Shedding light on detritus: Interactions between invertebrates, bacteria and substrates in benthic habitats

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Chapter 12

Concluding remarks

This thesis identified processes linking biotic and abiotic components of two contrasting benthic detrital food webs on either soft bottom sediments or on hard mangrove root substrates. This concluding chapter evaluates the importance of biotic-abiotic interactions in these two habitats and attempts to identify general drivers for detritus processing in benthic detrital food webs.

Organic matter composition

Organic matter in natural ecosystems varies widely in chemical composition. Some components of detritus are readily utilized, while other components resist degradation (recalcitrant carbon) or inhibit microbial and invertebrate consumers (Gessner and Chauvet, 2002; Cornwell et al., 2008; Hladyz et al., 2009). This thesis demonstrated that organic matter composition drives decomposition in different natural and manipulated benthic habitats.

Firstly, mangrove-derived OM, originating from decaying leaves and leachates from mangrove roots, is mainly composed of tannins and polyphenolic compounds (Maie and Jaffe, 2006). These recalcitrant substrates were shown to enhance recruitment only of specific mangrove-associated sponge species, while other species were suppressed (Chapter 8). In addition, it was demonstrated that exposure to mangrove-derived OM can kill sponge species that do not naturally colonize on mangrove roots within few days (Chapter 11). The capacity of the sponge species to grow on mangrove roots appeared to concur with the capacity of their associated bacterial symbionts that appeared to benefit from degrading recalcitrant organic substrates (Chapter 9). Therefore, the sorting of sponge holobionts capable or incapable of colonizing mangrove roots is essentially caused by the chemical composition of mangrove-derived OM.

Secondly, in this thesis the development of freshwater bacterial communities was monitored on two contrasting substrates: freshly collected plant biomass (ground nettle) and recalcitrant peat. In the experiment reported in Chapter 5, the metabolization of common, easily degradable compounds was used as a proxy to detect differences in the functional characteristics that ideally would involve also the metabolization of more recalcitrant substrates such as aromatic compounds in peat. It was shown that the functional composition of bacterial communities develops differently depending on the substrate type (Chapter 5). These observations are consistent with substrate-dependent developments of bacterial communities in humic lakes (Eiler et al, 2003) and soils (Brant et al., 2006)

Thirdly, a decomposition and consumption tablet (DECOTAB) with a defined chemical composition was developed to gauge detritus processing rates *in situ* (Chapter 4). Two different DECOTABS were composed and tested: a standard DECOTAB composed mainly of cellulose, and a more complex DECOTAB containing additional plant and soil extracts. It was demonstrated that microbial organic matter processing rates can differ depending on organic matter composition, while no differences in feeding rates were observed in the litter shredding isopod *Asellus aquaticus*. This indicates that organic matter composition has stronger and more direct effects on the microbial community than on the invertebrate communities in soft bottom sediments. Recently, litter decomposition rates in stream beds and forest floors have been compared in conjunction with consortia of invertebrates and microorganisms, and differences between both habitats were demonstrated (Gessner et al., 2010, and references therein). For instance, terrestrial detritivores accelerated decomposition of recalcitrant leaf species, while stream detritivores confronted with diverse litter fed preferentially on high-quality leaves, resulting in lowered OM processing rates. The observed difference in the effect of organic matter composition on invertebrates in soft sediments and mangrove root substrates suggests that different mechanisms underlie the effect organic matter composition on links between biota and OM processing rates. The present thesis demonstrates that organic matter composition invokes direct effects on either microbes or invertebrate-bacterial consortia, thereby affecting the development of specific invertebrate-bacteria consortia on large spatio-temporal scales. Thus the insight that organic matter composition is an important driver for OM processing rates highlights the need to study organic matter composition as driver for the long-term development of detritus based communities.

Invertebrate-Bacteria-Substrate interactions

Invertebrates and microorganisms are tied together in the processing of organic matter, and both groups of organisms can provide mutual benefits. This thesis also addressed these two sides of the same coin.

This thesis demonstrated that sediment reworking by invertebrates strongly promote bacterial respiration and organic matter processing in aquatic sediments, in which the magnitude of bacterial activity and detritus processing relied heavily on the type invertebrate bioturbation (Chapter 2 and 3). Moreover, invertebrate bioturbation also influenced the structure of the bacterial community and the spatio-temporal redox (Eh) conditions within the sediment. Thereby sediment reworking by invertebrates strongly facilitated and promoted bacterial growth in (sub)surface sediments.

Positive feedback between fauna and bacteria is even stronger in sponges. Sponges provide a physical substrate for microorganisms that colonize sponge voids or are actually incorporated in sponge tissues, in which symbiotic microorganisms can make up a large part (> 50%) of the holobionts biomass (e.g. Taylor et al., 2007). Sponge hosts actively filter tremendous amount of particulate and dissolved OM and the microbial symbionts play a role in the transfer of carbon substrates to its sponge host (Freeman and Thacker, 2011; Ribes et al., 2012). However, exact metabolic pathways and exchange routes of organic substrates between sponge cells and bacterial symbionts remain completely unresolved to date (Thacker and Freeman, 2012). Results presented in this thesis show that specific sponge-bacterial consortia living on mangrove roots were capable of degrading recalcitrant organic matter leaching from mangrove roots (Chapter 9), while sponge-bacterial consortia occurring on reefs can not utilize mangrove-derived OM (Chapter 9), nor survive exposure to mangrove-derived OM (Chapter 10, 11). This indicates that sponge-bacterial consortia interact in (D)OM metabolism facilitating growth on mangrove roots and persistence in mangrove ecosystems.

The results presented in this thesis show that bacteria and invertebrates co-act in the process of OM degradation. Mutual benefits are evident in sediments that support free-living fauna and free-living microbes, but appears to be even stronger in sessile sponge-bacteria associations. These facilitative interactions potentially act via the joint accumulation and digestion of detritus (OM) by the faunal-bacterial consortia, yet the provision of a physical substrate and transport of OM, oxygen and other substrates by fauna is fundamental in both soft sediment and hard substrate communities.

Anthropogenic stressors and organic matter processing

Species-specific intolerance to abiotic constrains such as temperature, pH, salinity, or anthropogenic stressors like eutrophication and metal pollution, eventually limit the occurrence of aquatic organisms to certain ranges of natural environments (e.g. Kiffney et al., 1994; Bervoets et al., 1996). Thus, abiotic conditions may restrict the ecological processes sustained by these species. In particular, there is ample evidence for reduced detritus degradation in natural habitats. An obvious example is provided by peat-ecosystems that are characterized by the conservation of organic matter by water logging and acidic conditions (Freeman et al., 2001) and forest humic layer thickening (e.g. Jobbagy and Jackson, 2000). Thus, diversity losses induced by abiotic conditions can also results in deminished ecosystem functioning. For instance, at a small scale, the manipulated disturbance of populations of suspension-feeding caddisflies was observed to negatively affect organic matter fluxes in streams (Cardinale and Palmer, 2002) probably with downstream effects on aquatic communities. Therefore, interactions between selective abiotic conditions, biodiversity at different trophic levels, and overall process rates in detritivore communities are tightly linked, and an integrated approach is essential to understand emerging patterns in interactions between biodiversity and ecosystem functioning. This thesis considered metal pollution as a potential driver influencing interactions between biota and organic matter processing and will be discussed below.

Effects of anthropogenic stressors are currently assessed by monitoring shifts and decreases in species composition of natural communities rather than subsequent changes in ecosystem processes. As a consequence, environmental policies aim at the protection of species, assuming inherent protection of ecosystem functioning. However, abiotic pressures may have various indirect effects via e.g. the reduction of food quality, invertebrate fitness or habitat suitability (e.g. Van der Geest et al., 1999; O'Halloran et al., 2008). This thesis therefore evaluated chemical and physical stress on invertebrate and bacterial detritivorous communities in relation to changes in ecosystem processes.

The response of a simplified soft bottom community to chemical stress was analyzed (Chapter 3). It was demonstrated that copper exposure affected the burrowing behavior of the isopod *Asellus aquaticus*, which resulted in reduced bacterial activity and organic matter processing; thereby illustrating that sub-lethal effects on invertebrates can cascade toward disordering ecosystem processes. Sub-lethal, physiological effects of pollution have also been observed in marine sponges, in which it was shown that OM filtration and clearance rates in sponges are reduced with increasing copper levels (Cebrian et al., 2006). Thus, antrophogenic stressors precede effects on biodiversity requiring a longer period of time to emerge, and therefore functional parameters (e.g. decomposition rate) may serve as more sensitive and reliable parameters for assessing ecological water quality and ecosystem functioning.

Metal pollution was thus found to exert strong effects on the performance of benthic communities and the inherent processing of organic matter. The profound impact of anthropogenic stressors on OM processing strengthen the insight that abiotic variables dictate organic matter processing both directly and indirectly and this warrants a key stone position in environmental protection aiming at protecting the species composition of communities, as well as protecting the essential functioning of ecosystems and the services they provide.

Effects of solar radiation on benthic environments

Solar radiation, and especially UV radiation, is known to exert negative effects on organisms and these effects depend strongly on the climate zone, climate changes and the transmission of radiation in local waters. Our current understanding of the effects of solar radiation is based on studies focusing on terrestrial systems and plankton communities, and it remained uncertain whether these observed effects extend towards the benthic environment. Evidence is provided here that solar radiation is a currently overlooked, but important driver for benthic communities that can mask or even decouple invertebrate-bacterial interactions in detrital food webs. (Chapters 5 and 6). It is also shown that solar radiation at levels common in the temperate zone can indirectly affect benthic communities via most likely an altered organic matter composition and effects on microbial community composition (Chapter 5) as well as via altered redox conditions within soft bottom sediments (Chapter 6). A number of sponge species are also known to be negatively affected by increased radiation intensities in the tropics, and a reduced performance was observed in a reef sponges transplanted to shallow, experimental mangrove stands exposed more directly to solar radiation (Chapter 10). The detrimental effects in the tropics are currently attributed to stress responses of phototrophic symbionts (e.g. Diaz et al., 2012). However, DOM composition in coastal waters has been shown to change substantially due to solar radiation that induced photodegradation and photosensitization (Kattner et al., 2006; Dittmar et al., 2006), hinting that effects of solar radiation might also be more complex and seize upon different attributes of tropical benthic ecosystems. Hence, although the results presented in this thesis are based on short term incubations in simplified settings, they indicate that solar radiation is a currently neglected, but potentially profound abiotic variable influencing OM processing in benthic detrital food webs.

Organism traits and detritus processing

It is argued in Chapters 2, 3, 5, 6 and 10 that a functional characterization of communities, i.e. identifying invertebrate and bacterial species according to their traits that likely affect ecosystem processes (e.g. body size, feeding strategy, locomotion, substrate preference) is essential to understand overall ecosystem processes, in particular detritus processing. This argument accords with the meta-analyses by Gessner et al. (2010) and Stewart et al. (2013) of biodiversity effects on aquatic and terrestrial food webs, which stressed the paucity of observations on functional traits in detrital food webs. Following a similar consideration, Naeem and Bunker (2009) and Mulder et al. (2012) argued that the identification and quantification of functional traits relevant to ecosystem properties is a key issue that requires further assessment and consolidation. This thesis therefore considered functional traits of both invertebrates and microorganisms in organic matter processing.

In soft bottom sediments, this thesis demonstrated that the rate of organic matter processing was not related to taxonomic diversity of an aquatic invertebrate community, but directly related to the functional (bioturbation type) composition of the aquatic invertebrate community

(Chapter 6), highlighting the importance of functional traits in soft bottom sediments (Nogaro et al., 2009; Hillebrand and Matthiessen, 2009). In contrast to the well studied invertebrate communities in soft bottom sediments, the functional role of sponges remains underexposed. Only a few seminal studies considered sponge functional traits, based mainly on body size and morphology, in relation to sponge species composition (Wulff, 2001; Bell, 2007, 2008; De Voogd and Cleary, 2007), yet consequences of shifts in sponge community composition for ecosystem functioning to date remain uncertain. However, sponges are of major importance for the processing of DOM and POM that is unavailable to metazoans (Bell, 2008; De Goeij et al., 2008; Thacker and Freeman, 2012), and transfer substantial amounts of dissolved carbon substrates in the form of particulate organic matter to higher trophic levels, thereby facilitating and sustaining biodiversity hotspots under oligotrophic conditions (De Goeij et al., submitted). Differential responses of sponges (Chapter 9, 10 and 11) and symbiont bacteria (Chapter 9) to mangrove-derived DOM and differences in OM resource preferences (cf. Granek et al., 2009; Van Duyl et al., 2012), however, point to an interplay between DOM composition and resource niches of sponge-bacterial consortia, and therefore DOM resource niches provide a promising functional trait linking sponge community composition to organic matter processing (Chapter 10).

Similarly, microorganisms can utilize a limited number of resources depending on physiological ability to metabolize organic substances. Bacterial communities likely respond to changes in the chemical composition of available organic matter, while alterations in bacterial community structure and functioning can become evident as the metabolic potential of the bacterial community studied. In this thesis, bacterial functional diversity was considered as bacterial resource niches, i.e. the type of substrates that are utilized by the consortium (e.g. Salles et al. 2009). This characterization proved useful to gain insight in the metabolic differentiation of sponge-associated bacterial symbionts (Chapter 9), and to describe changes in the functional composition of bacterial communities in response to various drivers such as including bioturbation (Chapter 3), organic matter quality (Chapter 5), and solar irradiation (Chapter 5). The results gained in this thesis thus demonstrated that the metabolic potential of bacterial communities provides valuable information about bacterial communities responsible for the processing of organic matter. This would have been overlooked when bacterial communities would have been characterized via their taxonomy, thereby supporting the notion that ecophysiological traits are valuable and worth extending to allow for an integrated assessment of bacterial taxonomic identity and metabolic capacity in the future.

Overall, this thesis identified functional traits for both bacteria and invertebrates. It was shown that trait diversity is more important than species diversity, thus demonstrating that functional traits are good vehicles to analyze the linkage between biodiversity and ecosystem processes.

Conclusion

This thesis identified interactions between fauna and micro-organisms degrading organic matter in two contrasting benthic systems: soft bottom sediments and hard mangrove root substrates. It was found that the chemical composition of OM and abiotic conditions, such as the presence of pollutants and solar radiation, greatly modulate biotic interactions.

Invertebrate fauna, free living in sediments and fauna attached to solid substrates (sponges) were found to facilitate the activity and composition of bacterial consortia, while vice versa bacterial development conditioned organic matter that was either refractive (peat) or less palatable (mangrove phenolics) for fauna. These refractory components of mangrove organic matter structured the sponge species distribution over mangrove and coral reef substrates. Biotic interactions appeared to be affected via faunal bioturbation modifying sediment redox conditions, or immobilization thereof by a model toxicant (Cu). Susceptibility of the detrital food web to copper has been demonstrated to interfere with detritus degradation, thereby demonstrating that effects of anthropogenic stressors on ecosystem processes precede effects on biodiversity. For that reason functional parameters for measuring ecosystem integrity are promoted. Solar radiation influenced the redox conditions of the sediment, thereby blurring the concurrent effects of bioturbation, and overriding the faunal effects on sediment bacteria. Although biodiversity or species composition has served as a touchstone for environmental protection, throughout the present study I found better explanations for detritus decay dynamics when using functional parameters of fauna and bacterial consortia.


I Lived Because I Dreamed
I Dream No More
DiTerlizzi and Black