

The importance of biodiversity for ecosystem processes in sediments:

experimental examples from the Baltic Sea

Johan Näslund



Doctoral thesis in Marine Ecotoxicology
Johan Näslund, Johan@ecology.su.se

Department of Systems Ecology
Stockholm University
SE-106 91 Stockholm, Sweden

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*"Now here, you see, it takes all
the running you can do, to keep
in the same place."*

– Lewis Carroll

List of papers

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

- I Karlson AML, Nascimento FJA, Näslund J & Elmgren R. "Higher diversity of deposit-feeding macrofauna enhances phytodetritus processing" *Ecology* 91 (5): 1414-1423.
- II Karlson AML, Näslund J & Blomgren-Rydén S. "Effects of a polychaete invader on soft-bottom ecosystem functions" (manuscript).
- III Näslund, J. "The enemy release hypothesis may contribute to explain the invasion success of *Marenzelleria arctica* (Polychaeta) in the Baltic Sea" (manuscript).
- IV Näslund J, Nascimento FJA & Gunnarsson JS. "Meio-fauna reduces bacterial mineralization of naphthalene in marine sediment". *ISME Journal*, in press.
- V Näslund J, Hedman J & Agestrand C. (2008) "Effects of the antibiotic ciprofloxacin on the bacterial community structure and degradation of pyrene in marine sediment" *Aquatic Toxicology* 90 (3): 223-227.

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My contribution to the papers:

Participating in the experimental design (I, III-V), execution of the experiment (I, III-V), performing molecular analyses (IV-V), data analysis (participating in I, II, IV performing in III, V) and writing the papers (participating in I, II, main writer in III-V).

Additional publication by the author of this thesis:

Nascimento FJA, Karlson AML, Näslund J & Gorokhova E. (2009) "Settling cyanobacterial blooms do not improve growth conditions for soft bottom meiofauna" *Journal of Experimental Marine Biology and Ecology* 368: 138-146.

Abstract

Aquatic sediments are, by surface, the largest habitat on Earth. A wide diversity of organisms inhabit these sediments and by their actions they have a large influence on and also mediate many ecosystem processes. Several of these processes, such as decomposition and remineralisation of organic matter are important on a global scale and are essential to sustain life on Earth. The main aim of this thesis was to use an experimental ecosystem ecology approach in order to study some of these ecosystem processes in marine sediments and how they are linked to biodiversity.

Paper I and II found that an increased species richness of sediment deposit feeders increases the processing of organic matter from phytoplankton settled on the sea-floor, and that species-rich communities have a more efficient resource utilization of deposited organic matter. The results in paper IV and V also suggest that there is a link between microbial diversity in sediments and the degradation of organic contaminants. Paper V also shows that antibiotic pollution is a potential threat to natural microbial diversity and microbially mediated ecosystem services. The introduction of invasive species to ecosystems is another major threat to biodiversity and was studied in Paper II and III, by investigating the ecology of *Marenzelleria arctica*, a polychaete worm recently introduced in the Baltic Sea. Paper II suggests that *M. arctica* mainly utilize food resources not used by native deposit feeders, thus potentially increasing the benthic production in the Baltic Sea by increasing resource use efficiency. Paper III, however, show that *M. arctica* is protected from predation by the native benthic invertebrate predators, due to its ability to burrow deep in the sediment, suggesting that predation on *M. arctica* by higher trophic levels is restricted, thereby limiting trophic transfer.

In conclusion, this thesis gives some examples of the importance of marine biodiversity for the generation of a few key ecosystem processes, such as organic matter processing and the degradation of harmful contaminants.

Keywords: Biodiversity • Soft-bottom sediment • Ecosystem processes • Ecosystem function • Benthic-pelagic coupling • Baltic Sea • Trophic interactions • Pollutant biodegradation • Organic matter mineralization • Deposit feeder • Detritivore • Invasive species

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Introduction

Oceans cover approximately 70 % of our planet. Under the water surface, lies the sea floor, mainly in the form of soft-bottom sediments. This constitutes, by area, the largest ecosystem on Earth in terms of spatial coverage (Snelgrove, 1997), and a wide range of ecological processes is taking place here. These ecosystem processes are essential for the maintenance of a well functioning ecosystem, and allow the continuous transfer of energy and nutrients between biotic and abiotic compartments of the ecosystem. All organisms within ecosystems, including humans, are dependent on functions generated by ecosystem processes, such as recycling of organic matter and the maintenance of clean air and water. In order to ensure well-functioning ecosystems, that provide ecosystem services to human society, it is necessary that we understand how key ecosystem processes function. With a proper understanding how important ecosystem services are generated, we can hopefully one day achieve a sustainable management of Earth's ecosystems. In several cases around the world today, anthropogenic disturbance (e.g. eutrophication, overfishing, habitat destruction and pollution) due to improper or absent management, have caused large-scale changes in marine ecosystems.

The main aim of this thesis was to study a few key ecosystem processes in marine sediments and how these processes are linked to biological diversity. More specifically, I have:

- Experimentally tested how biodiversity in the form of species richness and community composition affect the cycling of carbon and nitrogen deposited from settling phytoplankton blooms (I-II)
- Investigated the ecology of the, by humans, introduced species *Marenzelleria arctica* and how it has affected a few ecosystem processes in the Baltic Sea ecosystem (II-III)
- Experimentally studied the degradation of organic pollutants in sediments and how this process is linked to the diversity of bacteria (IV-V) and the abundance of meiofauna (IV) and how anthropogenic pollution by pharmaceuticals may affect the degradation of other organic pollutants (V).



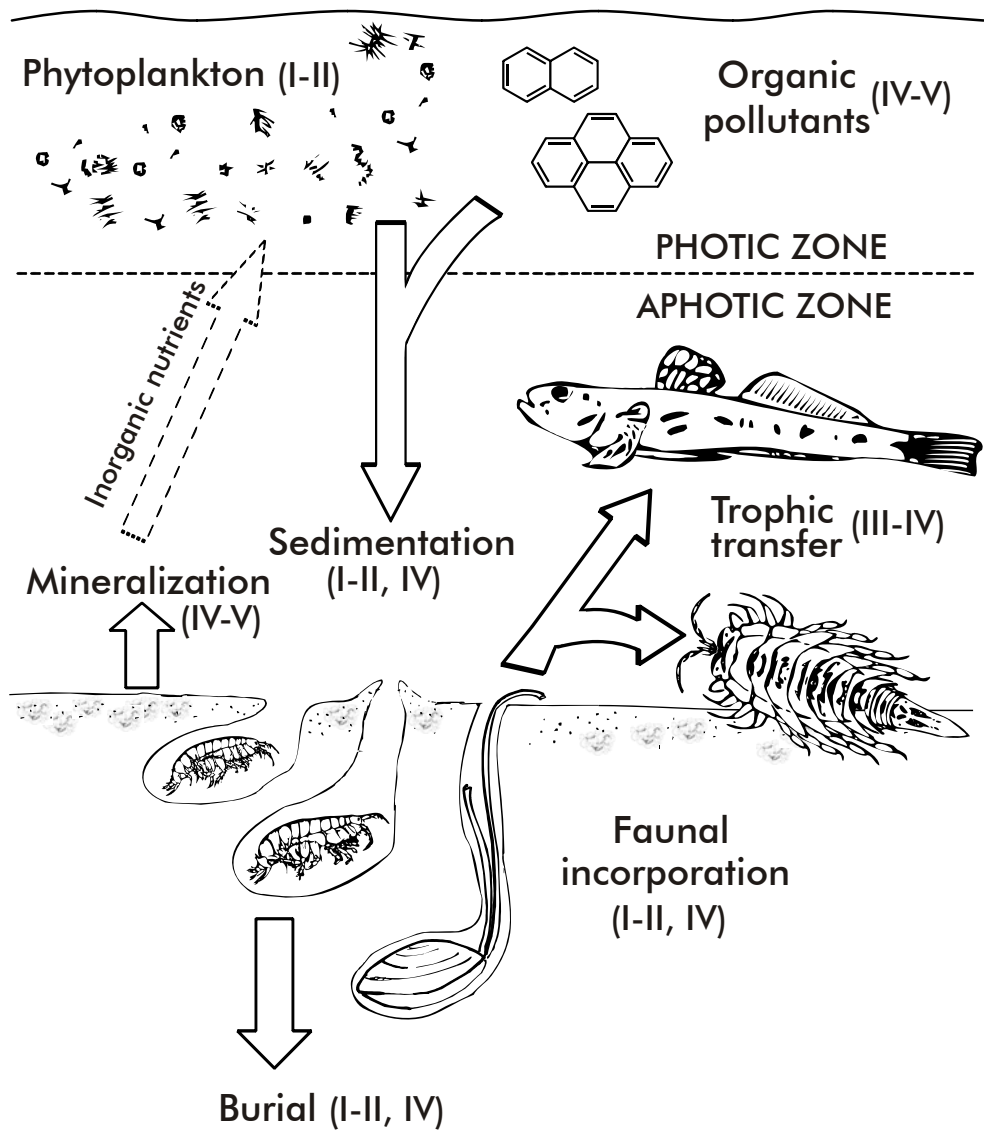


Figure 1. A schematic overview of the major sediment ecosystem processes examined and discussed within this thesis. Modified from Karlson (2010).

Ecosystem processes in marine sediments

An ecosystem is composed of organisms that interact with each other and their environment (Tansley, 1935). Physical, chemical and biological actions or events that occur at the ecosystem level can be defined as ecosystem processes. These processes link organisms and their environment together, forming an ecosystem, where energy is transformed and matter is cycled. At a basic functional level, ecosystems contain primary producers that harvest an energy source, such as sunlight, and convert it into chemical energy by transforming inorganic compounds into organic matter. Consumers feed on the organic matter created by primary producers, and so do decomposers, who also break the organic matter back into its inorganic components.

A majority of the world's sea floor is situated below the photic zone, where the light levels are too low for photosynthesis. Since only a small amount of primary production occurs below the photic zone in oceans (by chemoautotrophs), sediment ecosystems are fundamentally dependent on imported energy in the form of organic matter to maintain their structure. Mostly, organic matter input is supplied from settling phytoplankton, produced in the photic zone. Consumers living in and on the sea floor process organic matter that sediments down to and settles on the sea floor (Paper I-II, IV). The energy and matter originating from the settled organic matter is then available for further transfer to secondary consumers and predators at higher trophic levels (Paper III), constituting the marine food web. Decomposers eventually process and recycle organic matter into inorganic compounds (e.g. nutrients) that can be transferred back to the photic zone (Paper I-II, IV-V). This coupling of energy and matter between the benthic and pelagic system is commonly referred to as benthic-pelagic coupling, and it is a fundamental process for the functioning of marine ecosystems.

All nutrient cycles on Earth are by majority driven by microbial activity. For example, bacteria and fungi perform almost all of the carbon mineralization on earth (90 %) in addition to playing a leading role in the nitrogen, phosphorous and sulphur biogeochemical cycles (Atlas and Bartha, 1998). Microorganisms also play a crucial role in the degradation of organic contaminants in sediments (Eggleton and Thomas, 2004; Gilbert *et al.*, 1996; Helm *et al.*, 2000, Paper IV-V), helping to maintain clean water and sediments. The activity of microbes can be controlled by a set of environmental factors such as temperature, pH, Eh (redox potential) and nutrient availability (Atlas and Bartha, 1998; Eggleton and Thomas, 2004), of which some can in turn be affected by organisms living within the ecosystem.



Sediment-living fauna modify and rework soft sediments by their activities, often summarized by the term bioturbation. This term includes all types of faunal activity, for example burrowing, feeding, defecation, ventilation and irrigation of biogenic constructions. Bioturbation has been accepted as a key process that modify biological (e.g. other fauna and bacteria), chemical (e.g. nutrient concentrations) and physical (e.g. grain size) properties of marine sediments (Rhoads, 1974). Bioturbation also increases particle and water transport within sediments, allowing the burial of organic matter and harmful contaminants, as well as influencing the transport of solutes such as inorganic nutrients.



Figure 2. Bioturbating *Marenzelleria arctica* with biogenic constructions (burrows)

Marine biodiversity in sediments and the link to ecosystem processes

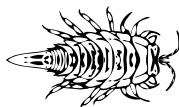
Biodiversity (biological diversity) is a wide term, encompassing all measures of biological variability from genes to ecosystems. The number of species present is the most common measure of biodiversity, usually referred to as "species richness". Other types of biodiversity, for example at genetic, community or landscape level are naturally also of major importance, depending on the temporal and spatial scale, or which processes that are considered.

Microorganisms are by abundance the far most dominant in all ecosystems on Earth. The total number of prokaryotes (Bacteria and Archaea) present on Earth has been estimated to $4\text{--}6 \times 10^{30}$ individuals (Whitman *et al.*, 1998), which, on a total carbon basis, equals the biomass of all plants on Earth. Microorganisms are generally classified as organisms too small to be seen with the human eye, which generally includes Bacteria, Archaea, viruses, Fungi, Algae, protozoans and small metazoans (Lim, 1998). However, this definition is problematic as there are several species and groups that are in a grey zone, for example the world's largest known bacteria, *Thiomargarita namibiensis*, can reach a size of $750\text{ }\mu\text{m}$ (Schulz *et al.*, 1999), which makes it observable by eye only. Many metazoans are also too small to be seen without a microscope

(e.g. many nematodes) but are mostly referred to as meiofauna when smaller than 500-1000 μm . Many organisms also go through microscopic juvenile stages, thus functioning as temporary microorganisms/meiofauna. Regardless of what is included in the term, it is clear that the microbial diversity is outstanding and at present time it is likely that we only have discovered a fraction of the total biodiversity of organisms on Earth. This is clearly displayed by extrapolation estimates on the total number of Prokaryote species (Archaea and Bacteria) that has been made by using molecular techniques in combination with statistics (Curtis and Sloan, 2004; Pedros-Alio, 2006; Torsvik *et al.*, 1998; Torsvik *et al.*, 2002; Ward, 2002). These estimates are staggering and range up to 10^9 species. Considering this large species richness, it is even more fascinating that an extensive genetic and functional versatility can exist within a single bacterial species (see e.g. Walsh *et al.*, 2009), highlighting the magnitude of the fact that all species are unique.

The question of what limits Earth's overwhelming species diversity was brought up early in natural history. Historically, the major assumption has been that biodiversity is a dependent variable responding to changes in the environment or in the ecosystems' processes (Naeem, 2002). For example the microbial ecologist Baas Becking, claimed in the 1930s that "everything is everywhere, but, the environment selects" (de Wit and Bouvier, 2006). Similarly, much research has been done on the effect of various abiotic environmental factors on biodiversity, for example factors such as oxygen and nutrient availability, sediment type, organic matter content, climate and pH (Buckley *et al.*, 2006; Freitag *et al.*, 2006; Hewson *et al.*, 2003; Hunter *et al.*, 2006; Moss *et al.*, 2006), just to name a few. Environmental factors, such as low oxygen concentrations in benthic habitats can also be negative on a local scale for biodiversity but on the other hand, may be positive on a larger scale as it creates habitat heterogeneity (Gooday *et al.*, 2010; Vanreusel *et al.*, 2010), and actually increases the biodiversity on a larger scale. A large spatial and temporal heterogeneity has also been shown to be necessary in order to sustain a high microbial diversity (Lozupone and Knight, 2007; Torsvik *et al.*, 2002) allowing a higher biodiversity in more complex environments.

The role of abiotic factors in regulating the occurrence and abundance of organisms was described in the early 1900s by Shelford (Shelford, 1913) in his "law of toleration", which states that for survival and growth each organism requires a complex set of conditions to be fulfilled, and gave examples of limiting factors such as temperature and low nutrient conditions. These thoughts were developed later-on by other ecologists, and in 1958,



Hutchinson defined the n-dimensional niche concept, where each dimension is represented by an environmental variable that limits the survival of a specific species. These environmental restrictions equate to the *fundamental niche*, which defines the space and resources a species can utilize in the absence of biotic interactions. Biotic interactions such as competition and predation are, however, present in the real environment, and restrict the fundamental niche space to the *realized niche* (Krebs, 2001).

That species may utilize resources with varying degree of efficiency, thereby implying that biodiversity is important for ecosystem processes, has been recognised and studied for a long time in science with described experimental studies dating back at least as far as 1825 (Sinclair, 1826). Due to the recent, rapid speed of biodiversity loss caused by human activities, research has intensified during the last decades in order to better understand the consequences of biodiversity loss on ecosystem function and the provision of ecosystem services. Three main hypotheses have been suggested on the relationship between biodiversity (species richness) and ecosystem function (see e.g. Lawton, 1994): 1) All species contribute to ecosystem function - the “rivet hypothesis”. 2) Species can be lost without consequences, as long as the functional groups are still present – the “redundancy hypothesis” 3) Species contribution to ecosystem function is unpredictable, due to context-dependency and the complexity of ecosystems – the “idiosyncratic hypothesis”. See Figure 3 for a graphic illustration of these three hypotheses.

Most of the research on the relationship between biodiversity and ecosystem function has been performed on a relatively small scale, and mostly by manipulating species richness at a single trophic level. Microbial species richness has for example been positively

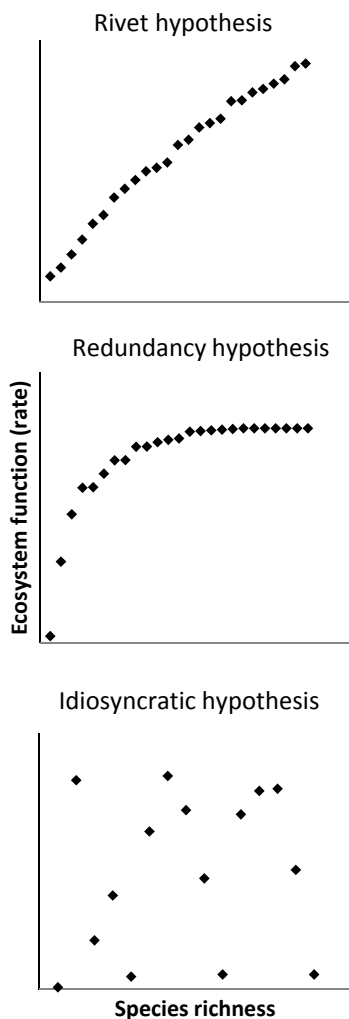
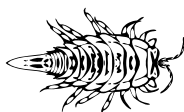


Figure 3. Three hypotheses on the relationship between species richness and ecosystem function. Adapted from Lawton (1994).

linked to community respiration rates (Bell *et al.*, 2005; McGrady-Steed *et al.*, 1997) and to the range of organic substrates that can be decomposed (Naeem *et al.*, 2000). The importance of species richness of burrowing macrofauna in sediments for ecosystem processes such as oxygen and nutrient fluxes has also been shown (e.g. Waldbusser *et al.*, 2004). Some, however, have argued that only the functional diversity (i.e. number of species traits) is important, not the species richness *per se*, for these processes (e.g. Raffaelli *et al.*, 2003), in accordance to the redundancy hypothesis. To a large degree, this is based on the assumption that species can perform the same roles in an ecosystem and have completely overlapping fundamental niches. However, even if this assumption would be true, this does not mean that species (for which the ecosystem potentially possess functional redundancy) may be lost without consequences, because species will always differ to some extent in some specific function or characteristic (Jax, 2005; Rosenfeld, 2002), e.g. the species being lost might be tolerant to a specific pollutant (and the replacer might not be).

The argument that mainly functional diversity is important, and the validity of the "functional redundancy hypothesis", is likely on a narrow or limited scale, but as the scale of focus increases and when several ecosystem processes/functions are considered simultaneously (Stachowicz *et al.*, 2007; Stachowicz *et al.*, 2008), it is more likely that species richness is positively linked to ecosystem function (rivet hypothesis). Recently, it has also been shown that food-web structure can interact to affect the relationship between biodiversity and ecosystem function (Duffy *et al.*, 2005), stressing the importance of increasing the complexity within biodiversity-ecosystem function research. An increased complexity can be achieved through several approaches, e.g. by including a food-web ecology perspective (Srivastava *et al.*, 2009) or include an increased spatial and temporal heterogeneity (Hillebrand and Matthiessen, 2009).

The last decades of biodiversity research have nevertheless accumulated evidence that there is a positive relationship between biodiversity (species richness) and ecosystem processes (Cardinale *et al.*, 2006; Duffy, 2009). This has successfully challenged one of ecology's central beliefs, namely that biodiversity is primarily a consequence of environmental factors and ecosystem processes, secondarily structured by community interactions (Naeem, 2002). A recent view on the relationship between environment, biodiversity and ecosystem processes is illustrated in Figure 4.



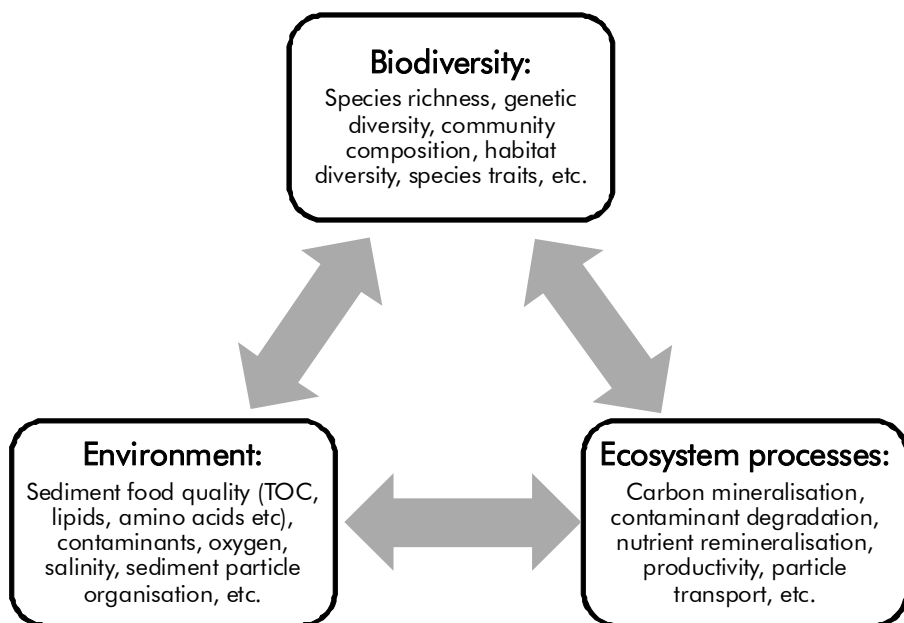


Figure 4. The links between biodiversity, ecosystem processes and the environment in marine sediment ecosystems. Adapted from Loreau (2010).

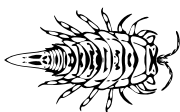
Marine ecosystems, like any other ecosystem have a capacity to resist and recover from various types of disturbance. The term resilience has been used as a definition for the amount of disturbances an ecosystem can absorb (or resist or buffer against changes) before changing into an alternative stable state (Gunderson *et al.*, 2002; Holling, 1973). Some evidence point towards that biodiversity may be even more strongly linked to stability (i.e. resistance, resilience, reduced variability) than ecosystem processes themselves (Stachowicz *et al.*, 2007). This may in part be explained by differences in species' response to environmental fluctuations, allowing a stabilization of community and ecosystem dynamics (Elmqvist *et al.*, 2003; Leary and Petchey, 2009).

Study system: The Baltic Sea

The Baltic Sea is one of the world's largest brackish water bodies with a surface area of more than 400 000 km² (Weaver, 2003). The Baltic Sea is divided into several basins with the Baltic Proper being the largest, occupying the southern half of the Baltic Sea. The other major basins are Bothnian Bay, Bothnian Sea, Gulf of Finland, Gulf of Riga and Kattegat (see Figure 5). The Baltic Sea can be seen as an "estuarine-type water body" (Reid and Orlova, 2002) with a salinity regime driven by a balance between freshwater inflow, mostly from rivers in the North, and inflow of saltwater from the North Sea, via the narrow Danish Straits (Reid and Orlova, 2002; Weaver, 2003). Because of the large catchment area of approximately 1.7 million km² (indicated in grey in Fig 6), more than four times than the Sea itself, the freshwater input to the Baltic Sea is large, compared to the intrusions of salt water from the North Sea, which only take place at very specific weather conditions that occur irregularly (Schinke and Matthaus, 1998).

Because of its special bathymetry, the Baltic Sea's water exchange through the Danish Straits creates a strong salinity stratification (halocline) at approximately 60-80 m depth. This generates a stagnant water layer below the halocline that is oxygen-poor throughout much of the deeper Baltic Proper due to the limited water mixing. A salinity gradient also occurs in the surface water, with salinities ranging from approximately 1-2 (expressed using the practical salinity scale) in the Bothnian Bay to 20 in the Danish Straits (Reid and Orlova, 2002; Weaver, 2003). A sharp thermocline also develops in the surface waters during the summer, and divides the surface waters into two distinct layers: the top layer down to 10-25 m depth, which is mixed by winds and a deeper and colder layer that extends down to the halocline or the bottom (Weaver 2003). The water temperature in deeper waters is generally around 4-6°C throughout the year. During the winter months, ice forms and usually covers a significant part of the Baltic, especially in the northern, colder parts that also have a lower salinity (Reid and Orlova 2002).

Soft mud is the most dominant bottom type and covers most of the Baltic Sea seafloor (Jansson, 1980), with accumulation bottoms dominating below 50 metres depth (Håkanson, 1993). The benthic macrofaunal diversity is low with a handful species, constituting a low number of functional groups (Ankar, 1977; Bonsdorff and Pearson, 1999). The meiofauna community is more species rich with



about 50-60 dominant species in the Baltic Proper, with nematodes, copepods and ostracods dominating in biomass (Ankar and Elmgren, 1976; Elmgren, 1978). Salinity is one of the main factors that affects the distribution patterns of Baltic Sea metazoans, as only a few species of marine origin thrive in the low salinity waters of the northern parts and only a few species of freshwater origin thrive in the salty southern parts (Foberg, 1994) (Laine, 2003; Weaver, 2003). The microbial diversity within the Baltic Sea is not as extensively studied as the diversity of larger organisms, but studies have shown that the Baltic Sea contain diverse and unique communities of bacteria, ciliates and flagellates (Edlund, 2007; Edlund *et al.*, 2008; Stock *et al.*, 2009). Studies of pelagic bacteria have also shown that it is most likely that Baltic Sea microbial communities have both a marine and freshwater origin (Riemann *et al.*, 2008; Sivonen *et al.*, 2007).

The nutrient status of the Baltic Sea has been greatly altered during the last century, due to anthropogenic and natural causes, resulting in a eutrophication situation. The major anthropogenic cause contributing to the eutrophication is the demographic increase in modern time; approximately 85 million people live in the Baltic's catchment area today. In addition to the last century's increased pollution from industries, agriculture and sewage, large saltwater inflows during the 1950s caused a mass release of phosphorous from the bottom sediments. The release of phosphorous in turn induced a high level of nitrogen fixation from phosphorous limited cyanobacteria, thus causing a large increase in primary production and sedimenting organic matter, starting the eutrophication cycle (Österblom, 2006). Large areas of the Baltic Sea seafloor are today either seasonally or permanently affected by low oxygen

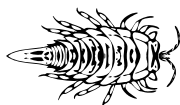


Figure 5. The six major basins of the Baltic Sea with their respective drainage area in light grey.

levels (hypoxia) or anoxia (oxygen free conditions), which has had large effects on sediment living fauna (Karlson *et al.*, 2002; Pearson and Rosenberg, 1978).

A large number of non-indigenous species have been introduced by humans into the Baltic Sea, mainly by unintentional transport through shipping and release of ballast water. The rate of species introduction into the Baltic Sea today is fast, with about 70 identified species that have established a reproducing population only during the last decades (Leppäkoski *et al.*, 2002; Olenin and Leppäkoski, 1999). These invading species have had effects on the Baltic Sea ecosystem such as altered food-web structure, community composition and ecosystem processes. The high invasion success of many species into the Baltic Sea may potentially be explained by the relatively low native species diversity, as higher biodiversity is known to enhance invasion resistance (Stachowicz *et al.*, 1999).

Anthropogenic pollution is also a major threat to the organisms of the Baltic Sea. Many man-made contaminants have been released in the past for example DDT and PCBs, and many are still released e.g. PAHs (polyaromatic hydrocarbons), dioxins, TBT (tributyltin), PBDEs (brominated flame retardants), lead, copper, cadmium, radioactive compounds and mercury (Helcom, 2005; Weaver, 2003). The concentrations of contaminants in fauna and sediments are high in comparison to other marine environments and the current levels of dioxin in several fish species exceed the limit set by the European Union for human consumption (Isosaari *et al.*, 2006; Wiberg *et al.*, 2009). Luckily, pollution loads into the Baltic Sea have decreased greatly during the last 30 years thanks to enhanced management and technology, and the situation has improved somewhat, although the pollution situation is still problematic (Bignert *et al.*, 1998; Helcom, 2004; Wiberg *et al.*, 2009).



Methods used

Experimental ecosystems (I-V)

Ecosystem ecology is often studied today using experimental methods of science, either by using field studies that manipulate some component of natural ecosystems or by constructing ecosystems in the laboratory. Ecosystems constructed in the laboratory are often called micro- or mesocosms, depending on the spatial scale used. Laboratory ecosystems contain suitable environmental constituents together with interacting organisms. As natural ecosystems are very challenging to recreate in laboratory conditions due to their innate complexity, experimental ecosystems are often forced to be relatively simple and limited in size, and it can be difficult to draw conclusions that are applicable on larger scales (i.e. spatial or temporal). The main advantage

of laboratory ecosystems, however, is that they allow the study of effects of one or several treatments, while maintaining all other variables constant. It is thus easier to study cause-effect relationships, compared to field studies, which often rely to large extents on correlational data, or where many unknown variables may confound the results. Furthermore, laboratory ecosystems can also be manipulated in ways that are either difficult or ethically very questionable to do in natural ecosystems (e.g. deliberately polluting the ecosystem with nutrients or harmful contaminants).



Figure 6. A few of the microcosms used in paper I, approximately 45 cm in height and 8 cm in diameter.

Mechanistic interpretation of biodiversity-ecosystem function experiments (I-II)

The analysis and interpretation of experiments on the relationship between biodiversity and ecosystem function has developed from simple observations and comparisons of primary production (Sinclair, 1826) to examining changes in relative yield (or

performance) within and among treatments for a range of communities and ecosystems. Yield can be defined as the outcome (amount) of the measured process, for example biomass increase or degradation of organic matter.

A challenge within this research field has been to acquire ecological understanding of the mechanisms responsible for observed relationships. Three general ecological mechanisms have been proposed: (1) Facilitation, where coexisting species enhance a process through direct interaction (Cardinale *et al.*, 2002) (2) Niche differentiation, where interspecific competition is reduced by e.g. resource partitioning of food (Griffin *et al.*, 2008) (3) Dominance, or selection effect, in which dominant species through selective processes such as interspecific competition outperform other species (Fox, 2005; Loreau and Hector, 2001). Facilitation and niche differentiation are commonly collectively referred to as complementarity effects. In experiments, an artefact called sampling effect also exists, which refers to the increased probability of including a species with particular traits as species richness increase (Huston, 1997). An underlying question in this research has been to identify and quantify the cause of observed over-yielding by communities with higher species richness. Over-yielding (when positive) and under-yielding (when negative) refer to the deviation between the total community yield in a mixed-species community and the sum of expected yields based on species' yields in monocultures (single species communities).

In order to calculate the relative performances of individual species in a community, the process studied must be possible to measure on species level (e.g. production or incorporation of labelled compounds). The relative performances of species can then further be used to partition the net diversity effect (the difference between observed and expected yield in the mixed community) into complementarity (trait-dependent and trait-independent) and dominance components, in order allow an ecological interpretation of the observed effects (Fox, 2005; Loreau and Hector, 2001). The partitioning of the net diversity effect according to the tripartite equation proposed by Fox (2005) is summarized in Box 1, and the (mechanistic) ecological interpretations of the resulting diversity components are given in Box 2.



Tripartite partitioning of the net diversity effect

The net diversity effect, ΔY , is calculated as the difference between the observed yield of a multi-species community and its expected yield. The diversity effect can be partitioned into three diversity components according to the following equation:

$$\Delta Y = Y_O - Y_E =$$

$$N \overline{\Delta RY_i} + N \operatorname{cov} \left(S_i, \frac{RY_{O,i}}{\sum_i RY_{O,i}} - RY_E \right) + N \operatorname{cov} \left(S_i, RY_O - \frac{RY_O}{\sum_i RY_{O,i}} \right) =$$

T-IC + Dominance + TDC

$\Delta Y = Y_O - Y_E$ = deviation from total expected yield in the multi-species community

$Y_O = \sum_i Y_{O,i}$ = total observed yield of the multi-species community

$Y_{O,i}$ = observed yield of species i in the multi-species community

$Y_E = \sum_i Y_{E,i}$ = total expected yield of the multi-species community

$Y_{E,i} = RY_{E,i} S_i$ = expected yield of species i in the multi-species community

$RY_{E,i}$ = expected relative yield of species i in the mixture, which is simply its original frequency in the community

S_i = yield of species i in the single species community

$RY_{O,i} = Y_{O,i}/Y_O$ = observed relative yield of species i in the multi-species community

$\Delta RY_i = RY_{O,i} - RY_{E,i}$ = deviation from expected relative yield of species i in the multi-species community

N = number of species in the multi-species community

Box 1. Ecological interpretations the of the diversity components calculated from the tripartite partitioning equation (Fox, 2005). S_i = yield of species i in a single species community.

	Positive value (contributes to over-yielding)	Negative value (contributes to under-yielding)
Trait-independent complementarity	Facilitation and/or niche differentiation Species increase their yield without affecting other species' yield.	Competition and/or inhibition Species decrease their yield at the expense of other species' yield.
Trait-dependent complementarity	Nested niches Species with a high S_i increase their yield without affecting other species' yield.	Nested niches Species with a low S_i increase their yield without affecting other species' yield.
Dominance (selection)	Overlapping niches Species with a high S_i dominate mixtures at the expense of other species' yields.	Overlapping niches Species with a low S_i dominate mixtures at the expense of other species' yields.

Box 2. Tripartite partitioning of the net diversity effect, after Fox (2005). T-IC = Trait-independent complementarity, TDC = Trait-dependent complementarity.

Isotope tracing (I-II & IV-V)

Isotope tracing involves a powerful set of techniques for studying ecosystem processes and are commonly used in ecological studies in order to follow biogeochemical cycles and examine food web structures (Fry, 2006). Isotopes are atoms that have the same number of protons but differ in the number of neutrons, thus leading to atoms of the same element that vary in mass. Natural carbon for example, is a mixture of three isotopes, ^{12}C , ^{13}C and ^{14}C . Isotopes are either stable (e.g. ^{12}C or ^{13}C) or unstable (e.g. ^{14}C or ^3H), depending on if they decay with time or not. Isotopes that are unstable (radioactive) are generally quantified through the energy they release as they decay, for example by using a scintillation counter. Stable isotopes, on the other hand, are quantified by using a high accuracy mass spectrometer, and the ratio between the heavy and light isotopes is determined. The resulting isotopic ratio is thereafter compared to an international reference standard in order to describe the isotopic signature (normally expressed in ‰, or δ). Both stable (^{13}C and ^{15}N) and radioactive (^{14}C) isotopes have been used as tracers in this thesis, in order to follow the cycling of phytodetritus and organic contaminants.

Assessing microbial diversity (IV-V)

An obvious question when studying microbial organisms and their activity is “How do you study something that you cannot see?”. Early in microbial ecology research, microorganisms were isolated from their natural environment, and subsequently cultured and studied in the laboratory. However, recently it has been shown that not even 1 % of all bacteria can be grown using current cultivation methods (Beebee and Rowe, 2004). Microorganisms can also be studied using microscopes, for example by counting the total number of bacteria. However, microscopic investigations of bacteria give little information on what type of bacteria is being studied and is difficult for soil and sediment samples due to the presence of interfering particles.



A common strategy today is to assess microbial diversity and abundance using DNA or RNA extracted from environmental samples. These nucleic acids can be studied using several molecular methods, of which most studies involve ribosomal rRNA genes (16S or 18S) but it is also possible to study other genes, such as those involved in specific functions. The 16S rRNA gene is the most commonly used gene to identify different bacterial groups or species (Weisburg *et al.*, 1991) and methods that assess the microbial community profile, for example (DGGE) (Muyzer *et al.*, 1993), terminal restriction fragment length polymorphism (T-RFLP) (Liu *et al.*, 1997) are also applicable. T-RFLP was used in Paper IV-V in order to assess the microbial community of sediments, see Figure 7 for an illustration of the method. Most of the recent community profiling methods are based on the amplification of a specific gene (by PCR), from the total genes of the community present in the sample. Usually bacterial community analyses are made using the 16S rRNA gene. However, the limited length of the 16S rRNA gene as well as the possibility that multiple copies of the same gene are present in the same individual bacteria can be a problem, therefore, the use of other genes has been suggested (Dahllöf *et al.*, 2000).

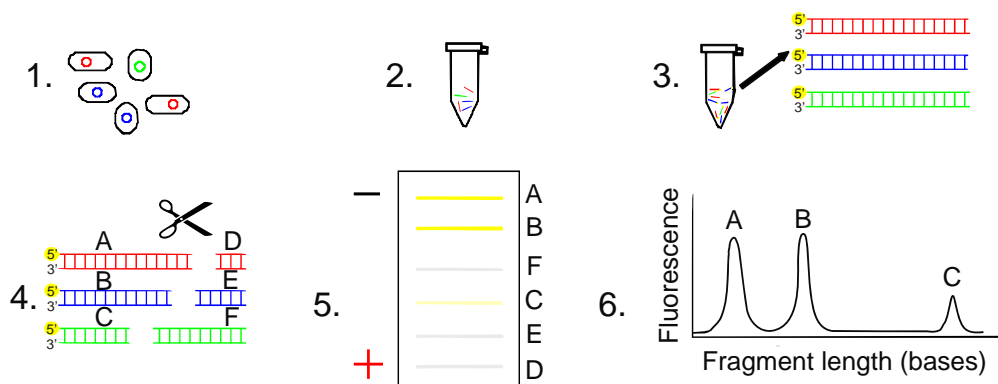


Figure 7. An overview of T-RFLP. 1) Sampling of the community 2) DNA extraction and purification 3) PCR-amplification of the gene of interest using a fluorescently labelled primer 4) Amplicon cutting using a restriction enzyme recognizing four specific bases (e.g. GG⁺CC) 5) Fragment separation by using e.g. capillary electrophoresis 6) Fragment detection and quantification of the fluorescently labelled fragments. The relative fluorescence for each peak (A, B, C) depends on the relative abundances of gene copies present in the sampled community.

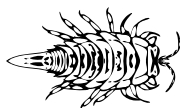
Summary of the thesis' research papers and major findings

Paper I and II found that an increased biodiversity of benthic deposit feeders increases the processing of organic matter settled on the sea-floor, suggesting that species-rich communities utilize this resource (i.e. sedimented organic matter) more efficiently. Paper II and III investigated the ecology of the recently introduced species *Marenzelleria arctia*, a polychaete spionid worm introduced with ballast water into the Baltic Sea. Our results show that both the ability to use different food resources than native fauna, and the lack of natural predators may have contributed to its invasion success in the Baltic Sea. In paper IV and V we studied the degradation of organic contaminants, and the results from Paper IV indicate that the structure of the food web in sediments is linked to this ecosystem process and may also affect the bacterial community diversity. Paper V shows that anthropogenic pollution by pharmaceuticals pollution is a potential threat for both microbial diversity and microbially mediated ecosystem processes.

Paper I

Higher diversity of deposit-feeding macrofauna enhances phytodetritus processing

This paper focuses on the link between cycling of organic matter and species diversity of benthic deposit feeding macrofauna. A natural phytoplankton bloom was enriched with stable isotopes, ^{13}C and ^{15}N , and the fate of the enriched phytodetritus was followed in benthic communities with varying species richness and composition, representing the natural communities found in sediments of the species-poor Baltic Sea. The use of stable isotopes allowed a quantification of the resource use (incorporation of ^{13}C and ^{15}N) at the species level, in both single- and multi-species communities. The incorporation rate of carbon and nitrogen, originating from settled phytodetritus, were different among all three species and communities with higher species diversity incorporated more C and N than expected from their respective single-species treatments. The incorporation of N in the most species-rich community also



exceeded N incorporation of the best-performing single-species community, which is evidence of transgressive over-yielding. This transgressive over-yielding was primarily due to a positive complementarity effect in all treatments. The results suggest that benthic communities of the Baltic Sea with a higher diversity of deposit feeders have higher phytodetritus processing rates and use organic-matter deposited carbon and nitrogen at higher efficiency, thus mainly supporting the rivet hypothesis. These findings highlight the importance of biodiversity for ecosystem processes of major importance for marine ecosystem function.

Paper II

Effects of a polychaete invader on soft-bottom ecosystem functions

Much due to a large increase in shipping, and transport of ballast water, the introduction of non-indigenous species is considered one of the major threats to marine ecosystems today. This paper examines the ecology of the recently introduced polychaete *Marenzelleria arctia*, now spread throughout the Baltic Sea, and investigates its potential effects on a few key benthic ecosystem processes. Stable isotope tracers were utilized in order to measure the incorporation and burial of carbon and nitrogen from a simulated spring phytoplankton bloom in different benthic communities, containing various combinations of one to four species of deposit-feeding macrofauna. Macrofaunal growth was also assessed in order to quantify community biomass production. The results showed that the non-indigenous *M. arctia* increased more rapidly in biomass than the native species, *Monoporeia affinis*, *Pontoporeia femorata* (Amphipoda) and *Macoma balthica* (Bivalvia), but incorporated and buried carbon and nitrogen, originating from the settled phytodetritus, at rates similar to the native species. Communities with higher species richness generally had higher incorporation values of carbon and nitrogen than what can be expected from the yields obtained in single-species communities (over-yielding). The mechanism behind the observed over-yielding was mainly facilitation and/or niche differentiation and was more evident in communities including *M. arctia*. In contrast, multi-species treatments generally had lower biomass production than expected due to competition and negative dominance effects. These contrasting results suggest that there is a low niche overlap in resource utilization of deposited phytodetritus between *M. arctia* and native species, but indicates a greater inter-specific competition for old organic material in sediments. The reliance on old organic

material for *M. arctia* was further supported by its low natural $\delta^{13}\text{C}$ -values. In conclusion, the results indicate that the invasive species *M. arctia* may potentially enhance benthic productivity by increasing resource use efficiency in Baltic Sea sediments. However, whether this potential increase in resource efficiency use is valid at larger spatial and temporal scales, and whether *M. arctia* is efficiently preyed upon by higher trophic levels in the Baltic Sea ecosystem remain to be studied.

Paper III

The enemy release hypothesis may contribute to explain the invasion success of *Marenzelleria arctia* (Polychaeta) in the Baltic Sea

Several hypotheses have been suggested for the great invasion success of the non-indigenous *Marenzelleria arctia* in the Baltic Sea. Predation experiments containing the three major invertebrate predators in the area, *Saduria entomon* (Isopoda), *Halicryptus spinulosus* (Priapulida) and *Bylgides sarsi* (Polychaeta) were performed in order to test if the enemy release hypothesis (lack of natural predators in the new ecosystem) may potentially explain the invasion success of *M. arctia*. The results showed that due to its ability to bury deep down in the sediment, *M. arctia* was protected from all three native invertebrate predators, and the enemy release hypothesis may thus potentially explain its successful invasion into the Baltic Sea. Furthermore, this paper describes the current community interactions among Baltic Sea sedimentary macrofauna, after the introduction and successful establishment of a reproducing population of *M. arctia* and discusses the consequences this introduction has had on the benthic community interactions. The results question if *M. arctia* is efficiently preyed upon by higher trophic levels, potentially leading to large implications in Baltic Sea food-web dynamics.

Paper IV

Meiofauna reduces bacterial mineralization of naphthalene in marine sediment

In paper IV, the degradation of organic pollutants in sediments was studied, by investigating the role of sediment-living meiofauna. Studies on the significance of meiofauna for benthic ecosystems are lacking, and their potential importance for several important



ecosystem processes in sediments are largely unknown. In this paper, we studied the role of meiofauna on the mineralization of naphthalene, a polycyclic aromatic hydrocarbon. A method to extract live meiofauna from sediments using density gradient extraction was developed. This method was applied in order to experimentally modify the sediment food web structure by changing the abundance and diversity of native meiofauna. In addition to quantification of the naphthalene mineralization rate, we assessed the number of cultivable naphthalene-degrading bacteria as well as the microbial community diversity in the sediment. Results showed that meiofauna had a significant effect on the bacterial community composition and that the naphthalene mineralization rate was negatively related to meiofauna abundance and biomass, due to top-down control by meiofauna on pollutant degrading bacteria. This study suggests that sediment-living meiofauna may significantly affect microbial community structure and microbially mediated ecosystem processes, stressing their potential functional importance in benthic ecosystems.

Paper V

Effects of the antibiotic ciprofloxacin on the bacterial community structure and degradation of pyrene in marine sediment

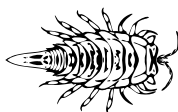
The antibiotic use worldwide is increasing and was estimated to 100 000 – 200 000 tonnes in 2002 (Wise, 2002). Antibiotics are used within human and veterinary medicine, aquaculture and agriculture and often pass through metabolic systems without being particularly degraded or transformed and have been found in the environment. The ecological consequences of antibiotic pollution for the aquatic environment is a recent issue of concern due to the potential risk for negative effects in the environment on microbial diversity and microbially mediated ecosystem processes. In this study, natural communities of sediment microorganisms were exposed to five different concentrations (0-2 mgL⁻¹) of the fluoroquinolone antibiotic ciprofloxacin in order to assess the potential effects on the microbial community diversity (determined using molecular methods) and the ecosystem's capacity to degrade the organic pollutant pyrene (traced by using ¹⁴C-labelled pyrene). The results showed a significant dose-dependent inhibition of pyrene mineralization as well as significant effects on the bacterial community structure due to exposure to ciprofloxacin. Our results show that antibiotic pollution can potentially be a threat to both microbially mediated ecosystem processes and bacterial diversity in aquatic sediments.

Final remarks

The sediment ecosystem processes studied in this thesis such as decomposition of organic matter and degradation of harmful contaminants are crucial for human society and are supplied by marine ecosystems worldwide. In this thesis I have studied how these ecosystem services are linked to various types of biological diversity in marine sediments (Paper I-V).

Paper I and II are, to my knowledge, the first studies to experimentally test the importance of macrofaunal deposit feeder diversity on the burial and incorporation of nitrogen and carbon of settled phytoplankton blooms. The results show that a higher richness of deposit feeders increases the processing of organic matter settled on the sea-floor, and that diverse communities have a more efficient resource utilization of the deposited resources. These results imply that a high biodiversity in marine sediments increases the efficiency of benthic-pelagic coupling of elements, thus potentially increasing both primary production in the photic zone and the trophic transfer of nutrients to secondary consumers and predators. The low species diversity and the distribution gradient of deposit feeders in the Baltic Sea along its salinity gradient presents an interesting aquatic ecosystem that is more simple to study and manipulate experimentally than more species-rich benthic ecosystems. Results from laboratory studies on Baltic Sea soft-bottom systems are also easier to extrapolate to actual field situations, since experimental communities can easily be manipulated to represent actual species compositions found in the field. The importance of deposit-feeder richness for benthic-pelagic coupling processes is probably also valid in other sediment systems, where detritivores drive organic matter processing. Community composition was also significant for the studied processes, due to species-specific differences in yield among the four species. This suggests that the four species of Baltic Sea deposit feeding macrofauna all belong to different functional groups, mainly supporting the “rivet hypothesis”. However, the low species richness in the Baltic Sea also makes it difficult to test the validity of the “redundancy hypothesis” in this system.

Paper II and III investigate possible reasons why the invading species *Marenzelleria arctica* has successfully colonized the Baltic Sea. In paper II, the positive complementarity in communities containing *M. arctica* suggest a low niche overlap with native deposit feeders for newly deposited organic matter, supporting the



suggestion that *M. arctia* may use a previously empty niche in the Baltic Sea. This is further supported by both the observed ability of *M. arctia* to grow fast when only supplied old organic matter as food resource and the natural $\delta^{13}\text{C}$ -values close to bulk sediment. It is thus possible that the introduction of *M. arctia* has had a positive effect on the secondary production of benthic deposit feeders in the Baltic Sea, as it is not dependent on newly settled phytodetritus to the same extent as the native species. However, as shown in Paper III, *M. arctia* is also well protected from the native invertebrate predators, suggesting that protection from predation is another factor that may help explain its invasion success. The ability to avoid at least some of the Baltic Sea predators also highlights the questions of “To what extent is *M. arctia* predated upon in the Baltic Sea?” and “Is the trophic transfer limited?”. Even if the introduction of *M. arctia* has not caused an increased interspecific competition among deposit feeders for food resources, competition for space may be significant. The negative effects of *M. arctia* on biomass production observed in Paper II may be due to an increased competition for space and/or interference competition. *M. arctia* is also likely to have a competitive advantage compared to the native species due to its superior ability to avoid predators. However, it is difficult to couple potential negative effects from increased interspecific competition on the native species in the field as large scale population declines of the amphipods *Monoporeia affinis* and *Pontoporeia femorata* occurred before the introduction of *Marenzelleria* spp. to the Baltic Sea. This stresses the fact that other factors than interspecific competition are also important for determining the abundance and distribution of fauna.

In paper IV, we describe a method we developed in order to extract live meiofauna from sediments, allowing experimental manipulation of meiofauna abundance. The results suggest that this commonly overlooked faunal group of the sediment ecosystem is of significant importance, by affecting both the microbial community diversity and the system’s ability to degrade organic contaminants. This study provides new information on the understanding of the degradation of organic contaminants in sediments. Paper V also investigates the degradation of organic contaminants by sediment bacteria, and shows that antibiotic pollution may be a threat to both microbial diversity and essential ecosystem services provided by microorganisms. Paper V also draws attention to the large anthropogenic influence on Earth’s ecosystems, which has caused large losses in global biodiversity and negative effects on the generation of ecological services (Chapin *et al.*, 2000). Anthropogenic disturbance on marine ecosystems is considerable across all scales and is caused by many factors, such as overharvesting of resources, eutrophication, the spreading of harmful contaminants, habitat

destruction and introduction of non-indigenous species (Snelgrove *et al.*, 2004). It is difficult to predict how these disturbances interact in the field and how large the cumulative effects are (Crain *et al.*, 2008). It is difficult to rank which anthropogenic disturbances that are most severe, due to variation in scales, the complexity of ecosystems and the question of the subjectivity of value(s). Nevertheless, the introduction of non-indigenous species (studied in paper II-III) has been ranked as one of the major threats to marine biodiversity, with large historical impacts on marine ecosystems and accelerating invasion rates (Carlton, 2001; Snelgrove *et al.*, 2004). Pollution by nutrients and environmental contaminants (studied in paper IV-V) are other high ranked threats to biodiversity, and despite our increasing ecological awareness and knowledge, new chemicals of environmental concern continue to emerge, and to be released into the environment. One of the main issues regarding current pollution levels is management, and much of the current global pollution is due to poor or non-existing management of waste in large parts of the world (Corcoran, 2010). Marine fisheries are likewise poorly or foolishly managed, and excessive fishing has altered the marine food webs on a global scale (Pauly *et al.*, 1998; Richardson *et al.*, 2009; Worm *et al.*, 2006). Human induced global changes in land use, biogeochemical cycles and climate are affecting biodiversity on an unprecedented level (Hassan *et al.*, 2005), and along with decreasing biodiversity, ecosystem processes as well as the provision of ecosystem services are affected, see Figure 8 (Chapin *et al.*, 2000; Hooper *et al.*, 2005).

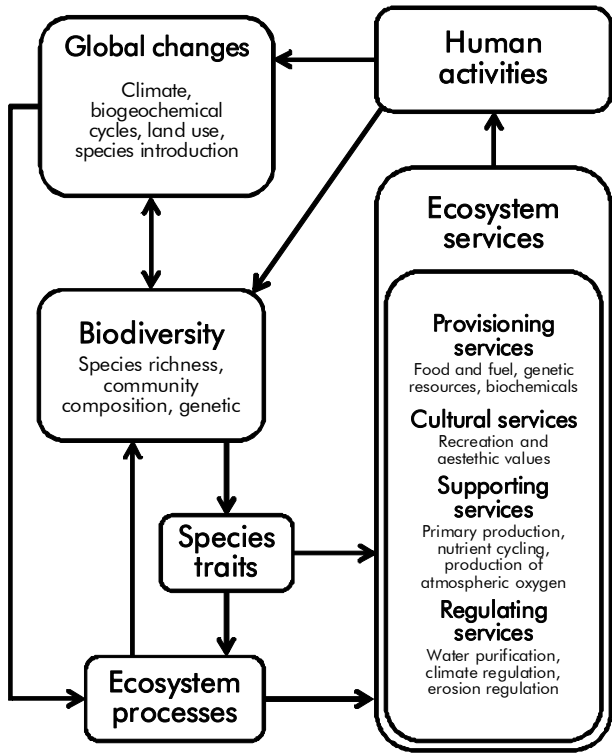
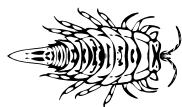


Figure 8. A conceptual model illustrating how anthropogenic activities is linked to sediment ecosystem processes and the provisioning of ecosystem services. Adapted from Chapin *et al.* (2000).



Four general reasons have been proposed in arguing that biodiversity is highly valuable and necessary to protect from extinction by humans (Ehrlich and Ehrlich, 1992): (1) Ethical reasons, i.e. what right do humans have to exterminate species for all eternity? (2) Esthetics, i.e. the beauty of nature's diversity is worth preserving (3) Economic value, i.e. nature provides innumerable resources of economic value to human society (4) Biodiversity provides essential supporting and regulating ecosystem services. This thesis is mainly focused on the role of biodiversity to supply ecosystem services, although I would argue that all of the four reasons above are valid for Baltic Sea sediment biodiversity. And after all, economic calculations will never be reasonable, due to the difficulty in making economic valuations based on ethical or esthetic measures, and the impossibility of predicting potential future values, questioning the sense in making economic calculations (Nunes and van den Bergh, 2001). However, estimations such as the ones made by Costanza et al. (1997), on the incredible economic value of marine ecosystem services worldwide, provide quite convincing economic arguments, why preserving biodiversity should be a prioritized issue for human society. Large economic benefits are also to be expected when restoring diversity, as exemplified by benefits gained in the creation of marine protected areas, where large increases in productivity, ecosystem stability and generation of tourism revenues have been observed (Worm *et al.*, 2006).

This thesis, in summary, illustrates in various ways, how biodiversity may influence a few selected ecosystem processes that occur in the Baltic Sea, and in other aquatic sediments across the world. It highlights the need to preserve marine biodiversity, which is important due to a number of reasons, one of which is the beauty of sedimentary organisms. The preservation of biodiversity is also undoubtedly beneficial for human society, both in a short and long-term perspective.



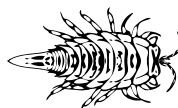
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