



## Long-term change in the copepod community in the southern German Bight<sup>☆</sup>



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### ABSTRACT

The North Sea has undergone considerable change in recent years, with several reported regime shifts in the last decades, the most recent of which is thought to have occurred in the final years of the last century. As biological evidence corroborating this most recent regime shift is still rare, we investigated the reaction of the copepod community of the Helgoland Roads sampling site to this perceived shift. We observed that the densities of calanoid copepods have declined to values which are roughly 25% of the peak densities in the mid 1980s and link the decrease to the decreasing nutrient inputs into the North Sea. The initial increase in the densities of non-calanoid copepods seems to have reversed, and currently most of the copepods of the community in the southern North Sea are below their long-term average. These strong declines in densities could have major consequences for recruitment of higher trophic levels. We expect a stronger dependence of copepod densities to the larger oceanographic phenomena such as inflows of Atlantic water into the North Sea, as now that the large anthropogenic riverine inputs of nitrogen and phosphorus have decreased and these inflows were the main source of nutrients into the North Sea.

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### 1. Introduction

The southern North Sea has undergone considerable change in the last decades, and many examples exist describing changes in the physical environment (e.g. Siegismund and Schrum, 2001) and as a result also in the living compartments of the ecosystem (Attrill et al., 2007; Beaugrand, 2004; Reid et al., 2003; Wiltshire and Manly, 2004; Wiltshire et al., 2008). In the plankton, we have seen changes in phenology (Edwards and Richardson, 2004; Greve et al., 2005; Wiltshire and Manly, 2004), species composition (Beaugrand, 2003; Boersma et al., 2007), and species densities (Martens and van Beusekom, 2008). However, many studies have either focused on whole communities with elaborate multivariate approaches to investigate regime shifts and ecosystem responses to the changing environment (Alvarez-Fernandez et al., 2012; Schlüter et al., 2008; Weijerman et al., 2005) or on single (or very few) species reactions to changing climatic conditions (e.g. Attrill et al., 2007; Payne et al., 2009). Here, we will consider the copepod community of the sampling station at the Helgoland Roads site,

describe the changes, and investigate potential factors related to these changes.

It is now well established that large change has occurred in the North Sea. Many authors have interpreted these changes as regime shifts. Discussing what regime shifts are exactly, and whether the observed changes classify as regime shifts (e.g. Andersen et al., 2009; Kraberg et al., 2011) is outside the scope of this paper. Hence, we use the common biological terminology here: meaning periods of sudden change in the system. The first regime shift for the North Sea falling within the observational period of this paper was around the end of the 1970s, and a second 10 years later. Some indications exist that a further 10 years later (ca. 1998) a third regime shift occurred (Weijerman et al., 2005). The data series for the zooplankton around Helgoland only starts in 1975, so we cannot investigate the changes in the copepod community related to the first regime shift, but we will explore the second and the third one. The 1988 regime shift (Reid et al., 2001a) was connected to temperature changes combined with stronger inflows of highly saline Atlantic water (Heath et al., 1991), and resulted in an increase in the phytoplankton biomass (Reid et al., 1998), combined with increasing calanoid copepod diversity (Beaugrand and Ibanez, 2002). The shift at the end of the 1990s coincided with another incursion of warm oceanic water from the north (Reid et al., 2001b). Only very few studies have considered this last shift in great detail. The 1998 regime shift changed the nutrient chemistry of the water, with an increase of dissolved nitrogen in the water in southern Norway (Frigstad et al., 2013), and a decrease in dissolved nitrogen, increasing

<sup>☆</sup> This paper is dedicated to all the people who carried out the sampling in all sorts of weather during the 50 years of the Helgoland Roads Time Series, and to those who analysed and counted these innumerable samples. Without them, there would be no data and no time series.

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diatom counts, a decrease in densities of dinoflagellates, and lower densities of copepods in the central North Sea (Alvarez-Fernandez et al., 2012). As the latter analysis is based mainly on the CPR data with relatively low temporal resolution, it remains to be seen here whether using data which have been collected with a much higher resolution show a similar result. Furthermore, since there still is a paucity of studies dealing with the potential regime shift in the late 1990s, we will investigate whether we find similar patterns for our dataset in the southern North Sea. As stated above, we will not define the regime changes but rather take these as a given and analyse whether the datasets available for Helgoland Roads allow for the differentiation of the different regimes, with a special emphasis on the copepod communities.

## 2. Materials and methods

In 1962, the Biologische Anstalt Helgoland initiated a long-term monitoring programme at Helgoland Roads (54° 11, 3'N, 7° 54, 0'E). Apart from temperature recordings, this programme involves monitoring nutrients (SiO<sub>4</sub>, NO<sub>2</sub>, NO<sub>3</sub>, NH<sub>4</sub>, PO<sub>4</sub>), salinity, light penetration (measured as Secchi depths), and phytoplankton species composition on a work-daily basis. Phytoplankton is counted to species level whereby 370 species are recognized (Hickel et al., 1993; Wiltshire and Dürselen, 2004; Wiltshire and Manly, 2004). From 1975 onwards, zooplankton sampling was added to the time series at Helgoland Roads (Greve et al., 2004). This involves sampling three times a week, at the same time as the phytoplankton and nutrient samples of the daily time series. Several zooplankton taxa are identified to species level, but many have been counted to genus level only (Greve et al., 2004). Since especially with the copepods counting to species is very time consuming and tedious for many genera, the standard protocol for most genera was originally (Greve et al., 2004) established using specific taxonomical units. The calanoids: *Acartia* spp. (mostly *A. clausi*, but some *A. tonsa*; Halsband and Hirche (2001), *Centropages* spp. (a combination of *C. hamatus* and *C. typicus*; adults were counted separately, copepodites were not; Wesche et al. (2007)), *Temora* sp. (exclusively *T. longicornis*; Gentsch et al. (2009)); *Pseudocalanus/Paracalanus* spp. (mostly *Pseudocalanus. elongatus*; Renz et al. (2008) and *Paracalanus parvus*; Knotz et al. (2006)), *Calanus* spp. (a mixture of *Calanus finmarchicus* and *Calanus helgolandicus*; Beaugrand et al. (2003)), the cyclopoid *Oithona* spp.; (mainly *O. similis* some *O. nana* and *O. plumifera*; Fransz et al. (1991)), the poecilostomatoid *Corycaeus* sp. (*Corycaeus. (Ditrichocorycaeus) anglicus*; Fransz et al. (1991), and the harpacticoids *Microsetella* sp. (*M. norvegica*; Fransz et al. (1991)) and *Euterpina* sp. (*E. acutifrons*; Greve et al. (2004)). Sporadic accounts for other species have also been noted, but the densities of those species were too low to warrant inclusion into this analysis. These taxonomical units will be used in the analyses in this study.

The basis for this study is the computed weekly average densities (in number per m<sup>3</sup>) of the five calanoid, the two harpacticoid, and the cyclopoid and poecilostomatoid taxa. Based on these weekly averages we computed annual average densities. These average densities were used in the analyses. Furthermore, we also looked at the temporal dynamics of the diversity of the copepod community, thus, expanding the dataset that was previously published in Wiltshire et al. (2010). For this, we computed the annual averages of the Shannon-Wiener Diversity index (Shannon and Weaver, 1949).

For the potential food of the zooplankton, we used the same data for three groups of phytoplankton, and using the biovolume calculations by Hillebrand et al. (1999), we established the total biovolume (in μm<sup>3</sup> l<sup>-1</sup>) for diatoms, dinoflagellates, and smaller flagellates. Biovolume was selected rather than densities per volume of water (compare Wiltshire et al. this volume and Wiltshire and Dürselen (2004)) to allow for the interpretation of food levels, as the average size of the phytoplankton species present at Helgoland Roads varies greatly.

We summarized the nutrients into two different categories, total dissolved P (mol l<sup>-1</sup>) and total dissolved N (mol l<sup>-1</sup>), which is the sum of NO<sub>2</sub>, NO<sub>3</sub> and NH<sub>4</sub>, and also used annual average values of these measures for the current analysis. We realize that in all cases we omit the large intra-annual variation, but since in this study we were not interested in intra-annual variation, we accepted the averaging out of the large within-year differences in nutrients, copepods, and algae.

As an indication of potential predation pressure, we used the herring larval abundance (<11 mm) from the Southern North Sea as obtained from the standard surveys of the ICES working group (ICES, 2013).

Before the analysis, all data were standardized, i.e., the mean was subtracted and divided by the standard deviation, similar to the standard reporting format of the ICES Zooplankton Status Reports (O'Brien et al., 2013), with the additional advantage that by dividing by the variance the interpretation of the anomalies is easier, a value of +1 indicates that the measurement under consideration is one standard deviation higher than the mean, whereas in the WGZE format a value of 1 indicates a 10-fold difference between the actual measurement and the grand mean. Moreover, the WGZE format also uses the method of Mackas et al. (2001), first computing the anomalies per month for any given year, and then averaging these over the months of the year. Where this may be appropriate for those data series that are low in frequency or have gaps in the series, this approach effectively causes the average of all of the anomalies to be lower than zero, making the interpretation of the graphs somewhat difficult. However, obviously the interpretation of the analyses does not depend on this choice of standardization.

For the analyses of the different regimes we separated the complete dataset (1975–2011) in three periods and contrasted the periods with respect to the measurements: pre-1989 (I, omitting the values from 1975–1978), 1990–1999 (II), and 2000–2011 (III), using discriminant function analyses. Further, we used multidimensional scaling (MDS) including all available taxon densities to investigate whether we could differentiate between the three different regimes.

## 3. Results

The small calanoid copepods all showed a very similar behaviour throughout the time series (Fig. 1a,b). In general, there was an increase in densities until the mid 1980s, after which we observed a decrease in the densities, such that the current annual averages of the calanoid copepod densities are now around one quarter of those observed at the peak in 1985. The non-calanoids *Corycaeus*, *Euterpina*, and *Oithona* showed a different behaviour. We also observed changes in the annual averages of these taxa, but the peaks in density were clearly 5–10 years later than those of the calanoids (Fig. 1c). *Microsetella* showed very high densities in the first year of our observations (1975) and was virtually absent after that. All in all the densities of the calanoids at Helgoland Roads were much higher than those of the non-calanoids, but we observed a significant change in the proportion of calanoid copepods to the total copepod community ( $r^2 = 0.47$ ;  $p < 0.001$ , Fig. 2), whereby this change is caused more by the almost constant decrease in the calanoid densities than by the increase in the densities of the other groups (Fig. 3). The consequence of the changing relative densities of the different taxa can be summarized in the Shannon-Wiener Diversity index,  $H'$  (Fig. 2). The regression line relating  $H'$  with the year has a significantly positive slope and explains 27% of the variation in  $H'$ . However, in the last 5 years of our data series, the diversity of the copepod zooplankton seemed to decrease again.

The biomasses of diatoms, dinoflagellates, and other flagellates showed considerable variation in the time series. The flagellates (data not shown) had low densities in the earlier year of the time series and then increased in biomass. This, however, was likely not a result of changes in the densities in the field but rather of changes in the methodology of counting (compare Wiltshire and Dürselen (2004) with Hickel

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