



Temperature–parasitism synergy alters intertidal soft-bottom community structure



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ABSTRACT

The abundant amphipod *Corophium volutator* is an ecosystem engineer in soft-bottom intertidal communities due to its grazing and bioturbation activity. However, the amphipod commonly serves as second intermediate host for detrimental microphallid trematodes. This host–parasite association is potentially very sensitive to climate change as the transmission rate of larval trematodes (cercariae) from first intermediate hosts (mud snails) to amphipods, and hence infection intensity-dependent amphipod mortality, generally accelerates with increasing temperature. Given the ecosystem engineering role of *C. volutator*, we hypothesized that elevated temperature, indirectly through increased parasite-induced amphipod mortality, significantly affects the structure of the surrounding benthic community. To test this, we performed a three-month outdoor mesocosm experiment exposing a natural soft-bottom community of benthic plants and animals to four different treatments: relatively low mean water temperature (18 °C) with low (<4%) and high (c. 31%) trematode prevalence in the snail population, and relatively high mean water temperature (22 °C) with low and high trematode prevalence. Both temperature and snail parasitism had a significant impact on amphipod abundance and resulted in their almost complete eradication at the warm temperature with high parasitism. Aside from the amphipod hosts, increased temperature affected the abundance of eight faunal species out of 22 in total (36%), whereas increased level of parasitism or the parasite–temperature interaction influenced the density of three species (14%). The treatment-determined *Corophium* abundance played an isolated role for several species, particularly the polychaetes *Hediste diversicolor* (positive) and *Polydora ligni* (negative). Regarding primary producers, the overall frequency distribution of 21 species of benthic diatoms differed between all four treatments. Species-specific effects were few and weak, however, and microalgal abundance (chlorophyll-*a*) was statistically unaffected by treatments, together suggesting a rather resilient plant community towards the experimental perturbations. At the community level, the non-host macrofaunal diversity decreased with temperature in the low parasitism treatments whereas it increased with temperature in the high parasitism treatments. This suggests that sufficiently high levels of parasitism may turn a negative effect of elevated temperature on macrofaunal biodiversity into a positive effect. Hence, our experiment demonstrates that the synergy between parasitism and a relevant temperature increase, e.g. in lieu of climate oscillations or global warming, may have broad ecological consequences for the organization and function of soft-bottom communities, in part through elevated parasite-induced mortality of a central community member.

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1. Introduction

Parasitism has been acknowledged as a major factor that can regulate the abundance of host populations (Scott, 1987), alter the structure of plant and animal communities (Minchella and Scott, 1991; Mouritsen and Poulin, 2002a; Poulin, 1999; Wood et al., 2007), and affect the functioning of ecosystems (Sousa, 1991; Thomas et al., 2005). At the same time, there has been a growing awareness that climate change

may increase the frequency of parasitic diseases in both terrestrial and aquatic environments (Harvell et al., 1999, 2002; Marcogliese, 2001). In particular, it has been emphasized that the transmission of marine trematodes is sensitive to even small temperature changes (e.g. Mouritsen, 2002; Mouritsen and Jensen, 1997; Poulin, 2006; Studer et al., 2010; Thieltges and Rick, 2006). Given that parasitism is capable of organizing natural ecosystems and that trematodes appear particularly sensitive to temperature, it becomes imperative to elucidate the potential responses of host–parasite systems to climate fluctuations, including climate warming. Accordingly, recent reviews have focused their attention on understanding the consequences of such temperature–parasite synergism on entire coastal ecosystems (Marcogliese, 2001, 2008; Mouritsen and Poulin, 2002b; Poulin and

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Mouritsen, 2006). There remains, however, great uncertainty about how and to what extent environmental factors affect marine host–parasite systems, and in turn the ramifications to the surrounding community of plants and animals. Specifically, to our knowledge, no studies have examined the potential effects of increasing temperature on coastal benthic community structure through elevated parasite-induced mortality rates of a single ecologically important community member.

The amphipod *Corophium volutator* is often a dominant macrofaunal organism in intertidal soft-sediment environments on both sides of the North Atlantic, occasionally reaching densities of 100000 individuals m^{-2} . *Corophium volutator* is an important prey item for demersal fishes, benthic invertebrates and migratory shorebirds (Daborn et al., 1993; Mouritsen, 1994; Pihl, 1985). It belongs to the infauna and lives in U-shaped burrows in the upper layer of the sediment. Due to the amphipods burrowing and grazing activities they may alter sediment characteristics of mud-flats and influence benthic community structure (Daborn et al., 1993; Gerdol and Hughes, 1994a; Mouritsen et al., 1998). Hence, amphipods may be regarded as ecosystem engineers in soft-bottom intertidal communities (Jones et al., 1997).

Corophium volutator acts as second intermediate host for a variety of microphallid trematodes. The most common microphallid species along eastern Atlantic coasts belong to the genera *Maritrema* and *Microphallus* (Deblock, 1980; Jensen and Mouritsen, 1992). The complex life cycle of these parasites also includes the mud snail *Hydrobia ulvae* as first intermediate host, and shorebirds as definitive hosts. After the parasite eggs are ingested by the mud snail, larval trematodes are continuously produced asexually within the snail's gonads and released as free-swimming cercariae that seek out and penetrate the cuticle of *C. volutator*. The cercariae encyst as metacercariae within the body cavity of the amphipods and await ingestion by an appropriate shorebird host in order to complete their life cycle. This host–parasite system is very sensitive to environmental factors, particularly temperature. Usually, increasing temperature accelerates the development of larval trematodes within the snails, as well as triggering their release (Meissner and Bick, 1999a; Mouritsen, 2002; Mouritsen and Jensen, 1997). This temperature-mediated increase in cercarial output in turn increases severe infection intensity of amphipods, as the transmission efficiency (proportion of cercariae successfully reaching the second intermediate host) remains roughly constant with increasing temperature within naturally occurring ranges (Mouritsen and Jensen, 1997; Studer et al., 2010). Consequently, the infection intensity-dependent parasite-induced amphipod mortality is likely to increase as temperature rises (Jensen and Mouritsen, 1992; Larsen et al., 2011; Meissner and Bick, 1999a,b; Mouritsen and Jensen, 1997; Mouritsen et al., 2005). Indeed, parasite-induced mass mortality in a local amphipod population has been observed in the Danish Wadden Sea during a period of unusual high temperatures (Jensen and Mouritsen, 1992). The disappearance of the tube-building amphipod led to increased sediment erosion and significant changes of the sediment characteristics (see Mouritsen et al., 1998). However, the direct as well as indirect consequences of such temperature–parasitism synergy on surrounding benthic flora and fauna have not yet been thoroughly quantified (Larsen et al., 2011; Mouritsen et al., 1998).

Here, we use the above mentioned host–parasite system to elucidate the effect of temperature–parasitism synergy on intertidal community structure. We hypothesize that temperature-dependent parasite-induced amphipod mortality leads to significant structural changes of the surrounding benthic community. To test this, we performed a three-month outdoor mesocosm experiment designed to unravel (1) the combined effect of temperature and microphallid parasitism on the density of *C. volutator*, (2) the ramifications on the community of benthic microalgae, meiofauna and macrofauna that may follow, and (3) the community consequences of altered temperature and parasitism stemming from other processes than parasite-mediated reduction in amphipod density.

2. Materials and methods

2.1. Experimental design

The outdoor mesocosm experiment was conducted at Rønbjerg Marine Biological Station, Limfjorden, Denmark, from 6 July to 21 September 2009. The experimental mesocosm unit was a circular PVC container, 16.5 cm in height and an inner diameter of 15 cm resulting in a 177 cm² bottom surface area. Two cm below the top of the container, 4 holes (each 0.8 cm²) covered with a 500 μ m polyethylene mesh were used as a drain, which hence allowed for a certain level of emigration of smaller resuspended organisms. To help maintaining the desired water temperature (see below) the containers were insulated on the outside with flexible polyurethane foam (10 mm).

Four different treatments were assigned to 28 such containers (i.e. $n = 7$ per treatment), fully randomized in a 4×7 block design: (1) low water temperature and low parasitism, (2) low water temperature and high parasitism, (3) high water temperature and low parasitism, and (4) high water temperature and high parasitism (high and low parasitism refer to prevalence of infection in the experimental snail population; see Section 3.2.2 for realized infection levels across treatments). The low water temperature treatment was designed to reflect the present mean summer temperature of coastal areas in Denmark (c.18 °C; data available at <http://www.seatemperature.org/>), whereas the high water temperature treatment aimed at a temperature 4 °C above the present level (22 °C). The latter corresponds to the expected rise in ambient air temperature in Denmark within this century (Christensen et al., 1998, 2001), bound to also affect near-coastal water temperature.

Each container was supplied with 6.5 cm substrate (see Section 2.2) and its own seawater supply (25–30‰) at a flow rate of 0.16 L min^{-1} . The latter corresponds to a retention time of approximately 9 min of the resulting water column of 8.0 cm (water volume: 1.4 L). This relatively high flow rate served to achieve the required temperature and to ensure well-oxygenated mesocosms. In order to avoid invasion of non-experimental organisms the applied seawater was filtered through a sand filter followed by a 25 μ m pleated polyester filter and a 5 μ m string wound filter. The filtered water was then directed through coiled tubes submerged in either cooled or heated water baths to achieve out-flow temperatures of 18 and 22 °C, respectively. The cooled and heated water was directed into two separate insulated PVC tubes ($\varnothing = 5$ cm, length = 230 cm) functioning as water reservoirs. This was done to obtain a constant water flow to each experimental mesocosm unit in addition to equal water temperature among containers within each of the two temperature treatments. Finally, short silicon tubes connected to these PVC tubes were used to supply each container with desired seawater quality. During experimentation, the water temperature was measured every 30 min by temperature loggers submerged in two haphazardly chosen experimental mesocosm units from each temperature treatment. The resulting water temperature in the low and high temperature treatments was 17.9 ± 0.01 and 22.0 ± 0.01 °C (mean \pm SE), respectively (Fig. 1). The experimental set-up allowed to a certain extent for the influence of fluctuating ambient temperatures and influx of sun radiation, thereby reflecting greater realism. Based on daily measurements at 15:00 PM and 03:00 AM, the variance in water temperature was statistical similar between the high and low temperature treatments over the course of the experiment (Levene's test, $F_{1,304} = 2.795$, $p = 0.096$). On July 27 (experimental day 22), the water temperature dropped to 17.8 °C during a two hours period in the high temperature treatment due to technical problems with the thermostat. However, this short-termed temperature drop is judged to have no significant bearing on obtained results.

2.2. Sediment, microflora and meiofauna

The sediment used in the experiment contained naturally occurring microflora and meiofauna community of initially unknown composition.

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