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Benthic ciliate diversity and community composition along water depth gradients: a comparison between the intertidal and offshore areas

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Abstract

The diversity of marine benthic ciliates is largely known from the intertidal zone. No comparative data are available for the change of ciliate communities from the intertidal to offshore sediments in the Yellow Sea. We investigated the community composition and diversity of benthic ciliates at two intertidal (sandy and silty-sand) stations and eight offshore stations along a latitudinal transect in the Yellow Sea. The ciliate abundance and biomass decreased almost linearly with increasing water depth and distance from the intertidal zone. Diversity indices showed a similar trend. By contrast, the total species richness and taxonomic diversity were much higher in the offshore sediments than in the intertidal area. Among the total of 94 species identified, only 20 species were shared by the two habitats, which were characterized by different dominant ciliate assemblages. Carnivorous ciliates always constituted the primary feeding type in terms of biomass at all offshore stations and the intertidal sandy station, whereas at the intertidal silty-sand station the primary feeding group varied throughout the period of sampling. Multivariate analyses indicates the ciliate communities were significantly different between the two habitats. Bottom water temperature and sediment grain size were the key factors that explained the ciliate community structure.

Keywords: Benthic ciliates; Community comparison; Diversity; Water depth gradient; Yellow Sea

Introduction

Ciliates exist in a wide variety of aquatic and terrestrial habitats. They are a fundamental component of both pelagic and benthic microbial food webs, feeding on bacteria, algae, other protozoa, and even small metazoa, and serve as an important mediator of energy transfer from pico- and nano-sized organisms to higher trophic levels (Azam et al. 1983; Epstein 1997a; Fenchel 2008; Weisse 2017). While the community structure and functional role of pelagic ciliates is reasonably well studied, research on marine benthic ciliates is generally poorly understood. Knowledge of the diversity and community structure of ciliates in marine sediments is still in its infancy due to undersampling and insufficient data,

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which are the key factors affecting the observed diversity and distribution patterns of these organisms (Foissner et al. 2008).

Most research on benthic ciliates has been carried out in intertidal and upper subtidal areas and mainly addresses their quantitative importance, distribution and dynamics (e.g., Azovsky et al. 2013; Du et al. 2012; Epstein 1997a,b; Hamels et al. 2005). In subtidal and intertidal sediments, ciliate diversity depends mainly on local habitat conditions (depth and sediment properties) (Azovsky and Mazei 2005). Sublittoral ciliate faunas tend to exhibit higher species diversity but a lower total abundance than intertidal faunas (e.g., Azovsky and Mazei 2007; Fernandez-Leborans 2000).

Although data on ciliates in offshore sediments are rather scant, previous studies indicate a remarkable difference in the ciliate community structure and feeding preference between the intertidal and offshore sediments (e.g. Du et al. 2012; Hamels et al. 2005; Meng et al. 2012; Zhou and Xu 2016). These studies, however, were conducted either in widely separated sea areas or in different habitats (estuary vs. continental sea). To date, only Meng et al. (2012) and Zhou and Xu (2016) have reported the community structure, diversity and trophic role of ciliates in offshore sediments from the Yellow Sea. No study has attempted to compare the ciliate communities from the intertidal to offshore sediments in the Yellow Sea. Thus, the distribution patterns of benthic ciliate communities in these two contrasting habitats are still unknown.

We investigated marine benthic ciliates from the intertidal to offshore area along a latitudinal transect (36°N) in the Yellow Sea off the northern coast of China. Qualitative and quantitative investigations of the ciliate diversity and community composition were carried out using the Ludox-QPS method (Xu et al. 2010). The main aims of this study are: (i) to compare ciliate diversity and community composition between intertidal and offshore sediments; and (ii) to gain a better understanding the environmental factors regulating the ciliate communities.

Material and Methods

Study sites and sample collection

Two intertidal stations about 200 m apart in Qingdao Bay, on the Yellow Sea coast of northern China, were selected for the study: a silty-sand station near the high tide mark and a sandy station near the low tide mark (Fig. 1). Intertidal sediment samples were collected during ebb tides on 29 July 2007, 19 May 2008 and 2 July 2008. A total of six samples, each with three replicates, was obtained for the intertidal sediments.

The offshore sediment samples were collected from eight stations (S1–S8), with water depths ranging from 33 m to 86 m, along the transect 36°N in the southern Yellow Sea (Fig. 1). Stations S1, S3, S4, S5, S7 and S8 were sampled on 15–16 June 2007, and stations S1, S2, S3, S4, S6 and S7 were sampled on 26–27 July 2008. Thus, stations S1, S3, S4 and S7 were sampled twice. A total of 12 samples, each with three replicates, were obtained for the offshore sediments.

In the intertidal zone, eight core samples were randomly collected at each station in an area of about 10 m^2 by coring sediments to a depth of 2 cm using a modified syringe with an inner diameter of 23 mm. In the offshore sea areas, sediment samples were first taken using a 0.1 m^2 modified Grey-O'Hara box corer and syringe core samples was taken from these. One syringe core sample was obtained from each of three box corer replicates grabbed at each station. A fourth syringe core sample was taken as backup. The sediment was carefully extruded through the bottom of the syringes, sliced into a 0–2 cm sediment layer, and immediately fixed with an equal volume of ice-cold glutaraldehyde (2% v/v final concentration). The fixed samples were stored at 4 °C in the dark until processed. For the measurements of environmental factors, the corresponding layer of another four syringe cores (three replicates plus a pseudo-replicate in the offshore area) were pooled and immediately stored at −20 °C in the dark until analyzed.

Ciliate identification and enumeration

Ciliates were analyzed following the Ludox-QPS method (Xu et al. 2010). Briefly, ciliates were extracted from the sediment samples by Ludox density gradient centrifugation and stained with the quantitative protargol stain (QPS). The slide-prepared ciliates were identified and enumerated with a Nikon E80i microscope at a magnification of 200× to 1000×. Most ciliates were identified to genus/species level using published guides (e.g., Kahl 1930–1935; Lynn and Small 2002; Song et al. 2009). Systematics and classification follow the schemes of Lynn (2008) and Adl et al. (2012). For each taxon, at least 20 cells (or all cells encountered if fewer than 20) were measured and the biovolumes were estimated by geometric approximation. The biomass was calculated using the conversion factor of 200 fg C μm^{-3} for aldehyde-fixed protozoa (Børsheim and Bratbak, 1987; Hamels et al., 2005). Based on their food preferences, which were either indicated from literature (e.g. Fenchel 1968) or from our own observations of the contents of food vacuoles, ciliates were classified into four feeding groups: bacterivores, carnivores, algivores, and omnivores. Bacterivorous ciliates encompass those that feed primarily or entirely on bacteria. The ciliates feeding mainly on microphytobenthos, in particular diatoms, were defined as algivores. Carnivores are those that feed on heterotrophic flagellates, other ciliates and even small metazoans. Omnivores are those ciliates that graze on a variety of food sources including bacteria, microphytobenthos and protozoans. Cysts, possibly belonging to ciliates, were found during the study but could not be identified so were excluded from the analyses. No tintinnid loricas were found in the sediment.

Species richness referred to the number of species per station. Margalef (d), Shannon (H') and Pielou (J') diver-