ICES Journal of Marine Science, 53: 972–977. 1996

Far-field control of long-term changes in Northumberland (NW North Sea) coastal zooplankton

Christopher L. J. Frid and Niette V. Huliselan

Frid, C. L. J., and Huliselan, N. V. 1996. Far-field control of long-term changes in Northumberland (NW North Sea) coastal zooplankton. – ICES Journal of Marine Science, 53: 972–977.

Zooplankton at a station 5.5 nautical miles off the Northumberland coast has been monitored monthly since 1968. Multivariate statistics distinguish two groups in the samples, with a change in community structure around 1979. These groups are not the result of dramatic changes in the occurrence of key species, but reflect small changes in abundance of many species. This study investigates the relationship between temporal changes in this community and local meteorological factors, far-field hydrographic/meteorological factors and internal, biotic, feedbacks, including availability of phytoplankton and abundance of predators. The results indicate good correlations for both zooplankton abundance and community structure with the position of the north wall of the Gulf Stream. Implications are discussed.

Key words: coastal waters, Gulf Stream, North Sea, time series, zooplankton.

Christopher L. J. Frid, and Niette V. Huliselan: Dove Marine Laboratory, University of Newcastle, Cullercoats, North Shields, NE30 4PZ, England, UK.

Introduction

The zooplankton community at a station off the Northumberland coast has been sampled monthly from 1968 to the present (see Evans, 1985; Roff *et al.*, 1988; Evans and Edwards, 1993). These studies have characterized the seasonal patterns of species abundance (Roff *et al.*, 1988), the annual productivity of the dominant copepods (Evans, 1985), the inter-annual variability of the zooplankton (Evans and Edwards, 1993), and established a relationship between productivity and standing stock of "over-wintering" copepods (Roff *et al.*, 1988).

Seasonal and inter-annual trends in copepod abundances, zooplankton composition and productivity have been examined in relation to macro-zooplankton, phytoplankton, and temperature in the North Sea (e.g. Vidal, 1980; Evans, 1981; Colebrook, 1979, 1982a,b, 1984, 1985a,b; Colebrook and Taylor, 1984; Roff *et al.*, 1988; Daan, 1989; Hannon and Joiris, 1989; Fransz *et al.*, 1991; Evans and Edwards, 1993). Some of these authors (Evans, 1981; Colebrook, 1979, 1982b, 1984, 1985b; Roff *et al.*, 1988; Fransz *et al.*, 1991; Evans and Edwards, 1993) have concluded that the size of the over-wintering stock of copepods plays a major role in determining total abundance of zooplankton and densities of specific species (e.g. *Acartia clausi* and *Pseudocalanus elongatus*) in the following summer.

Colebrook (1986) noted that there was a long-term decline in zooplankton abundance in CPR data for the western North Sea (including Northumberland waters) between 1950 and 1980. This decline was also recorded by Evans (1985; Roff *et al.*, 1988; Evans and Edwards, 1993). At the Northumberland station, the changes in abundance of some groups varied considerably. For example, *Acartia clausi* and *A. longiremis* were more abundant in the 1970s than in the 1980s. In contrast, the chaetognath *Sagitta elegans* was rare in the 1970s and increased in abundance in the 1980s. Overall, the holozooplankton reached a peak of abundance in 1975, declined sharply to 1980, and recovered in the 1980s (Evans and Edwards, 1993).

Different mechanisms have been proposed as the cause of inter-annual and longer-term changes in zooplankton communities. Long-term changes recorded by the CPR surveys have been correlated with the prevalence of either northerly or westerly winds (Colebrook and Taylor, 1979, 1984; Dickson *et al.*, 1988; Aebisher *et al.*, 1990). These winds would lead to changes in the degree of penetration of Atlantic Water into the North Sea (Taylor and Stephens, 1980; Taylor *et al.*, 1992), which may cause a direct injection of Atlantic species or alter species composition by changing the characteristics of North Sea water. Taylor and Stephens (1980) pointed out that the biological changes in the North Atlantic have occurred on a similar

1054–3139/96/060972+06 $18.00/0

temporal scale to the changes in the position of the Gulf Stream, with annual fluctuations in the number of copepods in the years 1966–1977 following the pattern of displacements in the Gulf Stream. Furthermore, Taylor and his co-workers (Taylor and Stephens, 1980; Aebisher *et al.*, 1990; Taylor *et al.*, 1992; Hays *et al.*, 1993; Taylor, 1995) have established a relationship between both the total abundance of North Sea zooplankton and various individual taxa, and the position of the north wall of the Gulf Stream. This relationship is again based on CPR data and the mechanism underlying the correlation is suggested to be the north–south displacement of storm tracks (Taylor *et al.*, 1992; Taylor, 1995).

It remains unclear whether and to what extent the zooplankton is responding directly to changes in hydrography associated with these mechanisms, or to changes in food supply, which are in turn controlled by variations in hydrography. There is a relationship between the abundance of copepods and the density of phytoplankton, as estimated by the green coloration of the meshes, in both the CPR data (Colebrook, 1984, 1986) and the Northumberland time series (Roff *et al.*, 1988; Evans and Edwards, 1993). The increased abundance of "Atlantic indicator species" in certain years suggests that at least some of the variation is the direct result of a greater penetration of Atlantic water into the North Sea.

This study presents analyses of the zooplankton at the Northumberland station for the period August 1968 to December 1993. The full data set is used to investigate the role of physical processes, i.e. displacements of the Gulf Stream position and local rainfall as an index of freshwater inflow to coastal waters and biological factors, such as phytoplankton and predator abundance, in controlling the observed long-term changes.

Materials and methods

Monthly sampling of zooplankton organisms at a fixed station about 5.5 nmi east of Blyth on the Northumberland coast at 55°07′N, 01°20′W was initiated in August 1968. The programme has run continuously up to the present, except in 1989 when only four months were sampled. The data set analysed here covers the period 1968 to 1993, excluding 1989. Sampling consisted of four vertical hauls, from a depth of 50 m to the surface (water depth approximately 53 m) to give a sample equivalent to a 200 m water column, using a 200 μm meshed WP2 net (UNESCO, 1968) with a mouth area of 0.25 m^2. A flowmeter was mounted in the mouth of the net to allow determination of the exact volume of water filtered. The catch from the four hauls was pooled and preserved immediately in 4% buffered formaldehyde in sea water.

In the laboratory, zooplankton was identified to species level whenever possible and counted. Certain taxa were subdivided into sexes, or were categorized as juveniles and adults.

The data used in this study are estimates of monthly abundances (number of individuals m^{-3}) of species and annual means. Prior to analysis, data were transformed (log (x+1)). Because of the large size of the biological/ecological data matrix, the analysis focuses on community parameters such as total abundance or key groups, i.e. copepods. The time series was initially examined using trend analysis with the fitting of linear, quadratic, growth and Pearl-Reed logistic models. Minimization of the mean absolute percentage error (MAPE) was used as the criteria for the selection of the most appropriate model. Both univariate (regression and product–moment correlation) and multivariate (principal component analysis) statistical methods were used to elucidate species assemblages and their temporal patterns. For multivariate analysis the data were reduced prior to analysis by maintaining only those species which comprised 75% of the community by abundance.

The environment was characterized by three variables: (i) the position of the north wall of the Gulf Stream (derived from the first principal component of its position at six longitudes; see Taylor and Stephens (1980) for details), (ii) local freshwater inputs (and associated inputs of nutrients from coastal sources) as indexed by the rainfall recorded at the local (Blyth, Northumberland) gauging station, and (iii) phytoplankton abundance as recorded by the CPR Net Colour Index (see Buchanan (1993) for details and justification). Predation pressure was indexed by two variables, consisting of the total abundance of "winter" (chaetognaths, hyperiid amphipods, and euphausiids) and "summer" (ctenophores, medusae, and fish larvae) predators each year (following Roff *et al.*, 1988).

Results

Principal component analysis of the species abundance matrix (annual means) showed that the first three axes explained approximately 40% of the total variance in the zooplankton community. The taxa that contributed most to the formation of the first two axes were *Calanus* spp., *Pseudocalanus elongatus*, *Paracalanus parvus*, *Metridia lucens*, *Centropages typicus*, *Acartia clausi*, *A. longiremis*, *Sagitta elegans* and *Semibalanus balanoides* (nauplii and cyprids). Most of the dominant species had high positive values for the first eigenvector, indicating that the first component represented species/taxa that were common to all years. There was a tendency for the years up to 1980 to separate on PCA axis 2 (Fig. 1), a pattern that was more distinct in multi-dimensional

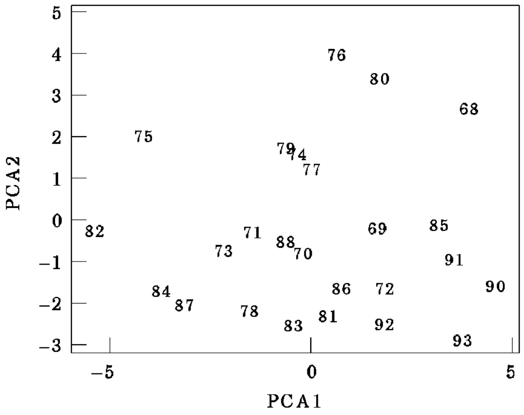

Figure 1. Principal component scores of the species abundance matrix, 1968–1993. PC axis 1 accounts for 19% of the variation and PC axis 2 for a further 11%.

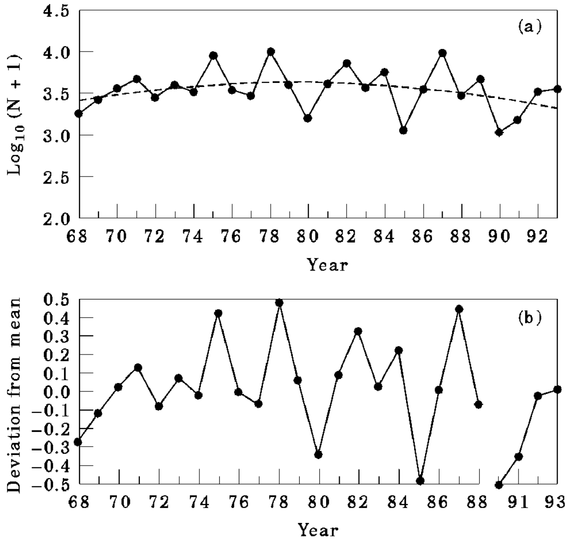

Figure 2. Total abundance of copepods, 1968–1993. (a) Annual abundance (solid line) and trend line produced by fitting a quadratic model (MAPE=5.18%; dashed line); (b) abundance as deviations from the long-term mean.

scaling ordinations of the 1968–1988 data set (see Evans and Edwards, 1993).

The annual mean abundance of total copepods appears relatively constant through time (Fig. 2a). Trends are more apparent when the deviations from the long-term mean are plotted (Fig. 2b). Trend analysis showed that the time series was best modelled (MAPE=5.1%) by a quadratic model (Fig. 2a). Total copepod abundance tended to increase from the beginning of the time series until 1979; the observed abundance in 1980 was very low and there was then a downward trend until 1990/91, with the exception of a high in 1987.

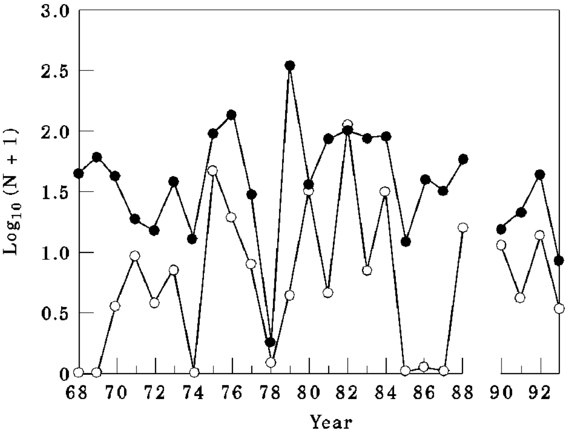

Figure 3. Abundance of winter (chaetognaths, hyperiid amphipods and euphausiids – ●) and summer (ctenophores, medusae and fish larvae – ○) planktonic predators, 1968–1993.

None of the principal predatory groups showed any clear long-term trends, either individually or when combined into seasonal groups (Fig. 3).

Possible explanations for the changes in total zooplankton, total copepods, and community structure (as indexed by PCA1; Bakus, 1990) were investigated by the use of multiple regression models. The independent variables used were: the position of the north wall of the Gulf Stream (Fig. 4a), the CPR net colour index (Fig. 4b), the rainfall at Blyth (Fig. 4c), and the abundance of summer and winter predators (Fig. 3). In addition, time-lags of 1 and 2 years were imposed between the zooplankton data and the possible forcing functions.

For each of the dependent variables examined, the position of the north wall of the Gulf Stream explained around 20% of the variation (Table 1, Fig. 5). The correlation of total copepods with the Gulf Stream position (GSP) was negative, i.e. copepod populations were suppressed in years when the north wall was further north. However, there were only 3 years with a large northward shift of the GSP (Fig. 5). Including additional factors did not greatly increase the amount of variation explained by the regression models. The abundance of summer or winter predatory plankton was not significant in any model. A time-lag of 2 years increased the variation explained by rainfall and phytoplankton (Table 1), but the proportion explained was still minor compared to the contribution of the GSP. A time-lag of 1 year had no effect on the explained variation (results not shown).

Discussion

The last 25 years have seen considerable inter-annual variation in the zooplankton off the Northumberland coast. This variation is apparent in both the abundance

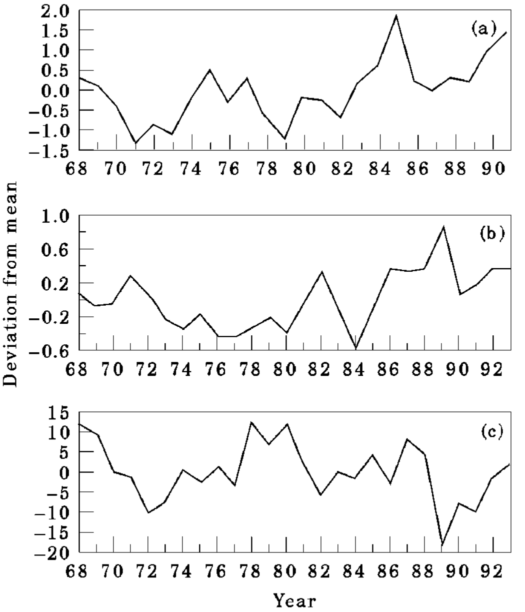

Figure 4. Time series of environmental factors, 1968–1993. (a) The first principal component of the Gulf Stream position; (b) CPR net colour index for area C2; and (c) rainfall recorded at Blyth.

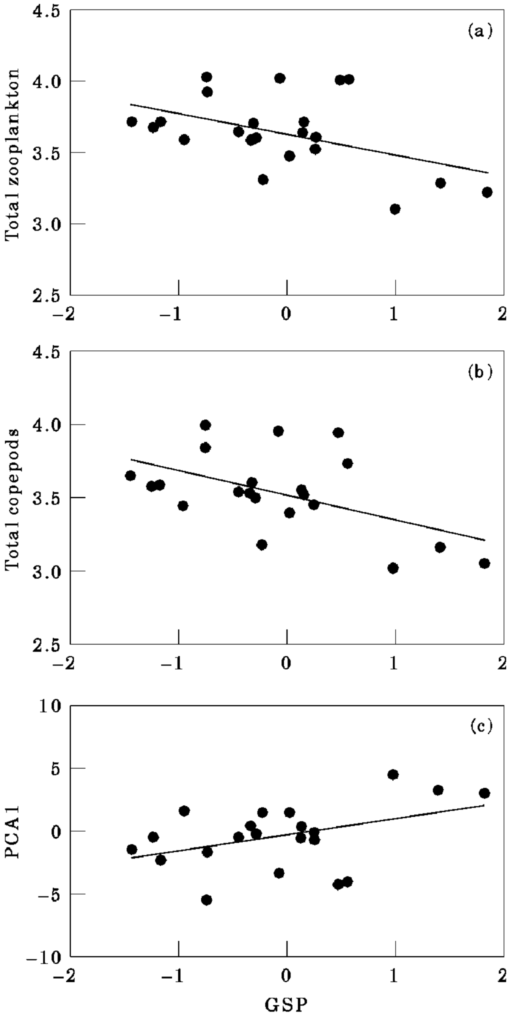

Figure 5. Regressions (n=22, significant, $p<0.01$, in all cases), 1968–1993. (a) Total zooplankton ($Y=3.616-0.1502$ X; $r^2=0.22$) vs Gulf Stream position (GPS): (b) total copepods ($Y=3.510-0.1731$ X; $r^2=0.27$) vs GPS; and (c) the first principal component axis of the species abundance matrix ($Y=-0.14+1.370$ X; $r^2=0.18$) vs GPS.

and the community structure. Analysis of the benthos at the same station has shown a change in the dynamics of the system in 1981, which was correlated with a change in the dynamics of the phytoplankton 2 years earlier, i.e. 1979 (Buchanan, 1993; Frid *et al.*, this volume). This event coincides with a marked shift in the structure of the zooplankton community (Evans and Edwards, 1993) and raises the possibility that both the zooplankton and the benthos at this site are closely coupled with the dynamics of the local phytoplankton.

Roff *et al.* (1988) showed that at the Northumberland station the abundance of copepods between April and July was highly correlated with the abundance of phytoplankton 2 months earlier. They took this to imply an annual period of food limitation/resource control. In both CPR data from the North Sea (e.g. Colebrook, 1979, 1984) and the Northumberland time series (Roff *et al.*, 1988; Evans and Edwards, 1993), there is a correlation between the size of the over-wintering copepod population and the abundance the following summer. The amount of over-winter mortality is, at least partially, determined by predation, especially by hyperiid amphipods and chaetognaths (Frid *et al.*, 1994). Thus, there is strong evidence for regulation of copepod numbers by biological factors, predation, and food limitation, during much of the year. However, these factors do not appear to play a major role in determining the inter-annual variation (Table 1).

The results clearly demonstrate a correlation of both zooplankton abundance and community structure with Gulf Stream position. Taylor and his co-workers (Taylor and Stephens, 1980; Aebisher *et al.*, 1990; Taylor *et al.*, 1992; Hays *et al.*, 1993; Taylor, 1995) have already demonstrated such relationships for CPR data from areas to the west of the British Isles and in the northern North Sea. However, a relationship was absent in area C2 (offshore from Northumberland) and in the southern North Sea. They attributed this to the lack of seasonal stratification in these areas and hence a lack of coupling between production and wind-induced mixing (Taylor and Stephens, 1980; Taylor *et al.*, 1992; Taylor,

Table 1. The amount of variation explained (coefficient of determination – r^2) by various multiple regression models for the independent variables "total zooplankton" (log (N+1) m^{-3}), "total copepods" (log (N+1) m^{-3}), and "community structure", as indexed by Principal Component Axis 1. (NCI=Net Colour Index; GSP=Gulf Stream Position).

Factors in model (independent variables)	Explained variation (%) in Total zooplankton	Total copepods	PCA1
Rainfall	N.S.	N.S.	N.S.
NCI	N.S.	N.S.	N.S.
GSP	21.9	27.2	18.3
GSP and rainfall – 2 yr time-lag	22.6	25.3	14.0
GSP and NCI – 2 yr time-lag	15.5	22.0	9.2
GSP, NCI and rainfall – 2 yr time-lag	21.6	24.9	9.2

1995). In those areas where a relationship existed it was always positive, i.e. northward movements of the GSP increase the abundance of total copepods. For the coastal waters of Northumberland, in contrast to the adjacent CPR box, the relationship is as strong as those demonstrated for the northern North Sea. However, it is an inverse relationship, i.e. total copepod abundance is lower in years when the GSP is more northerly.

George and Harris (1985) identified a climatic influence on the abundance of crustacean zooplankton in Lake Windermere, a freshwater lake in NW England (54°22′N, 02°56′W). These fluctuations have also been correlated with the position of the Gulf Stream (Taylor, 1995). Unlike the zooplankton in the northern North Sea and NE Atlantic, but like the Northumberland zooplankton, the sign of the correlation was negative.

The relationship between Gulf Stream position and zooplankton is thought to be an indirect one, through changing weather patterns over the North Atlantic, and involves a biological magnification of the climatic signal (Taylor and Stephens, 1980; Taylor, 1995). In Lake Windermere, the direct control of zooplankton is thought to be via a reduction in mixing depth and an earlier phytoplankton bloom. This leads to a decreased match between populations of grazers and their food in years when the Gulf Stream track is more northerly. Off Northumberland, changes in the timing of the spring increase in phytoplankton may affect the productivity of grazing copepods. Roff *et al.* (1988) have shown phytoplankton limitation of copepod production during April–July, although there is no correlation between annual phytoplankton production and copepod abundance. In nearshore waters, the input of nutrients and detritus may both vary in response to changing weather patterns. These may influence the dynamics of inshore zooplankton but not be sufficiently far-ranging as to affect populations in the offshore areas sampled by the CPR.

While internal biological interactions play an important role in the within-year dynamics of the zooplankton at the station investigated (Roff *et al.*, 1988), this study shows that between-year variation is the result of climatic forcing. It is important to test the generality of the difference in sign of the relationship of zooplankton to Gulf Stream position between the coastal and freshwater habitats and that for CPR boxes in more oceanic areas. Oceanic areas may be responding directly to climatic variations, while coastal and freshwater systems may be responding indirectly, via changes in nutrient/detrital fluxes.

Acknowledgements

Data collection has been supported by funds from many sources, including the Natural Environment Research Council, the Manpower Services Commission, and the Asian Development Bank. The authors especially thank the Department of Marine Sciences, University of Newcastle and Dr Stewart Evans and Professor Nicholas Owens for continuing to fund the sampling when time series were unfashionable. The time series was initiated by Dr Frank Evans (15 Thirlmere Avenue, North Shields NE30 3UQ, UK), who would be pleased to assist research workers wishing to use his 1969–1988 data in further plankton studies. CPR Greenness data were kindly provided by Dr Andy Warner at the Sir Alister Hardy Foundation for Ocean Science and rainfall data were made available by the National Rivers Authority. Our thanks to both of them, and to Arnold Taylor of the Plymouth Marine Laboratory for copies of work in press. Thanks also to the masters and crews of the research vessels who have assisted in sampling over the last quarter of a century!

References

Aebischer, N. J., Coulson, J. C., and Colebrook, J. M. 1990. Parallel long-term trends across four marine trophic level and weather. Nature, London, 347: 753–755.

Buchanan, J. B. 1993. Evidence of benthic pelagic coupling at a station off the Northumberland coast. Journal of Experimental Marine Biology and Ecology, 72: 1–10.

Colebrook, J. M. 1979. Continuous Plankton Record: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. Marine Biology, 51: 23–32.

Colebrook, J. M. 1982a. Continuous Plankton Record: persistence in time-series and the population dynamics of *Pseudocalanus elongatus* and *Acartia clausi*. Marine Biology, 66: 289–294.

Colebrook, J. M. 1982b. Continuous Plankton Record: seasonal variation in the distribution of plankton in the North Atlantic and the North Sea. Journal of Plankton Research, 4: 435–462.

Colebrook, J. M. 1984. Continuous Plankton Record: relationship between species of phytoplankton and zooplankton in the seasonal cycle. Marine Biology, 83: 313–323.

Colebrook, J. M. 1985a. Sea surface temperature and zooplankton, North Sea, 1948 to 1983. Journal du Conseil International pour l'Exploration de la Mer, 42: 179–185.

Colebrook, J. M. 1985b. Continuous Plankton Record: overwintering and annual fluctuations in the abundance of zooplankton. Marine Biology, 84: 261–265.

Colebrook, J. M. 1986. Continuous Plankton Record: the distribution and standing crop of the plankton of the shelf and ocean to the west of the British Isles. Proceedings of the Royal Society, Edinburgh, 88B: 221–237.

Colebrook, J. M., and Taylor, A. H. 1979. Year-to-year changes in the sea temperature, North Atlantic and North Sea, 1948 to 1974. Deep-Sea Research, 26A: 825–850.

Colebrook, J. M., and Taylor, A. H. 1984. Significant time scales of long-term variability in the plankton and the environment. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 183: 20–26.

Daan, R. 1989. Factors controlling the summer development of copepod population in the Southern Bight of the North Sea. Netherlands Journal of Sea Research, 23: 305–322.

Dickson, R. R., Kelly, P. M., Colebrook, J. M., Wooster, W. S., and Cushing, D. H. 1988. North winds and production in the eastern North Atlantic. Journal of Plankton Research, 10: 151–169.

Evans, F. 1981. An investigation into the relationship of sea temperature and food supply to the size of the planktonic copepod *Temora longicornis* Muller in the North Sea. Estuarine and Coastal Shelf Science, 13: 145–158.

Evans, F. 1985. The marine fauna of the Cullercoats district. 16. Zooplankton. Report of the Dove Marine Laboratory, Cullercoats, Northumberland (series 3), No. 3. 119 pp.

Evans, F., and Edwards, A. J. 1993. Changes in the zooplankton community off the coast of Northumberland between 1969 and 1988, with notes on changes in the phytoplankton and benthos. Journal of Experimental Marine Biology and Ecology, 172: 11–29.

Fransz, H. G., Colebrook, J. M., Gamble, J. C., and Krause, M. 1991. The zooplankton of the North Sea. Netherlands Journal of Sea Research, 28: 1–52.

Frid, C. L. J., Buchanan, J. B., and Garwood, P. R. 1996. Variability and stability in the benthos: 22 years of monitoring off Northumberland. ICES Journal of Marine Science, 53: 978–980.

Frid, C. L. J., Newton, L. C., and Williams, J. A. 1994. The feeding rates of *Pleurobrachia* (Ctenophora) and *Sagitta* (Chaetognatha), with notes on the potential seasonal role of planktonic predators in the dynamics of North Sea zooplankton communities. Netherlands Journal of Aquatic Ecology, 28: 181–191.

George, D. G., and Harris, G. P. 1985. The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. Nature, London, 316: 536–539.

Hannon, B., and Joiris, C. 1989. A seasonal analysis of the southern North Sea ecosystem. Ecology, 70: 1916–1934.

Hays, G. C., Carr, M. R., and Taylor, A. H. 1993. The relationship between Gulf Stream position and copepod abundance derived from the Continuous Plankton Recorder Survey: separating biological signal from sampling noise. Journal of Plankton Research, 15: 1359–1373.

Roff, J. C., Middlebrook, K., and Evans, F. 1988. Long-term variability in North Sea zooplankton off the Northumberland coast: productivity of small copepods and analysis of trophic interaction. Journal of the Marine Biological Association UK, 68: 143–164.

Taylor, A. H. 1995. North–south shifts of the Gulf Stream and their climatic connection with the abundance of zooplankton in the UK and its surrounding seas. ICES Journal of Marine Science, 52: 711–721.

Taylor, A. H., Colebrook, J. M., Stephens, J. A., and Baker, N. G. 1992. Latitudinal displacements of the Gulf Stream and the abundance of plankton in the North-East Atlantic. Journal of the Marine Biological Association UK, 72: 919–921.

Taylor, A. H., and Stephens, J. A. 1980. Latitudinal displacements of the Gulf Stream (1966 to 1977) and the relation to changes in temperature and zooplankton abundance in the NE Atlantic. Oceanologica Acta, 3: 145–149.

UNESCO. 1968. Zooplankton sampling, Monogr. Oceanogr. Method. 2., D. J. Tranter J. H. Fraser (eds). UNESCO Public., Paris, 174 pp.

Vidal, J. 1980. Physioecology of zooplankton. IV. Effects of phytoplankton concentration, temperature, and body size on the net production of *Calanus pacificus*. Marine Biology, 56: 203–211.