Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data

Sophie G. Pitois and Clive J. Fox

Data from the Continuous Plankton Recorder (CPR) survey over the past 40 years have shown that the abundance of copepods in many parts of the North Atlantic has declined, indicating geographical shifts in the plankton communities. Because the CPR does not sample all zooplankton species with equal efficiency, these observations may give a biased view of the overall changes. Here, we compensate for CPR undersampling by using previously published species-specific correction factors derived from comparisons of catches made with WP-2 ring-nets and the CPR. Based on such corrected data, the southern North Sea showed the highest concentrations of biomass, in contrast to maps based on uncorrected data, in which the areas of highest biomass were in the northern North Sea. Trend analysis confirmed the previously reported general decrease of total biomass. There has also been a general decrease in the mean size of zooplankton over time in the northern North Sea, but this has not been observed elsewhere. The results indicate the importance of smaller zooplankton species in the ecology of the Northwest European shelf. The changes in community structure may have general implications for energy transfer efficiency to higher trophic levels, and for the sustainability of fisheries resources.

S. G. Pitois and C. J. Fox: The Centre for Environment, Fisheries and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 OHT, England, UK. Correspondence to S. G. Pitois: tel: +44 1502 527785; fax: +44 1502 513865; e-mail: s.g.pitois@cefas.co.uk.

Introduction

Many studies on long-term changes in zooplankton abundance and species composition for the European shelf seas have been based upon data collected by the Continuous Plankton Recorder (CPR). The CPR consists of a towed body which is deployed from ships of opportunity along commercial routes. Great efforts have been made to preserve consistency in CPR sampling and in the analysis of the collected samples. For these reasons, the CPR provides a unique marine ecological time-series, particularly for the Northwest European shelf. Although providing excellent spatial and temporal coverage, the CPR has characteristics that potentially restrict the use of the data. In particular, the sampler is towed at a fixed depth of about 10 m, has a small mouth opening, and carries silk with a mesh of 270 μm (Batten *et al.*, 2003). Because of these factors, the sampler does not collect the full range of planktonic organisms with equal efficiency, and most analyses to date have used CPR data to provide relative indices of abundance. There is,

however, an urgent need to better understand marine ecosystem functioning, and in particular how climate change may affect primary and secondary production. Such climate-induced change may impact ecosystem functioning, by cascading up the foodweb to higher trophic levels, including fish. Uncovering these links is particularly pressing because fish stocks at low levels of biomass may be particularly sensitive to environmental change, perhaps compromising plans for stock recovery (Brander, 2005).

For the European shelf seas, investigating these links has largely been undertaken by deriving correlations between fisheries data, environmental time-series, and CPR-derived indices, an approach that has been criticized as unreliable and potentially misleading (Beverton and Lee, 1965; Aebischer *et al.*, 1990; Svendsen *et al.*, 1995; Myers, 1998; O'Brien *et al.*, 2000; Heath, 2005). There is clearly a need to move beyond such studies towards better mechanistic understanding, in order to untangle the drivers affecting stock sustainability, to aid the design of realistic stock recovery plans, and to be able to evaluate claims that

natural changes, as opposed to fishing, are responsible for stock collapse (Beaugrand *et al.*, 2003a; Clark *et al.*, 2003; Schiermeier, 2004). Such a move will require data to be collected on absolute zooplankton abundance and biomass in order to develop and test models of fish early life-stage survival, as has been done on Georges Bank and elsewhere (Hermann *et al.*, 2001; Lynch *et al.*, 2001).

Observations of recent geographic shifts in North Atlantic plankton communities along with some significant correlations with fisheries recruitment data suggest that abundance, timing of production, size, and possibly quality of fish larval prey may be key influences (Cushing, 1990; Mertz and Myers, 1994; Beaugrand *et al.*, 2003a). It is difficult to deal with all these factors in models, but focusing on prey size may provide a way to summarize complex planktonic communities (Bremigan and Stein, 1994). The availability of prey of suitable size coincident with the needs of the developing pre-recruiting fish may be a significant factor determining recruitment success (Pearre, 1986; Astthorsson and Gislason, 1995; Munk, 1997; Pepin and Penney, 1997). Moreover, the distribution of plankton sizes is a fundamental determinant of energy transfer efficiency in marine ecosystems, and may determine the overall biomass of higher trophic levels that can be supported in different systems or system-states (Sheldon *et al.*, 1972; Thiebaux and Dickie, 1993).

Unfortunately the CPR is known to underestimate zooplankton abundance, compared with other data sets, and the sampler does not collect quantitative information on phytoplankton and micro-zooplankton other than the colour index and counts of some selected taxa (Batten *et al.*, 2003). On the other hand, the CPR is the only long-term data set covering the offshore European shelf, so it seems worthwhile to examine the impact of applying published correction factors to investigate long-term changes in the distribution of zooplankton sizes for the region. In particular, we were interested in testing whether the well publicized decline in total copepod abundance over the past four decades (Colebrook *et al.*, 1984) has in fact resulted in a uniform decrease in biomass of all size classes over the whole region, or whether there are regional differences that might impact the ecology of the different regions.

Material and methods

Sampling and species and area selection

The Continuous Plankton Recorder (CPR) survey has now been running for more than 70 years, and has provided one of the longest and most extensive ecological time-series in the world, providing a unique source of long-term, large-scale information covering more than 300 species of zooplankton in the North Atlantic (Beare *et al.*, 2003; Reid *et al.*, 2003a). The CPR is towed by "ships of opportunity" at speeds of 15−20 knots and at an approximate depth of 10 m. Water enters the recorder through a square aperture of 1.62 cm^2, and is filtered through a continuously moving band of silk with an average mesh size of 270 μm. The plankton organisms

are covered by a second band of silk, and this double band is wound into a storage tank containing formalin. When returned to the laboratory for processing, the roll of silk is unwound and divided in sections representing 10 nautical miles (18.52 km) of tow, equivalent to about 3 m^3 of filtered seawater. Methods of counting and data processing are described by Colebrook (1975) and Batten *et al.* (2003).

Information on the abundance of copepods and cladocerans (a total of 60 taxa) was extracted from the CPR database for the period 1958−2003 and covering the area delimited by latitudes 45−63°N and longitudes 15°W−10°E. This area was subdivided into five smaller areas of study on the basis of biogeography: northern North Sea, southern North Sea, western Channel and Celtic Sea, Irish Sea and west of Ireland, northwest of Scotland (Figure 1). Copepods and cladocerans were selected because they are important prey for many fish larvae, and identification in CPR samples is generally carried out to species or genus level for these groups (in some other taxonomic groups, identification is limited to family or higher categories). Out of the original 60 species, only those contributing at least 0.1% of total biomass in at least one of the five subareas were kept, resulting in data on 29 key species being retained, accounting for >99% of total biomass (Table 1).

Abundance to biomass conversion

Raw CPR data are supplied as estimates of organism abundance per 3 m^3, based on subsampling analysis of silk lengths corresponding to tow lengths of 10 nautical miles (Colebrook, 1975; Batten *et al.*, 2003). In order to convert abundances to biomass, we used two different methods, one for copepods and one for cladocerans. For copepods, we calculated average lengths and widths of prosome and urosome based on sizes extracted from the literature (Sars, 1903; Rose, 1933; Massuti and Margalef, 1950) and ICES Identification Leaflets for Plankton (www.ices.dk/products/fiche/Plankton/START.PDF). Average lengths and widths of females were used as representative measures of the corresponding species, because females constitute the majority of copepod species identified by the CPR (Richardson *et al.*, 2006). Individual volumes for copepod species were calculated by approximating the body shape of a copepod as an ellipsoid for the prosome and a cylinder for the urosome, from Equation (1); volumes were then converted to wet weights by application of a specific gravity factor of 1.025 (Chojnacki, 1983), and the wet weights were converted to dry weights using a factor of 0.2 (Postel *et al.*, 2000):

$$V_{copepod} = \frac{\pi w_p^2 l_p}{6} + \frac{\pi w_u^2 l_u}{4}, \qquad (1)$$

where V is the body volume, w_p the prosome width, w_u the urosome width, l_p the prosome length, and l_u is the urosome length.

Because the volume of cladocerans cannot be approximated to an ellipsoid with equal semi-minor axis, and because we could not extract from the literature all the
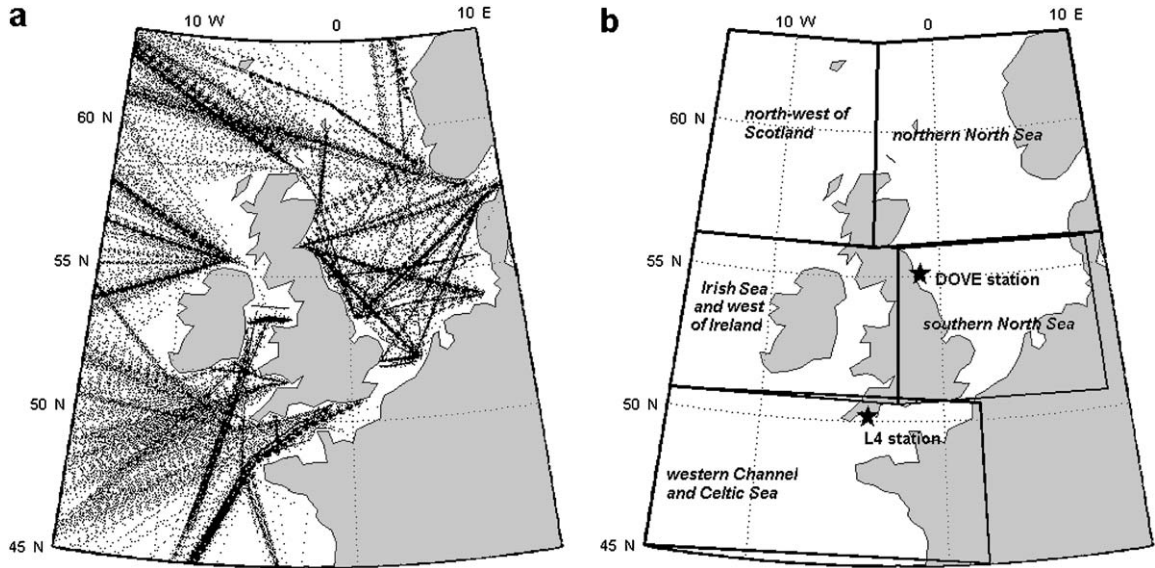
Figure 1. (a) Continuous Plankton Recorder (CPR) sample distribution and density (100 323 samples) within our area of study during the period 1958–2003. (b) Subdivisions to five smaller areas: northern North Sea, 56–63°N, 4°W–10°E; southern North Sea, 50°40′–56°N, 2°30′W–9°E; western Channel and Celtic Sea, 45–50°40′N, 15°W–2°E; Irish Sea and west of Ireland, 50°40′–56°N, 15–2°30′W; northwest of Scotland, 56–63°N, 15–4°W. The locations of the Dove Marine Laboratory Station (55°07′N, 1°20′W) and Station L4 (50°15′N, 4°13′W) are also shown.

necessary information regarding cladoceran morphometrics, we chose to apply a length–weight regression equation (Rose *et al.*, 2004) to obtain their individual dry weight:

$$\log_{10}(\text{DW}) = 1.05 \ \log_{10}(L) - 2.59, \tag{2}$$

where DW is the organism dry weight in mg, and L is the body length in mm. The results obtained from Equation (2) are similar to the dry weight values used by Hay *et al.* (1991), Walve and Larsson (1999), and J. A. Lindley (SAHFOS, pers. comm.).

Conversion of individual abundance data to total biomass for a species/taxa followed:

$$\text{Biomass}\,(\text{mg m}^{-3})$$
$$= \frac{\text{Dry weight}(\text{mg}) \times \text{Abundance (number/3 m}^3)}{3}. \tag{3}$$

Correction factors: WP-2/CPR ratios

Correction factors for undersampling by the CPR were obtained from published studies on the comparison of CPR data with results from fixed sampling stations, namely by the Dove Marine Laboratory station off the NE English coast (Clark *et al.*, 2001) and the L4 station off Plymouth, UK (John *et al.*, 2001; Figure 1b). Sampling at these sites was undertaken using vertically integrated hauls from approximately 50 m to the surface with 200-μm WP-2 nets; such nets are assumed to be 100% efficient for organisms of the same size range captured by the CPR. Substantial differences in absolute organism abundances were found when comparing records from the CPR with either the L4 or the Dove series; these are the result of three factors: the difference in mesh size, the fact that the CPR collects surface samples at 10 m covering a wide area whereas the WP-2 samples the entire water column but from a single site, and avoidance of the CPR compared with WP-2 nets. However, in each area (i.e. North Sea and English Channel), the overall long-term changes and seasonal cycles recorded by the two devices were similar (Batten *et al.*, 2003). Clark *et al.* (2001) and John *et al.* (2001) calculated ratios of abundance between the WP-2 and CPR samples for the main species in the North Sea and the English Channel, respectively. From these we calculated a mean ratio from each available species, although we acknowledge that such ratios are a crude approximation, because we assume that the two WP-2 stations are representative of the entire area at any given time.

Unfortunately, WP-2/CPR ratios were not available for all species selected in this study. We therefore used the relationship between WP-2/CPR ratios and dry weight for existing data in order to extract the missing correction factors.

$$\text{CF} = 3.8 \ \log_{10}(\text{DW})^2 + 2.2\text{DW} + 2.2, \tag{4}$$

where CF is the expected WP-2/CPR ratio (i.e. the correction factor), and DW is the organism dry weight in mg.

Data analysis

The CPR survey collects samples at different times of day and at locations that do not follow a regular grid. The data therefore need to be spatially interpolated and regularized in time and space before being subjected to numerical analyses (Beare

Table 1. List of species contributing to at least 0.1% of the total biomass in at least one of the five subareas. Species are listed in increasing dry weight, and the composition of the five size groups is also given. Correction factors were calculated from comparative studies in the North Sea (Clark *et al.*, 2001) and English Channel (John *et al.*, 2001). An asterisk indicates a missing value that was calculated from the relationship between available WP-2/CPR ratios and zooplankton dry weights.

Species in increasing order of size	Dry weight (mg)	Correction factor (mean WP-2/CPR ratio)	Group
Evadne spp.	0.0018	18.2	G1
Oithona spp.	0.0022	45.4	
Penilia spp.	0.0034	20.1[*]	
Podon spp.	0.0036	5.1	
Para-Pseudocalanus spp.	0.0042	13.9	
Corycaeus spp.	0.062	26.8	G2
Acartia spp.	0.0082	8.7	
Clausocalanus spp.	0.0106	10.3	
Pseudocalanus elongatus	0.0109	11.6	
Metridia I−IV	0.0124	20.0	
Temora longicornis	0.0126	18.3	
Calanus I−IV	0.013	2.4	
Isias clavipe	0.0134	11.6[*]	
Centropages hamatus	0.0147	1.7	
Candacia I−IV	0.0237	8.8[*]	G3
Centropages typicus	0.036	1.7	
Calanoides carinatus	0.0533	5.7[*]	
Metridia lucens	0.0623	20.0	
Euchaeta hebes	0.0798	4.5[*]	
Candacia armata	0.1062	3.8[*]	
Calanus helgolandicus	0.1096	2.4	
Pleuromamma robusta	0.1877	2.7[*]	G4
Euchaeta acuta	0.2372	2.4[*]	
Euchirella rostrata	0.3045	2.1[*]	
Eucalanus crassus	0.3055	2.1[*]	
Calanus finmarchicus	0.3192	2.4	
Undeuchaeta plumosa	0.3281	2.1[*]	
Euchaeta norvegica	2.8411	2.4[*]	G5
Calanus hyperboreus	2.85	2.4	

et al., 2003). This was undertaken on a 50 × 50 nautical mile (92.6 × 92.6 km) grid using Inverse Distance Interpolation (Lam, 1983; Legendre and Legendre, 1998). We used a search radius of 150 miles (i.e. 277.8 km), and a minimum and maximum number of neighbours of 5 and 100, respectively. These values were chosen as a compromise between numerical efficiency and the need to keep the number of missing values in the interpolated grid to a minimum. CPR data also show major seasonal and diel patterns (Beare *et al.*, 2003; Beaugrand *et al.*, 2003b), and these were taken into account when calculating annual values of biomass. The procedure used was adapted from Beaugrand *et al.* (2000b, 2001). The 100 323 CPR samples covering the European shelf over the period 1958−2003 were grouped into day and night periods for

each month and year; day/night periods were defined from calculation of sun zenith angle at each sampling location. Spatial interpolation was performed for each month for both day and night, resulting in 24 matrices per year that were then combined to produce 46 annual matrices covering the period 1958−2003. These resulting tables were averaged over 10-year periods to produce decadal maps of both corrected and uncorrected biomass distributions.

In order to characterize the trends in annual biomass over the past four decades for each area, the data were smoothed using a moving average with a five-year window (Legendre and Legendre, 1998). Trend analysis was performed on single species in each area, and on species groups defined according to linear size classes. The 29 species identified as major contributors to biomass were divided into five size groups, labelled G1−G5 in increasing size order (Table 1). The trends in annual mean individual weight of the organisms in each of the studied subareas were also calculated as

$$\text{Mean weight} = \overline{W} = \frac{\sum_{i=1}^{29} w_i n_i}{\sum_{i=1}^{29} n_i} = \frac{\sum_{i=1}^{29} b_i}{\sum_{i=1}^{29} n_i}, \tag{5}$$

where w_i and n_i are the dry weight and abundance of species i, respectively, and b_i is the biomass of species i.

Results

General patterns in zooplankton distribution

Based on CPR data uncorrected for undersampling, the highest biomass concentrations were found on the Norwegian shelf (Figure 2). However, this area has not been sampled in recent years by the CPR because of changes in the availability of ships of opportunity. Uncorrected maps suggest an overall decline in total biomass of key copepod and cladoceran species over the European shelf over the period 1960−1999, but the application of undersampling correction factors has a substantial impact on the distribution patterns observed. Applying undersampling corrections shifts the area of highest biomass concentration from the northern North Sea to the southern North Sea, and to a lesser extent to the Irish Sea and west of Ireland, and northwest of Scotland. However, the Irish Sea and west of Ireland is not particularly well sampled by the CPR. Again the overall impression is of a general decline in total average biomass concentration across the whole region over the past four decades, but the decline may be greater in some areas than in others.

The overall trends (Table 2) were not affected by application of undersampling correction factors, which only scale one species relative to another. While many species showed an overall decline, there were notable exceptions. For instance, *Temora longicornis*, *Centropages typicus*, *Calanus helgolandicus*, and *Podon* spp. have all increased. The use of correction factors changed the order of species in terms of their relative biomass contributions, as shown
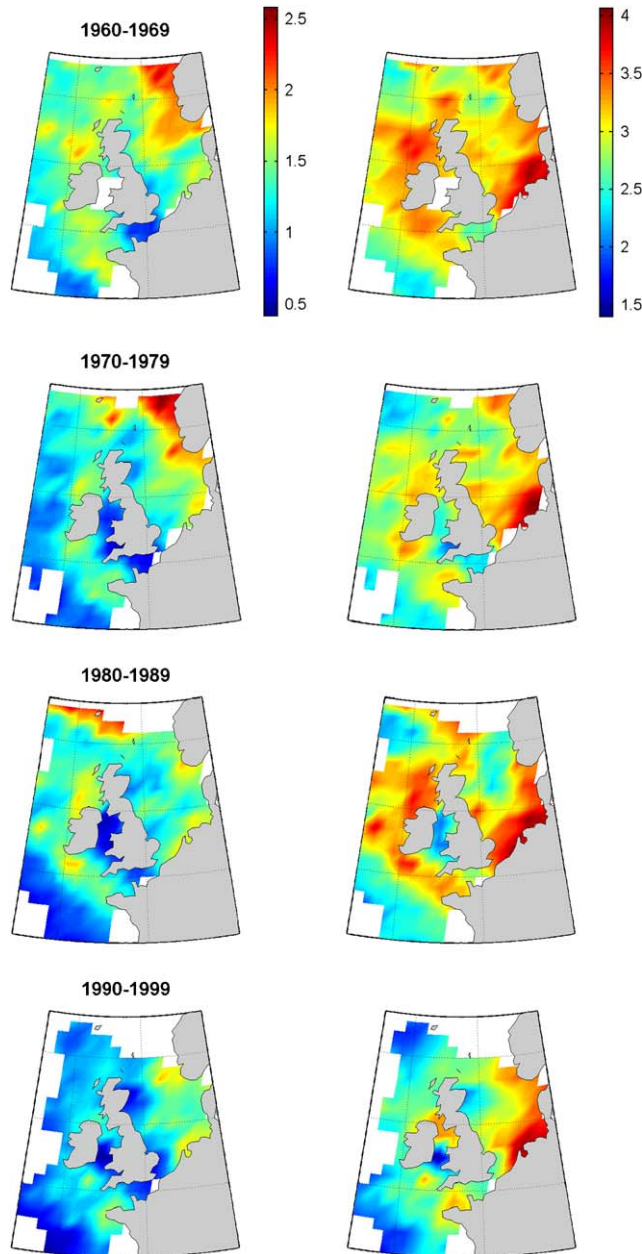
Figure 2. Decadal spatial distribution of total biomass concentration $(mg\,m^{-3})$ as $\log_{10}(x+1)$, based on the 29 major species/taxa of copepods and cladocerans recorded in the CPR for the northwestern European shelf. Maps were created using inverse square distance interpolation (see Material and methods). Left column, CPR data not corrected for undersampling; right column, CPR data corrected using species-specific WP-2/CPR ratios (see Material and methods).

in Table 3, with undersampled species gaining importance at the expense of well-sampled ones.

Trends in biomass

All five areas of study experienced a decline in total biomass concentration during the period 1958−2003 (Figure 3), and the application of undersampling correction factors increased the slope of the biomass evolution trend. This effect varies in amplitude in each area, and is the strongest in the western Channel and Celtic Sea, Irish Sea and west of Ireland, and northwest of Scotland. When no correction factor is applied, the northern North Sea undergoes the steepest biomass decrease, followed by the Irish Sea and west of Ireland, northwest of Scotland, the southern North Sea, and the western Channel and Celtic Sea. After application of

Table 2. Overall trend in biomass concentration over the entire 45 years of study: D = declining, I = increasing, C = constant, — indicates biomass contribution of <0.1%. The group number in parenthesis indicates size grouping to which that species/taxon was assigned. An asterisk indicates the main subareas in which the species/taxa was found.

Species/taxon	Entire region	Northern North Sea	Southern North Sea	Western Channel and Celtic Sea	Irish Sea and west of Ireland	Northwest of Scotland
Calanus finmarchicus (4)	D	D*	D	C	D	D*
Acartia spp. (2)	D	I*	C	C	D*	D*
Centropages typicus (3)	I	I	C	D*	C	I
Calanus I–IV (2)	D	D*	D	C	D	C*
Para-Pseudocalanus spp. (1)	C	C	D*	C*	D*	I
Podon spp. (1)	I	I*	I*	I	C	I
Temora longicornis (2)	I	I	I*	C	C	C
Calanus helgolandicus (3)	I	I	I	C*	C*	I
Pseudocalanus elongatus (2)	D	C	D*	D	D*	I*
Evadne spp. (1)	C	I*	D*	C	C	C
Euchaeta norvegica (5)	D	D	—	D	D	D*
Oithona spp. (1)	D	D*	D*	C*	D*	D*
Metridia lucens (3)	D	C	C	C*	D*	D
Centropages hamatus (2)	C	C	C*	D	C	C
Clausocalanus spp. (2)	I	C	C	I*	C	C
Calanus hyperboreus (5)	D	D	—	—	—	D*
Pleuromamma robusta (4)	D	—	—	D	D	D
Corycaeus spp. (2)	I	—	I*	C*	C	—
Penilia spp. (1)	I	I*	I*	—	—	—
Candacia armata (3)	—	I	—	C*	D*	—
Euchirella rostrata (4)	—	—	—	C*	—	—
Candacia I–IV (3)	—	—	—	C*	D	—
Metridia I–IV (2)	—	—	—	C*	D	D
Euchaeta hebes (3)	—	—	—	C*	I	—
Calanoides carinatus (3)	—	—	—	D*	—	—
Undeuchaeta plumosa (4)	—	—	—	C*	—	—
Euchaeta acuta (4)	—	—	—	I*	—	—
Isias clavipe (2)	—	—	C*	—	—	—
Eucalanus crassus (4)	—	—	—	C*	—*	—

correction factors, the Irish Sea and west of Ireland undergoes the steepest biomass decrease, followed by northwest of Scotland, the northern North Sea, the western Channel and Celtic Sea, and the southern North Sea. Overall, this implies a reorganization of the zooplankton communities that is specific to each area. Results from Table 2 further indicate that temperate species (e.g. *Centropages typicus*, *Podon* spp., *Para-Pseudocalanus* spp., *Calanus helgolandicus*, *Pseudocalanus elongatus*, and *Evadne* spp.) have spread northwards, and that boreal species (i.e. *Calanus finmarchicus* and *Euchaeta norvegica*) have declined.

Changes in biomass per size group

When plotting the evolution of total mean annual biomass by organism size group (Figure 4), the correction factors act as scaling, so both corrected and uncorrected plots were almost identical as a result. For this reason, we have only included plots corrected for undersampling. The smallest species/taxa considered (Group 1, G1) declined in all areas except the most northern ones (the northern

North Sea and northwest of Scotland). The relative biomass contribution shifted from the southern North Sea, which was the dominant area until 1980, to a more equal partitioning among the five subareas. Group 2 (G2) species declined everywhere except in the northern and southern North Sea. Group 3 (G3) species increased in the northern North Sea, but remained fairly constant in the southern North Sea, the western Channel and Celtic Sea, and northwest of Scotland, and decreased in the Irish Sea and west of Ireland. Group 4 (G4) species decreased in all regions except in the western Channel and Celtic Sea, and Group 5 (G5) species decreased everywhere; these boreal species (*Calanus hyperboreus* and *Euchaeta norvegica*) are still mostly located off the northwest of Scotland.

Around 1980, there was a sudden decline in total biomass of G1 and G2 species in all areas except the Irish Sea and west of Ireland for G2 species. G3 species also declined in the North Sea and in the western Channel and Celtic Sea then, but they increased in the Irish Sea and west of Ireland and northwest of Scotland. G4 species declined in the northern North Sea. When looking at individual species, the sharp

Table 3. Rank of species in each area in term of relative biomass over the entire 45 years of study, without (U) and with use of under-sampling correction factors (C). — indicates species/taxon for which the biomass contribution is too low for them to be ranked.

Species/taxon	Entire region		Northern North Sea		Southern North Sea		Western Channel and Celtic Sea		Irish Sea and west of Ireland		Northwest of Scotland	
	U	C	U	C	U	C	U	C	U	C	U	C
Calanus finmarchicus (4)	1	4	1	1	3	6	9	13	2	7	1	2
Acartia spp. (2)	2	1	3	3	2	2	3	2	1	1	2	1
Centropages typicus (3)	3	8	4	10	4	8	1	6	4	10	6	11
Calanus I−IV (2)	4	7	2	7	6	9	5	10	6	9	3	5
Para-Pseudocalanus spp. (1)	5	3	5	4	5	3	4	1	5	2	5	4
Temora longicornis (2)	6	2	6	2	1	1	7	3	8	4	9	8
Calanus helgolandicus (3)	7	11	8	11	8	11	2	7	3	8	8	12
Pseudocalanus elongatus (2)	8	5	7	5	7	4	6	5	7	3	7	9
Euchaeta norvegica (5)	9	14	9	13	—	—	12	15	10	14	4	6
Oithona spp. (1)	10	6	11	6	11	5	11	4	11	5	11	3
Metridia lucens (3)	11	9	12	9	—	14	10	9	9	6	10	7
Evadne spp. (1)	12	10	10	8	10	7	16	12	12	11	12	10
Centropages hamatus (2)	13	17	14	15	9	13	14	19	13	19	—	—
Clausocalanus spp. (2)	14	12	—	—	—	—	8	8	16	13	—	17
Podon spp. (1)	15	15	13	12	12	12	13	14	14	16	13	14
Calanus hyperboreus (5)	16	18	15	16	—	—	—	23	—	—	15	16
Pleuromamma robusta (4)	17	—	—	—	—	—	15	16	15	17	14	15
Corycaeus spp. (2)	18	13	—	14	13	10	17	11	20	15	—	—
Candacia armata (3)	19	—	—	—	—	—	21	20	18	—	—	—
Euchirella rostrata (4)	20	—	—	—	—	—	18	22	—	—	—	—
Penilia spp. (1)	—	—	—	17	13	16	—	—	—	—	—	—
Candacia I−IV (3)	—	—	—	—	—	—	20	18	19	18	—	—
Metridia I−IV (2)	—	17	—	—	—	—	25	15	17	12	16	13
Euchaeta hebes (3)	—	16	—	—	—	—	19	17	—	—	—	—
Calanoides carinatus (3)	—	—	—	—	—	—	24	19	—	—	—	—
Undeuchaeta plumosa (4)	—	—	—	—	—	—	22	21	—	—	—	—
Euchaeta acuta (4)	—	—	—	—	—	—	23	—	—	—	—	—
Isias clavipe (2)	—	—	—	—	14	15	—	—	—	—	—	—
Eucalanus crassus (4)	—	—	—	—	—	—	26	—	—	—	—	—

decline of biomass around 1980 is also seen for a majority. Following this sharp decline there was a recovery of biomass in the mid to late 1980s to the early 1990s, visible for G1 and G2 species, and to a lesser extent for G3 species; this second event can also be seen for most individual species. Both these events seem to affect smaller species more than larger ones; they have been reported and studied by other authors, and are discussed later. From the 1990s onwards, G1 and G2 species have declined in all areas except northwest of Scotland, while G3 species have increased in the North Sea and western Channel and Celtic Sea, but remained stable in the Irish Sea and west of Ireland, and northwest of Scotland. G4 and G5 species seem to have remained very low.

Evolution of mean size of organisms per area

Patterns of change of average organism mean dry weight over time (Figure 5) differed among regions as a result of the reorganization within the zooplankton communities. In the northern North Sea, average individual dry weight

dropped sharply in the 1980s, to reach a minimum in the early 1990s, but has recovered somewhat since. While the decline in abundance of *Calanus finmarchicus* ceased in the 1990s, the abundance of other smaller species has been increasing (i.e. G3 species), so leading to an overall decrease in individual mean dry weight. A similar pattern was seen in the western Channel and Celtic Sea, but the dramatic decline in the northern North Sea in the 1980s was not so acute in the western Channel and Celtic Sea. In the southern North Sea and in the Irish Sea and west of Ireland, there was a sudden increase in dry weight in the late 1970s, followed by a sharp drop in the early 1980s, attributable to a combination of declining biomass of smallest species with an increasing biomass of aver-age-sized species. The southern North Sea is traditionally thought of as being dominated by smaller species. In the late 1970s, smaller species (G1 and G2) decreased, and G4 and G5 species briefly increased in the southern North Sea (hence the peak of average dry weight). Since the 1990s, there has been a decline in some of the smallest
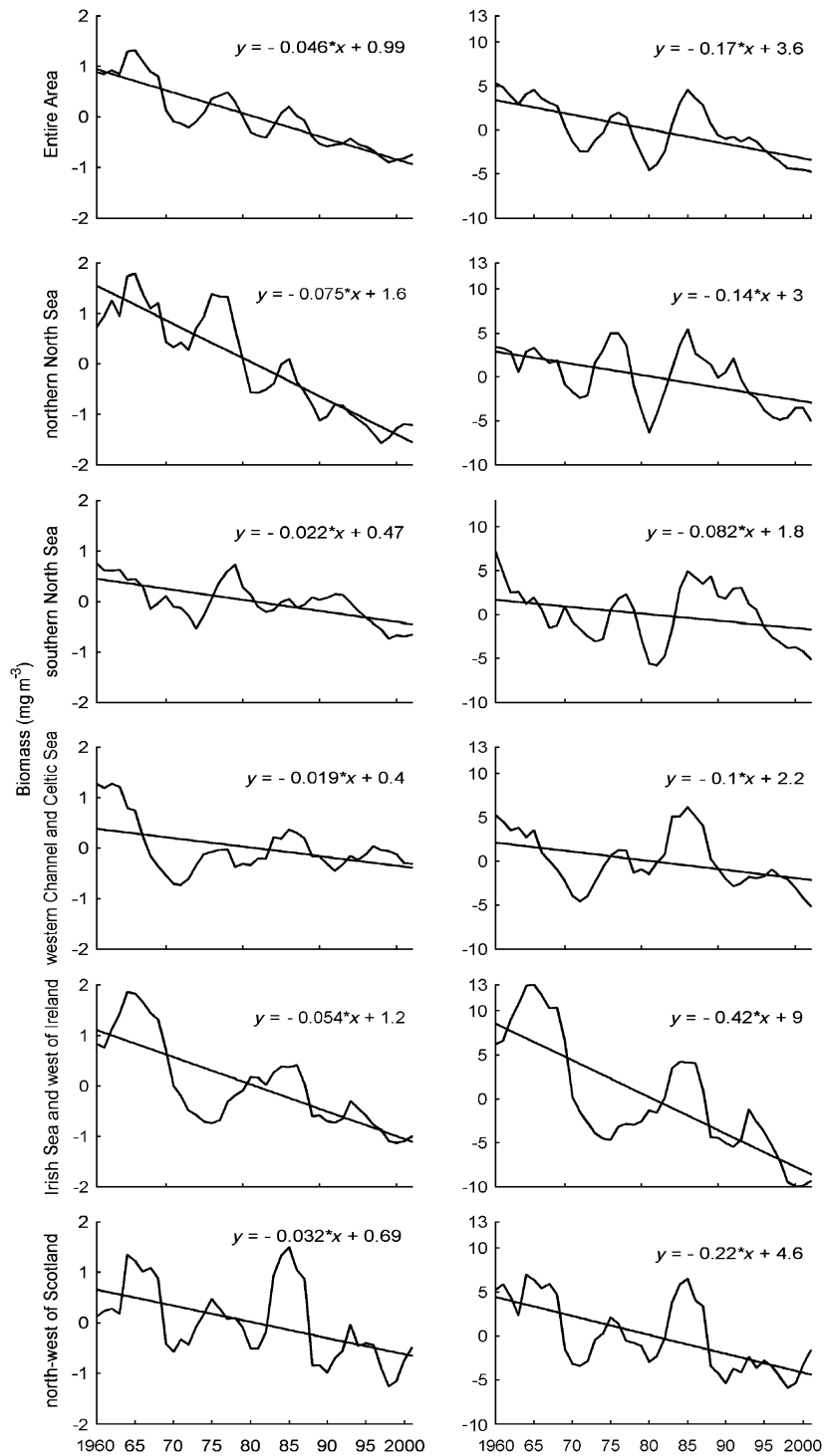
Figure 3. Evolution of annual average biomass concentration (mg m^{-3}) trend anomalies for 29 major species/taxa of copepods and cladocerans over the entire area and each of the five subareas. Annual average values were smoothed using a 5-year running window, so the smoothed results over the period 1960−2001 are shown. Plots for uncorrected biomass values are displayed on the left side, and plots for corrected biomass values on the right side.
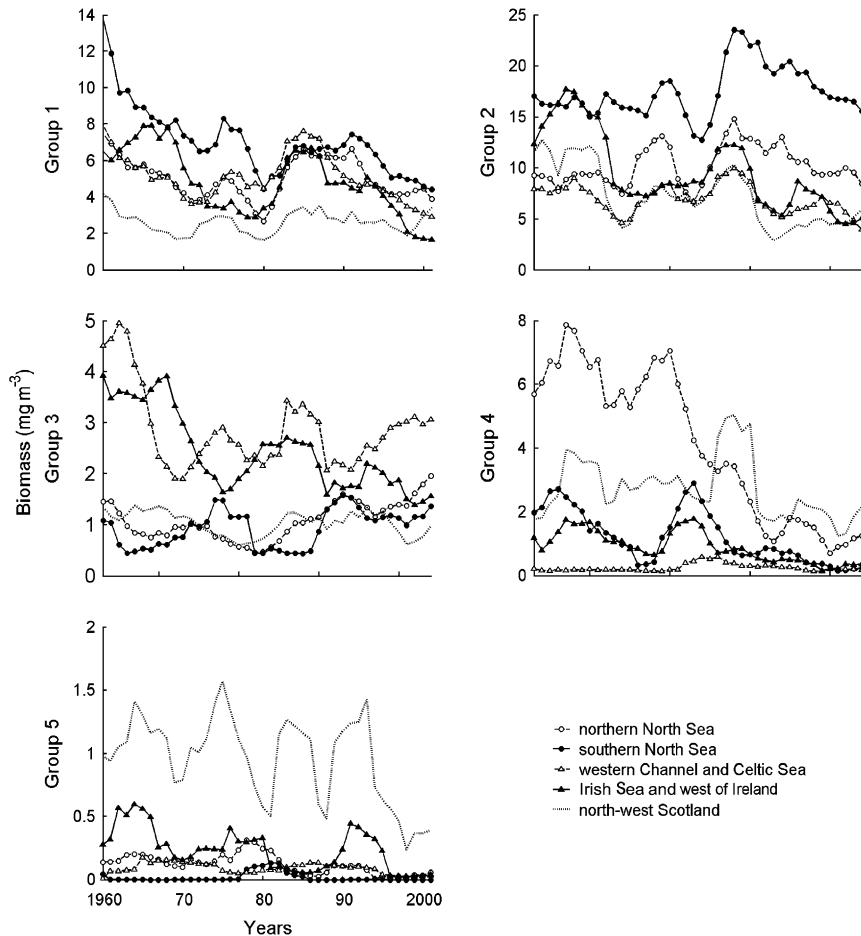
Figure 4. Evolution of average annual biomass concentration (mg m^{-3}) based on CPR data corrected for undersampling by size group of species in each of the five subareas. Annual average values were smoothed using a 5-year running window, so smoothed results over the period 1960−2001 are shown.

species (G1 and G2), while medium-sized species from G3 and G4 have either remained constant or even increased slightly. This also explains the upward trend in mean individual dry weight, which is emphasized when WP-2/CPR correction ratios were applied. The same could be said for the Irish Sea and west of Ireland. Northwest of Scotland, a sudden drop in mean dry weight can be seen from the 1990s on, owing to the decline in G5 species.

The northern North Sea and northwest of Scotland are the only subareas that showed an overall decrease in mean individual dry weight, probably a consequence of the steady decline of *Calanus finmarchicus*, the dominant species in that area until the 1980s in the northern North Sea, and G5 species off the northwest of Scotland. The trend in mean dry weight remained rather constant in the western Channel and Celtic Sea, and the Irish Sea and west of Ireland, while it was positive in the southern North Sea. This can probably be explained by the decline in smaller species (G1 and G2), combined with rather constant

levels of G3 species and the persistent low levels of G5 species, although G4 species did increase too. Again, the use of the WP-2/CPR correction factor modifies the shape of the plots as well as the slope of the general trend, according to whether smaller or larger species are most affected by the changes.

Discussion

The general decline in abundance of key species of zooplankton on the European shelf over the period 1958−2003 has been noted by many authors (Colebrook *et al.*, 1984; Lindley *et al.*, 1995; Reid *et al.*, 1998; Reid and Edwards, 2001). At the same time, there is evidence of structural changes within the zooplankton communities, particularly around the 1980s and early 1990s (Lindley *et al.*, 1995; Beaugrand, 2003, 2004b). Community changes have also been observed in the benthos of the North Sea (Austen *et al.*, 1991; Lindley *et al.*, 1995). Correction of
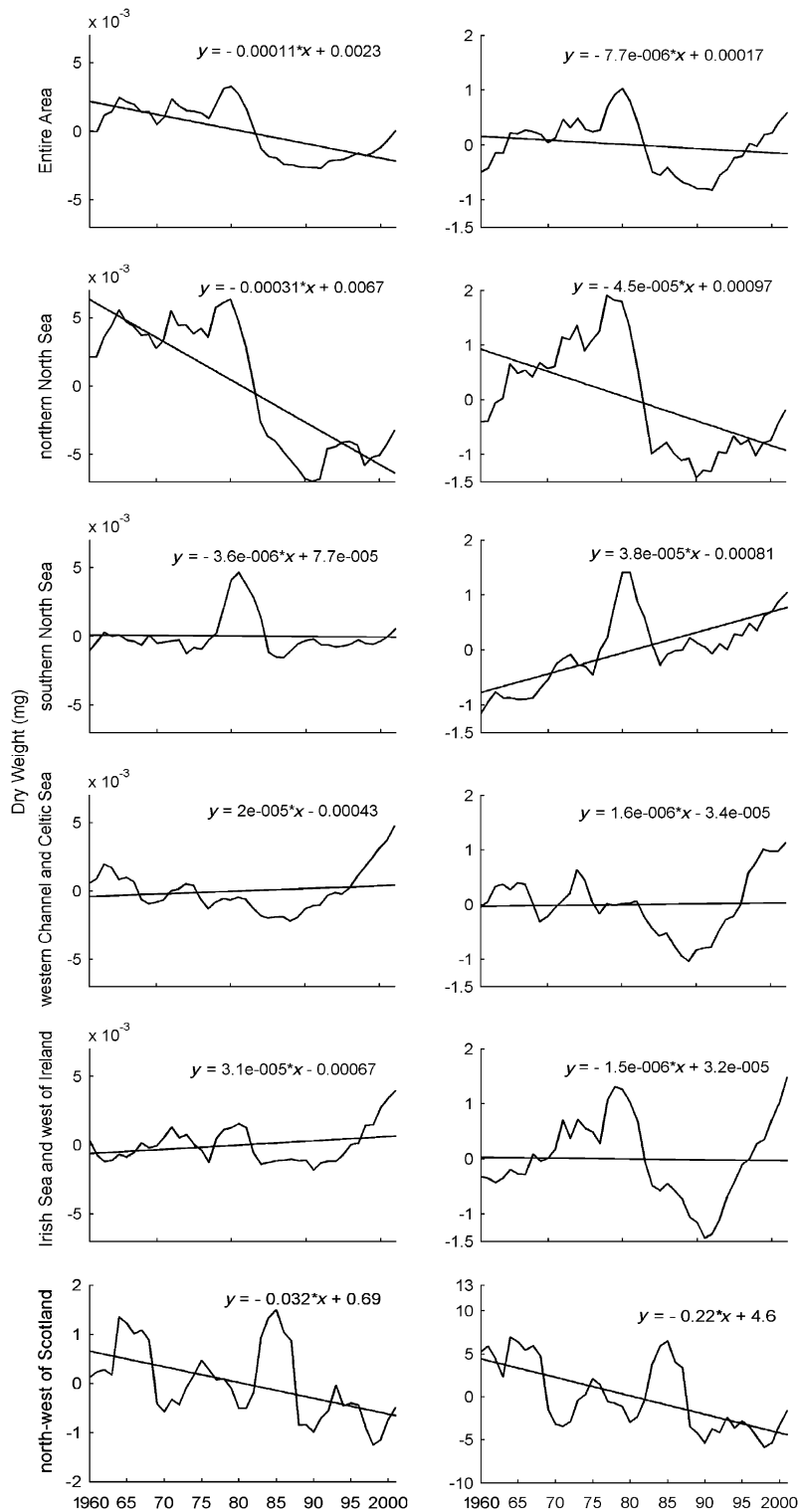
Figure 5. Evolution of the annual mean individual dry weight (mg) in the entire area and each of the five subareas. Data covering the period 1958–2003 were smoothed using a 5-year running window, so smoothed results over the period 1960–2001 are shown.

general biomass distribution for CPR undersampling results in a dramatic change to the areas of greatest concentration, which shifted from the northern North Sea to the southern North Sea. This is because species that are less well sampled by the CPR (i.e. those with the highest WP-2/CPR abundance ratios) often happen to be the smaller ones which, as Krause and Martens (1990) also stated, are also more abundant in the southern part of the North Sea.

The many changes in biological composition observed at the end of the 1980s and that persisted throughout the 1990s have been of a sufficiently large scale to be referred to as a regime shift (Reid *et al.*, 2001a; Beaugrand, 2004b). The regime shift that occurred in the northeastern Atlantic, and in particular in the North Sea, represents dramatic changes in abundances and species composition, from phytoplankton to fish, and reflects a shift in the ecosystem towards a warmer dynamic equilibrium (Reid and Edwards, 2001; Beaugrand *et al.*, 2002; Beaugrand, 2004a; Beaugrand and Ibañez, 2004). Various factors have been hypothesized to be responsible, including climate drivers (Planque and Taylor, 1998; Reid *et al.*, 1998; Ottersen *et al.*, 2001), changes in circulation (Reid *et al.*, 2001b, 2002, 2003b), and fisheries impacts (Reid *et al.*, 2000). Many other studies have established relationships between plankton and hydroclimatic variables in the North Atlantic Ocean (Colebrook, 1991; Frid and Huliselan, 1996; Fromentin and Planque, 1996; Beaugrand *et al.*, 2000a; Planque and Batten, 2000; Edwards *et al.*, 2002), but the mechanisms underlying such relationships, as well as the processes linking successive trophic levels within the marine ecosystem, are complex and not yet well understood (Richardson and Schoeman, 2004).

Our analysis suggests that the decreases in the early 1980s followed by the subsequent partial recovery have affected most species. Copepod species with an affinity for cold water (e.g. *Euchaeta norvegica*, *Calanus hyperboreus*, and *Calanus finmarchicus*) tend to be larger than temperate species (e.g. *Centropages typicus*, *Podon* spp., *Para-Pseudocalanus* spp., *Calanus helgolandicus*, *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp., and *Evadne* spp.), and it has been suggested that the larger species might provide more suitable prey for pre-recruit stages of fish such as cod (Sundby, 2000; Beaugrand *et al.*, 2003a). This study shows that reorganization within zooplankton communities is also seen through changes in mean size, in particular a maximum reached in the early 1980s coinciding with the cold episodic event, followed by a sudden drop in the late 1980s and early 1990s coinciding with the warm episodic event, and then some recovery (Figure 5). This is in agreement with the suggestion by Beaugrand *et al.* (2003a) that the decline in the mean size of calanoid copepods is a probable consequence of major changes in the community structure of calanoid copepods in the Northeast Atlantic, changes attributed to increasing temperature, and hydrographic changes. The increase of mean size since the late 1990s is driven by some recovery in abundance of these species and indicates that the zooplankton community is still undergoing structural change.

The fact that the CPR undersamples zooplankton has been well recognized, and has resulted in the data being used mainly to provide relative indices of abundance (Clark *et al.*, 2001; John *et al.*, 2001; Richardson *et al.*, 2004, 2006). Despite this, the unique spatial and temporal coverage of the CPR means it remains one of the few data sets available to parameterize and validate ecological models (Broekhuizen *et al.*, 1995; Heath, 2005). Most of these approaches have involved bulk-scaling of CPR data to try and account for the undersampling already mentioned. However, the limited work so far undertaken comparing CPR data with results from fixed site sampling has produced species-specific correction factors that can be used, albeit cautiously, to correct CPR data in a species-/taxon-specific manner.

There are several possible causes of the undersampling of zooplankton by the CPR. The filtering silk has a mesh of 270 μm, which does not retain very small species efficiently. For example, *Oithona* has the highest undersampling correction factor, as calculated by Clark *et al.* (2001) and John *et al.* (2001). The younger juvenile stages of many zooplankton are also not sampled efficiently; neither the CPR nor the WP-2 at a 200-μm mesh size are suited to capturing such small zooplankton, and even if the gear used operated at a constant efficiency rate, the abundance, corrected or not, would be underestimated. Some species similar in size to *Oithona*, e.g. *Temora longicornis* and *Centropages hamatus*, have markedly lower correction factors, so size is not the only factor. CPR towing speeds have increased over the years as average ship speeds have increased, but this does not have any significant influence on either filtration efficiency or retention of plankton (Hays and Warner, 1993; Hays, 1994). A third factor influencing catch efficiency is the vertical distribution of species. Because the CPR samples at an approximately constant depth of 10 m, the technique will be biased towards species that favour surface waters. A fourth factor is the diel vertical migration of some organisms, although the effects of diel variability have been taken into account when performing data analysis in this study. The final and apparently most significant factor is active avoidance of the CPR by zooplankton, as proposed by Clark *et al.* (2001) and Richardson *et al.* (2004). As avoidance is related to the behaviour of animals, it is species-specific (Fleminger and Clutter, 1965), explaining the markedly different correction factors for different species. Unfortunately, this means that correcting for undersampling by the CPR cannot be achieved using a universal factor.

Correction factors were missing for a number of species, and there is a risk that extrapolating missing values using a relationship between dry weight and correction factor will lead to unreliable estimates of abundance. This was a particular problem for species in size groups 3 and 4, and although most of the missing species in those groups were not numerically dominant, the estimation of overall biomass for them

may be less reliable than for other size groups. In the largest size category (G5), there is no published correction factor for *Euchaeta norvegica*, a species which can be a major contributor to biomass, particularly northwest of Scotland. It is also important to note that, because seasonal cycles recorded by the CPR are similar to those from other time-series, applying correction factors will only modify the relative abundances among species, without affecting the long-term trends. Whether correction factors derived from WP-2 collections made at a fixed location, usually in coastal waters, can be taken as representative of entire species/taxa is also open to debate (Hunt and Hosie, 2003; Richardson *et al.*, 2004). The WP-2 nets used to obtain the correction factors used here have a mesh size of 200 μm, and will not sample small species with total efficiency. As stated above, this will lead to underestimating the abundance of the smallest zooplankton, regardless of whether it has been corrected. The results on the distribution of plankton sizes derived in this study therefore exclude organisms with a carapace width smaller than 165 μm (Nichols and Thompson, 1991).

As well as correcting for undersampling, our approach involved estimating average copepod biomass based on morphometrics. This step may also lead to some error, because there may well be seasonal variation in body sizes. Our estimates of individual copepod biomass were comparable with measurements made by Lindley *et al.* (1997). Unfortunately, however, we could not use the same method to estimate the biomass of cladocerans because of a lack of information on morphometrics in the existing literature. Notwithstanding, selecting here a length−weight regression equation (Rose *et al.*, 2004) produced individual dry weights that were similar to the dry weight values used by Hay *et al.* (1991), Walve and Larsson (1999), and J. A. Lindley (pers. comm.).

Most fish larvae feed primarily on zooplankton, so changes in their food quantity and quality, as well as seasonal timing, will affect their survival. Bottom-up control is thought to be a significant factor determining year-class strength (Bremigan and Stein, 1994). Beaugrand *et al.* (2003a) reported that the regime shift that started in the mid-1980s radically changed the food environment for cod larvae, and this is reflected in North Sea cod year-class strength. However, these results are still based on correlation, and significant correlations have also been established for North Sea cod recruitment time-series and other environmental factors, such as temperature. In terms of stock conservation and recovery plans, it will be important to understand the causes of long-term zooplankton variations in biomass and community composition, as well as how these changes translate up the foodweb to higher trophic levels. Such results emphasize the need to take more of an ecosystem approach and to include these effects in fishery management. In future work, it will also be important to derive the zooplankton seasonal biomass dynamics in order to detect how changes in mean dry weight relate to seasons and how they influence first-feeding fish larvae. Further

effort to derive reliable undersampling correction factors for the CPR as well as additional monitoring, research, and modelling targeted at the smaller zooplankton species are also required.

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