Program Conference: "Bioturbation: An update on Darwin's last idea"

Linking bioturbation, biogeochemistry, and biodiversity

23 -27 August 2008 Renesse (The Netherlands)

SATURDAY 23 August 2008	
13:00 - 17:00	Arrival and Check-in
17:00 - 18:00	*Ice Breaker reception*
18:00 - 20:00	*Dinner*
20:00 - 20:30	Welcome: **Filip Meysman** (Vrije Universiteit Brussel) "BIOTURBATION: AN UPDATE ON DARWIN'S LAST IDEA"
20:30 - 21:30	Keynote Lecture: **Bob Aller** (Stony Brook University) "STRUCTURE AND BIOGEOCHEMICAL FUNCTION IN THE BIOTURBATED ZONE"
21:30 -	*Bar time*

SUNDAY 24 August 2008	
07:30 - 08:30	*Breakfast*
	Session A: The impact of bioturbation from local to global scales
	Discussion Leader: Stefan Hulth (Göteborg University)
09:00 - 09:45	Invited: **Gerald Matisoff** (Case Western Reserve University) "FRESHWATER BIOTURBATION: WHAT DO WE KNOW AND WHAT DO WE NEED TO KNOW?"
09:45 - 10:30	Invited: **Rob Wheatcroft** (Oregon State University) "THE ROLE OF BIOTURBATION IN A SOURCE-TO-SINK WORLD"
10:30 - 11:00	*Coffee break*
11:00 – 11:45	Invited: **Herman Eijsackers** (Wageningen University) "BIOTURBATION ON SOLID GROUNDS"
11:45 – 12:30	Invited: **Gary Banta** (Roskilde University) "BIOTURBATING INFAUNA AND SEDIMENT ASSOCIATED POLLUTANTS – A TWO WAY INTERACTION"
12:30 – 14:00	*Lunch*
14:00 – 16:00	*Free time*
16:00 – 17:00	**Workshop: What is bioturbation really?**
	The term "bioturbation" is understood in many ways, and these diverging interpretations have generated some misunderstanding. This session will

examine whether we can arrive at a more uniform interpretation of bioturbation and related terms like reworking and bio-irrigation.

Discussion Leader: Erik Kristensen (University of Southern Denmark)

Tapas Session I: Short appetizers of novel research

Chair: Fransesc Montserrat (Netherlands Institute of Ecology)

17:00 – 17:15 **Lorna Teal** (University of Aberdeen)
"NOVEL IN-SITU TECHNIQUES FOR LINKING BIOLOGICAL ACTIVITY TO SEDIMENT FUNCTION"

17:15 – 17:30 **Gil Penha-Lopes** (Universidade de Lisboa)
"EFFECTS OF DOMESTIC SEWAGE DOSING ON EPIFAUNAL BIOTURBATION IN MANGROVE SEDIMENTS"

17:30 – 17:45 **Laura Pischedda** (Centre d'Océanologie de Marseille)
"BIOTURBATION AND OXYGEN HETEROGENEITY IN MARINE SEDIMENTS: INFLUENCE ON THE OXYGEN FLUX"

17:45 – 18:00 **Anna Villnäs** (Finnish Institute of Marine Research)
"THE IMPORTANCE OF THE LOSS OF KEY SPECIES FOR ECOSYSTEM FUNCTIONING"

18:00 - 20:00 *Dinner*

POSTER SESSION

20:00 - 21:30 A perfect match of exotic cocktails and intriguing posters
(or equally, intriguing cocktails and exotic posters)

MONDAY 25 August 2008

07:30 - 08:30 *Breakfast*

SESSION B: The role of bioturbation in the biodiversity-ecosystem functioning debate

Discussion Leader: Martin Solan (Aberdeen University)

09:00 - 09:45 Invited: **Steve Widdicombe** (Plymouth Marine Laboratory)
"THE RELATIONSHIP BETWEEN BIOTURBATION AND BENTHIC BIODIVERSITY"

09:45 - 10:30 Invited: **Jack Middelburg** (Netherlands Institute of Ecology)
"ECOSYSTEM FUNCTION LOSSES FOLLOWING THE DEFAUNATION OF SEDIMENTS"

10:30 - 11:00 *Coffee break*

11:00 – 11:30 Invited: **Erik Kristensen** (University of Southern Denmark)
"DO INVASIVE SPECIES AFFECT THE BIOGEOCHEMICAL FUNCTIONING OF MARINE SEDIMENTS? THE MARENZELLERIA VIRIDIS CASE IN THE NORTH SEA-BALTIC SEA AREA"

11:30 – 12:00 Invited: **Karl Norling** (Norwegian Institute for Water Research)
"ECOSYSTEM FUNCTIONS IN BENTHOS: HOW IMPORTANT ARE BIOTURBATION AND BIODIVERSITY FOR MINERALIZATION AND NUTRIENT FLUXES?"

12:00 – 12:30 Speaker: **Sally Woodin** (University of South Carolina)
"TRANSIENT PRESSURE PULSES, POREWATER FLUX, AND ASSEMBLAGE CHARACTERISTICS"

12:30 – 14:00 *Lunch*

14:00 – 16:00 *Free time*

16:00 – 16:45 **Workshop: An Update on the Nereis Park Experiment**

Presented by: Franck Gilbert (Université de Toulouse III - Paul Sabatier)

Tapas Session II: Short appetizers of novel research

Chair: Lois Nickell (Scottish Association for Marine Science)

16:45 – 17:00 **Peter Stief** (MPI Bremen)
"NITROUS OXIDE EMISSION BY AQUATIC MACROFAUNA"

17:00 – 17:15 **Deena Pillay** (University of Cape Town)
"CALLIANASSID BIOTURBATION AS A MECHANISM FOR DECADAL CHANGES IN FISH AND INVERTEBRATE COMMUNITIES IN AN ESTUARINE EMBAYMENT"

17:15 – 17:30 **Ana Queirós** (Bangor University)
"CLIMATIC REGULATION OF INVASION IMPACTS ON NATIVE DIVERSITY AND ECOSYSTEM FUNCTIONING"

17:30 – 17:45 **Stina Lindqvist** (University of Gothenburg)
"IMAGING PARTICLE REDISTRIBUTION IN BIOTURBATED SURFACE SEDIMENTS"

17:45 – 18:00 **Sandra Lagauzere** (Institut de Radioprotection et de Sûreté Nucléaire)
"THE INFLUENCE OF BIOTURBATION ON BIOGEOCHEMICAL CYCLE OF URANIUM IN FRESHWATER SEDIMENTS"

18:00 - 20:00 *Dinner*

SESSION C: Merging ecological and evolutionary perspectives on bioturbation

Discussion Leader: Pete Jumars (University of Maine)

20:00 - 20:45 Invited: **Sören Jensen** (Universidad de Extremadura)
"A BRIEF HISTORY OF THE RISE OF BIOTURBATION"

20:45 – 21:15 Invited: **Kelly Dorgan** (University of California at Berkeley)
"DO WISE CRACKS CAUSE BIOTURBATION?"

TUESDAY 26 August 2008

07:30 - 08:30 *Breakfast*

SESSION D: Novel developments in experimental data acquisition and modeling approaches

Discussion Leader: Antoine Grémare (Université de Bordeaux)

09:00 - 09:45 Invited: **Bernie Boudreau** (Dalhousie University)
"INDIVIDUAL-BASED MODELS OF BIOTURBATION: A REVIEW"

09:45 - 10:30 Invited: **Martin Solan** (University of Aberdeen)
"BIOTURBATION: THE ELEPHANT IN THE DARK AND RECONCILING CONTRARIETIES WITH IMAGING"

10:30 - 11:00 *Coffee break*

11:00 – 11:30 Invited: **Nils Volkenborn** (Alfred Wegener Institute)
"FLUSHING OF INTERTIDAL SAND BY LUGWORMS: FROM INDIVIDUAL HYDRAULIC ACTIVITIES TO LARGE SCALE IMPLICATIONS"

11:30 – 12:00 Speaker: **Socrates Papaspyrou** (University of Essex)
"MICROBIAL REACTION RATES AND BACTERIAL COMMUNITIES IN SEDIMENT SURROUNDING BURROWS OF BENTHIC FAUNA"

12:00 – 12:30 Speaker: **Emma Michaud** (SUNY Stony Brook)
"SEDIMENTARY ORGANIC MATTER DISTRIBUTIONS AND BURROWING ACTIVITY: NATURAL PATTERNS AND EXPERIMENTAL ARTIFACTS "

12:45 – 14:00 *Lunch*

Excursion to Dutch Delta Area

14:00 – 18:00 Bike (or bus) ride from the conference site to the small port of Burghsluis (9 km) and 2 hour boat trip to the Oosterschelde Nature Reserve area.
Guide: **Peter Herman** (Netherlands Institute of Ecology)

18:00 - 20:00 *Conference dinner*

20:00 - 21:00 Keynote lecture: **Ronnie Glud** (Scottish Association for Marine Science)
"BENTHIC OXYGEN DYNAMICS AND THE IMPORTANCE OF FAUNA: FROM MICROMETER TO GLOBAL SCALE"

21:00 - Poster awards - End of conference ceremony

WEDNESDAY 27 August 2008

07:30 - 08:30 *Breakfast*

09:00 Departure with bus to Rotterdam Central Railway Station

POSTER SESSION

QUANTIFYING THE BIOTURBATION OF *COROPHIUM VOLUTATOR* (Crustacea, Amphipoda): EFFECT OF DENSITY, TIME AND PHYSICAL VERSUS BIOLOGICAL ACTIVITY
De Backer, A., Van Coillie, F., Vincx, M. and Degraer, S.

MACROFAUNA STRUCTURING THE SEA FLOOR: IS THERE ANY SEASONAL, DENSITY OR FUNCTIONAL IDENTITY EFFECT?
Braeckman, U., Provoost, P., Gribsholt, B., Vangansbeke, D., Middelburg, J., Vincx, M., Soetaert, K. and Vanaverbeke, J.

BIODIVERSITY EFFECTS ON NUTRIENT FLUX ARE MODIFIED BY FAUNAL RESPONSES TO HABITAT COMPOSITION
Bulling, M.T., Solan, M., Dyson, K.E., Hernandez-Milan, G., Luque, P., Pierce, G.J., Raffaelli, D., Paterson, D.M. and White, P.C.L.

INTERACTION BETWEEN BENTHIC FAUNA AND BIOFILM IN THE HYPORHEIC COMPARTMENT: A COLUMN-MODELING APPROACH
Davit Y., Dedieu, K., Aspa, Y., Sauvage, S., Debenest, G. and Gérino, M.

THE ROLE OF BENTHIC FAUNA AND BIOFILM ON DETOXICATION RATES IN THE HYPORHEIC COMPARTMENT
Dedieu, K., Davit, Y., Montuelle, B., Frédéric, J., Sauvage, S., Vervier, P., Sánchez-Pérez, J-M. and Gérino, M.

IMPACT OF TEMPORAL VARIATIONS IN A LAGOON ASSEMBLAGE ON SEDIMENT REWORKING IN COASTAL MARINE ECOSYSTEM
Duport, E., Gilbert, F. and Stora, G.

FOLLOW – UP OF THE SPATIOTEMPORAL DYNAMICS OF IN SITU BIOTURBATION ON THE LIPPENBROEK PILOT SITE (BELGIUM)
Ciutat, A., Beauchard, O., Munoz, T., Barbe-Barrailh, F., Maris, T., Meire, P., Stora, G., Tackx, M. and Gérino, M.

HOW ORGANISMS INTERACTIONS INFLUENCE SEDIMENT REWORKING BEHAVIOUR IN A MACROBENTHIC COMMUNITY?
Gilbert, F., Poggiale, J-C., Hulth, S. and Stora, G.

EFFECTS OF BIODIVERSITY AND HABITAT STRUCTURE ON BIOTURBATION INTENSITY AND NUTRIENT GENERATION
Godbold, J.A., Bulling, M.T. and Solan, M.

EXPLORING THE IMPACT OF BIOTURBATION ON SEASCAPE EVOLUTION USING SEDFLUX-2.0
Hannisdal, B. and Hutton, E.W.H.

NITROUS OXIDE EMISSION BY MARINE MACROFAUNA
Heisterkamp, I. and Stief , P.

BIOTURBATION AND BIODIVERISTY: HOW DOES THE ROLE OF FACILITATION VIA BIOENGINEERING CHANGE WITH ENIRONMENTAL STRESS?
Johnson, G.E., Hiddink, J. and Kaiser, M.J.

COMPLEX BURROWS OF THE MUD SHRIMP *LAOMEDIA ASTACINA* AND THEIR GEOCHEMICAL IMPLICATIONS IN THE TIDAL SEDIMENTS
Koo, B.J., Koh, C.H. and Shin, S.H.

INDIRECT EFFECTS OF NON-LETHAL PREDATION ON SEDIMENT BIOTURBATION
Maire, O., Merchant, J., Bulling, M.T, Teal, L., Grémare, A. and Solan, M.

BENTHOS-MEDIATED SEDIMENT DYNAMICS
Montserrat, F.

PARTICLE AND SOLUTE TRANSPORT IN ORGANICALLY ENRICHED SEDIMENTS
Nickell, L.A., Walpersdorf, E., Burke, K. and Black, K.D.

DEVELOPMENT OF AN INTEGRATED INDICATOR OF SEDIMENT CARBON CYCLING – REDOX AND BIOTURBATION?
Parker, R., Birchenough, S. and Brooks, L.

MACROFAUNAL IMPACT ON THE DENITRIFYING BACTERIAL COMMUNITY IN FRESHWATER SEDIMENT
Poulsen, M., Stief, P. and Schramm, A.

MODELING BIODIVERSITY EFFECTS ON THE FUNCTIONING OF A SEDIMENTARY, DETRITUS-BASED ECOSYSTEM
Provoost, P.

REVISITING THE ALLER TUBE-IRRIGATION MODEL: INFINITE VERSUS FINITE BURROW VENTILATION
Van Frausum, J., Meysman, F. and Middelburg, J.

EFFECTS OF BIOTURBATION ON BENTHIC RECRUITMENT OF *NODULARIA SPUMIGENA*
Karlson, A., Nascimento, F., Näslund, J., Suikkanen, and S., Viitasalo, S.,

TOWARDS A MECHANISTIC UNDERSTANDING OF BIODIVERSITY-ECOSYSTEM FUNCTIONING RELATIONSHIPS IN MARINE SEDIMENTS: SIMPLE SPECIES INTERACTIONS, COMPLEX OUTCOMES
Waldbusser, G.G. and Meile, C.

ABSTRACTS (in alphabetic order)

STRUCTURE AND BIOGEOCHEMICAL FUNCTION IN THE BIOTURBATED ZONE

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Benthic community biogeochemical functions are often taken as synonomous with properties such as nutrient regeneration and organic matter remineralization efficiency in the seabed. A virtually infinite set of conditions is possible when experimentally exploring the effects of benthos on an ecosystem function. From a purely physical-chemical perspective, how do the geometries of biogenic structures formed by benthos, and their temporal dynamics and spatial scaling in sediments, relate to a property or function such as nutrient regeneration or organic matter storage efficiency? In terms of structural diversity, can the effects of populations of single species of varied size and density be differentiated from those of multi-species mixtures, that is, do biodiversity and functional group diversity matter? Characteristics of the sedimentary environment and particle reworking are critically important: the same community of benthic species may impact net fluxes differently depending on distributions of labile substrate and average remineralization rates within a deposit. In the face of this complexity, it is desirable to identify master variables that might be used for practical predictive purposes, and to apply and interpret them within a well described sedimentary context. Simple geometric relationships relating single species to structural scaling properties may be viable options. Allometric, density dependent, and species mixture impacts on such structural properties must be established. One thing is clear: there is a dearth of mechanistic observations on which to base theory. Modern tools such as planar optode sensors, radiography, and finite element models of transport – reactions in complex geometries offer a means to move beyond statistical testing of arbitrary species configurations to a more mechanistic basis for predictions and to reveal novel interactions.

QUANTIFYING THE BIOTURBATION OF COROPHIUM VOLUTATOR (CRUSTACEA, AMPHIPODA): EFFECT OF DENSITY, TIME AND PHYSICAL VERSUS BIOLOGICAL ACTIVITY

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Corophium volutator is an abundant species in mudflats. It lives in U-shaped tubes, and population densities of *C. volutator* frequently reach > 20.000 ind. m^{-2}. The high population densities make this amphipod an important part of many mudflat ecosystems. *Corophium* is considered as an important bioturbator, however the impact and the magnitude of the bioturbation process is still under debate.

This study investigated the magnitude of the bioturbation process of *C. volutator* by performing a lab experiment with luminophores. Five treatments were used to examine the density effect, and the effect of physical versus biological activity: control, low density, high density, low density only tubes (physical activity), high density only tubes. For the time effect, experimental units were sampled after 1 day, 1 week, and 2 weeks.

Only high densities of *C. volutator* affected the magnitude of bioturbation, low densities or the presence of burrows alone (physical activity) didn't significantly affect the bioturbation pattern. The 'burrow only' treatments didn't differ from the control treatment. So, it is the biological activity in these tubes that is the driving factor in sediment reworking. There was also an effect of time, differences between high density and control treatments became more distinct as bioturbation lasted longer and the biodiffusion rate was significantly higher after 1 day than after 14 days.

BIOTURBATING INFAUNA AND SEDIMENT-ASSOCIATED POLLUTANTS – A TWO-WAY INTERACTION

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Bioturbating infauna come in close contact and interact with sediment-associated pollutants in a number of ways. On the one hand, infauna affect the fate of these pollutants through a number of direct and indirect mechanisms. Bioturbating fauna alter the distribution, transportation and transformation processes for pollutants in similar ways that they do so for many compounds in sediments (e.g., organic matter, nutrients). This includes direct effects related to transport of pollutants or indirect effects related to alterations in sediment biogeochemistry, hereunder conditions for microbes, which affects the fate of pollutants. Infauna themselves also directly alter the fate of sediment-associated pollutants via their own uptake and metabolism of pollutant compounds. On the other hand, infauna are themselves potentially affected by sediment-associated pollutants. These effects include lethal as well as sublethal effects, such as altered growth, reproduction and bioturbation activities. As a result the ecological and ecosystems engineering role of infauna species can be altered dramatically by the presence of pollutants. Thus, there is a complicated feedback system of two-way interactions where fauna affect pollutants and pollutants affect fauna. The outcome of these interactions is variable and depends on the species and pollutants involved as well as the specific conditions of the case considered. Mechanistic models provide useful tools to help predict the outcome of these complicated interactions, but a reasonable level of insight into the mechanisms involved in the specific pollutant-fauna interactions is required to produce such models.

INDIVIDUAL-BASED MODELS OF BIOTURBATION: A REVIEW

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A fundamental understanding of the quantitative effects of bioturbation faces daunting obstacles. Foremost, sediments are opaque, limiting direct observation. The frequency of bioturbation events varies widely in time and space. The mode of sediment displacement by various bioturbating organisms is not always well known. Additionally, some measurement methods, e.g., isotopes, are highly integrative and not diagnostic of mechanism.

Faced with these impediments, researchers have resorted to less conventional approaches. One such strategy is direct computer models of sediments and the individual organisms therein. Sediment can be approximated by "particles" on a lattice and organisms as computer-based entities that "live" on the lattice by following a set of rules that govern their behavior. By labeling the particles and mapping their positions in time, it is possible to derive vital statistical information about this computer-based bioturbation that should be applicable to real sediments.

This talk reviews the formulation and operation of such "lattice-automaton" models and the interpretation of the synthetic data they produce. Two important results that have been obtained is that the widely used diffusion model of bioturbation generates inconsistent results for various types of tracers, both steady state and transient. Many tracers will produce greater values of the apparent diffusivity than actually exist. These false results are directly attributable to a violation of the underlying assumptions of the diffusion model; specifically, such tracers usually do not integrate enough mixing events.

MACROFAUNA STRUCTURING THE SEA FLOOR: IS THERE ANY SEASONAL, DENSITY OR FUNCTIONAL IDENTITY EFFECT?

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To assess the effects of density declines and species loss on benthic ecosystem functioning, we investigated the importance of three different functional groups of macrobenthos in the benthic processes of the Belgian Continental Shelf. As macrobenthic activity depends on temperature and food availability, we performed two mesocosm experiments: before sedimentation of the phytoplankton bloom and after. Single – species treatments of key-species belonging to three different functional groups (*Abra alba*, *Lanice conchilega* and *Nephtys* sp.) were added to microcosms at three density levels (average natural - lower - very low) to account for possible density declines. Oxygen and nutrient fluxes as well as bioturbation were measured.

Both before and after phytoplankton bloom, *L. conchilega* had more pronounced influences on benthic respiration and nutrient release than *A. alba* and *Nephtys* sp.. *A. alba* appeared to be a more effective bioturbator than *Nephtys* sp.. Moreover, ecosystem functioning (as benthic respiration, nutrient fluxes and bioturbation) seems to be related to animal densities. Therefore, a decrease in densities (due to anthropogenic or natural disturbances) may have implications for ecosystem functioning rates at the study area.

FORAMINIFERA AS INDEX TAXA OF SEDIMENT BIOGEOCHEMISTRY

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Macrofaunal bioturbation and the biogeochemistry of the sediment are closely coupled. Bioirrigation brings oxygen and carbon deeper down in the sediment. Chemical and microbiological changes in the sediment due to bioturbation may deepen the habitable zone for foraminifera. Due to their high fossilitation potential and high abundances over time, foraminifera could be excellent index taxa of these various biogeochemical states of the sediments.

BIODIVERSITY EFFECTS ON NUTRIENT FLUX ARE MODIFIED BY FAUNAL RESPONSES TO HABITAT COMPOSITION

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Bioturbation is a key link between benthic biodiversity and ecosystem processes such as nutrient flux. Heterogeneity is a well-recognized feature of natural environments, and the spatial distribution and movement of individual species is primarily driven by resource requirements. As such habitat heterogeneity has the potential to be a key factor in determining the level and spatial distribution of bioturbation, and therefore a major determinant of the relationship between biodiversity and ecosystem process. In laboratory experiments designed to explore how different species drive ecosystem processes, habitat heterogeneity is often seen as something which must be rigorously controlled for. Most small experimental systems are therefore spatially homogeneous, and the link between environmental heterogeneity and its effects on the redistribution of individuals and species and on ecosystem processes has not been fully explored. Here we used a mesocosm system to investigate the relationship between habitat composition, species movement and sediment nutrient release by four contrasting species of marine benthic invertebrate macrofauna. Various habitat configurations were generated by selectively enriching patches of sediment with macroalgae, a natural source of spatial variability in intertidal mudflats. We found that the direction and extent of faunal movement between patches differs with species identity, density and habitat composition, and these differences were concomitant with changes in levels of nutrient release.

ROLE OF INTERACTIONS BETWEEN BENTHIC FAUNA AND BIOFILM ON BIO-PHYSICAL FUNCTIONING OF THE HYPORHEIC COMPARTMENT: A COLUMN-MODELING APPROACH

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In regard to aquatic ecosystems, bioturbation often refers to sediment mixing by benthic fauna, excluding solute transport. Etymologically speaking, the signification extends to all kinds of perturbation induced by living organisms. In macroporous media of the hyporheic compartment, particles are too big to be significantly displaced by invertebrates. However, fauna still extensively modifies physical, chemical and biological properties of the medium, mainly by interacting with the biofilm. Here, we investigate this interaction on the freshwater ecosystem of the French river Garonne. Our approach is based on coupling columns experiments with modeling tools. In this presentation, we focus on the modeling part, which aims to estimate modifications induced by fauna on effective reaction and transport parameters of a porous medium containing biofilms. We also highlight some difficulties which appear in modeling such multi-scales problems.

THE ROLE OF BENTHIC FAUNA AND BIOFILM INTERACTIONS ON DETOXICATION RATES IN THE HYPORHEIC COMPARTMENT

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Bioturbation acts to alter the physical structure as well as the biological and chemical nature of the sediment. In fine sediments, biogeochemical processes dominated by microbial activity are tightly linked to particle and solute displacements driven by macrofauna. In porous media such as hyporheic sediments where benthic organisms and particles sizes are on the same order of magnitude, bioturbation is mainly performed by biofilm grazing that modifies pore water flow and the associated transport of various solutes. In such sediments, advective transports are known to control microbial metabolism and solutes exchanges whereas grazing interferes in the relative efficiency of biofilm by altering community composition and physical structure. Consequently, the role of biofilm in the retention and transformation of natural material and pollutants may be affected by the presence of macrofauna.

The purpose of this study is to link biodiversity and ecological processes involved in toxic transformations of porous media from ground-/surface-water interfaces (i.e. river bed sediments). To test the role of biodiversity on detoxication rates, analysis of the herbicid diuron and metabolites were performed in water flowing through a series of microcosms reproducing a portion of water sediment interface. The community combinations in microcosms were tested by comparison of several experimental conditions setting with and without toxic. The toxicity of water at the outflow of microcosms was assessed with different toxicity models. The effects of pollutant exposure and invertebrate interactions on microbial diversity change were also investigated. Profiles and drift in diversity (estimated by molecular profiling) was carried out in all experimental conditions.

DO WISE CRACKS CAUSE BIOTURBATION?

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New understanding suggests that most animals burrow through muds by crack propagation; even a simple spade works by this same principle. Muds crack because their mechanical behavior is governed by the mucopolymer matrix holding grains together. Movements of individual grains in this composite material depend strongly on the bulk mechanical properties of the polymer and the spatial heterogeneity of those properties. Fundamental arguments of energetics would suggest that less energy would be expended in burrowing if grains are not rearranged, and the crack simply closes behind a burrower. Friction, theoretically resulting in small movements of grains, is a drag and should be minimized. This point of view overlooks two potentially important details, however. One is that sediments have low resilience and release some of their stored elastic energy through time-dependent creep. The second is that many burrowers are subsurface deposit feeders that cannot gain energetic benefit without freeing particles from the sedimentary matrix for ingestion. Moreover predatory burrowers may favor power over efficiency, requiring superior speed to capture prey, perhaps warranting enough tensile forces to propagate an unstable crack and cause massive plastic deformation. Testing these ideas requires new mechanical measurements and experiments with burrowers on specific time and space scales, but has implications from the scales of individual-individual interactions to those of the geological record.

IMPACT OF TEMPORAL VARIATIONS IN A LAGOON ASSEMBLAGE ON SEDIMENT REWORKING IN COASTAL MARINE ECOSYSTEM

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The lagoon assemblage, in which *Nereis diversicolor* is one of the dominant species, is widely distributed in brackish intertidal areas in the temperate zone of the northern hemisphere, along both the European and the North American coasts. The aim of this work was to quantify at seasonal scale the sediment mixing induced by the organisms of this lagoon assemblage in the Saint-Antoine canal (Gulf of Fos, Mediterranean Sea, France). This assemblage is essentially dominated by three species belonging to two different functional groups (i.e. sediment mixing modes): the gallery-diffusors *N. diversicolor* and *Cyathura carinata* and the biodiffusor *Streblospio shrubsolii*. In order to assess the impact of different ecological factors that could influence the intensity of sediment mixing by this community, a 1-D model was used to measure biodiffusion-like transport (*Db*: diffusion analogue) and biotransport (*r*: non local exchange analogue). Results showed that sediment reworking intensity differed with particle size: biodiffusion-like and biotransport for small particles were 1.25 and 1.49 higher than for larger particles. This difference was due to a selective particle size class resulting from both trophic and mechanical effects. In seeking an explanation for the sediment reworking performed by this community, we were only able to highlight not a single major but rather a combination of biological factors functional composition and total density of the assemblage, associated with the direct and indirect influence of environmental factors such as water temperature and sedimentary organic matter content.

BIOTURBATION ON SOLID GROUNDS

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Soil formation is steered by geological, physical and biological processes, each with their own time span. Bioturbation (time span: days to decades) comprises physical replacement of soil particles by pushing or burrowing, chemical processes like gut passage and addition of excretions (slime, exo-enzymes) and biological processes like litter layer fragmentation and re-mixture of litter material with mineral soil particles.
Bioturbators are invertebrates (earthworms, beetles, ants, termites) or vertebrates (moles, mice). Also plant(roots) bioturbate, which seems to be underestimated.

The impact of bioturbation by earthworms differs between groups: anecic worms with vertical burrows bringing soil to the soil surface, endogeic worms eating their way through the soil, totally remixing it, and epigeic worms comminuting and remixing litter material with superficial soil layers. Earthworms can change soil profiles. The introduction of European earthworm species in North American deciduous forests is recently presented as a major (alien) threat ("ecosystem invasional meltdown"). Results from Dutch research in grassland soils will provide realistic time and spatial frames.

Bioturbation also contributes to:

- better drainage and aeration of soils,
- mixing of organic matter and improving nutrient status
- replacement of buried contaminants, (surfacing of heavy metal contaminants in flood plain soils)
- stimulated breakdown of organic contaminants, like PAHs in dredged sediments

FOLLOW - UP THE SPATIOTEMPORAL DYNAMICS OF IN SITU BIOTURBATION ON THE LIPPENBROEK PILOT SITE (BELGIUM)

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The pilot project Lippenbroek tests the functioning of a Controlled Reduced Tidal area (CRT), as a response to a need for flood protection in the Freshwater tidal area (FTA) of the Scheldt estuary. The CRT occupies 10 ha of land which was used for agriculture in the past. In this newly created CRT, terrestrial communities are being replaced by aquatic communities in a primary benthic succession. The species composition of the benthic community influences the type and the intensity of the bioturbation activity and its resulting effect on biogeochemical fluxes. To quantify the bioturbation potential of this newly created ecosystem, bioturbation measurements (fluorescent particulate tracers) were done in situ on the Lippenbroek site, at different periods of the year (winter 2007, spring 2007, summer 2007, autumn 2007, winter 2008), and at three different places located along a gradient of immersion. Together with bioturbation measurements, the determinations of the composition of the benthic communities were also achieved in the same cores to analyze the relation between the biodiversity of the developing benthic communities and their function of bioturbation. The Lippenbroek pilot site provides a unique experimental opportunity to follow up the bioturbation activity of an installing aquatic benthic community, and its effects on chemical exchanges of natural and anthropogenic elements with the estuary.

HOW ORGANISMS INTERACTIONS INFLUENCE SEDIMENT REWORKING BEHAVIOUR IN A MACROBENTHIC COMMUNITY?

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In order to investigate potential changes in sediment reworking behaviour within different macrobenthic communities, a laboratory experiment was carried out with more or less complex reconstructed communities. Different combinations of 3 species (*Amphiura filiformis*, *Scalibregma inflatum* and *Abra nitida*) sampled in the Gullmarsfjord (Western Sweden) were introduced in experimental mesocosms, with identical densities (795 ind. m^{-2}), for 10 days. Sediment reworking was studied by quantifying downward and upward movements of fluorescent inert tracers (luminophores). Luminophores with different colour were initially deposited both at the sediment surface and within the sediments. For monospecific communities, tracers reworking coefficients ranged from 0.6 to 0.9 $cm^2\ y^{-1}$ and 0.9 to 2.8 y^{-1}, respectively for the biodiffusive-like and non-local transports. Combined species communities demonstrated changes in organisms' location within the sedimentary column with a general deeper positioning pattern. This was also reflected in the sediment reworking coefficients that were either decreased (biodiffusive-like coefficient) or increased (biotransport coefficient). These results suggest changes in behaviour for the individuals and in the reworking intensity for the communities due to organisms ' interactions, which have to be discussed.

BENTHIC OXYGEN DYNAMICS AND IMPORTANCE OF FAUNA: FROM MICRO TO GLOBAL SCALE

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Recent advances in microsensing and planar sensing has taught us that the oxic environment of marine sediments is far more dynamic than previously anticipated. Further, it has allowed for a much more detailed investigation of how bioirrigation and bioturbation interrelate to the solute dynamics, diagenesis and microbial community structure of sediments. The presentation will review present knowledge on benthic O_2 dynamics and the interrelation to fauna activity. The discussion will be based on a series of laboratory case studies and concerted in situ deployments of microelectrodes, chambers, planar optodes and the eddy correlation approach. A central challenge for discussion is how we move on from case and point studies to large-scale integrative approaches covering temporal and spatial scales relevant or benthic element cycling.

EFFECTS OF BIODIVERSITY AND HABITAT STRUCTURE ON BIOTURBATION INTENSITY AND NUTRIENT GENERATION

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Habitat fragmentation and homogenisation are expected to substantially affect global biodiversity over the next century, but their effects on ecosystem processes are still unclear. Manipulative experiments explicitly testing the relationship between biodiversity and ecosystem processes have largely been carried out in isolated, homogenous environments that do not incorporate structural heterogeneity. Here we experimentally investigated the effects of biodiversity, faunal movement and habitat heterogeneity on bioturbation and nutrient generation in marine benthic communities. Communities were established within a multi-patch mesocosm system, in which patches were either isolated or connected by corridors. Our results show that bioturbation intensity and nutrient generation are enhanced in more diverse systems, but that the magnitude of effect is underpinned by the presence of a dominant species. Moreover, increasing the openness of the system and allowing fauna to move and select patches, positively affected both bioturbation and nutrient generation. Collectively our findings suggest that the effects of species loss are likely to be more dramatic in fragmented habitats and that some ecosystem processes are best maintained by retaining habitat heterogeneity.

EXPLORING THE IMPACT OF BIOTURBATION ON SEASCAPE EVOLUTION USING SEDFLUX-2.0

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The biological imprint on seascapes and its importance relative to physical processes remains poorly understood. Biogenic mixing of marine surface sediments is pervasive, and by renewing the seafloor sediment distribution it potentially affects the rates of reworking and downslope transport by physical processes (e.g., storms). Does bioturbation leave a recognizable signature on seascapes, and if so, under what conditions? Here we explore this possibility through numerical experiments with the sediment transport model Sedflux-2.0. Using estimated paleobathymetry and sediment supply for the Po River as a starting point, the model predicts stratigraphy and morphodynamics under ever-changing boundary conditions. Surface plumes distribute and deposit sediment on the delta, where the flux of sediment along the seafloor is driven by cross-shore currents and wave orbital velocity, acting on multiple sediment grain types. Bioturbation is modeled as a 1D diffusion, and interacts with the other processes through the evolving grain size distribution of the uppermost sediment layers. Experiments so far show that in wave-dominated settings, bioturbation continually exposes fine-grained sediment to wave resuspension, thus increasing nearshore erosion and transport of fine sediment, affecting shoreline position and delta slope on a time scale of centuries. We discuss possible criteria for describing the morphodynamic effect of bioturbation, and identify some outstanding challenges.

NITROUS OXIDE EMISSION BY MARINE MACROFAUNA

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In aquatic ecosystems, bioturbating invertebrates interact with microbes by modifying water and sediment fluxes and hence altering biogeochemical processes. Beside these external animal-microbe interactions, also internal associations involving the presence of microbes in the alimentary tract of the animals influence microbially mediated element cycling. Recently, the gut microenvironment of many freshwater invertebrate species has been shown to stimulate the activity of ingested denitrifying bacteria that preferentially produce the greenhouse gas N_2O. Here we report on the N_2O emission of several marine invertebrate species sampled at various coastal sites. Highest N_2O emission rates were observed for filter-feeders, followed by deposit-feeders and grazers, while N_2O emission by predators was not significant. N_2O production obviously correlates with the amount of ingested microbes that is higher for filter- and deposit-feeders than for predators. Surprisingly, some of the most prominent deposit-feeders in coastal sediments (*Arenicola*, *Nereis*) did not emit N_2O at all. Laboratory experiments suggest that the production of N_2O by these infaunal species is absent due to the very low nitrate availability in their subsurface habitat and consequently their gut, which contrasts with nitrate-exposed epifaunal species. Thus, apart from the feeding guild, also the microhabitat of aquatic invertebrates determines their potential to emit N_2O.

A BRIEF HISTORY OF THE RISE OF BIOTURBATION

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The extent of bioturbation depends on a number of factors including the rate and manner in which organisms rework the sediment, the nature of the sediment and whether sedimentation is continuous or episodic. Across Earth history the evolution of animals becomes an additional factor. Only after about 560 Ma before the present is there a continuous record of animal activity in the form of trace fossil. For the first 15 million years or so this animal activity was essentially restricted to simple horizontal traces made close to the surface of the ocean floor. Deeper burrowing and more complex biogenic structures appeared in the Cambrian but the extent of bioturbation remained for the most part comparatively modest. It is only in the late Palaeozoic or even the Mesozoic that the intensity and style of bioturbation compares to that seen today. The rise of bioturbation had far-reaching consequences for the ocean floor including the restriction of extensive microbial mats and the creation of a more diffuse water-sediment boundary. The purpose of this talk is to provide an overview of the early history of bioturbation and the effects that the rise of bioturbation had on the ocean floor and early organism communities.

BIOTURBATION AND BIODIVERISTY: HOW DOES THE ROLE OF FACILITATION VIA BIOENGINEERING CHANGE WITH ENIRONMENTAL STRESS?

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Global environmental change is predicted to alter levels of biodiversity at all scales. Positive interactions through ecosystem engineering could help mediate species loss by ameliorating environmental stress. Two experiments examined how the importance of facilitative bioturbation changes with anoxic stress in the intertidal zone. First, a descriptive study examined populations of the lugworm, *Arenicola marina*, and associated communities *in situ* at varying levels of anoxic stress. Interactions between *Arenicola* density and sediment properties explained variation in biogenic mixing depth (BMD). When environmental- and bioturbation-induced effects on BMD were coarsely partitioned, bioturbation appeared to have a greater effect on BMD at low-energy sites.
Secondly, abundances of *Arenicola* and BMDs were manipulated *in situ*. Bioturbation altered BMD to a greater extent, with positive effects on associated species at low-energy sites. Thus, as stress increased, species interactions shifted in importance and positive interactions with *Arenicola* became relatively more important than negative interactions.

These studies show that bioengineers play an important role in stressed communities, increasing niches and allowing species to survive in environments that would not otherwise have been tolerable. In the face of global environmental change, facilitative interactions will become more important and may buffer species loss to a degree.

COMPLEX BURROWS OF THE MUD SHRIMP *LAOMEDIA ASTACINA* AND THEIR GEOCHEMICAL IMPLICATIONS IN THE TIDAL SEDIMENTS

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An interesting landscape created by the mud shrimp, *Laomedia astacina*, was found on the upper part of Saemangeum tidal flat in the west coast of Korea. One mound and several funnels constitute the surface structure of one burrow system, built and maintained by a couple of the shrimp. *Laomedia* had a huge and unique burrow system and the architecture was largely different from that of other thalassinidean mud shrimp in having several galleries vertically interconnected by spiral tunnels. The burrow of *Laomedia* (body length ranged from 5.4 to 8.4 cm) had an average of 840 cm (±347 cm) in total length and reached down to 142 cm sediment depth. Burrow volume varied between 3,986 and 16,276 cm^3, and burrow surface-area was between 5,690 and 18,685cm^2. At the observed abundances, the extensive burrows increase the total area of the sediment-water interface by roughly 1,044%. This value may be the highest among the reported data on increase in sediment-water interface by marine invertebrates. *In situ* continuous oxygen measurements at 12cm sediment depth revealed that *Laomedia* maintained burrow-water oxygen concentrations at 3.7 to 77.9 % of air saturation with respect to tides. Under the condition of excluding the shrimp from the burrow, an oxygen diffusion rate into the burrow by the passive irrigation was insignificant (0.16±0.07 $mgl^{-1}h^{-1}$) compared to the rate by active irrigation of the shrimp (16.91±13.05 $mgl^{-1}h^{-1}$). Bio-pumping of *Laomedia* plays an important role on providing the oxygen into tidal sediments and, subsequently, might affect biogeochemical processes in sediment-water interface.

DO INVASIVE SPECIES AFFECT THE BIOGEOCHEMICAL FUNCTIONING OF MARINE SEDIMENTS? THE *MARENZELLERIA VIRIDIS* CASE IN THE NORTH SEA – BALTIC SEA AREA

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Species composition and functional diversity of benthic fauna are known as major regulators of sediment biogeochemistry and microbial dynamics, with major implications on ecosystem functioning. Several invasive infaunal species, such as the polychaete *Marenzelleria viridis* from North America, have been introduced to the North Sea and Baltic Sea area during recent decades. The associated changes of macrobenthic species composition in coastal areas are likely to influence key sediment processes. This presentation aims to describe known effects of *M. viridis* and related invasive species on sediment biogeochemistry in shallow coastal sediments in Northern Europe. The interactions between *M. viridis* and native species will first be evaluated with emphasis on functional groups. Evidence will then be provided of how changes in species composition may affect benthic metabolism, electron acceptor availability and bacterial diversity.

THE INFLUENCE OF BIOTURBATION ON BIOGEOCHEMICAL CYCLE OF URANIUM IN FRESHWATER SEDIMENTS

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The biogeochemistry of sediments inhabited by *Chironomus riparius* larvae and *Tubifex tubifex* worms was investigated during 12-day laboratory experiments through high resolution measurements of oxygen uptake using a planar oxygen optode device, and of solute profiles using DET-gel probes. Additional experiments were carried out within uranium-contaminated sediment to assess the impact of bioturbation on the behaviour of this metal. As expected, both the two invertebrate species significantly increased the oxygen uptake of sediments (13-14%) but only *T. tubifex* maintained a high bioturbation activity in contaminated sediments. In these conditions, the combined effects of worms and uranium lead to an increase of 53% of the oxygen uptake, stimulated denitrification and nitrification processes, as well as sulphate-reducer metabolism. The bioconveying of sediment particles from the bottom layers to the surface induced the remobilization of uranium initially associated with sediments to the water column. This study confirmed the ecological importance of Chironomid larvae and Tubificid worms in freshwater sediments. Overall, it represents the first assessment of the influence of macro-invertebrate bioturbation on uranium cycle in freshwater ecosystems and highlights the necessity of further investigations in order to take into account the interactions existing between bioturbation, microbial metabolism and radionuclides.

IMAGING PARTICLE REDISTRIBUTION IN BIOTURBATED SURFACE MARINE SEDIMENTS

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In addition to pore water irrigation, a biologically induced transport of particles between redox zones (oxic/anoxic) may provide a reaction environment different from that in sediments devoid of fauna. In this work we have utilized non-destructive screening of luminophores to quantify 2-D particle transport by the polychaete Nereis diversicolor. Quantification was made using optical discrimination and CCD imaging of fluorescence according to principles of the Optical Reworking Coefficient (ORC). Imaging of particles may provide a powerful tool to experimentally verify the concept of functional groups, and in a more general sense further understand reworking by fauna in surface sediments. In conjunction with detection of small-scale (mm) particle displacements on a time resolution of minutes or less, transport processes on longer time scales (days) can be simultaneously quantified in the same experimental system. Thereby, eventual time-dependent (e.g. diurnal) cycles of particle transport can be evaluated. Results from a laboratory experiment using thin glass aquaria under light and dark conditions will be presented.

The present contribution is part of the collaborative Nereis Park Experiment 2007, performed as a tribute to Prof. Gaston Desroisiers.

INDIRECT EFFECTS OF NON-LETHAL PREDATION ON SEDIMENT BIOTURBATION

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Many benthic bivalves deposit feed at the sediment surface where recently settled organic material accumulates. Feeding above the sediment-water interface, however, makes individuals especially vulnerable to sublethal predation. We performed a series of mesocosm experiments to test the effects of predation avoidance on the feeding activity and bioturbation intensity of the bivalve *Macoma balthica*. Feeding activity at the sediment-water interface and bioturbation intensity (vertical incorporation of particle tracers) were monitored using image analysis techniques for treatments including and excluding the predatory shrimp, *Crangon crangon*. Detection of *C. crangon* resulted in an immediate retraction of the feeding siphon and a reduction in feeding activity for an extended period of time. *M. balthica* also buried deeper into the sediment. This predator avoidance behaviour indirectly affected sediment bioturbation, increasing the thickness of the bioturbated sediment layer as well as the non-local transport of sediment particles at depth. Conversely, feeding activity and bioturbation processes remained unaffected when *C. crangon* was present, but isolated from the sediment, suggesting that predator perception in *M. balthica* is tactile and induced by direct encounter rather than being chemosensory. Collectively, these results demonstrate that predatory avoidance behaviour by benthic infauna can significantly impact benthic bioturbation and the incorporation of organic matter into the benthic food web.

FRESHWATER BIOTURBATION: WHAT DO WE KNOW AND WHAT DO WE NEED TO KNOW?

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Freshwater macrobenthos through their burrowing, feeding, locomotive, respiratory, and excremental activities function similarly to marine macrobenthos and play similar roles in altering the physical and chemical properties of sediments. There are, however, some differences between freshwater and marine macrobenthos. Overall, freshwater organisms tend to be smaller than marine organisms, some taxa (echinoderms, burrowing shrimp) are absent, and the biogeochemistry of freshwater differs from that in seawater because sulfate concentrations are much lower. Particle mixing rates and depths are best derived from isotopic measurements using a Constant Initial Concentration (CIC) model for ^{210}Pb accumulation in marine settings whereas the Constant Rate of Supply (CRS) model is often used in small freshwater systems. ^{137}Cs may be used as a chronographic marker in freshwater sediments but it appears to be too mobile to use in marine systems. Future challenges in freshwater systems are to improve our understanding of the mechanisms and rates of exchange of oxygen and nutrients, especially phosphorus, between sediments and the water column to improve ecosystem modeling and predictions of hypoxia. In addition, the role of invasive species in altering mixing rates needs to be better understood and quantified. Other areas requiring future study include understanding the role of freshwater macrobenthos in the evolution of lakes and the geological history of the depth of mixing in freshwaters.

SEDIMENTARY ORGANIC MATTER DISTRIBUTIONS AND BURROWING ACTIVITY: NATURAL PATTERNS AND EXPERIMENTAL ARTIFACTS

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The coupling between biogenic reworking activity and reactive organic matter patterns within deposits is poorly understood and often ignored. In this study, we examined the influence of reactive organic matter distributions in muds on the burrowing behavior of the polychaete *Nephtys incisa*. Sediment and animals were recovered from a single subtidal site in central Long Island Sound, USA. The upper 15 cm of the sediment was sectioned into sub-intervals, and each interval separately sieved and homogenized. Three initial distributions of sediment and organic substrate reactivity were setup in a series of microcosms: (1) a reconstituted natural pattern with surface-derived sediment overlying sediment obtained from progressively deeper material to a depth of 15 cm (termed: natural); (2) a 15 cm thick sediment layer composed only of surface-derived sediment (termed: rich); and (3) a 15 cm thick layer composed of uniformally mixed sediment from the original 15 cm sediment profile (termed: rich+poor). This last treatment is comparable to that used in microcosms in many previous studies of bioturbation and interspecific functional interaction experiments. *Nepthys* were reintroduced and aquariums were X-rayed regularly over 3 months to visualize and quantify spatial and temporal dynamics of biogenic structure. The burrowing behavior of adult populations having similar total biovolume, biomass, abundance, and individual sizes differed substantially as a function of initial reactive organic matter distributions. For example, burrows in sediment with natural organic reactivity gradients were much shallower than those in microcosms without substrate reactivity gradients. In addition to demonstrating how species may respond to physical sedimentation events (e.g., homogenization) and patterns of reactive organic matter redistribution, these experiments suggest that infaunal species interactions in microcosms may be subject to artifacts depending on exactly how sediments are introduced experimentally.

ECOSYSTEM FUNCTION LOSSES FOLLOWING DEFAUNATION OF SEDIMENTS

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Most biogeochemical processes are mediated by microbes and consequently much research within biogeosciences is directed towards micro-organisms at the expense of higher organisms. Nevertheless, higher organisms (macrophytes, animals) govern many ecosystem processes and are essential components of the system Earth. Here we present the results of a deliberate hypoxia experiment resulting in the mortality of macrofauna. The disappearance and subsequent recovery of macrofauna has major consequences for ecosystem functioning. We will show that some ecosystems functions are rapidly restored following oxygen exposure (oxygen penetrations, benthic primary production), while functions governed by benthic animals remained different for months. Our data clearly show that key ecosystem functions such as sediment stability, sediment mixing, nitrogen loss (via denitrification), re-oxidation of sulfides and carbon flow from microbes to higher trophic levels are governed by macrofaunal communities. The slow recovery of macrofaunal communities following disturbances causes a linked delayed response of some ecosystem functions that are microbial mediated.

BENTHOS-MEDIATED SEDIMENT DYNAMICS

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Intertidal sediments are governed in their dynamics not only by environmental forcing variables, but also by their habitants. In a series of defaunation/exclusion experiments we assessed the influence of benthic communities on sediment properties in replicated 16m^2 plots on a tidal flat in the Westerschelde estuary (SW Netherlands). We compared microphytobenthos and benthic macrofauna recovery and recolonisation between control and defaunated sediments during eight months following the defaunation, focussing on how the temporal scale of biological responses interact with the temporal scale of sedimentological developments (grainsize, bed level, erosion threshold). In other defaunated plots we conducted a parallel experiment by applying inert sediment tracers (luminophores) and extracting cores through time for approx. one month. We used novel techniques and in-house developed analysing routines to quantify the vertical distribution of sand and mud fractions by the present macrofauna. Both experiments showed that the influence of both microphytobenthos and macrobenthos is profound, and that these interact in complex ways. Bed level, mud percentage (sediment cohesiveness) and erosion threshold differed significantly between treatments. Also, the vertical distribution of mud and sand fractions differed greatly between treatments. Mud was shown to be more mobile than sand and more so through the macrofaunal effects, causing the overall effect of macrofauna to be erosive. Small changes in sediment bulk parameters, caused by the absence of macrofauna, resulted in great changes in sediment behaviour.

PARTICLE AND SOLUTE TRANSPORT IN ORGANICALLY ENRICHED SEDIMENTS

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The activities of benthic organisms disrupt the sediment matrix and have complex influences upon chemical and biological processes contributing to fluxes of material across the sediment-water interface. As part of a study employing *in situ* methods of observation and measurement in coastal environments to assess benthic ecosystem function, a moored multi-chambered benthic lander was used to make a simultaneous comparison of solid and solute mixing rates under differing conditions of organic enrichment along a gradient provided by the presence of an Atlantic salmon fish farm. Luminophores and bromide were added to chambers and the resulting sediment profiles were used to make simultaneous estimates of particle and solute mixing rates. Comparisons of bioirrigation and bioturbatory activity were used to show the relative importance of each at sites of varying organic content to determine the sensitivity of each to the influence of organic carbon. We discuss the merits of these integrated measures of activity in the assessment of the impact of anthropogenic activity in coastal environments.

ECOSYSTEM FUNCTIONS IN BENTHOS: HOW IMPORTANT ARE MACROFAUNAL BIOTURBATION AND BIODIVERSITY FOR MINERALIZATION AND NUTRIENT FLUXES?

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Knowledge of benthic macrofauna importance for ecosystem functions is still limited. Reasons for this are that macrofaunal diversity is high, activities among species are diverse and the mechanisms between activities and ecological functions are complex and rarely quantified. However a limited number of species have been studied in detail (*e.g. Nereis* and *Hediste*). These studies suggest that bioturbating fauna, interacting with microbial communities in sediments, is essential for the transport and transformation of organic matter and nutrients.

The two benthic ecosystems studied, the brackish Baltic proper and the marine Skagerrak, consist of different species and diversity, due to an increasing salinity gradient from the Bothnian Bay to the North Sea. Interactions between macrofaunal species, micro-organisms, sediments and overlying water were investigated in a series of experiments and field studies.

The marine ecosystem was characterized by steeper abiotic gradients, higher functional diversity and greater fluxes of solids and solutes compared to the brackish. Highlights from the performed studies and the literature will be used to describe why macrofaunal bioturbation and functional group diversity (instead of species diversity) may be important for the measured functions (*e.g.* sediment reworking, organic matter mineralization and nutrient recirculation).

MICROBIAL REACTION RATES AND BACTERIAL COMMUNITIES IN SEDIMENT SURROUNDING BURROWS OF BENTHIC INFAUNA

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The activity and composition of bacterial communities from sediment surrounding burrows of marine infauna with different life habits was studied. Sediment from the burrows of two closely related, but behaviourally different polychaete worms (*Nereis diversicolor* and *Nereis virens*) was collected from Kertinge Nor, Denmark, while that from the burrows of the decapod *Pestarella tyrrhena* was collected from Vravrona Bay, Greece. Burrow linings and walls exhibited always higher organic matter mineralisation rates and bacterial abundance than surrounding sediment. The bacterial community fingerprints (based on 16SrDNA) of burrow linings and walls resembled the ambient anoxic sediment rather than the oxic sediment surface. On the other hand, the bacterial fingerprints of the sediment surrounding the burrows was markedly different for the two polychaete species suggesting either a site-specific difference in sediment parameters or a significant species-specific impact of the burrow inhabitants. These results show that burrow walls are not simple extensions of the oxic surface layer, but should rather be considered as unique biofilms subject to distinctive environmental conditions. In addition, the different life habits of even closely related infaunal species may significantly affect bacterial abundance and community composition.

DEVELOPMENT OF AN INTEGRATED INDICATOR OF SEDIMENT CARBON CYCLING – REDOX AND BIOTURBATION?

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To date, significant effort has been made develop indicators of ecosystem health, which can be used as tools to support various European legislative and policy frameworks in relation to the management of human activities. Central to to these goals, espcially under the European Marine Strategy Directive (2007) is the maintenance of ecosystem biodiversity, goods and services by focusing on structure & function when undertaking the assessment of impacts.

For the sediment system, this involves the development of indicators looking at the sediment state, the role organisms play in maintaining ecosystem function and how this is affected by human impacts. Regional datasets have been examined to explore the utility of a combined metric which describes the relative capacity and rates of the sediment to cycle carbon. Benthic assemblage information is described as a functional 'bioturbation metric' (Solan et al., 2004) and links to a carbon or nutrient cycling function via redox state (aRPD – apparent Redox Potential Discontinuity or BMD – Biological Mixed Depth) as determined from Sediment Profile Images (SPI).

Preliminary results investigate the regional performance of these metrics with respect to response to human impacts (disposal sites, trawling) and natural and regional variability (North Sea). These will be presented alongside more detailed biogeochemical information at key North Sea sites. This contrast will allow exploration of questions relating to the challenges involved in moving from in-depth, site specific bioturbation or biogeochemical studies to regional scales effects and the wider ramifications of biodiversity change on sediment carbon cycling.

EFFECTS OF DOMESTIC SEWAGE DOSING ON EPIFAUNAL BIOTURBATION IN MANGROVE SEDIMENT

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Mangroves are considered capable of filtering domestic sewage and thus prevent coastal pollution. However, this ecosystem service has not yet been conveyed to coastal management, nor has the filtration capacity and the role of phytoremediation, and especially zooremediation, been exploited. Studies have during the last years proved that benthic macrofauna affects the physical, chemical and biological properties of the substratum. A pilot wetland (mangrove wastewater treatment facility) located near Dar es Salaam, Tanzania, was built to develop an optimum wastewater treatment protocol using mangrove ecosystems. The present study focuses primarily on the direct and indirect filtration role of selected faunal species due to their bioturbation activities. The effect of different sewage concentrations on sediment reworking activities by the gastropod *Terebralia palustris* and by the fiddler crabs *Uca annulipes* and *U. inversa* was addressed, as well as the burrow characteristic (volume, format, surface and depth) of the latest. The consequences of these bioturbation effects to the wetland functioning, under different sewage concentration, will be addressed.

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CALLIANASSID BIOTURBATION AS A POSSIBLE MECHANISM FOR DECADAL CHANGES IN FISH AND INVERTEBRATE COMMUNITIES IN AN ESTUARINE EMBAYMENT

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Long term-monitoring of an intertidal sandflat in Durban Bay, South Africa, indicated a major shift in the macrofauna of the region, with bivalves dominating in 1994 (950 ± 273 ind.m^{-2}) but declining to 37 ± 3.3 ind.m^{-2} in 2002. This shift coincided with increases in density of the sandprawn *Callianassa kraussi* in the region, which was rare in 1994, but currently averages 130 ± 17.5 ind.m^{-2}. Moreover, bottom-feeding fish dominated the ichthyofaunal community in 1994, and bivalve siphon tips were a significant component of their diets. In 2002, the fish community was dominated by zooplanktivorous fish, and bivalve siphons were absent in the stomachs of benthic fish. In this paper, we present evidence for a hypothesis that these changes in fish and macrofauna are related to an increase in *C. kraussi* density. Field caging experiments showed a significant negative effect of *C. kraussi* on densities of bivalves, particularly *Eumarcia paupercula*, as well as its survival, condition and microalgal ingestion. We also demonstrated negative effects of *C. kraussi* on sediment microbial biofilms and recruitment of macrofauna, specifically bivalves. We hypothesise that unfilmed sediments act as negative settlement cues for larval macrofauna, or that the increased erodibility of unfilmed sediments results in post-settlement mortality. These results collectively provide evidence that increases in *C. kraussi* density between 1990 and 2002 played a role in altering macrofaunal composition, with likely cascading influences on the fish community through negative effects on food sources. Our findings also suggest that the effects of *C. kraussi* on the macrofauna ripple through higher trophic levels.

BIOTURBATION AND OXYGEN HETEROGENEITY IN MARINE SEDIMENTS. INFLUENCE ON OXYGEN FLUX.

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Macrofaunal bioturbation activities introduce oxygen heterogeneity in marine sediments and control oxygen diffusive fluxes across the sediment-water interface. This is of major importance since the availability of oxygen greatly influences in microbial diagenetic processes of organic matter in sediments. The study of oxygen heterogeneity was addressed in two ways. The first study was based on 2-D oxygen images of sediments inhabited by the biodiffusor *Cyclope neritea* and by the polychaetes gallery-diffusors, *Nereis diversicolor* and *Nereis virens*. In order to compare the impact of these species on oxygen distribution, we have defined a variability index reflecting the degree of spatial heterogeneity of oxygen in sediments. Results have shown that all species increased oxygen distribution heterogeneity and that the diffusive flux, integrated per surface unit, increased with increasing heterogeneity. The second study was performed in order to characterize oxygen heterogeneity and dynamic distribution within a macrofaunal biogenic structure. Two-D oxygen concentration was monitored every 2 minutes in a complete *Nereis diversicolor* burrow during 4 hours. The burrow lumen exhibited a strong heterogeneous oxygen distribution and dynamics that influenced the burrow wall oxygen dynamics since concentrations followed the same pattern as in the lumen. Also, burrow oxygen concentration and the nature of the burrow wall appeared to greatly influence oxygen diffusive flux across the sediment water interface.

MACROFAUNAL IMPACT ON THE DENITRIFYING BACTERIAL COMMUNITY IN FRESHWATER SEDIMENT

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Sediment-dwelling macroinvertebrates alter their habitat by transporting oxic water into the sediment and enriching it for organic matter, thereby affecting microbial processes in the sediment. Here we report that burrowing macroinvertebrates can also have a pronounced effect on microbial diversity, with nitrate-reducing and denitrifying bacteria as examples. The diversity of these functional groups was compared in sediment microcosms with and without *Chironomus plumosus* larvae, using the genes encoding nitrate reductase (*narG*) and nitrous oxide reductase (*nosZ*) as functional markers. The estimated phylotype richness of *narG* increased from 68 in sediment without larvae to 170 in sediment with larvae. Part of this increase in *narG* diversity could be explained by metabolic activation of certain nitrate-reducing bacteria in the gut of *C. plumosus*, since 18.3 % of the additional phylotypes were found actively expressed in the gut contents of *C. plumosus*. The remaining increase may be due to the creation of a (on the microscale) more structured habitat by larval activities like burrow construction, bioturbation, and water pumping, possibly combined with a general activation of microbes by enriching the sediment with partly degraded organic material excreted by the larvae. In contrast to *narG*, *nosZ* phylotype richness was unaffected by the presence of chironomid larvae, and very few *nosZ* phylotypes were actively expressed in the larvae gut. Our results suggest that burrowing macroinvertebrates affect the microbial diversity in sediments, both indirectly by their behaviour and directly by activating certain functional groups of microorganisms passing through their gut.

MODELING BIODIVERSITY EFFECTS ON THE FUNCTIONING OF A SEDIMENTARY, DETRITUS-BASED ECOSYSTEM

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The functioning of marine coastal and shelf sediments greatly influences global carbon and nutrient cycles, through processes such as carbon burial and nutrient removal by denitrification. As these systems become increasingly subjected to anthropogenic stress, there is a need to get a better understanding of how their dynamics and functioning react to external changes. In this modeling study we explore how extinctions influence the functioning of a sedimentary, detritus-based ecosystem, and how the system recovers from perturbations such as organic pollution through natural succession. The dynamic model considers functional effect and response traits, as well as trophic interactions and life history traits. Although sparse, we try to use data from experimental studies in order to parametrize bioturbation activity, bio-irrigation activity, and sulfide tolerance of the macrofaunal species in the model.

CLIMATIC REGULATION OF INVASION IMPACTS ON NATIVE DIVERSITY AND ECOSYSTEM FUNCTIONING

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Invasive ecosystem engineers are high impact species because they modulate resources and contribute disproportionably to ecosystem functioning. These invasions can lead to changes in native diversity that relate to trade-offs between competitive ability and abiotic stress tolerance of invasive (and native) species. We investigated how climate regulates invasion impacts on biodiversity and ecosystem functioning, through changes in functional importance of invasive species.

Abundance distributions of the invasive bioturbating clam *Ruditapes philippinarum* were determined at four sites across a latitudinal temperature gradient in Europe. Species richness increased with the oxygenation depth of superficial sediments (estimated from Sediment Profile Imagery), which was explained by higher densities of *R. philippinarum*. This relationship was stronger when climatic conditions were optimal for the invasive, and when bioturbation contributed more to sediment oxygenation relative to environmental processes. Experimental manipulation of community evenness, and richness, across temperature treatments corroborated the functional importance of this species in invaded communities. Bioturbation was enhanced where the species was present, and dominant, and when temperature was optimal for *R. philippinarum*.

This study provides evidence for climatic regulation of the link between biodiversity and bioturbation trough changes in species functional importance.

NITROUS OXIDE EMISSION BY AQUATIC MACROFAUNA

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Many macrofauna species co-ingest large quantities of microorganisms some of which survive the gut passage. Denitrifying bacteria, in particular, become metabolically induced by anoxic conditions, nitrate, and labile organic compounds in the gut of invertebrates. A striking consequence of the short-term metabolic induction of gut denitrification is the preferential production of nitrous oxide rather than dinitrogen. These observations were made in detailed studies on the larvae of the freshwater insects *Chironomus plumosus* and *Ephemera danica* which both can be very abundant in lake and stream sediments, respectively. Aside from these case studies, we screened more than 20 macrofauna species in various aquatic habitats for nitrous oxide production. Filter- and deposit-feeders that ingest large quantities of microorganisms were the most important emitters of nitrous oxide. In contrast, predatory species that do not ingest large quantities of microorganisms produced insignificant amounts of nitrous oxide. With increasing eutrophication, filter- and deposit-feeders often become the dominant feeding guilds of benthic communities. Thus, with increasing nitrate pollution, aquatic macrofauna has the potential to further heighten nitrous oxide emission from aquatic ecosystems.

BIOTURBATION: THE ELEPHANT IN THE DARK AND RECONCILING CONTRARITIES WITH IMAGING

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The advent of complex bioturbation is one of the most significant events in the evolution of marine ecosystems and its importance in mediating global biogeochemical processes provides a compelling reason for wanting to quantify in situ rates of bioturbation. Several approaches have been developed for estimating the rate and extent of bioturbation, although multiple approaches are seldom used in concert and the bioturbation intensity coefficient (D_b) has become the common currency of comparison. Whilst the computation of D_b (or equivalent coefficients) provides a convenient and mechanistic understanding of infaunal activity, it is fundamentally important that the assumptions behind these models are developed with reference to biological understanding. Yet, the bioturbation literature base is effectively comprised of two subsets; studies which develop and present new models of bioturbation that are largely based on theory, versus studies that attempt to fit such models to data obtained from named species. The tale of the blind men and the elephant reminds us that reality may be viewed differently depending upon one's perspective; what seems an absolute truth may be relative due to the deceptive nature of half-truths. Here I provide an overview and examples of how a combination of existing bioturbation models and imaging technology can inform the next generation of bioturbation models and argue that, by adopting such an approach, we will accelerate our understanding of how the activities of benthic biodiversity are causally linked to key ecosystem processes.

NOVEL IN-SITU TECHNIQUES FOR LINKING BIOLOGICAL ACTIVITY TO SEDIMENT FUNCTION

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In order to link biological data on bioturbation to ecosystem processes in the sediment, such as nutrient regeneration, simultaneous in-situ measurements of both biology and sediment chemistry conditions are required. A novel in-situ technique has been developed for measuring sediment porewater trace metal profiles (redox conditions) alongside biological activity (bioturbation) by combining DGT gels and time-lapse sediment profile imaging (t-SPI). The SPI including the gels (g-SPI) was deployed at two sites within the North Sea (Oyster ground and Dogger Bank) that support different biological communities. The profile images show higher biological activity at the Oyster ground than the Dogger Bank. The DGT profiles further suggest that background diagenetic processes are more highly affected by biological activity at the Oyster ground then the Dogger. The method was validated by taking gels from cores retrieved at the same sites, the common method used for DGT. Ongoing work is combining the g-SPI technique with tracking sediment particles in order to link in-situ sediment reworking rates to observed redox conditions. The link between biology and chemistry provides a key step towards determining the function of macrofauna in relation to reaction rates within the sediment.

REVISITING THE ALLER TUBE-IRRIGATION MODEL: INFINITE VERSUS FINITE BURROW VENTILATION

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Up to now, models describing burrows and their bio-irrigation effects on their surrounding sediment use the Aller tube model, which assumes that the oxygen concentration at the burrow wall equals the concentration in the overlying water. This requires an infinite ventilation rate. This approximation is very crude: benthic organisms typically achieve a finite pumping rate so that O2 concentrations in the burrow water are markedly lower than in the overlying water. Here we investigate an adaptation of the Aller model with a finite ventilation rate. The actual O2 concentration at the burrow wall is determined from an O2 mass balance over the burrow water volume. In total three different model approximations were made, which simplify this mass balance, so one does not need to revert to computationally demanding numerical software. A first, baseline model assumes that non-local flushing is the only transport mechanism in the burrow (no downward diffusion) and that burrow walls are flat. A second, more refined model also implements non-local flushing but accounts for the curvature of the cylindrical burrow wall. A third model adds downward diffusion as transport in addition to non-local flushing, while keeping the burrow walls flat. In each of these models, we compared the effects on oxygen consumption and penetration depth in the surrounding sediment, and evaluated the results of the sequential refinements.

EFFECTS OF BIOTURBATION ON BENTHIC RECRUITMENT OF *NODULARIA SPUMIGENA*

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The harmful bloom-forming cyanobacterium *Nodularia spumigena* produces resting cells (akinetes) that are deposited on the seabed and potentially play a role in initiating the future blooms. Activities by benthic deposit feeders may alter the recruitment success of *N. spumigena* from these sedimented propagules, thereby notably contributing to ecosystem processes. In this study we investigated the influence of bioturbation and possible grazing by various soft-sediment zoobenthic communities on the fate of benthic cells and germination potential of *N. spumigena* by means of a 4-week laboratory experiment. Akinetes and filaments of *N. spumigena*, labeled with a stable isotope, were introduced to natural intact sediment cores collected from shallow soft-sediment archipelago sites, dominated by either the bivalve *Macoma balthica* or the polychaetes *Marenzelleria* spp. In addition, cores from an anoxic site devoid of fauna were included. Germination of akinetes and filaments was determined once a week by means of inverted traps deployed above the sediment surface and removed after 2 d. Additionally, abundances of vegetative cells as well as nutrient concentrations in the water column were determined once a week. At the end of the experiment, a subcore from the sediment was collected to determine the vertical distribution (faunal-mediated mixing) of labeled akinetes. Macrofauna and meiofauna were analyzed for stable isotope signature to assess benthic grazing on *N. spumigena* cells. The effect of deposit feeders along a gradient of changing diversity and species dominance on the benthic recruitment success of *N. spumigena* will be discussed.

THE IMPORTANCE OF THE LOSS OF KEY SPECIES FOR ECOSYSTEM FUNCTIONING

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Rapid changes in biodiversity are occurring globally, yet the ecological impacts of diversity loss are still poorly understood. A central question is how the loss of biodiversity might alter the functioning of ecosystems. Shifts in biodiversity associated with the removal of functionally important species are predicted to have wide ranging implications for the resilience of ecosystems, and to be crucial for predicting recovery potential of anthropogenically affected sea areas. Large deep-burrowing bivalves often play a pivotal role in benthic-pelagic coupling and can have important facilitating effects on surrounding communities. Disturbance results in a loss of such long-lived key-species. Even though the functions of suspension-feeding bivalves have been investigated under laboratory conditions, the role of their presence or absence in disturbed areas has not been evaluated in field conditions. Hence, the functions of large, long-lived suspension-feeding bivalves (*Macoma balthica* and *Mya arenaria*) were investigated in a recovering habitat (one year after disturbance; no large bivalves present), in a treatment with elevated bivalve densities as well as in a control community. In situ flux chambers were used for measuring the impact of the suspension feeders on water and sediment nutrient fluxes. The results indicate clear differences in ecosystem responses, both for oxygen consumption and nutrient fluxes, and further studies will thus be necessary for defining resilience. This will especially be of importance in the degraded benthic habitats of the Baltic Sea, where hypoxia severely has altered the way benthic communities contribute to ecosystem processes.

FLUSHING OF INTERTIDAL SAND BY LUGWORMS: FROM INDIVIDUAL HYDRAULIC ACTIVITIES TO LARGE SCALE IMPLICATIONS

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Hydraulic activities of the lugworm *Arenicola marina* were found to induce widespread porewater pressure signals in intertidal sediments. To link lugworm hydraulic behaviors and porewater fluxes, we monitored pressure fluctuations in sandwich aquaria, in sync with 2-dimensional oxygen imaging with planar optodes and time-lapse photography. Certain lugworm activities, such as defecation, burrowing, and pumping, generated characteristic porewater pressure signals and induced dynamic oxygen distributions above and below the sediment surface. Most of the time lugworms pumped water through the open tail shaft into the blind ending burrow, raising porewater pressures and causing percolation of anoxic water out through the sediment-water interface. Pressure-driven transient flow reversal caused a percolation of oxygen rich surface water through the sediment-water interface into the sediment. Based on porewater pressure gradients measured in the field, the modeled porewater fluxes imply a complete turnover of porewater once per day within a spheroidal region 10-15 cm in diameter centered on the feeding pocket of the animal. Porewater nutrient profiles from 400 m² plots of a large-scale exclusion experiment confirmed that the concentrated hydraulic activities of lugworms result in a continuous flushing of the sediment to a depth of 15-20 cm. We conclude that hydraulic activities of lugworms have fundamental implications for benthic-pelagic coupling and biogeochemical processes in Wadden Sea sediments over spatial scales of thousands of square kilometers.

TOWARDS A MECHANISTIC UNDERSTANDING OF BIODIVERSITY-ECOSYSTEM FUNCTIONING RELATIONSHIPS IN MARINE SEDIMENTS: SIMPLE SPECIES INTERACTIONS, COMPLEX OUTCOMES

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Correlative relationships between biodiversity and ecosystem functioning (BEF) have been illustrated in many habitats, though the underlying mechanisms are poorly understood. In communities of bioturbating infauna, biodiversity effects may lead to changes in behavior due to direct species interactions thereby affecting ecosystem functioning indirectly through modification of physical and biogeochemical processes. The well established link between bioturbation and biogeochemical processes makes marine sediments an excellent test bed for examining BEF relationships. For example, the impact of increased burrow surface area for solute exchange is well documented; however how these surface areas vary as a function of species interactions is poorly understood. Knowledge of the behavior of a limited number of key species affords the opportunity to utilize them in experimental systems that allow for simplified and controlled species interactions and the quantification of their effects on physical and biogeochemical processes. Results from field and laboratory studies utilizing such simplified infaunal communities show that their effects on ecosystem function are often complex, but may be rooted in simple physical and biogeochemical processes. The experimental outcomes are examined in the context of species interactions and implications for "biodiversity effects". Additionally, future research objectives examining the role of species interaction and their effects on sediment biogeochemistry are presented.

THE ROLE OF BIOTURBATION IN A SOURCE-TO-SINK WORLD

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Recent efforts to study the transport of sediment and associated constituents (e.g., POC, contaminants) from the land to the sea and the development of the stratigraphic record have taken a whole-margin "source-to-sink" perspective. Thus, phenomena ranging from hill slope sediment erosion to floodplain storage to deep-ocean stratigraphy are measured and modeled. Bioturbation plays an important role in the source-to-sink world, but its primary effect changes as one moves through the dispersal system. On the hill slope (the source), bioturbation by plants and animals is a major source of sediment movement, whereas in the marine realm (the sink) bioturbation primarily destroys signals. This talk will explore bioturbation effects throughout the land-ocean continuum and examine how system(s) behavior might be different in the absence of Darwin's last idea.

THE RELATIONSHIP BETWEEN BIOTURBATION AND BENTHIC BIODIVERSITY

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The organisms which inhabit marine sediments make up some of the most diverse communities on the planet. This diversity ultimately results from complex interactions between the prevailing environmental conditions and a number of biological processes. A large number of these biological processes are primarily interactions between organisms at either the individual or population level. Such interactions can occur directly (e.g. predation) or indirectly, as organisms alter the environmental conditions within which the rest of the community must exist. Within sediment communities a key process responsible for these interactions is the disturbance created by the movement and feeding activities of infaunal and epifaunal organisms, a process known as bioturbation. Many studies have demonstrated strong links between macro-, meio- and micro-organisms with bioturbation playing a key role. Consequently, it is accepted that bioturbation can be instrumental in setting community structure. Whilst all organisms will create a disturbance simply by their presence within the sediment, it is clear that the activity of particular organisms can have a disproportionately large bioturbatory effect, in relation to their abundance. These organisms, known as ecosystem engineers, have the potential therefore to modify, maintain and/or create habitats. In light of theoretical relationships between disturbance and diversity (e.g. Intermediate Disturbance Hypothesis, Dynamic Equilibrium model and spatio-temporal mosaics) it is also clear that seasonal and spatial patchiness in the distribution of bioturbating organisms can influence community heterogeneity and maintain species diversity.

TRANSIENT PRESSURE PULSES, POREWATER FLUX, AND ASSEMBLAGE CHARACTERISTICS

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Pressure sensors can measure transient pressure pulses generated by infauna, both in the field and in the laboratory. Using such measurements for common large infauna, one can calculate the biogenic advective forces and resulting porewater flux both for an individual and for an assemblage comprised of several species. We have now measured such pressure transients for a variety of species that are the dominant large infauna in several sedimentary assemblages both in Europe and in the United States and have associated the wave forms of the pressure transients with particular behaviors. Interestingly in some cases animal behaviors by large infauna do not result in detectable pressure transients. In all cases this absence results from one of the following: (1) uninterrupted connections between the animal and the overlying water column, (2) very high permeability of the sediment column, or (3) highly reinforced burrow walls. Several species of thalassinid crustacean for example do not appear to generate transient pressures in sediments due to highly reinforced burrow walls. In contrast, many large and abundant infauna such as arenicolid and nereid polychaetes and tellinid bivalves do generate such pressures. Using these data we ask what are the expected rates of porewater flux as a function of the composition and species density of several infaunal assemblages.