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ZOOPLANKTON PREY FIELD VARIABILITY DURING COLLAPSE AND RECOVERY OF PELAGIC FISH IN THE NORTHEAST SHELF ECOSYSTEM

K. Sherman[1], J. Green[1], A. Solow[2], S. Murawski[3], J. Kane[1], J. Jossi[1], and W. Smith[4]

[1]National Marine Fisheries Service
Northeast Fisheries Science Center
Narragansett Laboratory
Narragansett, RI 02882-1199

[2]Woods Hole Oceanographic Institution
Woods Hole, MA 02543

[3]National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole Laboratory
Woods Hole, MA 02543

[4]National Marine Fisheries Service
Northeast Fisheries Science Center
James J. Howard Marine Science Laboratory
Highlands, NJ 07732-0428

ABSTRACT

Since the mid-1970s, three pelagic fish species--herring, *Clupea harengus*; mackerel, *Scomber scombrus*; and sand eel, *Ammodytes* spp.--have undergone significant flips in biomass. The herring and mackerel stocks that declined from dominant to subordinate positions in the 1970s recovered to a present combined biomass exceeding 5 million metric tons. Sand eels, whose population levels exploded in the late 1970s and early 1980s, are now in decline. The effects of several million metric ton changes in biomass among these three species of zooplanktivores are examined in relation to possible density-dependent variability in zooplankton and pelagic fish within the Northeast Shelf Ecosystem.

CHANGES IN FISH ABUNDANCE WITHIN THE ECOSYSTEM

In an effort to reduce scientific uncertainties in fisheries management, increasing attention has been focused over the past few years on synthesizing available information on factors influencing the natural productivity of marine fish biomass from an ecosystems perspective (AAAS, 1993). One of the results of this effort has been a series of reports on the large-scale changes in fishery biomass yields of the Northeast Shelf Ecosystem during the past 30 years (Sissenwine, 1986; Murawski, 1991; Anthony, 1993).

From 1963 to the present, high valued groundfish species (gadoids, flounders) have declined to unprecedented low levels. Other demersal species, with low market value (spiny dogfish, *Squalus acanthias*; and skates[1]) have increased in abundance (Fig. 1). Another category of species, the principal pelagics, Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*), have undergone precipitous declines for the decade 1968 through 1978, followed by population recoveries from the 1980s to the present time (Fig. 1). Their recovery is attributed to reduced fishing effort (Murawski, 1991). The observed biomass "flip" of the principal pelagics from high levels in the 1960s to historically low levels in the 1970s and the present high biomass has been the dominant factor in the population explosion of sand lance, *Ammodytes* spp., during the latter half of the 1970s (Sherman et al., 1981), and the precipitous 4-yr decline in abundance from 1982 to 1985. Based on predator-prey studies, it was concluded that predation of sand lance in their early, planktonic developmental stages by the principal pelagics depressed the population of sand lance, following a period of approximately 6 yr (1976-1982) when the predation pressure was significantly reduced (Fogarty et al., 1991) (Fig. 2).

LONG-TERM TRENDS IN HERRING AND MACKEREL ABUNDANCE

The principal pelagics and sand lance are zooplanktivores (Bowman et al., 1984; Maurer, 1976; Michaels and Grosslein, in prep.). The long-term inverse relationship in abundance of the principal pelagics as discussed by Skud (1982) appears to have shifted during the past 30 yr from the trends in a 90 yr time series of landings data examined from 1870 through 1960. Based on an analysis of herring and mackerel catches in relation to temperature trends, Skud (1982) concluded that when one of the species was dominant, the other was subordinate in response to a combination of temperature and density-dependent competition between the two species. He argued that density (abundance) of the two species is "governed by the carrying capacity of the ecosystem and [that] the species apparent response to climate change is dependent on its position in the dominance hierarchy and its population size relative to its equilibrium density." Since 1960, this apparent relationship has

[1]Species of skates include: little skate (*Raja erinacea)*, winter skate (*R. ocellata*), barndoor skate (*R. laevis*), thorny skate (*R. radiata*), briar skate (*R. eglanteria*), leopard skate (*R. garmani*) and smooth-tailed skate (*R. senta*).

been modified by the high levels of fishing mortality from the late 1960s through the mid 1970s for Atlantic herring and mackerel (Murawski, 1991). Since 1982, the depressed mackerel stock has been undergoing significant rebuilding from an estimated stock biomass level of approximately 650,000 metric tons (mt) in 1982 to 2.8 million metric tons (mmt) in 1992. The rebuilding of the herring stock during the same decade has progressed from less than 100,000 mt to 2.7 mmt. Neither species can be considered subordinate. Both have undergone recovery and are at high abundance levels, simultaneously (Figs. 3 and 4), with as yet, no apparent adverse impact on the "carrying capacity" of the ecosystem, as suggested by Skud (1982).

ZOOPLANKTON COMPOSITION AND ABUNDANCE

The zooplankton of the Northeast Shelf Ecosystem has been examined for broad-area spatial and temporal trends in abundance and species composition since the mid-1960s (Sherman et al., 1983, 1988; Kane, 1993; Jossi and Goulet, 1993), and during four earlier periods. The first was the classic measurements of zooplankton volumes and species made by Bigelow during the first two decades of the century (1912 through 1920). The second, the volume measurements made by Bigelow and Sears in the late 1920s through the 1940s. The third covered the late 1930s to the 1960s, with the biomass and species demographic studies of Fish (1936a,b), Clarke and Zinn (1937), Clarke (1940), Redfield (1941), Clarke et al. (1943), Riley and Bumpus (1946), Deevey (1952, 1956, 1960a,b), Grice and Hart in 1962; and the fourth, the more contemporary measurements of Judkins et al. (1980), Dagg and Turner (1982), Davis (1984a,b), Townsend and Cammen (1988), and the recent study of Durbin and Durbin (in press) who examined the regulatory processes of the Northeast Shelf zooplankton (e.g., temperature, food, and predation).

During the decade 1977 to 1986, samples were collected using 0.333-mm mesh bongo nets towed obliquely through the water column to a maximum depth of 200 m. Tows of 15-min duration at 1.5 knots were made at 200 sampling stations in a grid network at 35 km spacing within the entire ecosystem, six or more times per year (Sibunka and Silverman, 1984, 1989) (Fig. 5). In addition to point-samplings with nets, the Northeast Fisheries Science Center (NEFSC) staff have completed monthly Continuous Plankton Recorder (CPR) transects across the Gulf of Maine since 1961. This transect series has been augmented by a second transect from New York to Bermuda, across the Mid-Atlantic Bight of the Northeast Shelf Ecosystem since 1976 (Jossi and Goulet, 1993).

The total zooplankton measured as displacement volumes during the Marine Resource Monitoring Assessment and Prediction Program (MARMAP) surveys of the shelf from 1977 to 1981 did not differ significantly from the earlier estimates of zooplankton standing stock of the shelf ecosystem from 1912 through the 1960s (Sherman et al., 1988). The zooplankton composition included 394 taxa, with 50 dominant in at least one location in one or more seasons, including copepods, chaetognaths, barnacle larvae, cladocerans, appendicularia, doliolids, brachyuran larvae, echinodermata larvae, and thaliaceans (Sherman et al., 1988).

ECOSYSTEM LEVEL RESPONSE TO PELAGIC PERTURBATIONS

The more recent observations of zooplankton volumes on the shelf, reported by Kane (1993), for the Georges Bank area of the Shelf Ecosystem and Jossi and Goulet (1993) for the Gulf of Maine and the Mid-Atlantic Bight reveal interannual variability in zooplankton abundance. Examination of the CPR trend-data for the transect across the Mid-Atlantic Bight from 1976 through 1990 revealed a declining trend for the MARMAP decade 1977-1986 ($p = 0.026$). However, the interannual variability observed from net tows for the entire time series was not statistically significant as a declining trend ($p = 0.30$) (Fig. 6). The numbers of zooplankton on the northern CPR transect across the Gulf of Maine generally increased in abundance from 1961 through 1990 ($p = 0.054$), interrupted by a downward trend during the MARMAP decade ($p = 0.06$) (Fig. 7). Based on MARMAP net sampling for Georges Bank, Kane reported volumes higher than the 10-yr median biomass (cc/100 m^3) for 1977, 1978, and 1979, and lower volumes for 1982, 1983, and 1984. According to Kane (1993) the higher volumes may have contributed to the increases in sand lance, *Ammodytes* spp., during the late 1970s. In contrast, Payne et al. (1990) reported an inverse relationship between sand lance and the copepod, *Calanus finmarchicus*, during the population explosion of sand lance, suggesting density-dependent grazing control of the standing stock of zooplankton. This observation, however, was limited to a relatively restricted area of the Northeast Shelf Ecosystem known as the Stellwagon Bank area (Payne et al., 1990). On Georges Bank, where sand lance, herring, and mackerel are present in relatively high numbers in spring, zooplankton biomass in spring, measured as displacement volumes per 100 m^3 was abundant during the population explosion of sand lance, 1971-1981, with median annual volumes equal to or exceeding the 22-yr (1971 through 1992) long-term median value of 43 cc/100 m^3 (Fig. 8).

Examination of the temperature information for the Northeast Shelf Ecosystem during the last two decades indicates that the temperatures during 1978 to 1982, a period of population depression for the principal pelagics, was intermediate between a slightly warmer period of the mid-1980s (1983 to 1986) and moderately cooler waters of the mid-1960s (Holzwarth and Mountain, 1992). The influence of temperature on the survival of early developmental stages of sand lance, mackerel, and herring is not well understood and requires further study. The correlation between temperatures and positive and negative correlations with herring and mackerel dominance reported by Skud (1982) is not supported by the present study, wherein both species show population declines and increases attributed to excessive fishing effort in the 1970s and included sharp declines in the economically important demersal species during the same period (Anthony, 1993; Murawski, 1991). Whereas the excessive fishing mortality has persisted for the demersals, it has been significantly reduced for the principal pelagic species, and is considered the principal factor in their recovery (Murawski, 1991). The lowest period of larval herring abundance from

1971 through 1992 occurred from 1976 to 1984, spanning the intermediate and warm temperature periods. This is in contrast to the warming and cooling correlation and analysis of changes in herring distribution reported by Skud (1982), and lends support to the predominant influence of excessive fishing mortality to the decline in both herring and mackerel abundance (Fig. 9). The influence of temperature on the interannual variability of a dominant zooplankter, the copepod, *Calanus finmarchicus*, on Georges Bank is suggestive of a relationship (Meise-Munns et al., 1990). Further studies are presently underway to examine more closely the relationship between seasonal and interannual environmental variability and changes in zooplankton production (GLOBEC, 1991, 1992).

Earlier observations indicate that the zooplankton component of the Northeast Shelf Ecosystem has been relatively coherent in resilience, abundance, and biodiversity from the first decade of the century to the 1980s (Sherman et al., 1988). Based on the present analysis of nearly 10,000 zooplankton volume measurements (9,942) for the MARMAP decade, 1977 through 1986, we find that the zooplankton was in a declining trend during the 1980s. The declining trend is highly significant for the whole ecosystem (Fig. 10a), and for three of the four subareas, the trend is significant at the $p < 0.05$ level (Fig. 10b, c, and d). The declining trend for Georges Bank was more variable than for the other three subareas ($p = 0.10$) (Fig. 10e). The persistent downward trend coincided with the increase in abundance level of the principal pelagics, and the increase in biomass of another pelagic zooplanktivore, the butterfish, *Peprilus triacanthus*, (Fig. 11). During the years 1977, 1978, and 1979, the highest numbers of zooplankters, based on CPR sampling (Fig. 6), coincided with the first three years of the seven-year depressed state of the herring and mackerel biomass (Figs. 3 and 4). From a top-down examination of the ecosystem, the zooplankton component has been sufficiently robust, even through the period of declining trend, to sustain the recovery of both herring and mackerel to a level of 5.5 mmt. In addition to this biomass, the zooplankton prey field is needed to support the recovery of the depressed gadoid and flounder stocks during their larval stages, posing another significant biomass to be considered in estimating the carrying capacity of the ecosystem. Whether the decline reflects a response to increasing predation by the growing biomass of the pelagic fish species, or a biofeedback response to an environmental signal remains an important unanswered question. From the spring and autumn volume data, based on bongo tows over Georges Bank from an extended data set encompassing 1971 through 1992, it appears that zooplankton standing stock may again be increasing (Fig. 12a and b).

For insights to the possibility of an environmentally induced biofeedback, the zooplankton time series was examined for shifts in biodiversity using the annual time series of log abundance of 5 zooplankton species--*Calanus finmarchicus*, *Pseudocalanus* spp., *Centropages typicus*, *Metridia lucens*, and *Centropages hamatus*--for four regions: Georges Bank, Gulf of Maine, Mid Atlantic Bight, and Southern New England, for the period 1977-1987. Annual time series were constructed by averaging all samples within a year and also by taking the maximum sample within a year. In terms of temporal behavior, there were no real differences between these two approaches, so the average values were analyzed. The methods used are described in Solow (1994) to extract an overall trend from the five species for each of the four regions. There was no significant trend for the Mid-Atlantic Bight ($p = 0.785$), or Southern New England ($p = 0.128$). There were significant trends for Georges Bank ($p = 0.031$) and the Gulf of Maine ($p = 0.014$). The trends are shown in Fig. 13 and are highly correlated. The correlations between these trends and the five species are given in Table 1. From an examination of biodiversity, it appears that the dominant copepod community is undergoing a shift from *Calanus finmarchicus*, *Pseudocalanus* spp., *Metridia lucens*, and *Centropages typicus*, toward an increasing abundance of *Centropages hamatus* on Georges Bank and in the Gulf of Maine (Fig. 14). This apparent shift in species abundance may be environmentally induced, as it is unlikely that the principal pelagics would selectively avoid preying on *C. hamatus*. The ecosystem monitoring program presently underway by the Northeast Fisheries Science Center, in cooperation with EPA, is designed to provide more definitive information on density-dependent predation between the principal pelagics and their prey field, and density-independent environmental signals that may be the cause of apparent changes in the dominance structure of the zooplankton community. Pedator-prey studies being conducted as part of NOAA's Coastal Ocean Program are examining the fine-scale temporal and spatial interrelation between the principal pelagics and their prey-field (Michaels and Grosslein, in prep.).

The present state of the ecosystem remains stressed. The shift since the 1960s from a demersal assemblage of fish dominated by gadoids to the present state dominated by spiny dogfish and skates coinciding with the increase in the abundance level of the pelagic fish species (Fig. 1), raises an ecological question. How will fishing effort reduction measures initiated in 1994 (New England Fishery Management Council, 1994) affect the recovery process for the depressed state of highly-valued demersal species (e.g., cod, haddock, flounders)? The consequence of reduced biomass of gadoids and flounders has been an increase in targeting fisheries on abundant elasmobranch species. Nevertheless, these species are at historically high levels. Implications of the removal of an increasing fraction of the elasmobranch biomass on other fish components of the ecosystem will be closely monitored. The ecosystem level consequences associated with this adaptive management strategy have been reviewed by Sissenwine and Cohen (1991), who list several alternative species that could become major fish predators. With regard to the zooplankton component of the system, the changed state of the fish community has introduced uncertainty to any forecast of recovery for the demersal populations, dependent on the zooplankton prey-field during the early developmental stages of cod, haddock, and flounders. Unlike the gadoids and flounders, the present high biomass of elasmobranchs are independent of the zooplankton prey field during early development. The estimated biomass level of herring and mackerel, prior to the 1960s is not well documented and is likely, according to data presented by Skud (1982), to have been less than the present estimated level of 5.5 mmt. The questions posed by Skud with regard to the "carrying capacity" of the ecosystem will require further study as the Northeast Shelf undergoes a significantly altered ecological state within which greater numbers of predators will be dependent on a zooplankton prey field that may be undergoing a shift in biodiversity. The recent simulations of the pelagic components of the ecosystem by Overholtz et al. (1991) will be extended to include the zooplankton component in an effort to examine the capacity of the ecosystem to support recovering populations of pelagic and demersal fish and baleen whale species.

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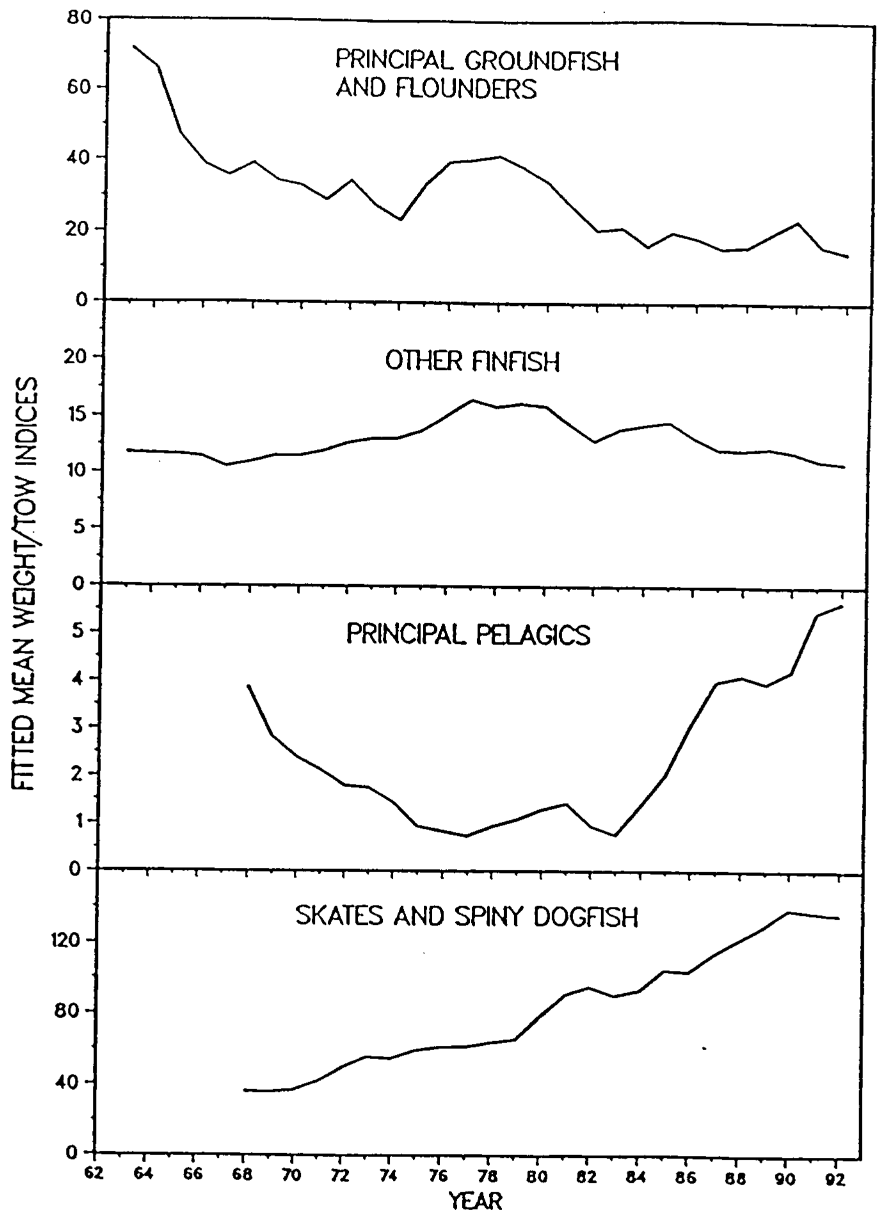


Fig. 1. Trends in indices of aggregate abundance (catch in weight per survey trawl haul) for four species groups, reflecting the major changes in fishery resources, 1962-1992. (From the NEFSC, 1993.)

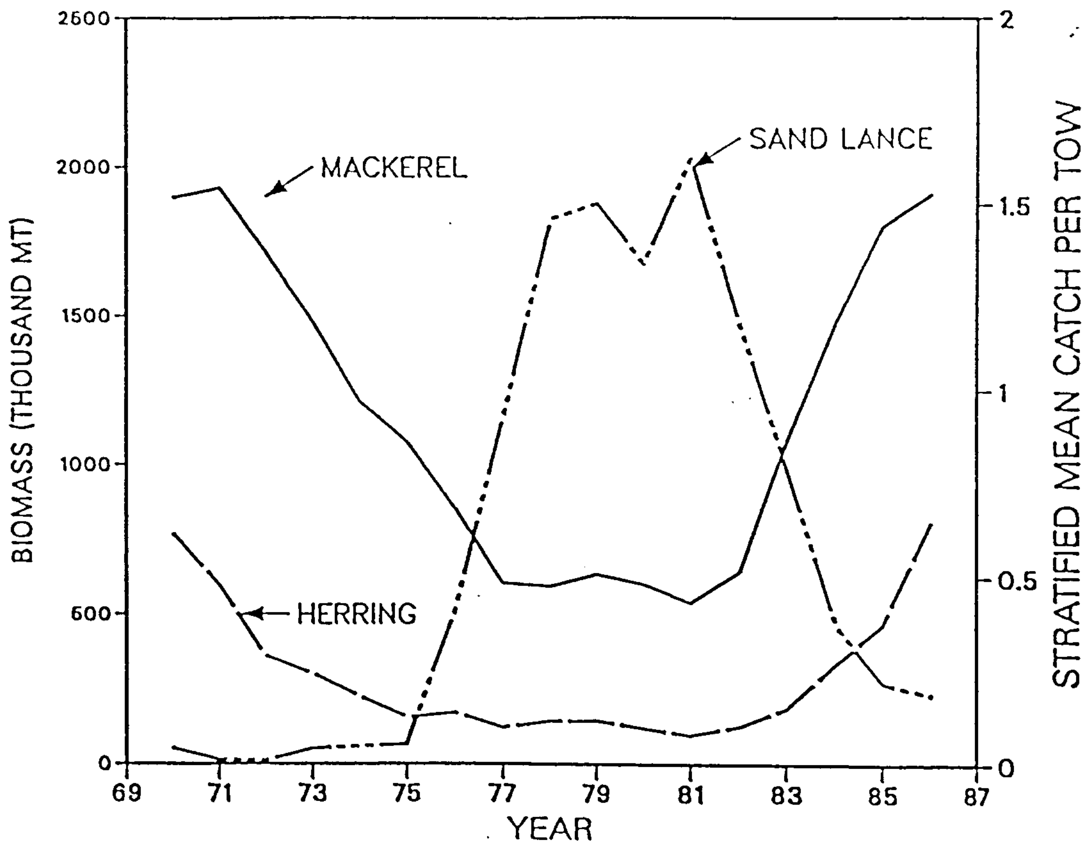


Fig. 2. Trends in biomass of mackerel (age 1+) and herring (age 3+) derived from virtual population analysis and trends in relative abundance (stratified mean catch per tow (kg)) of sand lance (age 2+) based on research vessel surveys. (From Fogarty et al., 1991.)

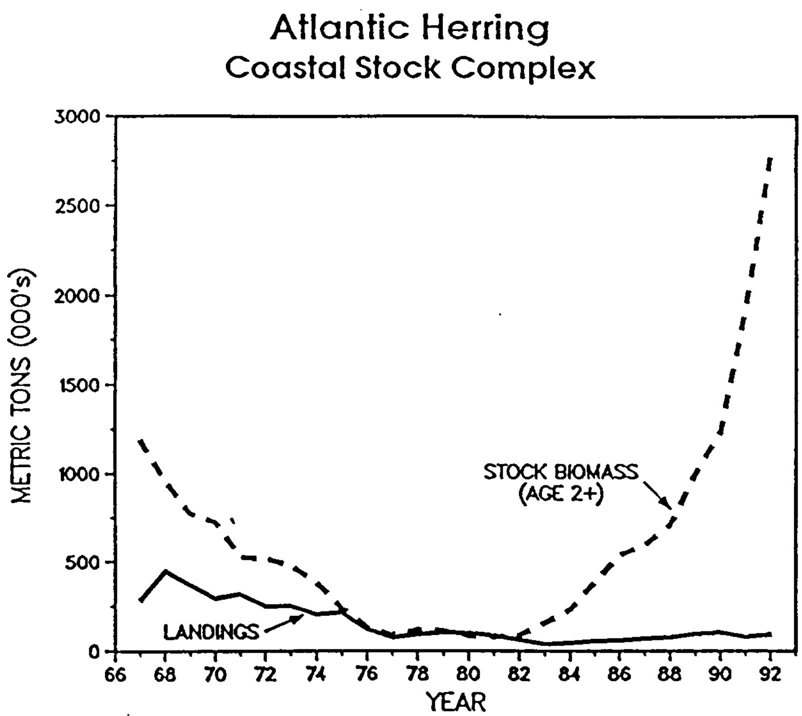


Fig. 3. Atlantic herring commercial landings and stock biomass, 1967 through 1992 (thousand metric tons). (From the NEFSC, 1993.)

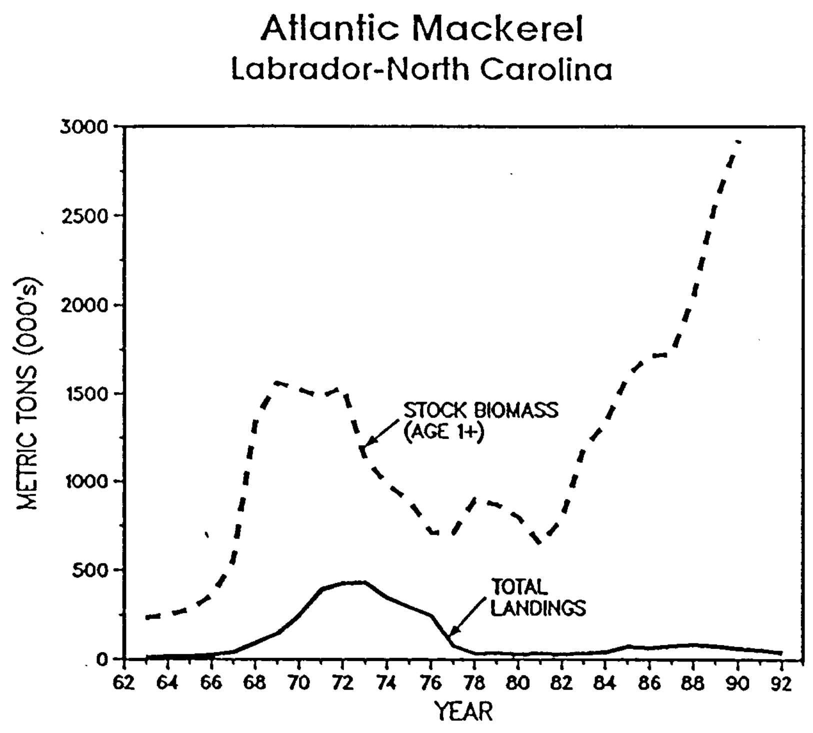


Fig. 4. Atlantic mackerel commercial landings and stock biomass, 1963 through 1992 (thousand metric tons). (From the NEFSC, 1993.)

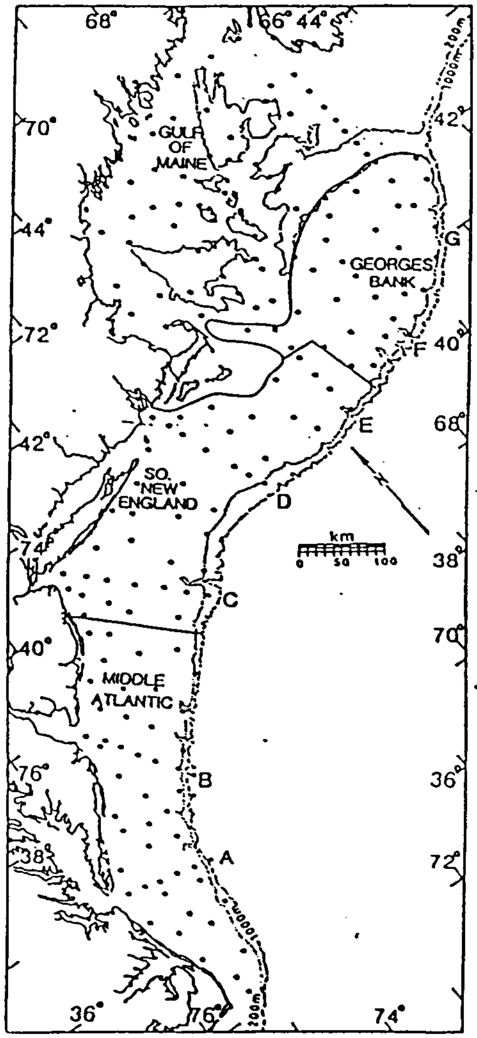


Fig. 5. Zooplankton sampling locations on MARMAP surveys of the Northeast Continental Shelf Ecosystem.

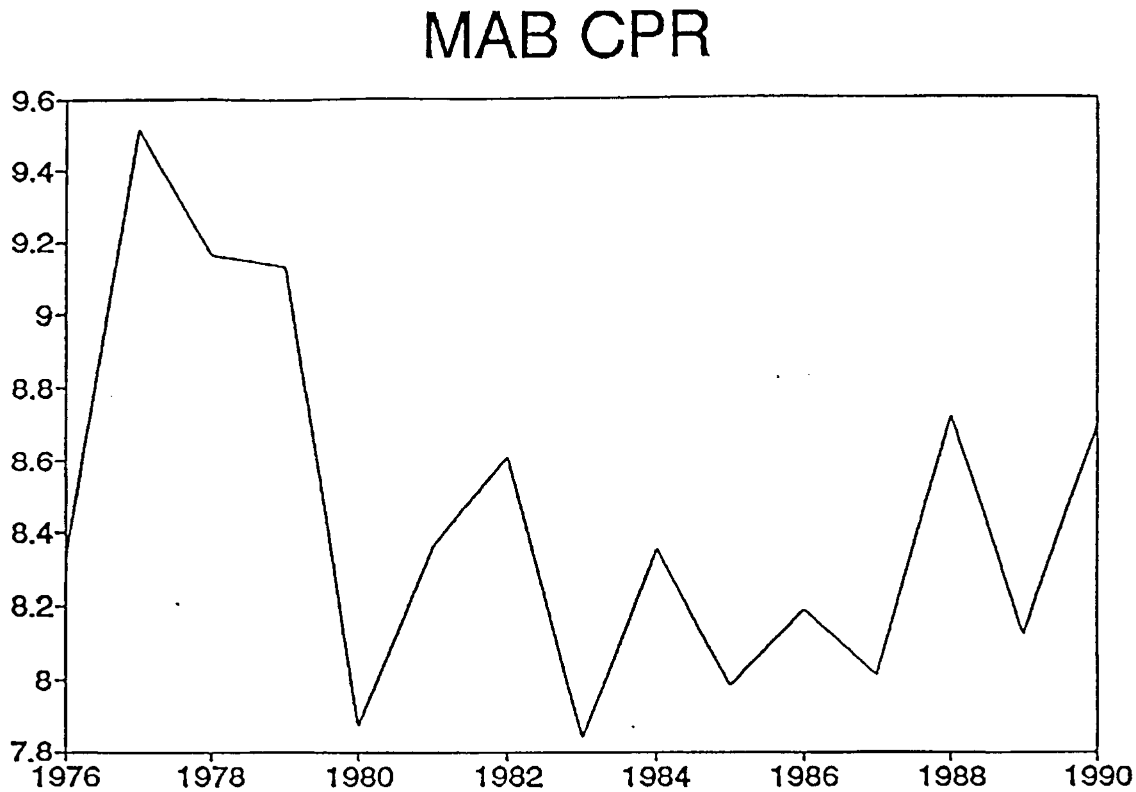


Fig. 6. Continuous Plankton Recorder trend data for the transect across the Mid-Atlantic Bight, 1976-1990. Rank Correlation Test for Trend; p = 0.026, 1977-1986; p = 0.30, 1976-1986. The ordinate values represent $\log_e$ transformed numbers of total zooplankton per 100 m^3/yr of water strained.

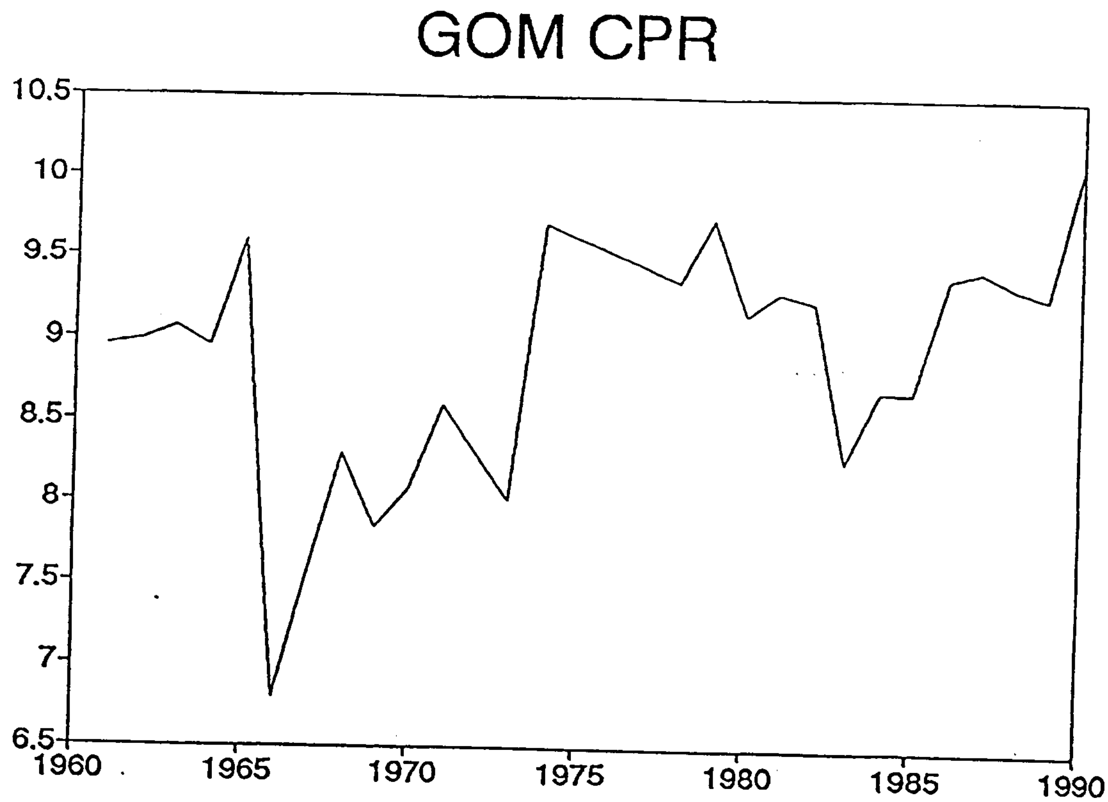


Fig. 7. Continuous Plankton Recorder trend data for the transect across the Gulf of Maine, 1961-1990. Rank Correlation Test for Trend; p = 0.054, 1961-1990; p = 0.062, 1977-1986. The ordinate values represent $\log_e$ transformed numbers of total zooplankton per 100 m^3/yr of water strained.

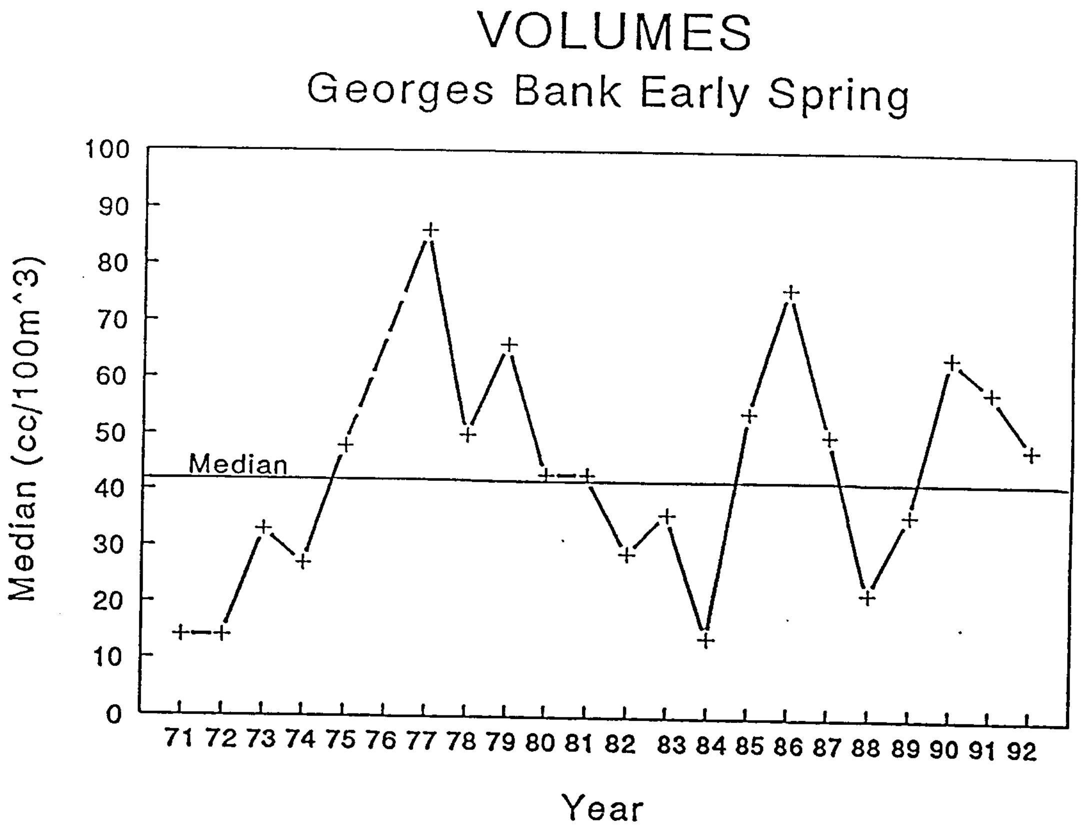


Fig. 8. Annual zooplankton median volumes (cc/100 m^3) for Georges Bank during early spring, 1971-1992, with the 22-yr median for the total time series; N = 733. Data for 1976 are not available.

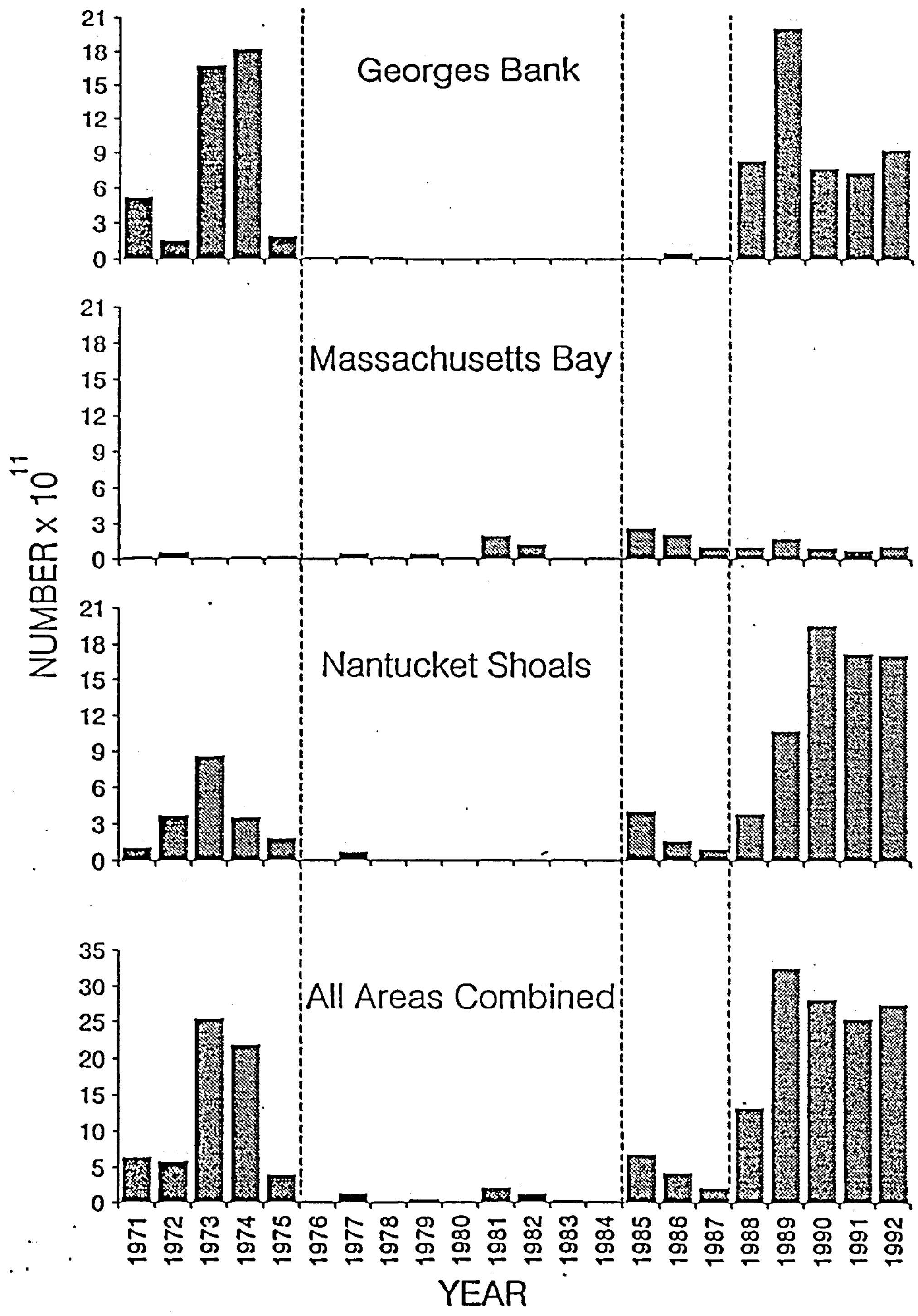


Fig. 9. Changes in abundance of Atlantic herring *Clupea harengus* larvae in the Georges Bank area between 1971 and 1990. Intervals represent multi-year periods that reflect the most apparent changes in spawning patterns.

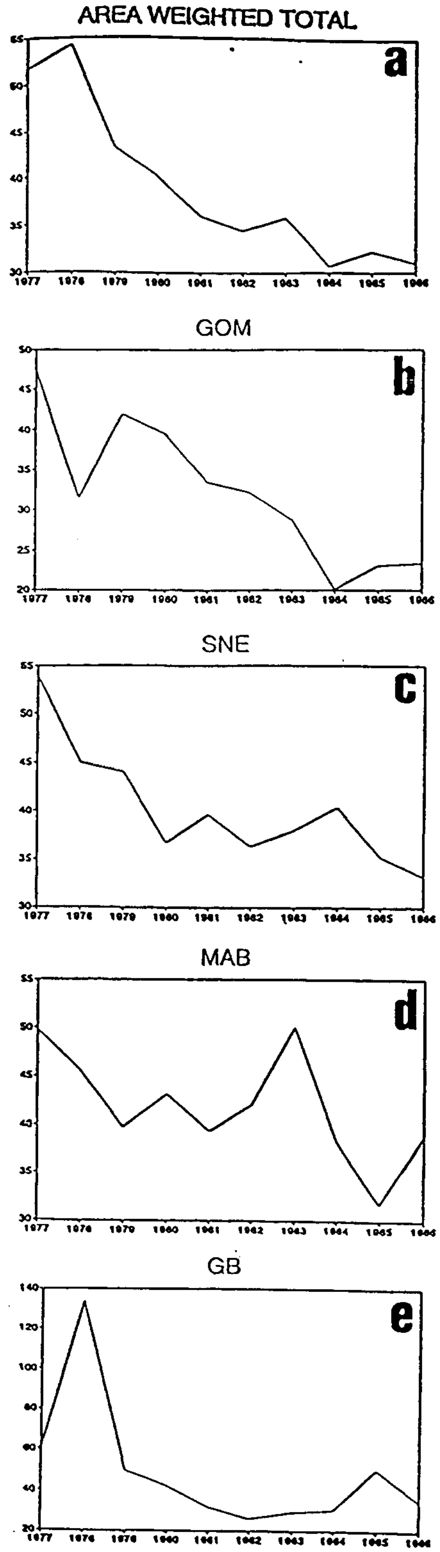


Fig. 10. Mean annual volumes in cc/100 m^3 for the Northeast Continental Shelf Ecosystem, 1977-1986. Data were combined for the four subareas--Gulf of Maine, Southern New England, Mid-Atlantic Bight, and Georges Bank--based on a Rank Correlation Test for Trend for the area weighted total (a) $p = 0.001$. The results of the test are given separately for each of the four subareas, b) Gulf of Maine, $p = 0.006$; c) Southern New England, $p = 0.006$; d) Mid-Atlantic Bight, $p = 0.040$; and e) Georges Bank, $p = 0.130$.

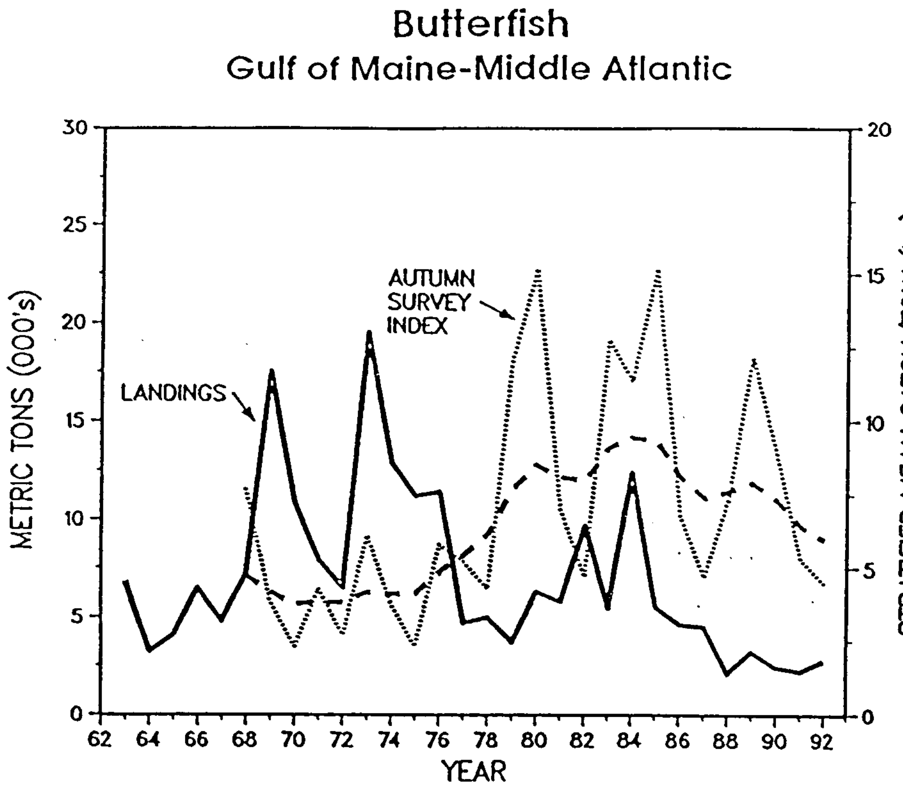
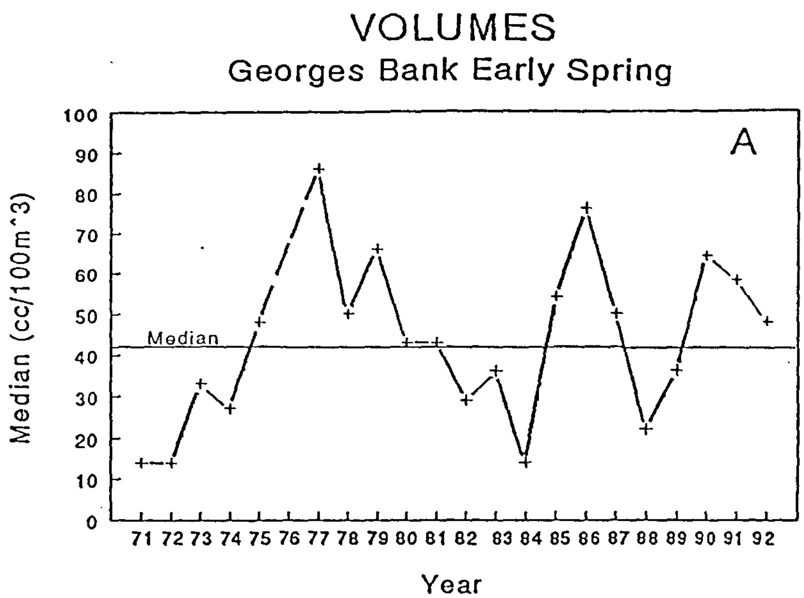


Fig. 11. Commercial catches of butterfish for the Northeast Continental Shelf Ecosystem (1000 mt) and stratified mean catch per tow (kg) based on the autumn bottom trawl survey index, Northeast Fisheries Science Center, 1963-1992. (From NEFSC, 1993.)



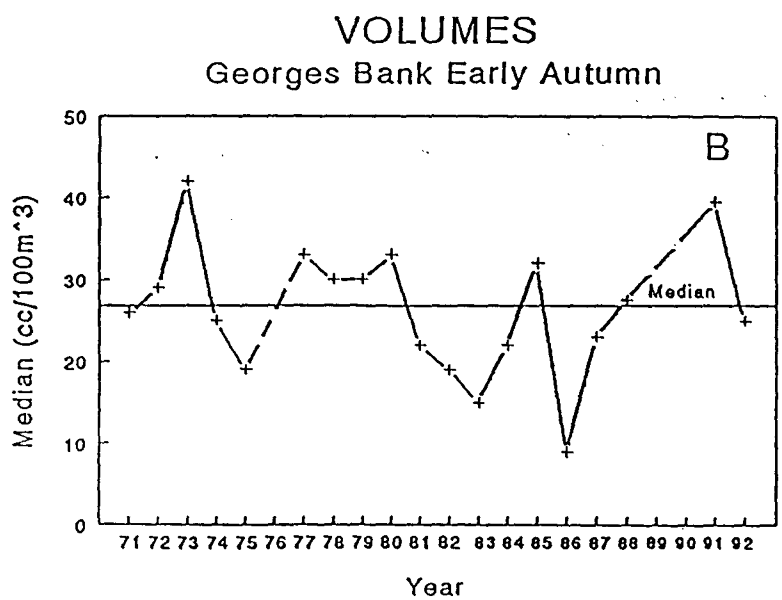


Fig. 12. The annual median zooplankton standing stock in displacement volumes/100 m^3 for: a) early spring, 1971 to 1992, and b) autumn, 1971 to 1992, based on bongo net tows made during spring and fall bottom trawl surveys of the Northeast Continental Shelf Ecosystem. Data missing for 1976, 1989, and 1990.

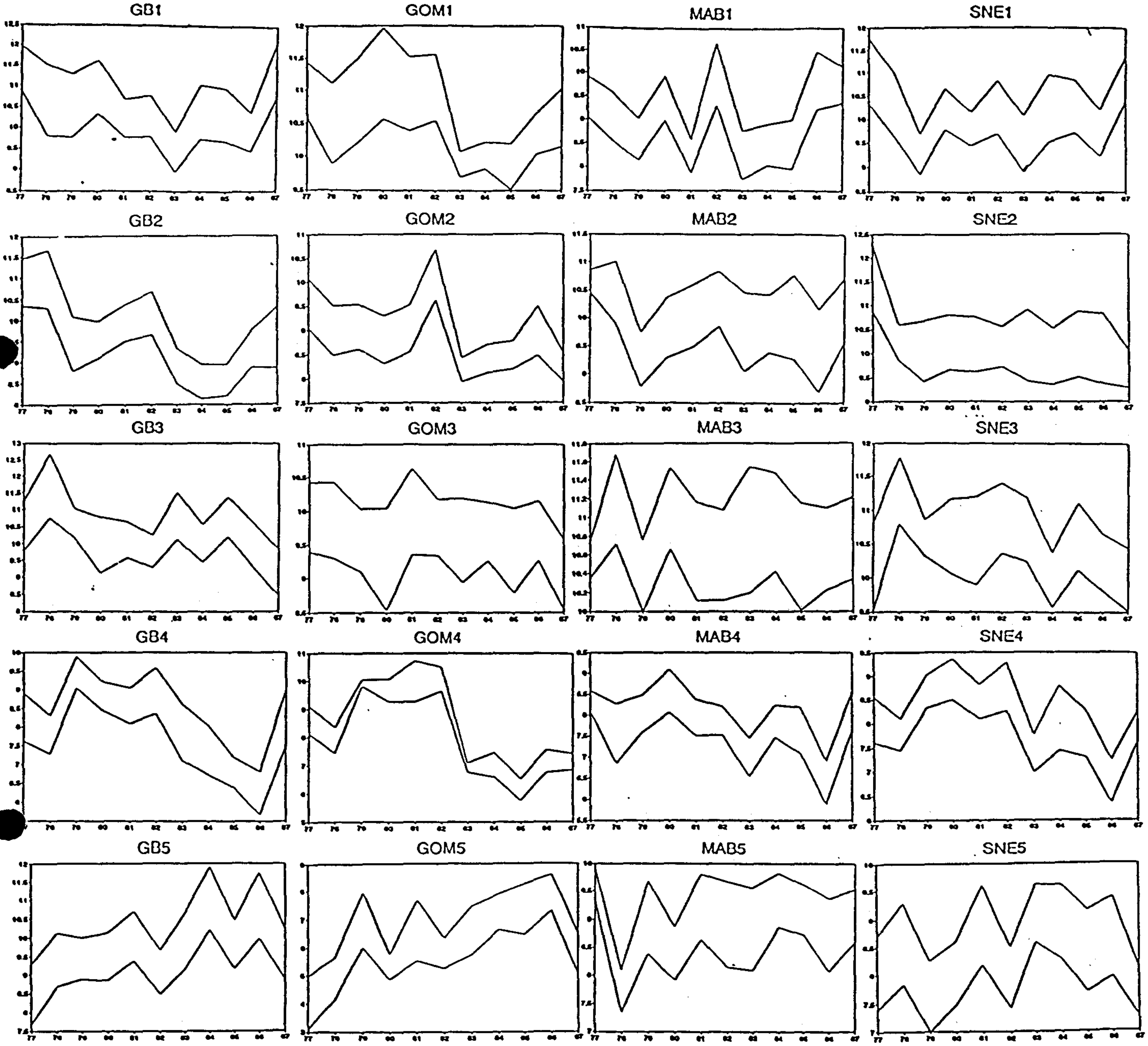


Fig. 13. Abundance trends for five species of dominant zooplankton species--*Calanus finmarchicus* (1), *Pseudocalanus* spp. (2), *Centropages typicus* (3), *Metridia lucens* (4), and *Centropages hamatus* (5)--within four regions of the Northeast Shelf Ecosystem--Georges Bank (GB), Gulf of Maine (GOM), Mid-Atlantic Bight (MAB), Southern New England (SNE)--for the period 1977 through 1987. Annual time series are based on averaging all samples within one year. Plots show relationship between $\log_e$ transformed sample means (lower trend line) and $\log_e$ transformed maximum sample abundances (upper trend line) for each year within the time series. Number designations for each species are given in parentheses.

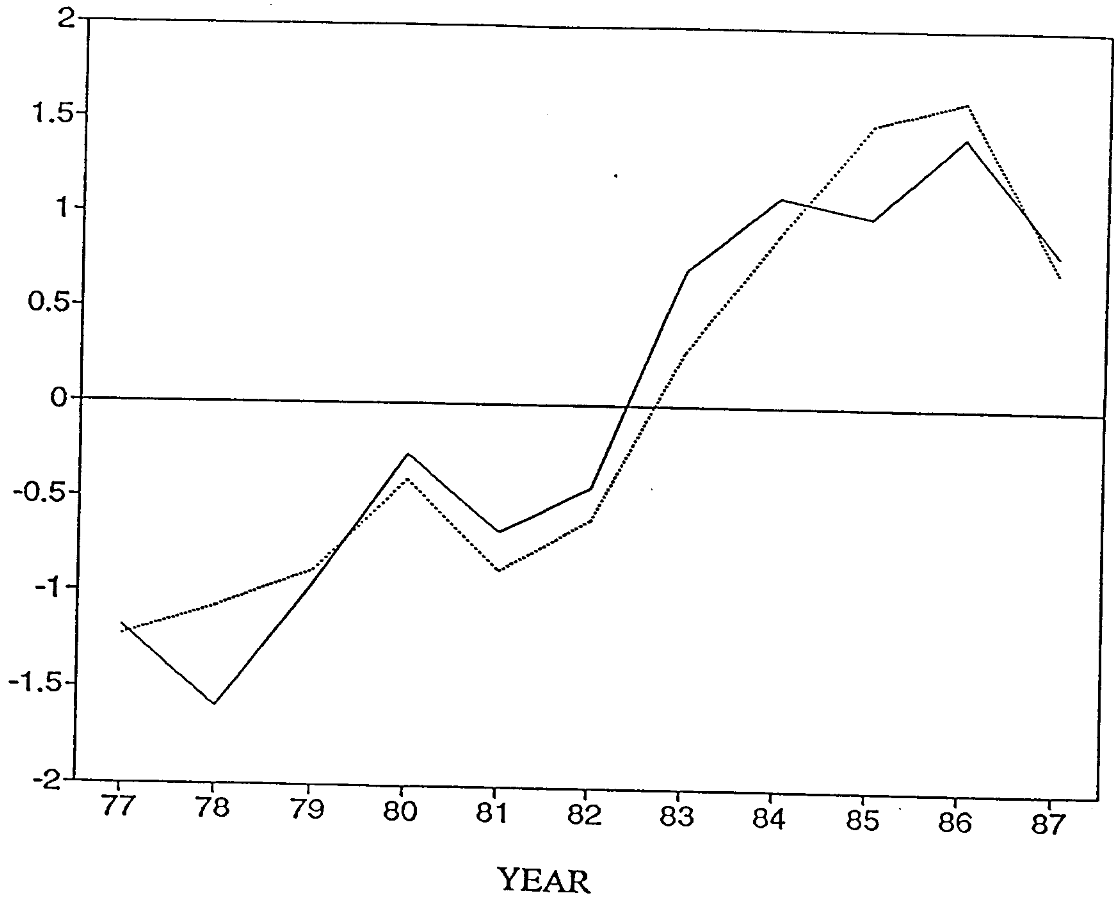


Fig. 14. Minimum-maximum Autocorrelation Factor (MAF) plot showing the monotone trend toward *Centropages hamatus* from 1977 to 1987, for Gulf of Maine (dotted line) and Georges Bank (solid line), (standardized to mean 0 and variance 1). Randomization test probability values calculated following Solow (1994) were: p = 0.031 for Georges Bank, and p = 0.014 for the Gulf of Maine. The trends were not significant for Southern New England, p = 0.128, and P = 0.785 for the Mid-Atlantic Bight subareas and are not plotted.

Table 1. Correlations between the five copepod species and the time trends found by MAF analysis for Georges Bank and the Gulf of Maine subareas of the Northeast Shelf Ecosystem (Solow, 1994).

Species	Georges Bank	Gulf of Maine
Calanus finmarchicus	-0.32	-0.64
Pseudocalanus spp.	-0.82	-0.54
Centropages typicus	-0.44	-0.35
Metridia lucens	-0.69	-0.77
Centropages hamatus	0.70	0.76