

7 Overview of trends in plankton communities

Priscilla Licandro (corresponding author), Erica Head, Astthor Gislason, Mark C. Benfield, Michel Harvey, Piotr Margonski, and Joe Silke

7.1 Introduction

Phytoplankton and zooplankton occupy pivotal positions within marine ecosystems. These small organisms fuel and support the foodwebs upon which almost all higher organisms depend. Fisheries and related economic activities are highly dependent on the production, size, and composition of zooplankton which, in turn, rely on primary production by phytoplankton. In addition to their role as prey for herbivorous zooplankton, phytoplankton absorb enormous quantities of dissolved CO₂ via photosynthesis. Zooplankton then plays an essential role in the biological pump by consuming phytoplankton and transporting carbon from the upper ocean to the deep ocean, where it is sequestered for hundreds to thousands of years (Ducklow *et al.*, 2002).

Given the ecological and economic importance of phyto- and zooplankton, it is essential to understand and predict how they are likely to respond to climate change. This is a complex problem, but recent research suggests that both groups are especially sensitive to climate-induced change in the physical and chemical properties of the upper ocean, and that their responses have implications for fish stocks and fisheries (Edwards, 2009).

In addition to light, the concentration of nutrients in the euphotic zone is the major factor controlling phytoplankton production in the oceans. This process is believed to be affected by warming of ocean water, with different responses in the cold and warm regions of the Northeast Atlantic (Reid *et al.*, 1998; Richardson and Schoeman, 2004). Thus, in the colder regions (north of approximately 50°N), sea surface warming is accompanied by increasing phytoplankton abundance, whereas the opposite is true in the warmer regions (south of 50°N). This apparent contradiction is thought to arise because colder waters tend to be strongly mixed and nutrient-rich, whereas warmer waters farther south are more stratified and nutrient-poor. Warming in the relatively well-mixed waters in the north will thus lead to only moderate stratification that will be beneficial to phytoplankton growth, whereas, in the south, the increased warming will enhance the already existing stratification, thus limiting admixture of nutrients into the euphotic zone even further and leading to a reduction in phytoplankton growth. Evidence that the climate impact on growth of phytoplankton depends on the physical structure of the water column is seen off the north and northwest coasts of Spain (Valdés *et al.*, 2007). There, primary production is predicted to decline over the long term in the more stratified regions while increasing in regions where upwelling is relatively intensive (Valdés *et al.*, 2007).

Climate-related hydrographic changes may also directly affect the abundance and composition of zooplankton, shifting the distribution of dominant species (Beaugrand *et al.*, 2002; Möllmann *et al.*, 2005), changing the structure of the zooplankton community (Reid *et al.*, 2001b; Beaugrand, 2004), and altering the timing, duration, and efficiency of zooplankton reproductive cycles (Bunker and Hirst, 2004; Edwards and Richardson, 2004).

Superimposed on these climatic factors, ocean acidification through increased carbon dioxide dissolution in the upper ocean is lowering the pH in surface waters (Makarow *et al.*, 2009). A lower pH could impair the physiology and ultimately the

abundance of many phytoplankton and zooplankton species, especially those that produce calcareous structures.

Recruitment success of fish stocks depends to a large extent on whether or not spawning occurs in close spatial and temporal proximity to blooms of phytoplankton and zooplankton prey. If young fish cannot secure sufficient food, they will starve, and few will survive to adulthood. Changes in the temperature of the upper ocean are likely to alter the timing and intensity of phytoplankton blooms and zooplankton peak abundance, and when, where, and how they occur, thus altering the availability of plankton to fish larvae and juveniles. Shifts in temperature and other hydrographic properties can result in pronounced changes in the distributional range of zooplankton. As warm-water species of zooplankton tend to be smaller than species from higher latitudes, changes in temperature can alter the size distribution, life-history pattern, and nutritional value of zooplankton assemblages. Consequently, these changes may have major effects on fish stocks that depend on zooplankton (Cushing, 1990; Platt *et al.*, 2003; Head *et al.*, 2005).

For all of these and other reasons, it is important to understand how phytoplankton and zooplankton are likely to respond to climate-induced changes in the ocean. This section explores what is known about the sensitivity of phytoplankton and zooplankton to climate change and summarizes the trends that are evident in plankton communities within the ICES Area.

7.2 Plankton time-series: indicators of change

The distribution and abundance of phytoplankton and zooplankton are highly variable in time and space at both small and large scales. Seasonal and interannual changes reflect the recurrent variability of their milieu from season to season and from year to year. Longer-term trends and patterns in abundance, species composition, and spatial distribution can only be identified by examining patterns that emerge over long time-series. By researching such changes in the context of hydrographic shifts, hypotheses regarding cause and effect can be developed and tested. There are currently 39 time-series (including some from the Mediterranean) whose data are summarized by ICES through the Working Group on Zooplankton Ecology (WGZE; Figure 7.1 and Table 7.1; O'Brien *et al.*, 2008). In these time-series, zooplankton are collected using a variety of sampling nets (with mesh sizes of between 90 and 333 μm), and at various sampling frequencies (mostly only a few times a year), for a minimum of 10 to a maximum of more than 70 years. Generally, the sampling methods are targeted to monitor the mesozooplankton (i.e. planktonic organisms between 0.2 and 20 mm in length) and provide only limited information on plankton outside this size range. The Continuous Plankton Recorder (CPR) survey is the monitoring programme that covers the greatest spatial (tens to thousands of kilometres) and temporal (monthly to multidecadal) scales, providing data on plankton near the surface of the ocean. Of the 31 North Atlantic time-series, 12 are within the area covered by the CPR and are thus available for comparison with the results of this survey. These time-series and the patterns described by the CPR were generally in agreement for total copepod abundance (O'Brien *et al.*, 2008). Comparisons between phytoplankton time-series and CPR results have not yet been made.

The CPR surveys began in the North Sea in 1931, but have only been extended over much of the ICES region since 1960 (Figure 7.1). Phytoplankton and zooplankton are collected between continuously advancing rolls of silk gauze as the CPRs are towed behind ships of opportunity (Batten *et al.*, 2003; Reid *et al.*, 2003a), and they are

counted and identified to species/taxa once the samples are returned to the laboratory. The Phytoplankton Colour Index (PCI) is derived from the greenness of the silk mesh and is used as a proxy for phytoplankton biomass. Comparison of this visual assessment with SeaWiFS (Sea-viewing Wide Field-of-view Sensor) satellite measurements has demonstrated that the PCI is a good indicator of phytoplankton standing stock (Raitos *et al.*, 2005).

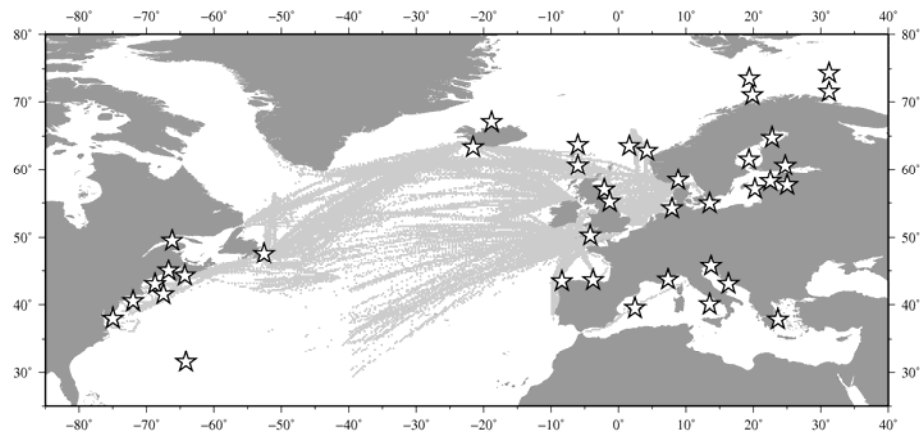


Figure 7.1. Locations of zooplankton time-series (☆) and sample positions as dots (pale grey) for the Continuous Plankton Recorder (CPR) survey (1931–2008). (Source: O'Brien *et al.*, 2008.)

7.3 Changes in phytoplankton

7.3.1 Distribution and abundance

A large increase in phytoplankton biomass (i.e. annual mean PCI) has been recorded in the Northeast Atlantic since the mid-1980s, particularly in the North Sea and in the area west of the British Isles (Figure 7.2), which appears in part to be related to increasing sea surface temperatures (SSTs; Reid *et al.*, 1998; Edwards, 2000; Edwards *et al.*, 2001b, 2007). In the same area, an extension of the duration of the seasonal maximum of the PCI has also been observed.

In contrast to previous observations, Boyce *et al.* (2010) have recently indicated a global decline in phytoplankton standing stock of up to 1% of the median phytoplankton biomass per year. However, the validity of this study is currently under debate because the heterogeneities of the data and the methodology used are considered to have biased the results presented by Boyce and co-authors (Mackas, 2011; McQuatters-Gollop *et al.*, 2011; Rykaczewski and Dunne, 2011).

Table 7.1. Summary of available time-series data on zooplankton compiled by the ICES Working Group on Zooplankton Ecology (WGZE). Data summarized by O'Brien *et al.* (2008) and table courtesy of Todd O'Brien, National Oceanic and Atmospheric Administration–National Marine Fisheries Service (NOAA–NMFS).

Ocean Region	Western North Atlantic										Icelandic-Norwegian Basin					Barents Sea			Baltic Sea						North Sea / English Channel				Bay of Biscay / Iberian Coast			Mediterranean						North Atlantic		
Country	USA					Canada					Iceland	Faroe Islands		Norway		Norway			Finland	Estonia	Latvia		Germany	Norway	Germany	UK	UK	Spain	Spain	Spain	France	Italy	Italy	Croatia	Greece	UK				
Sampling / Monitoring Programme	NMFS-NEFSC					AZMP					MRI-Iceland	FFI-Faroe Islands		IMR-Bergen			HELCOM Monitoring						National monitoring programme of Latvia	LatFRA-monitoring	IOW	IMR	BSH and DZMB	FRS-MLA	L4-PML/UK	IEO-Spain	IEO-Spain	LOV-France	SZN-Italy	UNIT S-Italy	IZOR-Croatia	HCMR-Greece	Continuous Plankton Recorder			
Sampling Site Name	MAB	SNE	GOM	GBK	Princ e 5	Halifax Line 2	Gaspé Current	Anticosti Gyre	Station 27	Selvogsbanki Transect	Siglufoes Transect	North ern Transect	Faroe Shelf	Svina y Transect West	Svina y Transect East	Fugloy a-Bjerna ya Transect North	Fugloy a-Bjerna ya Transect South	Vard a-Nord North	Vard a-Nord South	Bothni an Bay	Bothni an Sea	Tallin n Bay	Pärnu Bay	Station 121	Eastern Gotland Basin	Arkona Basin	Arendal Station 2	Helgoland Roads	Stonehaven	Plymouth L4	Santander	A Coruña	Balear es Station	Villefran che Point B	Gulf of Naples	Gulf of Trieste	StonCica	Saronik os-511	CPR Surveys	
Sampling Location	Mid-Atlantic Bight	South ern New England	Gulf of Maine	Georges Bank	Bay of Fundy	Scotti an Shelf	Gulf of St. Lawrence	Gulf of St. Lawrence	Newfoundl and Shelf	South Iceland	North Iceland	North Faroe Islands	Sout h Faroe Islands	Norwegian Sea	Western Barents Sea	Eastern Barents Sea	Northern Baltic Sea	Gulf of Finland	Gulf of Riga	Central Baltic Sea	Southern Baltic	Northern Skagerrak	Southeast North Sea	Northwest North Sea	English Channel	Southern Bay of Biscay	Northwest Iberian Peninsula	Balearic Sea	Cote d'Azur	Tyrrhenian Sea	North ern Adriatic	Middle Adriatic Sea	Aegean Sea	Continuous Plankton Recorder Surveys						
Sampling Duration	1977 - present	1977 - present	1977 - present	1977 - present	1999 - present	1999 - present	1999 - present	1999 - present	1999 - present	1971 - present	1961 - present	1990 - present	1990 - present	1996 - present	1996 - present	1994 - present	1994 - present	1994 - present	1994 - present	1979 - present	1979 - present	1993 - present	1957 - present	1993 - present	1960 - present	1979 - present	1994 - present	1975 - present	1997 - present	1988 - present	1991 - present	1990 - present	1994 - present	1974 - present	1984 - present	1970 - present	1959 - present; 1991; 1995 - present (unprocessed)	1987 - present	1946 - present	
Sampling Frequency	Cross-monthly surveys six times per year.					Monthly / Biweekly					Annually (May–June)		Annually (late May)		4 - 6 times per year		3 - 6 times per year		3 - 4 times per year		August		up to 10 times per year	monthly to weekly in non-ice months	at least 3 times per year	seasonally	seasonally	twice per month	Every Monday, Wednesday, and Friday	Weekly (52 weeks per year)	Weekly (~40 weeks per year)	Monthly	Monthly	monthly (up until 2006)	monthly	monthly	monthly	monthly (with gaps)	seasonally (1987-1998); monthly after 1999	Monthly (with gaps)
Sampling Gear (diameter)	Bongo Net					Ring Net (75 cm)					1971–91: Hensen Net; 1992–present: WP-2 Net		1990–1991: Hensen Net; 1992–present: WP-2 Net		WP-2 Net (56 cm)		WP-2 Net (56 cm)			WP-2 Net (56 cm)	Juday Net (36 cm)	WP-2 Net	Juday Net (36 cm)	WP-2 Net	WP-2 Net	Hydrobios and Calcofi	Bongo Net (40 cm)	WP-2 Net	Juday Net (50 cm)	Juday Net (50 cm)	Bongo Net (20 cm)	Juday-Bogorov Net	Nansen Net (113 cm)	WP-2 Net	Hensen Net (73 cm)	WP-2 Net	CPR (1.24 cm)			
Sampling Mesh (µm)	333 µm					200 µm					200 µm		200 µm		180 µm		180 µm			100 µm		90 µm	100 µm	160 µm	100 µm	180 µm	150 µm, 500 µm	200 µm	200 µm	250 µm	1971–96: 250 µm; 1996–present 200 µm	100/250 µm	330 µm	200 µm	200 µm	330 µm	200 µm	280 µm		
Sampling Depth (m)	0 to 200 (or bottom)					0 to bottom					0 to 50		0 to 50		0 to 200		0 to 100			0 to bottom		0 to bottom	0 to 50	0 to 100	0 to 25	0 to 50	0 to bottom	0 to 50	0 to 50	0 to 50	0 to 50	0 to 50	0 to 100	0 - 75	0 - 50	0 - 18	0 to 100	0 to 75	sub-surface (7-10 m)	

In the North Sea a pronounced increase in SST and windspeed after the 1980s resulted in an extension of the season favourable for phytoplankton growth, particularly in the southern North Sea. However, McQuatters-Gollop *et al.* (2007) and Llope *et al.* (2009) found that nutrient concentrations were not an important contributory factor to the observed changes in phytoplankton standing stock.

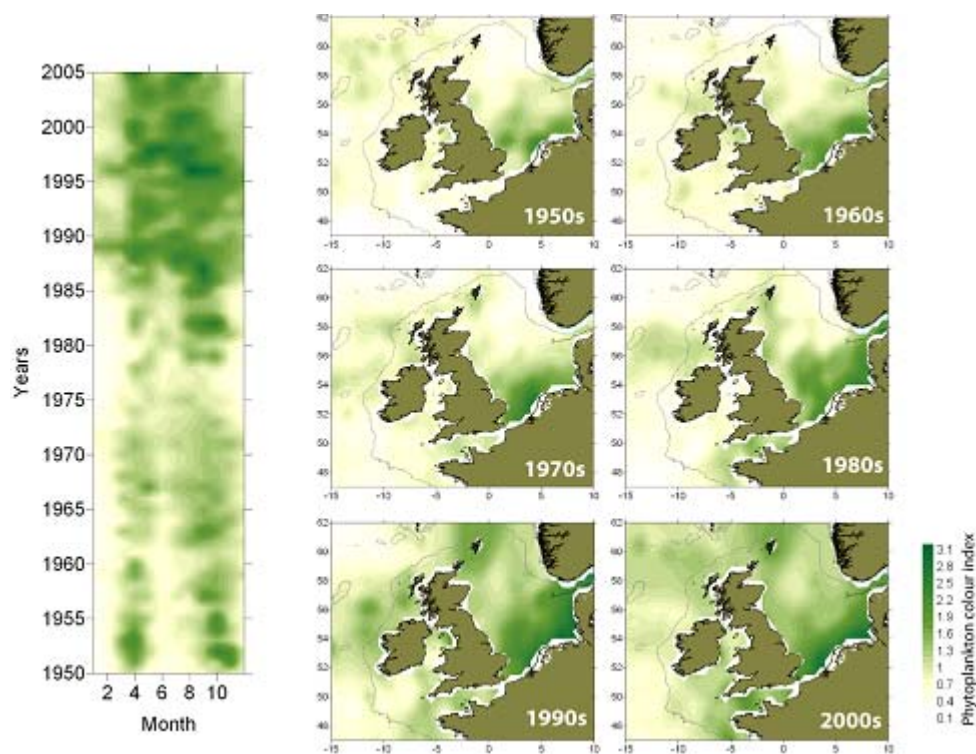


Figure 7.2. Mean spatial distribution of phytoplankton standing stock (Phytoplankton Colour Index, or PCI) per decade from the 1950s to the present. A considerable increase in PCI has been recorded since the mid-1980s, particularly in the North Sea and in the area west of the British Isles in relation to increasing sea surface temperature (SST). (Source: Edwards, 2009.)

In the waters around Iceland, particularly in the north–northeastern region, hydrographic changes (i.e. changes in currents and hydrography related to large-scale climate variability) may have an important influence on annual mean spring productivity. Primary production tends to be higher in years with a high inflow of relatively warm Atlantic Water than in years when this inflow is not so pronounced (Gudmundsson, 1998). A model developed by Ellingsen *et al.* (2008) demonstrates that primary production is likely to increase in a similar way in the Barents Sea under a warming scenario.

In the Northwest Atlantic, an increase in phytoplankton standing stock has been recorded in the past decade in both shelf and deep-ocean regions. The observed changes on the continental shelf and in the Gulf of Maine have been related to changes in the circulation and freshwater export from the Arctic Ocean, which are considered to be a consequence of climate warming (Greene and Pershing, 2007; Head and Sameoto, 2007), whereas, in the Subpolar Gyre, they are thought to be the direct result of increasing stratification caused by rising temperature (Head and Pepin, 2010).

In the Baltic Sea, it is difficult to distinguish the effects of changing climate, fishing, and eutrophication on phytoplankton biomass and species composition (Casini *et al.*, 2008). Wasmund *et al.*, (1998) consider that the spring increase in chlorophyll *a* in the

Bornholm and southern Gotland basins is related to eutrophication, whereas the reduction in diatoms in favour of the dinoflagellates is related to mild winters. The intensity of surface blooms of cyanobacteria is regulated by a combination of climatic factors, such as water temperature, solar radiation, and windspeed (Kahru *et al.*, 1994; Wasmund, 1997; Stal *et al.*, 2003).

7.3.2 Community structure

Regional climate variability has been related to changes in phytoplankton community structure observed in data from the CPR survey since the 1960s in the North Sea, with an increase in dinoflagellate abundance and a decrease in diatom abundance in response to warmer sea temperature (Leterme *et al.*, 2005; Edwards *et al.*, 2006a). The abundance of dinoflagellates is positively correlated with the North Atlantic Oscillation (NAO) and SST, whereas diatom abundance is negatively correlated with the NAO and SST (Edwards *et al.*, 2001a, 2006a). The marked hydrographic changes that have occurred in the North Sea since the late 1980s, and which have continued to the present, have resulted in an environment that appears to favour the growth and earlier succession of dinoflagellates (Edwards and Richardson, 2004; Edwards *et al.*, 2006b). In the North Sea, studies based on long-term phytoplankton datasets other than the CPR have noted similar ecological changes in the Northeast Atlantic in the late 1980s or in more recent years and, in particular, an increase in the ratio of dinoflagellates to diatoms in the southern North Sea (Hickel, 1998) and the western English Channel (Widdicombe *et al.*, 2010). Against this background of change, the abundance of the most common species of the armoured dinoflagellate *Ceratium* (e.g. *C. furca*, *C. fusus*, and *C. horridum*) has decreased markedly in the North Sea since the early 2000s (Edwards *et al.*, 2009).

In recent decades, in parallel with the rise in dinoflagellates, increasing records of harmful algal bloom (HAB) taxa have been reported in some regions of the North Sea. Anomalously high frequencies of HABs were recorded in the late 1980s in the Norwegian coastal region and in the Skagerrak, and HABs continued to be common in the Norwegian coastal region thereafter (Figure 7.3; Edwards *et al.*, 2006a). These modifications, which could merely be a consequence of a change in the centre of the distribution of HABs, are thought to be related to regional climate change, particularly to changes in temperature, salinity, and the NAO. In Gullmar Fjord on the Swedish coast, a possible link between the occurrence of toxin-producing *Dinophysis* spp., primary production, and the NAO index was hypothesized by Belgrano *et al.*, (1999).

Warming temperatures at higher latitudes appear to be providing conditions conducive to the northward expansion of warm-water plankton and possibly some HAB species. For instance, fossil records collected over the past few thousand years have revealed increased densities of *Lingulodinium polyedrum* and species similar to toxic *Gymnodinium catenatum* during periods of relatively warm temperatures in Scandinavian waters (Dale and Nordberg, 1993; Thorsen and Dale, 1997).

Blooms of *L. polyedrum* have been described from off the Portuguese coast since the 1940s, and the toxic autotrophic dinoflagellate *G. catenatum* has been associated with upwelling events along the Iberian coast since 1976 and farther off the Portuguese coast since 1986 (Pinto, 1949; Margalef, 1956; Moita *et al.*, 1998; Amorim and Dale, 2006; Ribeiro and Amorim, 2008).

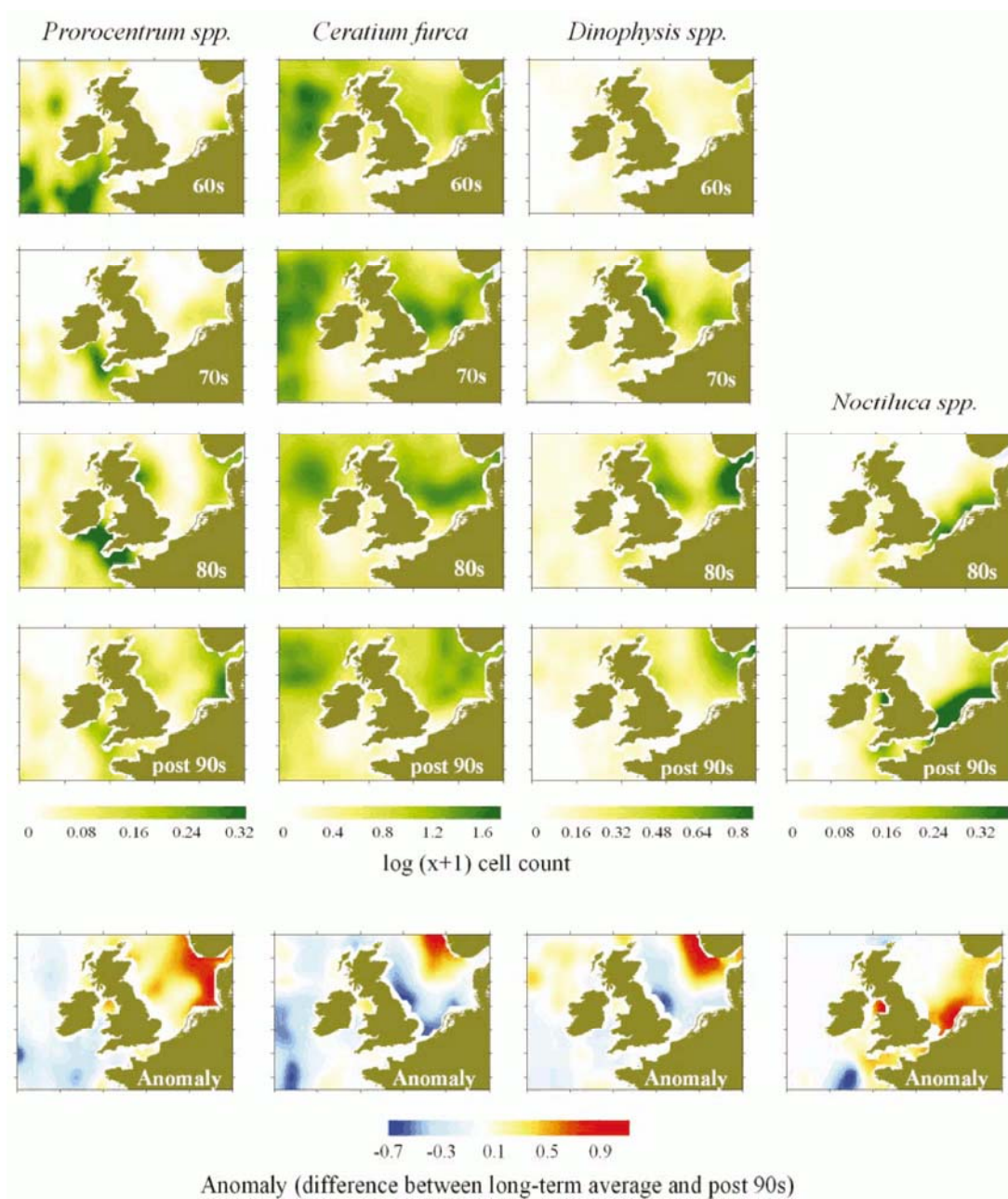


Figure 7.3. Top: mean spatial distribution of four dinoflagellate taxa in the Northeast Atlantic derived from Continuous Plankton Recorder (CPR) data. Estimated cell counts were $\log_{(x+1)}$ transformed. Bottom: anomaly maps showing the difference between the long-term mean (1960–1989) and the post-1990s period (1990–2002). Red = values above the long-term mean; blue = values below the long-term mean; white = mean values. (Source: Edwards *et al.*, 2006a.)

Within species-specific physiological limits, the metabolic and growth rates of many phytoplankton species increase with rising temperature. The balance between metabolism (respiration) and growth (via photosynthesis) may not change with increases of the order of 1–2°C, but greater changes could lead to a decline in primary production. Changes will depend on the geographical location and the type of phytoplankton species (cold- or warm-adapted). For most of the phytoplankton species in the Baltic Sea, temperature has had only a limited impact on algal growth (Dippner *et al.*, 2008), but some of the species have their own preferred temperature ranges, so that the community composition may change as temperature rises further (Wasmund, 1994). Here and elsewhere, however, direct effects of temperature will be

in addition to those caused by processes contributing to stratification (Wasmund *et al.*, 1998).

Increases in the intensity and frequency of winter storms, and increased rainfall, have been predicted for certain areas of the North Atlantic as consequences of global warming (McGrath and Lynch, 2008). These conditions will lead to increases in both the depth of deep winter mixing in the ocean and in freshwater run-off, with secondary effects on phytoplankton abundance and composition. On one hand, higher freshwater run-off will increase estuarine circulation and the dilution rate of many coastal regions, thereby constraining the accumulation of biomass. Freshwater can also create a shallow surface mixed layer in which irradiance is sufficient for net production, despite the water column as a whole being turbid. On the other hand, the large amounts of dissolved organic matter (*gelbstoff*) contained in some river outflows will reduce the depth to which photosynthetically active radiation can penetrate, thus confining photosynthetic cells to an upper shallow layer and limiting primary production (Heath *et al.*, 2009). Under these circumstances, species adapted to low light will have a competitive advantage in both oceanic and coastal regions. Moreover, an earlier stratification of the water column, evidence for which has been already reported in the Northeast Atlantic (MCCIP, 2008), may advance the onset of the phytoplankton bloom in spring.

River run-off normally contains high concentrations of dissolved nutrients derived from the weathering of soils, agriculture, and other human sources. Increased precipitation may lead to eutrophication and/or an increase in contaminant loads. An increase in the number of flash floods in summer could result in a pulsed supply of nutrients to nutrient-depleted coastal water, which could influence the timing and abundance of summer phytoplankton blooms. The HABs are also often triggered by events associated with loading from local rivers after heavy rainfall (Smayda, 2006). Local wind patterns can also affect water-column stability and nutrient availability below the pycnocline. This is particularly evident in regions where upwelling occurs (e.g. off the Iberian Peninsula). Changes in the intensity and frequency of local prevailing winds will affect the amount of fresh nutrient input to the euphotic zone and new primary production. The increased warming of the sea surface and thermal stratification should mitigate against wind-mixing events, if it were not for the expected movement towards a more variable climate with more extreme weather events.

7.3.3 New or non-native species

In recent years, an increasing expansion to new areas and abundance of warm-water phytoplankton species has been reported in the Northeast Atlantic. For instance, warm-water *Ceratium* spp. (e.g. *C. hexacanthum*) has been recorded in the North Sea (Edwards and Richardson, 2004).

The non-indigenous diatom *Coscinodiscus wailesii*, originally native to the Pacific Ocean, was first reported in the English Channel in the late 1970s. This species has subsequently spread to other European shelf seas and, since the mid-1980s, has become well established and abundant in the North Sea and around the British Isles (Edwards *et al.*, 2001b; Wiltshire *et al.*, 2010).

As summarized by Dippner *et al.*, (2008), several phytoplankton species that have invaded the Baltic Sea are thermophilic (e.g. *Alexandrium minutum* and *Gymnodinium catenatum*). Large blooms of diatoms (*Cerataulina pelagica*, *Chaetoceros brevis*, *Dactyliosolen fragilissimus*) that have recently formed massive blooms in Lithuanian

waters, are believed to have been introduced by warm-water inflow from the Kattegat (Hajdu *et al.*, 2006).

The first records in the North Atlantic of the Pacific subpolar diatom *Neodenticula seminae* have been related to the melting of sea ice in the Arctic caused by climate warming. This species was first found in CPR samples from the central Irminger Sea south of Greenland during spring, following the ice-free period in 1998 (Reid *et al.*, 2007). The progressive spread of *N. seminae* in the Northwest Atlantic was confirmed by the presence of large numbers in the Gulf of St Lawrence in 2001 (Starr *et al.*, 2002).

Although many studies increasingly report new occurrences of species of non-native dinoflagellates (including some that are potentially harmful) and diatoms, it has been argued that they are cosmopolitan species that have been misidentified in the past (Gómez, 2008).

7.4 Changes in zooplankton

7.4.1 Distribution and abundance

Hydrographic variability in the North Atlantic has been related to changes in the population dynamics of key zooplankton species. Several studies have noted changes in the distribution of relatively large copepods (e.g. *Calanus* spp.) that have had an important effect on total zooplankton abundance and biomass. For example, the abundance of the cold-water species *C. finmarchicus*, a key component of the planktonic ecosystem of the North Atlantic, has changed in several regions since the 1950s, and this has been associated with increases in sea temperature (Planque and Fromentin, 1996; Pershing *et al.*, 2004).

The decrease in *C. finmarchicus* in the North Sea over recent decades has led to a significant reduction in total zooplankton standing stock, namely 70% in total biomass between the 1960s and post-1990s (Edwards *et al.*, 2006b, 2007). In the Northwest Atlantic, changes in the circulation patterns of slope water in the 1990s led to an apparent decrease in the abundance of *C. finmarchicus* and in zooplankton biomass in the Gulf of Maine and on Georges Bank (Greene and Pershing, 2003), although *C. finmarchicus* abundance increased again in the 2000s (Pershing *et al.*, 2010).

In the North Sea, warmer temperature conditions and increased phytoplankton abundance earlier in the year since the late 1980s have been accompanied by an increasing abundance of meroplankton (i.e. temporary planktonic larvae of benthic species), particularly echinoderm larvae, which may now control the trophodynamics of the pelagic ecosystem by competitive exclusion of the holozooplankton (i.e. permanent planktonic species; Kirby *et al.*, 2007). This change in foodweb structure may have had an important effect by rerouting energy flow from the pelagic ecosystem to the benthos.

Dippner *et al.* (2008) have reviewed climatic and environmental effects on mesozooplankton based on long-term observations in the Baltic Sea. Salinity, eutrophication, temperature, predation by pelagic fish, and non-indigenous planktonic invertebrates are all considered to have contributed to changes in zooplankton abundance. These and other authors have concluded that expected future increases in water temperature will have a secondary effect on mesozooplankton standing stock, mostly affecting winter survival and summer growth/reproduction (Viitasalo *et al.*, 1995; Möllmann *et al.*, 2000, 2005; Dippner *et al.*, 2001).

Data collected during the ICES-coordinated surveys in the Norwegian Sea, which have been conducted annually in May since 1995, have demonstrated a progressive reduction (by 80%) in zooplankton biomass since 2002, especially in Atlantic waters, which is probably related to hydrographic variability (Figure 7.4). In this region, the average biomass of zooplankton in Atlantic waters in May was formerly significantly correlated with the average NAO for the March–April period in the previous year, but the relationship broke down in 2003 (Figure 7.4). It has been suggested that the drop in zooplankton biomass in the Norwegian Sea may be the consequence of higher predation pressure, because the planktivorous fish stock abundance has increased markedly in recent years in that region, although no clear conclusion has been drawn as yet (ICES, 2010a).

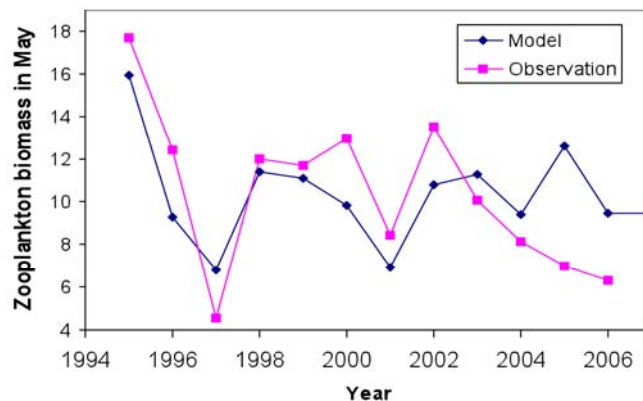


Figure 7.4. Observed and modelled zooplankton biomass (dry weight, g m^{-2}) in May for the upper 200 m of the Atlantic sector of the Norwegian Sea. Model: $\text{biomass}(\text{year}_{n+1}) = 2.3 \cdot \text{NAO}_{\text{year}_n} + 10.1$; $r^2 = 0.44$, $p = 0.02$. (Source: Melle, 2008.)

Other studies confirm a connection between hydrographic variability and plankton in different subregions of the Nordic seas. For instance, the zooplankton biomass north of Iceland is influenced by the inflow of warm Atlantic Water into the area. Thus, in warm years, when the flow of higher salinity Atlantic Water onto the northern shelf is enhanced, the zooplankton biomass can be almost twice as high as in cold years, when this inflow is not as evident (Astthorsson and Gislason, 1995). This is probably related to better feeding conditions for the zooplankton, not only because of higher levels of primary production in warm years, but also because the incoming Atlantic waters have higher levels of zooplankton. There is a marked year-to-year variability in the community structure of zooplankton in the waters around Iceland, which again is largely determined by hydrography (Gislason *et al.*, 2009). In the Barents Sea, both field studies (Dalpadado *et al.*, 2003) and simulation exercises (Ellingsen *et al.*, 2008) demonstrated an increase in zooplankton productivity with increasing temperature.

Variability has also been observed in the plankton over the shelf and in open-ocean regions of the Northwest Atlantic. The Scotian and Newfoundland shelf regions are influenced by the outflow of water from the Arctic, whose contribution to the total flux increased in the 1990s. This change probably contributed to increased stratification in the water column, earlier and more intensive phytoplankton blooms, and changes in the zooplankton community. For example, although the abundance of the boreal–temperate species *C. finmarchicus* decreased on the Newfoundland Shelf, two species of Arctic *Calanus* (*C. glacialis* and *C. hyperboreus*), which had previously been relatively rare, increased in numbers in the 1990s and remained abundant in the 2000s. In the Northwest Atlantic Subpolar Gyre, temperature may have had a more direct effect, contributing, in recent years, to increased levels of phytoplankton and

primary production (via increased stratification), and to increased production/survival of young *Calanus* copepodites and small copepods (Head and Pepin, 2007, 2010). In contrast, over the North Atlantic as a whole, Reygondeau and Beaugrand (2011) have demonstrated that the frequency of occurrence of *C. finmarchicus* (particularly early copepodites) decreases with increasing stratification.

There are indications that pelagic cnidarians and ctenophores (i.e. gelatinous zooplankton predators, or “jellyfish”) have increased in abundance throughout the world in recent years (Mills, 2001). Jellyfish outbreaks appear to be more frequent (Purcell *et al.*, 2007), although much uncertainty surrounds the issue because of the scarcity of reliable baseline data. Many species of jellyfish are difficult to sample and to culture; consequently, there is a lack of information concerning their ecological impact on zooplankton communities and especially on fish larvae. An increase in the frequency of occurrence of some jellyfish has been related to hydroclimatic changes in the Northeast Atlantic during the last decade (Lynam *et al.*, 2004; Attrill *et al.*, 2007). Such increases are not limited to shelf areas but have also been observed in oceanic waters (Figure 7.5; Gibbons and Richardson, 2009; Licandro *et al.*, 2010). Notwithstanding our still limited understanding, increasing temperature appears to be one of the main triggering mechanisms for exceptional outbreaks of these gelatinous carnivores (CIESM, 2001; Purcell, 2005). The timing of jellyfish seasonal peaks over the shelf and in oceanic waters appears to be regulated by temperature rather than food (Gibbons and Richardson, 2009), which may explain why swarms of warm-temperate species have been observed more frequently in the Northeast Atlantic in recent years (Licandro *et al.*, 2010). Improved and systematic monitoring of marine and coastal areas for jellyfish needs to be implemented in order to obtain a comprehensive overview of their spatial, vertical, and temporal distribution.

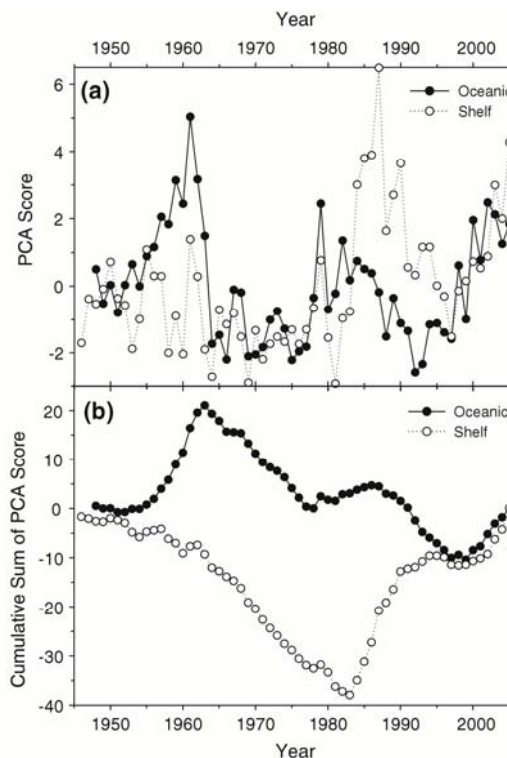


Figure 7.5. (a) First principal components of interannual variation in oceanic and shelf jellyfish from 1946 to 2005 derived from Continuous Plankton Recorder (CPR) data. (b) Cumulative sums of (a), highlighting the major step changes in the time-series. (Source: Gibbons and Richardson, 2009.)

7.4.2 Community structure

Pronounced biogeographic shifts or translocations have been recorded for zooplankton species over the entire North Atlantic by means of CPR sampling. These have been attributed to increasing regional sea temperatures. Calanoid species with warmer-water affinities have moved north by as much as 10° latitude in the Northeast Atlantic over the past few decades, and northward movement has continued to the present (Figure 7.6; Beaugrand, 2005; Edwards *et al.*, 2006b; Beaugrand *et al.*, 2009). In some North Atlantic regions, latitudinal changes have led to an increase in zooplankton diversity and parallel reductions in the mean size of the dominant zooplankton species (Beaugrand *et al.*, 2010).

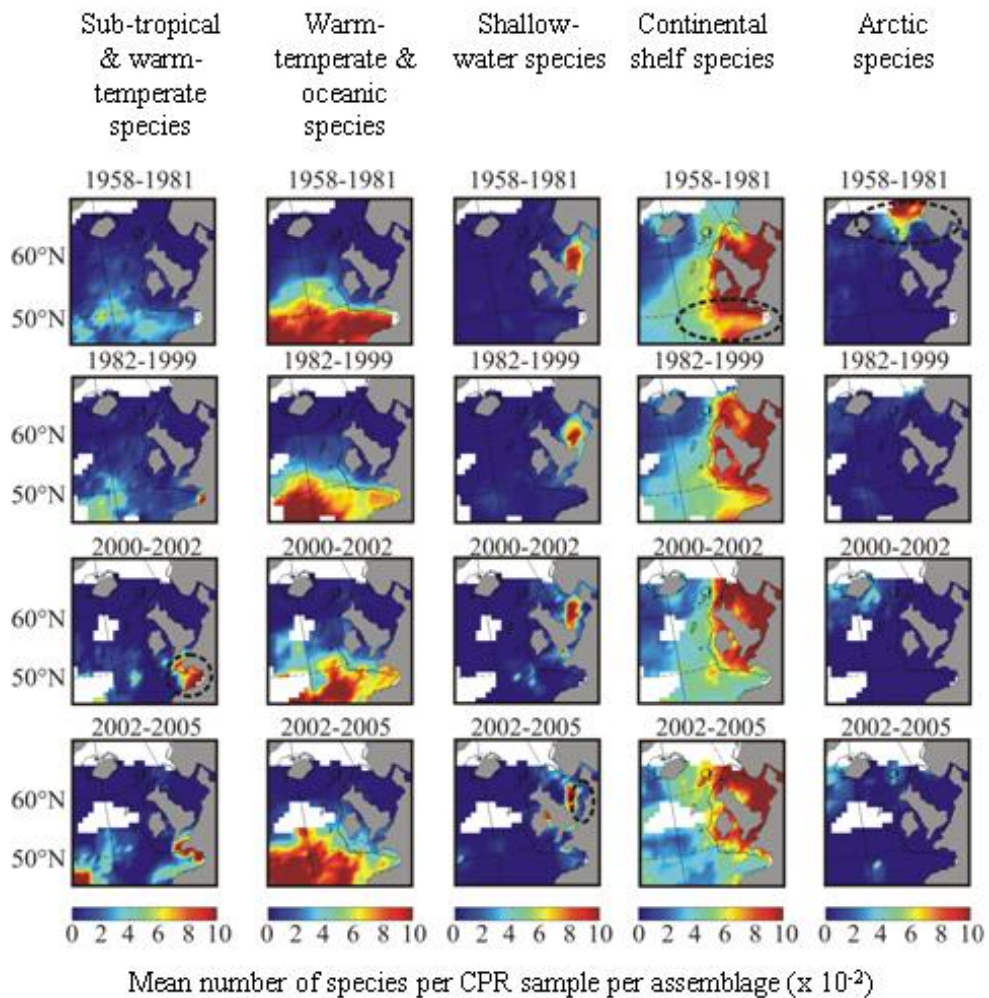


Figure 7.6. Maps showing biogeographic shifts of calanoid copepod communities in recent decades based on Continuous Plankton Recorder (CPR) data, with warm-water species shifting north by more than 10° of latitude and cold-water species retracting to the north. (Source: Beaugrand *et al.*, 2009.)

Examples of warm-water species/groups that have undergone changes in distribution include: increasing densities of *Calanus helgolandicus* in the North Sea and Bay of Biscay (Bonnet *et al.*, 2005; Helaouët and Beaugrand, 2007); the positive relationship between temperature and change in the abundance of *Centropages typicus* in the seas around the UK (Beaugrand *et al.*, 2007); the increase in species richness related to warmer waters in the western English Channel (Eloire *et al.*, 2010); and the northward shift of *Temora stylifera* into the Bay of Biscay (Figure 7.7; Valdés *et al.*, 2007) and of *Penilia avirostris* into the North Sea (Johns *et al.*, 2005). In Fram Strait (west of

Spitsbergen), northward shifts of the Atlantic hyperiid amphipods *Themisto abyssorum* and *T. compressa* have been observed since 2000, and are thought to be related to the increased influence of warm Atlantic waters (Kraft *et al.*, 2010). Euphausiids form a significant part of the zooplankton biomass in the North Atlantic, where they may play an important role as conveyors of energy between trophic levels. In the Barents Sea, euphausiid biomass (mainly *Thysanoessa inermis* and *T. raschii*) has increased since 2000, probably as a result of the recent warming, which provides favourable conditions for growth and survival of these species (Eriksen and Dalpadado, In press).

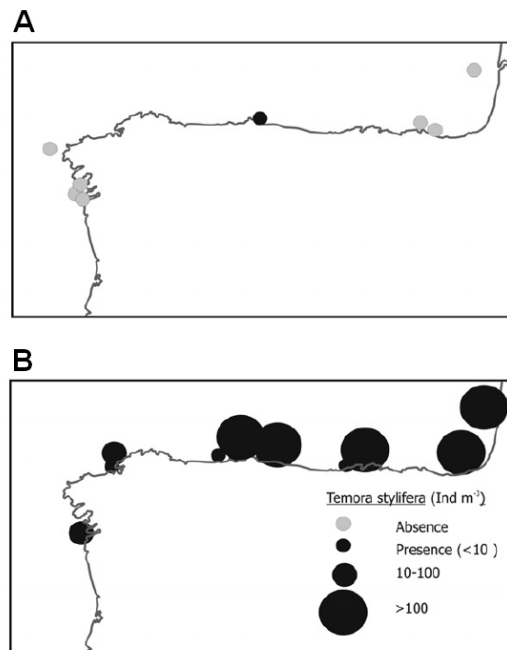


Figure 7.7. Abundance of the warm-water calanoid copepod *Temora stylifera* in transects off Vigo, Coruña, and Santander: (a) before 1982 and b) after 1982 (sampling by the Radiales project). Based on historical monitoring in the North–Northwest Iberian peninsula, *T. stylifera* was absent before 1978. Since the first record in the Cantabrian Sea in 1980, this species has become progressively more abundant in the Santander region, and a marked increase has been observed since the mid-1990s (Valdés *et al.*, 2007).

In the Baltic Sea, changes in temperature have had their greatest effect on organisms living in near-surface waters (Möllmann *et al.*, 2000, 2003, 2005), whereas those located deeper in the water column have been mostly affected by changes in salinity (Hansen, F., *et al.*, 2006). As a consequence, projected longer periods of higher water temperature and lower salinity during summer may strongly influence the pelagic foodweb, benefiting the growth of cladocerans, rotifers, and copepods, such as *Acartia* spp. (Viitasalo *et al.*, 1995; Möllmann *et al.*, 2000). In winter, higher temperatures may affect the survival of overwintering resting stages of copepods, cladocerans, and rotifers in sediment.

On the western side of the North Atlantic basin, in contrast to the Northeast Atlantic, a substantial movement south of Arctic species has occurred in areas where outflow from the Arctic has increased (Head and Sameoto, 2007; Head and Pepin, 2010). For example, on the Newfoundland Shelf, the abundance of the boreal–temperate species *C. finmarchicus* decreased in the 1990s, whereas abundance of two species of Arctic *Calanus*, which had previously been rare, increased and remained relatively abundant in the early 2000s (Head and Pepin, 2010). Similarly, the Arctic hyperiid amphipod

Themisto libellula increased in abundance in the 1990s in the Gulf of St Lawrence, where it has since become an abundant, full-time resident (Harvey *et al.*, 2009).

7.4.3 New or non-native species

As mentioned in Section 7.4.2, the calanoid copepod *Temora stylifera* has been recorded moving north into the Bay of Biscay from more southern waters (Valdés *et al.*, 2007). It was only observed north of the Iberian peninsula after 1978, and it has been cited as an example of a species that has shifted its distribution as a result of global warming (Villate *et al.*, 1997).

Penilia avirostris, a marine cladoceran typically found in subtropical and Mediterranean waters, was recorded at the Helgoland Roads time-series sampling station in 1990 and has increased in CPR samples collected in the North Sea since 1999 (Johns *et al.*, 2005). The increase in abundance is thought to be caused by higher SSTs, particularly during autumn. This species may have arrived in the North Sea by northward advection of adults in warmer waters or as resting eggs in the ballast water of ships (Johns *et al.*, 2005).

The ctenophore *Mnemiopsis leidyi* is a gelatinous predator originating on the American east coast. This species is believed to have been accidentally introduced into the Black Sea in the early 1980s via the ballast water of merchant ships (Shiganova, 1998). From the Black Sea, *M. leidyi* expanded into the Azov, Marmara, Mediterranean, and Caspian seas, and it is now increasingly being found in the Baltic Sea and in coastal waters of the North Sea from Bergen to the Netherlands (Leppäkoski *et al.*, 2002; Faasse and Bayha, 2006; Javidpour *et al.*, 2006). A persistent and increasing abundance of *M. leidyi* in the Northwest Atlantic has been related to warming water temperature (Purcell, 2005).

In the Baltic Sea, the first observations of *M. leidyi* were in the southwest in October 2006 (Javidpour *et al.*, 2006). Several publications have indicated a progressive eastward spread (Javidpour *et al.*, 2006; Janas and Zgrundo, 2007; Kube *et al.*, 2007; Lehtiniemi *et al.*, 2007). It should be noted here, however, that the invasive ctenophore *Mertensia ovum* has been wrongly identified as *M. leidyi* in the northern Baltic (Gorokhova *et al.*, 2009). As pointed out by these workers, further studies using molecular techniques are needed to elucidate the extent of invasion into European waters by *M. leidyi*. As stated by Javidpour *et al.* (2006), in the particular case of the Baltic Sea, it is not yet clear whether *M. leidyi* can severely affect zooplankton and fish populations directly, by feeding on fish larvae and eggs, or indirectly by competing for zooplankton food. However, taking into account the expected increase in water temperature and the remarkable ability of this invader to double its population size in a short time, it is a matter of concern and a challenge in predicting future risks to Baltic Sea ecosystems.

Unprecedented changes in the Arctic (including increased precipitation, river discharge, glacial and sea-ice melting) related to climate warming have led to changes in the plankton populations of the Northwest Atlantic, including marked increases in the abundance of Arctic species. Thus, the Arctic hyperiid amphipod *Themisto libellula* has been recorded since the early 1990s in the Gulf of St Lawrence (Figure 7.8; Harvey and Devine, 2008), where its abundance was positively correlated with the volume of Labrador Shelf Water advected into the Gulf through the Strait of Belle Isle during winter in the early 2000s, although not since 2006. The geographic expansion of *T. libellula* coincides with observations made by Drinkwater and Gilbert (2004) that the core temperature in the cold intermediate layer in the Gulf of St Lawrence in the

1990s was, on average, the coldest seen in the previous five decades. In addition, an increased contribution of Arctic Water to the Canadian continental shelf regions and the Gulf of St Lawrence in the 1990s led to increases in the abundance of cold-water copepods, such as *C. glacialis* and *C. hyperboreus*, on the Scotian Shelf in the early 2000s (Head and Pepin, 2010). In the past few years, however, the relative importance of some of these cold-water species has diminished in some regions (e.g. *C. glacialis* off Halifax and on the Grand Banks, *T. libellula* in the lower St Lawrence Estuary, northwest Gulf of St Lawrence, and Grand Banks), perhaps as a result of warming ocean temperatures and a reduction in the volume and extent of the cold intermediate layer.

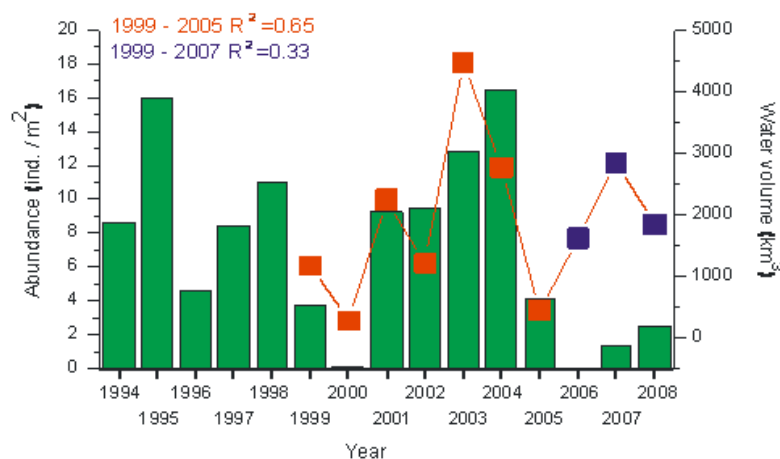


Figure 7.8. Relationship between the annual volumes of Labrador Shelf Water advected into the St Lawrence Estuary in winter (■) and the annual mean abundance of the hyperiid amphipod *Themisto libellula* (bars) in the lower St Lawrence Estuary and northwest Gulf of St Lawrence. (Source: Harvey and Devine, 2008.)

7.4.4 Phenology and life history

Climate-induced warming has triggered changes in the timing of occurrence (phenology) of many zooplankton taxa (Figure 7.9; Greve *et al.*, 2001; Edwards and Richardson, 2004; Edwards *et al.*, 2006b). The changes in phenology have varied among species, functional groups, and trophic levels, leading to potential mismatches in prey–predator relationships (Edwards and Richardson, 2004; ICES, 2006). In addition, recent investigations have demonstrated that winter temperature influences the time of spawning of some commercially important North Sea fish species, with warmer sea temperature being associated with earlier fish recruitment (Greve *et al.*, 2005).

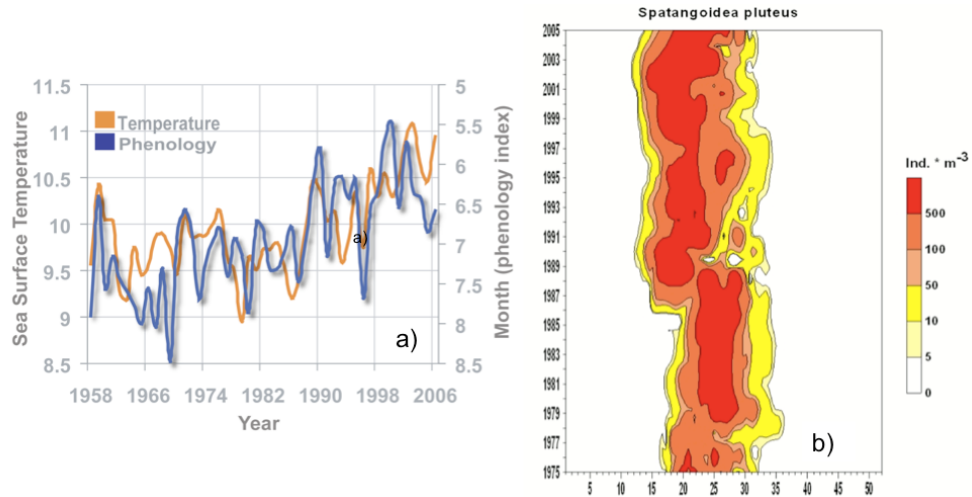


Figure 7.9. (a) Plot of the timing of the seasonal cycle (phenology) of echinoderm larvae from the Continuous Plankton Recorder (CPR) survey against sea surface temperature (SST) from 1958 to 2004, showing a close correlation between the larvae and SST (Edwards *et al.*, 2006b). (b) Contour plot showing abundance and seasonality of spatangoid plutei (i.e. echinoderm larvae) from 1975 to 2005, also showing a shift to an earlier timing. Data from the Helgoland time-series, southeastern North Sea. (Source: Greve *et al.*, 2001.)

In the central Labrador Sea, a key population centre for *Calanus finmarchicus*, there has been an increase in late winter–spring (and annual) average SST of ca. 1°C since the mid-1990s (Figure 7.10). Over the same period, the start of the spring bloom has occurred earlier, and the percentage of young *C. finmarchicus* found during annual sampling cruises in late May has increased. The inference is that increasing temperatures and earlier blooms are leading to earlier reproduction and enhanced population development rates of *C. finmarchicus*. Future temperature increases will probably maintain this trend.

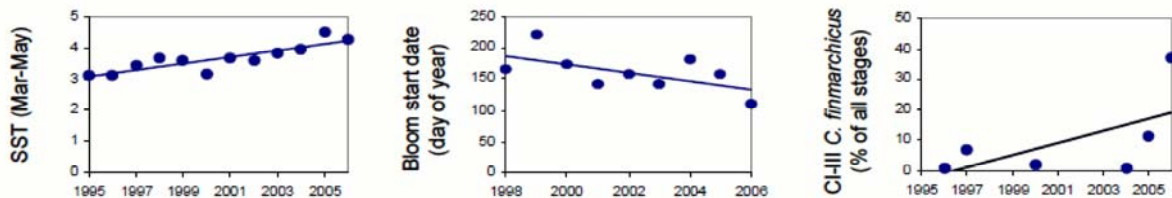


Figure 7.10. (a) Changes in late winter–spring temperatures; (b) the timing of the start of the spring bloom; and (c) the percentage of young *Calanus* (CI–CIII) present in late May in the central Labrador Sea. (Based on Department of Fisheries and Oceans (DFO), Canada time-series.)

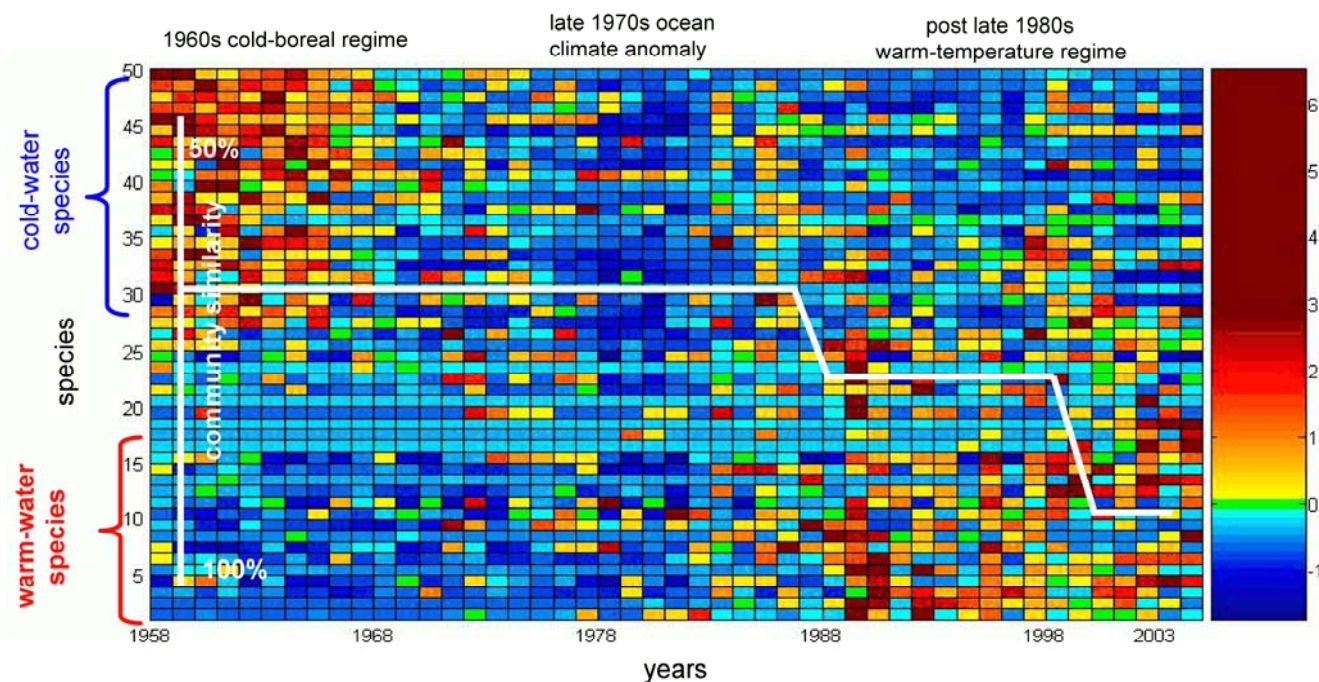


Figure 7.11. Continuous Plankton Recorder (CPR) data showing the results of a meta-analysis of 50 plankton species in the central North Sea (standardized abundance). The white line shows the community regime-shift index based on percentage similarity between 2006 and preceding years, calculated using displacement sequential regime detection (minimum regime shift = 10 years). (Modified from Edwards *et al.*, 2008.)

In the North Atlantic, substantial ecosystem changes seen across multiple trophic levels were demonstrated to be associated with temperature increases above a critical thermal boundary (Beaugrand *et al.*, 2008). This thermal threshold of 9–10°C, if crossed, will lead to changes in community structure, biodiversity, and carrying capacity. Such changes, especially when combined with fishing, may initiate a marked reduction in some fish stocks (e.g. the North Sea cod (*Gadus morhua*) stock).

Synchronous ecological regime shifts occurred in the central Baltic and North Sea in the late 1980s (Alheit *et al.*, 2005). The NAO index changed in the late 1980s (1987–1989) from a negative to a positive phase, which may have contributed to these regime shifts. Increasing SSTs were the main direct and indirect driving forces, however. After 1987, phytoplankton biomass in both systems increased, and the growing season was prolonged. The composition of phyto- and zooplankton communities in both seas changed conspicuously; for example, dinoflagellate abundance increased and diatom abundance decreased, whereas key copepod species, which are essential in fish diets, experienced pronounced changes in biomass (abundance of *Calanus finmarchicus* in the North Sea and of *Pseudocalanus sp.* in the Central Baltic fell to low levels, whereas *C. helgolandicus* in the North Sea and *Temora longicornis* and *Acartia spp.* in the Central Baltic were persistently abundant). The changes in biomass of these copepods had important consequences for the biomass, fisheries, and landings of key fish species.

The regime shift in the Baltic Sea was evident in all trophic levels, but zooplankton and fish were especially affected (Möllmann *et al.*, 2008). A copepod community dominated by *Pseudocalanus acuspes* changed to one dominated by *Acartia spp.*, which was attributed to lowered salinity and increased temperature. Although a link between hydrographic variability and changes in zooplankton and fish was recognized, it was noted that overfishing had probably amplified the climate-induced

changes at both trophic levels. This study indicated that (i) climatic and anthropogenic pressures may propagate through the foodweb via multiple pathways; (ii) both effects can act synergistically to cause and stabilize regime changes; and (iii) zooplankton play a crucial role in mediating these ecosystem changes.

In the Northwest Atlantic, a regime shift occurred in the early 1990s in response to changes in the freshwater export and circulation patterns in the Arctic Ocean (Pershing *et al.*, 2004; Greene *et al.*, 2008). This regime shift was associated with a freshening and stratification of shelf waters, which in turn led to changes in the abundance and seasonal cycles of phytoplankton, zooplankton, and organisms at higher trophic levels. On the other hand, it has been suggested that removal of top predators by overfishing would alter the plankton through a cascading effect (Frank *et al.*, 2005). It is likely that the recently observed ecological responses to Arctic climate change in the North Atlantic will continue into the near future if current trends in sea ice, freshwater export, and surface ocean salinity continue.

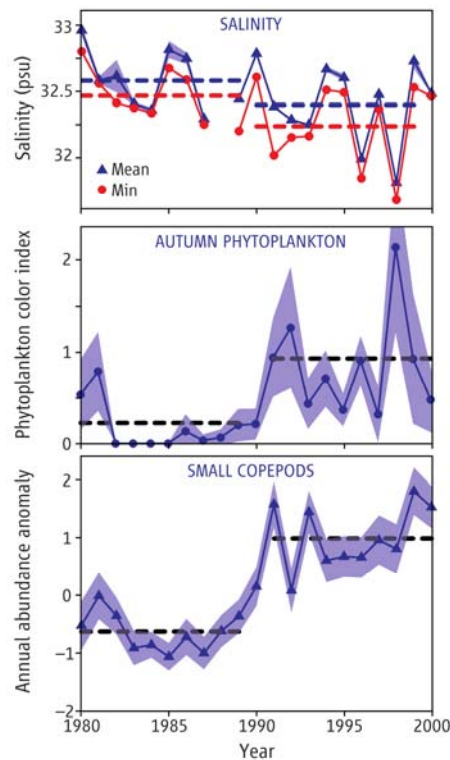


Figure 7.12. Salinity, phytoplankton, and zooplankton data from the Gulf of Maine and Georges Bank illustrate ecosystem changes associated with a regime shift. Dashed lines = mean values during 1980–1989 and 1990–1999; shaded areas = 95% confidence intervals. (a) Decadal mean salinities, based on annual mean (blue) and annual minimum (red) salinities (reported in Mountain, 2003): reduction after the regime shift. (b) Decadal mean autumn phytoplankton abundance, based on values of the annual mean Phytoplankton Colour Index (PCI; reported in Frank *et al.*, 2006): increase after the regime shift. (c) Decadal mean copepod abundance anomaly, based on the annual mean abundance of small copepods (reported in Durbin *et al.*, 2003): increase after the regime shift. (Source: Greene and Pershing, 2007.)

7.5 Effects on higher trophic levels: implications for fisheries

Given the importance of many zooplankton taxa as prey for larval and juvenile fish, the relative timing of zooplankton blooms and fish spawning is critical. This theory of the importance of trophic synchrony has been termed the “match–mismatch” hypothesis (Cushing, 1975). Climate change has the potential to alter the timing of fish spawning and egg development rates, as well as that of phytoplankton and

zooplankton blooms. Thus, poor “recruitment” in traditional fishery target species, such as cod, plaice (*Pleuronectes platessa*), and herring (*Clupea harengus*), is a potential consequence of climate change.

There is evidence that the seasonal timing of phyto- and zooplankton production has altered in response to recent climate change, and that this may have influenced predator species, including fish (Edwards and Richardson, 2004; Richardson and Schoeman, 2004; ICES, 2010a). In the Northeast Atlantic, warmer conditions now prevail earlier in the year; this appears to have led to changes in plankton biomass and in the seasonal timing of plankton production, and thus to poor recruitment of several commercially important fish species and low seabird breeding success, particularly in the North Sea (Beaugrand and Reid, 2003; Beaugrand *et al.*, 2003; Frederiksen *et al.*, 2006; Payne *et al.*, 2009). In the Baltic Sea, the change in hydrography has affected the reproductive success of several fish species, resulting in a change in dominance from the piscivorous cod to the planktivorous sprat (*Sprattus sprattus*; Möllmann *et al.*, 2008). Changes in hydrological conditions influenced fish recruitment both directly (e.g. by reducing the areas of cod reproduction) and indirectly (by altering feeding conditions).

Further future warming is likely to alter the geographic distributions of primary and secondary pelagic production, with indirect effects on oxygen production, carbon sequestration, and biogeochemical cycling. Changes in pH are also inevitable, with the lowest values mainly occurring in colder waters. All of these changes may place additional stresses on already-depleted fish stocks and have consequences for dependent species, such as mammals and seabirds.

Climate-induced change could also alter the relative abundance of permanent (holoplanktonic) and temporary (meroplanktonic) zooplankton species. In the North Sea, for example, a stepwise increase in sea temperature has coincided with an increase in the abundance of phytoplankton and meroplankton (particularly the larvae of the sea urchin (*Echinocardium cordatum*)) since the late 1980s (Kirby *et al.*, 2007). This change in foodweb structure, hypothesized to be the result of the competitive exclusion of the holozooplankton by the meroplankton, may have significantly diminished the transfer of energy towards top pelagic predators (e.g. fish) and increased the transfer to the benthos.

There are indications of an increase in the occurrence of jellyfish swarms in the Northeast Atlantic (Licandro *et al.*, 2010). Jellyfish feed on the eggs and larvae of commercially important fish (Greve, 1994; Bamstedt *et al.*, 1998), so outbreaks of jellyfish may ultimately lead to a reduction in the fish biomass available to fisheries. The introduction and continued presence of the ctenophore *Mnemiopsis leidyi* in the Baltic and North seas is of concern because this non-native species has had a pronounced negative impact on ecosystems in the southern seas of Europe (Javidpour *et al.*, 2006). The distribution pattern of *M. leidyi* in the Bornholm Basin has a substantial overlap with that of cod eggs. Predation of *M. leidyi* on cod eggs has the potential to alter recruitment success in this species, which is the top predator in the system, and thus to change the foodweb structure of the Baltic (Haslob *et al.*, 2007).

Although most studies demonstrate that hydrographic variability is the main factor controlling long-term changes in the plankton, recent research has suggested that removal of top predators from an ecosystem may also affect the trophic levels below by what is known as a “trophic cascade”. Studies in both the eastern and western North Atlantic suggest that climate and fishing may have synergistic effects on the

community composition and abundance of phytoplankton, zooplankton, and fish (Frank *et al.*, 2005; Casini *et al.*, 2008; Baum and Worm, 2009; Kirby *et al.*, 2009).

7.6 Conclusions

- An analysis of plankton time-series reveals that, in the North Atlantic, important changes have occurred in the abundance, distribution, community structure, and population dynamics of phytoplankton and zooplankton.
- These planktonic events appear to be responding to changes in regional climate, caused predominately by the warming of air and SSTs, and associated changes in hydrodynamics. Anthropogenic pressures (e.g. fishing) may also affect the community composition and abundance of plankton and may act synergistically with the climate.
- Changes in phytoplankton and zooplankton communities at the bottom of the marine pelagic foodweb may affect higher trophic levels (e.g. fish, seabirds), because the synchrony between predator and prey (match–mismatch) plays an important role (bottom–up control of the marine pelagic environment) in the successful recruitment of top predators, such as fish, seabirds, and mammals.
- The poor recruitment of several fish species of commercial interest and the low seabird breeding productivity recorded in recent years in some North Atlantic regions are associated with changes in plankton biomass and in the seasonal timing of plankton production.

7.6.1 Recommendations

- Long-term funding needs to be guaranteed in order to maintain the few time-series that exist at single sites and along transects, and to expand the CPR survey to cover unsampled and poorly sampled areas in the North Atlantic.
- Improved and systematic monitoring of jellyfish in coastal and offshore areas needs to be implemented in order to obtain a comprehensive overview of their spatial, vertical, and temporal distribution.
- Zooplankton should be included as a mandatory biological variable in the management of marine resources in different North Atlantic regions. In particular, abundance, biodiversity, and population dynamics (e.g. phenology) of zooplankton, as well as species that act as indicators of ecological status, should be monitored regularly.
- Anthropogenic activities (e.g. fishing) combined with climatic effects may put additional pressure on marine ecosystems. This possibility should be considered in the management of marine resources.

Acknowledgements

We thank the members of the ICES/IOC working groups on Zooplankton Ecology (WGZE) and Harmful Algal Bloom Dynamics (WG HAB) for assistance in preparing this report. Thanks are also due to A. Amorim and B. Dale for their helpful suggestions.