

Zooplankton response to a warmer northern Wadden Sea

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Abstract Weekly measurements of mesozooplankton (>76 µm) and hydrographic parameters have been carried out since 1984 in the List Tidal Basin (northern Wadden Sea). Monthly water temperature significantly increased by 0.04°C year⁻¹. The largest increase by 3°C in 22 years occurred in September, implying an extension of the warm summer period. Mean annual copepod abundance and length of copepod season correlated significantly with mean temperature from January to May. Except for an increasing *Acartia* sp. abundance during spring (April–May), no long-term trends in copepod abundance were observed. The percentage of carnivorous zooplankton increased significantly since 1984 mainly due to a sudden increase in the cyclopid copepod *Oithona similis* in 1997. We expect that global warming will lead to a longer copepod season and higher copepod abundances in the northern Wadden Sea.

Keywords Zooplankton · Copepods · Temperature · *Oithona* · Wadden Sea · Long-term change

Introduction

Given the importance of copepods as a food source for higher trophic levels and as a potential controlling factor of phytoplankton blooms it is important to know how this pivotal component of the pelagic ecosystem will respond to climate change and rising temperatures. Copepod abundance and diversity in the northeast Atlantic and in the North Sea is subject to large

interannual changes. Since 1948, a downward trend in abundance reversed during the early 1980s (Colebrook et al. 1984) and stabilized during the 1990s (Edwards et al. 2002). Several studies (e.g. Edwards et al. 2001; Reid et al. 2003a) linked changes in the plankton community of the North Sea and the Northwest European shelf to physical changes like the amount of Atlantic inflow or changes in the temperature regime. Beaugrand (2004) suggested that a shift in oceanic biogeographical boundaries along the European continental shelf was responsible for the observed changes in the plankton community. Edwards et al. (2002) and Beaugrand (2003) associated changes in the plankton community to exceptional hydro-climatic events. Richardson and Schoeman (2004) found a bottom-up control of herbivorous and carnivorous zooplankton dynamics in the northeast Atlantic and adjacent shelf. Phytoplankton abundance was positively related to sea-surface temperature at high latitudes where turbulent mixing and high nutrient concentrations prevail and negatively related to sea-surface temperatures at low latitudes where stratified conditions prevail. Changes in the phytoplankton and zooplankton may have important consequences for the entire ecosystem: Aebischer et al. (1990) suggested that changes in the plankton community (phytoplankton and zooplankton) propagated up in the food web across four trophic levels.

Most of the above information on long-term change in the zooplankton community is based on the continuous plankton recorder surveys (CPRS, e.g. Reid et al. 2003b). The CPRS uses a plankton recorder towed behind commercial ships. These plankton recorders are known to underestimate zooplankton abundance (Batten et al. 2003; Clark et al. 2001; John et al. 2001) and this may bias the observed trends. Pitois and Fox (2006) recalculated the CPRS data based on comparisons with vertical net hauls (Clark et al. 2001; John et al. 2001). Using species-specific correction factors, they reassessed biomass distribution and long-term

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trends in the North Sea. Pitois and Fox (2006) showed that the zooplankton biomass in the northern North Sea is lower than in the southern North Sea. They observed maximum biomass in the southeastern North Sea that was dominated by smaller copepods. A trend analysis indicated a decreasing trend in zooplankton biomass from 1960 to 2001.

The CPRS is not sampling shallow water. Therefore, little is known on long-term zooplankton trends in the shallow parts of the North Sea. Here we present data from a zooplankton time series started in 1984 in the List Tidal Basin lying in the northern Wadden Sea adjoining the southeastern North Sea. Nutrient and phytoplankton data suggest a general decrease in the eutrophication status and summer phytoplankton biomass (van Beusekom et al. 2005; van Beusekom et al. 2008). In addition, the offshore zooplankton populations show a general decrease in biomass (Greve et al. 2004; Pitois and Fox 2006). Given the bottom-up control found in the East Atlantic and adjacent shelf by Richardson and Schoeman (2004) we expected a decreasing trend in zooplankton biomass in the List Tidal Basin. We will show that in contrast to these expectations, (1) annual zooplankton abundance is not decreasing and (2) that higher winter and spring temperatures may lead to higher annual zooplankton abundances.

Materials and methods

Area description

The study was conducted in the List Tidal Basin (54°50′–55°10′N and 8°20′–8°40′E), a 404 km² semi-

enclosed bight in the northern Wadden Sea (North Sea, Europe). A single tidal inlet connects the basin to the open North Sea (Fig. 1). To the north and to the south two dams connecting the Island of Rømø and the Island of Sylt to the mainland close the basin laterally. Water volume at mean tidal level is about $845 \times 10^6 \text{ m}^3$. The mean water depth is 2.7 m (Loebl et al. 2007) but reaches up to 40 m in the main tidal channel. The water column is homogeneously mixed most of the time (Hickel 1980). Tides are semidiurnal and mean tidal range is about 2 m. During low tide, about 30% of the area is emerged. Monthly mean salinity and temperature reach seasonal minimum values around February and maximum values around August. Monthly mean salinity (1984–2005) ranges between 24.8 and 31.8 in February (mean: 28.1 ± 1.5) and between 28.6 and 33.4 in August (mean: 30.7 ± 1.1). Monthly mean temperature (1984–2005) ranges between -1.8 and $+5.3$ in February (mean: 2.3 ± 2.0) and between 16.3 and 21.9 in August (mean: 18.4 ± 1.4). Suspended matter ranges between 20 and 60 mg/l in winter to ~ 5 mg/l in later summer. Gätje and Reise (1998) give a detailed description of the area.

Sampling

Since 1984, measurements on zooplankton and temperature have been conducted regularly at a fixed station (55°01.30′N, 08°27.10′E) in the southernmost of three main tidal channels. In general, samples were taken twice a week depending on weather conditions. Mesozooplankton was sampled by taking 35 l seawater by bucket from the surface and sieving through a 76 μm net. High seston loads

Fig. 1 Map of the List Tidal Basin (situated in the south eastern North Sea). Indicated in the detailed map are the position of the sampling station, the extent of the tidal flats (hatched area) and the 5 m depth line (stippled line)

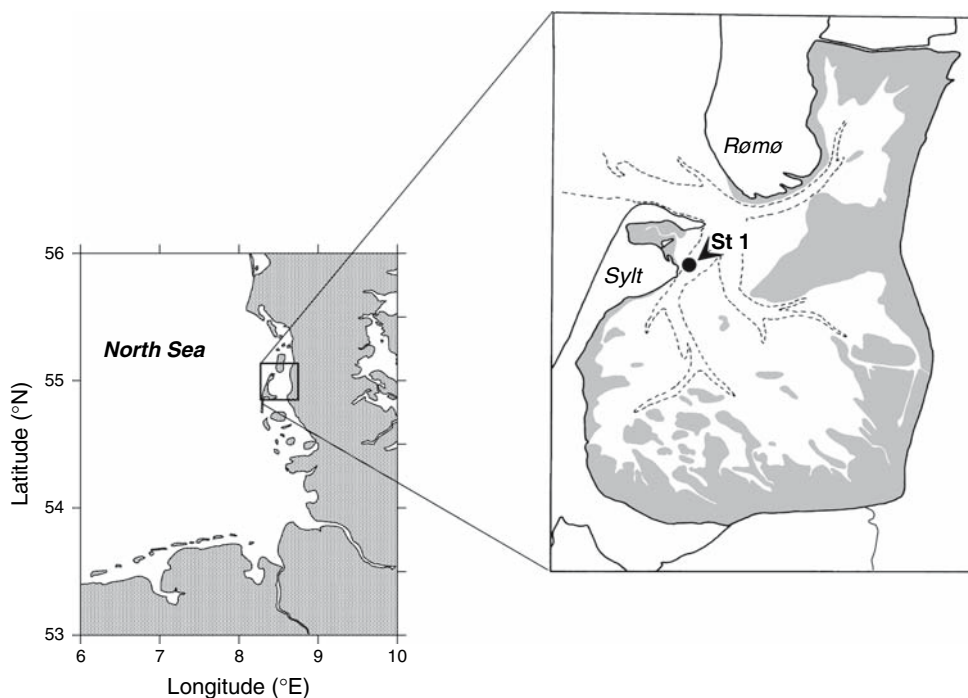


Table 1 Dry weight and feeding habit of zooplankton species in the List Tidal Basin (Martens 1975)

Species	Dry weight (μg)	Herbivorous	Carnivorous
Nauplii <i>Centropages hamatus</i>	0.11	X	
Nauplii <i>Temora longicornis</i>	0.11	X	
Nauplii <i>Acartia</i> sp.	0.11	X	
Nauplii <i>Oithona</i> sp.	0.11	X	
Nauplii <i>Para-</i> and <i>Pseudocalanus</i> sp.	0.11	X	
Nauplii Balanidae	4.50	X	
Cypris larvae Balanidae	16.00	X	
Copepodit <i>Centropages hamatus</i>	2.00	X	
Copepodit <i>Temora longicornis</i>	2.50	X	
Copepodit <i>Acartia</i> sp.	1.00	X	
Copepodit <i>Oithona</i> sp.	0.80	X	
Copepodit <i>Para-</i> and <i>Pseudocalanus</i> sp.	1.20	X	
<i>Centropages hamatus</i> adult	15.70	X	
<i>Temora longicornis</i> adult	18.40	X	
<i>Acartia</i> sp. adult	6.40	X	
<i>Oithona similis</i> adult	3.00		X
<i>Paracalanus parvus</i> adult	5.10	X	
<i>Pseudocalanus elongatus</i> adult	14.00	X	
Harpacticoidea (larvae and adult)	0.80	X	
<i>Noctiluca scintillans</i>	0.08	X	
<i>Oikopleura dioica</i>	10.00	X	
Larvae of Bivalvia	0.08	X	
Larvae of Gastropoda	2.00	X	
Trochophora larvae	0.15	X	
Metratrochophota of Spionidae	0.50	X	
Metratrochophora of other Polychaeta	0.50	X	
Nektochaeta of Spionidae	10.60	X	
Nektochaeta of other Polychaeta	10.60	X	
<i>Lanice conchilega</i>	12.00	X	
<i>Magelone papilicornis</i>	5.00	X	
Ophioplutei	1.20	X	
Echinoplutei	10.00	X	
Bipinnaria larvae	10.00	X	
Larvae of <i>Membranipora</i> sp.	1.00	X	
Rotatoria	0.07	X	
<i>Alaurina composite</i>	2.00		X
<i>Sagitta</i> sp.	10.00 per mm		X
<i>Podon</i> sp.	8.00		X
<i>Evadne</i> sp.	3.00		X
Zoea larvae	20.00		X
Megalopa larvae	50.00		X
<i>Rathkea oktopunctata</i>	14.30		X
<i>Sarsia tubulosa</i>	14.00		X
<i>Pleurobrachia pileus</i>	16.00		X
<i>Obelia geniculata</i>	15.20		X

of the water prevented the use of plankton nets due to clogging. The samples were preserved in 2% formaldehyde-seawater solution and counted under the microscope.

Zooplankton dry weight was computed after Martens (1975; Table 1). The water temperature was measured with a reversing thermometer attached to a TPN water sampler

(Transparent Plastic Nansen Water Sampler, System Hydrobios) or a Niskin-type water sampler. Strong turbulence prevents stratification in these waters (Hickel 1980). As part of these time series, water samples were also analyzed for hydrographic parameters (salinity, suspended matter, pH), nutrients and phytoplankton biomass (chlorophyll *a*). Details are given by van Beusekom et al. (2008) and Loebel et al. (2008).

We summarized the primary data to monthly mean values and calculated anomalies as the difference between the actual monthly value and the mean monthly value for the entire period of investigation (1984–2005). We tested for significant correlations with Pearson's regression analysis if the data were normally distributed (Shapiro–Wilk's *W* test) and otherwise we used the Spearman's Rank correlation coefficient (SR) [StatSoft, Inc. 2004. STATISTICA für Windows (Software-System für Datenanalyse) Version 6].

Results

Temperature

Monthly mean water temperature (Fig. 2a) shows a clear seasonal cycle with maximum values in August (mean of 1984–2005: 18.4°C) and minimum values in February (mean of 1984–2005: 2.3°C). Temperature anomaly (deviation from the mean monthly values 1984–2005) shows strong interannual variation (Fig. 2b). The conspicuous features are the cold winters of 1984–1987 and 1996, the warm winters 1988–1994 and 1999–2002, the relatively cold late summer (August–September) values until 1988 and the warm late summer values from 1995 onward. The monthly temperature anomalies are normally distributed (Shapiro–Wilk's *W* test) and correlate significantly with

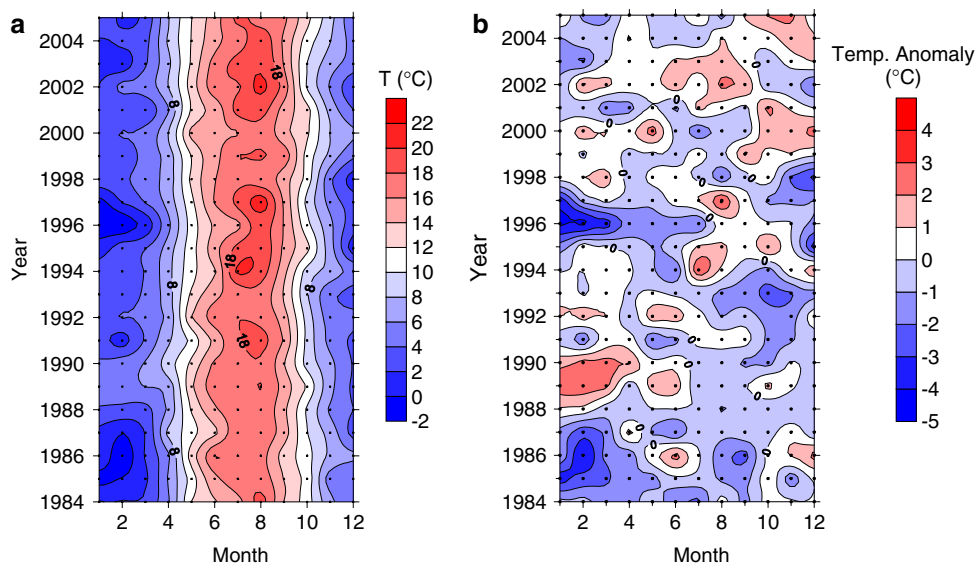
time ($P < 0.002$). The linear regression coefficient suggests a mean increase of about $0.04^{\circ}\text{C year}^{-1}$. However, the amount of variability explained by time is low and indicates high interannual variability in temperature anomalies and a minor long-term trend. A Spearman rank correlation for each month separately was only significant for September with a temperature increase of almost 3°C from values around $13\text{--}14^{\circ}\text{C}$ during the early 1980s to $14.5\text{--}17.5^{\circ}\text{C}$ during the early 2000s (Fig. 3). September temperatures are normally distributed and a Pearson's correlation is significant ($P < 0.001$) with a linear trend of $0.13^{\circ}\text{C year}^{-1}$. Based on this we conclude that during the past 22 years the warm summer period was extended by about 1 month.

Copepod dynamics

Monthly mean copepod numbers show large interannual differences (Fig. 4). Low spring densities indicate a late start of the growing season and prevail after cold winters (e.g. 1984–1987, 1996, 2001). *Centropages hamatus* and *Acartia* sp. are dominating copepods making up $75 \pm 5\%$ of total adult copepod numbers. The calanoid copepod *Acartia* sp. (Fig. 5a) shows a similar pattern as total copepods with low spring abundances and a late start of the growing season after cold winters. *C. hamatus* is an important holoplanktonic herbivorous species occurring from May/June until September but with strong interannual variations (Fig. 5b). Note again the low densities after cold winters (e.g. 1984–1987, 1996, 2001).

Figures 4 and 5 suggest that the copepod season tends to be shorter and that the seasonal development tends to start later in years with cold winters. We tested the influence of temperature on mean annual numbers with a correlation analysis using the mean winter and spring temperature as the independent variable (January–May). As mean annual

Fig. 2 Contour plot of monthly mean water temperature ($^{\circ}\text{C}$) (left) and monthly water temperature anomaly (deviation from the mean monthly temperature ($^{\circ}\text{C}$) (right) in the List Tidal Basin from 1984 until 2005



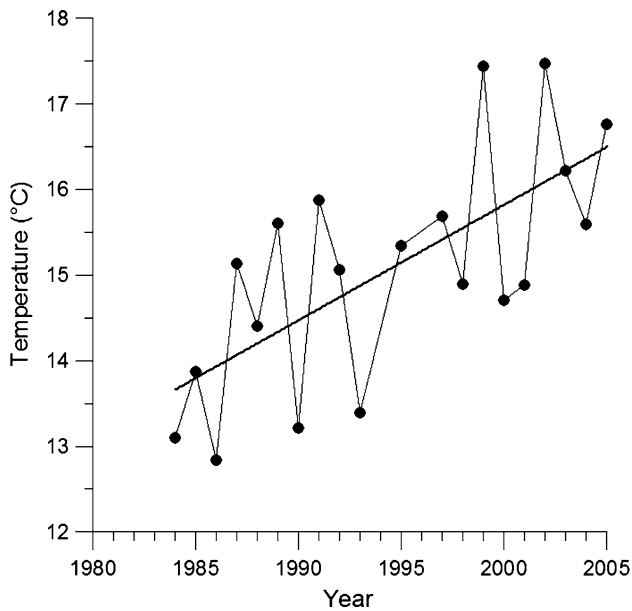


Fig. 3 Increase of water temperature in September in the List Tidal Basin ($R^2 = 0.46$; $N = 20$; $P < 0.001$; Data are normally distributed). The annual increase is $0.134^{\circ}\text{C year}^{-1}$

Acartia and *C. hamatus* numbers were not normally distributed, we used Spearman’s rank correlation. Mean annual copepod numbers were normally distributed and here we calculated Pearson’s correlation coefficients. In all cases, we found a significant correlation with mean winter and spring temperature (Table 2). Mean winter and spring temperatures explained about 40% of the interannual variance in total copepod numbers (Fig. 6).

We estimated the length of the copepod season by counting the number of months with abundances larger than

Fig. 5 Contour plot of (left) monthly mean adult *Acartia* sp. numbers (n m^{-3}) and (right) monthly mean adult *Centropages hamatus* numbers (n m^{-3}) in the List Tidal Basin from 1984–2005

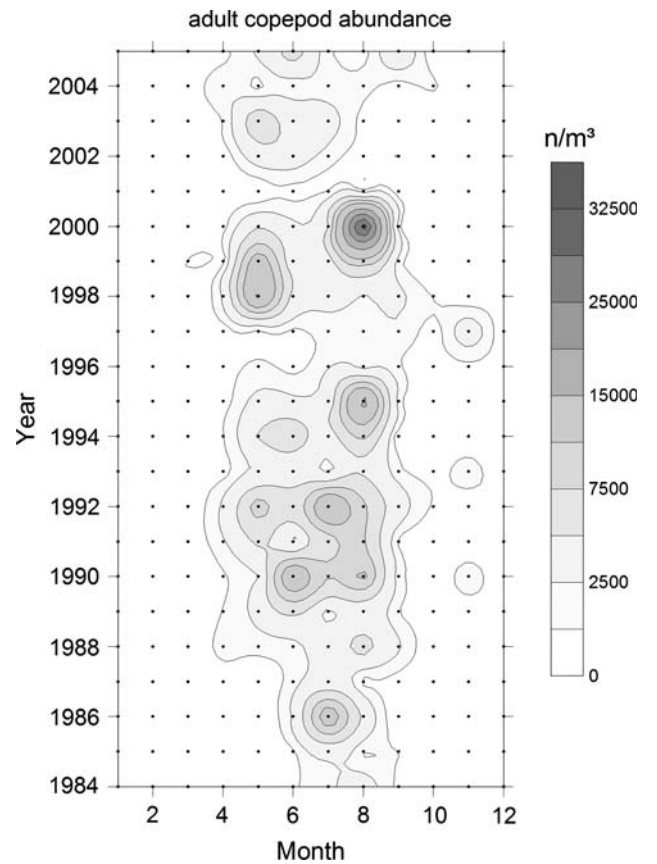
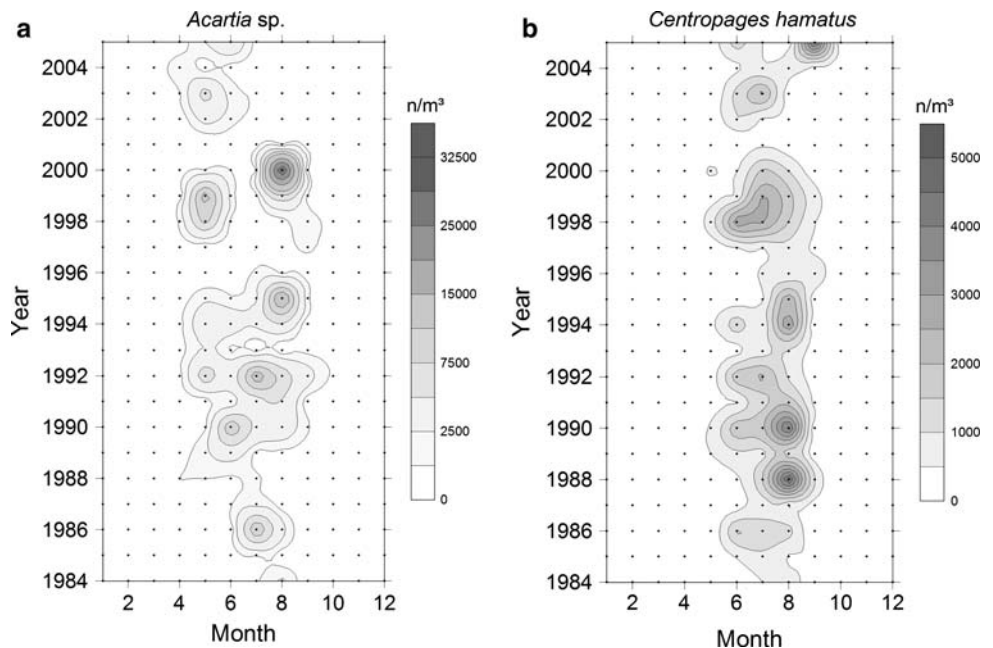


Fig. 4 Contour plot of monthly mean adult total copepod numbers (n m^{-3}) in the List Tidal Basin from 1984–2005

$1,000 \text{ m}^{-3}$ for total copepods and *Acartia* sp. and with abundances larger than 500 m^{-3} for *C. hamatus*. The season length was normally distributed and a Pearson correlation

Table 2 Results from the regression analysis between winter and spring temperatures (January–May) and mean annual *Acartia* sp. numbers and *Acartia* sp. season length (number of months with abundance > 1,000 m⁻³), mean annual *Centropagus hamatus* numbers

Independent value	Dependent value	Method	Result
Temperature	<i>Acartia</i> sp. (mean annual abundance)(season length)	Spearman Pearson	$R = 0.53; N = 21; P < 0.012$ $R^2 = 0.45; N = 21; P < 0.001$
Temperature	<i>C. hamatus</i> (mean annual abundance) (season length)	Spearman Pearson	$R = 0.61; N = 21; P < 0.0034$ not significant ($P = 0.41$)
Temperature	Total copepods (mean annual abundance) (season length)	Pearson Pearson	$R^2 = 0.40; N = 21; p < 0.002$ $R^2 = 0.38; N = 21; P < 0.003$

Data from 1989 were omitted (no data for April–June). *Acartia* sp. and *Centropagus hamatus* represent $75 \pm 5\%$ of total copepod numbers

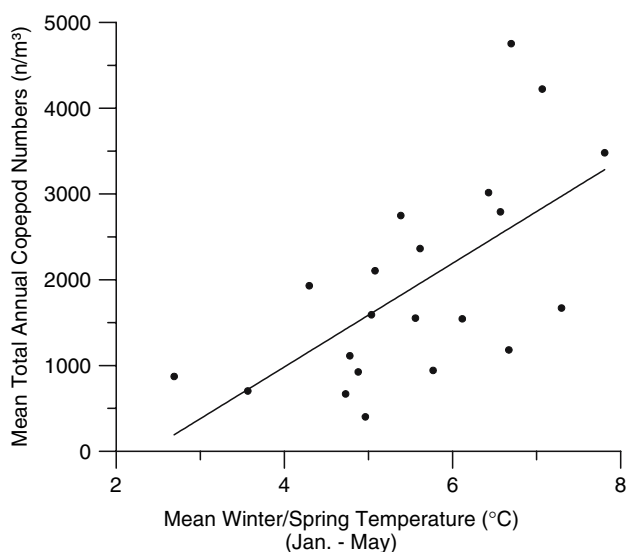


Fig. 6 Correlation between mean winter/spring temperature (January–May) and mean annual copepod numbers (n m⁻³) in the List Tidal Basin ($R^2 = 0.40; N = 21; P = 0.002$)

showed a significant influence of winter and spring temperature on the length of the season for total copepods ($R^2 = 0.38$) and for *Acartia* sp. ($R^2 = 0.45$; Table 2).

A multiple regression with time and temperature as independent variables revealed no significant temporal trend in total copepod abundance (Temperature January–May: $P < 0.0025$; Time: $P < 0.66$). Also, a simple linear regression showed no significant long-term trend in mean annual copepod numbers ($P < 0.93$). *Acartia* sp. abundance is on the borderline of not being normally distributed (Shapiro–Wilk’s W test: $P < 0.047$). A Pearson’s correlation with the mean temperature (January–May) is significant ($P < 0.0055$) and explains 34% of the variance of mean annual *Acartia* abundance. A multiple regression with time and temperature as independent variables showed that no significant trend is present (Temperature January–May: $P < 0.0055$; Time: $P < 0.51$). A simple linear regression showed no significant long-term trend in mean annual *Acartia* numbers ($P < 0.90$). *Acartia* abundance in spring (April and May)

and *Centropagus hamatus* season length (number of months with abundance > 500 m⁻³) and mean annual total copepod numbers and copepod season length (number of months with abundance > 1,000 m⁻³)

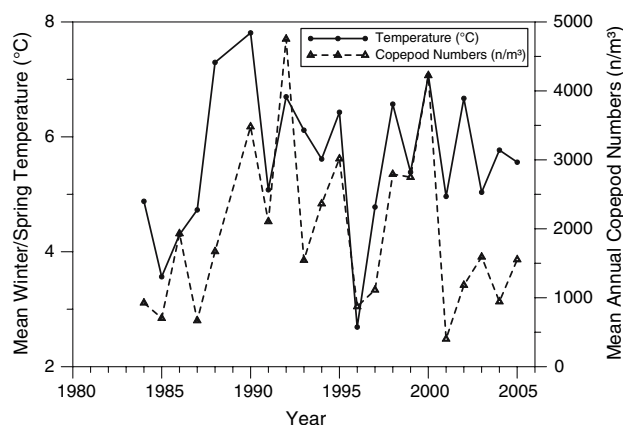


Fig. 7 Mean winter/spring temperature and mean annual total copepod numbers from 1984 until 2005

increased significantly (Spearman rank: $R = 0.45, P < 0.038$; Fig. 5a).

The impact of cold winters and springs is also evident from a plot of mean winter and spring temperature and total annual copepod numbers against time (Fig. 7). The graph highlights the large interannual differences in winter and spring temperatures of up to 3°C. These differences are large compared to the annual trend of 0.04°C year⁻¹ and suggest that at present any trend due to global warming is overridden by interannual dynamics. It is interesting to note that the mean copepod abundance since 2001 is on a similar level as during the early 1980s despite the much higher winter-spring temperatures indicating the effect of further, yet unidentified process involved in the seasonal copepod dynamics.

The long-term dynamics of *O. similis* (a carnivorous cyclopoid copepod) show low numbers before 1996 and high numbers after 1996 especially during late summer and autumn (Fig. 8). To compare long-term shifts between mainly carnivorous and mainly herbivorous species, the numbers per volume were converted to dry weight to exclude the effect of size differences between the species using factors of Martens (1975) (Table 1). The ratio

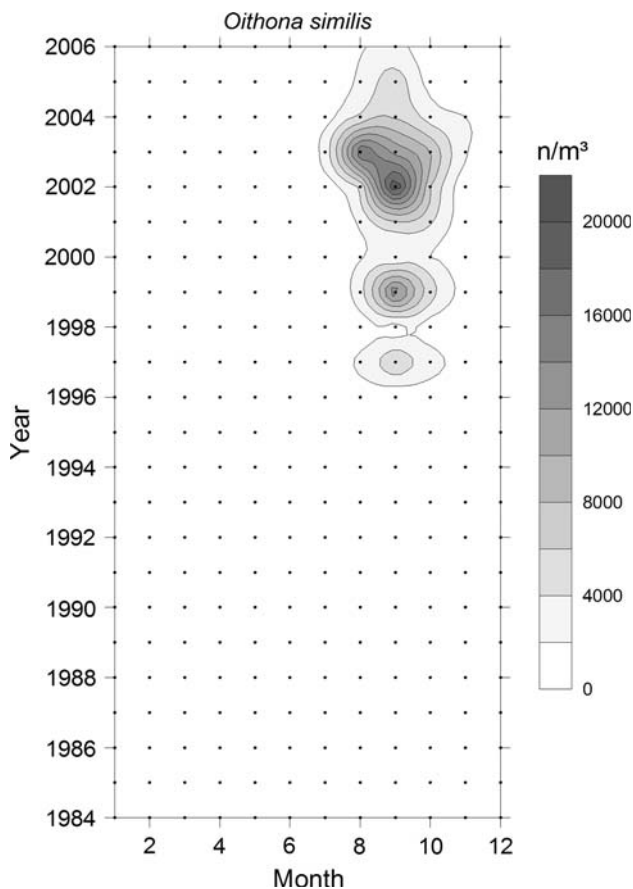


Fig. 8 Contour plot of monthly mean adult *Oithona similis* abundance (n m^{-3})

between herbivorous and carnivorous mesozooplankton biomass increased significantly from 1984 until 2005 (Spearman's rank; $P < 0.0001$; Fig. 9). This is mainly due to the increase of the mainly carnivorous (Lampitt 1978), "ambush feeding" (Svensen and Kiørboe 2000) copepod *O. similis*.

Discussion

Temperature increased by $0.04^\circ\text{C year}^{-1}$ during the past 22 years. The trend fits within a global warming trend (IPCC 2007) and within a warming trend in the North Sea and Baltic (van Aken 2003; Wiltshire and Manly 2004; MacKenzie and Schiedek 2007). However, the warming trend is minor compared to the interannual variation in the annual temperature regime. We found a significant effect of warmer winter and spring temperatures on the seasonal development of copepods. Based on this we suggest that global warming will lead to an earlier start of the copepod seasonal development and to a longer season and larger mean annual abundances in the List Tidal Basin.

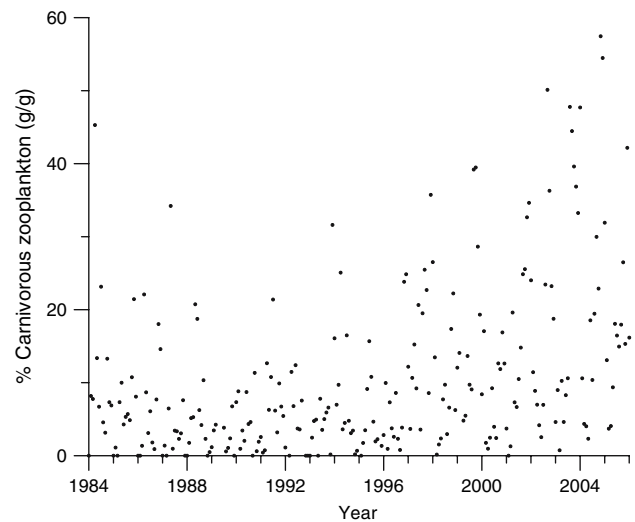


Fig. 9 Increasing percentage of the mainly carnivorous fraction of the whole mesozooplankton in the List Tidal Basin with time. Spearman's rank correlation coefficient: $RS = +0.405$; $P < 0.0001$

Temperature control of interannual copepod dynamics

In contrast to the decreasing trend of copepod numbers in the North Sea (Clark and Frid 2001; Greve et al. 2004; Pitois and Fox 2006) we observed no significant decreasing trend but found that the temperature regime of the preceding winter and spring (January–May) explained 40% of the interannual variability of the annual mean copepod abundance. During the 22 years of our observations, marked changes have occurred in the seasonal dynamics. Firstly, we observed a progressively earlier seasonal increase in *Acartia* sp. abundance and secondly we found that the share of carnivorous zooplankton in total zooplankton biomass has gradually increased. The latter increase was largely due to a proliferation of the copepod *O. similis*.

Our analysis further suggests that winter and spring temperatures have a strong impact on zooplankton dynamics in our area. This may be explained by the fact that many of the copepod species in the List Tidal Basin develop from benthic eggs (e.g. *Centropagus* or *Acartia*). The effect of temperature on hatching rates is well known (Arendt et al. 2005; Holste and Peck 2006). In addition, the increasing autumn temperatures and an extended growth season (better physiological conditions of females) may have stimulated egg survival.

Food availability seems to be of secondary importance. Although riverine nutrient loads are decreasing and despite a decrease in summer phytoplankton biomass (as chlorophyll; van Beusekom et al. 2005), this did not clearly affect zooplankton abundance. However, a closer look at the winter and spring temperatures and copepod abundance against time shows that during recent years copepod

numbers are on a similar level as during the 1980s despite much higher temperatures (Fig. 7). Three factors may contribute to this: a recent decline in food availability (a bottom-up effect related to decreased riverine nutrient loads), the proliferation of carnivorous zooplankton or an increased predation by fish larvae and small fish. Further studies are needed to clarify this. For the Wadden Sea no other time series on zooplankton are available but it is interesting to note that Fransz et al. (1992) noted that *Temora longicornis* biomass increased between 1973 and 1991 in the Western Dutch Wadden Sea (Marsdiep).

The proliferation of the carnivorous copepod *O. similis* contrasts with a general decrease observed in the rest of the North Sea (Pitois and Fox 2006). Apparently, conditions that support the development of this copepod in the List Tidal Basin have improved. We suggest that at least three factors contribute to this. Firstly, nutrient limitation intensified during recent years (Loebl et al. 2008). This may have lead towards a microbial loop dominated plankton community with a large share of ciliates being an important food source for the small carnivorous copepod *O. similis*. Secondly, increased September temperatures enhanced growth conditions. Thirdly, light availability and therefore phytoplankton growth conditions during September have improved (Loebl et al. 2008). The timing of the sudden increase of *O. similis* (in 1997) is striking as the September temperature increase was more gradual (Fig. 2) but coincides with a possible regime shift in the North Sea around 1997 (Weijerman et al. 2005).

Regime shifts in the North Sea

According to Beaugrand (2004) the North Sea underwent a dramatic regime shift during 1983–1988. A warm-biological dynamic regime followed a cold-biological regime, ecological processes being strongly dependent on hydroclimatic variability in the northeast Atlantic Ocean (Beaugrand and Ibanez 2004). Weijerman et al. (2005) analysed 28 abiotic and 50 biological time series in the North Sea and Wadden Sea and identified two major shifts around 1979 and 1988 and possibly a third minor shift in 1997–1998. Our time series are not long enough to identify these shifts with any certainty. However it is interesting to note that two marked changes in interannual copepod dynamics in the List Tidal Basin coincide with these shifts. Firstly, *Acartia* and total copepod increase started almost one month earlier after 1987. This change is most probably related to the extreme warm winter and spring temperatures in 1988/1989 as indicated by the relation between winter and spring temperature and copepod dynamics (Fig. 7; Table 2). The sudden increase of *O. similis* in 1997 coincides with the minor shift proposed by Weijerman et al. (2005). We could not provide a clear explanation for the timing of the sudden

Oithona increase after 1997. Probably, a yet unknown complex change comprising both abiotic and biotic components is involved in the latter shift.

Conclusions

Temperature has a strong and significant effect on the seasonal development of copepods in the List Tidal Basin with warmer winter and spring temperatures leading to a longer copepod season and higher mean annual abundances. Despite a warming trend since 1984 of $0.04^{\circ}\text{C year}^{-1}$ no significant temporal trends in copepod abundance were observed except for a progressively earlier start of the *Acartia* sp. season. September temperatures significantly increased $0.13^{\circ}\text{C year}^{-1}$ since 1984. Since 1997, *O. similis* developed a pronounced autumn bloom. We expect that global warming will lead to a longer copepod season and higher copepod abundances in the northern Wadden Sea.

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