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Mussels of a marginal population affect the patterns of ambient macrofauna: A case study from the Baltic Sea

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ABSTRACT

In contemporary ecosystems, organisms are increasingly confronted with suboptimal living conditions. We aimed to understand the role of ecosystem engineering species in suboptimal habitats from a population inhabiting the species range margin in naturally stressful conditions. We determined the impact of 2–4 cm sized patches of dwarfed mussels *Mytilus trossulus* close to its lower salinity limit in the North-Eastern Baltic Sea, on epibenthic community patterns. Mussels affected total macrofaunal abundance and biomass and the taxonomic and functional community structure based on abundances, as well as the species composition of macrofauna. Mussels did not affect ephemeral algae or sediment chlorophyll content, but increased the abundance, biomass, richness, and diversity of grazers, within a radius approximately twelve times the size of mussel patches. We can expect marginal populations of ecosystem engineers in suboptimal habitats to contribute to spatial heterogeneity in biotic patterns and eventual ecosystem stability.

1. Introduction

The biotic environment around us is created and maintained by a broad range of organismal activity at multiple spatial and temporal scales (Cech et al., 2010; Peterson et al., 2013; Strayer, 2014). Consumers often relocate matter in space either as constituents of their body or as separate organic or inorganic substances, thereby creating distinctive environmental patterns via both physical and/or chemical engineering (McIntyre et al., 2008; Gagnon et al., 2013; Seymour et al., 2014). The contemporary world is characterized by global environmental change and fast and progressively altering ecosystems (Steffen et al., 2007). Species are increasingly challenged by suboptimal living conditions rising from anthropogenically modified abiotic environments and/or climate change. Among others, important ecosystem engineers are also affected (Smith et al., 2006; Ridgwell et al., 2009).

Generally, organisms can survive at suboptimal environmental conditions until the stress level reaches some physiological threshold. However, population properties of affected taxa, in terms of demography, density, individual size, or biomass, are likely already altered by deteriorating habitat conditions above the survival threshold (Pörtner and Farrell, 2008). Altered abundance patterns of engineering organisms may modify the biotic environment for other taxa. Although the importance of suboptimal habitats has largely increased globally and can be predicted to increase into the future (Hobbs et al., 2014; Morse et al., 2014), the majority of studies explore ecological interactions in a relatively optimal environmental range (e.g., Paine, 1992; Menge, 1995; Bracken, 2004; Pfister, 2007; Aquilino et al., 2009). The main focus of studies concerning the ecological impact of global change has been on the ability of taxa to survive in rapidly changing abiotic conditions (Thomas et al., 2004; Hoegh-Guldberg et al., 2007; Carpenter et al., 2008; Gao et al., 2009; Pandolfi et al., 2011; Kamenos et al., 2013). It is still poorly understood, how stressed taxa with altered population properties function in species assemblages in suboptimal environmental conditions. This can be studied by experimentally manipulating environmental conditions on naive or recently disturbed populations, e.g. by simulating a disturbance like acidification or oxygen deficiency. However, long-term processes like adaptation, which affect populations in

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challenging environments and modify the real outcome of environmental change (Hoffmann and Sgrò, 2011) can be accounted for only by studying populations that already historically inhabit their environmental niche margins in stressful conditions.

In aquatic environments, sessile suspension feeders like mussels are often important ecosystem engineers. Mussels can increase the spatial heterogeneity in benthic processes by their structure and available biomass stock, by providing food for their predators and as hiding places and a secondary substrate for all associated organisms (Menge et al., 1994; Ragnarsson and Raffaelli, 1999; Lappalainen and Rask, 2001; Thiel and Ullrich, 2002; Norling and Kautsky, 2007). Strong evidence suggests that live mussels also affect benthic biota via their metabolic activity. In particular, mussels may fertilize surrounding benthic vegetation with their nutrient-rich excretions (Bracken, 2004; Pfister, 2007; Aquilino et al., 2009; Atkinson and Vaughn, 2015). Conspicuously, reports of mussel impact on benthic vegetation vary widely, ranging from enhancement to suppression (Reusch and Williams, 1998; Miyamoto and Noda, 2004; Pfister, 2007; Bracken and Nielsen, 2008; Vinther et al., 2012). In a few cases, an increase in invertebrate grazers has been observed related to mussels (Ragnarsson and Raffaelli, 1999; Norling and Kautsky, 2007; Kotta et al., 2009). The most frequently studied ecosystems are freshwater lakes and rivers, salt marshes, seagrass assemblages, tidepools and intertidal rocky shores, all with optimal conditions and high mussel densities, and present knowledge almost exclusively comes from assemblages hosting a large biomass of mussels (citations above). Limited evidence suggests density-dependent effects of mussels on benthic biota (Maggi et al., 2009; Koivisto et al., 2011), but the role of low-density populations of undersized specimens in shaping marine landscapes is poorly known, and there are extremely few studies from marginal populations (Norling and Kautsky, 2008; Kotta et al., 2009).

The Baltic Sea offers suboptimal conditions for lots of resident biota due to natural causes (low salinity, poor water circulation) combined with intense anthropogenic pressures (eutrophication, overfishing, various types of pollution) (Kautsky and Kautsky, 2000; Österblom et al., 2007; HELCOM, 2010; HELCOM, 2014). Individuals of the bay mussel (*Mytilus trossulus*) are dwarfed due to physiological salinity stress in the brackish Baltic Sea (Tedengren and Kautsky, 1986). As sessile benthic suspension feeders, mussels need sufficient water exchange to provide enough suspended food and satisfactory oxygen conditions (Hammond and Griffiths, 2004; Kotta et al., 2005). Accordingly, even the dwarfed mussels are able to build up high density populations at certain depths in areas with steep slopes and optimal exposure (Westerbom and Jattu, 2006; Kotta et al., 2015), while mussel populations in less favourable conditions, such as flat or more sheltered bottoms, consist of small scattered individuals with extremely low net biomass per area (Kotta et al., 2015). Therefore they fit well the definition of marginal population as one in which the individuals are relatively sparsely distributed and show effects of physiological stress (Soule, 1973).

The aim of the present study is to look at the role of a stressed, marginal population of an ecosystem engineer *M. trossulus* in generating biological patterns. We expect that patchily distributed marginal populations may increase the spatial heterogeneity in the biotic environment for other organisms. To confirm this, we expect ecosystem engineering species, such as *M. trossulus*, to be able to affect surrounding epibenthic biota even at low densities, and we test this in the North-Eastern Baltic Sea in suboptimal environmental conditions for this species. We predict changes in sediment organic matter and chlorophyll content, abundance of macrofauna, macroalgal and macrofaunal biomass, species richness and diversity; the functional and taxonomic dominance structure and species composition of epibenthic assemblages in the neighbourhood of low number of dwarfed mussels.

2. Material and methods

2.1. Experimental setup

An *in situ* experiment was run in a moderately sheltered bay (59.847 N, 23.253 E) adjacent to the Tvärminne Zoological Station in the North-Eastern Baltic Sea. The sediment in the shallow subtidal was mosaic; patches of hard rock surfaces combined with larger sediment accumulation areas of sand mixed with boulders. Salinity varied between 5.2 and 6.0 psu during the experiment. The experimental setup was designed to mimick the patchy occurrence of mussels on small boulders in flat shallow areas of the region (Malm and Isaeus, 2005; Liversage and Kotta, 2015). In the natural seascape, mussels can be distributed more or less evenly at different positions and on various sizes of boulders. Nevertheless, aggregation rates from one single to ten individuals clumped together are common in the depth zone dominated by macroalgae in the North-Eastern Baltic (Martin et al., 2013; Kotta et al., 2015). Plastic buckets (18 in total) with a height and top diameter of 20 cm were used as boulder mimicks. Each experimental unit consisted of one bucket and two cages attached to it (Fig. 1). Each bucket was covered with a lid, the central part of which (18 cm diameter) was made of a nylon mesh fabric previously confirmed as a suitable substrate for macroalgal attachment. We used the dominant epifaunal suspension feeder species of the Baltic Sea, the mussel *M. trossulus*, hereafter referred to as *Mytilus*, or simply ‘mussel’, for the experiment. The average shell length of *Mytilus* in the study area is around 1–2 cm (Database of the Estonian Marine Institute; Westerbom et al., 2002). We collected mussels from the adjacent sea area and planted them into cages made of plastic coated wire. We attached two cages containing 4–8 mussels to the opposite edges of the top of the bucket, corresponding to an average biomass (±SD) of 2.59 ± 0.87 g dry weight with shells m^{-2} and 0.41 ± 0.14 g of shell-free dry weight m^{-2} (Kotta et al., 2012). Initially, two different mussel densities were used: 6 replicates with 8 individuals and 6 replicates with 16 individuals, but as the effect sizes did not differ between the two mussel densities, these treatments were pooled for the simplicity of presentation. Six replicate buckets

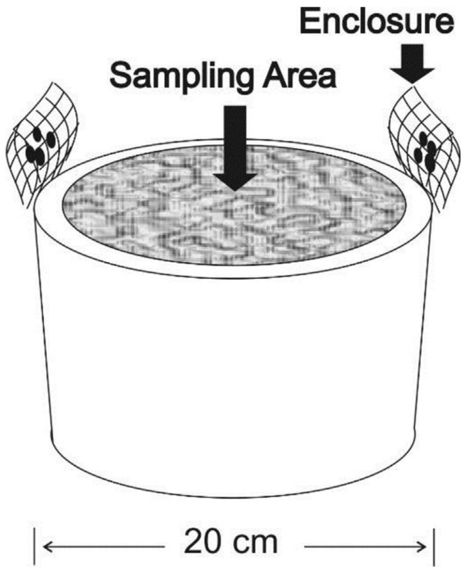

Fig. 1. The scheme of the experimental unit.