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Re-colonization of anoxic/sulfidic sediments by marine nematodes after experimental removal of macroalgal cover

Abstract In shallow beaches of the southern Baltic Sea drifting macroalgal mats frequently accumulate in the summer months, inducing anoxic and sulfidic conditions with devastating effects on most members of the benthic fauna. Our study describes the meiobenthic nematode fauna under such a natural drifting algal mat and its short-term (30 days) response to the removal of the mat, simulating natural displacement. The sediment under algal cover was characterized by high concentrations of total organic matter (3.9%) and sulfide (10.0 mmol l⁻¹). Sulfide was also detectable in the mat itself (2.2 mmol l⁻¹) and in the overlying water column (0.3 mmol l⁻¹). Thirty days after algal removal total organic matter had dropped to 1.7% and sulfide was present only in deeper sediment horizons. Changes in fauna composition of previously algal-covered sediments were compared with ambient reference stations by means of diversity indices and multidimensional scaling ordination. The nematode assemblage under the mat (prior to removal) was characterized by low diversity ($H' = 0.42$) and dominated by the deposit feeder *Sabatieria pulchra*, the only nematode present in algal-covered sediments in abundances similar to ambient reference stations. Significant changes in community composition in previously algal-covered sediments could be demonstrated after 30 days by means of multiple dimensional scaling techniques. At this time *Daptonema* sp. and *Chromadorita tenuis* dominated the nematode fauna and were present in significantly higher abundances than in the reference samples. While diversity indices showed no significant differences between treatments within 30 days, multidimensional scaling proved that differences between treatments were still significant, indicating that the recovery process had not finished. Reasons for the delayed re-colonization of nematodes are discussed.

Introduction

Disturbance, followed by re-colonization, is an important element in structuring species communities (e.g. Connell and Slayter 1977). The effect of disturbance mainly depends on its frequency and intensity. Disturbance events can be natural, like wave action, sedimentation or predation, as well as man induced. The increase of anthropogenic nutrient loading over the last decades has been recognized as a major threat to most coastal marine ecosystems around the world (Rosenberg 1985; Nixon 1990; Gray 1992). Particularly in the Baltic Sea, eutrophication in conjunction with density-stratified water masses frequently results in severe oxygen depletion of bottom waters, especially during the summer months, leading to hypoxic (dissolved oxygen concentration < 2 mg l⁻¹) or even anoxic (dissolved oxygen concentration of 0 mg l⁻¹) conditions (Rabalais et al. 1991; Turner and Rabalais 1991; Rosenberg et al. 1992). While most hypoxic events affect the fauna in deeper sublittoral regions below a thermo- or halocline, eutrophication has also been attributed to the increasing development of benthic macroalgae (Rosenberg 1985; Hull 1987; Raffaelli et al. 1991; Gray 1992; Kolbe et al. 1995). The resulting dislodged macroalgal material can accumulate, after detachment and fragmentation, as drifting mats in shallow regions and cover previously uncovered sediments. Thus, benthic communities, which had never been affected by hypoxia before, can become exposed or threatened by hypoxic/anoxic conditions (Olafsson 1988).
Drifting algal mats have been reported from shallow coastal areas worldwide (Koop et al. 1982; Hull 1987; Raffaelli et al. 1991; Dando et al. 1993; Bonsdorff et al. 1995) and have been most extensively studied in the Baltic Sea (Olafsson 1988; Bonsdorff 1992; Norkko and Bonsdorff 1996a,b,c; Norkko 1998). Here, algal mats seem to have increased in their frequency of occurrence and dimension over the last decades.

Such algal-covered sediments experience periods of severe oxygen depletion and develop toxic hydrogen sulfide as a result of anaerobic decomposition of organic matter (Reise 1983; Hull 1987; Dando et al. 1993). Consequently, many effects of algal cover are comparable to disturbance induced by periods of severe anoxia in density-stratified waters. Hypoxia and anoxia have been shown to have a great influence on all elements of marine benthic communities (for recent reviews see Diaz and Rosenberg (1995) for macrofauna and Wetzel et al. (2001) for meiofauna).

Within the benthic macrofauna community algal cover induces emigration or mass mortality (Bonsdorff 1992; Norkko and Bonsdorff 1996c), affects predator–prey interactions (Norkko and Bonsdorff 1996a; Norkko 1998), and impairs benthic community recruitment by preventing settlement of pelagic larvae (Olafsson 1988; Bonsdorff 1992; Bonsdorff et al. 1995). This strong effect is even enhanced by the irregular appearance of loose-lying algal mats, which mainly depends on the local seasonal flow regime (Olafsson 1988). Algal mats may remain stationary for some time, or become dislocated by changes in water currents or wave action. Depending on the duration of cover, the sediment will be left enriched to various degrees in organic and inorganic compounds. Hence, drifting algal mats can significantly contribute to the patchy distribution typical for many benthic communities (Olafsson 1988).

While the influence of drifting algal mats on macrofauna has been studied comprehensively, no information exists regarding their effect on meiofauna. Meiofauna (invertebrates ranging from 0.042 to 1 mm in size) are omnipresent in the marine benthos, where they play a significant role in energy flow and nutrient recycling (McIntyre 1969; Bell and Coull 1978; Hicks and Coull 1983; Grant and Schwinghamer 1987), serve as an important food source for macrofaunal invertebrates and juvenile fish (Gee 1989; Coull 1990; McCall and Fleeger 1995), and commonly demonstrate higher diversities than benthic macrofauna (e.g. Armonies and Reise 2000). Many meiobenthic species, in particular nematodes, which constitute up to 51–98% of all macrozoan meiofauna (cf. Coull et al. 1982; Heip et al. 1990; Montagna 1991; Guidi-Guilvard and Buscali 1995), are known to persist over extensive periods under hypoxic and anoxic conditions (see Wetzel et al. 2001, and references therein). Such resistant members of the meiofauna are likely to be unaffected by drifting algal mats, while other more sensitive species (mainly copepods) will disappear. This difference in resistive ability is also reflected in their different degree of mobility. Typically, copepods, compared to nematodes, are relatively capable swimmers and rapid dispersers (Sun and Fleeger 1994), and they may use this disposition to avoid low oxygen concentrations by emigration. Conversely, the same difference in swimming skills also influences re-colonization capability; copepods are usually mentioned among first settlers in studies monitoring the colonization of azoic sediments (e.g. Sherman and Coull 1980; Chandler and Fleeger 1983; Heip et al. 1985; Fegley 1988). However, in a few studies meiobenthic nematodes have been found to reach control abundances already within 1–2 days (Sherman and Coull 1980; Colangelo and Ceccherelli 1994), indicating that under certain circumstances fast re-colonization has to be expected by nematodes also.

The purpose of the present study was: (1) to document the metazoan meiofauna within and underneath a natural drifting algal mat, (2) to investigate possible short-term (30 days) successional changes in meiobenthic nematodes after mat displacement (simulated by partial removal of algal material), and (3) to identify early colonizers among meiobenthic nematodes. We compared changes in nematode fauna with ambient reference sediments by means of diversity indices and multidimensional scaling (MDS) ordination. Over the course of the experiment, sulfide gradients in the algal mat and their temporal changes compared to ambient reference sediments are presented.

Materials and methods

Study site

The study area is located on the southwest Baltic coast of Germany, known as the Bodden coast. Numerous barrier islands, peninsulas, and shallow embayments enclosed to various degrees are characteristic for this region. This study was conducted at a shallow and protected beach located on the east side of the small islet Fährinsel. This islet is located between the two larger islands Rügen and Hiddensee (54°30’N; 13°08’W). In the vicinity of Fährinsel, accumulations of dislodged macroalgal mats are known to occur frequently in the summer months (Gamenick et al. 1996, 1997). Water cover at this site is mainly influenced by wind direction and velocity; its depth varied between 10 and 40 cm during our study. During the experimental period (30 days, from 25 May to 25 June), a drifting algal mat (mainly composed of Fucus vesiculosus) had accumulated at a sheltered beach. The mat covered an area of approximately 30–40 m² (roughly 5–10 cm thick) and showed signs of increasing decomposition, with abundant patches of Beggiatiora spp. on algal material. In order to allow easy access and to minimize impact, a wooden platform was constructed a few days before the study was performed.

Experimental set-up and sampling

The experimental design consisted of 20 areas (each 0.3 m²) along the algal mat (“experimental sites”) and 8 similar areas of uncoved sediment, a few meters away (“reference sites”). The first samples at the experimental sites were taken shortly before the algal mat was removed (experimental sites, day 0). Thereafter the mat was carefully removed by hand, and additional samples were collected after 0.5, 1, 4, and 30 days. Reference samples were taken on days 0 and 30 only. At each sampling occasion, four experimental areas were selected randomly and sampled by means of destructive