

The importance of *Lanice conchilega* reefs in trophic linkages in intertidal areas

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Living organisms can have important impacts on physical and chemical processes occurring in their environment, as already stated by Charles Darwin in 1881 after having observed burrowing earthworms. However, the role of species in modifying habitats was only systematically defined in the late 20th century when Jones and co-authors introduced the concept of “ecosystem engineers”: organisms that directly or indirectly alter the availability of resources to other species, by modifying the physical environment. In the marine environment, ecosystem engineers show a high variety and have representatives in all kinds of habitats, ranging from coastal areas (e.g. burrowing mangrove crabs) up to the open waters of oceans and extreme environments such as the deep sea (e.g. zooplankton producing faecal pellets). Since ecosystem engineers tend to prevail in stressful environments (characterised by strong abiotic forces such as wave action or drought), coastal sediments harbour particularly large amounts of ecosystem engineering species such as sea grasses, burrowing invertebrates or feeding sting rays.

Some ecosystem engineers are capable of constructing biogenic reefs: solid structures created by an accumulation of organisms and forming a community or habitat which is very different from its surroundings. A prime example is the reefs constructed by the tube-building polychaete *Lanice conchilega* (Terebellidae), a well-known and widely distributed ecosystem engineer in soft-bottom environments. These *L. conchilega* reefs have profound structuring impacts on the benthic environment by altering the biogeochemical and physical properties of the sediment, which consequently affects the community composition, abundance and species richness of its environment.

Several studies have focussed on ecosystem engineers, biogenic reefs and on the polychaete *L. conchilega*, and they mainly contributed to our understanding of the role of these organisms in structuring their environment and the subsequent changes in the interactions between biotic and abiotic components (e.g. bioturbation). Nevertheless, significant knowledge gaps remain, especially dealing with the link between ecosystem engineers and food webs. Therefore, this PhD thesis aims at improving our understanding of the structural and functional role of reefs constructed by the ecosystem engineer *L. conchilega* in temperate soft-substrate coastal ecosystems. The study focusses on the French side of the English Channel, where substantial reefs of *L. conchilega* occur. An overview of the remaining knowledge gaps is outlined in Chapter 1, along with an elaborate description of the focal organism *L. conchilega* and a description of the two study sites in this PhD: the Bay of the Mont Saint-Michel (BMSM) and Boulogne-sur-Mer (Boulogne).

Biogenic reefs composed of *L. conchilega* are important from a conservation point of view, because they noticeably increase the biodiversity in otherwise species-poor environments. Most research however focusses on the effect of *L. conchilega* on a single ecosystem component at a time and this link is investigated at the local scale. In order to understand the general ecological function of the reefs beyond the local scale, the integrated effect of intertidal *L. conchilega* reefs on the major benthic-pelagic components of a soft-bottom intertidal ecosystem was studied in Chapter 2. The different components of the benthic community (i.e. macro-, hyper-, and epibenthos) were compared between an area dominated by *L. conchilega* and an area without any bioengineering species. Additionally, the effect of different local environmental characteristics on the structuring role of the reef habitat was investigated by including the two study sites. All three investigated benthic assemblages were positively affected by the presence of the *L. conchilega* reef structures. The magnitude of the effect depended on the link between the benthic assemblage and the sediment and was largest for the macrobenthos and least strong for the hyperbenthos (small animals living in the water column close to the seabed). The macro- and epibenthic community composition (benthic organisms living in and on the surface of the sediment respectively) was mainly structured by tubeworm density and macrobenthic food availability respectively, while the hyperbenthic community was rather structured by biotic environmental variables (such as total organic matter, chlorophyll a and suspended particulate matter). For the macro- and epibenthos, the reef effect was more pronounced in Boulogne than for in BMSM and was shown to be mainly driven by the higher tubeworm density in the intertidal area of Boulogne.

The high abundance, diversity and biomass of the macrofauna associated with *L. conchilega* render the reef areas exceptionally important feeding grounds for waders in otherwise uniform habitats, as shown in Chapter 3. Because of the high food availability, waders were attracted to the reef areas of the Bay of the Mont Saint-Michel and their densities in the reef exceeded densities in bare sand areas about 47 times. Based on faecal analysis, *L. conchilega* was the only identifiable polychaete species present in all bird species, however waders in the reef area tended to feed on the associated fauna, and especially crustaceans, rather than specifically on the tubeworm itself. The findings of this and the previous chapter reinforce the central role that *L. conchilega* reefs play in linking benthic, pelagic and air-borne compartments in soft-bottom intertidal areas.

While the importance of *L. conchilega* reefs for higher trophic levels was clearly demonstrated, there is no knowledge on the possible existence of reverse interactions; i.e. whether and to which extent predators affect the activity of *L. conchilega* within the reef habitat. A mesocosm experiment was set up to investigate the activity of the tubeworm in the absence and restricted and unrestricted presence of the predatory shrimp *Crangon crangon* (Chapter 4). The bioirrigation activity was quantified by the decrease of an artificially introduced bromide (Br⁻) tracer, while the feeding activity was measured from the incorporation of ¹³C via stable isotope analysis. The bioirrigation activity of the *L. conchilega* reef equalled about 30 L m⁻² d⁻¹ and was shown to remain unaffected in the presence of the predatory shrimp *C. crangon*. The food uptake of the tubeworm was however about three times lower in the unrestricted presence of *C. crangon*, presumably due to the retraction of the worm's body and tentacles in its tube, induced by physical contact with the predator. Hence, *C. crangon* exerts a trophic pressure on the tubeworm which affects its feeding activity, but not its bioirrigation activity, enabling the tubeworm to maintain its functional role in soft-bottom intertidal areas, even under high predatory pressure.

Notwithstanding the investigated bottom-up and top-down effects within bio-engineered *L. conchilega* reefs, the significance of the common and often influential process of ecosystem engineering on the food web structure and dynamics remains largely unknown. Moreover, most studies dealing with this issue have a theoretical nature and empirical evidence is largely lacking. Chapter 5 combined a classical and a more integrative stable isotope approach to explore the potential effect of *L. conchilega* reefs on the structure of the macroscopic soft-bottom intertidal food web of the two study locations. Despite the structural impacts of the ecosystem engineer on the associated macrofaunal community as reported in Chapter 2, the presence of *L. conchilega* reefs only has a minor effect on the structure of the food web. The isotopic niche width of the consumer communities of reef and control areas are highly similar, implying that consumer taxa do not shift their diet when feeding in a *L. conchilega* reef. Besides, species packing and hence trophic redundancy were not affected, pointing to an unaltered stability of the food web in the presence of *L. conchilega*. The ecosystem engineer's influence on the water column is probably too limited to substantially stir the global structure of the soft-bottom intertidal food web, which is mainly driven by water column-derived primary production.

Whereas the study in Chapter 5 looked at qualitative aspects, another important aspect of food web research consists in the quantification of food web flows, which yields a more thorough approximation of complex food webs. Therefore, Chapter 6 makes use of linear inverse models (LIMs) to present a comprehensive analysis of carbon cycling and dynamics of the food web of a soft-bottom intertidal area in the presence and absence of *L. conchilega* reefs; focussing on the macrofaunal part of the food web. The food web models were based on an empirical dataset from two study sites and two time periods, consisting of biomass and stable isotope data, and general physiological constraints from the literature. The carbon input into reef food webs was about 40 times higher compared to bare sand areas and was mainly derived from organic matter in the water column. The tubeworm focussed the organic matter which is produced in an area at least 15 times larger than the reef itself. Although most of the organic matter input towards these reefs was consumed by suspension feeding macrofauna, particularly *L. conchilega* itself, the worm was not an important source of carbon for other macrofaunal organisms. Rather, the tubeworm reinforces the benthic-pelagic coupling by establishing reef structures which act as a trap of organic matter, resulting in an overall high macrofaunal biomass in the presence of the tubeworm, and much more diverse and well-organised food webs.

The gained knowledge on the structural and functional role of the ecosystem engineer *L. conchilega* in natural soft-substrate coastal ecosystems is summarised and integrated in Chapter 7. This chapter is revolved around a conceptual diagram and discusses the potential of *L. conchilega* in linking community composition, feedback effects, food web structure and carbon cycling at the ecosystem level and beyond the local scale. The combined knowledge emphasises the added value of *L. conchilega* reefs in otherwise uniform intertidal areas. Additionally, the engineering effects of *L. conchilega* on the physical, biological and socio-economic aspects of the ecosystem are compared to the engineering effects of a variety of other ecosystem engineers. Whereas this PhD thesis

provides one of the first attempts to link food web structure/stability and ecosystem engineering in soft-bottom intertidal areas, the discussion thoroughly elaborates on the incorporation of these two research areas.

In conclusion, the ecosystem engineer *Lanice conchilega* facilitates the benthic-pelagic coupling in soft-bottom intertidal areas and it was proven to strongly affect the faunal community composition, diversity, abundance and biomass, even under high predatory pressure. Notwithstanding this strong structural and functional role provided by the *L. conchilega* reefs, no direct effects on the overall structure or stability of the intertidal food web were detected. The magnitude of the links between different food web compartments however is modified by the increased carbon input in the presence of the reefs.