Abstract.—Annual and seasonal variability of Georges Bank zooplankton biomass and dominant species abundance are described and related to variations in mean surface temperature and average depth distribution. Data were obtained from plankton samples collected bimonthly with a 0.333-mm mesh net throughout a ten-year period: 1977–86. Biomass was measured by displacement volume and the dominant species analyzed were the copepods *Calanus finmarchicus*, *Pseudocalanus minutus*, *Centropages typicus*, *Centropages hamatus*, and *Metridia lucens*.

Biomass levels were high in 1977 through 1979, low in 1982 through 1984. Biomass and copepod abundance in the spring of 1977 were extraordinary. Measurements over the entire bank were two to three times above a ten-year median. Unlike the first five years of monitoring, the average seasonal biomass cycle was not coherent from 1982 through 1986. Departures from the average seasonal cycle occurred several times during the second half of the time series.

Calanus finmarchicus and *Pseudocalanus minutus* abundance trends were nearly identical, suggesting that their populations may be affected by similar factors. *Centropages hamatus* abundance in the central shoal depth zone (<61 m) was related to surface temperature variability and its spring abundance estimates were indirectly proportional to the abundance of other dominant copepods. *Centropages typicus* counts in autumn 1985 were nearly double all other years, and *Metridia lucens* abundance surged in late spring 1979 but was low from 1983 through 1986.

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Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977–1986

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Zooplankton biomass has long been recognized as an important index for estimating the seasonal and annual variability of secondary production in marine ecosystems. Zooplankton play a key role in pelagic food chains, serving as the connecting link between primary producers and secondary consumers. The availability of zooplankton as food for larval fish is thought to be one of the key factors determining year class strength of commercial fish species (Cushing, 1978).

The rich fishing grounds of Georges Bank in the northwest Atlantic have been the focus of zooplankton studies since the turn of the century. The Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program (Sherman, 1980) has monitored the U.S. Northeastern continental shelf marine ecosystem from 1977 through 1987 with bimonthly surveys, measuring a variety of biological and physical parameters. During the first five years of MARMAP monitoring, zooplankton biomass on Georges Bank formed a coherent seasonal pattern, not changing significantly from year to year (Sherman et al., 1983). Comparison of this data to that collected by Bigelow (1926) from 1912 to 1920 showed that biomass levels, species composition, and abundance estimates of dominant species were essentially the same in both studies. Sherman et al. (1987) described in greater detail the seasonal cycle of Georges Bank zooplankton and how it relates to ichthyoplankton life histories. Additional studies (Davis, 1984; Meise-Munns et al., 1990) of Georges Bank zooplankton have used subsets of this large data base to help define and simulate seasonal cycles of dominant species in relation to environmental parameters.

The purpose of this paper is to further describe the Georges Bank zooplankton community by utilizing data collected during MARMAP surveys from 1977 to 1986. The annual and seasonal variability of zooplankton biomass captured with 0.333-mm mesh nets is reported and related to changes in the abundance of the five dominant zooplankton species (Sherman et al., 1987). The average depth distribution of biomass and dominant species abundance is described and departures from it are compared to overall population variability.

The sensitivity of the above parameters to surface water temperature readings is also examined to consider the potential effects of climatic change on Georges Bank zooplankton populations. This study is part of a continuing long-term investigation by the National Marine Fisheries Service (NMFS), which monitors the zooplankton component of the U.S. Northeast shelf ecosystem.

Methods

Plankton samples were collected at monthly to bi-monthly intervals at 32 station locations during MARMAP surveys on Georges Bank (Fig. 1).

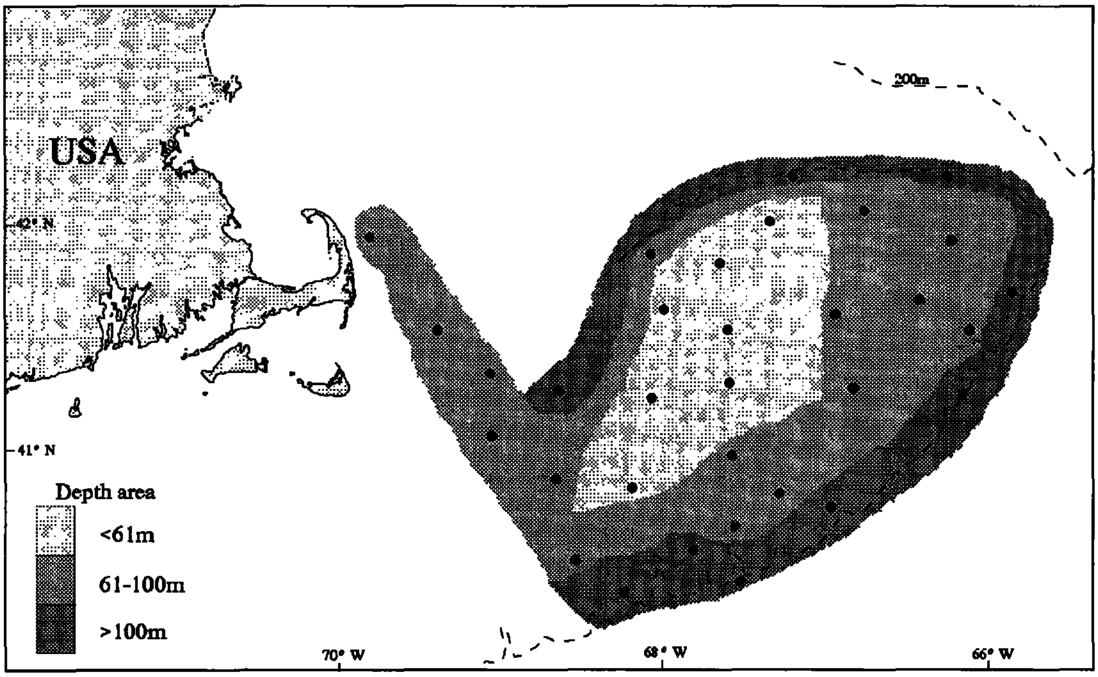

Figure 1
Location of standard MARMAP (Marine Resources Monitoring, Assessment, and Prediction program) stations on Georges Bank off the U.S. Northeast coast, 1977–86.

Plankton samples were also collected on trawl and dredge surveys at randomly selected locations that changed yearly. Areal coverage and sampling spacing on these surveys were similar to plankton cruises. Samples from different surveys, closely overlapping in time and space, were sometimes combined to ensure adequate coverage of the survey area.

Zooplankton was collected with a 61-cm bongo fitted with a 0.333-mm mesh net towed obliquely to a maximum depth of 200 m or 5 m from the bottom and back to the surface. Ship speed varied between 1 and 2 knots to maintain a 45 degree wire angle. Winter surveys in 1977 and 1978 towed bongos at 3.5 knots. A flowmeter was positioned in the center of the bongo frame to measure volume of water filtered during the tow. Samples were preserved in 5% formalin. At all stations, sea-surface temperature was measured with a stem thermometer to the nearest 0.1°C. Detailed sampling procedures, cruise tracks, and survey logistics are summarized by Sibunka and Silverman (1984, 1989).

Biomass was measured by displacement volume in the laboratory. Initially, organisms larger than 2.5 cm were removed. The plankton sample with preserving liquid was then measured in a graduated cylinder, poured through a mesh cone into a second cylinder, and drained until the interval between drops from the cone increased to 15 seconds. The liquid in the second cylinder was measured and the displacement volume of the sample was the difference between readings. Samples with high concentrations of gelatinous organisms were eliminated because the interstitial water retained by these animals leads to gross overestimates of zooplankton biomass. Samples were later subsampled by aliquoting to about 500 organisms and identified to species. Volumes (n=1937) are expressed as cc/100 m^3 of water filtered, and abundance (n=1839) as number/100 m^3.

The adults and late stage copepodites of the copepods *Calanus finmarchicus, Pseudocalanus minutus, Centropages typicus, Centropages hamatus,* and *Metridia lucens* were the dominant species analyzed. Depth distribution of biomass and species abundance was examined by subsetting the data into three geographic subareas according to bottom depth: 1) central shoal (<61 m); 2) intermediate (61–100 m); and 3) deep (>100 m). Seasonal shifts in biomass and community structure were investigated by grouping the data into the six seasons defined in Table 1. Extenuating circumstances prevented adequate areal coverage in only one season: winter 1979.

The Shapiro-Wilk test for normality was applied to each seasonal biomass and species data set. The null hypothesis that the data values were a random sample from a normal distribution was rejected (P<0.01). Zooplankton data are often log transformed to normalize zooplankton distributions. However, Roesler and Chelton (1987) found that transformation of zooplank-

Table 1

Seasonal median values of biomass and dominant species abundance by year and for all years combined during A) Winter, B) Early Spring, C) Late Spring, D) Summer, E) Early Autumn, and F) Late Autumn. *Centropages hamatus* abundance numbers are only from the central shoal depth area and *Metridia lucens* ones are restricted to the deep water depth area. Midpoint refers to the median day number of that years sampling. A '—' indicates no data were collected or processed.

A: Winter (1 Jan.–23 Mar.)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	51	61	—	62	64	66	20	18	17	34	48
Biomass	7	20	—	9	10	9	10	12	8	9	9
C. finmarchicus	1170	1523	—	2814	5539	1531	508	1191	639	1023	1258
P. minutus	1419	8678	—	1746	4814	3157	1131	1685	1701	954	2120
C. typicus	10	263	—	1253	145	2648	2988	1735	3720	2057	976
C. hamatus	0	77	—	1626	0	16	5709	1770	3021	10379	188
M. lucens	121	884	—	154	4334	1422	766	1112	340	49	444

B: Early spring (24 Mar.–4 May)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	115	105	101	102	112	116	103	95	92	104	101
Biomass	86	50	66	43	43	29	36	14	54	76	42
C. finmarchicus	44912	—	22680	15659	36957	27511	17600	5192	6729	19261	18100
P. minutus	19299	—	4483	7217	17032	17098	10654	3339	2449	4600	7217
C. typicus	0	—	1031	353	261	1300	89	34	108	182	207
C. hamatus	306	—	65	3889	549	115	4538	16	1702	10722	569
M. lucens	1666	—	5117	5210	4164	4373	213	1645	567	468	1621

C: Late spring (5 May–22 June)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	157	140	144	168	152	141	168	149	133	153	147
Biomass	137	89	95	42	50	37	15	38	46	21	50
C. finmarchicus	89437	59030	22748	15895	12429	20887	4590	15622	11221	9088	18255
P. minutus	43677	19034	19467	13727	19595	10765	2742	6853	4597	2833	9313
C. typicus	0	0	511	829	356	1274	0	0	0	9	51
C. hamatus	453	0	201	21188	21065	697	26190	13910	34157	7476	2657
M. lucens	8612	9147	24391	9963	2728	13486	117	1145	823	409	2568

D: Summer (23 June–12 Sept.)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	230	206	217	213	198	206	233	233	230	238	202
Biomass	43	37	43	33	46	15	25	25	16	25	31
C. finmarchicus	21856	5346	4737	4556	4667	875	5029	4693	2913	3473	4042
P. minutus	12205	8109	4655	5661	12908	5175	6328	1980	4354	7704	5776
C. typicus	7561	6739	11201	3416	4264	1678	22659	8954	6113	11225	6456
C. hamatus	9958	66547	89476	33095	97265	39490	27922	63458	67507	40335	46140
M. lucens	4040	635	12195	1879	1315	6280	1089	390	9	78	1597

E: Early Autumn (13 Sept.–9 Nov.)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	308	289	297	293	295	302	292	289	297	289	294
Biomass	33	30	30	33	22	19	15	22	32	9	24
C. finmarchicus	638	912	591	282	679	1364	429	454	971	347	587
P. minutus	5986	3472	2284	39	1285	3089	291	220	475	536	898
C. typicus	35103	33342	39431	39256	36453	11784	14322	18970	71184	5124	28431
C. hamatus	25608	17018	49178	10833	13524	14138	2024	17480	15068	5765	14138
M. lucens	2180	1020	4332	1895	3227	49	257	71	27	28	540

F: Late Autumn (10 Nov.–31 Dec.)

Year	77	78	79	80	81	82	83	84	85	86	All data
Midpoint	327	330	337	350	337	325	344	333	338	339	334
Biomass	22	23	24	11	13	27	7	12	18	6	16
C. finmarchicus	1186	573	133	683	419	1137	812	711	538	78	539
P. minutus	13752	7922	942	1826	799	2169	540	187	198	388	1030
C. typicus	17960	33013	24117	9200	21241	15835	9209	15646	50081	2594	16378
C. hamatus	4739	1691	23626	345	3999	21416	6057	24439	45741	10759	5523
M. lucens	1742	1570	7058	4773	4503	870	243	385	263	12	735

ton biomass can screen important biological events by repressing anomalous values. Therefore, nonparametric statistical techniques were employed to test for differences between years within the defined seasons. The Kruskal-Wallis ANOVA was used to determine if significant ($P<0.05$) differences existed between years within each season. The test showed that all biomass and species seasonal groupings had at least one pair of years different from each other. The Dunns multiple comparison procedure was applied to pinpoint the anomalous year(s).

Results

Annual cycle

Median biomass and dominant copepod abundance values for each of the defined seasons by year and for the ten-year study period are given in Table 1, A–F.

Biomass on average increased fourfold in early spring from its winter low. It peaked in late spring and then gradually declined through the summer and autumn seasons (Fig. 2). Overall, zooplankton standing stock was high from 1977 through 1979. Seasonal medians from early spring through late autumn were above time-series median values (Fig. 2A). The opposite pattern was evident from 1982 through 1984. Zooplankton standing stock was below average throughout these years, except for late autumn 1982 (Fig. 2B). Winter biomass showed little variation throughout the study period (Table 1A).

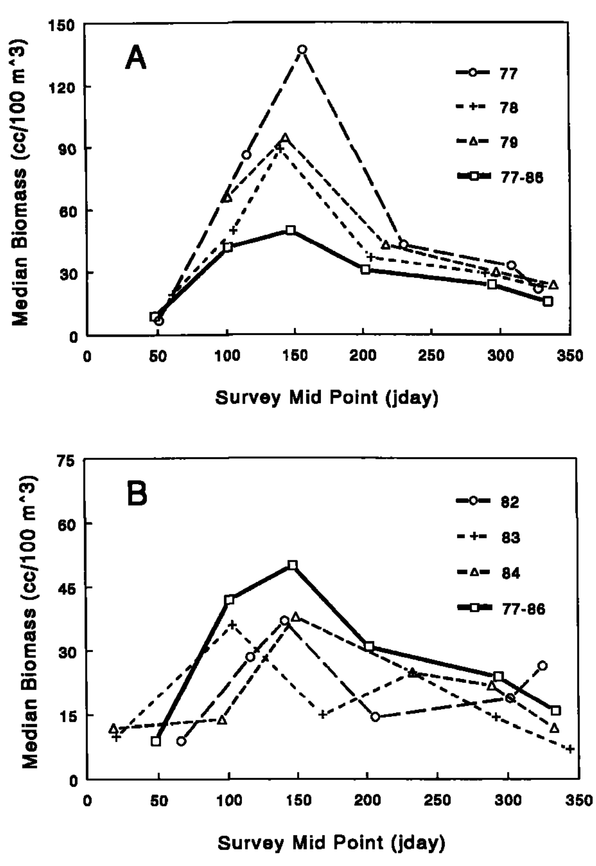

Figure 2

(A) Annual cycle of seasonal median biomass values in 1977 through 1979 and the ten-year median. **(B)** Annual cycle of seasonal median biomass values in 1982 through 1984 and the ten-year median.

The seasonal biomass cycle on Georges Bank from 1977 through 1981 was coherent; annual departures from the mean were insignificant (Sherman et al., 1983). However, substantial departures from the average seasonal cycle occurred on several occasions after 1981. Surveys in 1983, 1985, and 1986 recorded peak biomass in early spring instead of late spring and in two of those years, 1983 and 1986, there was an anomalous increase in biomass during the summer months (Fig. 3). However, because only below average summer levels were reached during these years, the latter increases appear to represent a recovery from the minimal levels measured in late spring, rather than a summer bloom. Zooplankton standing stock increased between summer and early autumn in only two years: 1982 and 1985 (Table 1, D–E). The usual decline in biomass between early and late autumn was not observed in 1982 (Table 1, E–F).

The average ten-year seasonal distribution of each variable as a function of bottom depth is depicted in Figure 4. There were no apparent long-term distribution shifts in biomass or species abundance during the ten-year period.

Calanus finmarchicus and *P. minutus* both dominated the zooplankton community in early and late spring. During the summer, their populations declined and *C. typicus* began to increase in abundance until it peaked in early autumn (Table 1). *Centropages hamatus* and *M. lucens* were only prevalent in specific depth strata (Fig. 4). *Centropages hamatus* was almost entirely restricted to the central shoal depth region, peaking there during summer months. *Metridia lucens* was most numerous in deep water where its large size caused it to be a major contributor to spring biomass. Overall, it was the only dominant species that exhibited a long-term abundance trend. Population estimates for *M. lucens* were low in 1983 through 1986 (Table 1).

All the above species showed departures from their average seasonal cycles during their periods of peak abundance. *Calanus finmarchicus, M. lucens,* and *P. minutus* all declined between early and late spring in 1983 and 1986 (Table 1, B–C). *Centropages typicus* departed from its typical annual abundance pattern during three years; population estimates in 1983 and 1986 declined from summer to early autumn and in 1982, *C. typicus* did not reach peak abundance until late autumn. The *C.hamatus* population was more variable than the other species. From 1977 to 1981, abun-

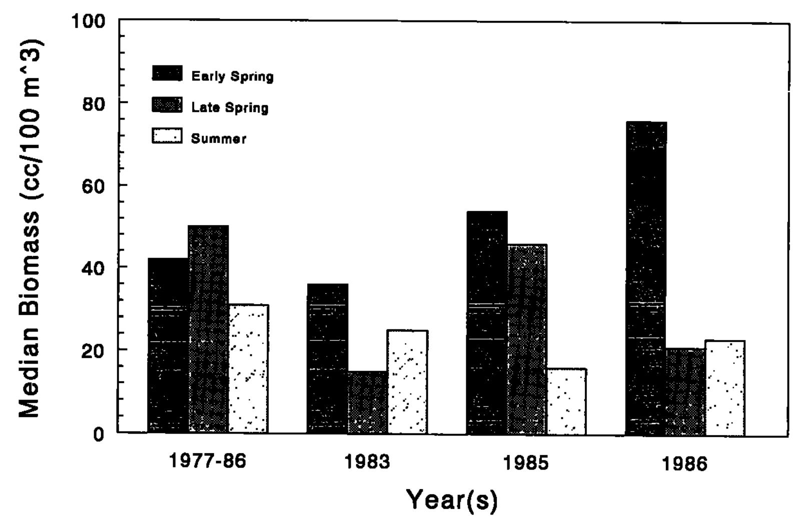

Figure 3
Departures from the ten-year (1977–86) median biomass cycle occurred between early spring and summer in 1983, 1985, and 1986.

dance decreased from early to late autumn. During the next five years, increases were recorded between seasons (Table 1, E–F). After an unusual pulse in early spring 1986 (Table 1B), *C. hamatus* declined in late spring and then rebounded to their average summer abundance. In one year, 1977, its annual high was delayed until early autumn (Table 1, D–E).

Surface temperature variability was examined by fitting seasonal medians (Table 2) to a harmonic regression (Fig. 5). The model depicted a strong annual cycle; $r^2 = 0.91$. Certain seasons in specific years had above or below average temperatures, but there were no prolonged warm or cool periods.

Interannual variability by season

Winter Zooplankton standing stock reaches its annual low and exhibits little interannual variation during the cold winter months (Table 1A). The only remarkable year was 1978, when median biomass was nearly double all other years. However, this may have been an artifact of survey logistics, rather than enhanced winter productivity. None of the usually low biomass stations along the northern and southern perimeter of Georges Bank were sampled that year.

Centropages hamatus was the only dominant species that demonstrated substantial interannual variation during the winter season. Population estimates in the central shoal depth zone from 1983 to 1986 were well above the ten-year median (Table 1A). These departures can be directly related to surface-temperature variability caused by dates of survey coverage. Throughout the winter time series, *C. hamatus* was virtually absent at stations where surface temperature was below 5°C (Fig. 6). Median surface temperatures for the years 1983–86 were all above 5°C (Table 2) and significantly higher ($P<0.05$) than the earlier years, which were all sampled later in the season when the annual minimum temperature on Georges Bank is normally reached. Biomass and the abundance of the other four copepod species were not affected by winter temperature regimes.

Early spring Zooplankton biomass in early spring was high at the beginning and end of the time series; 1977 and 1986 (Table 1B). Standing stock in 1984 was very low; significantly less ($P<0.10$) than all other years except 1982.

C. finmarchicus and *P. minutus* abundance (Table 1B) was similar to biomass trends in some years. Like biomass, abundance estimates for both species were highest in 1977 and low in 1984. In 1986, an unusual early spring pulse of *C. hamatus* (Table 1B) in the central shoals depth area elevated standing stock levels. The above average biomass levels recorded in 1985 could not be related to the low abundance estimates of the dominant species in that year (Table 1B). Notations made by shipboard personnel indicated that nets were frequently clogged with dense concentrations of phytoplankton. High biomass in 1985 was likely elevated by phytoplankton and entrapped organisms not usually captured with 0.333-mm mesh nets.

As in winter, the C. *hamatus* population was depressed by cold temperatures in early spring. Their highest early spring abundance occurred in 1986 when surface waters in the central shoals depth area were warmest (median=6.5°C) in this season. *Calanus finmarchicus* were also more abundant at stations where surface temperatures were 6°C or more. Annual changes in biomass and the abundance of other dominant species could not be related to surface temperature variability in early spring (Table 2).

Late spring Zooplankton biomass surged in the late spring of 1977 (Table 1C). The median volume was nearly three times higher than the seasonal 10-year median, and significantly different ($P<0.05$) from all years except 1978 and 1979. Though biomass declined from this peak in 1978 and 1979, median estimates in these two years were nearly double those recorded in

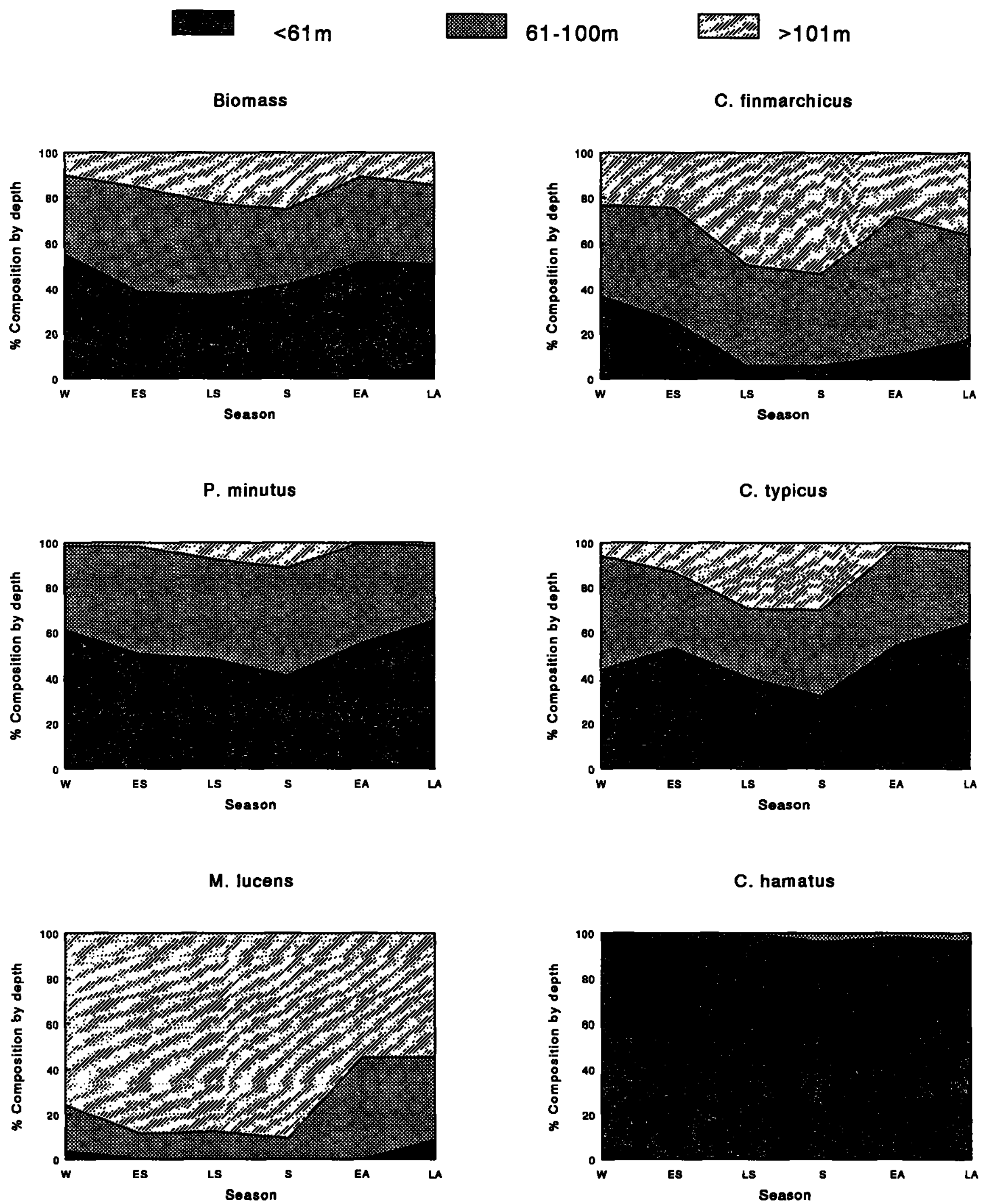

Figure 4
The average seasonal distribution of biomass and the five dominant species as a function of depth during the ten year study period. Season abbreviation key: W = Winter, ES = Early Spring, LS = Late Spring, S = Summer, EA = Early Autumn, and LA = Late Autumn.

the 1980's. Extremely low estimates were recorded in 1983.

Interannual fluctuations in late spring biomass were closely related to *C. finmarchicus* and *P. minutus* abundance (Table 1C). The similarities between abundance plots of both species during spring seasons (Fig. 7) suggest that their population dynamics may be controlled by similar factors.

Table 2
Seasonal median sea surface temperature (°C) by year and for all years combined. No data were collected in Winter 1979.

	Year										
Season	77	78	79	80	81	82	83	84	85	86	All data
Winter	4.9	4.6	—	4.8	4.2	3.4	7	5.7	6.9	5.7	5.2
Early spring	6.6	4.7	4.7	5.7	5.6	5.2	6.2	5.2	5.4	6	5.5
Late spring	9.6	7.4	8.5	11.6	10.2	7.2	10.4	8.9	7.9	9.2	9.1
Summer	16.4	14.7	16.7	18.1	15.0	15.6	16.1	18.2	16.8	15.3	16.1
Early autumn	14.0	13.5	14.4	14.9	12.5	12.9	14.3	14.1	13.8	13.6	13.6
Late autumn	10.6	11.6	10.4	7.4	9.9	11.5	9.2	10.8	9.8	10.6	10.2

There were two notable annual distribution shifts in late spring. *Calanus finmarchicus* abundance was usually sparse within the 60-m contour and evenly distributed offshore of it (Fig. 4). However, in the high biomass years of the late 1970's, the population thrived in central shoal waters. From 1977 to 1979, *C. finmarchicus* medians were 48,366, 33,397,and 15,364/ 100 m^3 respectively, while other years were all below 5000/100 m^3. *Metridia lucens* abundance in deep water peaked in 1979 (Table 3C) and they extended their range of dominance inshore across the 100-m contour line. Its high abundance (median = 22,015/100 m^3) in the intermediate depth zone, where its 10-year median was 365/100 m^3, elevated biomass there to nearly double the time-series median, despite only average *C. finmarchicus* abundance. The *M. lucens* abundance peak in 1979 accounts for the high biomass measured in that year.

Centropages hamatus was the dominant copepod species in the central shoals area during 1980 and 1981 and from 1983 to 1986. In other years, their numbers were sparse there; median values fell below 1000/100 m^3 (Table 1C). Their high years correlated with all but one (1981—*P. minutus*) of the low abundance years for *C. finmarchicus* and *P. minutus* (Fig. 8).

The strongest relationship between abundance and surface temperature variability in late spring (Table 2) was for *C. hamatus* numbers in the central shoals area. Five of the six years, during which they dominated those waters, temperatures were warmer than average, and three of the four years in which they were sparse were below the ten-year median temperature. Biomass and other dominant species abundance could not be related to interannual differences in median surface temperatures.

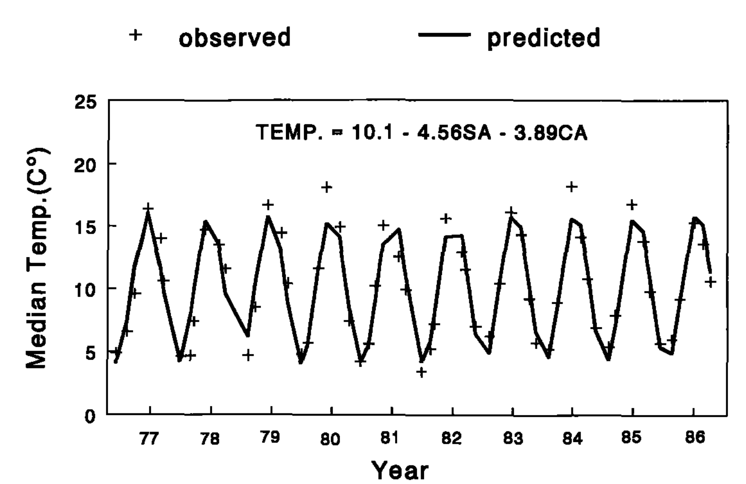

Figure 5
Seasonal median surface temperatures and the ones predicted from the harmonic regression model. Terms in the model are defined as follows: CA = Cos(0.0172*sampling midpoint(jday)); SA = Sin(0.0172*sampling midpoint(jday)).

Summer The spring zooplankton biomass surge of the late 1970's continued through the summer months. Biomass levels in those years and in 1981 were significantly different ($P<0.05$) from the low measures obtained in 1982 and 1985 (Table 1D).

Centropages hamatus was prevalent in the well mixed central shoals, but Georges Bank as a whole was not dominated by one copepod species during summer months (Table 1D). Biomass in 1977 was elevated when *C. finmarchicus* and *P. minutus* abundance reached near seasonal highs during the ten-year period. Notable in 1977 was that *C. hamatus* numbers in shallow water were minimal and *C. finmarchicus* abundance there (8386\100 m^3) was at its summer high, reinforcing the inverse abundance relationship observed between them in late spring. As it did in late spring, high *M. lucens* abundance outside the 60-m isobath raised biomass in 1979. Its abundance within the intermediate depth zone (4193\100 m^3) was well above its 10-year median there of 167\100 m^3. Biomass in 1981 was raised when both *P. minutus* and *C. hamatus* abundance estimates reached

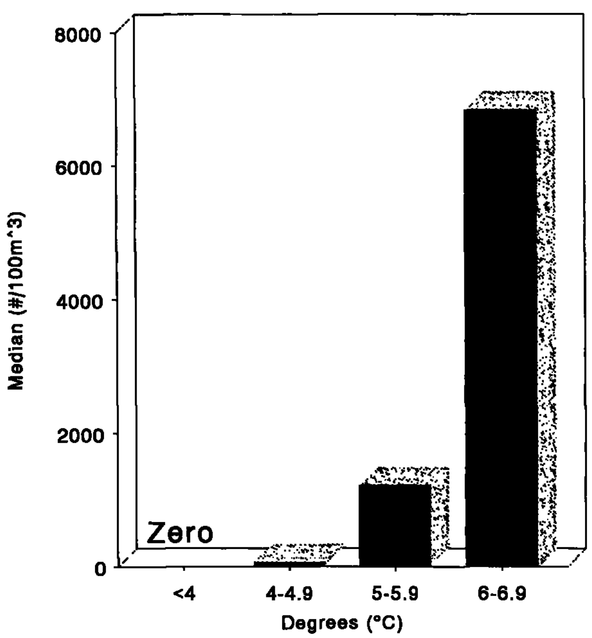

Figure 6
Ten-year median abundance of *Centropages hamatus* during the winter season at 1°C surface temperature intervals. Population estimates are from the central shoal depth area only.

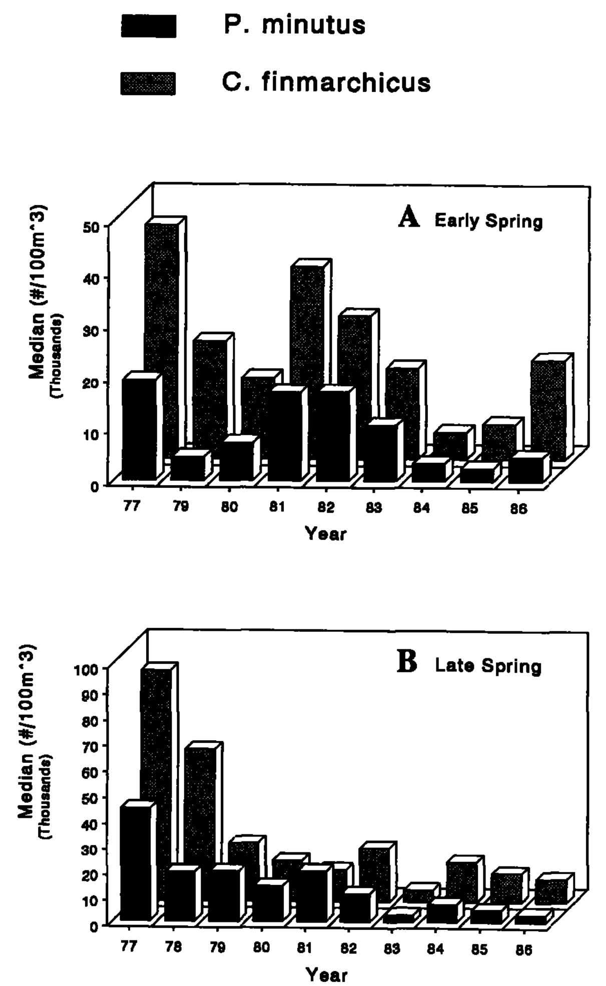

Figure 7
Median abundance of *Calanus finmarchicus* and *Pseudocalanus minutus* in 1977 through 1986 during (A) early spring and (B) late spring.

seasonal highs for the ten-year period. *Calanus finmarchicus, P. minutus,* and *C. typicus* were all below average abundance in the low biomass years of 1982 and 1985.

No strong correlation between median surface temperatures and biomass was evident during the summer. *Calanus finmarchicus* abundance estimates were highest at stations where surface temperatures had warmed above 17°C, reflecting their shift to warmer waters outside the 100-m isobath in summer (Fig. 4). This relationship is probably related to the cooler water found below the seasonal thermocline (Manning and Holzwarth, 1990), rather than to the warm surface layer where this cold water species is unlikely to concentrate. Abundance of other species was variable over the range of summer temperatures.

Early autumn Four high biomass years, from 1977 to 1980, were followed by diminishing ones through 1983 (Table 5E). Biomass began to climb in 1984 and again reached high levels in 1985. Standing stock fell to its lowest level in 1986. The depth distribution of the high biomass of 1980 differed substantially from average conditions (Fig. 4). Median biomass from the intermediate (39 cc/100 m^3) and deep (30.5 cc/100 m^3) water zones

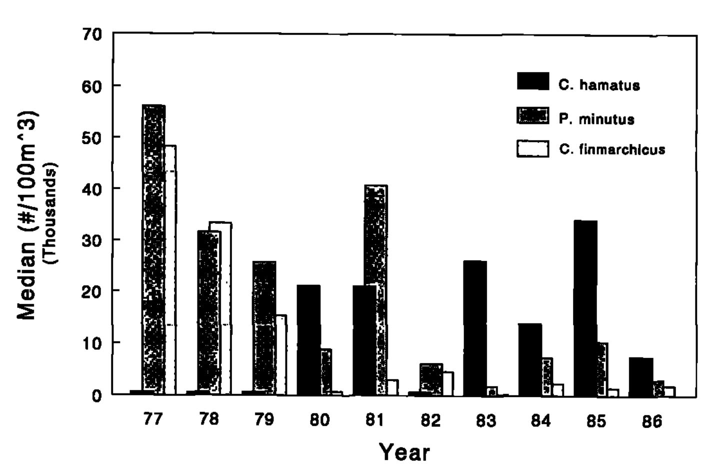

Figure 8
Median late spring abundance of *Centropages hamatus, Calanus finmarchicus,* and *Pseudocalanus minutus* in the central shoal depth region in 1977 through 1986.

were both higher than those from the central shoals area (27 cc/100 m^3), the region where biomass is usually concentrated.

Centropages typicus dominates the zooplankton population in early autumn; it makes up on the average 41% of total zooplankton abundance. Consequently, variation in its interannual abundance pattern nearly mirrored that of early autumn biomass. The only substantial deviation between patterns occurred in 1985 when *C. typicus* density soared to its ten-year high (Table 1E). Biomass was high in early autumn 1985, but not in proportion to this copepod's abundance. *Centropages typicus* abundance usually declined substantially offshore of the 100-m contour (Fig. 4). However, its abundance (10,805/100 m^3) in the deep-water depth area in 1980 was substantially higher than the time series median (1319/100 m^3). Consequently, offshore biomass in 1980 (30.5 cc/100 m^3) was also well above the deep-water 10-year median (7 cc/100 m^3). Though their numbers decline from summer, *C. hamatus* abundance continues to be a large component of zooplankton biomass in central shoal waters. Population estimates peaked in 1979 and, like biomass, were low in 1986 (Table 1E). Early autumn departures from average annual or seasonal cycles of biomass and species abundance and distribution could not be related to variations in surface water temperature (Table 2).

Late autumn The high zooplankton biomass of the late 1970's continued through late autumn (Table 1F). The seasonal peak recorded in 1982 was unexpected. Biomass increased from early autumn and pushed 1982 measurements above average for the first time. These high years were all significantly different ($P<0.05$) from the seasons lowest biomass measured in 1983 and 1986, the same years that were low in early autumn.

Centropages typicus continue to dominate the zooplankton as biomass declined towards its winter low. Its abundance was above average in the high biomass years of the late 1970's (Table 1F). The high biomass of 1982 was not related to total copepod or zooplankton numbers. Median counts of the five dominant copepod species and total zooplankton were not significantly different ($P>0.05$) from any of the other years. Cursory examination of other species abundance indicated that chaetognaths were prevalent and may have increased the biomass. The reverse occurred in 1985 when slightly above average biomass did not correlate to high zooplankton abundance. *C. typicus* and *C. hamatus* abundance in late autumn 1985 were three or more times above the ten-year median (Table 1F).

Warm late autumn temperatures appear to slow the decline of zooplankton biomass and abundance to the annual lows found in winter. High biomass years in late autumn all had above average surface temperatures (Table 2). The only high biomass levels of early autumn that were not sustained through late autumn were those collected in 1985, when surface temperature had fallen below the ten-year median. Consequently, it is not surprising that biomass and dominant copepod abundance were highest at stations where surface temperature was warm. The bimodal annual cycle displayed by *C. hamatus* in the mixed depth zone, that is to say the decline in numbers between early and late autumn from 1977 to 1981 and the increase in subsequent years (Table 1, E–F), cannot be explained by variability in autumn surface temperatures.

Discussion

The zooplankton population on Georges Bank exhibited considerable interannual and seasonal variability during the period from 1977 to 1986. Overall, biomass was above average from 1977 through 1979 and low from 1982 through 1984. Unique to the late seventies was the high late spring abundance of *C. finmarchicus* in the central shoal depth zone. The species was only a minor component of the zooplankton community there in later years. Compared with other years, 1977 biomass and copepod abundance levels in spring were extraordinary: two to three times above the ten-year median.

Calanus finmarchicus and *P. minutus* abundance fluctuations were nearly identical throughout the ten-year time series. This suggests that the annual abundance of these two species is regulated by similar processes and events, despite differences in their life cycles (Davis, 1987). This is in contrast to the results derived by Davis (1984) from model simulations of their seasonal cycles on Georges Bank. He concluded that predation pressure alone controls *P. minutus* population levels and that *C. finmarchicus* is regulated by both predation and food availability. The data presented here indicates that its unlikely that these species have different factors limiting their annual abundance. Furthermore, preliminary studies indicate that abundance estimates of both species on Georges Bank are correlated to chlorophyll levels in the water column[1]. Investigations on *P. minutus* population dynamics should not exclude food supply as a potential limiting factor.

Centropages hamatus abundance estimates were more variable and temperature sensitive than those for other dominant copepod species. Of special interest is that *C. hamatus* spring abundance pulses were inversely related to both *C. finmarchicus* and *P. minutus* population estimates. It is unlikely that temperatures which stimulate *C. hamatus* production would be detrimental to *C. finmarchicus* or *P. minutus*. Laboratory

[1] C. Meise, National Marine Fisheries Service, Narragansett, RI 002882, unpubl. data.

studies (Marshall and Orr, 1955; Corkett and McLaren, 1978) have shown that both *C. finmarchicus* and *P. minutus* grow and reproduce within the upper range of spring temperatures. There was no evidence in our data that either species had a strong response to spring surface temperature variability. One possibility is that the omnivorous *C. hamatus* may have depressed production in the other species by preying on their egg and naupliar stages, as Davis (1984) suggests they do in autumn months. Physical or behavioral responses to other changing spring conditions, such as daylight or thermocline formation, cannot be eliminated as potential factors that triggered or limited their production.

There is growing evidence that the earth's climate is changing (Mitchell, 1989). The impact of global warming on Georges Bank zooplankton could be substantial because the area is a faunal transition zone between northern boreal species and southern warm water plankton (GLOBEC, 1991). The sensitivity of the Georges Bank *C. hamatus* population to temperature indicates that the effects of a long-term warming trend might first affect the life cycle of this species. *Centropages hamatus* virtually disappears from the water column when surface temperature falls below 5°C. Marcus (1989) has shown it produces diapause eggs and reports that nauplii appeared after incubation of Georges Bank sediment. *Centropages hamatus* apparently overwinters as bottom resting eggs that hatch when water column temperatures rise to some threshold. If this phase of its life cycle is shortened or eliminated by global warming, growth and reproduction in the central shoals could continue year round and potentially limit the production of other copepod species. The early to late autumn rise of *C. hamatus* abundance from 1982 to 1986 suggests dormancy was postponed and an additional generation produced in these years. Since monthly anomalies of sea surface temperature for 1981–86 in the area indicate a warming trend (Wood and Tang, 1988), this may be the first signal that climatic change is affecting the marine ecosystem.

Interannual variability in the amount of food available to larval fishes is believed to be an important determinant of their survival and subsequent recruitment to adult populations. Field evidence for the linkage between larval survival and zooplankton prey concentrations is poor (Laurence and Lough, 1984; Leak and Houde, 1987). Though this report was not designed to examine the relationship between zooplankton variability and its effect on fishery resources on Georges Bank, it should be noted that zooplankton biomass patterns closely resembled those of northern sand lance (*Ammodytes dubius*) population estimates. Their population surged in the late seventies, responding to a reduction in predation and competition pressure caused by the fishery-induced collapse of herring and mackerel populations (Sherman et al., 1981). Relative abundance of the zooplanktiverous sand lance in survey trawls increased dramatically between 1977 and 1981, decreasing thereafter through 1986 (Nelson, 1990). The sand lance explosion may have been fueled by the high concentrations of zooplankton food stocks available in the late 1970's.

Interannual variations in time of sampling can bias estimates of biomass and abundance for predefined seasons. Early spring on Georges Bank is especially sensitive to this bias because the zooplankton population is beginning to harvest the late winter phytoplankton bloom and is rapidly transferring it to higher levels of the food chain. Obviously, the calendar definition of early spring used here to subset data may not be real in nature. The question arises whether the biomass estimates recorded in early spring 1984 were truly low or was sampling conducted too early? Median surface temperature in 1984 was only 0.3°C below the ten-year median of 5.5°C. There were other years with lower temperatures that had higher estimates of biomass. A biological sign of spring's arrival on Georges Bank is the presence of early copepodite stages of *C. finmarchicus* in the water column. The spring phytoplankton bloom triggers their spawning and, if spawning had not yet occurred, only overwintering stage-5 copepodites would be present (Davis, 1987). However, in 1984, 52.7% of the population was stage-2 and stage-3 copepodites, similar to the high biomass year of 1977 where 56.2% of the population were these early developmental stages. Thus, the low zooplankton biomass measured in early spring 1984 was probably real.

There is presently only a perceptual understanding of how physical processes affect the abundance and distribution of Georges Bank zooplankton. The success of a population depends not only on food availability and predator abundance but also upon the dynamics of its physical environment, which influence feeding efficiency, susceptibility to predation, transport, and recruitment success. Sea-surface temperature was the only physical parameter discussed in this report and its narrow range of variability could not be correlated to the comparatively large fluctuations of the zooplankton population. Monthly mean-derived wind stress components in the area (see Ingham and Wood, 1987) and anomalies in the volume of Georges Bank shelf water (Mountain, 1991) were also examined from 1977 to 1986 and no persistent correlation to biomass variability was evident. Ongoing studies are presently analyzing historical time series of physical and biological parameters to help direct future research efforts attempting to couple the physics and biology of the marine environment. Future monitoring surveys of the U.S. Northeast shelf ecosystem will continue to measure the variability of zooplankton and gather information to identify the key environmental and physical factors that drive their population dynamics.

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