Organisms as cooperative ecosystem engineers in intertidal flats

CrossMark

Claire Passarelli [a,*], Frédéric Olivier [a,b], David M. Paterson [c], Tarik Meziane [a], Cédric Hubas [a]

[a] UMR BOREA 7208 CNRS/MNHN/UPMC/IRD, Muséum National d'Histoire Naturelle, Bâtiment des Arthropodes, CP53, 61 rue Buffon, 75231 Paris Cedex 5, France
[b] ISMER/UQAR, CP3300, Rimouski, QC G5L 3A1, Canada
[c] Sediment Ecology Research Group, School of Biology, Scottish Oceans Institute, University of St Andrews, St Andrews KY16 8LB, UK

A B S T R A C T

The importance of facilitative interactions and organismal ecosystem engineering for establishing the structure of communities is increasingly being recognised for many different ecosystems. For example, soft-bottom tidal flats host a wide range of ecosystem engineers, probably because the harsh physico-chemical environmental conditions render these species of particular importance for community structure and function. These environments are therefore interesting when focusing on how ecosystem engineers interact and the consequences of these interactions on community dynamics. In this review, we initially detail the influence on benthic systems of two kinds of ecosystem engineers that are particularly common in tidal flats. Firstly, we examine species providing biogenic structures, which are often the only source of habitat complexity in these environments. Secondly, we focus on species whose activities alter sediment stability, which is a crucial feature structuring the dynamics of communities in tidal flats. The impacts of these engineers on both environment and communities were assessed but in addition the interaction between ecosystem engineers was examined. Habitat cascades occur when one engineer favours the development of another, which in turn creates or modifies and improves habitat for other species. Non-hierarchical interactions have often been shown to display non-additive effects, so that the effects of the association cannot be predicted from the effects of individual organisms. Here we propose the term of "cooperative ecosystem engineering" when two species interact in a way which enhances habitat suitability as a result of a combined engineering effect. Finally, we conclude by describing the potential threats for ecosystem engineers in intertidal areas, potential effects on their interactions and their influence on communities and ecosystem function.

© 2013 Elsevier B.V. All rights reserved.

Contents

1. Introduction

Interspecific competition has long been considered as the main process in structuring communities. Yet, in the last decades, the potential role of positive interactions between species has been increasingly recognised. Positive interactions involve at least two organisms, and benefit one or more organisms without negatively affecting any other organism (Bertness and Leonard, 1997). Positive interactions can be direct or indirect, obligatory or facultative and may be trophic or not. Among them, facilitative interactions describe non-trophic interactions where organisms promote, through their presence or activity, the settlement or development of other species. Facilitation and competition often occur simultaneously in communities, and the nature of the interaction between two individuals can even change according to growth stage or environmental conditions (Callaway and Walker, 1997). Also,

indirect facilitation of a species by another can offset the negative effects of competition between these organisms.

In this context, species contributing to the creation, modification or maintenance of habitats, and therefore having a crucial effect on other species, have been defined as ecosystem engineers by Jones et al. (1994). Ecosystem engineers can be found in terrestrial and aquatic ecosystems: for instance, earthworms that alter the composition of soils, beavers that create dams and seagrasses that modify local hydrodynamics (Fonseca et al., 1982), stabilise sediment (Gacia and Duarte, 2001), and provide a substratum for epibionts, are often referred to as ecosystem engineers. These can either transform living or non-living material in the environment from one physical state to another, or modify, through their physical presence and activity, the access to resources for other organisms. For instance, benthic macrofauna change the physical, chemical and biological properties of sediment through bioturbation (Braeckman et al., 2010), and thus are defined as allogenic ecosystem engineers. In contrast, submerged macrophytes, through their own structure, attenuate the light available for benthic organisms (Lee et al., 2001) and are therefore defined as autogenic ecosystem engineers.

The engineering effect may vary according to the considered species, and is therefore not always positive for the community in terms of diversity or abundance. For example, the exclusion of the lugworm *Arenicola marina* from intertidal sediment facilitates the development of tube-building worms, but hinders the settlement and growth of subsurface deposit feeders (Volkenborn and Reise, 2007). However, at large spatial and temporal scales, the overall impact of ecosystem engineers on ecosystems is generally positive (Jones et al., 1997). The global effect of an ecosystem engineer will mainly depend on 6 factors: the spatial distribution of its population; its density; the time period over which a population has been present at a site; the durability of impacts in the absence of the original engineer; the per capita activity of individual organisms and its lifetime; and, finally, the number and type of resources modulated by the engineer, and the number of species depending on these flows (Jones et al., 1994, 1997). Most engineers modify their environment with small-scale processes, which ultimately affect ecosystem functioning; yet, there are still questions about the links between effects at small or large spatial scales.

When considering the importance on these non-trophic interactions, it might be appropriate to replace the well-known food web by a more complete interaction web (Kéfi et al., 2012; Lawton and Jones, 1995). For instance, the influence of bioturbating worms on microphytobenthos cannot be easily predicted without considering non-trophic interactions (Fig. 1, Passarelli et al., 2012a). These authors demonstrated that while worms consume microphytobenthos, they also stimulate microalgal

growth through indirect facilitation, including mechanisms such as bioturbation redistributing nutrients.

Habitat creation, modification, and facilitation processes are crucial in some specific ecosystems. Indeed, biogenic habitat alterations can increase local diversity by allowing immigration of less well-adapted species by moderating harsh conditions (Bertness and Leonard, 1997; Hacker and Gaines, 1997). Therefore, ecosystem engineers play critical roles in intertidal areas, where species are subject to a large range of physical stresses: desiccation, variations of salinity and temperature (Little and Kitching, 1996). Also, numerous studies have shown the importance of facilitation and ecosystem engineering in these environments (Bertness and Leonard, 1997). The presence or absence of a single critical species can completely alter the structure of the whole community. For instance, the long-term exclusion of the bioturbating worm, *A. marina*, from a tidal flat modifies sediment properties, microbial and macrofaunal communities, by stimulating the development of sediment-stabilising organisms which are naturally excluded where *A. marina* is dominant (Volkenborn and Reise, 2007; Volkenborn et al., 2007, 2009). Such transitions between two stable ecosystem states are often prompted by positive feedback mechanisms, where organisms belonging to each community stimulate the development of its own community (Wilson and Agnew, 1992). For instance, the development of diatom biofilms on tidal flats will contribute to sediment stabilisation, therefore limiting the erosion of their own habitat, and stimulating their own population growth (van der Heide et al., 2007).

The common occurrence of ecosystem engineers in intertidal flats makes it an interesting system to study such interactions. These species are likely to interact in a manner which makes it difficult to differentiate the overall engineering effect of the association from the contribution of the individual species. This review focuses on soft-bottom intertidal areas in temperate waters, where numerous ecosystem engineers have been studied and described (Table 1). In this short review, we do not try to address every possible example but concentrate on systems that, in our experience, serve to highlight the co-engineering concept. Once introduced, this approach should be relevant to many other systems not considered in detail here, such as coral reef (Bozec et al., 2013), mussel and oyster beds (Grant et al., 2012; Lejart and Hily, 2011) among others. In addition, there is no reason to limit the approach to marine systems and expect terrestrial examples to emerge. Therefore, the role of some biogenic structures, which provide habitat complexity, is described first as spatial complexity that is important in maintaining local diversity (Bouma et al., 2009; Zühlke et al., 1998). The second part of the review will then focus on the ecosystem engineers which promote sediment stabilisation or destabilisation, and affect the settlement and growth of a large range of other species. Finally, the interaction of the engineers
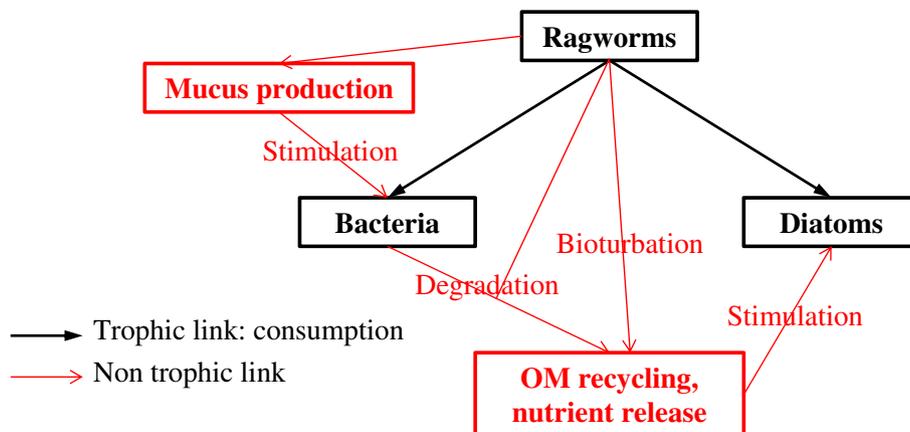

Fig. 1. Trophic web (in black) and interaction web (whole diagram) in a simplified benthic system with ragworms, diatoms and bacteria. Results from Passarelli et al. (2012a).

Table 1
Some examples of ecosystem engineers in tidal flats and their impact on their environment. Associated references.

Engineer	Activity	Impact	References
Polychaete *Lanice conchilega*	Tube building	Modification of hydrodynamics	Rabaut et al. (2007)
	Piston pumping of O_2 into sediment	Modification of O_2 repartition in sediment	Forster and Graf (1995)
Meiofauna	Bioturbation	Increase of nutrient fluxes in sediment	Aller and Aller (1992)
Macrofauna	Bioturbation	Increase in OM remineralisation and nutrient turnover	Braeckman et al. (2010)
Polychaete *Nereis diversicolor*	Burrow construction	Increase in O_2 concentrations in sediment	Scaps (2002)
		Increase of nutrients fluxes towards water column	
Kelp macroalgae	Presence	Modification of wave and current dynamics	Eckman et al. (2003)
Zostera sp.	Presence	Modification of hydrodynamics	Lee et al. (2001), van der Heide et al. (2007)
Bacteria	Biofilm production	Sediment stabilisation	Gerbersdorf et al. (2008)
Microphytobenthos	Biofilm production	Sediment stabilisation	Holland et al. (1974)
			Lubarsky et al. (2010)
Polychaete *Arenicola marina*	Bioturbation and bioirrigation	Modification of physico-chemical properties of sediment	Volkenborn et al. (2007)
	Formation of coiled faecal casts	Modification of hydrodynamics	Friedrichs and Graf (2009)
Salt marsh plants	Presence	Increase of habitat complexity	van der Wal and Herman (2012)
		Buffer of salinity and temperature	
		Modification of hydrodynamics	
Polychaete *Diopatra cuprea*	Tube building	Supply of substrata	Berke (2012)
		Predation refugia	
Oyster *Crassostrea giga*	Reef formation	Increase of substratum complexity	Lejart and Hily (2011)
		Supply of substrata	

and the consequences that can be expected at a community level will be discussed. In each of the first two sections, diversity of engineers will be quickly addressed but most attention will be given to common engineers, whose interactions with other species are numerous, and this will be discussed in the third section. Specifically, the influence of annelid tubes and biofilms as ecosystem engineers will be thoroughly investigated, and their possible cooperative engineering effect will be demonstrated.

2. Ecosystem engineers providing biogenic structures

For numerous benthic organisms, access to oxygen, nutrients or food resources is highly dependent on fluid dynamics at the sediment–water interface. Any organism capable of locally modifying the pattern of benthic boundary layer (BBL) flows by its presence or activity is therefore likely to act as an ecosystem engineer in an intertidal system. For instance, blades of the seagrass *Zostera marina* are able to modify the BBL dynamics within the seagrass bed affecting a large range of macrofaunal organisms (Lee et al., 2001). For tube-building species, such as the polychaete *Owenia fusiformis*, tube density will control characteristics of BBL flows in intertidal areas (Eckman et al., 1981); polychaete tubes are often the main structuring elements of soft-bottom tidal flats and have therefore been extensively studied in the past decades (Luckenbach, 1986; Zühlke et al., 1998). More recently the importance of maerl beds, created by the branching of calcareous algae, has been recognised as important on a European scale (Wilson et al., 2004). Like tube-fields these habitats enhance local biodiversity (Jackson et al., 2004) and often provide protection for commercially important species (Kamenos et al., 2004; Nelson, 2009). It should be noted that in some instances it is not necessary for the structuring organism to be alive to have the effect. Relict tube-fields still influence hydrodynamics while the calcareous remains of coralline algae from the maerl beds still protect benthic habitat although no longer active. The structures built by organisms have been defined as biogenic structures; polychaete tubes are a well-known example but illustrations are much more diverse, including mollusc shells, coiled faecal casts, maerl and furrows (Fig. 2).

Some of these engineers have a dual effect on benthic ecosystems: one is related to their impact on the surface roughness element, which modifies water flow at the BBL; while the second is related to the organism's biological activity. For instance, kelp macroalgae produce large quantities of exudates (Abdullah and Fredriksen, 2004) which can be consumed by other organisms and *Lanice conchilega* pumps water into the sediment thus affecting O_2 distribution and the turnover of organic matter (Braeckman et al., 2011; Forster and Graf, 1995). However,

most studies comparing the net effect of the whole organism with the influence of the roughness elements alone showed that the effect of these engineers was mainly due to the physical structure (Callaway, 2003; Thistle et al., 1984). Therefore, the influence of different artificial structures, or roughness elements, on water flow has been extensively used as model system to characterise the nature of such effects in flume experiments (Eckman et al., 1981; Friedrichs et al., 2000; Luckenbach, 1986; Nowell and Jumars, 1984; Wilkie et al., 2012). Three distinct patterns have been demonstrated to occur, depending ultimately on the density of roughness elements. At very low densities, the overall effect of a given cluster of biogenic structures (individual elements) can be considered as the sum of individual effects: every structure modifies the near-bed flow dynamics but these perturbations do not interact with each other; however the individual local effect on the sediment (scour) can be severe. When densities increase, interactive flow is established within the group of elements. When this becomes significant, which induces turbulence, an overall destabilisation of the substratum occurs. At higher element densities, most of the flow passes above the biogenic structures, and water velocity at the sediment surface is reduced, the turbulence being induced above the structure of the element (Paterson and Black, 1999). This "skimming flow" regime promotes both particle deposition and protection of the sediment. The threshold density of elements for reaching skimming flow will vary with the ambient velocity: for instance, Friedrichs et al. (2000) demonstrated that, for a current velocity of 5 cm · s^{-1}, skimming flow will develop as soon as roughness elements cover 2% of the surface of sediment. Yet, further studies showed that effects on water flow may vary according to the shape of the structures, as well as their stiffness (Friedrichs and Graf, 2009; Peralta et al., 2008) making absolute prediction problematic.

Because of their effect on hydrodynamics, sediment stability and nutrient availability, biogenic structures affect both recruitment and growth of benthic organisms. The effects of these structures on macrofaunal communities have been extensively characterised, with special attention to annelid tubes. These structures modulate the recruitment of benthic macrofauna, mostly by facilitating their settlements (Gallagher et al., 1983). Yet, the effect is species-specific, and inhibitory interactions have also been demonstrated (Bolam and Fernandes, 2002; Whitlatch and Zajac, 1985). The abundance and diversity of macrofaunal assemblages increase within and upon biogenic structures, both in the short and long-term (Callaway, 2003, 2006; Rabaut et al., 2007). There are species specific variations, so that the structure of the community also changes when tubes are present (Callaway, 2003; Zühlke, 2001). Similar effects on macrofauna have been demonstrated for other engineers, such as

Fig. 2. Diversity of biogenic structures. a. Mollusc shell. b. Macroalgal fragment. c. Tube of *Lanice conchilega*. d. *Zostera marina*.

Z. marina (Lee et al., 2001; Thistle et al., 1984). Other assemblages, particularly meiofauna, are also affected by polychaete tubes, but a general pattern is difficult to interpret as the effect of tubes on a species may vary according to its specific requirements regarding current velocity and organic matter content (Eckman, 1983). For instance, Zühlke et al. (1998) demonstrated that the abundance of a specific group of nematodes increases when tubes are present, while Passarelli et al. (2012b) showed a reverse tendency for most meiofaunal groups excepting the foraminiferal assemblages. Finally, biogenic structures were shown to prompt a short-term increase of bacterial abundances in flume experiments (Eckman, 1985), while no effect of these structures was demonstrated in situ at a longer temporal scale (Passarelli et al., 2012b). Nevertheless, polychaete tubes were shown to stimulate the development of microalgal biofilms (Passarelli et al., 2012b).

The effects of roughness elements on hydrodynamics can explain most of their influence on communities; however, these general patterns can become more intricate as some biogenic structures may also act as a refuge (Woodin, 1978), and the associated species richness may increase when biogenic structures becomes more complex (Bell, 1985). Also, many studies demonstrated that the engineering effects on communities may vary according to seasons: similar experiments that run at different times of the year generated different results, but patterns of variations were difficult to decipher (Bolam and Fernandes, 2002; Eckman, 1983). Differential effects on recruitments and development may explain why the influence of the engineers on both abundance and composition vary seasonally (Callaway, 2006). In addition, temporal effects may be accentuated, as the ecosystem engineer itself is likely to show seasonal development or variations in growth. For instance, *L. conchilega* tubes may be destroyed by waves, storms or freezing events and this may have an impact even when tubes are often rebuilt in the following 24 h (Zühlke, 2001). The seasonal and interannual dynamics of the engineer itself is likely to influence the composition and structure of benthic communities. For example, kelp forests damaged by winter storms take much longer to recover, and this can be affected by climatic conditions such as El Niño events (Dayton and Tegner, 1984).

3. Sediment stability in coastal sediments: a combination of physico-chemical factors and engineering effects

In coastal habitats, sediment erodibility depends ultimately on the balance between multiple erosive and resistive forces. Though it is well known that hydrodynamics is the major erosive driver in coastal habitats as flow generates shear stress on surface sediment layers; sediment also displays various physical, geochemical and biological characteristics that promote resistance to erosion (Black et al., 2002; Dade et al., 1992; Grabowski et al., 2011). Assessing which factors are the major resistive forces is not straightforward as they have complex and sometimes antagonistic effects on sediment stability. In addition, how the different factors may interact to promote resistance to sediment erosion has seldom been studied.

Average particle grain size and particle size distribution (i.e., percentages of clay, silt and sand) are important physical variables in the sediment that reflect mostly the exposure to water movements due to wave action and currents (Raffaelli and Hawkins, 1996). Notably, sediment cohesion increases with the amount of clays because fine particles with a high surface to volume ratio are subject to hydrogen bonding and this inter-particle attraction is important in bed cohesion (Grabowski et al., 2011). The extent of the attraction varies with packing and physico-chemical conditions so pore-water content (which is correlated to bulk density and porosity of the sediment, Avnimelech et al., 2001) and salinity are crucial.

Furthermore, microbial secretions of extracellular polymeric substances (EPS: a general term for polymers secreted from cells) have been increasingly recognised as a major stabilising factor in coastal sediments (Decho, 1990). In intertidal ecosystems, earlier studies have shown that persistent diatoms' vertical-migration rhythms within the sediment (Fauvel and Bohn, 1907; Palmer and Round, 1967) produce a mucilage that is responsible for the observed increased sediment stability (Paterson, 1989). This secretion induces the formation of an extensive matrix throughout the sediment surface as well as fine strands that attach grains together (Fig. 3). Coastal
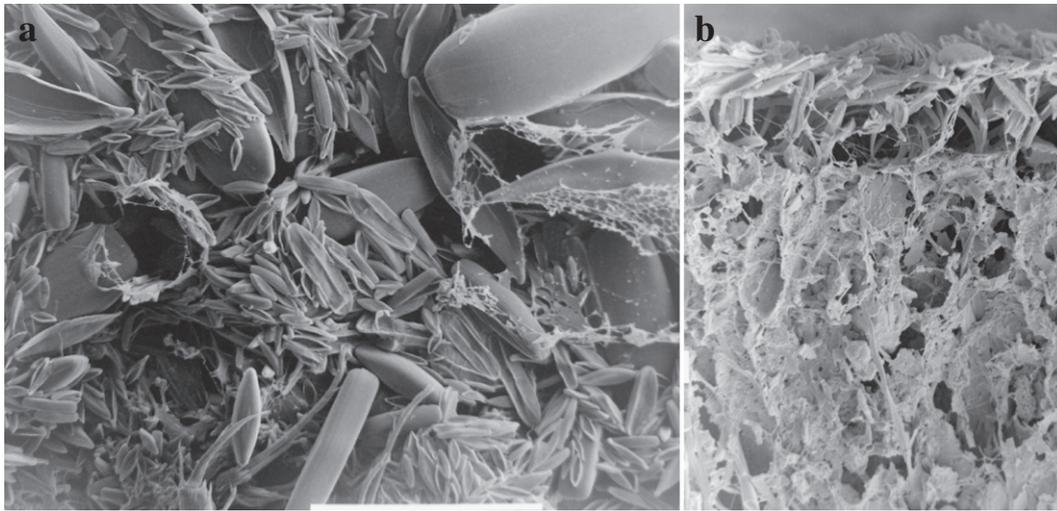
Fig. 3. LTSEM images of a microphytobenthic biofilm on sediment, showing the links between sediment particles through EPS. a. Surface of the biofilm. White bar: 100 μm. b. Fracture face; the sediment surface is at the top. White bar: 10 μm.

ecosystems are indeed characterised by strong physical and geochemical gradients under varied geomorphological settings, which create a multitude of habitats and niches (Raffaelli and Hawkins, 1996). In response to these environmental stresses, microbes have developed different strategies. In this context, EPS secretion can be seen as a protection mechanism against resuspension but has many other important roles (Decho, 1990). The demonstration of this hitherto unrecognised capacity of microorganisms to promote resistance to erosion (and particularly of diatoms in tidal ecosystems and estuaries), gave rise to numerous studies and the general acceptance that microbial EPS are a major stabilising force in coastal ecosystems (Gerbersdorf et al., 2008; Lubarsky et al., 2010; Raffaelli and Hawkins, 1996; Stal, 2010); therefore organisms responsible for these secretions are now considered as crucial ecosystem engineers in tidal environments.

Extracellular polymeric substances (EPS) have multiple roles in aquatic systems: attachment to substrata, feeding sources, protection against desiccation/UV/pollution, adhesion of microbes to surfaces, development of biofilms, cell to cell communication (Decho, 1990; Hori and Matsumoto, 2010; Leppard, 1995; Underwood and Paterson, 2003; Wotton, 2004). In the Arctic Ocean, it is suggested that EPS play an important buffering and cryoprotectant role for diatoms, against harsh winter conditions of high salinity and potential ice-crystal damage (Krembs et al., 2002). EPS are primarily composed of polysaccharides, proteins, various glycoconjugates and other macromolecules such as nucleic acids and humic acids. EPS are classified into bound EPS (including tightly bound EPS such as capsular polymer or loosely bound EPS such as mucilage) and soluble EPS or colloidal fractions released into bulk water. Thus EPS display a great molecular complexity and diversity, and have a multitude of forms, size, and activities (Decho, 1990). Nevertheless, regardless of the diversity of specific structure, species diversity and chemistry of coastal biofilms, EPS are a unifying biofilm component on which the integrity of the assemblages depends. In coastal ecosystems, EPS that enhance mineral inter-particle cohesion consist mainly of colloidal high-molecular weight compounds and also of tightly wound capsules at the microbial cell surface (Decho, 1990). Other molecules such as exoenzymes (e.g., beta-D-glycosidase, amino-peptidase) or signalling molecules (e.g., N-Acyl homoserine lactone which enables the coordination of group-based behaviour based on bacterial population density) are also secreted outside the cell wall and thereby indirectly influence sediment stability (Decho, 2000).

Microorganisms are not the only engineers capable of altering sediment stability. Meiofauna are small benthic invertebrates that live in both marine and fresh water environments (Higgins and Thiel, 1988; McIntyre, 1969). The term was first introduced in 1942 by Mare and refers to a size class of organisms (between c.a. 45/63 μm and 500 μm/1 mm) rather than to a taxonomic group (Mare, 1942). They are classically divided into two main categories (Giere, 2009): the permanent (which corresponds to organisms that spent their entire life cycle in this size category) and temporary meiofauna (which corresponds to juvenile stages of larger organisms: i.e., macrofauna). Macrofauna refers therefore to larger organisms (i.e., retained on a mesh of 500 μm/1 mm) that live on or in sediment. These benthic organisms have contrasting effects on sediment biofilms; depending on their size, abundance and behaviour they can cause a destabilisation of the sediment and therefore of the associated biofilms.

Bioturbation refers to the biological reworking of sediments. Faunal activities, such as burrowing, ingestion and egestion of sediment particles (e.g., such as by the lugworm *A. marina*), construction and maintenance of galleries and burrows, alter bed topography and are highly destructive for biofilms and therefore increase erodibility (Andersen, 2001; de Deckere et al., 2001). But any attempt to classify macrofaunal organisms as net destabilisers would be spurious. It has been proved that, despite an intense burrowing activity and a strong trophic pressure, the common ragworm *Hediste diversicolor* was able to enhance microbial activity and biofilm surface adhesion (Passarelli et al., 2012a). Indeed, bioturbators have strong implications for the biogeochemistry of sediments as they induce a modification of sediment texture, sediment compaction and porosity which in turn affect diffusion of solutes (Gerino et al., 2003; Meysman et al., 2006; Rhoads and Young, 1970). Bioturbation is therefore a major factor for molecular diffusion and solute transport in cohesive sediments, so that bioturbators have long been considered as engineers (Levinton, 1995). However, bioturbatory effects are likely to be less important in permeable sediments where wind, wave and tide driven currents are believed to be major drivers (Huettel and Webster, 2001). High levels of bioturbation may, in addition, make it difficult for juvenile macrofauna to remain in sediments or may otherwise mediate the immigration of new settlers (Olivier et al., 1996). Due to their small size, meiofauna organisms are generally not referred to as bioturbators but there is evidence that they also change sediment texture, induce a bio-irrigation and displacement of microorganisms and sediment particles. Nematodes, for instance, may improve oxygen and nutrient distribution in sediments by microbioturbation (Alkemade et al., 1992) and Harpacticoid copepods have been shown to be significant bioturbators (Hicks and Coull, 1983). These irrigation activities by meiofauna organisms generally promote microbial remineralisation of organic matter (Aller, 1994).

Another modifying effect of macrofauna and meiofauna on biofilm may result from grazing on microbes and egestion of faeces and nutrients. For instance, nematodes affect bacterial activity and organic matter degradation. Even at relatively low densities, they can significantly impact bacterial community composition in a very species-specific way (De Mesel et al., 2004). In addition, modifications of microbial assemblages by macrofauna grazing pressure have also been recorded by *Hydrobia ulvae* and *Corophium arenarium* (Hagerthey et al., 2002). This can have important implications for food–web interactions and ecosystem functions such as sediment stability (Orvain et al., 2004), and may result from differential food preferences or from more indirect interactions (Moens et al., 2005). However, grazing by meiofauna organisms on microbes is generally not considered sufficient to hamper biofilm development (Montagna, 1984). In contrast, grazing can significantly enhance microbial development and EPS secretions (Hubas et al., 2010), by fragmentation of organic matter particles, by preventing bacterial assemblages from rapidly reaching carrying capacity, and, most probably, by excretion of N-rich compounds which stimulate microbial growth (Ferris et al., 1998; Ingham et al., 1985), particularly by diatoms.

During locomotion and/or feeding, many meiofauna and macrofauna species secrete significant amounts of mucus, which, depending on their diverse properties such as their solubility, may bind sediment particles together and thus improve cohesion (e.g., mucus-net feeding polychaetes: Jørgensen et al., 1984; or nematode mucus secretion: Riemann and Schrage, 1978). It was suggested that nematode mucus tracks contain a substantial amount of polysaccharides which facilitate the development of specific strains of microbes (Moens et al., 2005), which are then grazed upon by the nematodes (i.e., mucus-trap hypothesis). Riemann and Helmke (2002) also suggested that several mucus secreting nematodes invest in a common enzyme pool with their "gardened" bacteria to enhance organic matter decomposition and therefore maximise nutrition and growth of both parties.

The complex interactions between different sediment physical, chemical and biological properties, which finally determine sediment stability, have been summarised (Fig. 4). It should be noted that the diverse organisms affecting sediment stability are likely to display seasonal variations, so that their effects and interactions might be temporally varied. Yet, if effects are strong enough, they will affect sediment stability on a yearly average basis. Stability is a critical factor for tidal flats because it modifies in depth the composition and depth of benthic communities (Reise, 2002)

and the stability of surface biogeochemical gradients which dominate the microbial ecology of benthic systems. First, sediment stabilisation is often associated with an increase of the fine particle fraction, and grain size is a key factor determining the composition of meiofaunal assemblages (Giere, 1993), which can in turn affect macrofaunal recruitment (Watzin, 1983). Also, stabilising and destabilising species tend to exclude each other (Volkenborn et al., 2009; Woodin and Jackson, 1979), so that communities are highly dependent on the stabilisation state of the sediment, and therefore on the ecosystem engineers which determine this state.

4. Associations of ecosystem engineers

The importance of ecosystem engineers for ecosystem functioning is now recognised, but data are missing on the potential interactions between two or more species of ecosystem engineers. The presence of one engineer may depend on the presence of others, forming what is called a "habitat cascade" (Altieri et al., 2007; Thomsen et al., 2010): a species promotes, through the modification of habitats, the development of another that in turn creates living space for different organisms. For instance, Altieri et al. (2007) demonstrated that cordgrass, by stabilising sediment with their roots, baffling wave impact and providing shade, promotes the development of a large assemblage of benthic organisms, including ribbed mussels. Those, in turn, provide a hard substratum and physical space for organisms like barnacles and amphipods. Such cascades are likely to have a crucial role for the development of benthic communities and examples are numerous. In the 1980s, Eckman et al. (1981) proposed that annelid tubes, by modifying the settlement of bacteria, may alter the recruitment of benthic organisms, as bacterial secretions often provide settlement cues. Invasive species may also drive large changes in benthic communities, by influencing the development or behaviour of a native ecosystem engineer, thereby transforming its influence on benthic assemblages (Gribben et al., 2009).

Non-hierarchical interactions between ecosystem engineers have also been demonstrated in the past years and studies show non-additive effects when two engineers impact the same habitat or resource (Crowe et al., 2011). For instance, Boyer and Fong (2005) studied the combined effects of the snail *Cerithidea californica* and the crab *Pachygrapsus crassipes* on macroalgal cover and functional properties of a salt marsh. These authors demonstrated that crabs alone decrease macroalgal
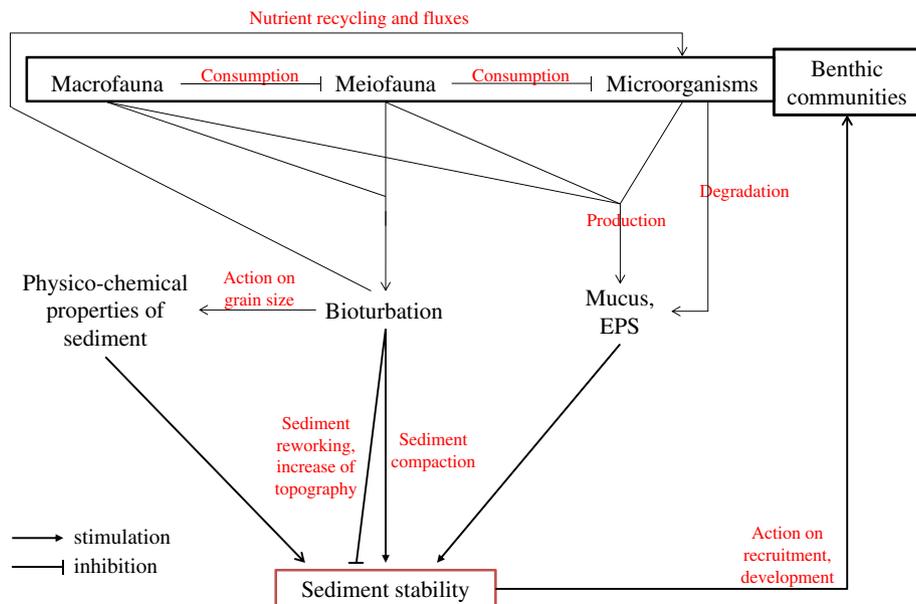
Fig. 4. Interplay between sediment stability and benthic communities in intertidal environments. Hydrodynamic features have not been displayed.

cover, while snails tend to increase it when macroalgae are at low density. Surprisingly, macroalgal cover was completely removed when both engineers were together. The authors pointed out that effects of both engineers together were not possible to predict from the knowledge of individual effects. These non-additive influences on benthic assemblage properties (over and under yielding) and ecosystem functions are difficult to assess and yet, are likely to occur commonly in natural systems (Emmerson et al., 2001). Also, these non-additive effects have been demonstrated to vary according to environmental conditions and context (Bulling et al., 2008; Caliman et al., 2011): for instance, the interactions between three different bioturbators change with the available sediment volume. Temporal variations of these interactions have also been demonstrated (Berkenbusch and Rowden, 2007; Berkenbusch et al., 2007).

No authors have, to the best of our knowledge, tried to formally characterise the different kinds of interactions between ecosystem engineers and their potential effects on community composition and ecosystem functioning. However, Passarelli et al. (2012b) describe an association between two ecosystem engineers, whose engineering effect has been assessed through an in situ experimental study. These authors tested the influence of artificial mimics of polychaete tubes on diatom development and sediment stability. When tubes reached a skimming flow density, they promoted the development of microphytobenthic biofilms in terms of both diatom and EPS content. Also, sediment adhesive capacity, which has been demonstrated to be a proxy for sediment stability (Lubarsky et al., 2010), was higher when these tubes were present.

These results show two different processes (Fig. 5.a). First, biogenic structures produced by benthic macrofauna facilitate the development of biofilms, which in turn stabilise the sediment. This stabilisation then facilitates the development of a specific benthic community, which differs from the assemblages present in non-stable sediments (Volkenborn and Reise, 2007; Volkenborn et al., 2009). The macrofauna and the biofilm are thus integral parts of a habitat cascade: an ecosystem engineer (infaunal worms) promotes, through the modification of habitats, the development of another one (diatom assemblages) that in turn creates niche capacity for different organisms (Altieri et al., 2007; Thomsen et al., 2010). Secondly, it is interesting to consider that sediment stability is affected by the hydrodynamic pattern at sediment surface and by the adhesion of sediment particles (Madsen et al., 1993). In this experiment, tubes modified near bed flow dynamics, and microbial communities produced EPS which coated sand grains and increased their cohesion. This association resulted in an overall increase of sediment stability within the biogenic structure bed but also in an enhanced capture of water born particles by the bed. These two groups of ecosystem engineers, although very different by size, organisation, and phylogeny, thus act cooperatively in a way which increases the engineering effect. Here we propose these groups to be called "cooperative ecosystem engineers", and hypothesise that other similar interactions are common in marine ecosystems.

5. Conclusion, and possible threats on ecosystem engineers

Ecosystem engineers, while modifying habitat for other organisms, may also provide what has been called "ecosystem services" for human populations (Millenium Ecosystem Assessment, 2005). Purification of water, stabilisation of soils and protection against natural catastrophes are some examples of ecosystem services provided by assemblages governed by ecosystem engineers. In this context, Odling-Smee (2005) highlighted that the limited resources available for nature conservation might be better invested in preserving species because of their functional value for the community or for humans. Ecosystem engineers are therefore potentially interesting conservation targets (Crain and Bertness, 2006; Godet et al., 2008b). For instance, erosions of soils and sediments are increasingly recognised as an environmental hazard for human development and well-being. The development of intensive agriculture for land and rising sea levels for coasts are some of the main drivers whereby erosion may increase in the next decades. An estimate of 1500 houses, and the land on which they stand, are lost due to coastal erosion in the U.S. each year; a loss of approximately $530 million per year for owners (Heinz Centre for Science Economics and the Environment, 2000).

Threats for ecosystem engineers are diverse (for examples, see Fig 5.b). First, natural catastrophes may destroy populations of engineers, and effects on community will then depend on the ability of these engineers to recover from such events. Also, long-term processes, such as global climate changes, will durably influence the functioning of systems. For instance, rising sea level will increase coastal erosion; this physical process could be enhanced by a diminished capacity for biofilms to stabilise sediment in response to antibiotics discharge in coastal waters (Lubarsky et al., 2012). Moreover, some biological invasions have been shown to produce great effects on the composition and functioning of some systems (see Boogert et al., 2006 for examples). These effects are not necessarily negative for biodiversity per se, but some alter either the development of the ecosystem engineer itself, or its ability to modulate resources fluxes and habitat for other organisms. A final example is
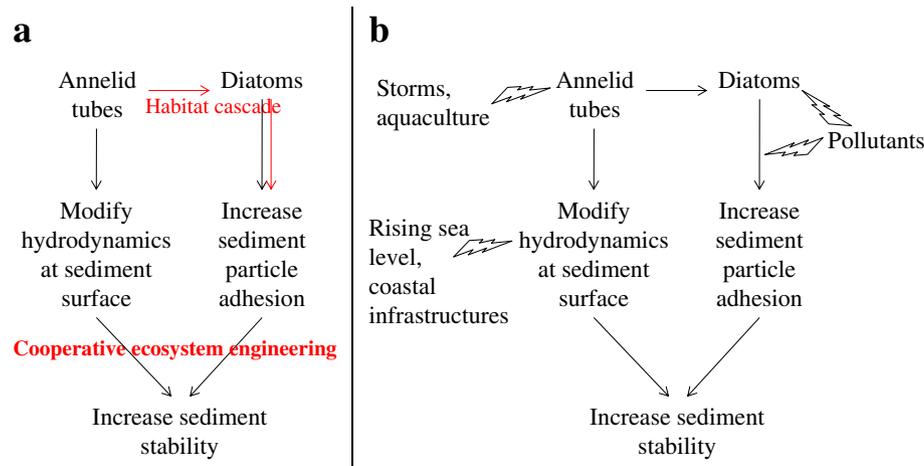

Fig. 5. a. Habitat cascade (red arrows) and cooperative ecosystem engineering (black arrows) as illustrated by the interactions between biogenic structures and biofilms (Passarelli et al., 2012b); b. potential threats on these species and process due to habitat change.

the direct destruction of ecosystem engineers; for instance, the development of Manila clam aquaculture leads to the destruction of the bed of *L. conchilega*, which is known to have a major structuring role in intertidal flats (Toupoint et al., 2008).

Loss of local diversity, change in ecosystem functioning and decrease in ecosystem services are among the main potential consequences of such threats. More durable and dramatic effects may occur if the perturbation of the ecosystem engineer is sufficient to prompt a switch to another stable state of the system (Eklöf et al., 2011). For instance, van der Heide et al. (2007) studied the non-recovery of *Z. marina* after the wasting disease in the 1930s. When present, these marine angiosperms decreased the nutrient concentration in seawater and limited the erosion of sediment by waves, thereby limiting the development of phytoplankton and epiphytes and reducing the amount of suspended sediment. After the disease, due to the destruction of the plants, turbidity dramatically increased in coastal waters. In turn, this increase in turbidity hindered the settlement and development of *Z. marina*, which prevent any recovery of these populations. This catastrophic switch is a good example of what might happen to current crucial ecosystem engineers due to environmental hazard combined with changes in their environmental conditions. In other conditions, *Z. marina* recovered well since the disease (Godet et al., 2008a), pointing out the complexity of interactions at stake.

Predicting how multiple changes in environmental conditions influence diverse ecosystem engineers and their interactions is an ongoing challenge for ecologists. A good understanding of how ecosystem engineers interact and, for instance, cooperate is therefore crucial in determining the key processes for ecosystem functioning and their future in changing conditions.

Acknowledgments

References

Abdullah, M.I., Fredriksen, S., 2004. Production, respiration and exudation of dissolved organic matter by the kelp *Laminaria hyperborea* along the west coast of Norway. Journal of the Marine Biological Association of the United Kingdom 84, 887–894.

Alkemade, R., Wielemaker, A., de Jong, S.A., Sandee, A.J.J., 1992. Experimental evidence for the role of bioturbation by the marine nematode *Diplolaimella dievengatensis* in stimulating the mineralization of *Spartina anglica* detritus. Marine Ecology Progress Series 90, 149–155.

Aller, R.C., 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chemical Geology 114, 331–345.

Aller, R.C., Aller, J.Y., 1992. Meiofauna and solute transport in marine muds. Limnology and Oceanography 37, 1018–1033.

Altieri, A.H., Silliman, B.R., Bertness, M.D., 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. American Naturalist 169, 195–206.

Andersen, T.J., 2001. Seasonal variation in erodibility of two temperate, microtidal mudflats. Estuarine, Coastal and Shelf Science 53, 1–12.

Avnimelech, Y., Ritvo, G., Meijer, L.E., Kochba, M., 2001. Water content, organic carbon and dry bulk density in flooded sediments. Aquacultural Engineering 25, 25–33.

Bell, S.S., 1985. Habitat complexity of polychaete tube-caps: Influence of architecture on dynamics of a meioepibenthic assemblage. Journal of Marine Research 43, 647–671.

Berke, S.K., 2012. Biogeographic variability in ecosystem engineering: patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. Marine Ecology Progress Series 447, 1–13.

Berkenbusch, K., Rowden, A.A., 2007. An examination of the spatial and temporal generality of the influence of ecosystem engineers on the composition of associated assemblages. Aquatic Ecology 41, 129–147.

Berkenbusch, K., Rowden, A.A., Myers, T.E., 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. Journal of Experimental Marine Biology and Ecology 341, 70–84.

Bertness, M.D., Leonard, G.H., 1997. The role of positive interactions in communities: lessons from intertidal habitats. Ecology 78.

Black, K.S., Tolhurst, T.J., Paterson, D.M., Hagerthey, S.E., 2002. Working with natural cohesive sediments. Journal of Hydraulic Engineering 128, 2–8.

Bolam, S.G., Fernandes, T.F., 2002. Dense aggregations of tube-building polychaetes: response to small-scale disturbances. Journal of Experimental Marine Biology and Ecology 269, 197–222.

Boogert, N.J., Paterson, D.M., Laland, K.N., 2006. The implications of niche construction and ecosystem engineering for conservation biology. Bioscience 56, 570–578.

Bouma, T.J., Olenin, S., Reise, K., Ysebaert, T., 2009. Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgoland Marine Research 63.

Boyer, K.E., Fong, P., 2005. Co-occurrence of habitat-modifying invertebrates: effects on structural and functional properties of a created salt marsh. Oecologia 143, 619–628.

Bozec, Y.-M., Yakob, L., Bejarano, S., Mumby, P.J., 2013. Reciprocal facilitation and nonlinearity maintain habitat engineering on coral reefs. Oikos 122, 428–440.

Braeckman, U., Provoost, P., Gribsholt, B., Van Gansbeke, D., Middelburg, J.J., Soetaert, K., Vincx, M., Vanaverbeke, J., 2010. Role of macrofauna functional traits and density in biogeochemical fluxes and bioturbation. Marine Ecology Progress Series 399, 173–186.

Braeckman, U., Provoost, P., Moens, T., Soetaert, K., Middelburg, J.J., Vincx, M., Vanaverbeke, J., 2011. Biological vs. physical mixing effects on benthic food web dynamics. PLoS One 6.

Bulling, M.T., Solan, M., Dyson, K., Hernandez-Milian, G., Luque, P., Pierce, G., Raffaelli, D., Paterson, D.M., White, P.C.L., 2008. Species effects on ecosystem processes are modified by faunal responses to habitat composition. Oecologia 158, 511–520.

Caliman, A., Carneiro, L.S., Bozelli, R.L., Farjalla, V.F., Esteves, F.A., 2011. Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. Oikos 120.

Callaway, R., 2003. Long-term effects of imitation polychaete tubes on benthic fauna: they anchor *Mytilus edulis* (L.) banks. Journal of Experimental Marine Biology and Ecology 283, 115–132.

Callaway, R., 2006. Tube worms promote community change. Marine Ecology Progress Series 308, 49–60.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78.

Crain, C.M., Bertness, M.D., 2006. Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56, 211–218.

Crowe, T.P., Frost, N.J., Hawkins, S.J., 2011. Interactive effects of losing key grazers and ecosystem engineers vary with environmental context. Marine Ecology Progress Series 430, 223–234.

Dade, W.B., Nowell, A.R.M., Jumars, P.A., 1992. Predicting erosion resistance of muds. Marine Geology 105, 285–297.

Dayton, P.K., Tegner, M.J., 1984. Catastrophic storms, El Niño, and patch stability in a Southern California kelp community. Science 224.

de Deckere, E., Tolhurst, T.J., de Brouwer, J.F.C., 2001. Destabilization of cohesive intertidal sediments by infauna. Estuarine, Coastal and Shelf Science 53, 665–669.

De Mesel, I., Derycke, S., Moens, T., Van Der Gucht, K., Vincx, M., Swings, J., 2004. Top-down impact of bacterivorous nematodes on the bacterial community structure: a microcosm study. Environmental Microbiology 6, 733–744.

Decho, A.W., 1990. Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. In: Barnes, M. (Ed.), Oceanography and Marine Biology: An Annual review. Aberdeen University Press, pp. 73–153.

Decho, A.W., 2000. Microbial biofilms in intertidal systems: an overview. Continental Shelf Research 20, 1257–1273.

Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. Limnology and Oceanography 28, 241–257.

Eckman, J.E., 1985. Flow disruption by an animal-tube mimic affects sediment bacterial colonization. Journal of Marine Research 43, 419–435.

Eckman, J.E., Nowell, A.R.M., Jumars, P.A., 1981. Sediment destabilization by animal tubes. Journal of Marine Research 39, 361–374.

Eckman, J.E., Duggins, D.O., Siddon, C.E., 2003. Current and wave dynamics in the shallow subtidal: implications to the ecology of understory and surface-canopy kelps. Marine Ecology Progress Series 265, 45–56.

Eklöf, J.S., Van der Heide, T., Donadi, S., van der Zee, E.M., O'Hara, R., Eriksson, B.K., 2011. Habitat-mediated facilitation and counteracting ecosystem engineering interactively influence ecosystem responses to disturbance. PLoS One 6, e23229.

Emmerson, M., Solan, M., Emes, C., Paterson, D.M., Raffaelli, D., 2001. Idiosyncratic effects of species diversity on ecosystem function. Nature 411, 73–77.

Fauvel, P., Bohn, G., 1907. Le rythme des marées chez les diatomées littorales. Comptes Rendus des Seances de la Societe de Biologie 62, 121–123.

Ferris, H., Venette, R.C., van der Meulen, H.R., Lau, S.S., 1998. Nitrogen mineralization by bacterial-feeding nematodes: verification and measurement. Plant and Soil 203, 159–171.

Fonseca, M.S., Fisher, J.S., Zieman, J.C., Thayer, G.W., 1982. Influence of the seagrass, *Zostera marina* L., on current flow. Estuarine, Coastal and Shelf Science 15, 351–358.

Forster, S., Graf, G., 1995. Impact of irrigation on oxygen flux into the sediment: intermittent pomping by *Callianasse subterranea* and "piston-pumping" by *Lanice conchilega*. Marine Biology 123, 335–346.

Friedrichs, M., Graf, G., 2009. Characteristic flow patterns generated by macrozoobenthic structures. Journal of Marine Systems 75, 348–359.

Friedrichs, M., Graf, G., Springer, B., 2000. Skimming flow induced over a simulated polychaete tube lawn at low population densities. Marine Ecology Progress Series 192, 219–228.

Gacia, E., Duarte, C.M., 2001. Sediment retention by a Mediterranean *Posidonia oceanica* meadow: the balance between deposition and resuspension. Estuarine, Coastal and Shelf Science 52, 505–514.

Gallagher, E.D., Jumars, P.A., Trueblood, D.D., 1983. Facilitation of soft-bottom benthic succession by tube builders. Ecology 64, 1200–1216.

Gerbersdorf, S.U., Manz, W., Paterson, D.M., 2008. The engineering potential of natural benthic bacterial assemblages in terms of the erosion resistance of sediments. FEMS Microbiology Ecology 66, 282–294.

Gerino, M., Stora, G., François-Carcaillet, F., Gilbert, F., Poggiale, J.-C., Mermillod-Blondin, F., Desrosiers, G., Vervier, P., 2003. Macro-invertebrate functional groups in freshwater and marine sediments: a common mechanistic classification. Vie et Milieu 53, 221–231.

Giere, O., 1993. Meiobenthology, Berlin.

Giere, O., 2009. Meiobenthology: The Microscopic Motile Fauna of Aquatic Sediments. Springer.

Godet, L., Fournier, J., Van Katwijk, M.M., Olivier, F., Le Mao, P., Retière, C., 2008a. Before and after wasting disease in common eelgrass Zostera marina along the French Atlantic coasts: a general overview and first accurate mapping. Diseases of Aquatic Organisms 79, 249–255.

Godet, L., Toupoint, N., Olivier, F., Fournier, J., Retière, C., 2008b. Considering the functional value of common marine species as a conservation stake: the case of sandmason worm Lanice conchilega (Pallas 1766) (Annelida, Polychaeta) beds. Ambio 37, 347–355.

Grabowski, R.C., Droppo, I.G., Wharton, G., 2011. Erodibility of cohesive sediment: the importance of sediment properties. Earth-Science Reviews 105, 101–120.

Grant, L., Archambault, P., Olivier, F., McKindsey, C., 2012. Influence of 'bouchot' mussel culture on the benthic environment in a dynamic intertidal system. Aquaculture Environment Interaction 2, 117–131.

Gribben, P.E., Byers, J.E., Clements, M., McKenzie, L.A., Steinberg, P.D., Wright, J.T., 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecology Letters 12, 1127–1136.

Hacker, S.D., Gaines, S.D., 1997. Some implications of direct positive interactions for community species diversity. Ecology 78, 1990–2003.

Hagerthey, S.E., Defew, E.C., Paterson, D.M., 2002. Influence of Corophium volutator and Hydrobia ulvae on intertidal benthic diatom assemblages under different nutrient and temperature regimes. Marine Ecology Progress Series 245, 47–59.

Heinz Centre for Science Economics and the Environment, 2000. Evaluation of erosion hazards. Report for Federal Emergency Management Agency, Washington, DC, p. 252.

Hicks, G.R.F., Coull, B.C., 1983. The ecology of marine meiobenthic harpacticoid copepods. In: Barnes, H., Ansell, A.D., Gibson, R.N. (Eds.), Oceanography and Marine Biology: An Annual Review. University College London Press, London, pp. 67–175.

Higgins, R.P., Thiel, H.e, 1988. Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington, D.C.

Holland, A.F., Zingmark, R.G., Dean, J.M., 1974. Quantitative evidence concerning the stabilization of sediments by marine benthic diatoms. Marine Biology 27, 191–196.

Hori, K., Matsumoto, S., 2010. Bacterial adhesion: from mechanism to control. Biochemical Engineering Journal 48, 424–434.

Hubas, C., Sachidhanandam, C., Rybarczyk, H., Lubarsky, H.V., Rigaux, A., Moens, T., Paterson, D.M., 2010. Bacterivorous nematodes stimulate microbial growth and exopolymer production in marine sediment microcosms. Marine Ecology Progress Series 419, 85–94.

Huettel, M., Webster, I.T., 2001. Porewater flow in permeable sediment. The Benthic Boundary Layer: Transport Processes and Biogeochemistry.Oxford University Press, Oxford 144–179.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers — effects on nutrient cycling and plant-growth. Ecological Monographs 55, 119–140.

Jackson, C.M., Kamenos, N.A., Moore, P.G., Young, M., 2004. Meiofaunal bivalves in maerl and other surbstrata; their diversity and community structure. Ophelia 58, 49–60.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Jørgensen, C.B., Kiørboe, T., Møhlenberg, F., Riisgård, H.U., 1984. Ciliary and mucus-net filter feeding, with special reference to fluid mechanical characteristics. Marine Ecology Progress Series 15, 283–292.

Kamenos, N.A., Moore, P.G., Hall-Spencer, J.M., 2004. Maerl grounds provide both refuge and high growth potential for juvenile queen scallops (Aequipecten opercularis L.). Journal of Experimental Marine Biology and Ecology 313, 241–254.

Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., Martinez, N.D., Menge, B.A., Blanchette, C.A., Iles, A.C., Brose, U., 2012. More than a meal… integrating non-feeding interactions into food webs. Ecology Letters 15, 291–300.

Krembs, C., Eicken, H., Junge, K., Deming, J.W., 2002. High concentrations of exopolymeric substances in Arctic winter sea ice: implications for the polar ocean carbon cycle and cryoprotection of diatoms. Deep-Sea Research Part I 49, 2163–2181.

Lawton, J.H., Jones, C.G., 1995. Linking species and ecosystems: organisms as ecosystem engineers. In: Jones, C.G., Lawton, J.H. (Eds.), Linking species & Ecosystems. Chapman & Hall, London, pp. 141–150.

Lee, S.Y., Fong, C.W., Wu, R.S.S., 2001. The effects of seagrass (Zostera japonica) canopy structure on associated fauna: a study using artificial seagrass units and sampling of natural beds. Journal of Experimental Marine Biology and Ecology 259, 23–50.

Lejart, M., Hily, C., 2011. Differential response of benthic macrofauna to the formation of novel oyster reefs (Crassostrea gigas, Thunberg) on soft and rocky substrate in the intertidal of the Bay of Brest, France. Journal of Sea Research 65, 84–93.

Leppard, G.G., 1995. The characterization of algal and microbial mucilages and their aggregates in aquatic ecosystems. Science of the Total Environment 165, 103–131.

Levinton, J., 1995. Bioturbators as ecosystems engineers: control of the sediment fabric, inter-individual interactions, and material fluxes. In: Jones, C.G., Lawton, J.H. (Eds.), Linking Species & Ecosystems. Chapman & Hall, London, pp. 29–36.

Little, C., Kitching, J.A., 1996. The Biology of Rocky Shores. Oxford University Press, Oxford.

Lubarsky, H.V., Hubas, C., Chocholek, M., Larson, F., Manz, W., Paterson, D.M., Gerbersdorf, S.U., 2010. The stabilisation potential of individual and mixed assemblages of natural bacteria and microalgae. PLoS One 5, e13794.

Lubarsky, H.V., Gerbersdorf, S.U., Hubas, C., Behrens, S., Ricciardi, F., Paterson, D.M., 2012. Impairment of the bacterial biofilm stability by triclosan. PLoS One 7.

Luckenbach, M.W., 1986. Sediment stability around animal tubes: the roles of hydrodynamic processes and biotic activity. Limnology and Oceanography 31, 779–787.

Madsen, K.N., Nilsson, P., Sundbäck, K., 1993. The influence of benthic microalgae on the stability of a subtidal sediment. Journal of Experimental Marine Biology and Ecology 170, 159–177.

Mare, M.F., 1942. A study of a marine benthic community with special reference to the micro-organisms. Journal of the Marine Biological Association of the United Kingdom 25, 517–554.

McIntyre, A.D., 1969. Ecology of marine meiobenthos. Biological Reviews 44, 245–288.

Meysman, F.J.R., Middelburg, J.J., Heip, C.H.R., 2006. Bioturbation: a fresh look at Darwin's last idea. Trends in Ecology & Evolution 21, 688–695.

Millenium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, DC.

Moens, T., dos Santos, G.A.P., Thompson, F., Swings, J., Fonseca-Genevois, V., Vincx, M., De Mesel, I., 2005. Do nematode mucus secretions affect bacterial growth? Aquatic Microbial Ecology 40, 77–83.

Montagna, P.A., 1984. Measurement of meiobenthic grazing rates on sediment bacteria and edaphic diatoms. Marine Ecology Progress Series 18, 119–130.

Nelson, W.A., 2009. Calcified macroalgae — critical to coastal ecosystems and vulnerable to change: a review. Marine and Freshwater Research 60, 787–801.

Nowell, A.R.M., Jumars, P.A., 1984. Flow environments of aquatic benthos. Annual Review of Ecological Systems 15, 303–328.

Odling-Smee, L., 2005. Dollars and sense. Nature 437, 614–616.

Olivier, F., Desroy, N., Retière, C., 1996. Habitat selection and adult-recruit interactions in Pectinaria koreni (Malmgren) (Annelida: Polychaeta) post-larval populations: results of flume experiments. Journal of Sea Research 36, 217–226.

Orvain, F., Sauriau, P.-G., Sygut, A., Joassard, L., Le Hir, P., 2004. Interacting effects of Hydrobia ulvae bioturbation and microphytobenthos on the erodibility of mudflat sediments. Marine Ecology Progress Series 278, 205–223.

Palmer, J.D., Round, F.E., 1967. Persistent, vertical-migration rhythm in benthic microflora. VI. The tidal and diurnal nature of the rhythm in the diatom Hantzschia virgata. The Biological Bulletin 132, 44–55.

Passarelli, C., Hubas, C., Nicolas Segui, A., Grange, J., Meziane, T., 2012a. Surface adhesion of microphytobenthic biofilms is enhanced under Hediste diversicolor (O. F. Müller) trophic pressure. Journal of Experimental Marine Biology and Ecology 52–60.

Passarelli, C., Olivier, F., Paterson, D.M., Hubas, C., 2012b. Impacts of biogenic structures on benthic assemblages: microbes, meiofauna, macrofauna and related ecosystem functions. Marine Ecology Progress Series 465, 85–97.

Paterson, D.M., 1989. Short-term changes in the erodibility of intertidal cohesive sediments related to the migratory behavior of epipelic diatoms. Limnology and Oceanography 34, 223–234.

Paterson, D.M., Black, K.S., 1999. Water flow, sediment dynamics and benthic biology. Advances in Ecological Research 29, 155–193.

Peralta, G., van Duren, L.A., Morris, E.P., Bouma, T.J., 2008. Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. Marine Ecology Progress Series 368, 103–115.

Rabaut, M., Guilini, K., Van Hoey, G., Magda, V., Degraer, S., 2007. A bio-engineered soft-bottom environment: the impact of Lanice conchilega on the benthic species-specific densities and community structure. Estuarine, Coastal and Shelf Science 75, 525–536.

Raffaelli, D., Hawkins, S., 1996. Intertidal Ecology. Springer.

Reise, K., 2002. Sediment mediated species interactions in coastal waters. Journal of Sea Research 48, 127–141.

Rhoads, D.C., Young, D.K., 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research 28, 150–178.

Riemann, F., Helmke, E., 2002. Symbiotic relations of sediment-agglutinating nematodes and bacteria in detrital habitats: the enzyme-sharing concept. Marine Ecology: Pubblicazioni della Stazione Zoologica di Napoli 23, 93–113.

Riemann, F., Schrage, M., 1978. The mucus-trap hypothesis on feeding of aquatic nematodes and implications for biodegradation and sediment texture. Oecologia 34, 75–88.

Scaps, P., 2002. A review of the biology, ecology and potential use of the common ragworm Hediste diversicolor (O.F. Muller) (Annelida: Polychaeta). Hydrobiologia 470, 203–218.

Stal, L.J., 2010. Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecological Engineering 36, 236–245.

Thistle, D., Reidenauer, J.A., Findlay, R.H., Waldo, R., 1984. An experimental investigation of enhanced harpacticoid (Copepoda) abundances around isolated seagrass shoots. Oecologia 63, 295–299.

Thomsen, M.S., Wernberg, T., Altieri, A., Tuya, F., Gulbransen, D., McGlathery, K.J., Holmer, M., Silliman, B.R., 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology 50, 158–175.

Toupoint, N., Godet, L., Fournier, J., Retière, C., Olivier, F., 2008. Does Manila clam cultivation affect habitats of the engineer species Lanice conchilega (Pallas, 1766)? Marine Pollution Bulletin 56, 1429–1438.

Underwood, G.J.C., Paterson, D.M., 2003. The importance of extracellular carbohydrate production by marine epipelic diatoms. Advances in Botanical Research 40, 183–239.

van der Heide, T., van Nes, E.H., Geerling, G.W., Smolders, A.J.P., Bouma, T.J., van Katwijk, M.M., 2007. Positive feedbacks in seagrass ecosystems: implications for success in conservation and restoration. Ecosystems 10, 1311–1322.

van der Wal, D., Herman, P.M.J., 2012. Ecosystem engineering effects of Aster tripolium and Salicornia procumbens salt marsh on macrofaunal community structure. Estuaries and Coasts 35, 714–726.

Volkenborn, N., Reise, K., 2007. Effects of *Arenicola marina* on polychaete functional diversity revealed by large-scale experimental lugworm exclusion. Journal of Sea Research 57, 78–88.

Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J.E.E., Reise, K., 2007. Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuarine, Coastal and Shelf Science 74, 331–343.

Volkenborn, N., Robertson, D.M., Reise, K., 2009. Sediment destabilizing and stabilizing bio-engineers on tidal flats: cascading effects of experimental exclusion. Helgoland Marine Research 63, 27–35.

Watzin, M.C., 1983. The effects of meiofauna on settling macrofauna: meiofauna may structure macrofaunal communities. Oecologia 59, 163–166.

Whitlatch, R.B., Zajac, R.N., 1985. Biotic interactions among estuarine infaunal opportunistic species. Marine Ecology Progress Series 21, 299–311.

Wilkie, L., O'Hare, M.T., Davidson, I., Dudley, B., Paterson, D.M., 2012. Particle trapping and retention by *Zostera noltii*: a flume and field study. Aquatic Botany 102, 15–22.

Wilson, J.B., Agnew, D.Q., 1992. Positive-feedback switches in plant communities. Advances in Ecological Research 23, 263–336.

Wilson, S., Blake, C., Berges, J.A., Maggs, C.A., 2004. Environmental tolerances of free-living coralline algae (maerl): implications for European marine conservation. Biological Conservation 120, 279–289.

Woodin, S.A., 1978. Refuges, disturbance, and community structure: a marine soft-bottom example. Ecology 59, 274–284.

Woodin, S.A., Jackson, J.B.C., 1979. Interphyletic competition among marine benthos. American Zoologist 19, 1029–1043.

Wotton, R.S., 2004. The essential role of exopolymers (EPS) in aquatic systems. In: Gibson, R.N., Atkinson, R.J.A., Gordon, J.D.M. (Eds.), Oceanography and Marine Biology: An Annual Review. Aberdeen University Press, pp. 57–94.

Zühlke, R., 2001. Polychaete tubes create ephemeral community patterns: *Lanice conchilega* (Pallas, 1766) associations studied over six years. Journal of Sea Research 46, 261–272.

Zühlke, R., Blome, D., van Bernem, K.H., Dittmann, S., 1998. Effects of the tube-building polychaete *Lanice conchilega* (Pallas) on benthic macrofauna and nematodes in an intertidal sandflat. Senckenbergiana Maritima 29, 131–138.