Vol. 119: 299-303, 1995 | MARINE ECOLOGY PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published March 23

NOTE

A change in the zooplankton of the central North Sea (55° to 58° N): a possible consequence of changes in the benthos

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ABSTRACT: The mesozooplankton taken in continuous plankton recorder samples from the central North Sea has changed from being numerically dominated by holoplanktonic calanoid copepod species from 1958 to the late 1970s to a situation where pluteus larvae of echinoid and ophiuroid echinoderms have been more abundant than any single holoplanktonic species in the 1980s and early 1990s. The abundance of the echinoderm larvae as a proportion of the zooplankton taken in the samples has followed a continuous increasing trend over the Dogger Bank, but off the eastern coast of northern England and southern Scotland the increase did not become obvious until the 1980s. This trend is consistent with reported increases in abundance of the macrobenthos. It is proposed that changes in the benthos have influenced the composition of the plankton.

KEY WORDS: Holoplankton · Meroplankton · Macrobenthos · Echinoderm · Larvae · North Sea

The benthos off northeastern England has been monitored since 1971 (Buchanan 1993) and in the Skagerrak-Kattegat area since 1973 (Josefson et al. 1993). In addition the abundance and biomass of macrobenthos on the Dogger Bank in the period 1950 to 1954 has been compared with those in the same area in 1985 to 1987 (Kröncke 1992). Numbers of benthic organisms at a station off northeastern England were stable during the period 1973 to 1981, with 2000 to 3000 ind. m^{-3} in samples taken in March of each year. Between 1982 and 1992 numbers were much more variable but were usually about double the values for the stable period. The biomass of the benthos in the Skagerrak-Kattegat area increased between 1973 and 1989 to levels 2 to 4 times those at the start of the period. Most of the increase has been since 1980. The biomass of the benthos of the Dogger Bank was 2.5 to 8 times higher in 1985 to 1987 than in 1950 to 1954.

Methods and results. Pelagic larvae of the benthic macrofauna occur in plankton samples taken by continuous plankton recorders (CPRs). The mesozooplankton of the North Sea has been monitored using CPRs towed at monthly intervals by merchant vessels on regular routes and analysed using consistent methods of analysis since 1946 (Rae 1952, Colebrook 1960, Edinburgh Oceanographic Laboratory 1973). Analyses of the year-to-year changes have shown a decline in abundance of the zooplankton until the late 1970s with a subsequent partial recovery, trends which correlate with climatic variables (Aebischer et al. 1990, CPR Survey Team 1993). These analyses have been based mainly on analyses of widespread and abundant holoplankton (Colebrook 1978). The long-term benthic studies have been compared with the results from the CPR survey (Austen et al. 1991) but the only meroplanktonic group included in the community analysis of the CPR data set was the decapod larvae.

Changes in dominance have been examined as part of a programme on year-to-year changes in diversity in the plankton taken by the CPR. The taxonomic resolution of the sample analysis has been constant since 1958. Initial analyses of diversity have been restricted, therefore, to the period 1958 to 1991. Numbers of each of the consistently identified taxa (species, genera or higher taxa) were extracted for 3 areas of the North Sea: 58° to 61° N, 55° to 58° N and south of 55° N. Dominance was measured by several indices including the Berger-Parker index ($d = N_{max}/N$, where N_{max} is the number of individuals of the most abundant taxon, and N is the total numbers of individuals). In the central North Sea (55° to 58° N) the dominant taxa (i.e. the source of N_{max} for each year) were holoplanktonic

*Deceased August 1994

Table 1. Dominant zooplankton taxa in continuous plankton records in the Central North Sea. Acartia: *Acartia clausi*; Calanus I–IV: *Calanus finmarchicus* s.l. copepodite stages I–IV; Para-Pseudo: *Paracalanus* spp. and *Pseudocalanus* spp.; Limacina: *Limacina retroversa*; Pelecypoda larvae: Pelecypoda (Bivalve) larvae; Echino. larvae: echinoderm larvae

Year	Total area	Area 1	Area 2	Areas 1 & 2
1958	Para-Pseudo	Para-Pseudo	Para-Pseudo	Para-Pseudo
1959	Para-Pseudo	Para-Pseudo	Para-Pseudo	Para-Pseudo
1960	Para-Pseudo	Limacina	Para-Pseudo	Para-Pseudo
1961	Limacina	Acartia	Limacina	Limacina
1962	Echino. larvae	Acartia	Para-Pseudo	Para-Pseudo
1963	Calanus I–IV	Pelecypoda larvae	Para-Pseudo	Pelecypoda larvae
1964	Calanus I–IV	Acartia	Calanus I–IV	Calanus I–IV
1965	Para-Pseudo	Acartia	Para-Pseudo	Acartia
1966	Calanus I–IV	Acartia	Echino. larvae	Acartia
1967	Acartia	Acartia	Para-Pseudo	Acartia
1968	Acartia	Acartia	Echino. larvae	Acartia
1969	Para-Pseudo	Acartia	Para-Pseudo	Para-Pseudo
1970	Calanus I–IV	Acartia	Echino. larvae	Echino. larvae
1971	Acartia	Acartia	Para-Pseudo	Acartia
1972	Para-Pseudo	Acartia	Para-Pseudo	Acartia
1973	Para-Pseudo	Acartia	Para-Pseudo	Para-Pseudo
1974	Para-Pseudo	Acartia	Echino. larvae	Acartia
1975	Para-Pseudo	Acartia	Echino. larvae	Acartia
1976	Acartia	Acartia	Echino. larvae	Acartia
1977	Calanus I–IV	Acartia	Para-Pseudo	Para-Pseudo
1978	Echino. larvae	Acartia	Calanus I–IV	Acartia
1979	Echino. larvae	Acartia	Para-Pseudo	Acartia
1980	Echino. larvae	Acartia	Calanus I–IV	Calanus I–IV
1981	Echino. larvae	Echino. larvae	Calanus I–IV	Calanus I–IV
1982	Echino. larvae	Acartia	Echino. larvae	Echino. larvae
1983	Echino. larvae	Acartia	Echino. larvae	Echino. larvae
1984	Acartia	Acartia	Acartia	Acartia
1985	Echino. larvae	Acartia	Echino. larvae	Echino. larvae
1986	Echino. larvae	Acartia	Echino. larvae	Echino. larvae
1987	Echino. larvae	Echino. larvae	Para-Pseudo	Echino. larvae
1988	Echino. larvae	Acartia	Echino. larvae	Echino. larvae
1989	Echino. larvae	Acartia	Limacina	Echino. larvae
1990	Echino. larvae	Echino. larvae	Echino. larvae	Echino. larvae
1991	Echino. larvae	Echino. larvae	Echino. larvae	Echino. larvae

calanoid copepods from 1958 to 1977 except for 1961 and 1962. From 1978 onward, echinoderm larvae were dominant in all years except 1984 (Table 1). The echinoderm larvae identified in CPR samples are almost entirely the pluteus larvae of echinoids and ophiuroids (Rees 1954) which are identified by their calcareous skeletal rods. The larvae of other echinoderms lack these rods and are rarely identified in the samples.

Due to changes in shipping routes a change in the sampling distribution occurred in the late 1970s, so the data were re-analysed to include only samples from 1° latitude × 2° longitude rectangles which had been sampled throughout the period. These could be grouped into an area adjacent to the east coast of northern England and southern Scotland (Area 1) and an area between 55° and 56° N from 1° W to 5° E (Area 2) (Fig. 1). In the former area echinoderm larvae were dominant only in 1981, 1987, 1990 and 1991 whereas in the latter area they were dominant in 2 years in the 1960s, 4 years in the 1970s, 5 years in the 1980s, and in 1990 and 1991 (Table 1). When data from the 2 areas were combined, echinoderm larvae were dominant in 1970 and then in every year from 1982 onward except for 1984.

The proportion of echinoderm larvae in the annual total counts of zooplankton (Pe) in CPR samples in the 2 consistently sampled areas, the combination of the 2 areas and the whole of the central North Sea are shown in Fig. 2. The plots show increased proportions of echinoderm larvae over the whole time period in all cases. The correlation coefficients (r) were 0.60 in Area 1, 0.61 in Area 2, 0.74 in Areas 1 and 2 combined and 0.61 in the whole area between 55° and 58° N. All of these were significant at the 0.1 % level. In the series from Area 1 and the total area the increasing trend is only consistent from the mid-1970s and values in the former clearly exceeded those from the late 1950s and early 1960s only during the 1980s. Comparing the

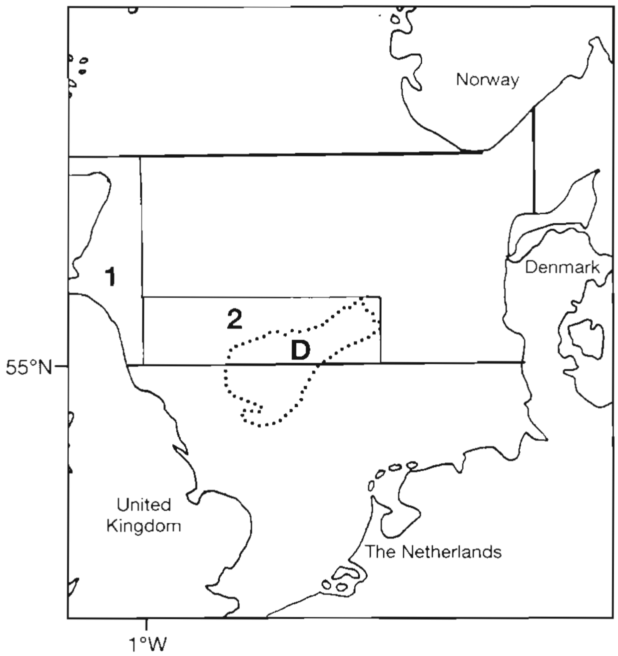

Fig. 1. The North Sea showing the boundaries of the central area, the consistently sampled areas (Areas 1 and 2) and the Dogger Bank (D)

results from the whole area with those from the regularly sampled sub-areas it is evident that the alteration in sampling distribution in the late 1970s exaggerated the abruptness of the change. In all cases the linear correlation is a very crude model for the pattern of variability and future application of techniques of time-series analysis may provide improved understanding of the changes.

The mean numbers per 3 m^3 sample (annual total count/annual total number of samples) and the 5 yr running means of echinoderm larvae and the 3 most abundant calanoid copepods over the whole area are shown in Fig. 3. The 5 yr running mean values for echinoderm larvae declined from 229 larvae per sample at the start of the period to ~100 in 1970 to 1971, then increased to >235 with highest values close to 300 from the mid-1980s (the correlation coefficient for the regression of numbers on time was 0.35, $0.01 < p < 0.05$). Abundance of *Acartia clausi* appears to follow a 9 to 10 yr cycle while *Calanus finmarchicus* and *Paracalanus* spp. combined with *Pseudocalanus* spp. both declined in abundance over the sampling period (r = 0.10 for *A. clausi*, −0.45 for *C. finmarchicus* and −0.60 for *Paracalanus* spp. with *Pseudocalanus* spp., not significant and significant at the 1% and 0.1% levels respectively). The recovery in abundance of echinoderm larvae started earlier than the general revival in numbers of zooplankton which started about 1980 (CPR Survey Team 1993).

Discussion. The most abundant echinoderm larvae in CPR samples from the North Sea in the period 1949 to 1951, the only period for which identifications have been published, were those of the echinoid *Echinocardium cordatum* (Rees 1954). In the Dogger Bank area the numbers of this species in the benthos appear to be stable (Kröncke 1992). The species of echinoderm associated with the increase in benthic biomass is the ophiuroid *Amphiura filiformis* (Kröncke 1992, Buchanan 1993, Josefson et al. 1993), the abundance of which appears to have been depressed in the early 1950s due to the cold winter of 1947 (Duinveld et al. 1987). This species is among the macrofaunal species

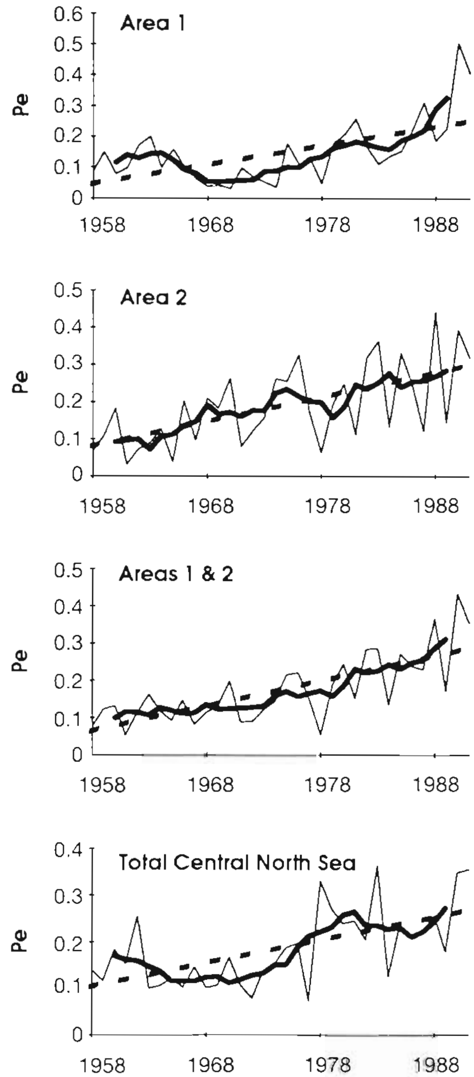

Fig. 2. Annual mean numbers per sample (——), 5 yr running means (▬▬) and linear regression (▪ ▪) of the abundance of echinoderm larvae as a proportion of the zooplankton counts (Pe) from CPR samples in Area 1, Area 2, Areas 1 & 2 and the whole central North Sea, 1958 to 1991

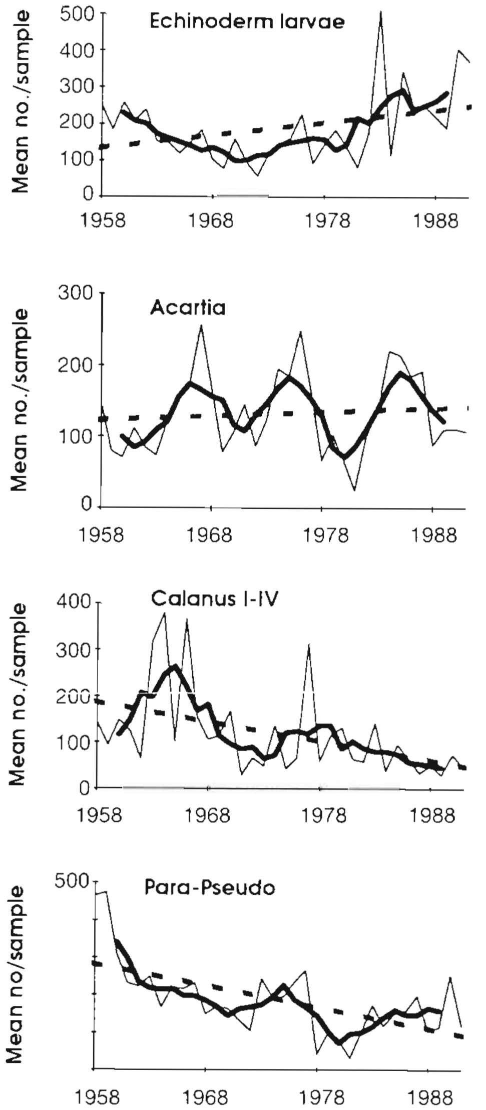

Fig. 3 Annual mean numbers per sample (-———), 5 yr running means (▬▬) and linear regression (▬ ▬) of echinoderm larvae, *Acartia clausi*, *Calanus finmarchicus* s. l. copepodite stages I–IV and *Paracalanus* spp. & *Pseudocalanus* spp. in the central North Sea

which increase in abundance in response to organic enrichment.

In 1949 to 1951 the larvae of *Echinocardium cordatum* and *Amphiura* spp. were most abundant in the summer, with maxima of the former in July and of the latter in July to September (Rees 1954). Preliminary inspection of seasonal cycles in the central North Sea from 1958 to 1991 shows the seasonal cycle with 1 to 3 mo of high abundance, centred between mid-June and mid-August in most years. The concentrated seasonal production of larvae provides possible competition with holoplanktonic filter feeders for food resources at the time of peak abundance of many planktonic copepods, cladocerans and appendicularians (Fransz et al. 1991) as well as larval stages of some euphausiids (Lindley 1980, 1982).

Interaction between the plankton and benthos influences the structure of both communities (Warwick et al. 1986). Changes in the amount of phytoplankton available to the benthos are directly related to the abundance and biomass of the benthic fauna (Pearson & Rosenburg 1978). Increasing abundance of the benthic fauna off northeast England has been correlated with increased phytoplankton in the CPR records from that area (Buchanan 1993); details of year-to-year variations in the benthos are closely related to the CPR phytoplankton with a time lag of 2 yr. Changes in the benthos in the Skagerrak-Kattegat area have been linked to eutrophication due to nutrients in land run-off, with high correlations between annual run-off and benthic macrofaunal abundance with lags of 0, 1 or 2 yr at different stations (Josefson et al. 1993). Kröncke (1992) considered that eutrophication was possibly a contributory cause of the increase on the Dogger Bank. However the low abundance of phytoplankton in CPR records in the 1970s was part of a pattern of change, correlated with climate, similar to that of zooplankton (CPR Survey Team 1993) with minimum values in the 1970s. The levels of phytoplankton abundance in the late 1950s were similar to or higher than those in the 1980s (Aebischer et al. 1990). Therefore, the increase in relative importance of echinoderm larvae may be at least partially independent of the annual levels of abundance of phytoplankton. The possibility remains that changes in seasonal cycles or composition of the phytoplankton may have preferentially benefited echinoderm larvae.

The North Sea Task Force (1993) has drawn attention to the effects on the benthos of anthropogenic activities. Epifauna is damaged by towed demersal fishing gear, and infauna particularly by beam trawls. The damage to the benthos resulting from beam trawling (Bergman & Hup 1992) is principally mortality of sessile forms and those with brittle shells or tests (Rumor & Krost 1991). Ophiuroid populations are damaged to a lesser extent than are echinoids (Bergman & Hup 1992). Species capable of exploiting the dead or damaged organisms or the products of their decay may benefit from the effects of fishing. Duinveld et al. (1987) suggested that reduction of flatfish stocks due to fisheries may have reduced predation pressure on *Amphiura filiformis*. It is possible, therefore, that fisheries may have influenced abundance of echinoderms and the relative abundance of the species producing the pluteus larvae. The intensity of beam trawling is lower in the area from the Dogger Bank northwards than in the Southern Bight; the bottom of parts of this area may be scoured more than once a year (North Sea

Task Force 1993). Any physical damage caused by fisheries to the populations of echinoderms which produce the larvae taken in the CPR appears to have been outweighed by increased phytoplankton production, the removal of predators, or other beneficial effects.

The increase in the relative importance of echinoderm larvae in the central North Sea indicates a possible effect on the pelagic ecosystem through the production of greater numbers of pelagic larvae by macrobenthos. The increase in the benthos reported from 3 areas of the North Sea suggests that it is unnecessary to seek explanations for the increase in the abundance of echinoderm larvae through improved larval survival or the consequences of changed vertical distributions on the results of single depth sampling by the CPR. However, there are no data available to test either of these possibilities. The consequences of the increased abundance of echinoderm larvae in the North Sea have yet to be explored but the role of meroplankton, including the fluxes between the benthos and the plankton at the beginning and end of pelagic development, need to be understood and quantified for modelling and managing the marine environment (Radford et al. 1988). Further research on the effects of anthropogenic nutrient input, fisheries, climatic change and natural variability in the populations on the plankton and the benthos are needed to establish with certainty the causes and consequences of the increase in abundance of echinoderm larvae.

Acknowledgements. We thank the owners, agents, masters and crews of the vessels which tow CPRs and all past and present members of the CPR Survey Team. The CPR survey is funded by the Ministry of Agriculture Fisheries and Food (UK), Department of the Environment (UK), Department of Fisheries and Oceans (Canada), NOAA/NSF (USA), the European Commission and Consortium (The Netherlands) and laboratory accommodation at PML is provided at subsidised rates by the Natural Environment Research Council (UK). The work of J.A.L. on this project constitutes part of the Plymouth Marine Laboratory Strategic Research Programme on coastal Biodiversity. We also thank the 3 anonymous reviewers for their helpful comments.

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This note was submitted to the editor

Manuscript first received: August 1, 1994
Revised version accepted: December 23, 1994