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# Changes of benthic fauna in the Kattegat – An indication of climate change at mid-latitudes?



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## ABSTRACT

Several predictions point to changes in the marine benthic macrofauna associated with climate change, but so far only a few and minor changes have been reported. This study relates observed changes in the species composition to climate change by looking on the past decades in the Kattegat between Denmark and Sweden. A reduction of the total number species and a reduction of species with a northern range parallel to an increase of species with a southern range have been observed. The most likely explanation of the changes is the increase in temperature of the bottom water. Increased temperature could change the species distributions but also decrease primary production which impacts recruitment and growth. Hypoxia and bottom trawling could also act synergistic in this process. A sparse occurrence of previously encountered Arctic-Boreal species and critical foundation species, which gives the area its special character, suggests a change in biodiversity and might therefore be designated as early warning signals of a warmer climate. The northern fauna below the halocline with limited capacity of dispersal and low reproduction potential, can be considered as sensitive with low adaptive capacity to climate change. Therefore, not only tropical and high-latitude species, but also benthos on deep bottoms at mid-latitudes, could be vulnerable to warming. As many species live at the edge of their range in the Kattegat, and also are dependent of distant recruitment, large scale changes will probably be detected here at an early stage. It is important to protect relatively undisturbed reference areas in the Kattegat for future studies, but also for preserving a large number of ecosystem services, biotopes, habitats, and fish species.

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## 1. Introduction

### 1.1. The aim of this study

This study aimed to identify long term changes of species composition related to geographic area of distribution with special emphasis on climate change. This is especially important as a rise in the bottom water temperature has been recorded in later years. Therefore, the faunal response to changes in bottom water temperatures was studied in a 24 year perspective. Trawling could result in changes of area of distribution of benthos (Hiddink et al., 2015), but the impact is not selective to northern or southern species. Dawson et al. (2011) points to three important factors considering vulnerability of climate change, exposure, sensitivity and adaptive capacity. An increased temperature also means that the fauna can be impacted both by hypoxia and high temperatures and these factors in combination.

### 1.2. Background

Observations of species responses that have been linked to anthropogenic climate change are widespread, but are still lacking for some taxonomic groups e.g., phytoplankton, benthic invertebrates, marine mammals (Poloczanska et al., 2016). However, several studies point to large changes in the benthic macrofauna associated with climate change (Thomas et al., 2004; Hiscock et al., 2004; Reiss et al., 2011; Birchenough et al., 2015). However, so far only relatively minor changes have been presented (Barry et al., 1995; Southward et al., 2004; Mieszkowska et al., 2006; Beukema et al., 2009; Hiddink et al., 2015). Changes in the fauna could also be related to the variability in the North Atlantic Oscillation climate index (Tunberg and Nelson, 1998; Kröncke et al., 1998, 2011).

Tropical and high-latitude species are considered particularly vulnerable to warming (Tewksbury et al., 2008). However, Meyer et al. (2016) report long-term variability of species number and abundance of epibenthos and demersal fish at a shallow site in the North Sea that could be related to climate impact. Singer et al.

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(2017) predicted significant changes in the range sizes and occurrences of most modelled species at the same site until the mid 21st century.

### 1.3. Study area

The Kattegat is a shallow sea area between Denmark and Sweden, situated on the border between the Skagerrak and the Baltic. The surface water is largely affected by the Baltic surface current from the south via the Sound and the Belt Sea with a salinity of about 10–15. Marine conditions are found at bottoms below 25 m depth with a salinity of about 30. A strong halocline at 10–20 m depth moves vertically, largely dependent on the rate of inflow from the Baltic. The strong stratification of the water column prevents vertical water exchange, especially in the southern part. Here, bottoms below the halocline are occasionally stressed by low oxygen concentrations in the autumn. The special hydrographic conditions creates the prerequisites for a diverse benthic macrofauna with a relative high share of Arctic-Boreal species (Brattström, 1941).

### 1.4. The northern fauna of the Kattegat

Brattström (1941) showed that the echinoderm fauna in the 1930s to a large part (approx. 20–30%) consisted of Arctic-Boreal species in the southern Kattegat and the adjacent Sound. The echinoderm fauna were then dominated by Mediterranean-Boreal and widely distributed species (about 60%). The Brattström (1941) description of the fauna still holds. The rather high Arctic-Boreal fauna element probably depends on the lower temperatures and narrower temperature range compared to adjacent sea areas. There are nowadays several examples of cold water species, common in the Arctic region, that are almost only abundant in the southern Kattegat and the Sound on the Swedish west coast, i.e. the bivalves *Musculus niger* and *Macoma calcarea*, and the gastropod *Euspira pallida*. As an example, *Macoma calcarea* can only withstand temperatures less than 11 °C long term. All three species are on the national red-list (<http://www.artdatabanken.se/en/the-red-list/>) and the two last on the Helsinki Commission (HELCOM) red-list of Baltic species (<http://www.helcom.fi/baltic-sea-trends/biodiversity/red-list-of-species>).

Moreover, the special temperature conditions in the deep water could be one of the explanations of recent highly diverse *Modiolus* beds and past *Haploops*-communities with a high share of Arctic-Boreal species, important for fishing. *Modiolus modiolus*, *Haploops tubicola* and *Haploops tenuis* are on the national and HELCOM red-list. *Modiolus* beds are also on the Oslo and Paris Conventions (OSPAR) list of threatened and/or declining species and habitats ([http://jncc.defra.gov.uk/pdf/0806e\\_OSPAR%20List%20species%20and%20habitats.pdf](http://jncc.defra.gov.uk/pdf/0806e_OSPAR%20List%20species%20and%20habitats.pdf)). Local temperature regimes plays a major role for several species. For example, for *Modiolus modiolus* it impacts the interacting processes of gametogenesis and spawning (Brown, 1984). This species does not tolerate large temperature changes (Davenport and Kjørsvik, 1982).

The Kattegat holds several high salinity demanding, more or less isolated, Arctic-Boreal species populations below the halocline. This depends on the relatively stable salinity conditions and on the special temperature conditions on the border of the Baltic, one of the largest brackish waters.

### 1.5. Structuring factors

Several factors structure the benthic macrofauna, both abiotic and biotic. Among abiotic factors temperature and depth are probably most important (Reiss et al., 2011). Rosenberg (1995)

suggested hydrodynamic processes and food to be most important for the benthic fauna in the adjacent Skagerrak. Recruitment of larvae of many benthic species on deep bottoms is strongly dependent of the supply from the south going current from the Skagerrak. Biotic factors are more difficult to study but predation is most likely of great importance for the benthic fauna (Moksnes et al., 2008).

Changes in the fauna in the Kattegat have been reported that could be related to eutrophication. Pearson et al. (1985) reported signs of eutrophication in comparing benthic fauna with Petersen's results from the early 1900s. Rosenberg et al., 1995 pointed to hypoxia, salinity and temperature as structuring factors for benthic communities in the especially eutrophicated Laholm Bay in the southeast Kattegat.

### 1.6. Factors influencing area of distribution of the benthic fauna besides temperature

The nutrient development along the entire Swedish coastline shows declining trends between 1975 and 2005 (Andersson and Andersson, 2006) and therefore an impact of eutrophication on the benthic fauna is likely reduced in later years. Concentrations of heavy metals and traditional organic xenobiotics are also generally being reduced in fauna and sediments, yet there are some concerns regarding new substances (Bignert et al., 2011) including micro plastics (Andrady, 2011). Bottom trawling fishery on Norway lobster *Nephrops norvegicus* is intensive and occurs more or less daily on the silty-clay bottoms deeper than 30 m in the central Kattegat. In this study the three deepest stations N10, N12 and N14 are probably impacted by this activity. Even if it is unknown how the benthic communities would have appeared without the trawl disturbance, species sensitive to physical disturbance showed higher abundance in areas with low trawl activity compared to areas with higher activity (Pommer et al., 2016).

The American invasive polychaete *Marenzelleria viridis* has been found since 2006, but only in low abundances at shallow bottoms (Göransson and Olsson, 2015). The ctenophore *Mnemiopsis leidyi*, originally native to the western Atlantic-coastal waters, was first recorded in 2006 at the Swedish west coast. This species could have significant impact on the ecosystem by preying on zooplankton (Purcell et al., 2001). It is also a powerful predator on pelagic benthos larvae (Ivanov et al., 2000).

### 1.7. Temperature and climate change

The temperature in the Kattegat has increased significantly both in the surface water (about 2 °C) and bottom water (about 1.5 °C) during the period between 1971 and 2009. This increase was largest in the 2000s (Palmbo and Andersson, 2010). Temperature increased also at all monitored stations in this study in the Kattegat between 1993 and 2013 (Hultcrantz and Skjevik, 2014). Potentially this might have a long term impact on the species composition. Primarily it could be expected that species with the southernmost area of distribution will increase or immigrate whilst the equivalent northern species diminish or disappear when water temperature increases (Hiscock et al., 2004; Birchenough et al., 2015). An increase in the water temperature also reduces its ability to dissolve oxygen which might elevate the frequency and duration of oxygen depletion in the bottom water (Altieri and Gedan, 2014). However, primary production might also decrease at an increase in temperature (Henriksen, 2009). Ocean acidification can also be related to climate change (Kroeker et al., 2013) but impacts are yet unknown in the studied area.

The sensitivity of the fauna in the studied area probably varies depending on the species composition. Temperature is especially

important for species with a southern or northern area of distribution. Northern species are consistently most sensitive since they live on their edges of ranges in the Kattegat and these species therefore probably also have the lowest adaptive capacity. They could not shift to other habitats or migrate to more suitable areas and they have often a low or slow reproduction capacity (Thorson, 1946). Some species are also dependent on distant transport of larvae from the north.

The sensitivity of the fauna is probably also dependent on depth. The shallow fauna above the halocline is adapted to a rather wide temperature range. However, the deep fauna below the halocline (>24 m) normally experience temperatures in the narrow 5–12 °C level, whilst there may be high exposure from minor increases in temperature in the Kattegat bottom water. Hence, since many Arctic-Boreal species live on their edges of ranges in the Kattegat, the results of studies from this area could provide an early warning signal of a warming trend in the marine environment.

## 2. Materials and methods

### 2.1. Sampling of benthic fauna

Benthic fauna data were chosen from 13 sampled stations in the Swedish side of the Kattegat, from the Kungsbackafjord in the north to the Laholm Bay in the south, with a depth interval of 15–50 m (Fig. 1 and Table 1). These stations were chosen as they together constitute a long time series of different seafloor environments in the Kattegat with different species composition. Stations were sampled annually 1993–2016 in the spring in a regular monitoring program, with the purpose of registering environmental changes, at the request of the County of Halland.

The soft bottom fauna is characterized by a mixture of *Amphiura*, *Abra* and *Chamelea*—communities, primarily on silty-clay-fine sand substrate. Five replicate samples were taken from each station using a modified Smith-McIntyre grab with a sampling area of 0.1 m<sup>2</sup>, and were immediately sieved through a 1.0 mm mesh. The samples were then transferred onboard in 4% formaldehyde (1997–2015) or 95% ethanol (1993, 1994 & 2016). In the laboratory, each grab sample was divided into 2 size fractions (>2 mm, 1–2 mm) by resieving in fresh water with nested sieves. The larger fraction was sorted by hand, while the smaller fraction was sorted under a stereo microscope (×6 magnification). All animals were generally identified to the species level, counted and total wet weight of each species was determined after blotting to remove excess water. For practical reasons biomass was always expressed without certain very large species (e.g. *Arctica islandica* and *Brissopsis lyrifera*) that completely obscured the biomass contributions of other species (National Swedish standards, Tunberg and Nelson, 1998).

After the analysis of species, abundance (for each species and total), and biomass wet weight (for each species and total), all animals were transported and archived at the Zoological Museum, University of Lund. Organic content was measured as loss on ignition (LOI) at 550 °C for at least six hours, at the uppermost 1 cm sediment layer. Data have been transferred to the national database at the Swedish Meteorological and Hydrological Institute (<http://www.smhi.se/klimatdata/oceanografi/havsmiljodata/marina-miljoovervakningsdata>). The total macrofauna data set 1993–2016 includes 1560 samples, 445 taxa and 375 well defined, identified species.

### 2.2. Comparability of benthic fauna

Benthic fauna data for this study were chosen from a limited area at the Swedish west coast to avoid larger differences in hydrography. However there is an increasing gradient in salinity

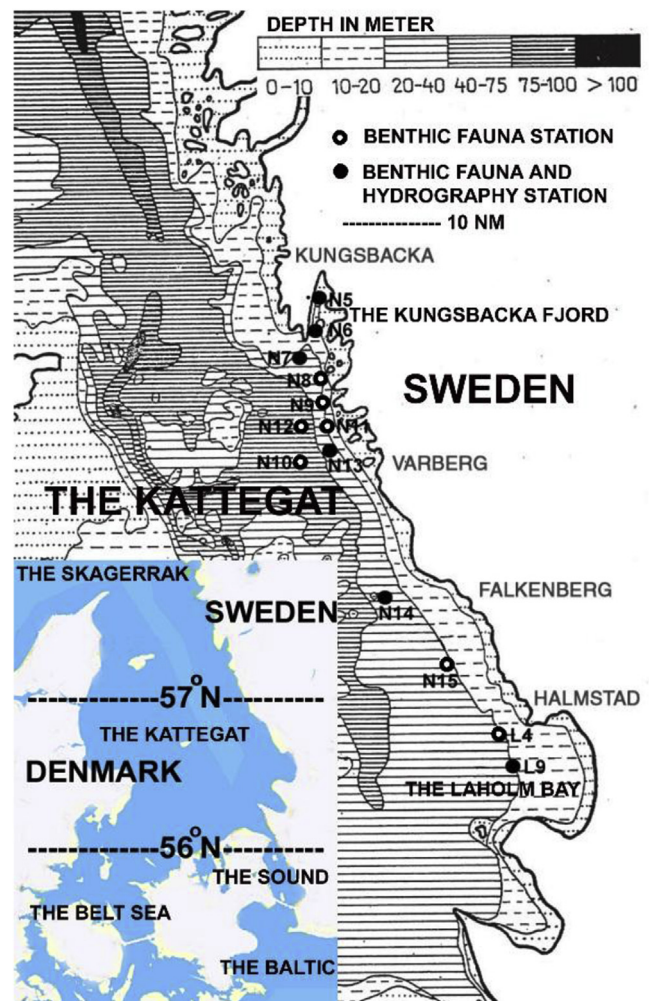


Fig. 1. Location of sampling stations in the Kattegat. (Original map with depths from Brattström, 1941; with permission from the author). Map with adjacent seas inserted.

south to north, mainly in the surface water, but bottom water is generally relatively stable above 30. A few stations could be influenced by point sources, but opportunistic species never dominated, however with a few exceptions.

Comparisons were primarily conducted at the species level, which is simple and also has the advantage of increasing the dynamic between years and periods. As every species has the same

Table 1

Positions in Latitude-Longitude, depth (m), dominating surface sediment and organic content (loss on ignition, LOI) for sampling stations (Stat).

Stat	Lat	Long	m	Dom. surface sed	LOI, %
L4	563700	123844	21	Sandy silt	1
L9	563390	124320	20	Sandy silt	1
N5	572440	120300	15	Silt	12
N6	572160	120175	27	Silty clay	9
N7	571820	115930	26	Silty clay	4
N8	571612	120500	19	Silty sand	2
N9	571350	120445	21	Silty sand	2
N10	570720	120118	50	Silt	11
N11	571080	120500	20	Sandy silt	1
N12	571080	120110	48	Silt	11
N13	570820	120640	24	Sandy silt	2
N14	565640	121270	31	Silt	7
N15	564330	122650	23	Silty clay	2

value regardless of abundance, the dynamic will increase markedly when there is a change in species composition. This is especially important to detect changes that depends on slowly migration by few individuals of single species.

Analyzes in 1993–1996 were conducted by the author and another person. However, comparison of number of species were only made on the time series 1997–2016 when the author alone was responsible for the analyses. This was important as differences could be considerable according to results from intercalibrations (ICES/HELCOM, 1995). The difference by using 4% formaldehyde or 95% ethanol in a few years may have been of some minor importance for comparisons of abundance and biomass but should not, in particular, give any bias regarding the range of species.

The long-term data set contains many species and the sampled area consists of different soft bottoms associations. This should mean that the results not only depend on local factors and reflect the development of species in a relatively large area.

### 2.3. Temperature, hydrography data and NAO index

Long term monthly measurement data between 1993 and 2016 exist from 6 of the 13 stations (N5, N6, N7, N13, N14 and L9), and was acquired from the national Swedish Meteorological and Hydrological Institute (<http://www.smhi.se/klimatdata/oceanografi/havsmiljodata/marina-miljoovervakningsdata>). The Hurrell NAO index was acquired from NCAR/UCAR <https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>.

### 2.4. Processing of data

All, well-defined, species were divided into four major groups according to their main geographical area of distribution. These groups were Arctic-Boreal species, Boreal species, Mediterranean-Boreal species and species with a wide distribution. Here Arctic-Boreal species were defined as species occurring in the Arctic region as well as the Boreal region. Boreal species were defined as species mainly occurring from northern Scandinavia to the southern North Sea including the English Channel. Mediterranean-Boreal species were species occurring in the Boreal region and into the Mediterranean. According to the European Commission the Boreal region in this study covers the Norwegian Sea to the Arctic Circle, the Baltic Sea, the North Sea and the Celtic Sea ([http://ec.europa.eu/maritimeaffairs/atlas/maritime\\_atlas](http://ec.europa.eu/maritimeaffairs/atlas/maritime_atlas)). The purpose of this approximate division was to provide an idea of distribution areas weighted towards north or south relative to the Boreal region. Occasional somewhat isolated occurrences were therefore not been taken into account. The distribution for most species were given by World Register of Marine Species (<http://www.marinespecies.org/>). The modes of reproduction were obtained from Thorson (1946) and Hartmann-Schröder (1996).

As the main interest concern long term changes in species composition only linear relationships were used, which provide useful and easily interpreted approximations (Altman and Krzywinski, 2015). Trends were tested by linear regression. Parametric correlations were performed on normal distributed data by using Pearson Product Moment Correlation. In addition to temperature, linear relationships between faunal abundance and other relevant parameters were also calculated (Salinity, Chlorophyll a, oxygen, regional runoff, Total nitrogen, Total phosphorus and NAO-index). These were tested as annual means with a lag of one or two years previous to sampling of benthic fauna. This is reasonable considering the impact on recruitment depending on growth from juvenile to adult (Thorson, 1946). A lag of one or two years was also used successfully by Tunberg and Nelson (1998). In addition to

benthic fauna, sediment organic content (LOI) was also recorded within this project. Additional data were received from other sources (2.3).

## 3. Results

### 3.1. Temperature, salinity, nitrogen, chlorophyll and oxygen

Significant temperature increases were recorded at all the stations but the most shallow during the study period (Table 2). The highest increases were generally recorded at the deepest stations, between 24 and 50 m depth, well below the halocline ( $r^2 = 0.688$ ,  $p = 0.041$ ). In the latest 24 years temperature increased on average  $0.05\text{ }^\circ\text{C}$  at the 15–50 m level. The increase was higher at the deepest stations and increased generally with depth. Bottom water oxygen concentrations also declined at all six monitored stations during the period 1993 to 2013 (Hultcrantz and Skjevik, 2014).

There were especially negative correlations between benthic fauna variables and temperature (6 significant correlations) but also positive correlations between benthic fauna variables and bottom water oxygen (3 significant correlations) and chlorophyll (3 significant correlations). The North Atlantic Oscillation index (NAO) was significantly correlated with the transport of total nitrogen from local waterways to the coast of Halland 1992–2015. This index was also significantly correlated with salinity, oxygen and chlorophyll concentrations on one of the six stations each. However, there was no significant linear correlation between benthic fauna and NAO with a one or two year lag.

### 3.2. The long term development of the benthic fauna 1993–2016

The benthic fauna of the thirteen stations has decreased in the period between 1993 and 2016. This applied primarily regarding the total number of taxa ( $r^2 = 0.436$ ,  $p < 0.001$ ) but also for abundance ( $r^2 = 0.243$ ,  $p = 0.014$ ) and biomass ( $r^2 = 0.385$ ,  $p = 0.001$ ). A slight reduction was also recorded concerning the organic content of the surface sediment ( $r^2 = 0.244$ ,  $p = 0.023$ ). There is a correlation between the total number of species and average bottom temperature with a one year lag for the latest twenty years (Fig. 2).

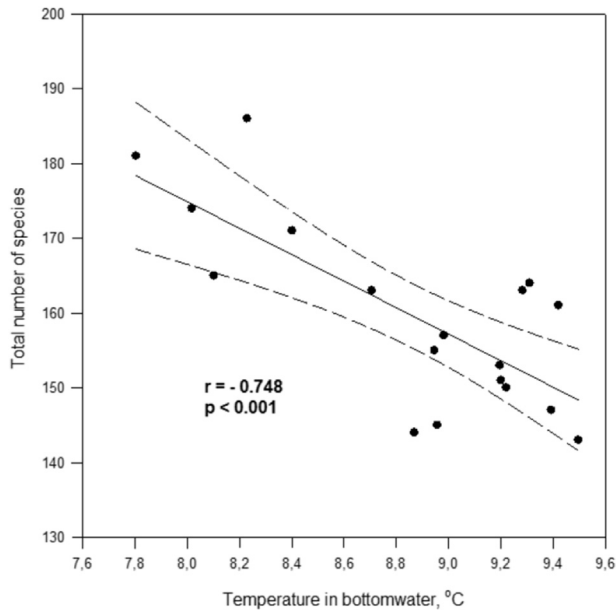
### 3.3. The long term development of the area of distribution of the benthic fauna 1993–2016

The four different zoogeographical groups varied considerably

**Table 2**

Changes in bottom temperature in the Kattegat 1994–2015. Linear regression of annual means for 6 stations and average (Fig. 1). Data from Swedish Meteorological and Hydrological Institute.

Station, depth m	$r^2$	p	Change per year $^\circ\text{C}$	Total change $^\circ\text{C}$
N5, 14–16 m	0.018	NS	+0.019	+0.40
N6, 25–29 m	0.370	0.004	+0.064	+1.34
N7, 26–30 m	0.296	0.013	+0.057	+1.20
N13, 20–24 m	0.299	0.013	+0.063	+1.11
N14, 25–31 m	0.376	0.020	+0.054	+1.13
L9, 18–20 m	0.216	0.039	+0.051	+1.07
Average, 14–31 m	0.365	0.005	+0.050	+1.05



**Fig. 2.** Total number of species for 13 benthic fauna stations in the Kattegat vs. average bottom water temperature with a one year lag for the period 1997–2016.  $N = 20$ . Pearson correlation.

during the period between 1993 and 2016 well below and near the halocline (Fig. 3). Development was similar at both depth intervals. The decrease of Arctic-Boreal species (northern) mirrors the increase of Mediterranean-Boreal species (southern) and both showed significant trends. The difference was greatest well below the halocline. The share of Boreal- and Arctic-Boreal species were slightly higher well below the halocline ( $p < 0.001$ , paired  $t$ -test) and conversely, the share of Mediterranean-Boreal and widely distributed species were slightly higher near the halocline ( $p < 0.001$ , paired  $t$ -test). There were negative correlations between the development of Arctic-Boreal species and Mediterranean-Boreal species, both well below the halocline ( $r = -0.852$ ,  $p < 0.001$ ), and near the halocline ( $r = -0.632$ ,  $p < 0.001$ ).

#### 3.4. Correlations between area of distribution and bottom water temperature

There was a negative correlation between the development of species with an Arctic-Boreal area of distribution and average bottom temperature with a one year lag for the period 1997–2016 (Table 3). There were also negative correlations between species with an Arctic-Boreal area of distribution and species with a Mediterranean-Boreal area of distribution and between the latter and species with a Boreal area of distribution.

#### 3.5. Development of individual species

Zoogeographical groups and mode of reproduction for species with a significant changed occurrence long term, between 1997 and 2016, are summarized in Table 4a–b. The number of significantly decreasing species is nearly three times higher than the group of increasing taxa. Of 48 species with a decreased occurrence, 20 (42%,  $p < 0.001$ ), have an Arctic-Boreal area of distribution. Non-pelagic reproduction also dominated in this group (61%,  $p < 0.001$ ). On the contrary there was a dominance of Mediterranean-Boreal area of distribution (40%,  $p < 0.001$ ) and pelagic reproduction (72%,  $p < 0.001$ ) in the group of decreasing species (Fig. 4).

## 4. Discussion

### 4.1. Temperature

The increases in temperature in the bottom water per year between 1994 and 2015 are at the same level as 1971–2009 (Göransson and Olsson, 2015). The increase is relatively large in the bottom water of the deepest areas where the fauna normally experiences temperatures in the range of 5–12 °C.

### 4.2. Development pattern of the fauna in the long term

The fact that a majority of species with a decreased abundance in later years have a northern range and species with an increased abundance have a southern range is probably a response to the increased temperatures. There are also examples of shifts from northern species to near related southern species with about the same traits and bioturbation potential (Queirós et al., 2013) as *Nuculana pernula* – *Nucula nitidosa*, *Brada villosa* – *Diplocirrus glaucus* and *Polyphysia crassa* – *Lipobranchius jeffreysii*. This also agrees with observations already made by Barry et al. (1995). The bottom water temperature is of great importance for the distribution of species (Künitzer et al., 1992; Reiss et al., 2011).

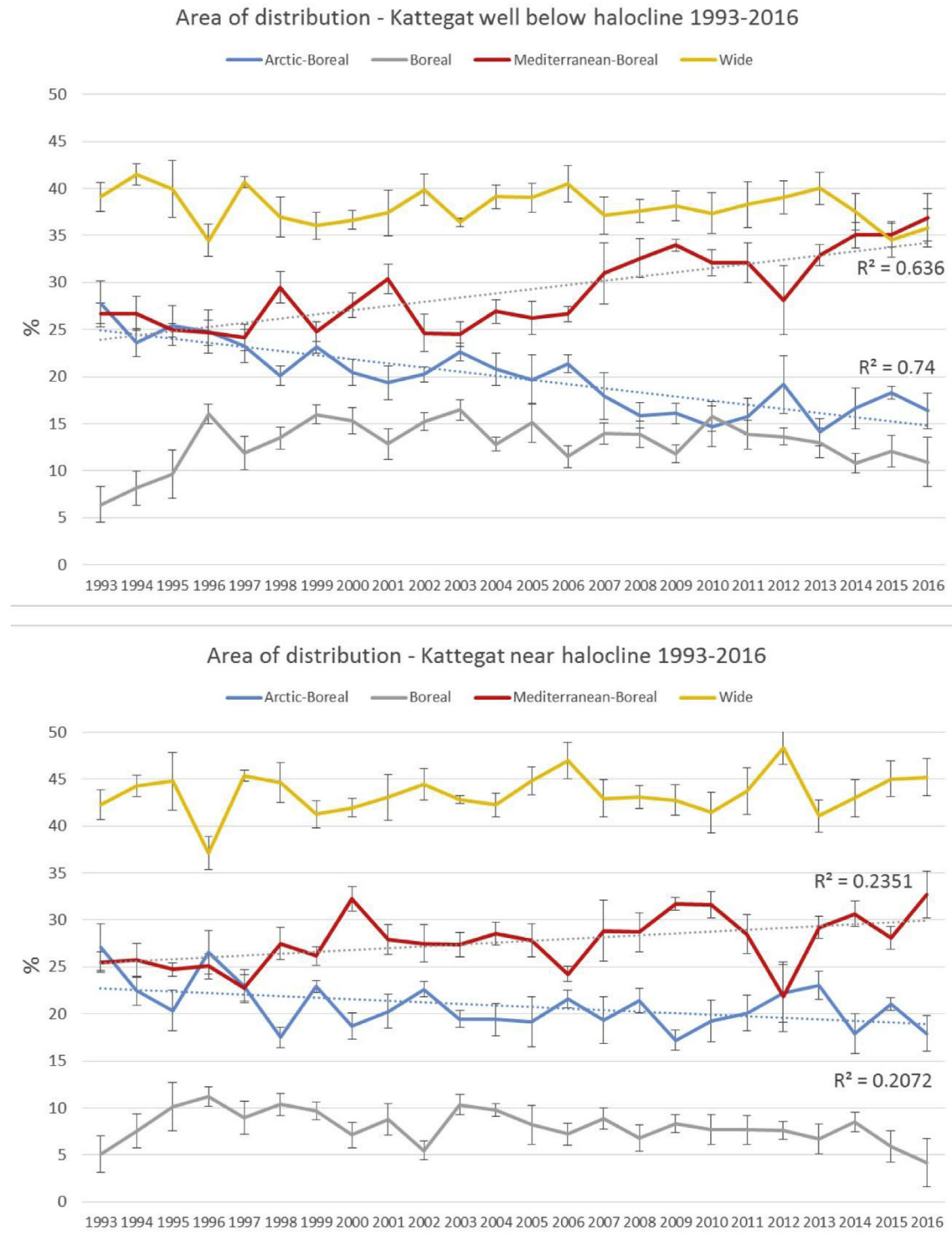
A similar development pattern for stations at different depth intervals is most evident for the counteraction between Arctic-Boreal and Mediterranean-Boreal species. The greater change well below the halocline also indicate that temperature is an important explanatory factor because the effect of a change increases with depth. The difference between depth intervals depends also on fewer northern species and more southern species on shallow bottoms. This is natural as the temperature decreases with depth.

The decrease in Arctic-Boreal species, especially on the deepest bottoms, in recent decades stands out, and should be followed by great attention given the current climate change. In the Kungsbackafjord, northern Kattegat, the share of Arctic-Boreal species, also was distinctly lower in the 2000s than in the 1930s (Göransson and Olsson, 2015). There is also a long term decline in Arctic-Boreal species in the Sound, south of the Kattegat (Göransson et al., 2010). This could indicate a larger scale regional change in faunal composition in later years in connection with an increase in water temperature. Northern species are especially vulnerable as they live in a narrow temperature range and often have limited capacity to dispersal and low reproduction potential (Thorson, 1946). Therefore, not only tropical and high-latitude species (Tewksbury et al., 2008), but also benthos on deep bottoms at mid-latitudes, is likely to be vulnerable to warming.

### 4.3. Other factors contributing to the decrease of the fauna

The benthic fauna is affected by many factors, both abiotic and biotic, and will probably give an integrated picture of conditions (Göransson, 2002; Zettler et al., 2017). It is of note that the number of significant decreasing species is nearly three times higher than the group of increasing taxa. As not only northern species are declining this suggests that more factors than just the species temperature requirements are important.

The decrease of the total fauna in both number of species, abundance and especially biomass, and an indication of lower organic content of the sediment, could be caused by a decrease in primary production. A large scale regional decline in primary production has also been shown by Henriksen (2009). This could depend both on decreased nitrogen load and increased temperature. The decline in primary production should have great significance for the organic load and faunal development (Pearson and Rosenberg, 1978). The decreased occurrence of the polychaete



**Fig. 3.** Area of distribution for species in the Kattegat between 1993 and 2016. Percentage of species in four zoogeographical groups. Stations well below halocline (24–50 m,  $n = 720$ ) above and stations near halocline (16–21 m,  $n = 840$ ) below. Regressions are significant for Arctic-Boreal species ( $p < 0.001$ , resp.  $p < 0.001$ ) and Mediterranean-Boreal species ( $p = 0.025$ , resp.  $p = 0.016$ ). Mean and standard error for 6 resp. 7 stations.

*Owenia fusiformis*, which was an opportunist and at times dominated the fauna in the Laholm Bay, is probably also a sign of reduced organic load. This bay has previously been regarded as a hotspot regarding eutrophication (Rosenberg and Loo, 1988).

Increasing temperatures can also impair oxygen conditions (Altieri and Gedan, 2014; Birchenough et al., 2015) and the bottom

water of the southern Kattegat is especially vulnerable, due to the strong stratification of the water column. There are also declining oxygen levels between 1993 and 2013 on all studied stations in the area (Hultcrantz and Skjevik, 2014). The last large decline of the *Haploops*-community in the adjacent Öresund could depend on synergy between hypoxia and high temperature in 2007

**Table 3**

Pearson correlation table for average bottom temperature and area of distribution for species. Correlation coefficient (above) and level of significance (below). NS = not significant.

	Arctic-Boreal	Boreal	Medit.-Boreal	Wide
Temp	−0.593	−0.036	0.379	0,090
	0.009	NS	NS	NS
Arctic-Boreal		0.254	−0.846	0.090
		NS	<0.001	NS
Boreal			−0.543	−0.150
			0.013	NS
Wide				−0.417
				NS

(Göransson et al., 2010).

Intense bottom trawling also may have contributed to the decline of sensitive species (Pommer et al., 2016) on the deepest bottoms. Both fishing impact and climate change were hypothesised as explaining the changes in the Dogger Bank macrofauna

communities (Kröncke, 2011). Furthermore there might also be an indirect effect on predation from the capture of keystone predators through fishing which could result in increased predation on benthos from small fish. However, studies on predation from fish on deep benthos are scarce and should be studied more extensively. The ctenophore *Mnemiopsis leidyi*, is an important predator on pelagic benthos larvae (Ivanov et al., 2000) but the decrease of benthic fauna in the Kattegat mainly concerns species with bottom living larvae.

The correlations between several variables and the North Atlantic Oscillation index (NAO) are additional indications of climatic importance which in turn affects the development of the fauna (Tunberg and Nelson, 1998; Kröncke et al., 1998; Kröncke, 2011; Zettler et al., 2017). However, the correlation of macrobenthic parameters and the NAO index is not consistent over a large time span (Dippner et al., 2014; Zettler et al., 2017). Temperature was the major abiotic determinant of macrobenthic temporal variability in the German Bight 1981–2011 (Shojaei et al., 2016), as in this study.

**Table 4a**

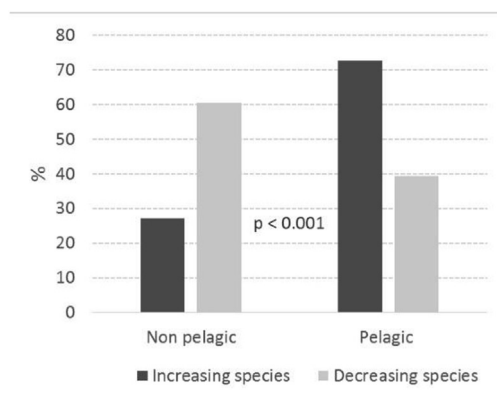
Compilation of species with a significant abundance decrease in the Kattegat between 1997 and 2016. Linear regression coefficient, level of significance, zoogeographical group and type of larvae. (Non pelagic e.g. non pelagic lecithotrophic or short pelagic. n = 1300).

Species	r <sup>2</sup>	p	Zoogeographical group	Larvae
<i>Ampelisca macrocephala</i>	0.295	0.013	Arctic-Boreal	Non pelagic
<i>Aphrodita aculeata</i>	0.491	<0.001	Wide	Pelagic
<i>Artacama proboscidea</i>	0.525	<0.001	Arctic-Boreal	Non pelagic
<i>Autonoe longipes</i>	0.280	0.016	Boreal	Non pelagic
<i>Brada villosa</i>	0.601	<0.001	Arctic-Boreal	Unknown
<i>Byblis gaimardi</i>	0.207	0.044	Arctic-Boreal	Non pelagic
<i>Calocaris macandreae</i>	0.342	0.007	Mediterranean-Boreal	Non-pelagic
<i>Diastylis lucifera</i>	0.427	0.002	Arctic-Boreal	Non pelagic
<i>Diastylis rathkei</i>	0.289	0.014	Arctic-Boreal	Non pelagic
<i>Echinocardium cordatum</i>	0.301	0.012	Wide	Pelagic
<i>Eudorella truncatula</i>	0.248	0.025	Wide	Non pelagic
<i>Gattyana amondseni</i>	0.257	0.022	Arctic-Boreal	Pelagic
<i>Glycinde nordmanni</i>	0.286	0.015	Boreal	Unknown
<i>Galathowenia oculata</i>	0.256	0.023	Arctic-Boreal	Pelagic
<i>Harmothoe impar</i>	0.337	0.007	Wide	Pelagic
<i>Labidoplax buskii</i>	0.469	<0.001	Arctic-Boreal	Non pelagic
<i>Laonice bahusiensis</i>	0.703	<0.001	Boreal	Unknown
<i>Leptopentacta elongata</i>	0.447	0.001	Mediterranean-Boreal	Non pelagic
<i>Leptostylis villosa</i>	0.412	0.002	Arctic-Boreal	Non pelagic
<i>Leucon nasica</i>	0.567	<0.001	Arctic-Boreal	Non pelagic
<i>Montacuta ferruginosa</i>	0.368	0.005	Mediterranean-Boreal	Pelagic
<i>Musculus niger</i>	0.228	0.033	Arctic-Boreal	Non pelagic
<i>Mya truncata</i>	0.204	0.045	Arctic-Boreal	Pelagic
<i>Maera loveni</i>	0.200	0.048	Boreal	Non pelagic
<i>Maldane sarsi</i>	0.788	<0.001	Wide	Non pelagic
<i>Montacuta tenella</i>	0.327	0.008	Boreal	Pelagic
<i>Nephtys ciliata</i>	0.321	0.009	Arctic-Boreal	Pelagic
<i>Nuculana pernula</i>	0.360	0.005	Arctic-Boreal	Non pelagic
<i>Ophiiodromus flexuosus</i>	0.335	0.007	Mediterranean-Boreal	Non pelagic
<i>Ophiura affinis</i>	0.326	0.009	Arctic-Boreal	Pelagic
<i>Ophiura albida</i>	0.418	0.002	Wide	Pelagic
<i>Ophiura ophiura</i>	0.221	0.036	Boreal	Pelagic
<i>Owenia fusiformis</i>	0.476	<0.001	Wide	Pelagic
<i>Panthalis oerstedii</i>	0.289	0.015	Mediterranean-Boreal	Unknown
<i>Phascolion strombus</i>	0.427	0.002	Wide	Non pelagic
<i>Phaxa pellucida</i>	0.369	0.005	Wide	Pelagic
<i>Philomedes brenda</i>	0.474	<0.001	Arctic-Boreal	Non pelagic
<i>Pista cristata</i>	0.292	0.014	Mediterranean-Boreal	Unknown
<i>Polyphysia crassa</i>	0.499	<0.001	Arctic-Boreal	Unknown
<i>Protomedea fasciata</i>	0.244	0.027	Arctic-Boreal	Non pelagic
<i>Rhodine gracilior</i>	0.553	<0.001	Wide	Unknown
<i>Saxicavella jeffreysii</i>	0.231	0.032	Wide	Pelagic
<i>Scoletoma fragilis</i>	0.326	0.009	Boreal	Unknown
<i>Sphaerodorum flavum</i>	0.383	0.004	Arctic-Boreal	Unknown
<i>Thyasira equalis</i>	0.364	0.005	Boreal	Non pelagic
<i>Thyasira sarsii</i>	0.209	0.043	Boreal	Non pelagic
<i>Trichobranchus roseus</i>	0.363	0.005	Boreal	Unknown
<i>Westwoodilla caecula</i>	0.536	<0.001	Wide	Non pelagic

**Table 4b**

Compilation of species with a significant abundance increase in the Kattegat between 1997 and 2016. Linear regression coefficient, level of significance, zoogeographical group and type of larvae. (Non pelagic e.g. non pelagic lecithotrophic or short pelagic. n = 1300).

Species	r <sup>2</sup>	p	Zoogeographical group	Larvae
<i>Abyssoninoe hibernica</i>	0.561	<0.001	Boreal	Unknown
<i>Cylichna cylindracea</i>	0.445	0.001	Mediterranean-Boreal	Pelagic
<i>Clausinella fasciata</i>	0.343	0.007	Mediterranean-Boreal	Pelagic
<i>Corbula gibba</i>	0.221	0.037	Mediterranean-Boreal	Pelagic
<i>Chone fauveli</i>	0.440	0.001	Arctic-Boreal	Unknown
<i>Diplocirrus glaucus</i>	0.241	0.028	Mediterranean-Boreal	Unknown
<i>Ennucula tenuis</i>	0.359	0.005	Arctic-Boreal	Pelagic
<i>Harpinia antennaria</i>	0.420	0.002	Wide	Non pelagic
<i>Hyalia vitrea</i>	0.629	<0.001	Wide	Pelagic
<i>Lipobranchius jeffreysii</i>	0.373	0.004	Boreal	Unknown
<i>Notomastus latericeus</i>	0.437	0.001	Wide	Pelagic
<i>Nucula nitidosa</i>	0.473	<0.001	Mediterranean-Boreal	Pelagic
<i>Orbinia sertulata</i>	0.332	0.008	Boreal	Unknown
<i>Pholoe pallida</i>	0.549	<0.001	Boreal	Non pelagic
<i>Praxillella praetermissa</i>	0.488	<0.001	Arctic-Boreal	Unknown
<i>Thracia convexa</i>	0.245	0.027	Mediterranean-Boreal	Unknown
<i>Thyone fusus</i>	0.349	0.006	Mediterranean-Boreal	Non pelagic
<i>Vitreolina philippi</i>	0.222	0.036	Wide	Pelagic



**Fig. 4.** Reproduction for increasing and decreasing species at 13 benthic fauna stations in the Kattegat 1997–2016. Percentage of species with dominating non pelagic and pelagic reproduction. N = 49. Chi-squared test.

#### 4.4. Reproduction and area of distribution

The mode of reproduction differs generally between the groups of species with increased and decreased abundance. In the decreasing northern, cold water species group, a reproduction connected to the seafloor dominates and in the increasing, southern/widely distributed species group, long pelagic planktotrophic reproduction dominates. This difference is also general between northern and southern species, known as Thorson's rule (Thorson, 1946) although many benthic invertebrates in the Boreo-Atlantic region also reproduce via pelagic larvae (Fetzer and Antz, 2008). This also means that the southern species are more rapid colonizers and have a greater capacity to spread than the northern species. This is probably one of the reasons why Mediterranean-Boreal species dominates the group with an increased abundance in later years. The Arctic-Boreal species, which dominate the group with a decreased abundance, probably recover slowly as they also must be recruited far away from the north. However, their general mode of reproduction, with direct development and lecithotrophic larvae, means that they can remain in an area for a long time. This is probably why many still occur in the Kattegat albeit in low numbers.

#### 4.5. Correlation between temperature and zoogeographical groups

This study found a linear relationship between the bottom temperature and the development of different zoogeographical groups. However, the mean temperature is probably a blunt instrument and the benthic animals more likely respond to extreme periods. Mueter and Litzow (2008) also report linear relationships between community distribution and bottom temperature, suggesting warming climate as the primary cause of changing biogeography of the Bering Sea continental shelf. Elevated temperatures may negatively impact population dynamics in a number of ways, i.e. via recruitment or mortality as well as growth (Thorson, 1946; Beukema et al., 2009; Birchenough et al., 2015) but could also impair reproduction during situations of hypoxia (Eriksson-Wiklund and Sundelin, 2001).

The negative correlation between the occurrence of northern species and bottom temperature with a one year lag seems realistic as there is a certain time for growth from larvae to the adult. However, there was also a significant correlation between total number of observed species and temperature. This indicates that the temperature, at this level, not only affects species composition, but also the total number of species.

#### 4.6. Important habitats and species

Distributional shifts of benthos associated with temperature change have been reported recently from other areas, but mostly on the single species level (Birchenough et al., 2015; Meyer et al., 2016; Sorte et al., 2017). In this study several red-listed species were recorded. A high proportion of these species has a northern area of distribution. Most important in this context is the threat to several regional ecologically important and typical habitats, as *Haploopsis*- and *Modiolus*-communities which previously have been found to decrease in the Sound and the southern Kattegat (Göransson, 2002; Göransson et al., 2010). The *Haploopsis*-community, including the brittle star *Ophiura robusta*, which earlier dominated large areas in the southern Kattegat (Petersen, 1913), share several species with occurrences in the Arctic region (Stephensen, 1916; Stewart et al., 1985; Kędra et al., 2010). This may be an example of species that cannot withstand change in thermal habitat (Hiddink et al., 2015) and therefore have declined gradually with increasing temperatures in the entire region.

There also seems to be a reduction in the *Modiolus*-beds. A reduction of the Boreal horse mussel will truly decrease the diversity in the deep water since they contain many associated northern species. Hiscock et al. (2004) predicted a particular decline of horse mussel in conjunction with climate change in the coastal waters of Britain and Ireland. Both *Haploopsis*-species and *Modiolus modiolus* are critical foundation species (Rigolet et al., 2014; Gerdali et al., 2017; Sorte et al., 2017) which creates three-dimensional habitats for several associated benthic species and with great importance for fishing.

#### 4.7. The deep Kattegat as an important protected reference area

A further increased temperature may have great impact on the deep fauna of the Kattegat which can be considered as sensitive and also with low adaptive capacity (Dawson et al., 2011) to temperature changes since many species live on their edge of ranges. Therefore large scale changes will probably be detected at an early stage (Birchenough et al., 2015). However, it is important to protect relatively undisturbed reference areas in the Kattegat for future changes in the marine environment, but also for preserving a large number of ecosystem services, not only on energy and matter cycles, but also essential habitats for a large part of the fish species.



The areas that are currently protected are not sufficient to maintain diversity in the Kattegat and suitable large protected areas are needed for the deeper fauna. The status of the deep fauna of the Kattegat also is of great significance for the conditions in the Sound as several salinity-tolerant species are recruited from the Kattegat (Thorson, 1946).

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## References

- Altieri, A.H., Gedan, K.B., 2014. Climate change and dead zones. *Glob. Change Biol.* 21, 1395–1406.
- Altman, N., Krzywinski, M., 2015. Points of significance: simple linear regression. *Nat. Methods* 12, 999–1000. <http://dx.doi.org/10.1038/nmeth.3627>, 2015.
- Andersson, P.M., Andersson, L.S., 2006. Long term trends in the seas surrounding Sweden. Part one – nutrients. *Swed. Meteorological Hydrological Inst.* 2006. Oceanography No 34.
- Andrady, A.L., 2011. Microplastics in the marine environment. *Mar. Poll. Bull.* 62, 1596–1605.
- Barry, J.P., Baxter, C.H., Sagarin, R.D., Gilman, S.E., 1995. Climate-related, faunal changes in a California rocky shore intertidal community. *Science New series (Issue 5198)*, 672–675 (Feb. 3 1995).
- Beukema, J.J., Dekker, R., Jansen, J.M., 2009. Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Mar. Ecol. Prog. Ser.* 384, 135–145.
- Bignert, A., Boalt, A., Danielsson, S., Hedman, J., Johansson, A.K., Miller, A., Nyberg, E., Berger, U., Borg, H., Eriksson, U., Holm, K., Nylund, K., Haglund, P., 2011. Övervakning av metaller och organiska miljögifter i marin biota 2011. Report nr 7: 2011, 224 pp. *Swed. Mus. Nat. Hist.*
- Birchenough, S.N.R., Reiss, H., Degraer, S., Nova Mieszkowska, N., Borja, A., Buhl-Mortensen, L., Braeckman, U., Craeymeersch, J., De Mesel, I., Kerckhof, F., Kröncke, I., Parra, S., Rabaut, M., Schröder, A., Van Colen, C., Van Hoey, G., Vincx, M., Wätjen, K., 2015. Climate change and marine benthos: a review of existing research and future directions in the North Atlantic. *WIREs Clim. Change* 2015 (6), 203–223. <http://dx.doi.org/10.1002/wcc.330>.
- Brattström, H., 1941. Studien über die Echinodermen des gebietes zwischen Skagerrak und Ostsee, besonders des Öresundes, mit einer übersicht über die physische geographie. Undersökningar över Öresund XXVII. PhD thesis. University of Lund. Gleerup – University of Lund, 1941.
- Brown, R.A., 1984. Geographical variations in the reproduction of the horse mussel, *Modiolus modiolus* (Mollusca: Bivalvia). *J. Mar. Biol. Ass. U. K.* 64 (4), 751–770.
- Davenport, J., Kjørsvik, E., 1982. Observations on a Norwegian intertidal population of the horse mussel *Modiolus modiolus* (L.). *J. Mollusc. Stud.* 48, 370–371.
- Dawson, T.P., Jackson, S.T., House, J.L., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing climate. *Science* 332, 53.
- Dippner, J.W., Möller, C., Kröncke, I., 2014. Loss of persistence of the North Atlantic Oscillation and its biological implication. *Front. Ecol. Evol.* 2, Article 57, 22 September 2014. <https://doi.org/10.3389/fevo.2014.00057>.
- Eriksson-Wiklund, A.K., Sundelin, B., 2001. Impaired reproduction in the amphipods *Monoporeia affinis* and *Pontoporeia femorata* as a result of moderate hypoxia and increased temperature. *Mar. Ecol. Prog. Ser.* 222, 131–141.
- Fetzer, I., Antz, W.E., 2008. Reproductive strategies of benthic invertebrates in the Kara Sea (Russian Arctic): adaptation of reproduction modes to cold water. *Mar. Ecol. Prog. Ser.* 356, 189–202.
- Geraldi, N.R., Bertolini, C., Emmerson, M.C., Roberts, D., Sigwart, J.D., O'Connor, N.E., 2017. Aggregations of brittle stars can perform similar ecological roles as mussel reefs. *Mar. Ecol. Prog. Ser.* 563, 157–167.
- Göransson, P., 2002. Petersen's benthic macrofauna stations revisited in the Öresund-area (southern Sweden) and species composition in the 1990's – signs of decreased biological variation. *Sarsia* 87, 263–280.
- Göransson, P., Bertilsson Vuksan, S., Karlfelt, J., Börjesson, L., 2010. *Haploops-samhället och Modiolus-samhället utanför helsingborg 2000-2009*. English summary. *Environ. Board Helsingborg* 2010.
- Göransson, P., Olsson, P., 2015. *Bottenfaunaundersökningar i Kungsbackafjorden 1969-2009 – med en återblick till 1930-talet*. *Engl. Summ. Cty. Halland* 2015.
- Hartmann-Schröder, G., 1996. Annelida, Borstenwürmer, Polychaeta. *Die Tierwelt Deutschlands*. Gustav Fischer Verlag, Jena.
- Henriksen, P., 2009. Long-term changes in phytoplankton in the Kattegat, the Belt sea, the Öresund and the western Baltic sea. *J. Sea Res.* 6, 114–123.
- Hiddink, J.G., Burrows, M.T., Molinos, J.G., 2015. Temperature tracking by North Sea benthic invertebrates in response to climate change. *Glob. Change Biol.* 21, 117–129.
- Hiscock, K., Southward, A., Tittley, I., Hawkins, S., 2004. Effects of changing temperatures on benthic marine life in Britain and Ireland. *Aq. Cons. Mar. Fresh. Ecosys* 14, 333–362. <http://dx.doi.org/10.1002/aqc.628>.
- Hultcrantz, C., Skjerveik, A.-T., 2014. Årsrapport 2013 Hydrografi & Växtplankton. Hallands kustkontrollprogram. SMHI nr 2014–13.
- Ivanov, V.P., Kamakin, A.M., Ushivtzev, V.B., Shiganova, T., Zhukova, O., Aladin, N., Wilson, S.I., Harbison, G.R., Dumont, H.J., 2000. Invasion of the caspian sea by the comb jellyfish *Mnemiopsis leidyi* (ctenophora). *Biol. Inv.* 2, 255–258, 2000. ICES/HELCOM, 1995. QA Intercalibration Exercise 1995. 15.1 1996. JNJ.
- Kędra, M., Gromisz, S., Jaskula, R., Legeżyńska, J., Maciejewska, B., Malec, E., Opanowski, A., Ostrowska, A., Ostowska, K., Włodarska-Kowalczyk, M., Węślawski, J., 2010. Soft bottom macrofauna of an biodiversity site: hornsund (77°N, svalbard). *Pol. Pol. Res.* 31 (Issue 4), 309–326.
- Kroeker, K.J., Kordas, R.L., Crim, R.N., Hendriks, I.E., Ramajo, L., Singh, G.G., Duarte, C., Gattuso, J.-P., 2013. Impacts of ocean acidification on marine biota: quantifying variation in sensitivity among organisms and life stages and at elevated temperatures. *Glob. Change Biol.* 19, 1884–1896.
- Kröncke, I., Dippner, J.W., Heyen, H., Zeiss, B., 1998. Long-term changes in macrofaunal communities off Norderney (East Frisia, Germany) in relation to climate variability. *Mar. Ecol. Prog. Ser.* 167, 25–36.
- Kröncke, I., Reiss, H., Eggleton, J.D., Aldridge, J., Bergman, M.J.N., Cochrane, S., Craeymeersch, J.A., Degraer, S., Dewarumez, J.-M., Gerard, C.A., 2011. Changes in North Sea macrofauna communities and species distribution between 1986 and 2000. *Est. Coast. Shelf Sci.* 94, 1–15.
- Kröncke, I., 2011. Changes in the Dogger Bank macrofauna communities in the 20<sup>th</sup> century caused by fishing and climate. *Est. Coast. Shelf Sci.* 94, 234–245.
- Künitzer, A., Basford, D., Craeymeersch, J.A., Dewarumez, J.M., Dörjes, J., Duineveld, C.A., Eleftheriou, A., Heip, C., Herman, P., Kington, P., Niermann, U., Rachor, E., Rumohr, H., J de Wilde, P.A., 1992. The benthic infauna of the North Sea: species distribution and assemblages. *ICES J. Mar. Sci.* 49, 127–143.
- Mieszkowska, N., Kendall, M.A., Hawkins, S.J., Leaper, R., Williamson, P., Hardman-Mountford, N.J., Southward, A.J., 2006. Changes in the range of some common rocky shore species in Britain – a response to climate change? *Hydrobiol.* 555, 241–251.
- Moksnes, P.O., Gullström, M., Tryman, K., Baden, S., 2008. Trophic cascades in a temperate seagrass community. *Oikos* 117, 763–777.
- Meyer, J., Kröncke, I., Batholomä, A., Dippner, J.W., Schükel, U., 2016. Long-term changes in species composition of demersal fish and epibenthic species in the Jade area (German Wadden Sea/Southern North Sea) since 1972. *Est. Coast. Shelf Sci.* 181, 284–293.
- Mueter, F.J., Litzow, M.A., 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* 18, 309–320.
- Palmbö, A., Andersson, L.S., 2010. Havet Nu. Oceanografi. [www.havet.nu/dokument/Havet2010-oceanografi.pdf](http://www.havet.nu/dokument/Havet2010-oceanografi.pdf).
- Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Ocean. Mar. Biol. Ann. Rev.* 16, 229–311.
- Pearson, T.H., Josefson, A.B., Rosenberg, R., 1985. Petersen's benthic stations revisited. I. Is the Kattegat becoming eutrophic? *J. Exp. Mar. Biol. Ecol.* 92, 157–206.
- Petersen, C.G.J., 1913. Havets bonitering II. Om havbundens dyresamfund og disses betydning for den marine zoogeografi. *Den danske biologiske station XXI*. København 1913.
- Poloczanska, E.S., Burrows, M.T., Brown, C.J., Molinos, J.G., Halpern, B.S., Hoegh-Guldberg, O., Kappel, C.V., Moore, P.J., Richardson, A.J., Schoeman, D.S., Sydeman, W.J., 2016. Responses of marine organisms to climate change across oceans. *Front. Mar. Sci.* 3, Article 62,04 May 2016. <https://doi.org/10.3389/fmars.2016.00062>.
- Pommer, C.D., Olesen, M., Hansen, J.L.S., 2016. Impact and distribution of bottom trawl fishing on mud-bottom communities in the Kattegat. *Mar. Ecol. Prog. Ser.* 548, 47–60.
- Purcell, E.P., Shiganova, T.A., Decker, M.B., Houde, E.D., 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiol.* 451, 147–176, 2001.
- Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M., Sommerfield, P.J., Van Colen, C., Van Hoey, G., Widdicombe, S., 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecol. Evol.* (11)
- Reiss, H., Cunze, S., König, K., Neumann, H., Kröncke, I., 2011. Species distribution modelling of marine benthos: a North Sea case study. *Mar. Ecol. Prog. Ser.* 442, 71–86.
- Rigolet, C., Dubois, S.F., Thiébaud, E., 2014. Benthic control freaks: effects of the tubicolous amphipod *Haploopsis nira* on the specific diversity and functional structure of benthic communities. *J. Sea Res.* 85, 413–427.
- Rosenberg, R., Loo, L.-O., 1988. Marine eutrophication induced oxygen deficiency: effects on soft bottom fauna, western Sweden. *Ophelia* 29, 213–225.
- Rosenberg, R., Loo, L.-O., Möller, P., 1995. Hypoxia, salinity and temperature as structuring factors for marine benthic communities in a eutrophic area. *Neth. J. Sea Res.* 30, 121–129.
- Rosenberg, R., 1995. Benthic marine fauna structured by hydrodynamic processes and food availability. *Neth. J. Sea Res.* 34 (4), 303–317.
- Shojaei, M.B., Gutow, L., Dannheim, J., Rachor, E., Schröder, A., Brey, T., 2016. Common trends in German Bight benthic macrofaunal communities: assessing temporal variability and the relative importance of environmental variables. *J. Sea Res.* 107, 25–33.
- Singer, A.J., Millat, G., Staneva, J., Kröncke, I., 2017. Modelling benthic macrofauna and seagrass distribution patterns in a North Sea tidal basin in response to 2050 climatic and environmental scenarios. *Est. Coast. Shelf Sci.* 188, 99–108. <http://>

- [dx.doi.org/10.1016/j.ecss.2017.02.003](http://dx.doi.org/10.1016/j.ecss.2017.02.003).
- Sorte, C.J.B., Davidson, V.E., Franklin, M.C., Benes, K.M., Doellman, M.M., Etter, R.J., Hannigan, R.E., Lubchenko, J., Menge, B.A., 2017. Long-term declines in an intertidal foundation species parallel shifts in community composition. *Glob. Change Biol.* 23, 341–352. <http://dx.doi.org/10.1111/gcb.13425>.
- Stephensen, K., 1916. Zoogeographical Investigation of Certain Fjords in Southern Greenland, with Special Reference to Crustacea, Pycnogonida and Echinodermata Including a List of Alcyonaria and Pisces. University of Copenhagen, 1916.
- Stewart, P.L., Pocklington's, P., Cunjaki, R.A., 1985. Distribution, Abundance and Diversity of Benthic Macroinvertebrates on the Canadian Continental Shelf and Slope of Southern Davis Strait and Ungava Bay, pp. 281–291. *Arctic* 38, No 4.
- Southward, A.J., Hiscock, K., Kerckhof, F., Moyse, J., Elfimov, A.S., 2004. Habitat and distribution of the warm-water barnacle *Solidobalanus fallax* (Crustacea: cirripedia). *J. Mar. Biol. Ass. U. K.* 84, 1169–1177.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. *Nature* 427, 145–148.
- Thorson, G., 1946. Reproduction and larval development of Danish bottom invertebrates. In: *Medd. Komm. Danm. Fisk Og Havunders. Ser Plankton. Bd 4. Nr 1*. University of Copenhagen, 1946.
- Tewksbury, J.J., Huey, R.B., Deutsch, C.A., 2008. Putting the heat on tropical animals. *Science* 320, 1296–1297 (2008).
- Tunberg, B.G., Nelson, W.G., 1998. Do climatic oscillations influence cyclical patterns of soft bottom macrobenthic communities on the Swedish west coast? *Mar. Ecol. Prog. Ser.* 170, 85–94.
- Zettler, M.L., Friedland, R., Gogina, M., Darr, A., 2017. Variation in benthic long-term data of transitional waters: is interpretation more than speculation? *PLoS One* 12 (4), e0175746. <http://dx.doi.org/10.1371/journal.pone.0175746>.