation is also spatially variable.
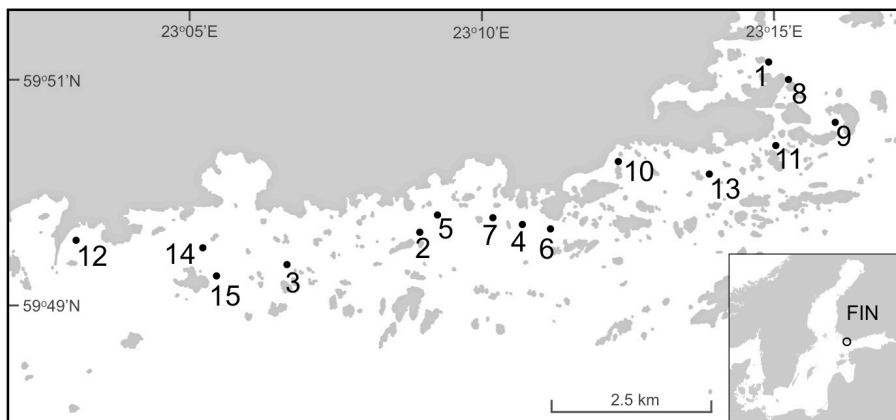
Figure 3. Geographic position of each study site (solid circles 1–15) within the Tvärminne-Hanko archipelago area. The insert shows the location of the study area (open circle) in south-western Finland (FIN). Sites are numbered in rank order of species richness (see paper 4).

Study sites span a broad-scale gradient of increasing exposure to wind and waves from the south-west (1–15, Fig. 3) with sediment surfaces varying from smooth to rippled, indicative of low to high-energy environments. All fieldwork was done sub-littorally using SCUBA. Prior to the selection of a site, an area with a radius of 25 m from the center of each site was visually inspected to ensure a similarly uniform sandy benthic landscape between sites. Salinity in the region varies between 5–6. Dominant taxa include typical estuarine soft-sediment taxa: Ostracoda, Oligochaeta, the bivalve *Macoma balthica*, the polychaete *Marenzelleria* spp. and the Gastropoda *Hydrobia* spp. (see Fig. 4, Table 3, papers 1–4). The region is also characterized by strong seasonality. For example, in 2006–

2007 the maximum recorded seawater temperature was 20.1°C in August and the minimum was -0.1°C in March, and with 53 days of ice cover in February and March of 2007. Over this period average monthly wind conditions were reasonably consistent, with highest monthly means in December 10.4 ms^{-1} and lowest in July 5.9 ms^{-1}.
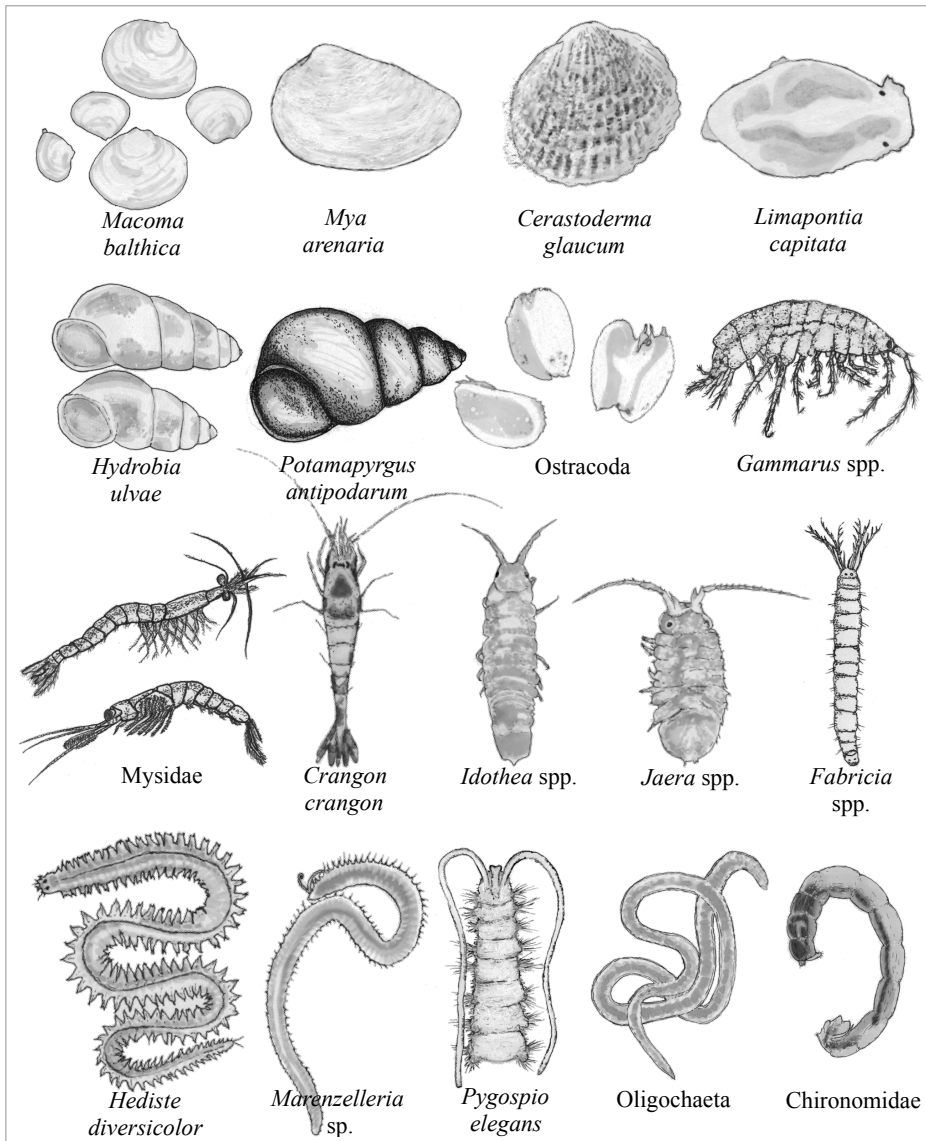

Figure 4. Picture panel showing the main taxa that formed community composition in studies for papers 1–4. Drawings by E. Valanko (2012) and are not drawn to scale. See also table 3 for detail on taxa.

2.2 Experimental design

The following summarizes the experimental setup of each study. Statistical analyses were done using SigmaStat, SAMS and PRIMER 6 PERMANOVA+. More detail can be found in respective papers.

Table 1. General spatial and temporal scales of investigation in respective studies of papers 1–4. Study sites used (see map Fig. 3) and the distance (km) between them is indicated. Dates when sampling occurred, as well as duration and frequency of sampling intervals are also given.

Scale		**Paper** 1	2	3	4
Spatial	Site	5,7,9,11	5,7,9,11	7	1-15
	Range (km)	1.3-7.0	1.3-7.0	0.05-0.25	0.5-13.0
Temporal	Duration	48h	6 x 48h	9 x 48h	0, 5, 35, 370 days
	Range: from	9.10.2007	31.7.2006	2.8.2007	20.8.2008
	– to		9.10.2007	20.8.2007	25.8.2009

Paper 1: **Dispersal strategies of benthic invertebrates**
In order to investigate dispersal strategies of benthic invertebrates a combination of traps were used allowing site-specific comparisons of different dispersal modes with respect to dominant hydrodynamics and sedimentary conditions, as well as the resident community (Table 2, Fig. 3). At each of the four sites traps were deployed at five replicate sampling blocks positioned along a 50 m transect, which allowed for a comparison of species either emerging from the sediment (Em), being transported in sediment bedload (Be), being transported in the water column (WaL and WaH) or settling from the water column (SetDw, see Fig. 5). At each site average ambient community abundance was estimated and the species presence/absence in different traps was noted. Site-specific grain-size characteristics, energy, exposure, sediment and algal material transport in the bedload were recorded. In addition, life-history dispersal related traits were compiled from existing literature for taxa. The contribution of each taxa to the average sample similarity for each trap-type was determined separately using the SIMPER routine (Clarke & Warwick, 2001).

Paper 2: **System- and species- specific bedload dispersal mechanisms**
In order to investigate underlying mechanisms of dispersal in the bedload, a study was designed to monitor ambient community and dispersing community composition using bedload traps (6 x 48 h) in 2006 and 2007, across four sites spanning a gradient of increasing exposure to waves and wind (Table 1 and 2, Fig. 3). At each site, five replicate sampling blocks of sediment bedload traps and ambient community sampling locations were positioned along a 50 m transect. This allowed site-specific comparisons of rates of bedload dispersal with respect to variation in environmental condition (local hydrodynamics and sedimentary conditions), seasonality, species-specific characteristics, as well as ambient community composition (Table 2). Both absolute (individuals in traps)

and relative (individuals in traps/individuals in ambient community) rates of dispersal were calculated separately for each taxa (see Commito & Tita 2002). Thresholds in site-specific relative rates of dispersal were investigated by looking at changes in upper quantiles (0.90 and 0.99) in response to consecutively larger amounts of algal and sediment transport defined on a logarithmic scale (Cade and Noon 2003). Spatial and temporal variation in absolute dispersal was examined for total abundance and number of taxa using a fixed factor 2-way ANOVA with site and time as factors. Size-dependent dispersal with increasing sediment transport was also investigated for two contrasting taxa; the bivalve *Macoma balthica* and the gastropod group Hydrobiidae.

Paper 3: **Dispersal and connectivity in <u>maintaining</u> local community composition**
To test whether varying rates of dispersal and connectivity would have an effect on local community composition a temporal study was designed. Replicate sampling locations were designated along a 50 m transect (10 m apart) running in an along-shore direction at one site (number 7 in map, Fig. 3). Nine consecutive 48 h sampling intervals were monitored for connectivity (hydrodynamic forcing), rates of dispersal (measured in different trap-types, Fig. 5), and change in ambient community composition (cores taken at beginning and end of each 48 h). The study period was 18 days long, which included sufficient variation in physical connectivity by wind-induced waves and currents (Soomere et al. 2008). At each 48 h interval, all sampling was carried out within 30 min using SCUBA. Taxa were grouped into either dispersing actively or passively. Linear regression modeling and distance-based linear modeling (DistLM; Legendre & Anderson 1999) was then used to test relationships between physical connectivity measures 48 h^{-1} (waves, currents, wind and cumulative energy) rates of dispersal (dissimilarity of different trap-types and ambient community composition every 48 h), and rates of change in community composition (dissimilarity between beginning and end community composition every 48 h). In addition, at all sampling intervals Pielou's evenness was calculated as a measure of temporal change in abundance distribution of species in the local community.

Paper 4: **Immigration across scales in community <u>assembly</u>**
To investigate how patterns of diversity change depending on rates of dispersal (α- versus β-diversity), as well as to evaluate the relative importance of different metacommunity processes a disturbance-recovery experiment was conducted at sites 1–15 simultaneously. Over time, both reassembling and control communities were monitored at each site. Assembly history can be viewed as the cumulative number of immigration events since initiation of assembly, which was re-set by defaunating 1m^2 plots at each site (Tischendorf & Fahrig 2000). The experiment was begun after the main larval recruitment period in late summer/early autumn, to ensure availability of post-larval dispersal and recruitment. Subsequent sampling intervals (i.e. assembly time) corresponded to 0, 5, 35 and 370 days since the initiation of experiment. Data analysis consisted of three parts. First, differences among-sites were tested between control and assembly manipulation community composition using a two-way PERMANOVA. This was done separately at all 4 sampling times, using both univariate (α-diversity) and multivariate (β- diversity) measures of

community composition. Secondly, among-site differences in community composition were investigated. This was done by looking at changes in the α- and β-diversity relationship, with site characteristics as represented by principal components analysis (PCA). Third, differences in metacommunity structure over assembly time were investigated. Overall diversity of the reassembling metacommunity (i.e. α-, β- and λ-diversity) relative to control was compared. At each interval variation in community composition (β-diversity) was decomposed into fractions explained by environmental, spatial and dispersal variables using 3-way variation partitioning (Legendre et al. 2005).

2.3 Biotic and abiotic variables

Ambient community composition was sampled along with a variety of direct and indirect measures of dispersal and used in combination with several abiotic variables in studies for papers 1–4. Community composition was determined in ambient cores (n=513), assembly manipulated cores (n=180), as well as in 6 different replicated trap-types (n=768). As propensity to disperse is also life-history and size-dependent (Whitlatch et al. 1998, Paper 2), taxa that exhibited large size differences were divided into different size categories before subsequent analyses were conducted (Table 3). Another important consideration was that sampling methods vary quantitatively, in for example, area or volume sampled (see Fig. 5). Appropriate transformations were therefore applied prior to comparing different methods. Below some of the main methods developed and used for studying dispersal of benthic invertebrates sub-littorally are presented (paper 1–4 = 1015 dives).

Ambient community
For all studies, ambient and reassembling community composition were sampled by taking replicate cores (diam. 5.6 cm, depth 10 cm) from the center of each designated sampling location. Samples were preserved in the laboratory by removing seawater using a 0.2 mm sieve, placing them into 70% ethanol and staining them with rose bengal for later analysis. All samples were sorted and enumerated using a binocular microscope after sieving through a 0.2 mm sieve. An elutriation and decanting technique was applied prior to sorting of ambient community samples, which contained large amounts of sediment coarser than 0.2 mm.

Assembly manipulation
Community assembly was re-set by conducting an *in situ* disturbance-recovery experiment at all 15 sites simultaneously. Defaunated 1 m² plots were established by covering the sediment surface with black low-density polyethylene (LDPE) plastic to induce anoxia to underlying sediments. The edges of the plastic sheets were held in place with metal rods secured with 30 cm metal pegs, which prohibited any water exchange from underneath the plastic. Plots were covered for a 16-day period to ensure complete defaunation and the experiment was started by carefully removing the plastic. For each site the ambient community was also sampled at a distance of 3 m from the reassembling community as a control.

Table 2. A summary of the main biotic and abiotic variables collected in each study for papers 1–4. Biotic variables collected include community composition of the ambient community, in the assembly manipulation and in the community dispersing in different trap-types (see also Fig. 5). A number of abiotic variables related to grain-size, energy, space, sediment and algal material transport in bedload traps (Be) were also collected. The range (min=minimum, max=maximum) and units of each parameter is indicated. U_* = estimated friction velocity, U_{*crit} = critical friction velocity, PCNM = principal coordinates of neighbor matrices. See also individual papers (1–4) for further detail.

Biotic variables		1	2	3	4	description
Ambient		X	X	X	X	control community
Assembly					X	community within defaunated 1m² plots
Dispersal	SetIn			X		settle into sediment
	Em	X			X	emerge out of sediment
	Be	X	X	X		bedload transport along bottom
	SeDw	X	X	X		settlement down from water column
	WaH	X			X	transport in the water column at 1 m
	WaL	X			X	transport in the water column at 0.3m

Abiotic variables		1	2	3	4	min	max	units
Transport (Be)	Sediment	X	X			0	0.4	g sed. 24 h⁻¹
	Algal material	X	X			0	10	g algae 24 h⁻¹
Energy	Wind	X	X	X	X	0	22	m s⁻¹
	Waves			X		3.5	58.3	cm s⁻¹
	Current			X		0.1	11.9	cm s⁻¹
	Cumulative		X	X	X	14.5	34.3	% gypsum lost
	U_*		X	X	X	0.2	1.6	cm s⁻¹
Grain size	Median		X		X	0.2	2.6	mm
	Graphic mean		X			0.2	1.4	mm
	Sorting		X		X	0.3	1.1	SI
	% mud		X		X	0.1	18.4	% <0.063mm
	% gravel		X		X	0.2	39.5	%>2mm
	U_{*crit}		X		X	1.2	3.6	cm s⁻¹
Space	North	X	X	X	X	50°49'04	59°51'18	Lat.
	East	X	X	X	X	23°02'81	23°16'05	Long.
	Depth	X	X	X	X	3.7	6.1	m
	Exposure	X	X		X	9249	127073	Iseaus model index
	PCNM			X		-	-	-

Dispersal

Dispersal was quantified directly using different trap-types, which were sampled over 48 h intervals. Six different trap-types were used in combination to estimate the relative importance of different dispersal modes (Fig. 5, see also paper 1 for more detailed description). All samples were preserved and enumerated in accordance with the method applied to cores used to sample the ambient community composition (see above).
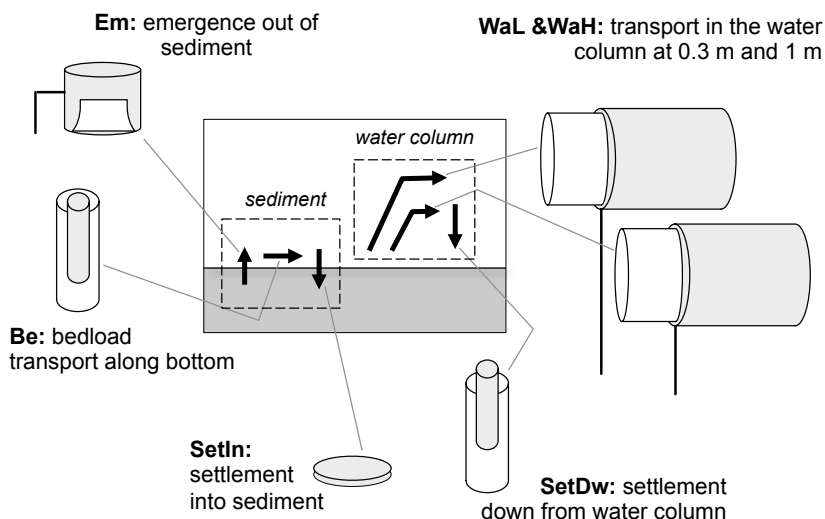

Figure 5. Trap-types used with the respective mode of dispersal they sampled: sediment associated dispersal (Em, Be, SetIn) and water column associated dispersal (WaL, WaH, SetDw).

- Emergence out of the sediment (Em) was sampled using two cylindrical emergence traps positioned on the sediment surface (diam. 9.5 cm, height 16 cm) at each replicate location, requiring species to swim 12 cm vertically in order to get caught.

- Bedload transport along the bottom (Be) was sampled using cylindrical bedload traps (diam. 3.7 cm, depth 29 cm). One bedload trap was deployed at each replicate location. Traps were positioned with their mouth opening flush with the sediment surface in pre-deployed outer sleeves.

- Settlement into the sediment (SetIn) was sampled using two settlement trays (diam. 9 cm, depth 1 cm) at each replicate location. The trays were filled with defaunated sediment and deployed with their upper edge flush with the ambient sediment surface. Defaunated sediment was prepared by elutriation and freezing of sediment from the site.

- Settlement down to the bottom from the water column (SetDw) was sampled using cylindrical settlement traps (diam. 3.7 cm, depth 29 cm), one at each replicate location. These traps were positioned vertically so that their mouth opening was 5 cm above the sediment surface in pre-deployed outer sleeves.

- Transport in the water column at 0.3 m and 1.0 m above the bottom (WaL and WaH) was sampled using water column traps with a vertical mouth opening (diam. 26 cm) that self-adjusted towards the current direction with a rudder and swivel shackle. Nylon net bags (<0.2 mm mesh, depth 51 cm) positioned horizontally onto trap ends were used to collect the sample over each consecutive 48 h interval at each replicate location at both heights.

Sediment and algal transport

During sorting animals were separated from the sediment and algal material collected in individual traps. Subsequently bedload transport of both sediment and macroalgal material content dry weight (48 h at 60°C) was determined from each trap. Sediment and algal material transport (flux) was expressed separately as g 24 h^{-1}. Traps that had >10 g sediment or >0.4 g algae trap^{-1} day^{-1} contained too much material to sample efficiently (aspect ratio too small) and were removed prior to analysis.

Sediment granulometry

Sediment grain size characteristics were determined for each site from replicate cores (diam. 2.1 cm, depth 5.0 cm) collected and frozen for subsequent analysis. Hydrogen peroxide (H_2O_2, 6%) was used to dissolve organic material. Grain sizes were separated into >3.00, >2.00, >1.00, >0.500, >0.250, >0.100, >0.063, <0.063 mm size class fractions using respective sieves. Dry weight (48 h at 60°C) was obtained for each grain size class. Median grain size (D_{50} mm), sorting (S_I), % > 2.00 mm (pebbles) and % <0.063 mm (mud) were calculated for each sample, from which a mean was obtained for each site (c.f. Folk and Ward 1957). In addition, critical values for initiation of sediment transport (U_{*crit}, cm s^{-1}) were calculated using the median grain size (D_{50} mm) of each site (Soulsby 1997, paper 2).

Direct measures of physical connectivity

In studies (1–4) a combination of different direct measures of physical connectivity were used, including average wind, current, wave and cumulative energy (Table 2). Wind speed and direction (10-min mean) at 30 min intervals were recorded at a nearby weather station (Jussarö, 59° 49′N: 23° 34′E) by the Finnish Meteorological Institute. In paper 3 at site 7, waves (orbital speed, cm s^{-1}) were recorded at the site by deploying a wave gauge (DOBIE). It measured pressure bursts at 5.4 m depth every 30 min, with each burst consisting of 2048 data points at a sampling interval of 0.2 s. At the same site, currents (cm s^{-1}) were recorded using an acoustic doppler current profiler (ADCP), which was mounted on a 0.5 m high platform facing upwards to record horizontal current speed and direction. It used a 300 kHz broadband consisting of 18 0.6-m bins, sampling every 30 min with 1000 pings at a 1.8 s interval. The ADCP's first valid cell was at 2.8 m from the sensor. To

estimate current speed at the same depth as the study site 7, the ADCP was deployed 270 m to the south in deeper water (10.4 m) and the 6th cell (depth 5.4 m) was used. For all studies and sites cumulative (48 h) wave and current energy combined was measured using a gypsum dissolution technique (e.g. Commito et al. 1995). Over 48 h sampling intervals replicate gypsum blocks (diam. 4.5 cm, height 2 cm) were deployed at each site and/or sampling interval onto metal rods 30 cm above the bottom (i.e. close to the bottom but still avoiding contact and abrasion). Gypsum blocks were dried (48 h at 60°C) and weighed, before and after 48 h deployment. Mean change in dry weight was expressed as percentage gypsum loss. Results were also related to an *in situ* calibration study across sites between gypsum blocks (48 h) and direct turbulence measurements using an acoustic Doppler velocimeter with a sampling frequency of 16 Hz (Oikkonen et al. unpubl.). Using this correlation (linear regression, $r^2=0.98$, $p<0.001$) friction velocity (U_*) for sites and/or sampling period was estimated. Friction velocity was expressed as a proportion of the site's critical value of initiation of sediment transport (U_{*crit}, cm s^{-1}), determined by the site's median grain size (D_{50} mm).

Indirect measures of physical connectivity

Indirect measures of connectivity between sites was calculated by constructing principal coordinates of neighbor matrices (PCNM) axes using geographic location at each of the 15 sites. This method creates an uncorrelated set of explanatory variables between sites that can be used to explain spatial dependence of communities across a range of scales (Borcard and Legendre 2002, Borcard et al. 2004). In addition, relative openness of sites to wind and waves was calculated between sites using a GIS-based wave exposure model developed by Isaeus (2004). This model did not use bathymetric data, but shoreline coastal shape together with main wind direction (SW), and a maximum fetch distance of 500 km at a 25 m^2 grid resolution.

3. RESULTS AND DISCUSSION

3.1 Synthesis of results

This thesis investigated post-larval dispersal strategies and mechanisms (paper 1 and 2). By direct quantification of post-larval dispersal, using a variety of trap-types, benthic invertebrates were observed to disperse in relative proportions that were distinctly different from the ambient community composition (paper 1, 2, 3). In contrast to the ambient community, community composition of the dispersing community was found to be highly variable over both space and time (paper 2 and 3). The majority of epifaunal species represented in the ambient community were also recorded within all dispersal modes, whereas infaunal species were less common. Several species-specific differences were observed between traps sampling species either emerging from the sediment, being transported in sediment bedload, being transported in the water column or settling from the water column (paper 1, Table 3). Dispersal in the bedload was found to be relatively more

common than other modes of dispersal (paper 1). Rates of bedload dispersal were found to depend on taxa- and site-specific characteristics, temporal and seasonal variability, as well as on fluxes of sediment and algal material (paper 2).

Another goal of this thesis was to determine whether variation in dispersal and connectivity can quantitatively affect local benthic community composition (paper 3). Higher rates of dispersal (48 h^{-1}, all trap types) were observed at times when connectivity was stronger, especially when wave energy dominated. This suggests that waves are an important prerequisite for post-larval dispersal (paper 3). The rate of change (48 h^{-1}) in local community composition of passively dispersing taxa was lower with increased connectivity, while the rate of change in community composition of actively dispersing taxa was unrelated to temporal variation in the strength of connectivity. This suggest that active dispersers are more efficient at maintaining their position than passive ones, as they are relatively more independent from vectors of dispersal (i.e. hydrodynamic conditions) and can actively select for suitable habitats. These findings highlight that even short-term temporal variation in physical connectivity and rates of dispersal can have important implications for metacommunity structure.

Over longer temporal scales (1 year) and across all 15-study sites, results demonstrate how metacommunity composition is assembled (i.e. immigration history) in response to small-scale disturbances (paper 4). In contrast to control communities, initial community composition of reassembling communities was found to be associated relatively more with local environmental conditions (species sorting), suggesting dispersal and recruitment of site-specific nearby dominants, sharing the same niche requirements. At later assembly time variation in community composition could also be explained by spatial variables, suggesting that sink species from source populations located further away also had time to disperse and establish (mass-effect). These *in situ* findings provide valuable insight into how dispersal and recruitment between soft-sediment benthic communities help maintain diversity at different scales (α, β and λ) in source-sink metacommunities.

3.2 Dispersal <u>strategies</u> of benthic invertebrates

Findings of this thesis provide evidence that benthic invertebrates in the non-tidal Baltic Sea disperse in relative proportions that are distinctly different from the relative composition of the resident community, suggesting differences in dispersal strategies between species (e.g. Commito et al. 1995). A significant proportion (40%) of taxa recorded in paper 1 were observed to lack a planktonic larval life-stage (Table 3). Similarly, Grantham et al. (2003) have shown that in California and Washington on average 66% of benthic soft-sediment taxa have short or no planktonic dispersal period. This would imply that benthic communities, also in the Baltic Sea, are composed of taxa with other equally successful post-larval and adult dispersal strategies. This thesis demonstrates how post-larval dispersal is age/size dependent, as well as species-specific (papers 1 and 2, see also Table 3). In paper 2 a threshold response in the upper quantiles (0.90 and 0.99) of mean relative rates of dispersal was demonstrated in relation to

increasing sediment and algal material fluxes measured in bedload traps. In paper 2 both absolute and relative rates of dispersal were reported, as considering only absolute rates of dispersal (i.e. the most commonly reported measure) provides little insight into the movement of animals in relation to ambient densities and bedload processes (Commito et al. 1995). Despite disturbance to shallow coastal areas by drift algae (Norkko et al. 2000), findings suggest that algal material can also provide an effective means of dispersal by rafting for benthic invertebrates (Highsmith 1985, paper 2).

If currents are fast enough and/or waves large enough (U_*, cm s^{-1}), sediments will also be brought into suspension in the water column to be transported by currents and deposited elsewhere. Many benthic invertebrates have also been recorded to actively use currents to be transported relatively greater distances (tens of km) in the water column than they would be able to in the bedload (Beukema & de Vlas 1989, Lundquist et al. 2004). In paper 1, very low numbers of species and individuals were observed dispersing in the water column and it is suggested that dispersal in the water column might be comparatively less important in the Baltic Sea where tidal currents are absent. In tidal-systems, however, both Commito et al. (1995) and Lundquist et al. (2006) also observed comparatively lower rates of dispersal in the water column than in the bedload. They also observed a greater number of individuals dispersing in the water column when wind-waves increased, and suggest storm-related transport to be an important process for long-distance dispersal (i.e. in the water column). Similarly in paper 3, an increased rate of dispersal in the water column was observed at both 0.3 m and 1.0 m from the bottom when wind-induced waves and currents increased.

It is interesting to hypothesize, whether episodic storm events provide the means for long-distance post-larval dispersal, connecting for example communities in the shallow coastal environments with communities in deeper offshore areas. Although short in duration, storms are considered a dominant process along many shores when much of the interaction between waves and the coast takes place (making studying such conditions extremely difficult, but see paper 3). Storms are usually accompanied by increases in sea-level, allowing waves to continue towards the coast unaffected by for example longshore sand bars that usually provide protection from coastal erosion. Thus large removal of sediment, potentially also associated benthic invertebrates, can occur during storm events (especially in autumn/early winter). Rather than assigning declines in population density in shallow coastal areas by default to mortality, an important consideration is emigration and long-distance dispersal to deeper water adult populations from which larval recruitment back to shallow coastal areas may occur in spring. Seasonal migratory rhythms between coastal and deeper offshore areas would allow successive life stages to reach the most suitable habitat, which warrants further studies in the Baltic Sea context. Such knowledge would also provide valuable insight into recovery processes of the increasingly larger and more frequent disturbances occurring in deeper offshore areas of the Baltic Sea due to hypoxia (Karlson et al. 2002, Diaz & Rosenberg 2008, Conley et al. 2009).

Table 3. The most important taxa recorded in studies for paper 1–4. Size-class grouping and dispersal-related traits (active or passive) are indicated for each taxa (x). Dispersal related functional characteristics are also described for each taxa (from paper 1). Summary of taxa recorded in the community and dispersing in different trap- types are shown (from paper 3). Ambient community mean (avg.) number of individuals (ind. core^{-1}) and standard errors (SE, n=45) are presented for taxa with one decimal place accuracy. (-) indicates not observed. Dispersal modes (48 h^{-1}) over the study period include: emergence out of sediment (Em); bedload transport along the bottom (Be); settlement into sediment (SetIn); water column transport at 0.3 m (WaL); water column transport at 1.0 m (WaH); settlement down from water column (SetDw). (+) = taxa recorded at least once in respective trap, (++) = taxa in trap with mean >1 ind. trap^{-1}, blank = not recorded in trap.

Species / Taxa	Size-class (mm)	Dispersal trait Active	Passive	Functional characteristics Living habit	Environmental position	Developmental mechanism	Adult longevity	Ambient avg. (SE) ind. core^{-1}	Sediment associated dispersal Em	Be	SetIn	Water column dispersal WaL	WaH	SetDw
Bivalvia *Macoma balthica*	>2		x	burrowing	infauna	planktotrophic	5-10 years	0.8 (0.1)			+			
	1-2		x	dweller	(0-30cm)			4.1 (0.5)	+	+	+	+		
	0.5-1		x					2.9 (0.3)	+	+	+	+	++	
	<0.5		x					-	+		+			
Mytilus edulis			x	hard bottom	epifauna	planktotrophic	18-20 years	0.1 (0.1)			+	+	++	+
Cerastoderma glaucum	>2		x	burrowing	infauna	planktotrophic	3-5 years	0.5 (0.2)	+		+			
	1-2		x	dweller	(0-5cm)			0.5 (0.1)	+	+	+	+		+
	<1		x					0.1 (0.0)	+	+	+			
Mya arenaria			x	burrowing dweller	infauna (0-40cm)	planktotrophic	10-15 years	0.1 (0.0)	+	+	+	+	+	+
Gastropoda *Hydrobia ulvae*	>1	x		free living	epifauna	planktotrophic	2-3 years	2.8 (0.3)	++	+	++	+		+
Potamopyrgus antipodarum	>1	x		free living	epifauna	direct/ internal brooding	2 years	0.8 (0.2)	++	++	++	+	+	+
Theodoxus fluviatilis	>1	x		free living	epifauna	lecitotrophic	3-4 years		+	+		+		+
juvenile gastropod	0.5-1		x	free living	epifauna/ infauna	-	<1year	1.4 (0.3)	++	+	++	+	+	+
	0.2-0.5		x					2.1 (0.4)	+	++	++	++	+	+
	<0.2		x					-	+					
Limapontia capitata		x		free living	epifauna	direct/ internal brooding	1-2 years	-			+	++	++	+

Continued on next page.

Table 3. continued from previous page.

Species / Taxa	Size-class (mm)	Dispersal trait		Functional characteristics				Ambient avg. (SE) ind. core^{-1}	Sediment associated dispersal			Water column dispersal		
		Active	Passive	Living habit	Environmental position	Developmental mechanism	Adult longevity		Em	Be	Setn	WaL	WaH	SetDw
Crustacea Ostracoda			x	free living	epifauna	direct/ internal brooding	1 year	22.6 (1.8)	++	++	++	++	++	++
Gammarus spp.	>6	x		free living	epifaun/ pelagic	direct/ internal brooding	2-4 years	-	+	+	+	++	++	-
	<6	x			pelagic	internal brooding		0.0 (0.0)	+	+		++	+	+
Jaera spp.	x	x		free living	epifaun/ pelagic	direct/ internal brooding	<1year	-	+		+	++	+	+
Idothea spp.	>4	x		free living	epifaun / pelagic	direct/ internal brooding	1-2 years	-	+			++	+	-
	<4	x			pelagic	internal brooding		-	+	+		++	+	+
Mysidae		x		free living	pelagic	direct/ internal brooding	<1year	-	+	+		++	+	+
Crangon crangon		x	x	free living	epifaun/ pelagic	spawn/ egg carrying	1-3 years	-	+	+	+	++		+
Polychaeta Hediste diversicolor	>1	x		burrow dweller/ freeliving	infauna (0-40 cm)	lecitotrophic	2-3 years	0.4 (0.1)		+	+			
	<1	x						0.8 (0.2)	+	+	+	+		
Pygospio elegans	x	x	x	burrow dweller	infauna (0-10 cm)	planktotrophic/ adelphophagic	1 year	0.6 (0.1)		+	+	+	+	
Manayunkia aestuarina	>2		x	burrow dweller	infauna (0-10 cm)	direct/ external brooding	1 year	1.4 (0.1)	+		+			
	<2		x					0.7 (0.2)			+			
Marenzelleria sp.	>1	x		burrow dweller	infauna (0-20 cm)	leciotrophic/ planktotrophic	2-3 years	1.9 (0.4)	+	+	+	+		
	<1	x						4.6 (0.4)	+	+	+	+	+	
Insecta Chironomidae			x	burrow dweller	infauna (<top 2cm)	other	1-2 years	0.1 (0.0)	+	++	+	++	++	+
Oligochaeta			x	free living	infauna (0-10 cm)	diverse	1 year	10.7 (1.2)	+	++	++	+	+	+
Nemertinea Prostoma obscurum		x		free living	epifauna	direct/ external brooding	1 year	1.2 (0.2)	+	+	+	+	+	+

On the west coast of North America, Lee (1966) observed size-dependent movement of the isopod (*Idothea montereyensis*) from shallow eel grass beds subjected to waves in winter to more protected deeper water red algae habitats. In other tidal systems seasonal migration between adult and juvenile habitats has also been shown for a number of species, for example, the lugworm *Arenicola marina*, shore crab *Carcinus maenas*, the brown shrimp *Crangon crangon* and the bivalve *Macoma balthica* (Beukema 1993). In general, individuals have been observed dispersing in a shoreward direction as juveniles in late spring and in an offshore direction in winter once they are larger, so that juveniles tend to be more abundant in the shallow upper shore while as adults they are less vulnerable and are found at a variety of depths. In the non-tidal Baltic Sea, Segerstråle (1960) suggested that the bivalve *M. balthica* will similarly also disperse in response to a shift in habitat preference over ontogeny (see also Bonsdorff et al. 1995).

Findings suggest that frequent small-scale dispersal as post-larvae also plays a role in the Baltic Sea (paper 1 and 2), having the potential to also affect benthic community composition quantitatively (paper 3). It is therefore relevant to consider whether in fact the contribution of later stage post-settlement dispersers is as important or even more important than the initial larval recruits to the mature adult population, due to the relatively higher survival rates and extended period of dispersal of the post-settlers (e.g. Pedersen et al. 2008). Importantly, by only studying a specific scale in isolation it is impossible to achieve a full mechanistic understanding of dispersal and resulting population dynamics (e.g. Pineda et al. 2009). It is therefore important to consider that different strategies of dispersal are often operating over disparate temporal and spatial scales when measuring how well connected soft-sediment communities are (e.g. Günther 1992, Palmer et al. 1996, Thrush & Whitlatch 2001).

3.3 Bedload dispersal <u>mechanisms</u>

In papers 2 and 3, findings suggest that the amount of sediment transported depends on dominant hydrodynamic forcing (currents and/or waves) and the amount of friction that is exerted per unit area of the bottom (bottom shear-stress, BSS). However, findings also suggest that rates of dispersal (sediment or invertebrates) do not have a simple linear or monotonic relationship with energy, but also depend on an intricate relationship between site-specific sediment characteristics, as well as species behavior (Fig. 6, paper 2).

Soft-sediments are mainly composed of mixtures of either mud (<0.063 mm), sand (0.063–2 mm) and/or gravel (>2 mm). All studies for this thesis were conducted on sandy (non-cohesive) soft-sediment sites, varying in mud content from 0.1 to 18.4% and in gravel content from 0.2 to 39.5% (depending on the site's exposure to the dominant south-westerly wind direction). Sediment stability counteracts wave/current energy at a locality, and is called the critical friction velocity (U_{*crit}, cm s^{-1}). Critical friction velocity depends on the median grain size (D_{50} mm) of sediment; coarser grained sediments require more energy to be transported. Across study sites median grain size ranged from 0.16– 2.61 mm, with corresponding critical friction velocities of 1.28– 3.58 cm s^{-1}. Thus, friction velocity

(U_*, cm s^{-1}) can also be expressed as a proportion of a locality's critical value of initiation of sediment transport (U_{*crit}, cm s^{-1}), determined by median grain size (D_{50}). This provides a good estimate of when sediment transport is most likely (see paper 2 and 3). Accordingly, highest rates of bedload dispersal (both in terms of abundance and number of species) were observed at site 7. This site was intermediately exposed relative to other sites, with an estimated friction velocity (U_*, cm s^{-1}) that was closest to its critical friction velocity (U_{*crit}, cm s^{-1}). For example, in non-cohesive sediments (i.e. sand) flume experiments have shown that the finer sand and the associated fauna have lower critical erosion thresholds than coarser grained sand and fauna (Hunt 2004).
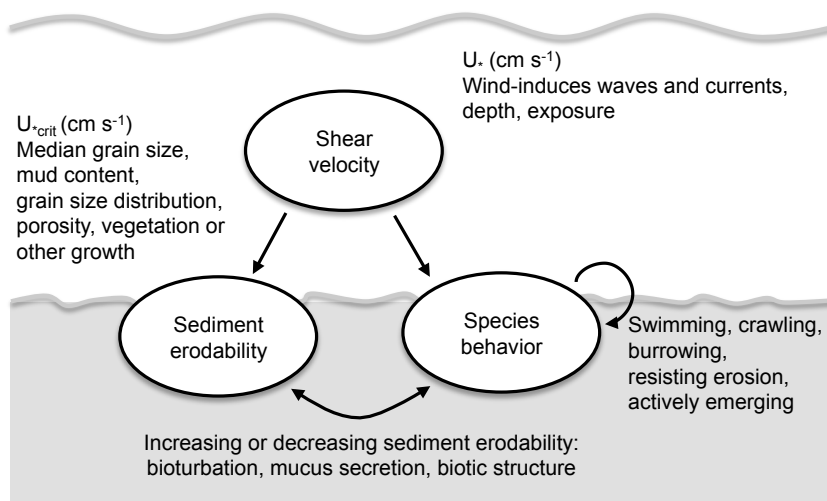
Figure 6. General scheme illustrating factors contributing to propensity for soft-sediment invertebrates to be eroded and dispersed. In addition to species behavior, dispersal will also depend on interactions between grain size characteristics and hydrodynamic conditions. Shear velocity or energy reaching the bottom will affect erosion rates of both benthic invertebrates and sediment. However, species are also able to behaviorally increase or decrease their erosion rates directly or indirectly by affecting erosion rates of their resident sediment. A combination of sediment characteristics and biotic interactions can also affect erosion rates of sediments (adapted from paper 2). U_* = estimated friction velocity, U_{*crit} = critical friction velocity.

Wind-induced waves in combination with longshore currents are important for the transport of sediment, especially in the absence of regular ebb and flood tides (e.g. Baltic Sea). Sediments will remain immobile if currents and wave energy are weak. However, when flow velocity slowly increases at a site above a long-term average, a threshold velocity will be reached when a few sediment grains will begin to move. The movement of particles in continuous or near-continuous contact with the bed or bedload transport will dominate at these times (Le Hir et al. 2007). In accordance with these predictions, paper 2 demonstrates a threshold response in the upper quantiles (0.90 and 0.99) of mean relative rates of bedload dispersal (48 h^{-1}) with increasing rates of sediment transport. This

threshold response was site-specific (D_{50} = 0.14– 0.60 mm, sites 5, 9, 7, 11). In general, the majority of epifaunal species of the ambient community were also recorded within all dispersal modes, whereas infaunal species were less common (paper 1 and 2). This suggests that, in the absence of regular tides, infaunal dispersal is more stochastic and will depend on wind-induced waves and currents exceeding a long-term average for sediment erosion to occur. Similarly in tidal systems, post-larval dispersal rates have been directly quantified and correlated with wind velocity and sediment fluxes (e.g. Commito et al. 1995, Norkko et al. 2001, Hunt et al. 2007).

The spatial distribution of hydrodynamic forcing depends on depth and how sheltered or open the coast is to wind-induced waves. In general beaches and their sub-littoral soft-sediment habitats are composed of sand, as wave energy that characterizes beaches is typically too high to permit fine particles to accumulate. Thus a site's long-term average hydrodynamic conditions, which depends on its relative depth and adjacent coastal configuration, will also determine the site's dominant sediment grain-size characteristics. Sites that are more exposed to wind-induced waves will have larger grain sizes and thus higher critical erosion velocity (U_{*crit}, cm s^{-1}) requiring greater bottom shear-stress (U_*, cm s^{-1}) for sediment erosion and transport (Table 2, Fig. 6, paper 4). It can therefore be expected that when current velocity or wave height exceeds a long-term average within a region (i.e. at all sites), connectivity will also be higher between benthic communities at these times. This can be expected as U_*/U_{*crit} will approach 1 at a greater number of localities within the region at the same time. Temporal persistency of dispersal between communities can thus be more a sharp transition between contrasting states of connectivity than a gradual continuum (paper 2 and 3), which has implications for metacommunity function (see next section Fig. 7, Filotas et al. 2010, Winegardner et al. 2011).

3.4 Dispersal and connectivity in <u>maintaining</u> local community composition

Paper 3 investigated whether variation in rates of dispersal and physical connectivity can affect local community composition. The study demonstrated how the number of dispersing taxa became higher with increasing physical connectivity. However, when connectivity was low and less taxa were recorded dispersing, local community composition exhibited an increased rate of change in community composition of passively dispersing taxa. This suggests that dispersal is required in order to maintain local community composition (mass effect, paper 4). This response was dependent on dispersal-related traits of taxa. Actively dispersing taxa will be relatively better at maintaining their position, as they are not as dependent on hydrodynamic conditions and can actively select for suitable habitats. Passive dispersers, on the other hand, will more easily enter the bedload or water column, to be transported passively by currents and deposited back down onto the sediment. Thus, if a species is able to actively choose its habitat instead of passively being transported, species will be more likely to maintain sorting along environmental gradients according to their niche requirements (species sorting model, see glossary).
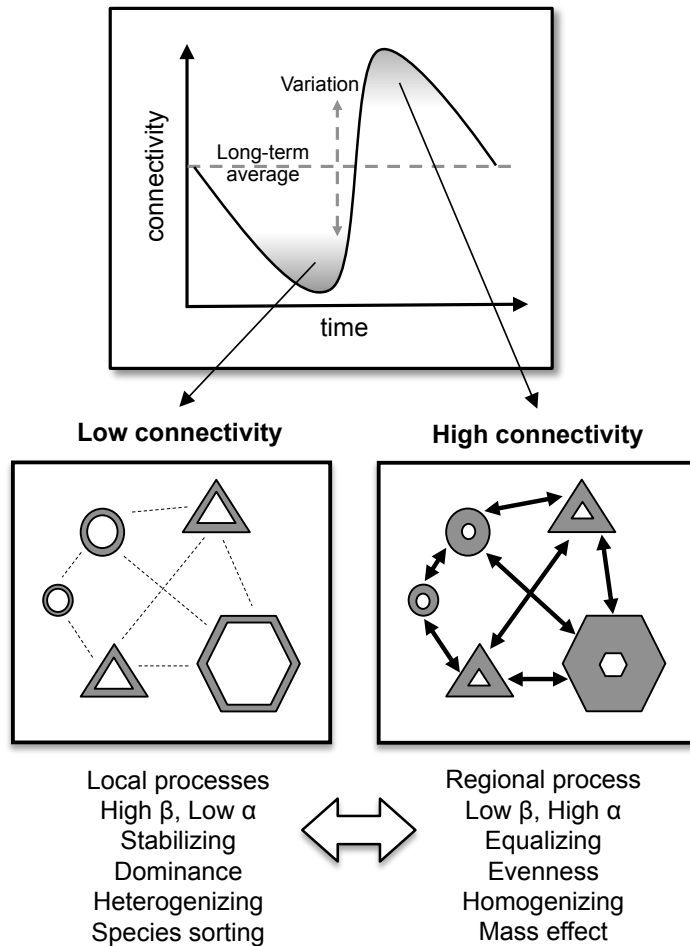
Figure 7. Conceptual model showing how rates of dispersal can either favor regional or local processes that differentially effect community composition (α- and β-diversity), without changing regional species richness (λ-diversity, Cadotte 2006). Temporal variation in hydrodynamic conditions (waves and currents) implies that connectivity can either be above or below a long-term average (paper 3). These alternating low and high connectivity periods can affect rates of dispersal and thus the number of species getting established in the neighboring communities. This, in turn, promotes either a low-similarity or a high-similarity metacommunity. Low connectivity = large white areas within different shapes (community type) indicates local dominance and dotted lines indicate limited dispersal between communities. High connectivity = large dark areas within different shapes (community type) indicates common species to all communities and arrows indicate higher rates of dispersal between communities. See glossary for terms used.

At times when physical connectivity is higher (Fig. 7), it can be expected that species with different dispersal capabilities will also be able to disperse over a relatively larger proportion of the region, thus favoring the establishment and persistence of sink populations (Hillebrand et al. 2008). However when physical connectivity is low (Fig. 7), it can be expected that a smaller proportion of neighboring communities will exchange individuals. At these times emigration (export) will continue, while immigration (import) of nearby dominant species will be favored over sink species that require immigration from source populations located at relatively greater distances away (Osman & Whitlatch 1998, Mouquet & Loreau 2003, Matias et al. 2012). In accordance with these predictions, in paper 3 the rate of change in local community composition was observed to be larger when dispersal became limiting.

Interestingly, the neutral model also predicts changes in community composition under varying rates of dispersal (Hubbell 2001). It predicts that sites which are located further away will be less likely to receive immigrants from its metacommunity (i.e. dispersal limited) and will thus be more likely to experience local extinctions over time due to stochasticity in local population dynamics (Bell 2001, Alonso et al. 2006). The neutral model assumes that species similarities, not differences, explain the high diversity of many natural communities. For benthic communities it has been demonstrated that there are species-specific dispersal-related traits (paper 1), that rates of dispersal relative to ambient community abundances vary between species (paper 2), and also that local environmental conditions (i.e. grain size characteristics) can explain variation in community composition between sites (paper 4). Thus findings would support niche-based models (deterministic, e.g. Kneitel & Chase 2004), so that when dispersal is low, local environmental conditions determine community composition (i.e. species-sorting, high β-diversity). In contrast, when rates of dispersal increase beyond the scale of underlying environmental heterogeneity sink species can "spill over" into sub-optimal sites and increase local species richness (mass effect model, low β-diversity).

3.5 Immigration across scales in community <u>assembly</u>

Community assembly and patterns of diversity across scales

In paper 4, changes in scale-dependent diversity (α-, β- and λ-diversity) were investigated over assembly time in response to increasing rates of dispersal. Community assembly was re-set simultaneously at 15 sites (i.e. dispersal history), after which reassembling and control community composition were monitored as recruitment into equal-sized $1m^2$ plots over time (Tischendorf & Fahrig 2000). As expected α-diversity was low in the reassembling communities and increased with time towards control levels (Fig. 8). β-diversity showed an opposite trend, and was already after 5 days significantly higher than in controls (Fig. 8). β-diversity then decreased towards control community levels over time with the subsequent arrival of additional recruits. This increase in similarity of reassembling community composition over time is in accordance with Mouquet & Loreau

(2003) who predict that with increasing proportion of dispersal between communities β-diversity should decrease, while α-diversity should increase as the number of shared species between communities increases.
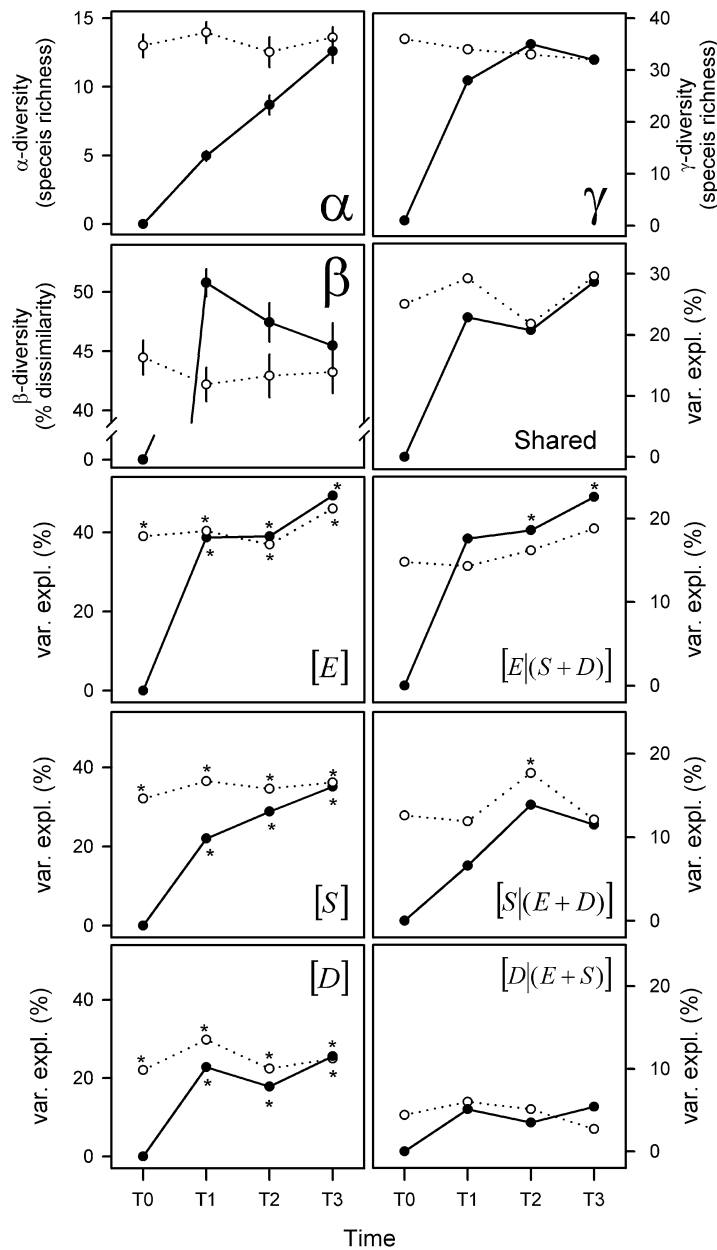

Figure 8. Changes in scale-dependent diversity patterns (α-, β- and λ-diversity) over assembly time (T0– T3), relative to control (see paper 4 for detail). Reassembling community (solid circle and line); control community (open circle dotted line). Assembly times = T0 (0 days), T1 (5 days), T2 (35 days), T3 (370 days). α-diversity = mean (±SE) species richness at a site, λ-diversity = pooled

species richness from all sites, β-diversity = mean (±SE) Bray-Curtis dissimilarity of a site to all other sites. Variation partitioning of control and reassembling community composition matrices sampled at different times. Forward selection procedure (R^2, p<0.05) identified the most significant combination of standardized variables to represent environmental (% mud, % gravel), spatial (PCNM2, PCNM3) and dispersal (energy) explanatory variable groups. var. expl. (%) = variation explained by respective pure and shared fractions expressed as a percentage, * = *P*-values showing significance (*P*<0.05) of each fraction of variation, estimated with 999 permutations. Shared = total variation shared between environmental (E) spatial (S) and dispersal (D) variables. [E] = variation explained by environmental variables, [E│(S+D)] = pure environmental variation, [S] = variation explained by spatial variables, [S│(E+D)] = pure spatial variation, [D] =variation explained by dispersal variables, [D│(E+S)] = pure dispersal variation.

Interestingly after 35 days regional species richness (λ-diversity) was higher in reassembling communities than in control communities (T2, Fig. 8). At this time average α-diversity in reassembling communities was only 70% of the control, but average β-diversity was 10% higher in reassembling communities. Thus reassembling communities collectively reflected regional species richness already after 35 days. Such a "pseudo-saturation" stage has been described by Mouquet et al. (2003) at early assembly time when only a subset of the apparent species pool is able to colonize a locality (i.e. nearby dominants). Subsequent assembly beyond this point (increased α-diversity with time) can therefore be considered mainly to be by commonly shared taxa between sites and having a homogenizing effect on community composition, reducing β-diversity between reassembling communities even further (Fig. 8). Interestingly, after 370 days (T3) a small but significant difference between control and re-assembled community composition was still observed, which could either be due to different assembly histories (e.g. Chase 2003) or due to differences in age of individuals, as community data was based on size-class subdivided taxa. Chase (2003) suggests that differences in recruitment history can result in differences in community composition between localities that have identical environmental conditions and connectivity to their metacommunity.

Local environmental (E) processes

Environmental heterogeneity tends to be spatially structured (e.g. broad-scale gradient of exposure over 15 study sites). One can therefore expect that a reassembling community will more likely share similar environmental conditions with a nearby community than with one located further away (e.g. Jacobson & Peres-Neto 2010). Following this logic, one would expect environment (E) to explain variation in reassembling community composition if initial recruitment is by site-specific nearby dominants (e.g. Osman & Whitlatch 1998). This is conditional to dominant taxa in the nearby source communities being dominant due to niche-environment relationship (species sorting). These assumptions were in accordance with observed patterns (Fig. 8), where E already after 5 days explained a significant proportion of variation in reassembling community composition (i.e. recruitment of nearby dominants at all sites). Furthermore, pure E was found to explain more of variation in reassembling community composition than in control

communities (which was not significant). A better environment match for reassembling community composition was probably due to the still relatively low number of regionally common taxa, which made control communities more homogenous in community composition (see diversity discussion above).

Regional spatial (S) processes

It can be expected that with time additional recruits will also arrive from further away (i.e. successful dispersal over larger spatial scales). Accordingly, space (S) was found to explain an increasing proportion of variation in reassembling community composition over time. Significant E and S have been attributed to a mass-effect metacommunity model, which suggests source-sink dynamics at work (Cottenie 2005, Fig. 8). Source populations located at greater distances can provide additional recruits to sink communities that are located in suboptimal environmental conditions for those species (Pulliam 2000, Mouquet & Loreau 2002). Over assembly time this can be expected as rates of dispersal among communities increase and α-diversity approaches control communities (i.e. saturation) and all species will have had enough time to disperse and reach all communities. Thus, reassembling communities become less recruitment limited with time (increasing α-diversity), despite an increase in variation explained by S. At later assembly time when sink populations are established, species composition can be expected to reflect a mass-effect metacommunity model (E with S). In such a case, sink species will be dispersal limited in their sink communities, but the community as a whole is less recruitment limited than it was at early assembly when α-diversity was lower (Fig. 8).

Physical connectivity, dispersal (D)

In addition, variation was also partitioned into the fraction explained by pure D (using friction velocity cm s^{-1} as a proxy, see paper 3). Pure D (dispersal) was found to be low and not significant (Fig. 8), suggesting that dispersal rates were fairly uniform between sites over the times sampled and the minimum dispersal distance aprox. 0.5 m (i.e. the center of a 1m^2 manipulation in a continuous landscape system) of this study. However, the dispersal proxy used was more a measure of "physical connectivity into the disturbed patch" and did not take into consideration differences in species-specific ability to disperse *per se*. For example, in soft-sediment communities dispersal in the larval phase is episodic over a large scale, while post-larval dispersal is more frequent but over smaller scales (Whitlatch et al. 1998, paper 1– 3). However, when comparing α- and β-diversity after 5 and 35 days a significant interaction was observed between the factors site and assembly-manipulation (see paper 4, two-way PERMANOVA $p<0.05$). This was most likely due to differences in α-diversity between sites, as it will take longer for species to assemble in more species-rich communities (i.e. to reach control α-diversity). It can also be assumed that species identity will also matter once the required scale of dispersal increases (patch dynamic model, Tilman 1994). For example, larger empty patches up to ≈60 000 km^2 have been recorded in deeper areas within the study region (i.e. seasonal anoxia, Conley et al. 2009). Lateral dispersal to the center of such an area, if moving passively at 5 cm s^{-1}

unidirectionally, would require about 40 days. In comparison, lateral dispersal at the same rate to the center of the 1 m^2 disturbed plots used in paper 4 would require only 14 seconds. For reassembling community composition to become dispersal limited due to hydrodynamic conditions (i.e. significant D), then the size of the disturbed patches (time and distance required to disperse) would need to be large enough relative to differences in dominant waves and currents between sites (e.g. Petraitis & Latham 1999).

3.6 Rates of dispersal and metacommunity structure

Dispersal operates over different temporal scales. Thus an initial step in any metacommunity study should be to define both the spatial and temporal scale of investigation (Fig. 9). For example, over temporal scales of many applied questions, the consequence of the neutral model (Hubbell 2001) is less obvious as it involves long-term evolutionary dynamics of large-scale systems (Bengtsson 2010). Over shorter time scales, Winegardner et al. (2012) have suggested that the amount of dispersal present between communities within a metacommunity can be used to differentiate between the patch-dynamic (limited dispersal), species sorting (efficient dispersal) and mass effect (high dispersal) models. In the benthos, dispersal will become limiting for some species if the scale of a newly created disturbed patch (relative to underlying habitat heterogeneity) exceeds a threshold value (Petraitis & Latham 1999). In such a situation, other species will be able to invade the newly disturbed patch (Hobbs & Huenneke 1992). Recruitment will depend on the dispersal ability of species, which will result in assembly that is historically contingent. In such a case a patch-dynamic model would be expected (Tilman 1994, Fig. 9). If however, a newly disturbed patch is very small relative to underlying habitat heterogeneity, then recruitment will most likely be by nearby dominant species (Osman & Whitlatch 1998, paper 4). In such a situation, dispersal will be sufficient allowing for species sorting (Fig. 9). The local community will thus consist of those species sharing the same niche-environment relationship (i.e. deterministic assembly). If dispersal becomes higher, as in for example dynamic soft-sediment habitats where it is more or less continuous (paper 1– 4), species will also persist in communities with sub-optimal environmental conditions so that α-diversity increases beyond what would be expected by purely species sorting (mass effect, Fig. 9).

Over the study area of this thesis, variation partitioning suggests a mass effect model at work (significant E and S, paper 4). In paper 3 local community composition (site 7) was maintained when rates of dispersal and connectivity were high (a mass-effect model). However, when rates of dispersal decreased, the rate of change in local community composition was found to increase for passively dispersing taxa. With lower connectivity, dispersal will become limiting for sink species (e.g. species emigration without immigration) and favor the locally dominant species, essentially shifting metacommunity structure more towards species sorting (Winegardner et al. 2012).
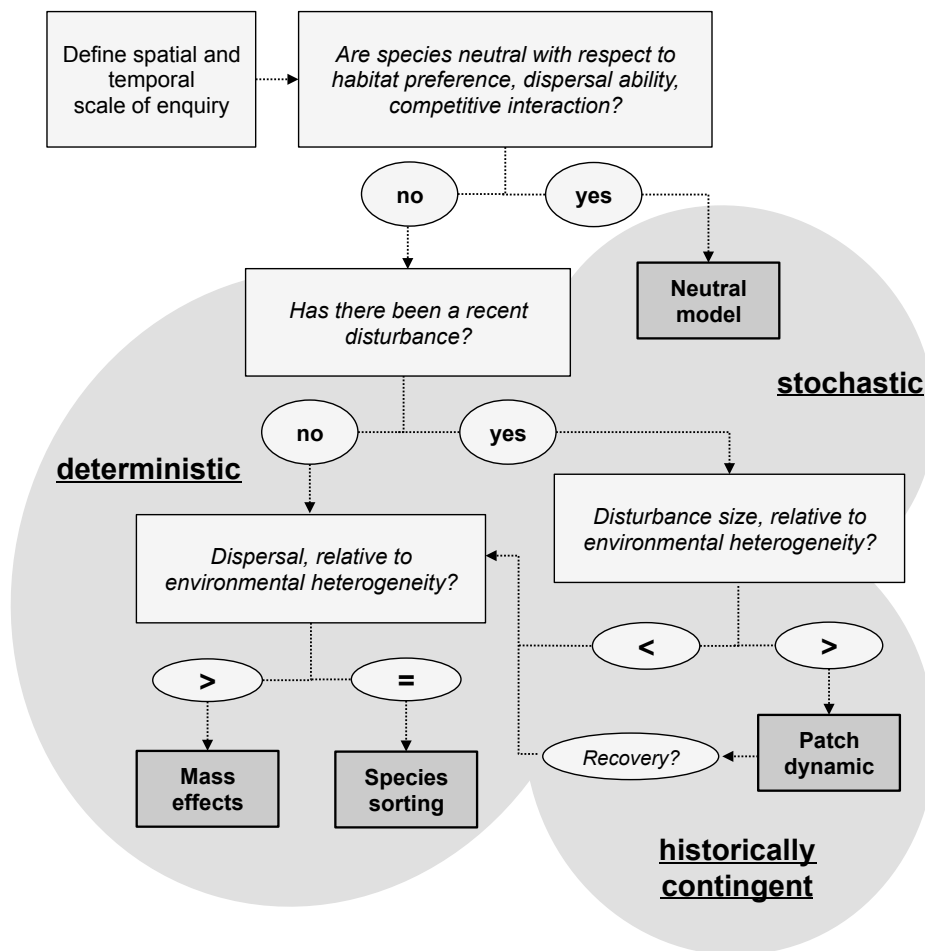
Figure 9. Flow chart demonstrating how metacommunity structure will change depending on rates of dispersal (e.g. Winegardner et al. 2012). First, both the spatial and temporal scale need to be defined. Significance of the neutral model (stochastic processes) can be expected when considering long-term evolutionary dynamics of large-scale systems (Hubbell 2001). If a disturbance size exceeds a threshold value, dispersal will become limiting for some species (patch dynamic, historically contingent). Relative to underlying environmental heterogeneity (deterministic processes), dispersal will either be sufficient (species sorting) or high (mass effect). See glossary for definition of terms.

Similarly in paper 4, metacommunity structure also changed according to predictions of Winegardner et al. (2012) as the cumulative number of immigration events increased over time. With increased dispersal, metacommunity structure first reflected a species-sorting model (significant E), and as dispersal became "high" a mass effect model metacommunity structure was observed (significant E and S). It can be predicted that if the disturbed patch ($1m^2$) would have been larger (greater dispersal distance) or if sampling had been conducted earlier, then dispersal could have been limiting for some species and a

patch dynamic model would have been observed. This has been suggested in a recent study in which reassembling community composition differed depending on the size of the disturbed patch (1, 4, and 16 m^2; Norkko et al. 2010). Similarly, Thrush et al. (2008) also suggest that recruitment limitation over time is both site-specific (due to dominant hydrodynamic conditions), as well as disturbance patch size-specific (depending on dispersal distance). Some species will be more dispersal limited than others, due to greater distance to their source population or due to temporal variability in hydrodynamic forcing (connectivity) and species-specific dispersal strategies (paper 1–3).

Understanding how dispersal operates, not only over spatial, but also over varying temporal scales can provide insight into metacommunity processes important in the assembly and maintenance of communities (paper 3 and 4, Fig. 7 and 9). Important for soft-sediment benthic communities is safeguarding environmental heterogeneity, which is essential in maintaining sufficiently different communities (β-diversity) that can act as sources of dispersal to a locality (α-diversity), thus maintaining overall regional diversity (λ-diversity, e.g. Hillebrand et al. 2008).

4. IMPLICATIONS AND FUTURE DIRECTION

A major issue in ecology is on which scales phenomena and processes should be studied (e.g. Peterson & Parker 1998, Hewitt et al. 2010). Even though benthic ecologists generally acknowledge the importance of scale in their studies, very few empirical studies explicitly measure and/or discuss the effects of scale on their results (Ellis & Schneider 2008). Findings from this thesis emphasize that patterns of community composition are a matter of scale, which in turn depends on the temporal frequency and spatial extent of dispersal relative to underlying environmental heterogeneity. Many applied questions in ecology will require both knowledge of ecological theory and intimate understanding of the natural history of the system under study to provide the appropriate context (e.g. Bengtsson 2010). However, many theoretical models often overlook environmental heterogeneity and assume constant rates of dispersal across scales and between species. This discrepancy highlights the dangers of allowing only theoretical predictions to guide management (and many empirical studies) in, for example, benthic ecology. Here are some important aspects that future studies should more explicitly consider in combination when interpreting results in benthic ecology:

- The underlying environment is heterogeneous. Environmental conditions should be considered as a continuum of overlapping gradients and a local community as a point in space (with specific environmental conditions) and time (providing dispersal has been sufficient to it) where multiple species' distributions happen to overlap.

- Species differ in their dispersal behavior and capability, thus rates of dispersal can vary in temporal frequency (seconds to seasons) and spatial extent (cm to kms).

- Dispersal can quantitatively affect local community composition by either supplementing birth rates or increasing loss rates. The existence of a local community at a specific scale is therefore largely trivial, as its member species also form part of a larger regional entity (i.e. the metacommunity).

Across the benthos, communities may vary in species' relative abundances distribution, as well as life-stage composition (i.e. biomass/ind.). Communities will therefore also vary in their propensity to contribute to function (traits and/or material production, Snelgrove et al. 1997, Weiher et al. 2011). Classical approaches to studying food webs or BEF (biodiversity and ecosystem function) have focused on patterns and processes occurring at the community level rather than the broader ecosystem scale, and often ignoring spatial aspects of the dynamics (Bengtsson 2010, Massol et al. 2011). However, management and conservation of BEF will ultimately also rely on understanding how communities are interacting (via dispersal), over spatial scales that greatly exceed the generally accepted extent of a local community (the metaecosystem, Massol et al. 2011). Future studies should thus better combine the movement of organisms (traits) and material across spatial and temporal scales (e.g. Gravel et al. 2010). In so doing, tackling for example, eutrophication in the Baltic Sea region can be better understood as its causes and effects on trophic interactions are spatially mediated within the region (Österblom et al. 2007, Conley et al. 2009, Villnäs et al. 2011).

5. CONCLUSIONS

Using a variety of direct and indirect measures of dispersal the thesis has investigated connectivity in marine soft-sediment benthic communities. Several system and species–specific dispersal related strategies have been demonstrated (paper 1 and 2), as well as underlying mechanisms by which communities are connected (paper 2 and 3). Large-scale manipulative field experiments reveal how patterns of community composition (α-, β- and λ-diversity) change depending on rates of dispersal. Findings complement several theoretical and laboratory-based studies (e.g. Cadotte 2006, Matias et al. 2012, Winegardner et al. 2012). In so doing, this thesis provides insight into how both dispersal and environmental heterogeneity contribute to the assembly (paper 4) and maintenance (paper 3) of spatio-temporal patterns of benthic community composition. Below the main conclusions are summarized for paper 1– 4:

Paper 1: **Dispersal strategies of benthic invertebrates**
Many benthic invertebrates (40–60%) do not have a larval dispersal phase. After initial colonization species will also continue to disperse as post-larvae (juveniles and adults), which can occur frequently and over small scales. This highlights the danger of assuming that recruitment is limited to larval dispersal when, for example, designing networks of marine protected areas (MPAs).

Paper 2: **System- and species- specific bedload dispersal <u>mechanisms</u>**
Dispersal of benthic invertebrates requires that site-specific energy (waves and currents) reaching the bottom is sufficient to initiate erosion and subsequent transport. The amount of energy needed depends on both the coarseness of the sediment at a site and species-specific traits (epifauna/infauna, active/passive), as well as age (size) of individuals. When wind-induced waves are above a long-term average within a region, site-specific critical erosion thresholds will more likely be exceeded, increasing the proportion of dispersal between communities in the region during these periods.

Paper 3: **Dispersal and connectivity in <u>maintaining</u> local community composition**
Environmental heterogeneity per unit area can support a number of different community types (species and relative abundances) that can collectively be called a metacommunity. High rates of dispersal enable species to also persist in communities other than the ones they do best in. However at times when connectivity is low, locally dominant species will be favored over sink species that depend on immigration from source-communities at relatively greater dispersal distances.

Paper 4: **Immigration across scales in community <u>assembly</u>**
In response to small-scale disturbances, recruitment will at first be by nearby dominant species after which species will successively arrive from further away. Dispersal acts to transfer regional differences in community composition (β-diversity) to a locality (α-diversity). Underlying environmental heterogeneity per unit area is therefore essential, in order to maintain sufficiently different communities that act as sources of dispersal to local communities (maintaining diversity).

ACKNOWLEDGEMENTS

GLOSSARY OF TERMS

Locality – the local scale, unit of observation, a site

Region – the scale that incorporates multiple localities of interest to the observer

Community – co-occurring species at a locality at a given point in time.

Environmental heterogeneity – variation in abiotic conditions per unit area, creating environmental gradients of differing local conditions within the region.

Dispersal – a process by which individuals move from a locality (emigration) to another locality (immigration). Rates of dispersal vary in temporal frequency and spatial extent. The effect of dispersal is twofold. Immigration will supplement local birth rates, while emigration enhances loss rates of the local population. Propensity to disperse depends on ontogeny of species (i.e. dispersal life-history strategy) and species-specific dispersal related traits, whether it is more passive (i.e. dependent on external energy) or active (i.e. own vagility).

Diversity components – Relationship between diversity at different scales, which can be partioned as α-, β- and γ-diversity.

Alpha (α) diversity – Number of species in a locality (within-community component).

Beta (β) diversity – Difference/variation in species composition between localities within a region (between-community component).

Gamma (γ) diversity – Total number of species in a given region.

Metacommunity – a set of potentially interacting local communities, connected by dispersal.

Neutral model – it assumes that species' similarities, not differences, explain the high diversity of many natural communities. The only driver of population dynamics is immigration and demographic stochasticity (random fluctuations in local births and death rates). It predicts that localities that are less connected to the metacommunity (dispersal limited) will experience a greater number of local extinctions over time (community drift).

Patch dynamic - predicts explicit trade-offs between species in their competition-colonization ability when recolonizing a locality. See also historically contingent.

Species sorting - assumes that species arriving at a locality are subject to trade-offs in response to underlying local environmental conditions due to niche differentiation, which leads to competitive exclusion of locally mal-adapted species from the community.

Mass effect - predicts that emigration and immigration between localities can act to promote coexistence beyond what would be expected by purely by local niche differentiation of species. Local persistence of species as bad competitors in sink localities is ensured by immigration from source localities in which they are good competitors.

Deterministic process – niche-based assembly, stabilizing, the effect of species interaction on community structure is determined by environmental conditions, with a differential response to a heterogeneous environment (i.e. niche differences).

Stabilizing – a species coexistence process by which negative intraspecific interactions relative to negative interspecific interaction increase. Relates to niche-based deterministic processes, examples include: resource partitioning or size-dependent predation.

Historically contingent – dispersal assembled communities, community structure diverge among localities as a result of stochastic variation in the history of species arrival, even under identical conditions and identical species pools.

Stochastic process – equalizing force, random fluctuations in birth and death rates, which may lead to extinction of species in a locality if rates of immigration are not sufficient.

Equalizing – a species coexistence process by which the average fitness differences between species is minimized, reducing large average fitness inequalities which might negate the effects of stabilizing mechanism.

(Definitions are modifications from the following sources: Chesson 2000, Hubell 2000, Leibold et al. 2004, Fukami 2010, Chase & Bengtsson 2010, Gravel et al. 2011, Heino 2011)

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SAMMANFATTNING (*abstract in Swedish*)

Spridning och metasamhällsdynamik i marina mjukbottenfaunasystem – hur väl är havsbottnen sammankopplat?

I naturen beror graden av konnektivitet på organismers spridning mellan samhällen. Spridning hos marina mjukbottenfaunasamhällen är en process som involverar mera än endast larvrekrytering från pelagialen. För att upprätthålla artsammansättningen och abundansen hos ett samhälle kan en fortsatt småskalig spridning av juveniler och fullvuxna vara lika viktig. Vår kunskap om spridningspotentialen efter larvstadiet hos marina evertebrater är dessvärre i allmänhet mycket begränsad. Det här gäller speciellt bentiska system utan tidvatten, såsom Östersjön, där spridningen inte har direkt kvantifierats förut. Förutsättningen för att kunna tolka diversitetsmönster på olika skalor (α-, β-, γ- diversitet) är att förstå hur och när individer sprider sig i relation till miljöns heterogenitet inom ett visst område. Det är dock svårt att konkret mäta spridningen i naturen, vilket har resulterat i att den empiriska forskningen ligger mycket efter den teoretiska utvecklingen, inom både metasamhälls- och metapopulationsekologin.

I denna avhandling har både direkta och indirekta mätningar av spridning använts för att undersöka konnektiviteten inom mjukbottenfaunasamhällen. Spridning av mjukbottenfauna (juveniler och adulter) mättes genom att använda olika typer av fällor. Mängden spridning samt den omgivande samhällsstrukturen kvantifierades för lokaler med olika miljöförhållanden (t.ex. sedimentstruktur och vågexponering) och under olika tidpunkter. Arterna spred sig i relativa proportioner som tydligt skiljde sig från samhällsstrukturen i kringliggande sediment. 40 % av arterna saknade helt pelagiska larver och var således beroende av spridning som juveniler och/eller adulter. Flera artspecifika spridningsstrategier påvisades samt mekanismer för hur och när mjukbottenfaunasamhällen är sammankopplade. Över tid förändrades mjukbottenfaunasamhällets artsammansättning mera då spridningsraten och den fysiska sammankopplingen (vågenergi och vattenströmmar) minskade. Detta mönster var tydligare för arter som sprider sig passivt, medan arter som sprider sig aktivt bättre behöll sin position eftersom de inte är så beroende av fysisk sammankoppling och passiv transport med strömmar.

Spridningsförmågans inverkan på koloniseringen och därigenom bottendjurssamhällets diversitet (α-, β- och λ-diversitet), undersöktes i ett storskaligt manipulativt fältexperiment som inleddes med lokal utrotning av bottenfaunan på flera lokaler. Spridningsförmågan kan vara en begränsande faktor för vissa arter och/eller livsskeden (patch dynamic model) i ett tidigt skede av koloniseringen, samt då det nyligen störda området är stort i förhållande till miljöfaktorernas heterogenitet i det kringliggandet område. Om störningen däremot är småskalig består den initiala rekryteringen av arter som dominerar i den omedelbara närheten, varefter arter från allt avlägsnare områden anländer efter hand. Om spridningen förblir hög mellan lokala samhällen inom ett område kan antalet samexisterande arter överskrida det som förväntas (enbart) på basen av existerande ekologiska nischer (species sorting model). Sålunda överförs regionala olikheter i

samhällssammansättningen (β-diversitet) till den lokala skalan (α-diversitet, mass effect model).

I motsats till enbart larvrekrytering kan en upprepad småskalig spridning som juveniler och adulter förlänga spridningsperioden och därmed bidra till upprätthållandet av bentiska samhällen när de är utsatta för störning. *In situ* resultat från denna avhandling kompletterar tidigare teoretiska och laboratoriebaserade studier genom att demonstrera hur så väl spridning av bottenfauna som miljöförhållandenas heterogenitet bidrar till att upprätthålla (temporala och rumsliga) diversitetsmönster i mjukbottenfaunametasamhällen.

NYCKELORD: spridning, diversitet, sammankoppling, störning, skala, metasamhälle, mjukbottenfauna, evertebrater, tidvattenfri, hydrodynamik, Östersjön

YHTEENVETO (*abstract in Finnish*)

Pohjaeläimien liikkuvuus ja niiden metayhteisödynamiikka meren pehmeillä pohjilla – kuinka hyvin merenpohja on kytkeytynyt?

Meren pohjaeläinyhteisöjen kytkeytyvyys toisiinsa riippuu näiden pohjaeläinten liikkuvuudesta. Pohjayhteisöihin vaikuttavat toisaalta toukkien ensimuutto (kolonisaatio ja rekrytoituminen) sekä toisaalta pienimuotoinen ja jatkuva pohjaeläinten toukkavaiheen jälkeinen liikkuvuus. Tämä toukkavaiheen jälkeen sekä aikuisvaiheessa tapahtuva liikkuvuus saattaa olla yhtä tärkeitä tai jopa tärkeämpiä yhteisörakenteen säilymisen kannalta kuin toukkavaiheessa tapahtuva liikkuvuus. Tietomme meressä elävien eläinten toukkavaiheen jälkeisen leviämisen merkityksestä on yleisesti kuitenkin hyvin rajoittunut. Erityisen vähän aihetta on tutkittu merissä, joissa ei esiinny vuorovettä. Esimerkiksi Itämeressä leviämistä ei ole aiemmin mitattu eikä määritelty lainkaan. Tieto siitä, milloin ja kuinka paljon yksilöt liikkuvat suhteessa elinympäristöjensä heterogeenisyyteen on tärkeää, jotta voidaan ymmärtää eläinyhteisöjen monimuotoisuutta eri mittakaavoilla (α-, β-, γ- monimuotoisuus). Eläinten todellista liikkuvuutta luonnossa on kuitenkin erittäin vaikea mitata suoraan. Tämä on johtanut teoreettisen tutkimuksen kehittymiseen huomattavasti empiiristä tutkimusta nopeammin sekä metayhteisö- että metapopulaatioekologiassa.

Tässä väitöskirjassa käytettiin sekä suoria että epäsuoria pohjaeläinten liikkuvuuden mittausmenetelmiä määritettäessä pehmeiden merenpohjien eläinyhteisöjen yhteyttä toisiinsa. Pohjaeläinten liikkuvuutta mitattiin käyttämällä erilaisia pyydysansoja, minkä jälkeen saatuja näytteitä verrattiin kyseisen havaintopaikan pohjaeläinnäytteisiin. Lisäksi tutkimuksessa otettiin huomioon havaintopaikkojen vaihtelevat ympäristötekijät (mm. sedimenttirakenne, alttius tuulille ja aalloille) ja mitattiin liikkuvuutta eri ajankohtina. Pohjaeläinten liikkuvuus ei ollut suhteessa sedimentistä havaittuun yhteisörakenteeseen. Suurelta osalta lajeista (40 %) puuttui planktinen toukkavaihe. Tutkimuksessa havaittiin useita lajikohtaisia liikkuvuustapoja sekä määriteltiin yleisiä mekanismeja (miten ja milloin), joilla pehmeiden pohjien eläinyhteisöt ovat yhteydessä. Pohjaeläinyhteisön rakenteen huomattiin muuttuvan enemmän, kun liikkumismäärät ja fysikaalisten tekijöiden (aallot ja virtaukset) voimakkuus vähenivät. Tämä muutos oli kuitenkin merkittävä vain niillä pohjaeläinlajeilla, jotka liikkuvat passiivisesti. Aktiivisesti liikkuvat pohjaeläinlajit eivät ole yhtä riippuvaisia fysikaalisista tekijöistä ja ovat siten vähemmän alttiita virtauksien kuljetettaviksi.

Laajoilla kenttäkokeilla tutkittiin, miten pohjaeläinten liikkumismäärät vaikuttavat monimuotoisuuden muodostumiseen eri mittakaavoilla (α-, β-, γ- monimuotoisuus). Osa alkuperäisestä pohjaeläinyhteisöstä poistettiin tarkoituksellisesti (aiheutettiin häiriö) ja niiden palautumista seurattiin ja verrattiin suhteessa ympäröivään häiriintymättömään pohjaeläinyhteisöön. Häiriötilanteen jälkeisessä varhaisessa palautumisessa pohjaeläinten vähäinen liikkuvuus voi rajoittaa joidenkin lajien ja/tai elinvaiheiden palautumista (patch dynamic model). Näin käy, jos häiriöalue on laaja suhteessa elinympäristön erilaisuuteen alueella. Toisaalta pienimuotoisissa häiriöissä

läheiset ja määrällisesti runsaat lajit liikkuvat ja palautuvat ensin, jonka jälkeen muita lajeja saapuu menestyksellisesti kauempaakin. Lajit asuttavat ensisijaisesti itselleen sopivia elinympäristöjä (species sorting model). Mikäli yleinen liikkuvuus on korkea, lajien määrä yhteisössä voi olla suurempi kuin mitä olisi odotettavissa pelkästään lajien ympäristövaatimusten perusteella. Lajit voivat silloin asuttaa elinympäristöjä, joita ne eivät asuttaisi muutoin. Näin kasvava liikkumismäärä voi siirtää yhteisöjen koostumusten alueelliset erot (β-monimuotoisuus) paikalliseen pohjaeläinyhteisöön (α-monimuotoisuus, mass effect model).

Toukkien ensimuuton lisäksi toukkavaiheen jälkeinen jatkuva pienimuotoinen liikkuminen voi pidentää lajin leviämisaikaa ja vaikuttaa siten positiivisesti pohjaeläinyhteisöjen elpymiseen häiriötilanteessa. Tämän väitöskirjan *in situ* tutkimustulokset täydentävät useita teoreettisia ja laboratorioperusteisia tutkimuksia osoittaen, että sekä eläinten leviäminen että alueen ympäristötekijöiden vaihtelu vaikuttavat pohjaeläinyhteisöjen monimuotoisuuden ylläpitoon.

AVAINSANAT: liikkuvuus, leviäminen, monimuotoisuus, kytkeytynyt, mittakaava, metayhteisö, pohjaeläin, vuorovedetön, aallot, virtaukset, häiriö, Itämeri

SEBASTIAN VALANKO

DISPERSAL AND METACOMMUNITY DYNAMICS IN A SOFT-SEDIMENT BENTHIC SYSTEM
– how well is the seafloor connected?

This PhD thesis deals with connectivity by investigating dispersal strategies of benthic invertebrates and looking at mechanisms of dispersal in a shallow marine soft-sediment system. Continued dispersal after initial larval recruitment and a locality's connectivity to its metacommunity are important in maintaining community composition. Thus having an understanding of how and when individuals are dispersing relative to underlying environmental heterogeneity within a given region is key to interpreting scale-dependent patterns of diversity (α-, β-, γ-diversity) and in predicting responses to, for example, different types of disturbances or management actions in conservation.

THE AUTHOR

Sebastian has a background in marine ecology, environmental policy and scientific diving from the UK and Finland. He started his PhD work in April 2006 with the Tvärminne Benthic Ecology Team. In his research he has adapted several techniques for underwater use to quantify dispersal of benthic invertebrates directly, a novelty in non-tidal systems such as the Baltic Sea. Underwater he has also made use of several hydrographic measures under varying conditions and conducted manipulative field experiments across several sites to test theoretical advances, *in situ*, in metacommunity ecology.