

# **Transport by Benthic Macrofauna: Functional Classification and Biogeochemical Response**

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For your unending love and support  
this book is dedicated to you, Emil

## Abstract

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Burrowing and reworking activities by benthic macrofauna regulate rates and pathways during organic matter mineralisation in bioturbated sediments. In so doing, they also affect the overall cycling of elements crucial in the biosphere (e.g. C, N, P, Fe, Mn and S). Feeding, burrowing, respiratory ventilation and construction activities by benthic fauna alter sediment structures, creating a mosaic of microenvironments within the sedimentary deposit. Fauna regulate input of organic material to the sediment and the vertical distribution of solids and solutes within the sediment, thereby influencing sediment-water exchange of gases and solutes such as carbon dioxide, oxygen and nutrients. While the existence of a relationship between faunal activity and biogeochemical responses is clearly established, the mechanisms behind this influence are not well constrained. In order to understand sediment response to changes, natural or anthropogenic, the role of benthic macrofauna for physical, chemical and biological processes need to be clarified. Because of the different behaviour of faunal species in sediments, observed effects of benthic macrofauna on biogeochemical variables are not necessarily directly and straight-forwardly coupled to the biomass of fauna. In fact, biomass has proven to be a relatively poor proxy for bioturbation throughout experiments presented in this thesis. Moreover, the relation may be non-linear and vary significantly between species and functional behaviour of fauna.

This thesis is based on results from several experiments designed to quantify the impact of bioturbation by individual species for element cycling in surface sediments, with focus on the small-scale transport mechanisms in bioturbated sediments. The functional behaviour of fauna and feedbacks between macrofauna reworking activities and chemical signals in sulphidic environments was studied by introducing two species (the brittle star *Amphiura filiformis* and the polychaete *Nephtys incisa*) to severely reducing sediments from beneath a mussel farm. The biogeochemical response to the different modes of reworking was significantly different between the two species. *Amphiura filiformis* generally enhanced bioadvective solute transport, while *Nephtys* sp. restricted the oxic zone and reduced benthic fluxes of nitrate and silicate.

Fauna in shallow sediments experience a daily light- and dark cycle. The diurnal light regime was experimentally demonstrated to significantly affect reworking activities by the polychaete *Hediste diversicolor*. An increased activity was observed for specimens of *H. diversicolor* that were exposed to a natural light cycle in comparison to those in constant darkness, probably related to a decrease in surface feeding. A light-dependent diurnal reworking behaviour has ramifications for the daily transformation of elements in shallow illuminated sediment systems.

An important result from this thesis is that activities by macrofauna in sediments and their significance for different biogeochemical processes, are too complex to be explained by only one or two bioturbation proxies. Assessments by multivariate analysis indicated that a general and repeatable comparison and classification associated with modes of bioturbation can be readily achieved by evaluating multiple experimental proxies for bioturbation. Similar functional groups were found by multivariate analysis on particle reworking by imaging or multiple transport processes in cores, i.e. independent of evaluation techniques for transport.

**Keywords:** Marine sediments | Early diagenesis | Bioturbation | Functional groups | Benthic fluxes | Imaging | Ecosystem function | Sediment reworking | Transport proxies | Fluorescent particles

## Populärvetenskaplig Sammanfattning

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Bioturbation är ett vidsträckt och komplext begrepp som innefattar olika aktiviteter av djur som lever på och i havets botten. Genom till exempel omblandning av sedimentpartiklar, konstruktion av gångar och hålrum, pumpning av vatten, födointag och exkretion av fekalier påverkar grävande djur sedimentets generella struktur. Deras aktiviteter leder till att transporthastigheter av partiklar och lösta ämnen förändras och att utbytet mellan bottenvatten och ytsediment stimuleras.

Ett ökat utbyte över gränssytan tillför sedimentet oxiderande ämnen från vattenmassan (t.ex. syre och nitrat) och minskar uppbyggnaden av giftiga och nedbrytningshämmande restprodukter (t.ex. svavelväte) i sedimentet. Syrerikt vatten som pumpas in i sedimentet via djurens aktiviteter leder till att stora delar av sedimentet i nära anslutning till gångar och hålrum syresätts. Detta ökar betydelsen av reaktioner som kräver syre i havsbottnarna och kan t.ex. leda till både ökad nedbrytning av organiskt material och till ökad bortförel av kväve ur haven.

Avhandlingen bygger på resultat från flera experiment där betydelsen av bioturbation för transport av partiklar och lösta ämnen har studerats. I en undersökning studerades möjligheten att använda grävande djur för att förbättra miljön i sediment med hög halt organiskt material (Artikel I). Det sediment som användes kom från botten under en musselodling, där fekalier och musslor faller ner och bidrar till en lokal övergödning under odlingarna. Två djurarter användes och det visade sig att ormsjärnan (*Amphiura filiformis*) generellt ökade transporten av vatten över sediment-vatten ytan. Därmed syresätts sedimentet och sannolikt ökade även nedbrytningshastigheten av det organiska materialet. Havsbortsmasken (*Nephtys incisa*), däremot, minskade generellt flöden av närsalter och syre.

Djur som lever i grunda bottenar upplever en daglig ljus- och mörkercykel, till skillnad från djur som lever i djupa bottenar dit ljuset inte når. I en annan undersökning studerades om aktiviteten av havsborstmasken (*Hediste diversicolor*) förändrades om den levde i mörker jämfört med en ljus- och mörkercykel (Artikel II). Det framgick att aktiviteten minskade under konstant mörker, vilket förmodligen är kopplat till ett minskat födosök på sedimentytan. Denna dagliga omgrävingscykel har betydelse för kretsloppet av t.ex. syre, mangan och järn i grunda havsmiljöer där bottenlevande alger finns.

En slutsats från avhandlingen är att betydelsen av aktiviteter av bottenlevande djur i sediment för olika biogeokemiska processer är för komplexa för att kunna förklaras av endast en eller två transportparametrar. I två experiment visas att man kan gruppera djur med olika grävbetende på ett objektivt sätt (Artikel III och IV). I och med att olika djur påverkar kemien i sedimentet på olika sätt är det nödvändigt att kunna gruppera djur med liknande egenskaper för att förstå hur biogeokemin fungerar i havsbottnarna under olika betingelser.

## PART A: Summary

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## PART B: Scientific Papers Included in the Thesis

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The thesis is based on work presented in the following papers. The papers are appended at the end of the thesis and referred to by their Roman numerals.

- Paper I** Lindqvist, S., Norling, K., Hulth, S. (2009) Biogeochemistry in highly reduced mussel farm sediments during macrofaunal recolonization by *Amphiura filiformis* and *Nephtys* sp.. *Marine Environmental Research*, 67: 136-145.
- Paper II** Lindqvist, S., Gilbert, F., Eriksson, S.P., Hulth, S. (2013) Activities by *Hediste diversicolor* under different light regimes: Experimental quantification of particle reworking using time-resolved imaging. *Journal of Experimental Marine Biology and Ecology*, 448: 240-249.
- Paper III** Lindqvist, S., Eriksson, S.P., Engelbrektsson, J., Hulth, S. Functional classification of bioturbating macrofauna in marine sediments using time-resolved imaging of particle displacement and multivariate analysis. *Manuscript*.
- Paper IV** Lindqvist, S., Eriksson, S.P., Norling, K., Hulth, S. Bioturbation by benthic macrofauna: experimental quantification and functional classification based on particle and solute transport. *Manuscript*.





# 1. Introduction and Aims

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## 1.1 Background

Processes occurring in marine sediments regulate the composition of the Earth's surface since the sediment surface is not only the interface between the ocean and the sea floor, but also the transition zone from the biosphere into the geosphere. Biotic and abiotic reactions in marine surface sediments control the global cycles of e.g. O<sub>2</sub>, C, and nutrients (Aller, 2014). Burial of organic carbon in sediments is generally considered to control the content of oxygen and carbon dioxide in the atmosphere over geological time scales (Bernier, 1982; Middelburg and Meysman, 2007). Thus, the balance between recycling of elements into the overlying water and burial into the sedimentary deposit determines the availability of elements essential for life. During mineralisation of organic matter in sediments, nutrients and other products from degradation are released to the pore water. These products are recycled to the overlying bottom water along concentration gradients. The supply of pore water solutes from benthic mineralisation may thus provide an important source of nutrients for primary production in the open ocean since nutrient availability is often limiting for primary producers. In coastal waters, nutrients released from the sea floor can supply 25-80 % of planktonic nutrient requirements (Middelburg and Soetaert, 2004).

Rates and pathways of organic matter mineralisation and the consecutive transport of organic and inorganic solutes across the sediment-water interface are tightly coupled to the redox state of the environment. In general, the redox condition of sediments depends on the availability and balance between oxidants (e.g. O<sub>2</sub>) and reductants (e.g. organic matter). A sequence of electron acceptors (oxidants) are used in organic matter mineralisation with oxygen as the thermodynamically most favourable oxidant, followed by nitrate, manganese- and iron oxides and sulphate (Froelich et al., 1979).

In sediments below oxygenated water, the activities of benthic macrofauna (> 1 mm) may significantly affect reaction pathways, sediment-water exchange and the composition of sediments eventually preserved (Aller, 1990). The sum of the activities by organisms in sediments and soils is termed bioturbation (Bernier, 1980; Darwin, 1881; Kristensen et al., 2012). Feeding, burrowing, tube construction and ventilation by benthic macrofauna result in particle and fluid transport. These transport processes influence reaction distributions, solute diffusion geometries and the relative and absolute rates of reactions in a deposit.

Bioturbating macrofauna influence the redox zonation in several ways, for example by translocating material between reaction zones and thereby altering the reaction distribution (Aller, 1982). Advective transport of material within the sediment and across the sediment-water interface is directly generated by benthic fauna activities (Rhoads, 1974). In bioturbated deposits, fauna create complex and time-dependent, three-dimensional transport-reaction patterns.

Today, significant efforts are devoted to understand consequences from anthropogenic stressors on essential ecosystem functions (Diaz and Rosenberg, 2008; Emmerson et al., 2001; Lohrer et al., 2004; Rhein et al., 2013; Solan et al., 2004a). Ecosystem function includes stocks of material such as carbon, water, minerals and nutrients and processes that involve transformation and dynamic exchange of energy and matter between trophic levels and between various environments. Examples of ecosystem functions are dynamics and transport

of carbon, oxygen and nutrients across phase boundaries. Another relevant term for the discussion of ecosystem function is ecosystem services, which can be described as the benefits that people obtain from ecosystems, within decision frameworks.

## **1.2. Scientific relevance**

While correlations and feedbacks between sediment biogeochemistry and benthic fauna are clearly established through numerous *in situ* and laboratory investigations, mechanistic controls and the exact effect of faunal communities for specific benthic responses are not well known (Meysman et al., 2006). For example, weak correlations between sediment metabolism and the number of species of macrofauna are frequently observed (Emmerson et al., 2001; Solan et al., 2004a). Therefore species-specific traits are increasingly recognised as important for benthic response of bioturbation (Norling et al., 2007). By continuously modifying the pore water/sediment matrix and altering the requisites for transport of particles and solutes, fauna has profound effects on mass transport and exchange of reactants between the sediment and the overlying bottom water.

There is a gap between transport models of bioturbation on one hand and experimental data on the other. Most models are either very general (e.g. the biodiffusion model, where biogenic transport is approximated as diffusive) or very specific, based on individual experiments on one species or a community). While the biodiffusion model might sufficiently describe bioturbation activities integrated over long time scales, it has proven difficult to assess biological transport by mathematical formulations on short time scales (Meysman et al., 2008a). In addition to the inherent difficulty of comparing macrofaunal transport between experiments due to site-specific properties, comparisons between reworking variables derived from different bioturbation models is often a challenging task. A general, but mechanistically correct model would unravel the need to better confine the solute and material transport by fauna in marine sediments. The concept of functional behaviour and functional groups of macrofauna based on transport of particles and solutes may pave the route for a better understanding of feedbacks between faunal activities and biogeochemical response in bioturbated environments. An improved understanding of the direct effects of bioturbation would also improve the knowledge on regulatory mechanisms of bioturbation (Maire et al., 2008; Meysman et al., 2006).

### **1.3. Aims**

The overriding aim of this thesis is to, by experimental procedures, describe and quantify feedbacks between biogeochemical responses (ecosystem functions) and bioturbation. In particular, efforts have been made to explore the feasibility of utilizing multivariate analysis to classify bioturbating fauna into functional groups based on a wide suite of proxies quantified from biogenic transport of particles and solutes. A general classification of bioturbating macrofauna, (specimens, species, and communities) based on proxies experimentally quantified from “transport functions” would improve the potential to predict the biogeochemical response from activities by benthic macrofauna.

In the first part of the thesis (Part A), sediment biogeochemistry is introduced with a brief overview of the coupling between structure and function of benthic systems, and macrofaunal reworking activities. In the second part (Part B), key hypotheses are tested by experimental procedures. In Paper I, the biogeochemical response from two species of bioturbating macrofauna with different reworking behaviour was investigated in highly reducing sediments. In Papers II- IV, the main focus was to experimentally quantify particle and solute transport by macrofauna. Studies included different species of macrofauna with a range in reworking patterns. Classification of fauna was made using a multi-proxy approach and multivariate analysis.

## 2. Early diagenesis in benthic ecosystems

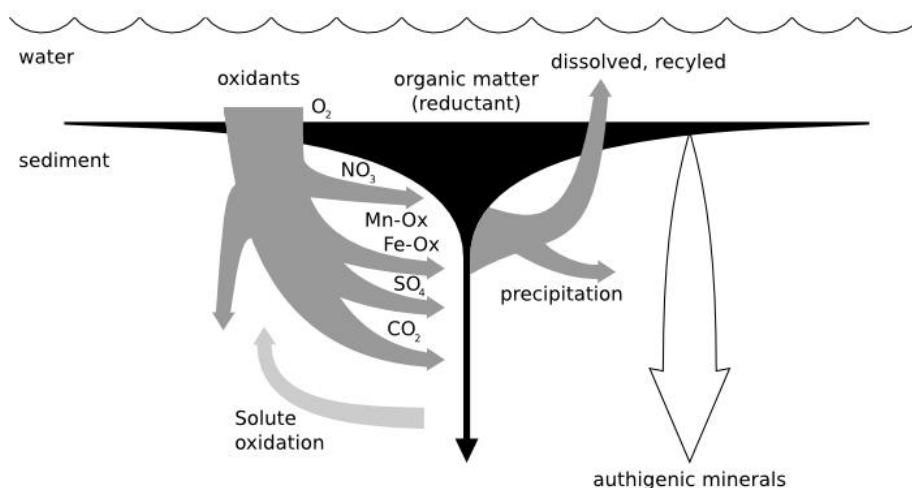
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### 2.1. Oxidation of organic material

As particulate matter settles through the water column, it is subjected to physical and biogeochemical processes that alter the size and chemical composition of the organic and inorganic material. These processes continue as the particles accumulate on the seafloor and eventually become buried (Figure 1). Particulate organic material reaching the sea floor will be subject to changes such as mineralisation, dissolution and geopolymerisation during its progressive burial into the deposit. *Diagenesis* refers to the sum of all changes that material undergoes once it reaches the seafloor and the successive burial into the sedimentary deposits at temperatures below 50 °C (Aller, 2014). This usually corresponds to a depth of a few hundred meters and a time span of a few thousand years. Most of these changes take place in the upper part of the sediment column, close to the sediment surface during *early diagenesis*. Some of the diagenetic changes lead to remobilisation of trace elements, nutrients and carbon. Thus, the balance between diagenesis and burial determines the degree to which the sediments act as a sink or source for any particular element.

Most chemical reactions in sediments during diagenesis are mediated by microorganisms as energy-yielding redox reactions driven by the oxidation of organic matter. Organic matter is a critical metabolic resource to heterotrophic benthic organisms. Dark benthic ecosystems (below the photic zone) generally rely on a supply of organic material from the overlying waters as energy source for metabolism. The organic matter in marine sediments is mainly derived from terrestrial, marine and anthropogenic sources and is carried to the oceans through numerous transport mechanisms. Besides continental shelves, which are deposits for terrestrial-derived material, most of the organic material reaching the sea floor is of marine origin, primarily from the photosynthetic fixation of carbon during primary production. Photosynthesis is responsible for most of the carbon fixation and hence organic matter production on this planet. Organic material transported to the sediment from the overlying water column is mainly agglutinated phytoplankton aggregates, fecal pellets and carcasses/detritus/dead organisms (Glud, 2008). As this "marine snow" sinks through the water mass, much of the particulate organic material will be decomposed by bacteria or consumed by higher trophic levels and thus recycled within the water column. The sinking process for particulate organic material can take hours, days or weeks depending on size, density and shape of the particles.

Heterotrophic microbes consume organic matter to fuel the respiratory metabolism that provides energy by redox reactions. Redox reactions involve oxidation and reduction reactions, where electrons are transferred between the oxidant (electron acceptors; e.g. O<sub>2</sub> or NO<sub>3</sub><sup>-</sup>) and the reductant (electron donors; e.g. organic matter), changing their respective oxidation state. Each reactant has a characteristic affinity for electrons and the greater the difference in electron affinity between the oxidising and reducing agents, the greater the free energy yield ( $\Delta G^{\circ}$ ) in the reaction. Due to its relative abundance and low electron affinity, organic matter is the most important reducing agent in the ocean. Oxygen is a molecule with



**Figure 1.** Schematic description of major diagenetic processes that associate with the remineralisation of organic matter. Modified from (Aller, 2004).

high electron affinity and is therefore an energetically favourable oxidising agent. Furthermore, the saturation concentration of oxygen in sea water is relatively high ( $\sim 250 \mu\text{M}$ ) compared to that of other potentially important oxidants. During oxygen respiration by microorganisms (bacteria and archaea), organic matter (represented by a carbohydrate in the reaction below) is oxidised by oxygen to carbon dioxide:



This reaction proceeds until oxygen has been consumed to drive the redox potential low enough to favour the next most energetically favourable redox reaction (Brewer et al., 2014; Froelich et al., 1979). For a more detailed description of potential reactions during the decomposition of organic matter see Table 1. Once  $\text{O}_2$  is depleted, nitrate will be utilized by nitrate reducing microorganisms. The main sources of nitrate in the sediment are the overlying water and nitrate produced by oxidation of ammonium (nitrification) – a terminal end product from mineralisation of organic matter. Nitrate is consecutively reduced in a stepwise fashion through a number of respiratory pathways to  $\text{N}_2$  or  $\text{N}_2\text{O}$ . The sum of these transformations is termed denitrification or nitrate/nitrite reduction. Denitrification is mediated by diverse groups of prokaryotes. This N-transformation pathway is considered a globally important sink for nitrogen since the reaction converts fixed, bioavailable nitrogen to nitrogen gas,  $\text{N}_2$ , thus removing nitrogen from the biological system. Because nitrogen is often considered limiting for phototrophs, denitrification may counteract effects of eutrophication.

With oxygen and nitrate depleted, the next most energetically favourable oxidising agent is manganese oxide, followed by iron oxides. Iron and manganese oxides are locally important electron acceptors, for example in the deepest trough of the north-eastern Skagerrak and in the deepest part of the Gullmar Fjord where 30-90 % of the carbon oxidation proceeded by metal oxide reduction (Canfield et al., 1993; Engström et al., 2005). Quantitatively, the second most important oxidising agent in marine sediments after oxygen is sulphate.

While oxic respiration dominates in deep-sea sediments, sulphate reduction is suggested as an equally important oxidant as oxygen in coastal sediments (Canfield et al., 1993). Shelf sediments cover an area of 8.6 % of the world's ocean, but  $\geq 90$  % of the oceanic sulphate reduction occurs in these areas. In coastal areas with low oxygen concentrations in the

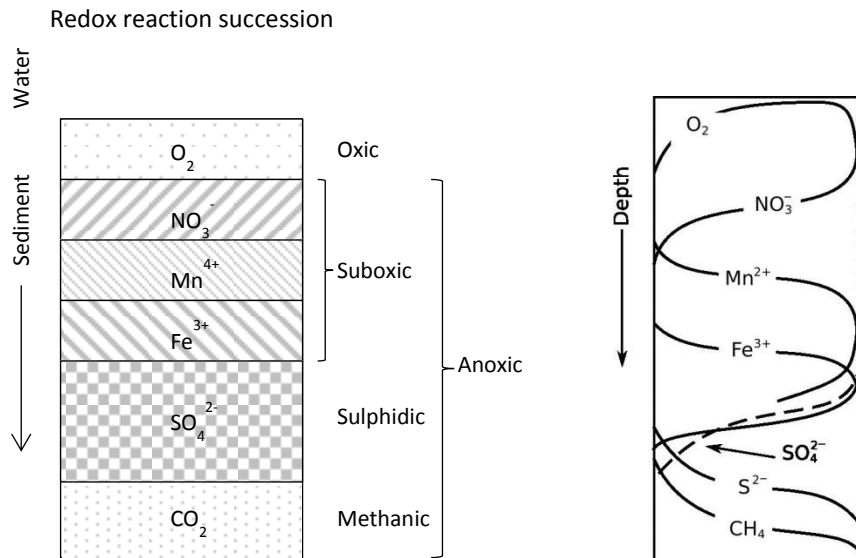
overlying sea water or with a high input of organic material, for example naturally stagnant fjords, bays or shallow waters affected by eutrophication, carbon oxidation proceeds mainly by sulphate reduction. An important consequence from sulphate reduction is the production of H<sub>2</sub>S, a gas extremely toxic for many species of benthic macrofauna as well as for humans. In sediments with oxygenated overlying water, H<sub>2</sub>S is quickly oxidized to elemental sulphur, thiosulphate or sulphate by various oxidants. To conclude the reaction sequence during early diagenesis, the least energetically favoured reaction is methanogenesis in which carbon dioxide is used for oxidant. Methanogenesis is normally not a quantitatively important reaction as sulphate concentration in sea waters is high (28 mM). Sulphate reducers inhibit methanogens by competing for common substrates and consequently it occurs mainly in very organically rich sediments, e.g. mussel and fish farms (Christensen et al., 2003; Jorgensen, 1982).

**Table 1.** Idealised stoichiometric reactions during organic matter oxidation. Organic matter is represented according to the Redfield ratios: 106:16:1 (C:N:P). Adapted from (Aller, 2014).

<i>Metabolic redox process</i>	<i>Overall reaction</i>
Aerobic respiration	$(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) + 138\text{O}_2 \rightarrow 106\text{CO}_2 + 122\text{H}_2\text{O} + 16\text{HNO}_3 + \text{H}_3\text{PO}_4$
Nitrate reduction	$5(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) + 424\text{NO}_3^- \rightarrow 106\text{CO}_2 + 318\text{H}_2\text{O} + 424\text{HCO}_3^- + 212\text{N}_2 + 80\text{NH}_3 + 5\text{H}_3\text{PO}_4$
Manganese reduction	$(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) + 212\text{MnO}_2(\text{s}) + 318\text{CO}_2 + 106\text{H}_2\text{O} + \rightarrow 212\text{Mn}^{2+} + 424\text{HCO}_3^- + 16\text{HNO}_3 + \text{H}_3\text{PO}_4$
Iron reduction	$(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) + 424\text{Fe}(\text{OH})_3 + 742\text{CO}_2 \rightarrow 424\text{Fe}^{2+} + 848\text{HCO}_3^- + 318\text{H}_2\text{O} + 16\text{HNO}_3 + \text{H}_3\text{PO}_4$
Sulphate reduction	$2(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) + 106\text{SO}_4^{2-} \rightarrow 106\text{H}_2\text{S} + 212\text{HCO}_3^- + 32\text{HNO}_3 + 2\text{H}_3\text{PO}_4$
Methane production	$(\text{CH}_2\text{O})_{106}(\text{NH}_3)_{16}(\text{H}_3\text{PO}_4) \rightarrow 53\text{CH}_4 + 53\text{CO}_2 + 16\text{HNO}_3 + \text{H}_3\text{PO}_4$

The thermodynamic difference in energy yield per mole carbon together with the competitive exclusion principle in ecology, suggests that carbon oxidation reactions occur in a succession (Aller, 1982). A zonation in successive dominating redox reactions is supported by the vertical distributions of reactants and reaction products with depth in marine sediments (Figure 2). The separation of redox zones is enhanced by the poisoning effect that some substances involved in one redox reaction have on enzymes of a competing process. For example, denitrification is usually inhibited both by oxygen and by H<sub>2</sub>S. Redox processes also tend to be separated in time and space due to the relative slow transport of solutes by diffusion. Molecular diffusion is the major mechanism by which solutes can be transported through the pore waters of sediments. As diffusive transport is often slower than the kinetics of chemical reactions, the attainment of redox equilibrium is controlled by diffusion. For further discussion on transport mechanisms in the sediment, see chapter 2.3.

Globally, including both deep sea and continental margins, oxygen is estimated to account for ~70% of the total organic matter oxidation in marine sediments (Emmerson and Hedges, 2003). Seawater may contain stronger oxidising agents than O<sub>2</sub> (e.g. H<sub>2</sub>O<sub>2</sub>), but these do not have a controlling influence on the redox chemistry of the ocean due to their relatively low concentrations. Occasionally, reactions may be controlled by reaction kinetics and slow rates of reactions. In comparison, nearly all reactions that involve O<sub>2</sub> proceed relatively rapidly as



**Figure 2.** Idealised, one-dimensional vertical zonation of major oxidants associated with organic matter mineralisation in marine sediments (left), modified from (Aller, 2014) and (Aller, 1982). Schematic vertical concentration distributions of key solutes during mineralisation of organic matter (right). Redrawn after (Bernier, 1980).

they are mediated by enzymes produced by a large variety of marine organisms. Without the catalytic effect of enzymes, many redox reactions would proceed at very slow rates. As organic carbon is buried, the easy degradable, labile fractions are preferentially consumed. Preferential mineralisation results in organic matter at depth to be more unreactive and refractory compared to the material originally deposited on the sediment surface (Middelburg, 1989). It has been shown that the labile fraction is mineralised equally fast in oxic as in anoxic regions (Hulthe et al., 1998). On the other hand, more refractory organic matter is mineralised faster by O<sub>2</sub> compared to by SO<sub>4</sub><sup>2-</sup> or NO<sub>3</sub><sup>-</sup> (Kristensen and Holmer, 2001). Oxygen in sediments is consumed both by heterotrophic O<sub>2</sub> respiration and by oxidising the reduced products of anaerobic organic carbon oxidation. These products include the reduced forms Mn<sup>2+</sup>, Fe<sup>2+</sup> and H<sub>2</sub>S as well as NH<sub>4</sub><sup>+</sup> liberated from organic matter during anaerobic oxidation. This reoxidation can, to a large extent, be attributed to O<sub>2</sub>, either directly or through a redox-cascade involving a series of complex abiotic and microbial catalyzed redox processes (Jorgensen, 1982).

If all reduced inorganic solutes from anaerobic mineralisation are fully oxidised within the sediment, the total benthic O<sub>2</sub> uptake represents a proxy of the total benthic carbon mineralisation. However, this approach disregards electron sinks like N<sub>2</sub> release from denitrification and the combined burial of Fe<sup>2+</sup> and sulphide as pyrite. Two processes that often are regarded as negligible and disregarded in budget calculations (Canfield et al., 1993; Jorgensen, 1982). Further, the approach does not account for the O<sub>2</sub> equivalents used for nitrification (Anderson and Sarmiento 1994).

In shallow-water environments where light reaches the sediment surface there is a potential for photosynthesis by benthic microalgae. These algae appear as a thin, brown layer and consist mainly of pennate diatoms. Through their production of oxygen and organic matter, they control important biogeochemical processes in the sediment (Dalsgaard, 2003; Sundback et al., 2000).

## 2.2. Transport of dissolved and particulate material

Diffusion is the net motion of matter resulting from the random motion of individual entities, e.g. ions or molecules (Berner, 1980). It is the net motion of matter driven by gradients in chemical potential. This random motion is sometimes called Brownian motion and is produced by collisions with other entities in the solution. The magnitude of diffusive transport in sediments ( $J_{\text{diff, sed}}$ ) is dependent on the sediment porosity ( $\Phi$ ), the whole sediment molecular diffusion coefficient for the compound ( $D_s$ ) and the concentration gradient ( $\delta C/\delta z$ ) according to Fick's first law of diffusion adapted to sediments (Berner, 1980):

$$J_{\text{diff, sed}} = -\phi D_s (\delta C/\delta z) \quad (2)$$

The whole sediment molecular diffusion coefficient has been empirically determined for sediments with a porosity  $> 0.7$  to be the molecular diffusion coefficient in free solution ( $D^0$ ) multiplied by the square of porosity,  $D_s = D^0 \times \Phi^2$  (Ullman and Aller, 1982). This diffusion coefficient is a constant for a given substance under a specific set of solution conditions (e.g. temperature, nature and concentration of the electrolyte). The negative sign in the equation means that when  $(\delta C/\delta z)$  is positive, the flux will be in the direction of decreasing concentration in order to eliminate concentration differences. There will be a larger degree of motion from high concentration to low than in the reverse direction, even though all molecules/ions have equal a priori probability of moving in either direction.

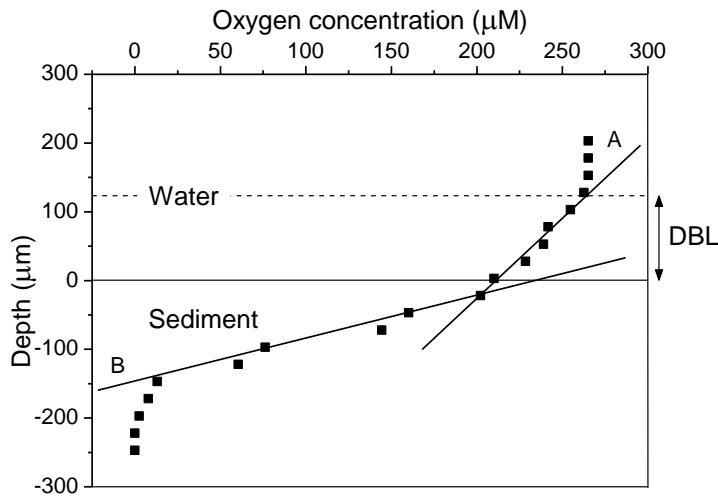
In liquids, molecules and ions continuously interact and their trajectories can be followed by random and erratic displacements. Within a time interval  $\Delta t$ , molecules will undergo various net displacements  $\Delta x$ , but the average of the square of their displacements has been found to be proportional to the time interval (Oxtoby and Nachtrieb, 1986):

$$\overline{(\Delta x)^2} = 6 \times D^0 \times \Delta t \quad (3)$$

Diffusion is thus an effective mechanism for motions over small distances, but the dependence of  $\Delta t$  makes the process slow for long distances. It is therefore most likely that mechanisms more efficient than molecular diffusion are required for the rapid transport of solutes over long distances in the sediment.

Diffusive fluxes ( $J_{\text{diff}}$ ) of e.g. silicate and oxygen can, together with benthic fluxes quantified during enclosed sediment-water incubations ( $J_{\text{tot}}$ ), be used to determine which transport mechanisms that govern solute fluxes across the sediment-water interface in benthic environments (Hulth et al., 1994). A  $J_{\text{tot}}/J_{\text{diff}}$  ratio  $> 1$  indicates that activities by benthic macrofauna may be important for solute transport. However, due to an irregular topography of the sediment surface, one dimensional diffusion models of solute fluxes (e.g. Fick's first law of diffusion, eq. 3) may severely underestimate rates of benthic fluxes (Gundersen and Jorgensen, 1990). Bioirrigation and/or potential artifacts in geometry when assuming a one-dimensional diffusive transport, may underestimate total solute fluxes several-fold (Rasmussen and Jorgensen, 1992). Water flow over the sediment surface will decrease in velocity closer to the surface. In a thin water layer, typically 0.5-1.0 mm, over the sediment surface, the main transport process for solutes is diffusion. This layer is termed the diffusive boundary layer (DBL), see figure 3.





**Figure 3.** Oxygen concentration measured in the pore water of a control core from Paper I. The upper limit for the diffusive boundary layer (DBL) is indicated with a dashed line, while the lower limit (the sediment surface) is drawn as a solid line. Linear regression depicts the area of diffusion-dominated transport in the water (A) and in the sediment (B). Oxygen flux can then be calculated from either of these by using Fick's first law.

Interdependable reaction and transport processes form the diagenetic processes where solutes and solids are produced or consumed within sediments. The main diagenetic change occurs vertically with sediment depth due to gravity forces acting upon the deposited organic material. As a consequence, diagenetic models are often conceptualised with depth as the only dimension.

The mass balance diagenetic equation in sediments explains vertical concentration patterns by reaction- and transport processes (Berner, 1980; Boudreau, 1997):

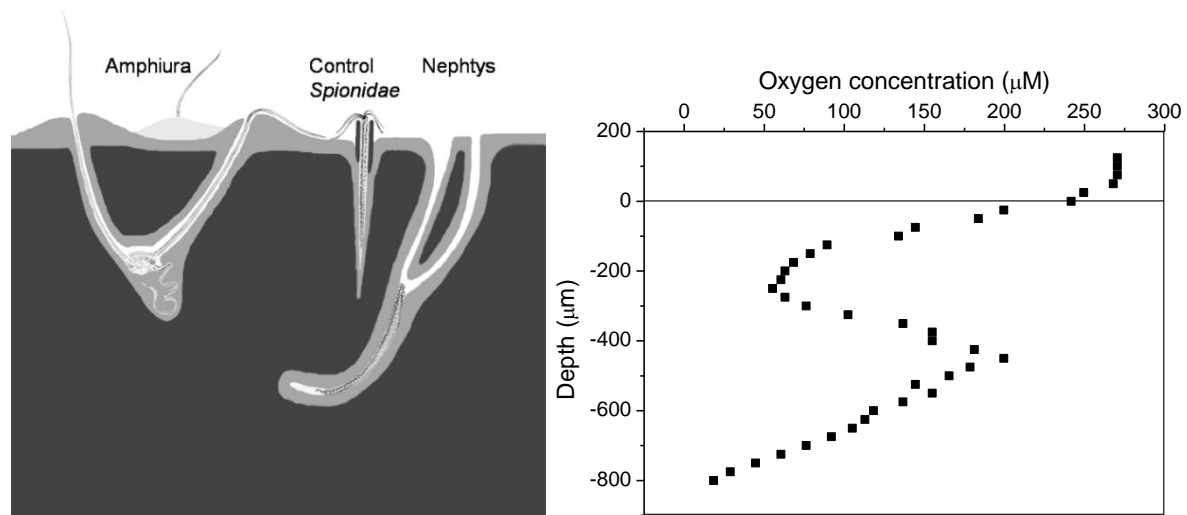
$$\frac{\partial(\phi C)}{\partial t} = \frac{\partial}{\partial z} (\phi D_s \times \frac{\partial C}{\partial z}) + \frac{\partial(v\phi C)}{\partial z} + \Sigma \phi R_i \quad (4)$$

*Diffusion          Advection          Reaction*

where  $C$  is solute concentration in pore water,  $t$  is time,  $z$  is sediment depth,  $\phi$  is porosity,  $D_s$  is the whole sediment molecular diffusion coefficient empirically corrected for the longer path of diffusion to circumvent particles in porous media,  $v$  is pore water advection or sedimentation rate and  $\Sigma R_i$  is the sum over all reactions affecting the solute. Solutions to this equation can then be used to describe and predict the distributions of a solute with time and depth (Aller, 2001).

Solute in the pore water may be transported by e.g. molecular diffusion or advection due to burial and compaction, or particle reworking and irrigation activities by benthic macrofauna. Similarly, particles may be relocated by advection due to burial, compaction or biological activity by bioturbation and by physical mixing caused by waves and currents (Jorgensen and Boudreau, 2001). Advection is a transport mechanism with a bulk motion of the fluid. For example, an upward advective flow of pore water occurs due to the increased weight of settling particles on the sea floor. Compaction causes the water content and porosity to decrease with depth as water is squeezed out. In permeable sediments, such as sands, pressure

gradients can impose an advective fluid transport (Timmermann et al., 2006). In this thesis, only low-permeable, consolidated mud- and silty sediments have been investigated, and the major transport mechanisms within the sediment are due to molecular diffusion and advective transport caused by faunal activities.

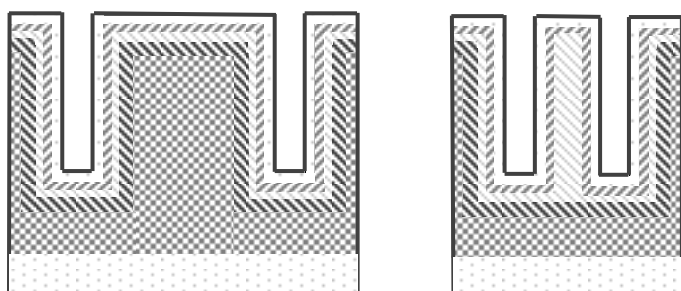


**Figure 4.** Schematic illustration of general bioturbation patterns of *A. filiformis*, *M. fuliginosus* and *Nephtys* sp. in Paper I (left). Note how irrigation activities by the fauna oxygenates burrow walls and tube linings, changing the oxygen distribution in the sediment. (B) An example of how oxygen distributions in the pore water may be affected by bioturbation activities (right). This was measured in an *Amphiura filiformis* core from Paper I. Note the short depth scale.

### 2.3. The influence of benthic macrofauna on early diagenesis

Bioturbation by benthic macrofauna is a major determinant of the physical, chemical and biological properties of the sediment in bioturbated deposits (Aller, 1982; Lohrer et al., 2004; Rhoads, 1974) and a comprehensive account of its feedbacks to the mineralisation of organic matter can not be covered in this chapter. Instead, some important functions of fauna will be highlighted, starting by their transport of material which structures many ecosystem functions in benthic environments.

Particles may be translocated both within the sediment (particle reworking), and into the overlying water (resuspension). Particle reworking can be so efficient that it more or less completely homogenises the upper sediment layers. Transport of solutes across the sediment-water interface may be attributed both to a diffusive flux along concentration gradients and proceed as a consequence of irrigation when benthic macrofauna flush burrows with overlying water for respiratory and feeding purposes (ventilation, Figure 4). In addition to the advective flux induced during burrow ventilation, the diffusive transport is simultaneously increased by sustaining gradients of reactants and products in the pore water immediately adjacent to burrows. The diffusive transport is also positively affected by the increase of interface area between water and sediment open for diffusive exchange (Fenchel, 1996; Kristensen, 2000).



**Figure 5.** Idealised, vertical zonation of major oxidants associated with organic matter mineralisation around ventilated burrow microenvironments in marine sediments, modified from (Aller, 2014) and (Aller, 1982). Redox layers are depicted by different patterns, compare figure 2. Abundance of benthic macrofauna will be important for the overall structure of redox zones, the effect of sparsely (left) and densely (right) populated sediments is displayed here.

Of particular importance is the relocation of solutes and particles that would not have occurred in defaunated sediments. Besides the introduction of oxygen and other oxidants to deep, anoxic layers, sediment mixing relocates newly settled, labile organic material and metal oxides downward into deeper, more reduced layers thereby changing metabolic pathways and rates for mineralisation of organic matter (Aller, 1990). In fact, high rates of Mn and Fe reduction can only be sustained if metal oxides are supplied to the zone of reduction by particle mixing (Thamdrup, 2000). In the absence of physical reworking such as waves or currents, bioturbation is commonly the main transport mechanism. The influence of benthic macrofauna on Mn and Fe cycling is therefore dependent on the ability of macrofauna to transport sediment into deeper sediment layers.

Bioturbated sediments are dynamic systems, continuously mixed during foraging, feeding and burrow maintenance activities by benthic macrofauna. In addition, burrows systems are subject to intermittent flushing of oxygenated water during ventilating (Forster and Graf, 1995). Burrows represent oxygenated microzones in the sediment and burrow walls are characterized by sharp gradients of reactants and products from organic carbon oxidation (Figure 5). The ventilation by fauna results in intermittent oxygenation and time-dependent redox oscillations in particular close to burrow walls.

### 3. Experimental methodology

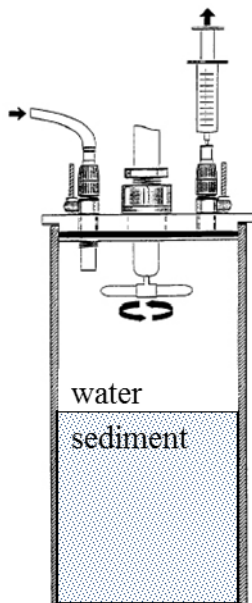
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#### 3.1. Experimental approach

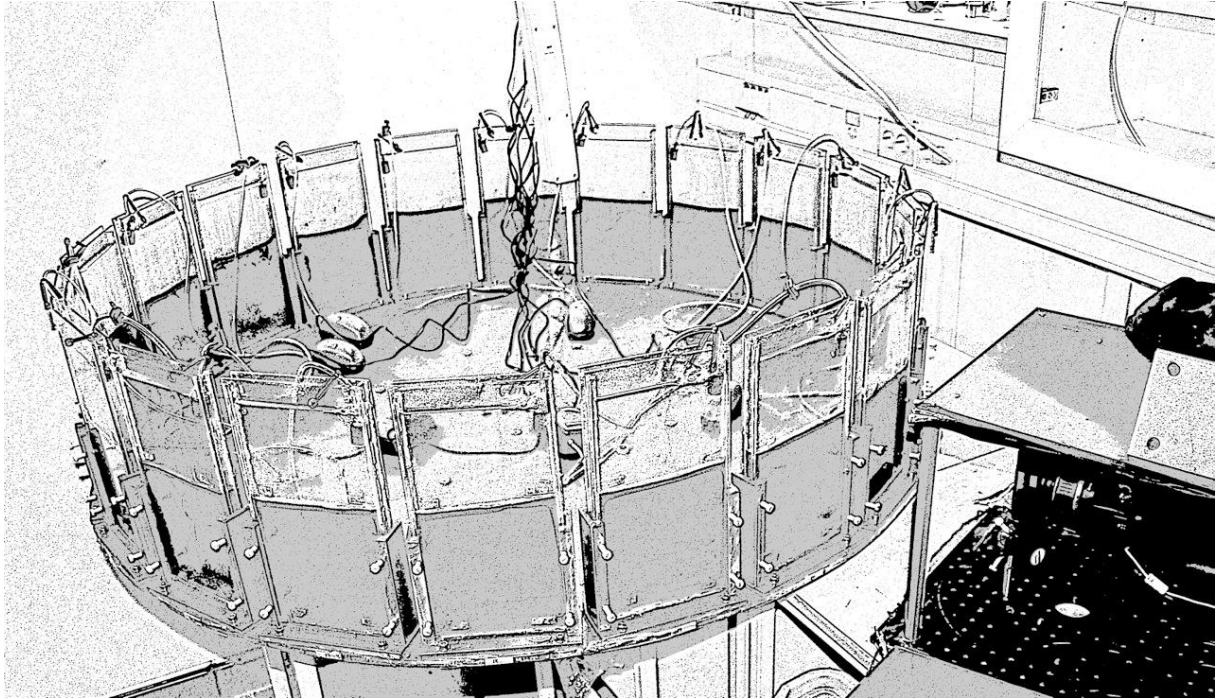
In this thesis, effects of bioturbation on biogeochemical processes and transport of solutes and particles have been investigated under controlled laboratory conditions at the Sven Lovén Research station at Kristineberg, on the west coast of Sweden. Experiments have also been performed at the Department of Chemistry and Molecular Biology in Gothenburg.

Plexiglass core tubes and thin glass aquaria filled with sediment and sea water were used as experimental microcosms. While cores were used for quantification of biogeochemical variables (e.g. transport of solutes and particles across the sediment-water interface and within the sediment, Figure 6), glass aquaria were used for quantification of particle reworking by means of side-view imaging of fluorescent tracers over time (Figure 7).

Benthic solute fluxes were measured by sediment-water incubations. By enclosing a known volume of sediment and overlying seawater to prevent exchange with the surrounding environment, concentration changes in the overlying water can be evaluated over time. Concentration changes are detected either by removing discrete water samples from the overlying water, or by applying continuous measurements of the overlying water using e.g. an oxygen microsensor (Clark-type electrode or optode).



**Figure 6.** Cross-section of the Plexiglass cores used during experiment with benthic flux measurement for Papers I, II and IV. Samples of overlying water are drawn through valves in the lid, while simultaneously adding replacement water. Stirring is obtained by a rotating Teflon coated magnetic stirring bar. Republished with permission (Hulth et al., 1997).



**Figure 7.** Experimental set-up for side-view imaging of particle reworking for Paper III. Fluorescently labelled particles were added to the sediment surface and images acquired from the optical set-up (LED light source, CCD-camera (CMOS image sensor) with a bandpass filter) Aquaria were individually positioned in a custom-built high precision rotation stage with a 24 sample cell turret. Image acquisition was controlled from an adjacent laboratory.

### **3.2. Functionality of species investigated**

Bioturbation activities by ten species of benthic macrofauna have been investigated during this work (Table 2). They belong to different Phyla and have previously been assigned to different functional groups in terms of feeding strategy, mobility and reworking behaviour. They also have several traits in common, e.g. all species are common at relatively high densities in the Skagerrak and the Kattegatt and they have a high reworking or ventilation potential (Gilbert et al., 2007; Hakonen et al., 2010; Rosenberg et al., 2002). As far as was practically possible, the species chosen were of a similar size range to facilitate inter-species comparisons (Figure 8).

More detailed descriptions of species behaviour can be found in respective papers.

**Table 2.** Functional behaviour in terms food resource exploited, mobility and reworking mode of the species investigated during this work.

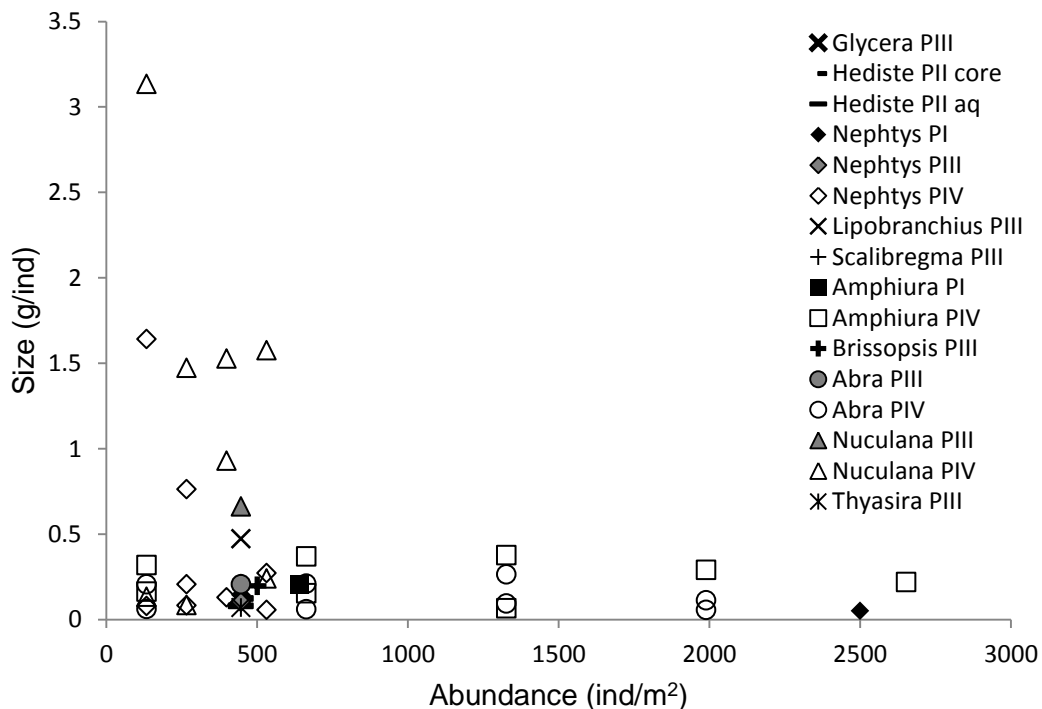
<b>Species</b>	<b>Feeding mode</b>	<b>Mobility</b>	<b>Reworking behaviour</b>	<b>References</b>
Annelida				
<i>Glycera alba</i>	Predator	Mobile	Gallery of burrows	1
<i>Hediste diversicolor</i>	Predator/Suspension/Deposit	Mobile	Gallery of burrows; Gallery diffusor	1,2
<i>Nephtys incisa</i>	Subsurface deposit/Predator	Mobile	Transient burrows; Biodiffuser	1,3,12
<i>Lipobranichius jeffreysii</i>	*Surface/subsurface deposit	*Mobile	*Gallery of burrows	
<i>Scalibregma inflatum</i>	Surface/subsurface deposit	Mobile	Gallery of burrows; Gallery diffusor	1,4
Echinodermata				
<i>Amphiura filiformis</i>	Suspension/Surface deposit	Semi-mobile	Biodiffuser/ Upward conveyor/ Gallery diffusor	4,5,6,7
<i>Brissopsis lyrifera</i>	Subsurface deposit	Mobile	Bulldozer/ Biodiffuser	5,8
Mollusca				
<i>Abra nitida</i>	Surface deposit/Suspension	Variable	Biodiffuser	4,9
<i>Nuculana pernula</i>	Subsurface deposit	Semi-mobile	Biodiffuser	10
<i>Thyasira sarsi</i>	Symbiotic	Semi-mobile	Burrows	11

1. (Fauchald and Jumars, 1979) 2. (François et al., 2002) 3. (Sanders, 1960) 4. (Gilbert et al., 2007) 5. (Duchene and Rosenberg, 2001) 6. (Buchanan, 1964) 7. (Lindqvist et al., 2009) 8. (Queiros et al., 2013) 9. (Wikander, 1980) 10. Paper III 11. (Dufour and Felbeck, 2003) 12. (Braeckman et al., 2010) \*No records of *Lipobranichius jeffreysii* found in the literature, groupings are according to *Scalibregma inflatum*, due to their close family relations and our observations (Paper III).

Efforts have been made to define functions related to particle reworking and solute irrigation by macrofauna of importance for element cycling and general ecology of the investigated sediments. Commonly, fauna have been classified based on properties or behaviour of the fauna itself such as feeding behaviour, mobility, and burrowing and ventilation activities (Fauchald and Jumars, 1979; Kristensen et al., 2012; Pearson, 2001). In an approach to classify fauna due to the potential and patterns of particle mixing, a classification has been suggested including the following functional groups; biodiffusers, upward-conveyors, downward-conveyors, re-generators (Boudreau, 1986a; Boudreau, 1986b; Francois et al., 1997; Francois et al., 2001; Gardner et al., 1987) (Figure 9). Some of the species investigated have previously been classified according to this approach (Table 2).

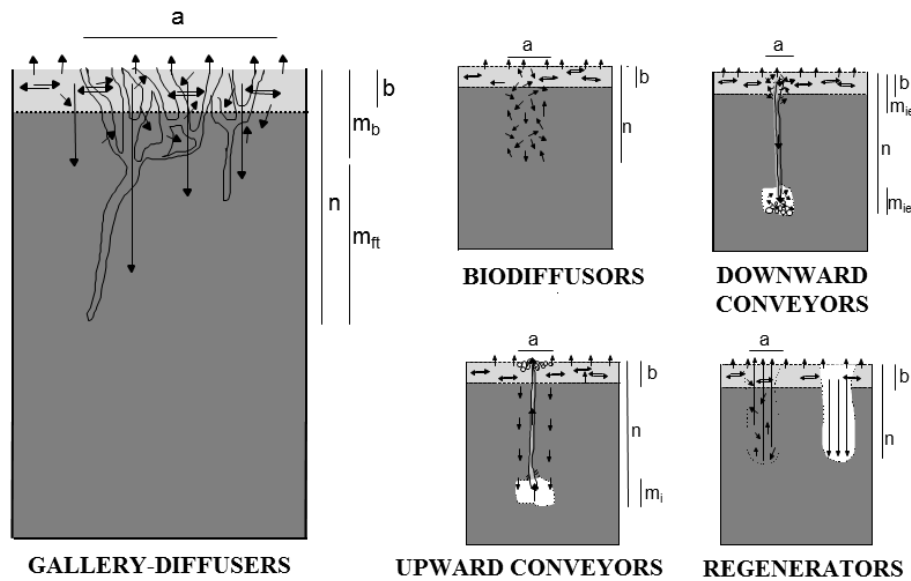
An important objective of this thesis was to quantify reworking behaviour and irrigation activities by macrofauna and use these experimentally derived proxies for particle and solute transport for functional classification of fauna. During experimental procedures, short-term incubations and side-view imaging or manual counting of luminophores in discrete sediment layers following deposition on the sediment surface have been used for evaluating particle transport into the sediment. The gallery-diffusor model was used to describe modes and

patterns of particle transport during all experiments in order to compare the species investigated. In this model, both diffusive- and advective-like transport are included and reworking proxies for these two modes of transport mechanisms can be approximated. The ability to describe both of these transport mechanisms was important due to the different reworking modes of the investigated species. The biodiffusion coefficient ( $Db$ ) and the non-local transport coefficient ( $r$ ) were calculated by minimising a weighted sum of squared differences between the observed and modelled tracer concentrations with depth in the sediment. (Francois et al., 1997; François et al., 2002).



**Figure 8.** Abundance and size of all faunal treatments for Paper I-IV. Some species recurs in several studies; *Nephtys incisa*/sp., *Amphiura filiformis*, *Abra alba*, *Nuculana pernula*.





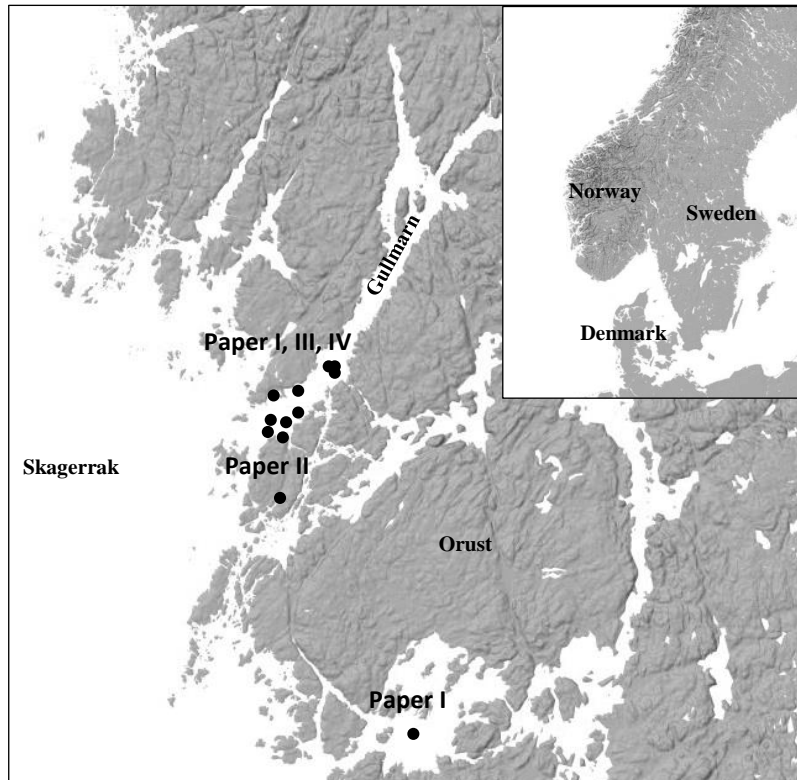
**Figure 9.** Schematic description of the physical and biological reworking mechanisms of the gallery-diffusers, biodiffusers, the downward-conveyors, the upward-conveyors and the regenerators. The letters indicate parameters used in the model. Arrows represent movement of sediment particles. Modified from (Francois et al., 2001).

Three main patterns of feeding behaviour were represented during experiments presented in this thesis. While the feeding behaviour was not a direct source for characterization and classification based on particle reworking, there were some implications worth highlighting. Suspension feeders actively or passively entrap suspended particles in the overlying water, thereby introducing organic matter into the sediment (Middelburg and Soetaert, 2004; Rhoads, 1974). The suspension feeder *A. filiformis* significantly influenced resuspension of the sediment surface and the concentration of particles in the overlying water (Paper IV). Interestingly, there seemed to be different mechanisms that controlled the net supply of particles to the overlying water depending on the applied mixing rate of the water (high or low stirring rate).

Although *N. incisa* is described as a deposit feeder in the literature (Sanders, 1960), it has also been described as a predator (Fauchald and Jumars, 1979) with direct implications for the oxygen penetration observed in Paper I and patterns of (surface) particle reworking demonstrated in Paper II. In Paper I, the depth of oxygen penetration decreased compared to both the control and to the *A. filiformis* treatment. This was suggested to be attributed to predation of small tube-building worms that were present in all treatments from start but disappeared due to predation in the *N. incisa*-treated cores. Similar patterns of predation by *N. incisa* were observed in Paper IV, where removal of surface luminophores was smaller and less variable in the *N. incisa* cores, compared to the control cores.

### 3.3. Study area

Sediment and fauna were sampled in the Skagerrak archipelago on the Swedish west coast (Figure 10). Most of the fauna and the sediment was collected from the Gullmar Fjord. During the work with sediments from beneath a mussel farm (Paper I), sediments were collected in Stigfjorden and for the work with *Hediste diversicolor* (Paper II), fauna and sediment were collected from a shallow site in the bay Rågårdsvik.

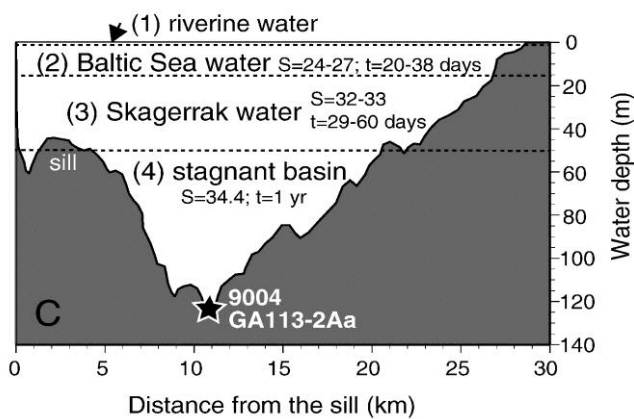


**Figure 10.** Map of the sampling sites on the Swedish west coast in the Skagerrak archipelago.

The Skagerrak is a continental margin sea in the north-eastern part of the North Sea. It has topographic characteristics similar to a large fjord with a sill depth of about 270 m. Maximum depth is 700 m. The water transported northward along the Swedish west coast originates from near-ocean salinity North Sea water, mixed with medium-salinity waters (~15-18) from the Baltic Sea and with riverine water from Sweden and Norway.

The land area in the Skagerrak archipelago is characterized by agriculture, rocks and patches of forest. The marine area consists of shallow bays and stratified fjords with bottom substrate characterised by rocky- and soft-bottom substrata depending on exposure and water exchange. The archipelago is influenced by gradients of lower salinity in shallow water from estuaries, shallow bays and fjords, and close to oceanic salinities in the outermost islands in the north and in the deep waters. The area is micro-tidal with an average tidal amplitude of 20-30 cm. During summer, shallow (0-1 m) coastal water salinity typically fluctuates between 14 and 24 (Pihl and Rosenberg, 1982). The water temperature ranges from 5 to 14 °C in spring and autumn and from 14 to 20 °C during summer. Occasionally, the temperature in the shallow bays reaches 30 °C.

Sampling of benthic macrofauna (PI, III and IV) and sediment (PIII, IV) was mainly performed in the Gullmar Fjord. It is a fjord with a sill depth of approximately 40 m and a maximum depth at the centre of the deep basin of 118 m. The fjord is 30 km in length and has a water volume of 2.05 km<sup>3</sup>. The water in the fjord is highly stratified with three distinct water masses (Figure 11). The surface water has a varying salinity and is a mixture of local riverine water, Baltic Sea water and Kattegatt/Skagerrak water. The intermediate water mass is dominated by surface water from the Skagerrak. The deep water mass below ~50 m of water depth has higher salinity (34 - 35) and is derived from the North Sea. The mean surface water residence time is 16-26 days for the water above the halocline (Arneborg, 2004), while the bottom water is renewed once a year during late winter or early spring. The salinity and temperature in the deep parts of the fjord corresponds to conditions at 200-300 m depth outside of the fjord with fairly constant temperatures of 5-6.5 °C throughout the year. Therefore, species of macrofauna that normally live in the deep Skagerrak are also observed in the Gullmar Fjord. The spring bloom normally occurs in late February or March and is largely dominated by diatoms, while the phytoplankton bloom during summer and autumn is generally dominated by dinoflagellates. The annual production ranges roughly between 180 and 230 g C m<sup>-2</sup> y<sup>-1</sup> (Lindahl, 1987).



**Figure 11.** Stratification of the Gullmar Fjord's water masses with salinity ranges and residence times. Republished with permission (Harland et al., 2013).

## 4. Quantification of bioturbation

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### 4.1. Multi-proxy approach

A general idea born and developed during this project is that activities by macrofauna and their significance for different biogeochemical processes in sediments are too complex to be explained by only one or two proxies for bioturbation. This idea is still in its infancy, but preliminary results indicate that a general and repeatable characterization and classification can be achieved by evaluating faunal reworking by multiple proxies and multivariate analysis. Similar patterns and groups in the data set are found from the multivariate models when based on proxies from independent methodologies such as particle reworking by imaging, or multiple transport processes during sediment-water incubations (Paper III and IV).

### 4.2. Particle reworking and ventilation

Net effects of particle reworking by macrobenthic communities are usually evaluated from vertical distributions of a particle-associated tracer. Common tracers for particle transport are either artificial (e.g. sediment grains coated with fluorescent dye - luminophores) or natural radioisotopes (e.g.  $^{210}\text{Pb}$  or  $^{234}\text{Th}$ ) (Maire et al., 2008). Natural radioisotopes are usually used for evaluating long-term particle mixing *in situ* while artificial tracers such as luminophores are normally used in short-term experiments. Fluorescently labelled particles have been widely used during the past 15-20 years for short-term *in situ* and *in vitro* experiments on bioturbation by benthic macrofauna e.g. (Gerino et al., 1994; Gerino et al., 1998; Mahaut and Graf, 1987). They were initially used for the ease of quantification in sediments due to their fluorescent properties. These properties were taken advantage of in the development of a technique for quantification by side-view imaging, thereby quantifying sediment transport in 2-D (Gilbert et al., 2003). Imaging also facilitated a high spatial ( $\mu\text{m}$  scale) and temporal (seconds to minutes) resolution in observation patterns. A number of experiments have been conducted using concepts originating from the fluorescence imaging approach (Maire et al., 2006; Piot et al., 2008; Schiffers et al., 2011), and the technique has also been adapted to *in situ* experiments (Solan et al., 2004b). The main potential disadvantage with the use of luminophores as tracers of biogenic transport concerns their ability to mimic naturally occurring sediment particles. Luminophores are sediment particles without a natural organic coating (biofilm) when introduced to the sediment system. Further, they are covered by a fluorescent dye and the effects of introducing artificial compared to indigenous particles on the selection by fauna for feeding and ingestion are not well known. Transport proxies obtained from the use of luminophores therefore represent a potential for the reworking of particles. Because some species of fauna are known to select particles with high organic content luminophores might be disregarded (Shull, 2001). Such effects would cause an underestimation in the transport of newly settled, organic-rich particles. Other species may preferentially select size-classes of particles. Such potential artifacts may be minimized by introducing a range of size classes during addition of luminophores.

Reworking proxies for particle transport by fauna are frequently quantified by fitting a reaction-transport model to the vertical distribution of the tracer obtained from experimental protocols. There are several models for quantification of particle reworking and the by far most frequently used models consider transport of particles by benthic macrofauna in diffusion-like manners (Meysman et al., 2010). Combining the conservation of mass and

Fick's first law of diffusion (Equation 2), a biodiffusion coefficient ( $D_b$ ) can be calculated in analogy to the molecular diffusion coefficient in solution (Boudreau, 1986b; Goldberg and Koide, 1962; Guinasso and Schink, 1975). There are models for particle reworking that also include transport by advection and account for biological transport of particles in a non-diffusive manner. Transport by fauna in a non-diffusive manner, for example by vertical translocation of substances over long distances is referred to as non-local transport, or anomalous reworking e.g. (Fisher et al., 1980; Meysman et al., 2010; Smith et al., 1986).

During the past years, significant efforts of the scientific community focused on bioturbation have been devoted to improve existing models for bioturbation. One of these approaches include the random walk model (Meysman et al., 2008b; Wheatcroft et al., 1990), which is based on the concept of random walk and Brownian motion. While Fick's first law describes bulk diffusion along concentration gradients, the random walk is conceptually analogous to molecular diffusion by individual atoms, molecules or ions. The transport of particles can be described by the waiting time, the jump length and the jump angle. By using the high temporal resolution achieved by fluorescence imaging, and a random walk approach, the reworking by *Hediste diversicolor* has been described (Schiffers et al., 2011).

While these models are theoretical in their approach to particle and solute transport by macrofauna, others have focused on an empirical approach. Activities associated with mobility and sediment particle reworking have been defined and given a score 0 – 4. Faunal species are then assigned to these groups and a Community bioturbation potential ( $BP_c$ ) can be calculated from the scores and the biomass of each species (Queiros et al., 2013; Solan et al., 2004a; Swift, 1993). This scheme allows for comparison of the total bioturbatory potential between different benthic communities.

Due to the diverse suite of methodologies to qualitatively and quantitatively describe particle reworking and solute ventilation, with new models continuously emerging and replacing older ones, it is a challenge to compare the output from models between different studies. For example, it is not straight-forward to compare  $D_b$  between the biodiffusor model (Francois et al., 1997) and the gallery-diffusor model (François et al., 2002). It is possible, though, to compare data that found the model (e.g. the horizontal and vertical distributions of tracers). In Paper III and Paper IV, observations support a close relation between  $D_b$ ,  $r$  and the fraction of luminophores buried beneath a shallow surface (0.5 or 1 cm) and a deeper (e.g. 2 cm) sediment layer. Presentation of rawdata provides a means for comparisons between experimentally derived transport proxies. Additionally, both the distribution of traces and proxies derived from bioturbation models depend on the duration of the tracer incubation.

The activities by benthic macrofauna are focused to the upper ~10-50 cm of deposits but may extend several meters into the seabed (Aller, 2014). Depth of reworking by fauna can provide important information as it relates to the vertical transportation of particles, overlying bottom water and pore water across redox zones. Depth and distribution of burrow constructions as well as the maximum depth of tracer penetration constitute bioturbation proxies that couple to both particle reworking and burrow ventilation. They are both readily quantified with high temporal and spatial resolution and are therefore possible to compare between experiments.

The imaging approach and experimental protocols to quantify reworking proxies from imaging of fluorescently labelled particles were significantly improved by the introduction of the Optical Reworking Coefficient (ORC) (Gilbert et al., 2003). Concepts of ORC were further developed during this work (Paper II and III) which resulted in three additional

reworking proxies derived from imaging of luminophore distributions. The basic concept was similar, i.e. the binary image of the luminophore distribution imaged over an aquaria side obtained at time  $t$  ( $\mathbf{M}_t$ ) was subtracted from the binary image at an earlier time. ( $\mathbf{M}_x$ ). The sum of the resulting matrix  $\mathbf{M}$  therefore described the total relocation of luminophores in the sediment.

The reworking proxy *2-D redistribution* was calculated from an image ( $\mathbf{M}_t$ ), subtracted by the image at the start of experiments ( $\mathbf{M}_0$ ). This follows the rationale of the ORC closely. Another reworking proxy, the *daily particle transport* was calculated from an image ( $\mathbf{M}_t$ ), subtracted by the image captured the previous day ( $\mathbf{M}_{t-24\text{ h}}$ ). The *transport rate* was then calculated from the sum of the daily transport divided by the number of experimental days.

In addition to the modifications of the ORC mentioned above, no further modelling was performed and results were directly presented as a function of incubation time. Further, in contrast to the ORC, absolute values of pixels ( $|X|$ ) were summed and results were not normalised for time.

The main advantage of the fluorescence approach is that reworking activities can be highly resolved in time by a non-destructive technique. The high spatial resolution, only limited by the capacity of the camera adds to the attraction. These positive properties of the technique could be utilized in a number of ways. One example is to further investigate the indication that *H. diversicolor*, and many other shallow-living species have a light-dependent reworking behaviour (Karlson, 2007; Rosenberg and Lundberg, 2004) and Paper II. The verification and increased temporal and spatial resolution of this behaviour is easily quantified by frequent imaging and subsequent quantification of bioturbation proxies.

There are some drawbacks with the imaging technique. For example, there are indications that imaging underestimates the reworking by benthic macrofauna in thin aquaria (Norling, 2007; Solan et al., 2004b) and Paper II. This potential artifact could relate to the 3D-structures created by the fauna, not necessarily represented by imaging of one side of the aquaria. Relatively few investigations have compared reworking proxies derived from imaging with proxies from the sectioning technique. While a study of *Abra nitida* and *Abra alba* achieved similar results comparing the two techniques (Maire et al., 2006), to my knowledge the other two studies exploring imaging and sectioning simultaneously suggest a significant difference between the techniques (Norling, 2007) and Paper II.

Based on the findings during the work with this thesis, I would recommend the following in performing experimental bioturbation studies:

- Quantify bulk transport of the material in question (solutes, particles) combined with a depth measure, and if possible, a “time-variable” that quantifies the variation of response with time.
- Biomass, abundance and size should be used cautiously for normalisation between species. Experimental designs with relevant abundances and sizes of the respective species of benthic macrofauna reveal more information and results from those are more readily applied to natural situations.
- Use imaging with caution for studies with major 3D variation. However, it is a suitable tool for time-resolved research questions.

## 5. Conclusions and Outlook

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### 5.1. Main conclusions

- In highly reduced sediments, the brittle star *Amphiura filiformis* generally enhanced bioadvective solute transport in contrast to the polychaete *Nephtys* sp. that restricted the oxic zone and benthic nitrate and silicate fluxes .
- The polychaete *Hediste diversicolor*, found in shallow sediments, had an increased particle reworking activity during a light- and dark cycle compared to in constant darkness.
- How good explanatory variables (e.g. biomass or abundance) correlate with the transport proxies (e.g. Db or maximum tracer depth) depends on the transport process in question.
- The correlation between measured transport proxies and explanatory variables (biomass, abundance, size) was highly species-dependent.
- Quantification of multiple bioturbation proxies in combination with multivariate analysis is a viable means of qualitative functional classification of benthic macrofauna.
- Three broad groups of bioturbators emerge from quantification of reworking proxies; the surface reworkers, the deep reworkers and the major reworkers. This classification seems to be independent of evaluation technique (particle reworking by imaging or multiple transport processes in cores).

## 5.2. Outlook

This work has largely focused on particle transport by benthic macrofauna. During the work, a promising method for general classification of fauna was explored, i.e. the quantification of multiple bioturbation proxies and subsequent multivariate analysis in order to classify and compare fauna. This concept is versatile and can be used for various research aims. For example, the next natural step would be to explore the ventilation and bioirrigation behaviour of fauna.

Further, the method can be readily adapted to explore bioturbation effects from multi-species investigations or community comparisons. The main, evasive aim of this work was to explore feedbacks between biogeochemical responses and bioturbation. By using the functional groups of fauna described in this work, attention could be turned to questions regarding benthic community effects on element cycling in benthic systems.

Quantification of reworking in 2D by imaging fluorescent tracers is a technique with potential for research questions regarding bioturbation activities with high resolution in time.

Finally, the knowledge about transport by benthic macrofauna presented here derives from empirical experiments. To do full justice of the data, this information should be incorporated into models to further generalise conclusions and to improve future experiments.



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