# COHERENCE IN ZOOPLANKTON OF A LARGE NORTHWEST ATLANTIC ECOSYSTEM[1]

K. SHERMAN,[2] J. R. GREEN,[2] J. R. GOULET,[2] AND L. EJSYMONT[3]

## ABSTRACT

Mesoscale measurements of zooplankton of the continental shelf off the northeast United States reveal previously unreported large-scale temporal and spatial coherence in the Gulf of Maine, on Georges Bank, off Southern New England, and in the Mid-Atlantic Bight. Unlike the apparent decline in zooplankton over the 30 years reported for the North Atlantic and North Sea, the zooplankton of the northeast shelf have not undergone any large-scale change in abundance or species composition since initial measurements made 70 years ago. Recent declines in fish populations of the shelf appear related more directly to excessive fishing mortality than to any changes in the abundance of zooplankton.

Zooplankton in marine ecosystems function as links between primary producers (phytoplankton) and predatory populations of fish, marine birds, and mammals. Mesoscale changes in zooplankton abundance have been associated with disruption of predator-prey relationships resulting in economically disastrous declines in fish stocks (Glover 1957; Glover et al. 1961; Williamson 1961; Jacobsen 1980). Although it has been demonstrated that large-scale (100-1,000 km) seasonal and annual variability in abundance of zooplankton has been associated with advective processes in the northeast Pacific and northeast Atlantic (Wickett 1967; Colebrook 1977, 1978a, b), we have not observed any large-scale changes in abundance of zooplankton off the northeast coast of the United States. The region has been under investigation since the turn of the century, but previous studies of zooplankton have been limited to restricted areas of the northeast shelf and covered relatively short periods of time (Fish 1925, 1936a, b; Bigelow 1926; Clarke and Zinn 1937; Bigelow and Sears 1939; Clarke 1940; Clarke et al. 1943; Deevey 1952, 1956, 1960; Grice and Hart 1962; Sherman 1968, 1970, 1976; Malone 1977; Judkins et al. 1980).

## METHODS

Our findings are based on 32 surveys of zooplankton conducted by the United States, Poland, Soviet Union, and German Democratic Republic between 1977 and 1981, as part of a joint MARMAP study of the ecosystem of the northeastern shelf (Sherman 1980). Between 6 and 8 surveys were done per year. Sampling was done in four subareas: Gulf of Maine, Georges Bank, Southern New England, and Mid-Atlantic Bight, each characterized by distinct bathymetry and circulation (Emery and Uchupi 1972; Butman et al. 1982) (Fig. 1). Zooplankton were collected at an average of 129 locations per survey situated 25-35 km apart, resulting in a total of 3,568 samples. The time-series analyzed for each subarea is shown in Figure 2. At each sampling location, tows for zooplankton, using a paired bongo-type sampler (Posgay and Marak 1980) with 60 cm openings and nets of 0.333 and 0.505 mm mesh, covered the water column obliquely from 5 m above bottom to the surface. These nets were towed at ship speeds from 1.5 to 3.5 kn, and were lowered at a wire speed of 50 m/min and retrieved at 20 m/min. Water filtered through the net was measured with a flowmeter and a time-depth recorder was used to measure the towing profile of the sampler.

Zooplankton samples were sorted, identified, and counted at the Plankton Sorting Center, Szczecin, Poland. The biomass of zooplankton is expressed as cc/100 m$^3$ of water strained; numerical abundance is expressed as numbers of zooplankters/100 m$^3$ of water strained. Patterns of abundance of the dominant zooplankters are based on the analysis of the size-fraction retained in the 0.333 mm net, which primarily captured late juvenile and adult copepods.

## RESULTS

### Coherent Patterns of Biomass

Displacement volumes expressed as cc/100 m$^3$ of

[1]MARMAP Contribution No. MED/NEFC 82-68.
[2]Northeast Fisheries Center Narragansett Laboratory, National Marine Fisheries Service, NOAA, South Ferry Road, Narragansett, RI 02882, U.S.A.
[3]Morski Instytut Rybacki, Zaklad Sortowania i Oznaczania Planktonu, 71-550 Szczecin, Poland.

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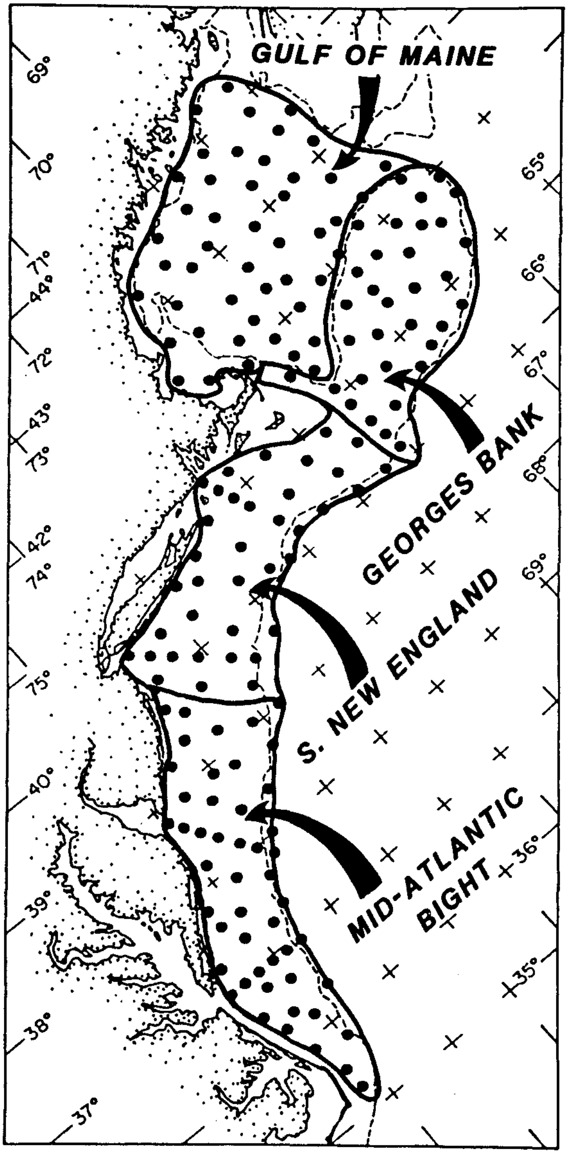



FIGURE 1.—The four geographic areas of the northwest Atlantic sampled for zooplankton during MARMAP operations from 1977 to 1981, with MARMAP station locations indicated by dots.

water strained are used to represent standing stocks of zooplankton. The seasonal patterns of zooplankton biomass observed each year and compared with the 5-yr means in each of the subareas, were coherent (Fig. 2a). The term coherent is used here to describe the recurring seasonal patterns of zooplankton biomass in which annual deviations from the 5-yr mean are insignificant at the 0.05 level (Table 1). On Georges Bank, the annual peak in spring (May) is followed by a sharp decline from late spring (June) through summer (August), and less precipitous decline from late summer through autumn to an annual low in winter. In the Gulf of Maine seasonal changes are not as pronounced as on Georges Bank, with the annual low in winter. The greatest change in biomass begins in April and reaches its annual high in May. From July until November, the standing stock does not undergo marked change, but declines gradually from November to a winter low in February. In Southern New England, zooplankton biomass is bimodal: an initial pulse occurs in May followed by a low in July, and a second peak occurs in August, followed by a decline in autumn and winter. In the Mid-Atlantic Bight biomass increases from an annual low in winter to an annual high in autumn.

TABLE 1.—Summary of probability statistics for the two-tailed Fisher-sign test for year-to-year coherence in the zooplankton volumes, dominance, and three dominant species—*Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus*. Annual departures from the MARMAP 5-yr mean annual cycle were tested for each subarea. The ranges of the probability of the Fisher-sign statistic are tabulated. Of the 100 tests (5 yr × 4 areas × 5 variables) only four reject the null hypothesis at 0.05 significance. $H_0$: annual cycle = 5-yr mean cycle; * = significant difference in the year indicated in parentheses.

| Survey variable | Subarea: Gulf of Maine | Georges Bank | Southern New England | Mid-Atlantic Bight |
|---|---|---|---|---|
| MARMAP | | | | |
| Volume | 0.344-0.875 | 0.031-0.910 | 0.227-0.656 | 0.109-0.812 |
| Dominance | 0.145-0.773, 0.007* (78) | 0.109-0.500 | 0.172-0.637 | 0.188-0.500 |
| *C. finmarchicus* | 0.344-0.773 | 0.109-0.891 | 0.500-0.656 | 0.188-0.812 |
| *P. minutus* | 0.344-0.773 | 0.188-0.891, 0.984* (79) | 0.344-0.656, 0.992* (79) | 0.500-0.812 |
| *C. typicus* | 0.227-0.891 | 0.344-0.891, 984* (77) | 0.227-0.891 | 0.500-0.891 |

## Coherence in Dominance

The Fager and McGowan (1963) index was used to identify the dominant zooplankters in each subarea by season. Of the 394 taxa in the samples, 50 were dominant in at least one location in one or more seasons. Summary statistics for all taxa, including rank, abundance, dominance, median abundance, and Delta-mean abundance (Pennington 1983), are available from the authors. Twelve taxa, all copepods, comprised 85% of the dominance—*Calanus finmarchicus*, *Pseudocalanus* sp., *Centropages typicus*, *Metridia lucens*, *Temora longicornis*, *Centropages hamatus*, *Acartia clausi*, *Acartia tonsa*, *Acartia* spp. (*A. clausi*-*A. longiremis*), *Oithona* spp., *Calanus* spp., and *Paracalanus parvus*. Among these 12 taxa, *Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* accounted for 75% of the total dominance.

## Species Shifts in Dominance

Although the three species co-occur on the shelf, their temporal and spatial patterns of dominance are different. These patterns are coherent among the 5 yr. The proportion of the total zooplankton accounting for these three dominant species is shown for each subarea as a function of time in Figure 2b. In the Gulf of Maine and over Georges Bank, *C. finmarchicus*, a species that overwinters in the cooler, deep waters of the Gulf of Maine (Bigelow 1926), is dominant in spring and early summer. During early autumn, when temperatures in the upper layer are warmest, dominance shifts to *C. typicus*, a species which undergoes greatest egg production in water warmer than 13°C (Dagg 1978). The shift from *C. finmarchicus* to *C. typicus* dominance occurs earlier (in late summer) on Georges Bank, where the change in abundance is of greater magnitude and persists to early winter. In the southern portion of the shelf, the dominance of *C. finmarchicus* in late spring is replaced by *P. minutus*, *C. typicus*, and other less-abundant zooplankters, including other copepods, cladocerans, larval echinoderms, salps, and barnacle larvae in Southern New England and principally cladocerans in the Mid-Atlantic Bight. Annual deviations in the dominance patterns of *C. finmarchicus*, *P. minutus*, and *C. typicus* from the 5-yr mean were insignificant at the 0.05 level in 95% of the comparisons made within the subareas (Table 1).

The numerical abundance of the three copepods were coherent within the envelope of one standard error of the mean and within the mean range in each of the subareas during the 5 yr (Fig. 2c). The zooplankton standing stocks, dominance patterns, and abundance levels of the principal species in each of the four subareas are different. The spring peak in zooplankton standing stock in the Gulf of Maine and on Georges Bank (Fig. 2a) is represented by *C. finmarchicus* in the Gulf of Maine and a combination of *C. finmarchicus* and *P. minutus* on Georges Bank, (Fig. 2b, c); the shift to *C. typicus* dominance in autumn is not of sufficient magnitude to register a secondary pulse in standing stock in the Gulf of Maine or Georges Bank.In Southern New England waters the bimodal peaks in zooplankton standing stock are represented by *C. finmarchicus* and *P. minutus* dominance in spring and early summer followed by large-scale *C. typicus* swarming in late summer and autumn (Fig. 2b, c). Further south in the Mid-Atlantic Bight, *C. finmarchicus* abundance is diminished, and is replaced by *P. minutus* and *C. typicus* in late winter and early spring, followed by an increase in the standing stock of zooplankton from summer through autumn (Fig. 2a) related to the growing abundance of cladocerans and other zooplankters in summer and large-scale swarming of *C. typicus* in autumn (Fig. 2b, c). Deviations from the 5-yr mean temporal patterns of abundance of the three dominant copepods were not significant at the 0.05 level in 95% of the comparisons (Table 1).

# DISCUSSION

Observations on the zooplankton of the northeastern continental shelf made during the past half century (Bigelow 1926; Bigelow and Sears 1939; Grice and Hart 1962; Judkins et al. 1980) can be divided into four periods: 1) The first measurement of volumes and species abundance made by Bigelow between 1912 and 1920, 2) the volume measurements by Bigelow and Sears from 1929 to 1932, 3) the volume and species measurements of Grice and Hart in 1960, and 4) the more contemporary measurements of species abundance made by Judkins et al. in 1975. Data from these studies were converted where possible from volumes per standard haul and volumes per square meter to volumes per 100 $m^3$; data from stations showing evidence of net clogging due to large amounts of gelatinous zooplankton, large number of organisms >2.5 cm length, or sampling gear and methods differing significantly from MARMAP methods were excluded. Throughout the sampling periods the mean seasonal zooplankton values of the earlier investigators were not significantly different from the mean values of the contemporary MARMAP data base (Table 2). The greatest range in biomass from year to year is on Georges Bank and is likely related to variability in retention of zooplankton resulting from the seasonal formation and decay of the Georges Bank gyre (Butman et al. 1982). In the earlier studies (Bigelow 1926; Bigelow and Sears 1939; Grice and Hart 1962; Judkins et al. 1980) copepods were the predominant zooplankters: *Calanus finmarchicus* and *Pseudocalanus minutus* were the most abundant species in the spring, with a shift to *Centropages typicus* in late summer and autumn. These three species are important links in the energetics of the shelf ecosystem since they provide food for larval, juvenile, and adult fish (Sherman and Honey 1971; Sherman and Perkins 1971; Marak 1974; Sherman et al. 1981b; Cohen and Lough 1982).

Our results provide evidence that the biomass and species compositon of zooplankton have not changed substantially over the past 70 yr. The persistent patterns of abundance and species dominance reflect coherence within the range of interannual variability observed since the early part of the century. These

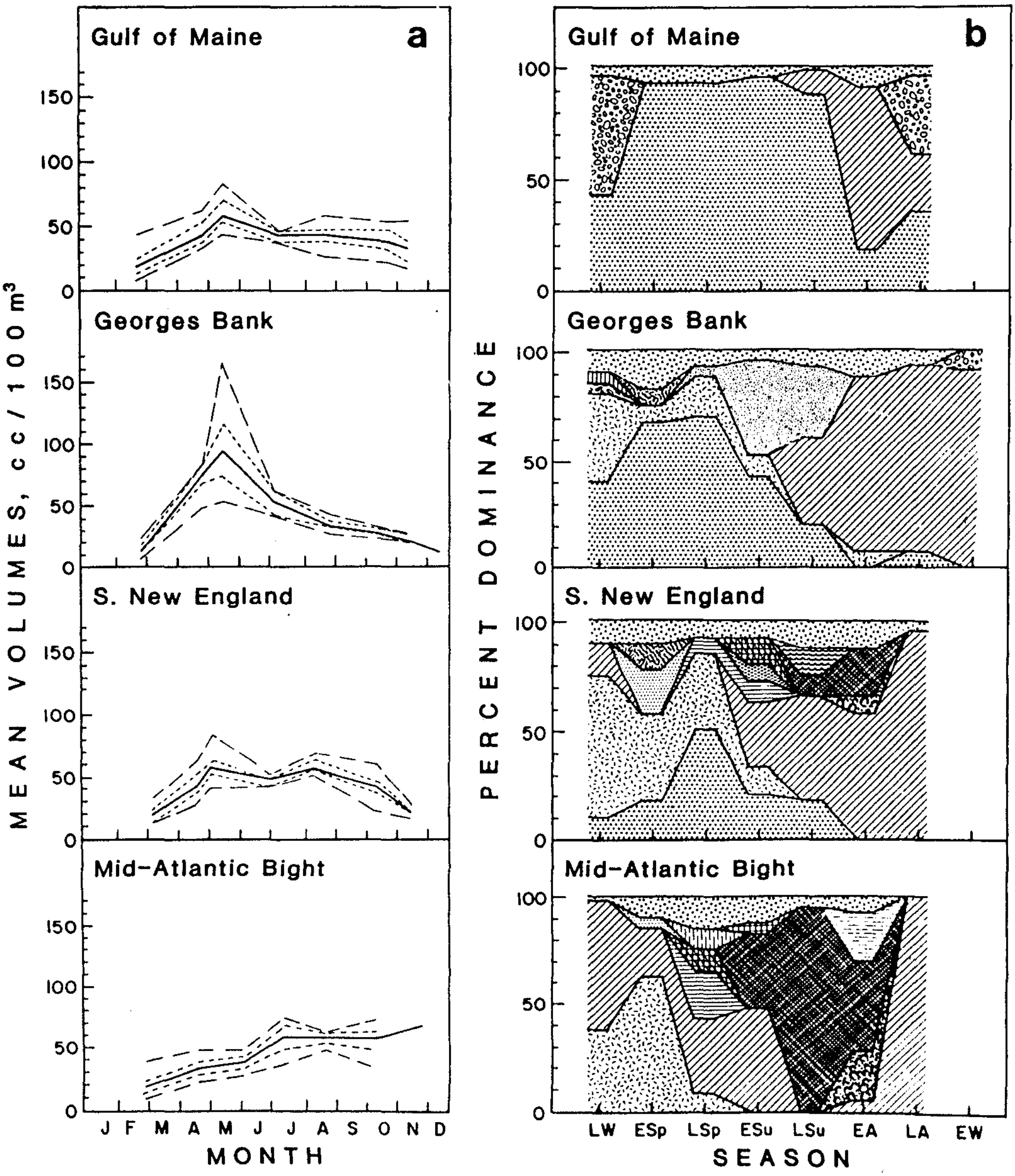
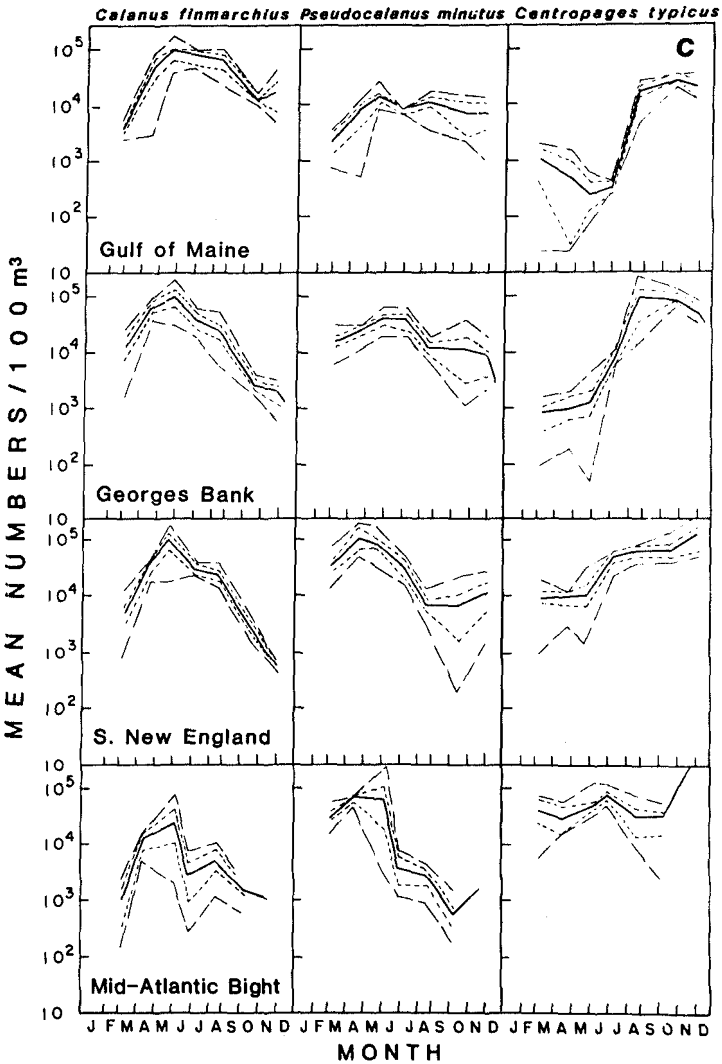



FIGURE 2.—Patterns of zooplankton coherence in four northeastern U.S. continental shelf subareas—Gulf of Maine, Georges Bank, Southern New England, and the Mid-Atlantic Bight. (a) Seasonal patterns in mean zooplankton standing stock (cc/100 m³) for the 5-yr MARMAP time-series; (b) seasonal patterns of dominance of zooplankters by subarea shown as a percentage of the samples with a dominant taxon on the 5-yr MARMAP time-series; (c) seasonal pulses in abundance of the three dominant copepod species—*Calanus finmarchicus*, *Pseudocalanus minutus*, and *Centropages typicus* (no./100 m³)—in each of the subareas for the 5-yr time-series. LW = late winter, ESp = early spring, LSp = late spring, ESu = early summer, LSu = late summer, EA = early autumn, LA = late autumn, EW = early winter, in panel b.




For b section

_____ = seasonal changes in mean abundance; ----- = one standard error above and below the mean; — — = minimum and maximum range above and below the mean, in panels a and c. = Calanus finmarchicus; = Pseudocalanus minutus; = Centropages typicus; = Centropages hamatus; = Penilia avirostris; = other (taxa <5%); = Metridia lucens; = Sagitta elegans; = Balanidae; = Temora longicornis; Acartia sp.; = Calanus sp.; = Evadne nordmanni; = Appendicularia; = Doliolidae; = Brachyura; = Echinodermata; = Thaliacea.

TABLE 2.—Comparisons of zooplankton volumes (cc/100 m³) by subarea between MARMAP data and the earlier studies on the northeast continental shelf. No significant differences were found between MARMAP data and earlier studies in comparisons of displacement volumes (Kruskal-Wallis $P > 0.05$). Volumes reported by Bigelow (1926) for late summer on Georges Bank were relatively high compared with those for the same season in MARMAP data. However, Bigelow's sampling was heavily biased towards the northeast peak of Georges Bank. The range of mean displacement volumes for that region in the MARMAP data is 24.4-191.7 cc/100 m³.

| | Late winter | Early spring | Late spring | Early summer | Late summer | Early autumn | Late autumn | Early winter |
|---|---|---|---|---|---|---|---|---|
| Gulf of Maine | | | | | | | | |
| MARMAP 1977-1981 | 10.9-47.0 | 34.6-65.2 | 44.0-83.2 | 40.3 | 31.8-58.0 | 23.3-57.5 | 18.4-53.9 | |
| Bigelow 1912-1920 | 17.8 | | | | 25.5-47.7 | | | |
| *P* | 0.380 | | | | 0.248 | | | |
| Georges Bank | | | | | | | | |
| MARMAP 1977-1981 | 11.4-24.0 | 50.2-86.5 | 56.2-166.0 | 46.2-65.8 | 31.4-43.9 | 25.8-37.2 | 23.2-28.8 | 13.9 |
| Bigelow 1912-1920 | 23.8 | | | | 74.9 | | | |
| *P* | 0.655 | | | | 0.157 | | | |
| Southern New England | | | | | | | | |
| MARMAP 1977-1981 | 13.2-33.5 | 32.0-66.5 | 46.7-85.4 | 43.4-54.4 | 57.4-69.2 | 24.2-60.9 | 21.4-28.4 | |
| Bigelow and Sears | | | | | | | | |
| 1929-1932 | 8.7-19.5 | 59.6-72.3 | 42.5-93.0 | 40.3-89.3 | | 38.0-40.6 | | |
| *P* | 0.180 | 0.101 | 0.631 | 0.157 | | 0.770 | | |
| Grice and Hart | | | | | | | | |
| 1960 | 12 | | | 40 | 61 | 38 | 14 | |
| *P* | 0.143 | | | 0.180 | 0.770 | 0.380 | 0.157 | |
| Mid-Atlantic Bight | | | | | | | | |
| MARMAP 1977-1981 | 11.8-39.6 | 25.2-51.5 | 29.5-50.9 | 41.0-73.2 | 50.4-66.0 | 37.4-76.0 | 70.1 | |
| Bigelow and Sears | | | | 38.6-52.4 | | | | |
| 1929-1932 | 33.6-39.1 | 27.0-48.7 | 24.7-75.1 | 0.248 | | 44.8 | | |
| *P* | 0.180 | 0.655 | 0.715 | | | 0.380 | | |

findings are in contrast with the 30-yr decline in zooplankton including the copepod component reported for large areas of the North Atlantic and North Sea (Colebrook 1978b). It appears that the climatic changes influencing the zooplankton decreases in the northeast Atlantic are more pronounced in the open ocean areas of the North Atlantic drift which in turn have greater impact on plankton in the North Sea (Colebrook 1978a, b, 1982; Garrod and Colebrook 1978). Based on MARMAP studies of the Northeast Fisheries Center, we have not detected large-scale influences of Gulf Stream eddies on populations of zooplankton or ichthyoplankton on the northwest Atlantic shelf (Laurence and Burns 1982; Cohen et al. 1982).

The fish stocks representing the mid-size predator component of the ecosystem of the northeast continental shelf have declined recently. During the period 1968 through 1975, the biomass of principle fish species declined about 50%. The decline was correlated with heavy fishing mortality (Clark and Brown 1977). The relative stability observed in both zooplankton standing stock and species composition when considered in relation to the decline in finfish biomass and subsequent population explosion of fast-growing, short-lived, zooplanktivorous sand eel (Sherman et al. 1981a) suggests that the reductions in fish abundance are not attributable to a lack of food at the lower end of the food chain. It appears that fishing mortality has imposed greater perturbations on fish populations of the northeast shelf than any changes in the abundance of zooplankton.

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