Long-term variability in the diversity of North Sea zooplankton

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Results from the Continuous Plankton Recorder survey were used to study long-term changes in the zooplankton of four regularly sampled areas of the North Sea. The trends in α-diversity are described and analysed. Species associated with inflow of oceanic or mixed waters from the Atlantic or shelf to the west and south of Britain have increased in abundance or frequency of occurrence. Meroplankton have also increased but resident holoplankton and those associated with colder oceanic or mixed waters have declined. These changes have resulted in an increase in the species richness in the areas in the north-western North Sea. There was a period of low diversity in the late 1970s and early 1980s in the most southerly area, furthest from the sources of inflow. The evidence for a long-term trend was stronger than relationships between diversity and either the North Atlantic Oscillation or variation in position of the Gulf Stream in the western Atlantic.

INTRODUCTION

The Continuous Plankton Recorder (CPR) survey has been operated in the North Sea since 1931 (Hardy, 1939). Methods of analysis of zooplankton have been constant since 1948 (Rae, 1952) and the taxonomic resolution of the analysis has been mainly stable since 1958 (Colebrook, 1960). Analyses of the survey data have demonstrated changes in the plankton correlated with climatic variables (see Reid et al., 1998 for a recent review). Lindley et al. (1995) identified a change in dominance in CPR samples from the central North Sea. The dominant taxa were calanoid copepods for most of the period from 1958 to 1978 but thereafter echinoderm pluteus larvae were usually the most numerous taxon in the samples.

There is latitudinal variation in diversity of holozooplankton with low diversity at high latitudes (Huston, 1979). This is the case for crustaceans (Turner, 1981; McKenzie, 1967; Abele, 1982), Foraminifera (Rutherford et al., 1999) and gelatinous groups (Fraser, 1947a,b; Bückmann, 1969; Pierrot-Bults & Nair, 1991). The existence of a latitudinal gradient for marine benthos as a whole has been challenged (e.g. Clarke, 1992; Kendall & Aschan, 1993). However Thorson (1950) demonstrated that the proportion of macrobenthic species with planktotrophic larvae in polar regions was lower than that at lower latitudes, so the species richness of the meroplankton should decline with increasing latitude.

Dana (1853) related distributions of marine Crustacea to isocrymes, indicating the mean temperature in the coldest 30-d period of the year. This is consistent with the correlation of plankton distributions with winter temperature (e.g. Colebrook, 1964), mass mortality of benthic fauna in cold winters (e.g. Crisp, 1965) and temperature limitations to successful reproduction both in the laboratory (e.g. Wear, 1974) and in the field (e.g. Lindley, 1987). The influence of temperature on pelagic biogeography has been reviewed by van der Spoel (1997).

If global warming is reflected in regional conditions then we would expect an increase in species richness in the North Sea plankton with examples of the more diverse fauna from lower latitudes spreading into the area. Kröncke (1992) and Kröncke et al. (1998) found evidence of increasing benthic diversity in sites in the North Sea with no indication that the changes were caused by disturbance.

Margalef (1967) found that diversity very often increases through a seasonal succession, sometimes decreasing again toward the final stage of succession. If the length of the productive season is a factor limiting diversity, then any increase in diversity due to temperature rise removing limits to distributions could be restrained by lack of appropriate 'temporal niches' in the seasonal cycle (Lindley, 1998).

Allen (1997) has analysed year-to-year changes in plankton community structure in four regularly sampled areas of the North Sea by similarity analysis and multi-dimensional scaling. Here significant changes in the proportions of taxa in the zooplankton counts, the changes in dominant taxa and gains and losses in these four areas are described and discussed as a contribution to understanding the temporal component of β-diversity in the North Sea zooplankton. Also long-term trends in changes of α-diversity indices and the relationships with two climatic indices are investigated and analysed. These indices are the Gulf Stream index (GSI), a measure of the position of the northern boundary of the Gulf Stream where it diverges from the American coast (Taylor, 1995)

and the North Atlantic Oscillation index (NAO), the variations in difference of normalized pressures in winter between Lisbon, Portugal and Stykkisholmur, Iceland (Hurrel, 1995).

METHODS

Continuous plankton recorders are towed by ships-of-opportunity, mainly merchant vessels, sailing on regular routes. Wherever possible, tows are taken along each route at monthly intervals. Warner & Hays (1994) describe the positions of tows up to 1993 and methods of analysis and taxonomic resolution of the CPR survey data. Among the zooplankton, calanoid copepods are identified mainly to species; cladocerans, cyclopoid and poecilostomatoid copepods are identified to genus and other groups are identified to higher taxonomic levels only. The results of analysis provide estimates of abundance of each of the taxa identified in samples each representing the plankton retained during 18 km of tow (assumed to be from 3 m^3 of water).

Four areas of the North Sea were selected on the basis of consistent sampling of groups of adjacent rectangles of 2° longitude×1° latitude over the period from 1958 to 1995. These areas were: (1) two rectangles, 58–60°N 01–03°W; (2) three rectangles, 55–58°N 01–03°W; (3) three rectangles 55–56°N 01°W–05°E and (4) two rectangles 53–55°N 01°W–01°E. (Note, areas 2 and 3 correspond with areas 1 and 2 of Lindley et al., 1995). The boundaries of the areas and the distributions of samples within these areas are shown in Figure 1. Total counts (sums of accepted values of estimates of abundance) of taxa identified in routine analysis of the CPR in each year were divided by the number of

samples taken in that year for each year from 1958 to 1995. The list of taxa found in the four areas is given in Table 1 with the abbreviations used in subsequent tables.

In order to detect linear trends that may be correlated with global warming or the forcing factors that are considered to drive it, the product moment correlation coefficient was calculated from the year to year changes in abundance of each taxon as a proportion of the total zooplankton counts in each area for the period 1958–1995.

Measures of α-diversity used were: S (species richness), number of taxa present; Margalef index, $D_{Mg}=(S-1)/\ln N$; Berger–Parker index*, $d=N_{Max}/N$; Shannon–Weiner index, $H'=-\sum p_i \ln p_i$; Shannon Evenness, $E=H'/\ln S$.

*In the analyses the reciprocal Berger–Parker index (1/d) was used as this follows the same trend as the other indices, i.e. high values=high diversity; where: S= number of taxa in sample(s); N=number of individuals; N_{Max}=number of individuals in the most abundant taxon; p_i=proportion of individuals in taxon i.

The values of these indices were calculated for the total zooplankton data for each area. In addition, data for calanoid copepods, the only group in the zooplankton that are identified mostly to specific level, were analysed. Linear correlations between these diversity indices and year from 1958 to 1995 and between the diversity indices and the NAO index, derived from the data of Hurrel (1995), in the same period were calculated. In area 4, sampling was poor in each year from 1978 to 1983, with samples taken in fewer than nine months of the year, so correlations within this area were also calculated excluding these years.

The index of position of the northern boundary of the Gulf Stream (GSI) was calculated by principal component analysis of the latitude at six longitudes (Taylor, 1995). The data were available from 1966 onward. The years were divided into three groups according to the values of the index. 'North years' for the 11 years when the northern boundary of the Gulf Stream was furthest north, 'south years' for the years when the boundary was furthest south and 'intermediate years', when the position was closest to the average for the period. Taylor (1995) presented graphs illustrating the variations in the index and the data from which they were derived. As no Gulf Stream position data were available before 1966, comparisons between the effects of this, the NAO and the long-term trend were based on the period 1966–1995 only. The NAO data for 1966–1995 were divided into years of high, medium and low NAO index values (high=1.6–5.1; low=−4.9–0.2). During periods of higher values the pressure difference between Iceland and Lisbon is greater than during periods of lower values. In order to compare results for the GSI and NAO with any long-term trend, the period was divided into three decades. The groups of years used to examine the effects of GSI, NAO and time are listed in Table 2. The means and standard deviations of annual values in the North Sea for sea surface temperature (data from the International Council for the Exploration of the Sea) and the CPR colour index (Warner & Hays, 1994) for these groups of years are also listed. The significances of differences in indices of diversity between groups of years within areas were assessed by *t*-tests. The analyses for area 4 were repeated excluding the poorly sampled years 1978–1993.
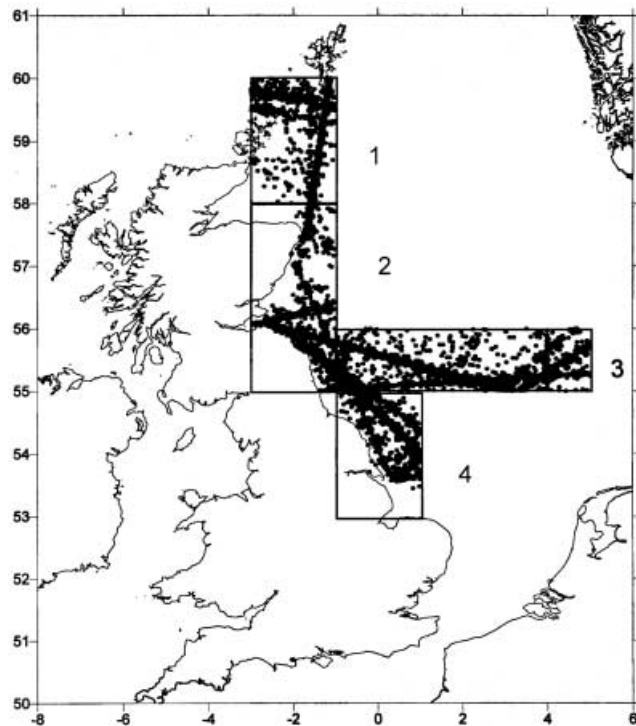
Figure 1. Boundaries of the four areas of the North Sea for which data are presented here with positions of CPR samples taken in those areas during the period 1958–1995.

Table 1. *Taxa identified from the CPR survey in the four areas illustrated in Figure 1 during the period 1958–1995 and used in the analyses presented here, and the abbreviated forms used in Tables 3 and 4.*

Taxon	Abbreviation	Taxon	Abbreviation
Crustacea: Copepoda: Calanoidea		Cladocera	
Acartia clausi Giesbrecht	*Acartia*	*Evadne* spp.	*Evadne*
Aetideus armatus (Boeck)		*Podon* spp.	*Podon*
Anomalocera pattersoni Templeton		Other Crustacea	
Calanus finmarchicus (Gunnerus)	*Cal fin*	Caprellidae	
Calanus helgolandicus Claus	*Cal hel*	Cirripedia larvae	Cirr larvae
Calanus spp. CI–CIV	*Cal I–IV*	Cumacea	Cumacea
Candacia armata (Boeck)	*Candacia*	Decapoda (larvae and post-larvae)	
Centropages hamatus Lillejeborg	*Cent ham*	Euphausiacea calyptopis	
Centropages typicus (Krøyer)		Euphausiacea furcilia and adult	Euph tot
Clausocalanus spp.		Gammaridea	Gammarid
Eucalanus crassus Giesbrecht	*Eucal cras*	Hyperiidae	
Euchaeta hebes Giesbrecht	*Euc hebes*	Isopoda	Isopoda
Euchaeta norvegica Boeck		Mysidacea	Mysid
Isias clavipes Boeck	*Isias*	Ostracoda	Ostracod
Labidocera wollastoni (Lubbock)		Mollusca	
Metridia longa (Lubbock)		Cephalopoda larvae	Cephalop
Metridia lucens Boeck	*Met lucens*	*Clione limacina* (Phipps)	*Clione*
Paracalanus spp. & *Pseudocalanus* spp.	*Para P*	*Limacina* spp.	*Limacina*
Pleuromamma gracilis (Claus)	*Pl gracilis*	Pelecypoda larvae	Bivalve
Pleuromamma robusta (F. Dahl)		*Pneumodermopsis paucidens* Boas	*Pneu pau*
Rhincalanus nasutus Giesbrecht	*Rhin nas*	Other Groups	
Scolecithricella spp.	*Scolecith*	Chaetognatha >8 mm	Chaet >8
Temora longicornis (O.F. Müller)	*Temora*	Chaetognatha <8 mm	Chaet <8
Other Copepoda		Ectoprocta: cyphonautes larvae	
Caligoidea	Caligoid	Polychaeta larvae	Poly larva
Copepod nauplii	Cop naup	*Tomopteris* spp.	
Corycaeus anglicus Lubbock		Echinoderm pluteus larvae	Ech larv
Clytemnestra spp.		Echinoderm post-larvae	
Euterpina acutifrons (Dana)		Appendicularia	Appendic
Harpacticoidea		*Branchiostoma lanceolatum* (Pallas)	*Branchios*
Oithona spp.	*Oithona*	Fish eggs	Fish eggs
Oncaea spp.		Fish larvae	Fish larvae

Table 2. *Groups of years used to identify effects relationships between Gulf Stream position, NAO and long term trend (decade) on diversity indices.*

Gulf Stream	South	Intermediate	North
Years	1970–74, 76, 78, 79, 81, 82	1967, 69, 75, 77, 80, 83, 86–88	1966, 68, 84, 85, 89–95
T°C	9.6 (0.4)	9.5 (0.4)	10.0 (0.6)
CPR colour	2.0 (0.2)	2.2 (0.4)	2.4 (0.4)
NAO	**Low**	**Intermediate**	**High**
Years	1968, 69, 70–72, 77–79, 85–87	1966, 67, 74, 76, 80, 82, 84, 86, 88, 91	1973, 75, 81, 83, 89, 90, 92–95
T°C	9.3 (0.3)	9.8 (0.3)	10.1 (0.5)
CPR colour	2.1 (0.3)	2.1 (0.4)	2.4 (0.4)
Decade	**First**	**Intermediate**	**Last**
Years	1966–75	1976–85	1986–95
T°C	9.6 (0.2)	9.6 (0.4)	10.1 (0.6)
CPR colour	2.1 (0.1)	1.9 (0.2)	2.6 (0.3)

CPR, Continuous Plankton Recorder; NAO, North Atlantic Oscillation; T, temperature.

RESULTS

Table 2 shows that decade of 1986–1995, the 'north years' for the GSI and the high NAO years had the highest values for both mean temperature and CPR colour index. Results of *t*-tests indicated that the most significant differences ($P < 0.001$) were between temperature in high NAO years and low NAO years and between colour in 1986–1995 and the each of the two preceding decades. The difference in temperatures between intermediate and low NAO years was very significant ($P < 0.01$). Differences in temperature between intermediate and north GSI years and the earliest and latest decades and in colour between north and south GSI years and 1966–1975 and 1976–1985 were significant at the 5% level.

Species that have increased or decreased significantly in relative abundance over time are listed in Table 3. Most taxa which increased are of the meroplankton, species usually associated in the North Sea with inflow of warm Atlantic or mixed waters, or Cladocera and diaptomoid calanoids which potentially can produce resting eggs which can remain dormant in the sediment (see Lindley, 1997). The others are multi-specific higher taxa or development stages.

Within the calanoids, *Metridia lucens* increased significantly in areas 2 and 3 as did *Candacia armata* in areas 2, 3 and 4. These species are associated with inflow of oceanic/mixed waters into central and southern North Sea (Corten, 2001). *Euchaeta hebes*, which is most abundant over the continental slope, and the oceanic calanoids *Eucalanus crassus* and *Rhincalanus nasutus* approach the northern limits of their distributions in the waters around northern Scotland (Corten, 2001). The variations in abundance of these three species in areas 1 and 2 during the period 1958–1995 are shown in Figure 2. Only *R. nasutus* occurred in area 1 regularly prior to the early 1980s but in recent years all have occurred regularly in that area and at least intermittently in area 2. *Rhincalanus nasutus* was found in area 3 in 1988 and 1991 and *Eucalanus crassus* has been recorded in area 4 in 1996 (data not illustrated).

These species were comparative rarities in the samples. The most abundant of the species increasing in abundance were the echinoderm larvae (echinopluteus and ophiopluteus) and *Acartia* spp., (a diaptomoid calanoid) and the cladoceran *Evadne* spp. (mainly *E. nordmanni*). Table 4 presents the dominant taxa in total zooplankton counts and in the counts of calanoid copepods only for the four areas from 1958 to 1995. It can be seen that echinoderm larvae have been dominant in areas 2 and 3 for most of the 1990s and in area 3 through the 1980s as well. *Acartia*, a potential resting-egg producer, has become the most frequently dominant calanoid and in many cases the dominant species in the zooplankton in recent years.

'Para-Pseudocalanus', mainly *Pseudocalanus elongatus* and *Paracalanus parvus*, was the most abundant group of calanoids identified in the CPR survey area in 1948–1956 (Colebrook et al., 1961) and was usually so in the early

Table 3. *Significant correlations between relative abundance (p_i) of zooplankton taxa in CPR samples in four areas of the North Sea and year.*

Positive

Area 1			Area 2			Area 3			Area 4		
Poly larva	M	0.485**	Ech larv	M	0.661***	Ech larv	M	0.607***	Cirr larva	M	0.598 ***
Cop naup		0.432**	*Candacia*	SR	0.611***	Cumacea	M	0.572***	Caligoid	M	0.455**
Euc hebes	S	0.422**	*Cal hel*	S	0.587***	Echino pl	M	0.566***	Candacia	SR	0.445**
Eucal cras	S	0.414*	Appendic		0.529***	*Branchios*	M	0.441**	*Acartia*	R	0.435**
Evadne	R	0.399*	Cop naup		0.526**	*Podon*	R	0.380*	Poly larva	M	0.372*
Podon	R	0.363*	*Euc hebes*	S	0.483**	Caligoid	M	0.369*	Euph tot		0.343*
			Fish larvae	M	0.480**	Cop naup		0.349*	*Cent ham*	R	0.334*
			Met lucens	S	0.475**	*Candacia*	SR	0.347*			
			Rhin nas	S	0.424**	*Met lucens*	S	0.344*			

Negative

Area 1			Area 2			Area 3			Area 4		
Pl gracilis	S	−0.336*	*Oithona*		−0.418**	Isopoda	M	−0.323*	Chaet <8		−0.399*
Scolecith		−0.341*	Ostracod		−0.430**	Fish eggs	M	−0.377*	Gammarid	M	−0.426**
Mysid	M	−0.378*	Gammarid	M	−0.493**	*Oithona*		−0.379*	Fish eggs	M	−0.429**
Clione		−0.380*	*ParaP*		−0.528***	Gammarid	M	−0.383*	*Isias*	R	−0.467**
Met lucens	S	−0.393*				Para P		−0.508**	*Limacina*		−0.490**
Caligoid	M	−0.420**				Chaet <8		−0.571***	*Oithona*		−0.500**
Limacina		−0.422**							Para P		−0.505**
Chaet >8		−0.433**									
Isopoda	M	−0.463**									
Euph tot		−0.492**									
Cephalop	M	−0.507**									
Oithona		−0.524***									
Pneu pau	S	−0.525***									
Cal fin		−0.536***									

M, larval meroplankton and epibenthos, hyperbenthos or parasites occurring temporarily in the plankton; R, Cladocera and diaptomoid Calanoida (resting egg producers, 'adult meroplankton'; s, southern (associated with inflow of warmer waters).
***, $P < 0.001$, **, $0.01 > P > 0.001$; *, $0.05 > P > 0.01$.

Eucalanus crassus

Euchaeta hebes

Rhincalanus nasutus
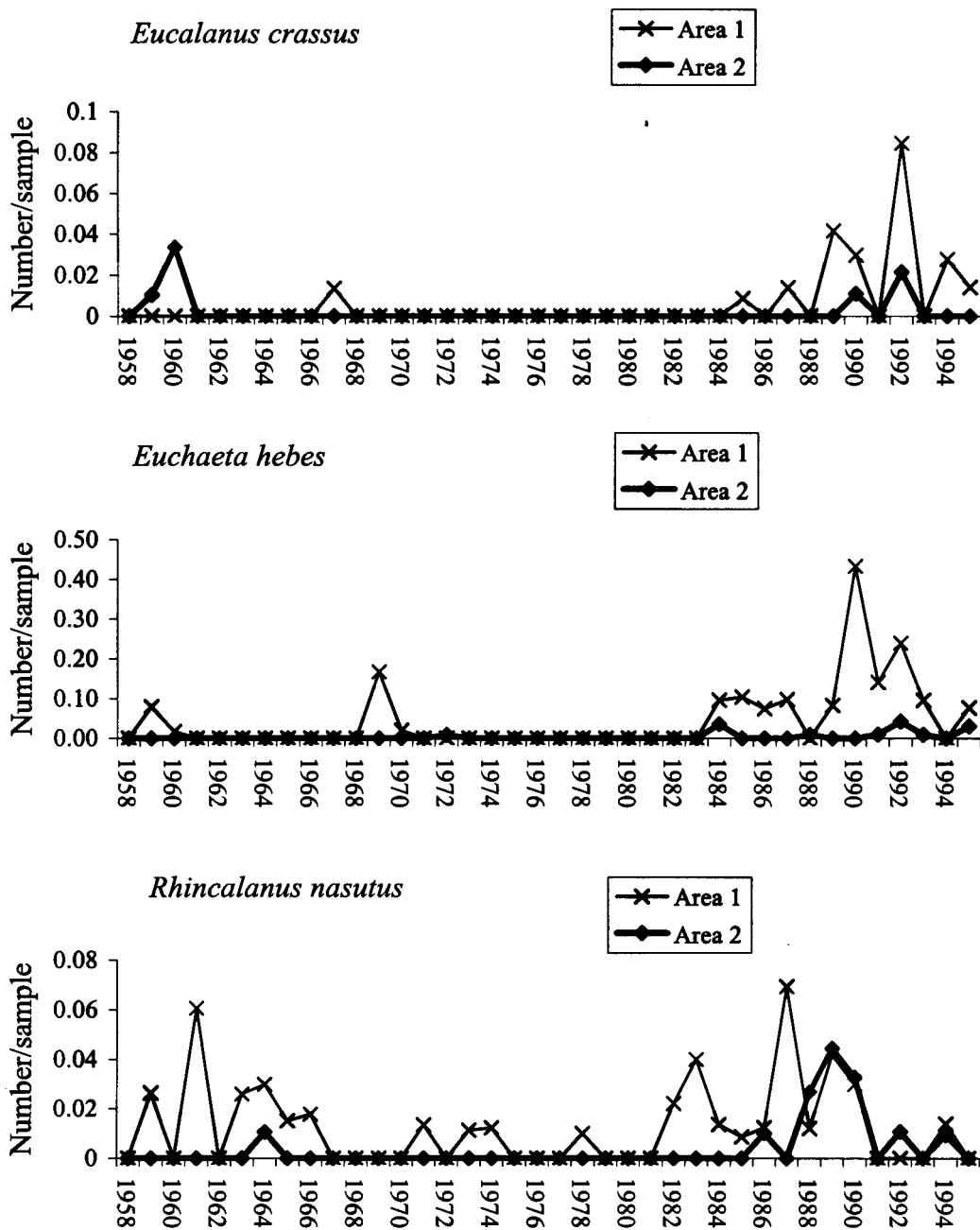
Figure 2. *Eucalanus crassus*, *Euchaeta hebes* and *Rhincalanus nasutus*. Annual variations in abundance in the areas 1 and 2 (Figure 1) 1958–1995.

part of the time period studied here. Numbers have declined significantly in areas 2, 3 and 4 and only in area 3 has '*Para-Pseudocalanus*' remained the dominant calanoid taxon but it had been overtaken in that area by the echinoderm larvae which have increased in abundance to become dominant taxon of the whole zooplankton. *Calanus finmarchicus* (only the sub-adult and adult C5 and C6 stages are identified to species) showed the most significant decline in area 1. Like *C. finmarchicus*, the planktonic gastropod *Limacina* spp. has its main centre of abundance within the CPR survey area in the oceanic waters of the Labrador-Irminger gyre. The genus has declined significantly in relative abundance in areas 1 and 4, being dominant in the former in five years between 1958 and 1966 but only twice subsequently.

The overall values of the α-diversity indices in the four areas are listed in Table 5. Diversity was highest (high species richness, lowest dominance and greatest evenness) in areas 1 and 3. In area 2, species richness was close to that of those two areas but dominance was highest and evenness least of the four areas.

Significant ($P<0.05$) product moment correlation coefficients indicating long-term trends in the five $\tilde{\alpha}$-diversity indices described above for total zooplankton and for calanoids are listed in Table 6A. Only two significant coefficients were negative out of a total of 11. Excluding data for area 4 in 1978–1983, when samples were taken in eight months or less of each year, did not result in any change in significance levels although the r value for $1/d$ became -0.446 $(0.05>P>0.01)$. In the calanoids, dominance

Table 4. *Single dominant taxa of the whole zooplankton and of calanoid copepods in CPR samples from the four areas of the North Sea, 1958–1995.*

Year	Total				Calanoids			
	Area 1	Area 2	Area 3	Area 4	Area 1	Area 2	Area 3	Area 4
1958	Cal I–IV	Para P	Para P		Cal I–IV	Para P	Para P	
1959	Para P	Para P	Para P	Para P	Para P	Para P	Para P	Para P
1960	Limacina	Limacina	Para P	Para P	Cal I–IV	Acartia	Para P	Para P
1961	Limacina	Acartia	Limacina	Para P	Para P	Acartia	Para P	Para P
1962	Para P	Acartia	Para P	Para P	Para P	Acartia	Para P	Para P
1963	Limacina	Bivalve	Cal I–IV	Ech larv	Temora	Acartia	Cal I–IV	Para P
1964	Cal I–IV	Acartia	Cal I–IV	Para P	Cal I–IV	Acartia	Cal I–IV	Para P
1965	Limacina	Acartia	Para P	Acartia	Cal I–IV	Acartia	Para P	Acartia
1966	Limacina	Acartia	Ech larv	Evadne	Para P	Acartia	Para P	Para P
1967	Acartia	Acartia	Para P	Para P	Acartia	Acartia	Para P	Para P
1968	Acartia	Acartia	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia
1969	Ech larv	Acartia	Para P	Para P	Para P	Acartia	Para P	Para P
1970	Acartia	Acartia	Ech larv	Cal I–IV	Acartia	Acartia	Para P	Cal I–IV
1971	Limacina	Acartia	Temora	Ech larv	Para P	Acartia	Temora	Acartia
1972	Acartia	Acartia	Para P	Temora	Acartia	Acartia	Para P	Temora
1973	Acartia	Acartia	Para P	Ech larv	Acartia	Acartia	Para P	Para P
1974	Acartia	Acartia	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia
1975	Temora	Acartia	Ech larv	Acartia	Temora	Acartia	Para P	Acartia
1976	Acartia	Acartia	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia
1977	Temora	Acartia	Para P	Para P	Temora	Acartia	Para P	Para P
1978	Temora	Acartia	Cal I–IV	Acartia	Temora	Acartia	Cal I–IV	Acartia
1979	Acartia	Acartia	Para P	Para P	Acartia	Acartia	Para P	Para P
1980	Cal I–IV	Acartia	Cal I–IV	Cal I–IV	Cal I–IV	Acartia	Cal I–IV	Cal I–IV
1981	Cal I–IV	Ech larvae	Cal I–IV	Evadne	Cal I–IV	Acartia	Cal I–IV	Acartia
1982	Evadne	Acartia	Ech larv	Limacina	Acartia	Acartia	Temora	Temora
1983	Limacina	Acartia	Ech larv	Ech larv	Para P	Acartia	Cal I–IV	Acartia
1984	Evadne	Acartia	Acartia	Acartia	Temora	Acartia	Acartia	Acartia
1985	Para P	Acartia	Ech larv	Acartia	Para P	Acartia	Acartia	Acartia
1986	Ech larv	Acartia	Ech larv	Acartia	Para P	Acartia	Para P	Acartia
1987	Bivalve	Ech larvae	Para P	Acartia	Para P	Acartia	Para P	Acartia
1988	Para P	Acartia	Ech larv	Acartia	Para P	Acartia	Para P	Acartia
1989	Para P	Acartia	Limacina	Cal I–IV	Para P	Acartia	Para P	Cal I–IV
1990	Ech larv	Ech larvae	Ech larv	Acartia	Para P	Acartia	Para P	Acartia
1991	Acartia	Ech larvae	Ech larv	Ech larv	Acartia	Acartia	Cal I–IV	Acartia
1992	Acartia	Acartia	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia
1993	Acartia	Ech larvae	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia
1994	Ech larv	Ech larvae	Ech larv	Acartia	Cal I–IV	Acartia	Temora	Acartia
1995	Acartia	Ech larvae	Ech larv	Acartia	Acartia	Acartia	Para P	Acartia

Table 5. *Overall values of α-diversity indices in the four areas shown in Figure 1.*

	Area 1	Area 2	Area 3	Area 4
Species Richness (S)	55	52	54	49
Margalef index (D_{Mg})	5.09	4.85	4.99	4.59
Inverse Berger–Parker index (1/d)	0.15	0.29	0.2	0.25
Shannon–Weiner index (H')	2.50	2.33	2.48	2.39
Shannon Evenness (E)	0.62	0.59	0.62	0.61

decreased (increase in diversity) in area 3 but in the total zooplankton there was no significant change. Equivalent data for correlations between diversity and the NAO index are listed in Table 6B. Only five of 40 coefficients were significant. Of these, four positive correlations were indices of species richness (S or D_{Mg}).

Differences between α-diversity indices for total zooplankton and for calanoids in the pairs of groups of years listed in Table 2 that were significant after the Bonferroni correction for multiple comparisons was applied are listed in area 7. Indices of species richness constituted the majority of the listed values. Most of those values are for differences between decades indicating that a long-term trend is having a greater effect than the year-to-year variations of the two climatic indices. Many of the listed differences are between the middle decade,

Table 6. *Significant correlations between α-diversity indices of the total zooplankton and calanoids and time (years) and the NAO index in four Areas of the North Sea for 1958–1995.*

A. *Time.*

Total			Calanoids		
Area	Index	r	Area	Index	r
1	S	0.446**	1	S	0.514***
1	H′	0.350*	1	D_{Mg}	0.469**
3	D_{Mg}	0.425**	1	E	−0.465**
4	1/d	−0.407*	2	D_{Mg}	0.593***
			3	1/d	0.478**
			3	H′	0.525***
			3	E	0.467**

B. *NAO.*

Total			Calanoids		
Area	Index	r	Area	Index	r
3	S	0.446**	1	E	−0.386*
3	D_{Mg}	0.490**	2	D_{Mg}	0.494**
			3	D_{Mg}	0.425*

***, $P < 0.001$; **, $0.01 > P > 0.001$; *, $0.05 > P < 0.01$.

Table 7. *Significant differences in α-diversity indices for total zooplankton and for calanoids between pairs of groups of years listed in Table 1 in four areas.*

Area	Year group	Index	High group	Mean (σ)	Low group	Mean (σ)
Total						
3	Decades*	S	1986–1995	40.3 (2.4)	1966–1975	37.4 (2.0)
3	Decades	S	1986–1995	40.3 (2.4)	1976–1985	33.8 (4.9)
3	Decades	D_{Mg}	1986–1995	5.66 (0.52)	1976–1985	4.93 (0.45)
3	Decades	H′	1966–1975	2.34 (0.14)	1976–1985	2.16 (0.10)
3	Decades	H′	1986–1995	2.31 (0.15)	1976–1985	2.16 (0.10)
4	Decades	D_{Mg}	1966–1975	5.18 (0.51)	1976–1985	3.62 (0.74)
4	Decades	D_{Mg}	1986–1995	4.99 (0.70)	1976–1985	3.62 (0.74)
4	Decades	1/d	1966–1975	3.95 (0.82)	1976–1985	2.77 (0.77)
4	Decades*	1/d	1966–1975	3.95 (0.82)	1986–1995	2.90 (0.79)
Calanoids						
1	GSI*	S	North GSI	13.3 (1.5)	South GSI	10.9 (0.8)
1	GSI*	D_{Mg}	North GSI	1.96 (0.24)	South GSI	1.59 (0.11)
1	GSI	1/d	Intermediate	2.82 (0.60)	North GSI	2.27 (0.48)
1	Decades	S	1986–1995	13.7 (1.3)	1976–1985	11.9 (1.4)
1	Decades*	D_{Mg}	1986–1995	2.03 (0.20)	1966–1975	1.69 (0.30)
1	Decades	D_{Mg}	1986–1995	2.03 (0.20)	1976–1985	1.72 (0.27)
2	Decades	S	1986–1995	10.3 (1.3)	1976–1985	9.0 (1.0)
2	Decades*	D_{Mg}	1986–1995	1.65 (0.15)	1966–1975	1.34 (0.16)
2	Decades	D_{Mg}	1986–1995	1.65 (0.15)	1976–1985	1.35 (0.15)
3	Decades	H′	1966–1975	1.50 (0.14)	1976–1985	1.43 (0.15)
4	Decades	S	1966–1975	10.6 (1.07)	1976–1985	7.5 (1.35)
4	Decades	S	1986–1995	9.9 (1.44)	1976–1985	7.5 (1.35)
4	Decades	D_{Mg}	1966–1975	1.55 (0.18)	1976–1985	1.17 (0.25)
4	Decades*	1/d	1966–1975	2.44 (0.41)	1986–1995	1.87 (0.42)

*, difference between extremes (North/South GSI, High/Low NAO, 1966–1975/1986–1995).

1976–1985 and the preceding or succeeding decades. There were only three cases (S, D_{Mg} and 1/d for calanoids in area 1) where the differences between groups of years classified according to GSI were significant. No differences between years grouped according to NAO values were significant. For area 4 the values were recalculated excluding the poorly sampled period 1978–1983 and the significantly different pairs are listed in Table 8. In area 4

Table 8. *Significant differences in α-diversity indices between groups of years listed in Table 1 in area 4 excluding data for 1978–1983.*

Area	Year group	Index	High group	Mean (σ)	Low group	Mean (σ)
Total						
4	Decades	D_{Mg}	1986–1995	4.99 (0.70)	1976–1985	4.21 (0.40)
4	Decades*	1/d	1966–1975	3.95 (0.82)	1986–1995	2.90 (0.79)
Calanoids						
4	Decades	S	1966–1975	10.6 (1.07)	1976–1985	8.5 (1.00)
4	Decades	D_{Mg}	1966–1975	1.55 (0.18)	1976–1985	1.12 (0.16)
4	Decades*	1/d	1966–1975	2.44 (0.41)	1986–1995	1.87 (0.42)

*, difference between extremes (North/South GSI, High/Low NAO, 1966–1975/1986–1995.

Table 9. *Numbers of species of holoplanktonic calanoid copepods and gastropods in CPR samples in North Sea six standard areas (B1–D2, see Taylor, 1995) from Edinburgh Oceanographic Laboratory (1973), recorded here as 'Atlas', and of Euphausiacea and the meroplanktonic larvae of benthic or hyperbenthic taxa from other studies.*

Standard Areas	Reference	Years	Bl	B2	C1	C2	D1	D2
Holoplankton								
Calanoida	Atlas	1958–1968	22	23	17	15	14	14
Cladocera	Atlas	1958–1968	3	3	5	5	3	5
Euphausiacea	Lindley, 1977	1966–1967	5	5	5	5	3	4
Gastropoda*	Atlas	1958–1968	3	3	3	4	2	3
Meroplankton								
Decapoda	Lindley, 1987	1981–1983	8	29	24	27	19	19
Bivalves	Rees, 1954a	1950–1951	nd	9	35	37	32	36
Echinodermata	Rees, 1954b	1947–1951	nd	13	11	12	8	10

nd, no data; *, holoplanktonic groups, Thecosomata, Gymnosomata, Heteropoda.

there was a notable depression in species richness and increase in dominance in the decade 1976–1985 that was not wholly eliminated by removal of data for the poorly sampled years and was reflected to some extent in the results for area 3.

DISCUSSION

The inflow of species associated with the warm oceanic or mixed inflow into the North Sea certainly appears to have been greater in the late 1980s and 1990s than previously (Lindley et al., 1990; Edwards et al., 1999; Corten, 2001). These biological indications are supported by hydrographic data, such as anomalously high salinities in the late 1980s and early 1990s in the Skaggerak (Danielssen et al., 1996), the Southern Bight (Laane et al., 1996) and in the northern North Sea (Heath et al., 1991) as well as the high temperatures (Table 2). Modelled flows indicate higher inflow into the northern North Sea from the west in the region of the Fair Isle passage, between the Orkney and Shetland Isles, in the late 1980s and early 1990s but decreased inflow from the Norwegian Sea east of Shetland (Stephens et al., 1998). An increase in the intensity of the shelf-edge current is implicated in an increase of Atlantic influence in the North Sea (Reid et al., 2001).

The influence of the GSI and the NAO probably cannot be separated from a general long-term trend in these data. The large proportion of northerly GSI years and high NAO years in 1986–1995 with the associated high values for temperature and colour means that any trend leading to high or low values in that period will tend to produce appropriate correlations with the GSI and NAO. However the earlier work of Taylor (1978) and Taylor & Stephens (1980) on the GSI demonstrated a link with zooplankton abundance before the concentrated mass of northerly years (1989–1995) was evident and Planque & Fromentin (1996) demonstrated relationships between the distribution of *Calanus finmarchicus* and the NAO.

The increase in species richness, particularly of calanoids, in the most northerly areas can be attributed to increased inflow, but at present the species which are increasing or adding to the numbers are not permanent components of the North Sea plankton but immigrants from warmer waters. The species of the meroplankton also constitute temporary components of the plankton, migrating from the benthos to the plankton for the pelagic phase of their life. This constitutes a significant challenge to analysis of pelagic diversity because the species richness of the groups treated in the current analysis as single taxa may exceed that of the holoplanktonic groups, as shown in Table 9. Even in the North Sea, where the fauna is well known, descriptions of larval stages are much less comprehensive than is the case with adults and identification may be problematic. The Cladocera and diaptomoid calanoids are usually considered to be holoplankton but, due to the presence of benthic

resting stages in their life history, they may be considered to be 'adult meroplankton' in comparison with the larval meroplankton (Marcus & Boero, 1998).

The importance of the larval meroplankton in the North Sea is emphasized by the abundance of echinoderm larvae, particularly in the areas 2 and 3. Lindley et al. (1995) suggested that the most likely source of the increase was the ophiuroid *Amphiura filiformis*. However, Kröncke et al. (1998) have reported that the echinoid *Echinocardium cordatum*, the most abundant species in the CPR samples in 1947–1951 (Rees, 1954b), is sensitive to low winter temperatures but dominated the benthic biomass off Norderney (Wadden Sea) after mild winters. Thatje & Gerdes (1998) found that both species were more abundant in the inner German Bight in 1995 than in earlier years. In the Northern Hemisphere, winter temperatures have shown a trend to higher values since the end of the 1960s (Jones, 1997) and the winter of 1996 was the first 'strong continental' (cold) winter in the North Sea since 1987 (Loewe, 1996).

Kröncke (1992) showed that the change in the benthos of the Dogger Bank between the early 1950s and mid 1980s included an increase in short-lived opportunistic species. This is paralleled in the plankton. In three of the four areas *Acartia* (mainly *A. clausi*) was the numerically dominant calanoid by the 1990s, replacing *Calanus* spp. and *Para-Pseudocalanus* (*Paracalanus* spp. and *Pseudocalanus* spp. combined) except in area 2 where *Acartia* has always been dominant. Colebrook (1982) showed a higher rate of population increase of *Acartia* than of *Pseudocalanus* in the spring, relating this to faster development times of the former (McLaren, 1978). It should be noted that free-spawning species such as *Acartia* tend to have a higher rate of egg production than those, like *Pseudocalanus*, that carry their eggs (Mauchline, 1998). *Calanus* spp., partly due to their relatively large size, also have longer development times than small calanoids like *Acartia* and *Temora*. However, the main centres of the populations of *C. finmarchicus* and *C. helgolandicus* in the CPR survey area are outside the North Sea (Planque & Fromentin, 1996). Maintenance of populations of these species in the North Sea is partly dependent on advection from those areas (e.g. Backhaus et al., 1994).

In the North Sea resident and colder water holoplanktonic species have declined in abundance, and meroplankton (adult and larval) and expatriates from warmer oceanic and mixed waters have increased, producing an increase in species richness at least in the northern areas. This leaves 'weight' the problem of whether the species temporarily (if regularly) in the plankton of a region can be given the same in analysis of diversity as permanent residents. Attempts to analyse the diversity of a geographical location or area are open to criticism, as the habitat of the plankton is the water mass, which is dynamic. However the meroplankton species, larval and adult, are linked to the more permanent habitats of the benthic phases of their life cycle.

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