Deep-Sea Research I 58 (2011) 839–864

Contents lists available at ScienceDirect

Deep-Sea Research I

journal homepage: www.elsevier.com/locate/dsri

Submarine ridges do not prevent large-scale dispersal of abyssal fauna: A case study of *Mesocletodes* (Crustacea, Copepoda, Harpacticoida)

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ARTICLE INFO

Article history:
Received 13 December 2010
Received in revised form
19 May 2011
Accepted 23 May 2011
Available online 31 May 2011

Keywords:
ANDEEP
Biogeography
Cosmopolitanism
Deep sea
Dispersal
DIVA
Meiofauna

ABSTRACT

We examined the large-scale distribution of deep-sea harpacticoid copepods at the species level, in order to clarify the underlying processes of copepod dispersal. The study was based on samples collected from 12 regions and a total of 113 stations: 57 stations at depths between 1107 and 5655 m on abyssal plains in the South and North Atlantic, Southern Ocean, southern Indian Ocean, and the Pacific Ocean, and 56 stations above 900 m in the North Atlantic and eastern Mediterranean Sea.

We chose the genus *Mesocletodes* Sars, 1909 as an ideal group to study the large-scale distribution of harpacticoid copepods in the deep oceans. Clear apomorphies and a comparatively large body size of about 1 mm allow rapid recognition of allied species in meiofauna samples. In addition, *Mesocletodes* represents more than 50% of the family Argestidae Por, 1986, one of the most abundant harpacticoid families in the deep sea.

The geographical distributions of 793 adult females of *Mesocletodes* belonging to 61 species throughout the South and North Atlantic, Southern Ocean, southern Indian Ocean, Pacific Ocean, and eastern Mediterranean Sea indicated that most species are cosmopolitan. Neither the topography of the sea bottom nor long distances seem to prevent species from dispersing. Passive transport by bottom currents after resuspension is likely the propulsive factor for the dispersal of Harpacticoida, while plate tectonics and movement of individuals in the sediment may play relatively minor roles.

1. Introduction

Topographic features arising from the sea floor are considered to be geographical barriers for the dispersal of deep-sea macrofaunal species that lack swimming life stages (e.g., Brandt et al., 2005; Gage and Tyler, 1991; McClain and Hardy, 2010). Metazoan meiofaunal organisms are traditionally considered to be primarily bound to the sediment and to show limited mobility, since adults as well as juveniles of most species dwell in the sediment and are poor swimmers. Land masses and undersea mountain ranges are therefore considered to prevent meiofauna species from dispersing (see Gage and Tyler (1991) for summary). Nevertheless, a few benthic deep-sea species in different groups of metazoan meiofauna have been recorded from mutually distant regions. These include copepods (Gheerardyn and Veit-Köhler, 2009; Gheerardyn and George, 2010; Mahatma, 2009; Menzel, 2011, in press; Menzel and George, 2009; Por, 1965b), foraminiferans (Lecroq et al., 2009; Pawlowski et al., 2007), gastrotrichs (Alexander Kieneke, personal comment), nematodes (Miljutin et al., 2010 and references therein), and tantulocarids (Mohrbeck et al., 2010). These studies suggest that meiofauna species may have an extremely wide distribution, although relatively few regions have been examined. However, knowledge of large-scale distribution patterns (> 1000 km) of metazoan meiofauna is so far confined mostly to nematodes at the genus level (e.g., Danovaro et al., 2009; De Bovée et al., 1990; De Mesel et al., 2006; Fonseca et al., 2010; Gallucci et al., 2009; Ingels et al., 2006; Lambshead and Boucher, 2003; Miljutina et al., 2010a, 2010b; Thistle and Sherman, 1985), and data at the species level are few (Bussau, 1993; Bussau and Vopel, 1999; Jensen, 1988; Miljutin et al., 2010).

Harpacticoid copepods are the second most abundant taxon in metazoan meiofauna samples, and may even exceed nematodes in terms of biomass (Seifried, 2004). Investigations of large-scale species distribution patterns using harpacticoids came to the fore only in recent years (George, 2006; George and Plum, 2009; George and Tiltack, 2009; Gheerardyn and George, 2010; Gheerardyn and Veit-Köhler, 2009; Mahatma, 2009; Menzel, 2011, in press; Menzel and George, 2009; Plum and George, 2009). Such studies require extensive sampling in the areas to be compared (*cf.* Rose et al., 2005), because small-scale diversity is extremely high in deep-sea sediments (e.g., Baguley et al., 2006; Coull, 1972; Menzel, unpublished data; Rose et al., 2005; Shimanaga et al., 2004; Thistle, 1978). To date, this requirement has been met only by the DIVA and ANDEEP campaigns, which have provided more meiofauna samples and individuals from the deep oceans at different spatial scales than have been available previously in a single study. The few studies on

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doi:10.1016/j.dsr.2011.05.008

large-scale harpacticoid distributions indicate a trend toward cosmopolitanism at the species level. Harpacticoids appear not to be restricted by geographical barriers such as ridges (George and Tiltack, 2009; Gheerardyn and Veit-Köhler, 2009; Menzel, 2011, in press), long distances (George and Tiltack, 2009; Gheerardyn and Veit-Köhler, 2009; Menzel, 2011; Menzel and George, 2009; Por, 1964b) or large land masses (Menzel, 2011; Por, 1964b).

The datasets used for previous studies of large-scale distribution patterns of (shallow water) harpacticoids were compiled from a variety of sources (e.g., Chertoprud et al., 2010; Veit-Köhler et al., 2010 most recently), but are only compatible with respect to the described species. For undescribed species or specimens with dubious specific allocation, data providers assigned working species names. However, since in contrast to coastal waters, deep-sea sampling yields extraordinarily large numbers of undescribed species, it is impossible to compile datasets from different providers. Studies on large-scale distribution patterns of deep-sea harpacticoids are only practicable if all specimens are identified by the same person; so far, only the present study and the study by Gheerardyn and Veit-Köhler (2009) on parts of the ANDEEP and DIVA samples have been carried out in this way.

The genus *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae) is a suitable group for large-scale biogeographical investigations since it is clearly a monophylum (Menzel and George, 2009) containing 35 species described to date (Menzel, 2011; Menzel and George, 2009; Wells, 2007), and is found in different ocean regions (*cf.* for summary Menzel, 2011). The well-defined diagnostic characters and the comparatively large body size allow rapid recognition of individuals in meiofauna samples. Moreover, in deep-sea samples, *Mesocletodes* comprises 30–60% of all members of the family Argestidae Por, 1986, a typical, though not exclusively deep-sea taxon. In the last decade, argestid species have been the subject of taxonomic (George, 2004, 2008; Menzel, 2011, in press; Menzel and George, 2009) and faunistic studies (e.g., Ahnert and Schriever, 2001; Baguley et al., 2006; George, 1999; Rose et al., 2005; Thistle and Sedlacek, 2004).

The objectives of this study were: (1) to compare the species composition of *Mesocletodes* in different regions in the South and North Atlantic, the central Pacific, the southern Indian Ocean, and the Southern Ocean at the morphospecies level; (2) to assess the distribution range of species of *Mesocletodes* in the deep sea throughout the Pacific, Atlantic, Indian and Southern Ocean abyssal plains and the eastern Mediterranean Sea; and (3) to assess morphological variability in deep-sea species of *Mesocletodes*.

2. Materials and methods

2.1. Sampling and sample processing

Meiofauna samples were collected during several research cruises in the ANDEEP, CROZEX, DIVA, NODINAUT and OASIS projects, and from the Porcupine Abyssal Plain (PAP), the Great Meteor Bank (GMB), and the eastern Mediterranean Sea. Twelve regions with 113 stations were sampled, 57 of them at depths between 1107 and 5655 m on the abyssal plains of the South and North Atlantic Ocean, Southern Ocean, southern Indian Ocean, and Pacific Ocean, and 56 samples from above 1000 m in the North Atlantic and the eastern Mediterranean Sea (Table 1, Fig. 1). The 113 stations yielded 149 multicorer (hereinafter: MUC) or megacorer hauls including 628 sediment cores, and 89 deployments of an epibenthic sledge (hereinafter: EBS), blade corer, Giant Box Corer (Groß Kasten Greifer, hereinafter: GKG), or Ockelmann trawl. Altogether, 717 samples were available for analysis, with a total of 3.09 m^2 quantitatively sampled (Table 1). Additionally, published data for type localities and repeated finds of known species are provided in Table 2.

The MUC and megacorer cores taken during the cruises of ANDEEP II (partly), CROZEX, NODINAUT, and at the PAP were sliced into 1-cm layers. For all other samples, the upper 5 cm of the cores were used for analyses. On board the research vessels, all sediment samples except the Ockelmann trawl samples were fixed in 37% formaldehyde solution, which was diluted to 4–7% using filtered sea water. The Ockelmann trawl samples were fixed in 70% ethanol. Only the sediments obtained from the GKG were rinsed on board with water and sieved over 40 μm mesh (OASIS [http://www1.uni-hamburg.de/OASIS/, November 29, 2010]).

In the laboratory the formalin-fixed samples were washed with tap water through a 40 μm sieve. Meiofauna and organic material were extracted from the remaining sediment by centrifugation with a colloidal silica polymer (Levasil®) as flotation medium and kaolin to cover the heavier particles (McIntyre and Warwick, 1984). The centrifugation was repeated three times at 4000 rpm for six minutes. After each centrifugation, the floating matter was decanted and rinsed with tap water. The copepods extracted from the CYPRUS samples were stored in ethanol. Copepods, including all argestids, were picked out with the aid of a Leica MZ 12.5 stereo microscope and mounted on slides in glycerin. Identifications are based on the original literature and comparison with type material, if currently available. As formal species names for most deep-sea copepods are essentially unavailable, we recognized working species and identified them to species level. Short species descriptions were prepared for all new species, and included information on the habitus, antennula, antenna exopod, mouthparts, Pereiopods P1–P5, and the chaetotaxy and arrangement of spinules on the furcal rami. Drawings were made with the aid of a drawing tube on a Leica DMLS microscope at maximum 1000 × magnification. The material is kept in the collection of Senckenberg am Meer in Wilhelmshaven (Germany), DZMB Department (Deutsches Zentrum für Marine Biodiversitätsforschung).

The females were described for all but two species of *Mesocletodes*, which were represented by males only. Approximately one-third of all species of *Mesocletodes* found in this material are (undescribed) males, but the extreme poecilandry (Menzel, 2011) made it impossible to associate males and females of the same species. Therefore, the present analysis was based only on females.

2.2. Statistical analyses

Statistical analyses were performed for the stations sampled quantitatively by MUC and megacorer that contained adult females of *Mesocletodes*. Samples taken with other gears were excluded from all statistical analyses in order to lessen the influence of sampling bias on the evaluation. Three stations (ANDEEP II 134, PAP May 1991, and PAP October 1997) were excluded from the analysis, because they contained no adult females of *Mesocletodes*.

A non-metric multidimensional scaling (nMDS), two-dimensional plot was produced to compare station similarity based on species composition. Due to differences in sample size and sampling effort at the different stations, the Sørensen coefficient was used as a similarity index, which is identical to the Bray–Curtis coefficient when the latter is calculated on presence/absence data (Clarke and Gorley, 2006). A one-way ANOSIM was carried out to test for the significance of the similarities in species composition between the different regions. Analyses were conducted using the PRIMER6 software (Clarke and Gorley, 2006).

3. Results

3.1. Overall data

In total, 78,377 Copepoda yielding 2850 adult Argestidae were analyzed (Table 1). Adult females of *Mesocletodes* totaled 793