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Light or tide? Effects on the emergence and recolonization of harpacticoid copepods from sand flats of the Wadden Sea (southern North Sea)

Alexandra Segelken-Voigt[a,*], Klaas Gerdes[a], Achim Wehrmann[b], Pedro Martínez Arbizu[a,c], Thomas Glatzel[a]

[a] Institute of Biology and Environmental Sciences, Carl von Ossietzky University Oldenburg, Carl von Ossietzky Str. 9-11, 26111 Oldenburg, Germany
[b] Marine Research Department, Senckenberg am Meer, Suedstrand 40, 26382 Wilhelmshaven, Germany
[c] German Centre for Marine Biodiversity, Senckenberg am Meer, Suedstrand 44, 26382 Wilhelmshaven, Germany

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ABSTRACT

The Wadden Sea is a highly productive coastal ecosystem and an important nursery ground for various demersal fishes of the southern North Sea. Copepods are one of the major food sources of the ecosystem, yet little is known about the movement patterns of this benthic meiofaunal group within both sediment and water column in the intertidal environment, where they would be more vulnerable for predation. The diversity and abundance of harpacticoids emerging and recolonizing intertidal sand flats were investigated during two diurnal and two nocturnal high tides, using specifically designed traps. Our study revealed no significant difference in the amount of copepods emerging from the sediment into the water column during the day and the night. Furthermore, the proportion of emerging adults and copepodids did not differ from each other and most individuals persisted in the sediment during high tide. Interestingly, the most abundant species *Arenosetella tenuissima* and *Tachidius discipes* showed an opposite emergence behavior, with the former migrating in higher numbers during the night and the latter during the day.

Although tidal inundation was the proximate factor initiating emergence, we suggest that sediment reworking by tidal currents, waves and bioturbation as well as water and food availability above and within the sediment may be additional factors controlling emergence of harpacticoids in the Wadden Sea, with light intensity playing a minor role.

Therefore, emergence and recolonization patterns of harpacticoids from subtidal ecosystems cannot directly be transferred to intertidal areas as the time for benthic pelagic processes is limited to high tides.

1. Introduction

Some meiofaunal organisms move actively in the water column for mating or to improve their living conditions by enhancing food resources or avoiding predation (Armonies, 1989; Decho, 1986; Hicks, 1986; Service and Bell, 1987; Thistle et al., 1995). This migrating behavior is regarded as an efficient energy exchange between benthic and pelagic and therefore as a trophic link between bacteria and larger fauna (Armonies, 1988a; Chandler and Fleeger, 1983). Emergence (i.e. actively leaving the sediment) and recolonization (i.e. active movement from the water column back into the sediment) are always related with the recruitment and colonization of new habitats (Alldredge and King, 1977; Chertoprud et al., 2013; De Troch et al., 2005; Sedlacek and Thistle, 2006; Thistle, 2003; Walters and Bell, 1986) and are affected by specific factors such as salinity, current velocity, wave action, exposure, temperature, grain size composition and roughness of the seabed (Armonies, 1988a; Chertoprud et al., 2005; Fleeger et al., 1995; Hockin, 1982; Palmer, 1988; Strickler, 1998). This behavior is characteristic for harpacticoid copepods (Armonies, 1989), but also occurs in other meio- and macrofaunal groups, e.g. amphipods, ostracods, polychaetes and turbellarians (Thistle et al., 2007).

Studies on the emergence of marine meiofauna organisms, especially on copepods, have been conducted since the end of the 1970s. These investigations were done predominantly in (sub-)tropical reef environments (Alldredge and King, 1977; Blackmon and Valentine, 2013; Hobson and Chess, 1979; Jacoby and Greenwood, 1988), subtidal seagrass meadows (Bell et al., 1989; De Troch et al., 2005; Kurdziel and Bell, 1992), on sandy sediments (Alldredge and King, 1980, 1985; Hicks, 1992; Thistle et al., 1995) and in the intertidal zone of cold-temperate environments (Gee, 1987; Joint et al., 1982).

It is assumed that emergence mostly occurs at night when predatory risk is lower (Ambrose, 1984; Armonies, 1988a). For example, a higher

* Corresponding author.
E-mail address: alexandra.segelken.voigt@uni-oldenburg.de (A. Segelken-Voigt).

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migration rate at night of meiofaunal taxa was observed in subtropical sand and seagrass habitats (Walters and Bell, 1994). Furthermore, Armonies (1994) investigated meiofauna in the tidal zone of the Island of Sylt (southern North Sea, Germany) by collecting the organisms from the water column applying different sampling methods. He focussed on 24 h temporal scales to reveal the dark-light cycle and detected a much higher percentage of copepods leaving the sediment during a single nocturnal high tide than during the day (Armonies, 1988a). However, standardized emergence traps were not used in that study and as many organisms temporarily occur in the water column (Hagerman and Rieger, 1981), it is difficult to distinguish between planktonic, passively eroded, or actively migrated meiofauna with these methods.

In addition, copepods can actively move several meters through the water column before resettlement (Boeckner et al., 2009; Fegley, 1988; Palmer, 1988); therefore, the water column pathway may be very important.

The simultaneous use of emergence and recolonization traps offers the possibility to determine whether parts of the harpacticoid population stay for a prolonged time in the water column or immediately return into the sediment.

As comparative studies about emerging copepods in the intertidal are rare, this investigation was initiated to examine the emergence and recolonization of harpacticoid copepods of that specific environment. For this purpose traps were developed adjusted to the regional hydrodynamic conditions.

The aim of this study was to determine the diversity and abundance of emerging and recolonizing harpacticoid copepods during nocturnal and diurnal high tides in an intertidal sand flat with no surficial water film during low tide. Except day light all other external abiotic factors (i.e. grain size, hydrodynamic regime, and vertical intertidal position) have been kept as constant as possible for both the diurnal and nocturnal experiments.

2. Material and methods

2.1. Study site

The experimental site (53° 46.895′ N; 007° 53.449′ E) was situated in the backbarrier tidal flats of Wangerooge Island in the central Wadden Sea, Germany (Fig. 1). As a moderate energy system (Hayes, 1979), sand flats of the Wadden Sea are continuously affected by wind, waves and tides, altering the substrate. The intertidal zone is strongly exposed to episodic storm surges which physically disturb and rework the intertidal habitat. Intertidal flats exposed during low tide are influenced by precipitation, evaporation and strongly fluctuating air temperatures. These physical factors control the environmental conditions within the emerged tidal sand flat such as highly varying salinities or ice formation during cold winters. However, the sedimentary system of the Wadden Sea is resilient enabling it to return to equilibrium immediately after disturbance (e.g. storm surges) (Wehrmann, 2016).

Small-scale wave ripples at the sediment surface indicate frequent reworking, transport and deposition of the uppermost sediment during each tide. The thickness of the uppermost oxic layer, as indicated by the bright brownish sediment color, was 1–3 cm. During sampling the water temperature ranged from 16 °C to 17 °C. The direction of tidal currents was eastwards with current velocities from 20 cm s^{-1} in the western part to 5 cm s^{-1} in the eastern part of Wangerooge (calculated by the modeling program of the Federal Maritime and Hydrographic Agency BSH; personal communications A. Schulz). The salinity had a value of 29.1. Average wind speed was 13.5 m s^{-1}. Mean tidal range southeast of Wangerooge is about 3.0 m.

2.2. Sediment analysis

Grain size frequency distribution of the sand fraction (63–2000 μm) was measured with a MacroGranometer™ settling tube (2 m height, 0.20 m diameter). For conversion of the raw data from settling velocities (psi) into particle diameters (phi) the software SedVar 6.2p was used. To analyze the amount of organic carbon in the sediment, nitrogen and carbon was measured with an Electron Corporation Thermo FlashEA 1112 Series NC Soil Analyzer for all sediment cores (n = 20).

2.3. Trap design

Similar to emergence studies by Hicks (1986), Walters and Bell (1986) or Thistle (2003), we modified the inverted-funnel (emergence-) trap.

The emergence trap (Fig. 2) consisted of one polymethyl methacrylate (PMMA) pipe with a height of 22 cm and an inner diameter of 10 cm. The lower part had a row of eight ports (inner diameter: 2 cm) and was pushed 5.0 cm deep into the sediment when the trap was in place. The upper part of the trap, which was above the sediment surface, had a row of eight mesh-covered (40 μm) ports and a removable, mesh-covered lid (40 μm). Two more mesh-covered (40 μm) ports were situated below the lid. These openings maintain water exchange during submergence. In the emergence traps, the funnel was attached inversely 5.0 cm above the sediment surface. Hence, the specimens had to actively move a distance of 15 cm from sediment surface in order to be trapped. The area of emergence was 78.53 cm^2 whereas the funnel mouth has only an area of 4.15 cm^2 (for potential recolonization after trapping see discussion).

The recolonization traps were designed in size and proportion analogue to the emergence traps and consisted of a funnel ending in the catch tube (Fig. 3). The bottom of the trap was covered with a removable lid and a drain screw to facilitate draining and extracting the samples after the sampling process. The inner diameter of the recolonization trap also scaled 10 cm and the top of each recolonization trap was covered with a 5 mm mesh to prevent macrofauna (e.g. polychaetes, decapods) from entering the trap.

To withstand wave action the pipes of both trap-types were attached to stabilizing rings. These rings had a diameter of 33 cm and were perforated (6 openings with 6 cm diameter and 3 openings with 4 cm diameter; see Fig. 4A) to maintain natural conditions and to avoid artifacts within the intertidal sand flat. Three reinforcing steel rods with a length of 120 cm were connected to the stabilizing ring and were inserted vertically 80 cm deep into the sediment. A spring cotter pin was put through each reinforcing steel bar to keep the stabilizing ring on the sediment surface.

2.4. Sampling design

Five emergence traps and five recolonization traps were placed at low tide randomly in an 8 × 8 m plot in the sand flat (Fig. 4A) ensuring a minimum distance of 2 m between the traps.

The experiment took place from 18th to 20th June 2011 (3 days after full moon) covering two complete diurnal (18th and 19th) and two nocturnal (19th and 20th) high water phases (Fig. 4B) and therefore four flood occurrences.

At low tide the traps were emptied, cleaned with 40 μm filtered sea water and repositioned on a new nearby (20–30 m) plot under comparable environment conditions for the next high tide sampling. All four plots were characterized by similar sedimentary conditions, i.e., thickness of the oxidized layer, small-scale sedimentary structures and the absence of a surficial water film at low tide. The samples were immediately sieved through 40 μm steel sieve mesh, putting the residual into plastic storage jars preserved with 37% formaldehyde and seawater (ratio 1:9) and stained with Rose Bengal. To facilitate comparisons of the number of copepods emerging, with the number persisting in the sediment, 5 cm long sediment cores, also with a diameter of 10 cm were taken from the middle of the stabilizing rings after removing the emergence traps. The core material was sampled in-situ and treated exactly the same way as the other samples.