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Invertebrate predators of zooplankton on Georges Bank, 1977–1987

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Abstract—Chaetognaths, primarily *Sagitta elegans*, were the most abundant and widespread invertebrate predator on Georges Bank during 1977–1987 MARMAP surveys. They were present in 79% of samples collected, and their average abundance was nearly an order of magnitude greater than that of any other predator taxon. Hydrozoan and scyphozoan medusae, euphausiid shrimp, and gammarid and hyperiid amphipods were also abundant. Diversity and abundance of predators was highest in the central, well-mixed region of the bank. In this region numbers of chaetognaths and cnidaria increased following increased abundances of *Calanus finmarchicus*. However, on a larger scale the density of *C. finmarchicus* populations was inversely correlated with number of predators because this herbivore was most abundant in deeper waters surrounding Georges Bank where predators were least numerous.

Chaetognaths and cnidaria were more abundant in 1978–1979 than in other years, and there was a statistically significant decline in the abundance of chaetognaths over the 10 year period. Abundance of both these groups was inversely correlated with temperature. Average numbers of chaetognaths in summer were low following a warm winter. Abundance of cnidaria in summer decreased with increasing summer temperatures.

INTRODUCTION

A basic understanding of the spatial and temporal distribution of zooplankton on the Georges Bank fishing ground has been gained through a number of surveys beginning in the early 1900s; their conclusions have been summarized by Davis (1987). One of the most recent and extensive surveys was conducted by the National Marine Fisheries Service Marine Resources Monitoring, Assessment and Prediction (MARMAP) program. The first 5 years of MARMAP monitoring were analyzed for seasonal cycles of dominant zooplankton species, primarily the herbivorous or omnivorous copepods and their apparent relationship to life history of fish (Sherman *et al.*, 1987) and environmental parameters (Meise-Munns *et al.*, 1990). Factors regulating copepod population dynamics also have been inferred using models based partly on this data set (Davis, 1984). Kane (1993) described patterns in zooplankton biomass and abundance of copepods over the full 10 year MARMAP time-series.

Much of the emphasis in the studies mentioned above was placed on describing distribution patterns of the numerically dominant copepod species. However, in addition to data on copepods, the MARMAP samples contain information about small and numerous zooplankton predators that were captured coincident with copepods in the same net tows. These include a variety of invertebrate taxa, chaetognaths, predatory copepods,

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amphipods, mysid and euphausiid shrimp (especially the younger and smaller juveniles), and cnidarians such as hydroids, hydromedusae, siphonophores and scyphomedusae.

The purpose of this study is to describe abundance and distribution of these predator species over the full 10-year time-series. Distribution patterns of zooplankton predators on Georges Bank have been described previously from somewhat more limited data sets (e.g. Cohen and Lough, 1982, and summarized by Davis, 1987). Our aim was to compare results from the 1977–1987 MARMAP survey with historic patterns as well as to provide a more complete basis for comparison with more recent studies such as the joint NSF-NOAA GLOBEC program. Our goal was to provide a foundation for studies of dominant factors controlling herbivore population dynamics on the Georges Bank region including physical processes, food limitation, and predation.

METHODS

Plankton samples were collected at monthly to bimonthly intervals during MARMAP surveys of the North Atlantic Ocean. Most of our analyses are based on data from 38 stations on Georges Bank that fit roughly within the 100 m isobath and bounded by latitudes 40.10–42.18 °N and longitudes 67.25–68.91 °W (Fig. 1). A total of 2352 samples collected during 1977–1987 were used for this analysis, 1190 or 50.6% of which were collected at night. The number of samples collected each year varied from 168 to 235 except during 1978 when increased sampling frequency in October and November resulted in 329

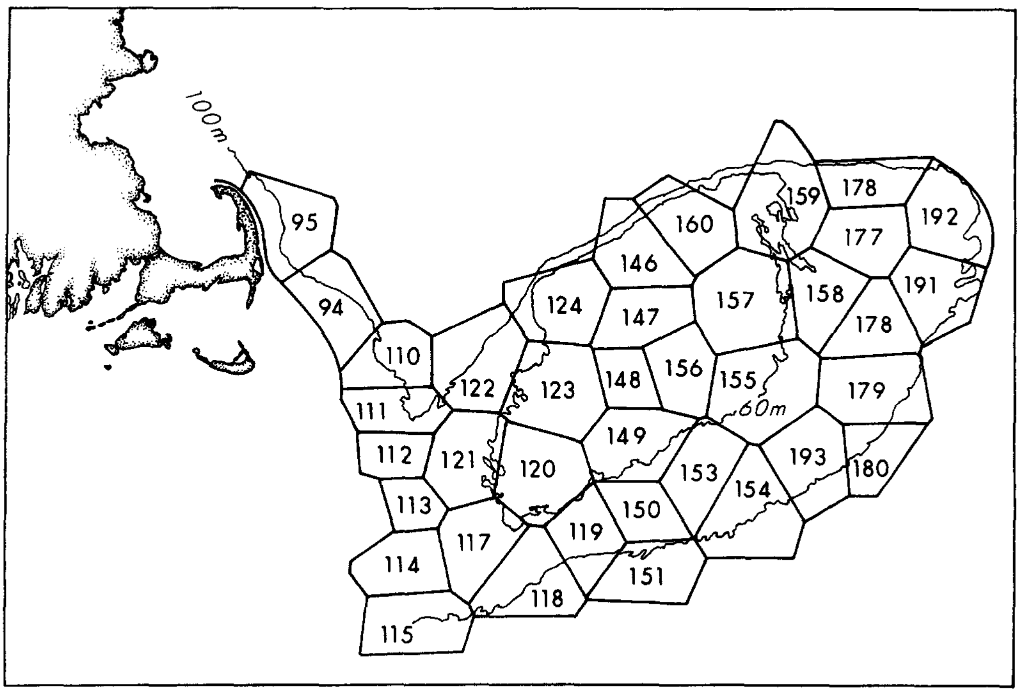


Fig. 1. MARMAP station locations on Georges Bank, 1977–1987, used for analyses reported here. The 60 and 100 m isobaths are indicated.

stations. Maps of seasonal and geographic distribution were generated using additional stations in the Gulf of Maine and Nantucket Shoals to make the maps comparable to those used for analysis of *Calanus finmarchicus* by Meise and O'Reilly (1996).

Zooplankton were collected with a 61-cm bongo frame fitted with a 0.333 mm mesh net towed obliquely to a maximum depth of 200 m or to within 5 m of the bottom and back again to the surface. Ship speed varied between 1–2 knots except during the winter surveys of 1977 and 1978 when is was 3.5 knots. Volume sampled was determined from a flowmeter suspended in the center of each bongo frame. Samples were preserved in 5% formalin. A mechanical time–depth recorder was attached to the wire above the frame. Surface temperature was measured at each station with reversing thermometers. Detailed sampling procedures and cruise tracks are summarized by Sibunka and Silverman (1984, 1989).

Zooplankton were sorted and identified to the lowest taxon possible at the Morski Instytut Rybacki, Szczecin, Poland. Those MARMAP taxa known to be predators on copepods and larval fish were selected for analyses (Table 1). We do not present information

Table 1. *Invertebrate predators on Georges Bank. Abundance statistics at standard MARMAP stations during the period* 1977–1987

Predator type	Samples present (%)	Average (no./100 m^3)	Median when present (no./100 m^3)	Maximum (no./100 m^3)
Total chaetognaths	79.1	6291.8	1525.9	383,547
Sagitta elegans		4616.8		383,547
Sagitta enflata		10.2		11,250
Sagitta serrodentata		8.5		3322
Cnidaria	12.2	630.2	478.4	206,811
Hydrozoa	9.9	366.2	336.7	83,872
Siphonophores	9.4	39.9	122.6	5944
Total euphausiid shrimp	47.3	592.6	264.9	153,673
Meganyctiphanes norvegica		56.3		106,389
Euphausia krohni		24.5		32,675
Nematoscelis megalops		1.9		2352
Thysanoessa raschi		1.3		608
T. longicaudata		0.9		548
T. inermis		0.5		244
T. gregaria		0.3		176
Gammarid Amhipods	33.9	581.9	261.7	80,563
Hyperiid Amphipods	33.5	271.9	224.4	69,456
Mysid Shrimp	11.0	167.2	234.2	36,576
Decapods				
Crangon septemspinosa	11.0	62.1	280.8	7984
Lucifer faxoni	1.8	6.2	114.9	8331
Total Euchaeta	12.8	16.6	59.1	1449
Euchaeta marina		0.7		493
Euchaeta norvegica		0.7		420
Isopods	2.9	4.2	67.2	1295
Ctenophores*	0.7	2.2	150.1	1294

*Ctenophores are not adequately represented in the MARMAP data because they cannot be preserved.

on the omnivorous copepod, *Centropages* spp. because temporal and spatial distribution patterns have been analyzed by Kane (1993).

Species level data were available only for chaetognaths, euphausiid shrimp and the copepod genus *Euchaeta*. For certain analysis we combined all species data. For example, we created the category "total chaetognaths" by adding Chaetognatha, *Sagitta* spp., *Sagitta elegans*, *Sagitta serrodentata*, and *Sagitta enflata*. The MARMAP category termed "coelenterates" has been changed here to "cnidaria" to reflect more recent taxonomic practice. While no species data were available for this category, we believe it includes primarily hydrozoan and scyphozoan medusae; siphonophores were enumerated under a separate heading. From 1979 to 1985 the category "hydrozoa" was also enumerated separately from other cnidaria; no information was available as to whether the medusa or hydroid stage, or both, were counted.

It is probable that accuracy of abundance estimates of the various zooplankton taxa reported here varies widely. Estimates of fragile ctenophores such as *Bolinopsis* spp. are the least reliable; the gelatinous nature of these ctenophores does not withstand collection and preservation procedures used. Some of the larger scyphomedusan jellyfish also do not collect or preserve well. In addition, abundances of large, rapidly swimming crustacean predators such as adult euphausiid and decapod shrimp are probably underestimated because these organisms evade collection with small nets.

Data analysis was performed using either the SAS statistical analysis program for the PC or Microsoft Excel. For Table 1 mean and maximum abundances were determined over the entire 10-year period. Many taxa were present in only a small number of samples; to create meaningful results despite the large number of zero values we calculated median values for the subset of samples with non-zero abundance. This statistic provides a realistic assessment of typical abundances during seasons when, or at locations where, a species occurs. Average values over specific depth ranges were calculated for the entire 10 year period for station depths 0–60 m, 0–100 m and > 100 m.

For all other analyses abundances were log-transformed [ln(abundance + 1)]. Seasonal mean abundances of transformed data were determined for four periods: winter (1 January–30 April), spring (1 May–14 June), summer (15 June–14 September), and fall (15 September–31 December) of each year. Mean surface temperature was calculated for the same periods. These means were used to examine temporal trends (1977–1987) and to investigate the influence of temperature on abundance. The Spearman Rank Order Correlation test was used to determine significance of relationships. To determine if observed patterns could be biased by sampling dates, which differed from year to year, correlation with a temperature anomaly also was examined. Temperature anomalies for the 0–30 m near-surface layer of Georges Bank, as a whole, were calculated with anomalies being determined relative to an annual cycle for the whole MARMAP data set (D. Mountain, personal communication, 1995).

Correlation of abundances of "total chaetognaths" and "cnidaria" with numbers of *Calanus finmarchicus* were calculated for stations on Georges Bank within the 60 m isobath. Coefficients of variation for these taxa were also calculated.

Contoured distributional maps of abundance over both Georges Bank and the Gulf of Maine region were generated using data over the entire 10-year period. Data were grouped, irrespective of year, into six 2-month intervals (January–February, March–April, May–June, July–August, September–October, and November–December). Abundance estimates of total chaetognaths, cnidaria, gammarids, and euphausiids were log-transformed

[$\log_{10}$(abundance + 1)], and maps for each 2-month period were generated using means grouped by MARMAP tile. Standard tile coordinates were transformed to map coordinates using Lambert's conic conformal map projection (Snyder, 1987), Surface III contouring software (Sampson, 1988), and a grid resolution of 5.4 km/grid.

RESULTS

I. Abundance of predator taxa

Chaetognaths were the most abundant invertebrate predators collected on Georges Bank during 1977–1987 (Table 1). *Sagitta elegans* was the most common species; *Sagitta enflata* and *S. serrodentata* were much less abundant. Chaetognaths were present in nearly 80% of the samples collected, and their average abundance far exceeded that of all other categories. The median for samples in which chaetognaths were present was 1526 per 100 m^3 and also exceeded that for other taxa. Thus, chaetognaths were present at abundances greater than 1526 per 100 m^3 in 40% of samples collected during the 10 year period (Table 1).

"Cnidaria", presumably hydrozoan and scyphozoan medusae, were also abundant on Georges Bank. The average number during the 10 year period was 630 per 100 m^3. However, they were present in only 12% of samples collected. Maximum abundance approached that of chaetognaths. Hydrozoa, when enumerated separately from other cnidaria, were present in 9.9% of samples and were much more abundant than siphonophores, which were found in 9.4% of samples.

Large crustaceans including euphausiid shrimp and gammarid amphipods were the next most abundant taxa. Hyperiid amphipods were somewhat less abundant. Euphausiid shrimp were collected in 47% of samples, at times reaching densities of > 100,000 per 100 m^3. *Meganyctiphanes norvegica* and *Euphausia krohni* were the most common species. Mysid shrimp and the decapod shrimp *Crangon septemspinosa* were collected less frequently, but when present were found in abundances similar to euphausiid shrimp and amphipods (Table 1). Small crustacean predators of the copepod genus *Euchaeta* were among the least abundant of the predators. Isopods and the decapod shrimp *Lucifer faxoni* also were infrequently observed.

Ctenophores were preserved and enumerated in only 18 samples collected primarily in June, July and September. Because some species preserve so poorly, numbers reported here are certainly underestimates of their abundance on Georges Bank.

II. Geographic and seasonal patterns in abundance

Predators were generally more diverse and more numerous in the shallow, well-mixed region of Georges Bank; a smaller number of species were characteristic of deeper waters surrounding the Bank (Table 2).

Shallow assemblage. All species of chaetognaths except *Sagitta serrodentata* were more abundant at depths ranging from 0 to 100 m than in deeper water (Table 2). Immature chaetognaths (*Sagitta* spp.) were more common within the 60 m isobath, while mature chaetognaths (identified as *S. elegans*) were found out to 100 m (Table 2). This pattern of maximum abundance concentrated within the mixed area of Georges Bank and on Nantucket shoals was typical for all seasons (Fig. 2). Cnidaria inhabited the shallowest

Table 2. Species composition of invertebrate predators versus station depth on Georges Bank. Numbers are abundances averaged during 1977–1987. Species are considered part of the assemblage only when average abundance exceeded > 50 per 100 m³. Data from October–November 1978 have been excluded from averages calculated for Sagitta elegans

	Number per 100 m³
Shallow assemblage (0–60 m)	
Sagitta elegans	4371
Gammarid amphipods	1552
Cnidaria	1305
Euphausiid shrimp*	461
Mysid shrimp	300
Hyperiid amphipods	203
Crangon septemspinosa	116
	8308 total
Mid-depth assemblage (60–100 m)	
Sagitta elegans	3871
Euphausiid shrimp	645
Cnidaria	453
Hyperiid amphipods	318
Gammarid amphipods	186
Mysid shrimp	154
	5627 total
Deep assemblage (> 100 m)	
Euphausiid shrimp†	650
Sagitta elegans	292
Hyperiid amphipods	248
Siphonophores	62
Euchaeta spp.	59
	1311 total

**Meganyctiphanes norvegica* was the most abundant species.
†*Euphausia krohnii* was the most abundant species.

regions of Georges Bank and were found primarily at stations less than 60 m deep (Table 2). Seasonal peaks occurred in May and June (Fig. 2). Gammarid amphipods were also more abundant in shallow waters on the central Bank within the 60 m isobath. Highest abundances were typically observed in summer and fall (Fig. 2). Mysid shrimp, isopods, *Crangon septemspinosa* and *Lucifer faxoni* were all characteristic of the shallow central Bank.

Deep assemblage. In contrast to most other predators, euphausiids were more abundant in waters deeper than 60 m, with highest densities in the southern and southwest flank and in the Gulf of Maine (Fig. 2). Seasonal peaks were observed in March–June. Hyperiid amphipods were more abundant on the southern Bank and found in deeper waters than the gammarids. Seasonal peaks occurred in the spring. *Euchaeta* spp. and siphonophores were found mostly in deeper waters and the Gulf of Maine (Table 2).

For most taxa, more animals were collected during the night than during daytime tows (Table 3). This was especially true for species in which diel migrations are known to be undertaken by mature animals, e.g. euphausiid shrimp and chaetognaths. Taxa for which

(a)

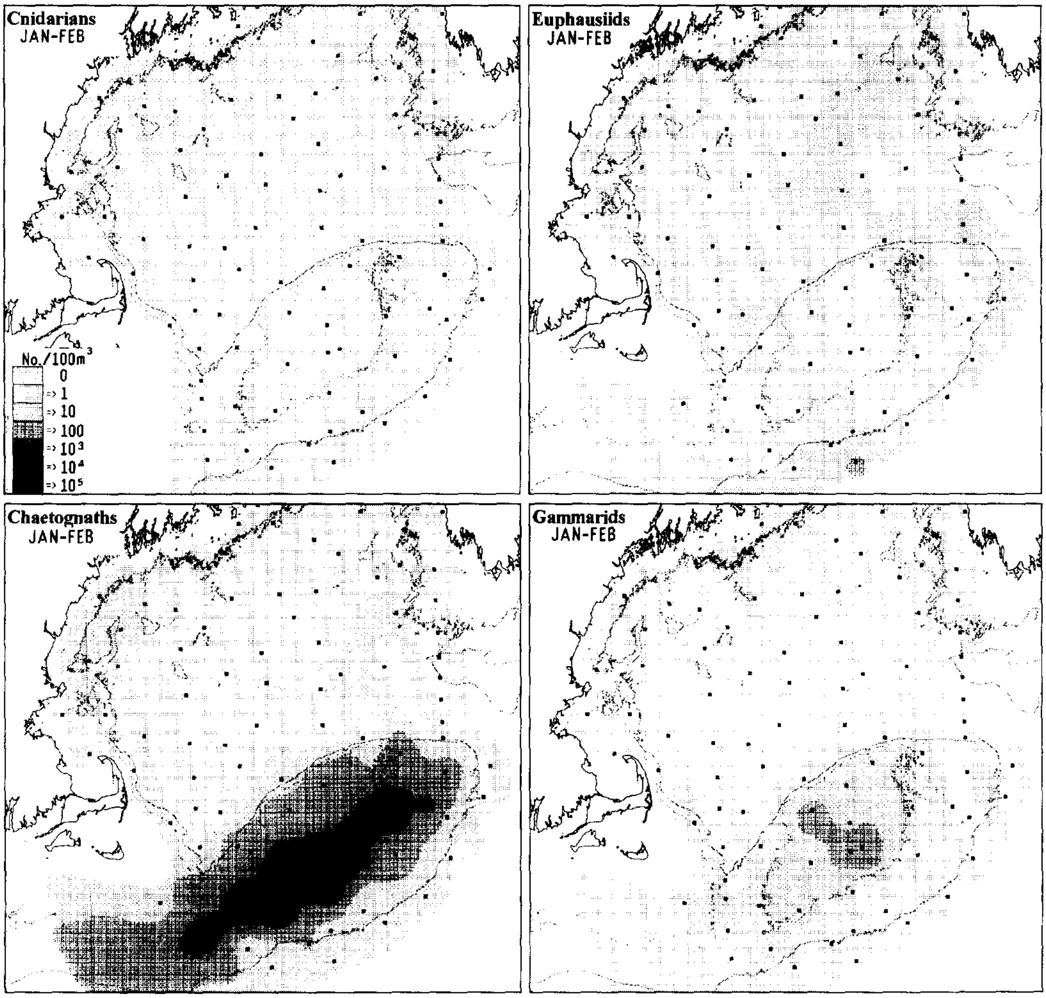


Fig. 2. Contoured distributional maps of abundant invertebrate predators in the Georges Bank–Gulf of Maine Region. Data plotted are 2-month means averaged over the entire 10-year period. Abundance estimates were log-transformed [$\log_{10}$(abundance + 1)] and maps for each 2-month period were generated using means grouped by MARMAP tile. Standard tile coordinates were transformed to map coordinates using Lambert's conic conformal map projection (Snyder, 1987), Surface III contouring software (Sampson, 1988), and a grid resolution of 5.4 km/grid.

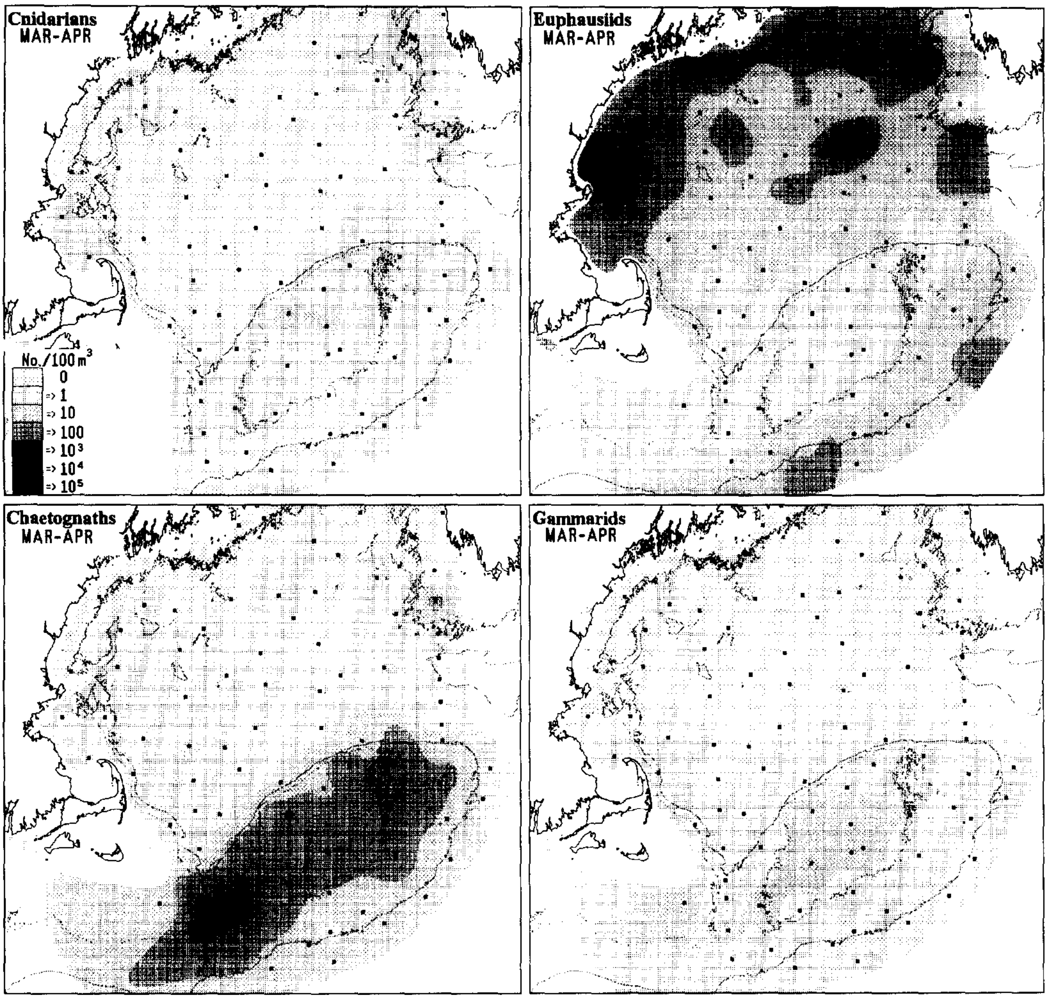

Cnidarians
MAR-APR
No./100 m³
0
=> 1
=> 10
=> 100
=> 10³
=> 10⁴
=> 10⁵
Euphausiids
MAR-APR
Chaetognaths
MAR-APR
Gammarids
MAR-APR

Fig. 2(b).

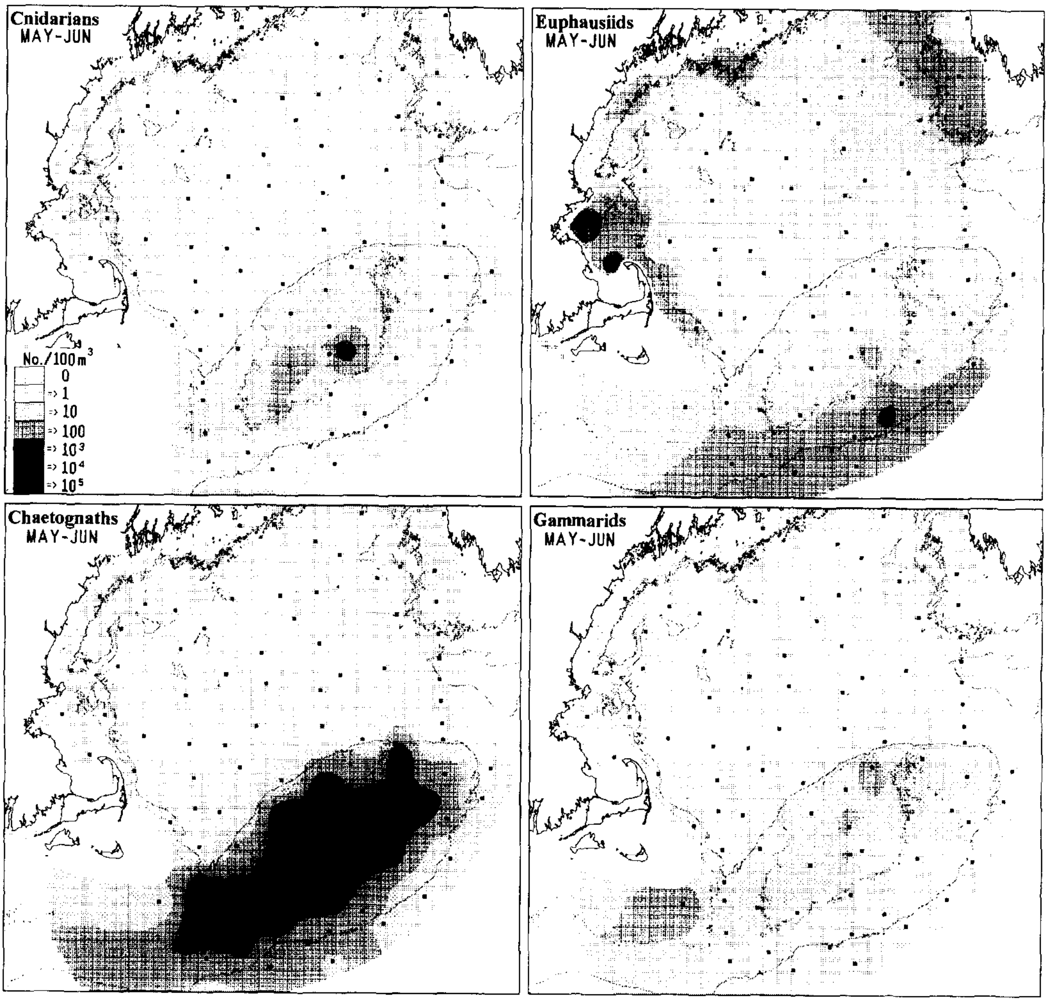

Cnidarians
MAY-JUN
No./100m^3
0
=> 1
=> 10
=> 100
=> 10^3
=> 10^4
=> 10^5
Euphausiids
MAY-JUN
Chaetognaths
MAY-JUN
Gammarids
MAY-JUN

Fig. 2(c).

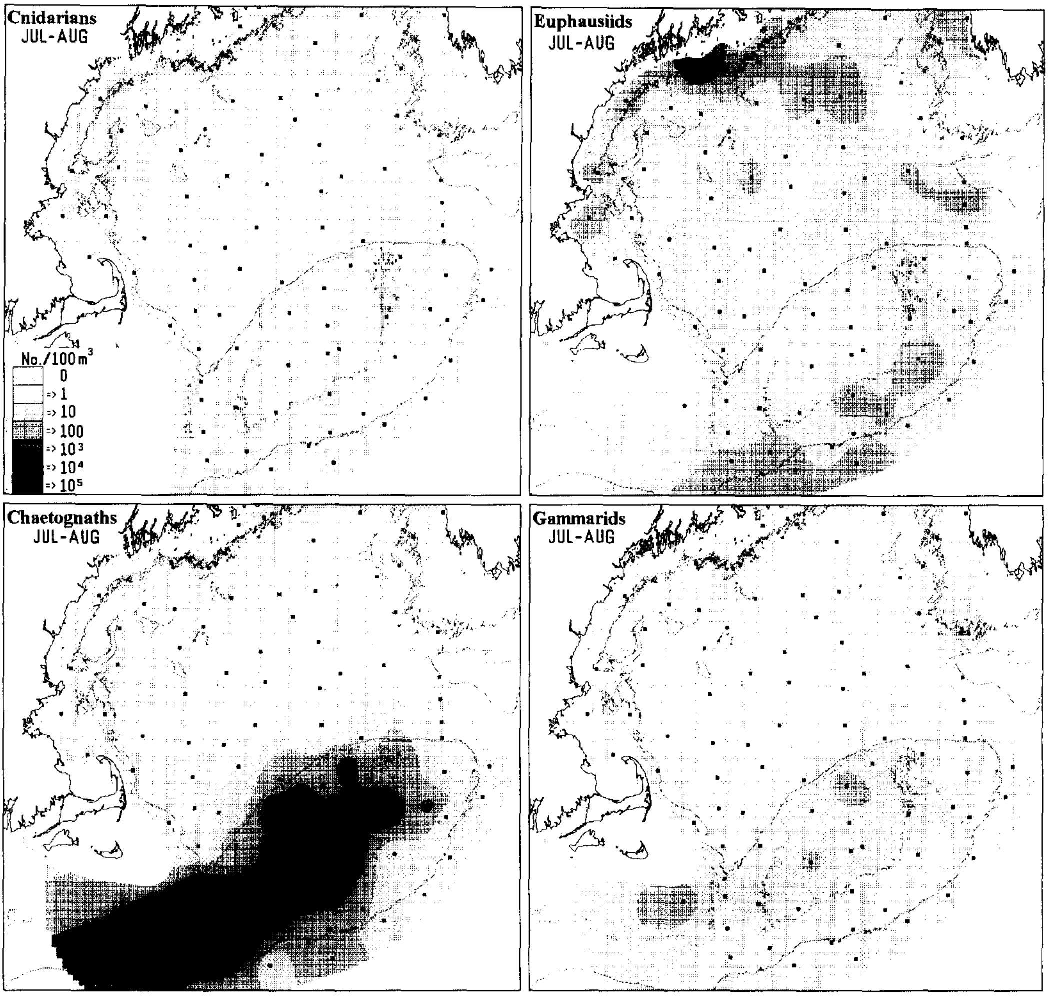

Cnidarians
JUL-AUG
No./100 m^3
0
=> 1
=> 10
=> 100
=> 10^3
=> 10^4
=> 10^5
Euphausiids
JUL-AUG
Chaetognaths
JUL-AUG
Gammarids
JUL-AUG

Fig. 2(d).

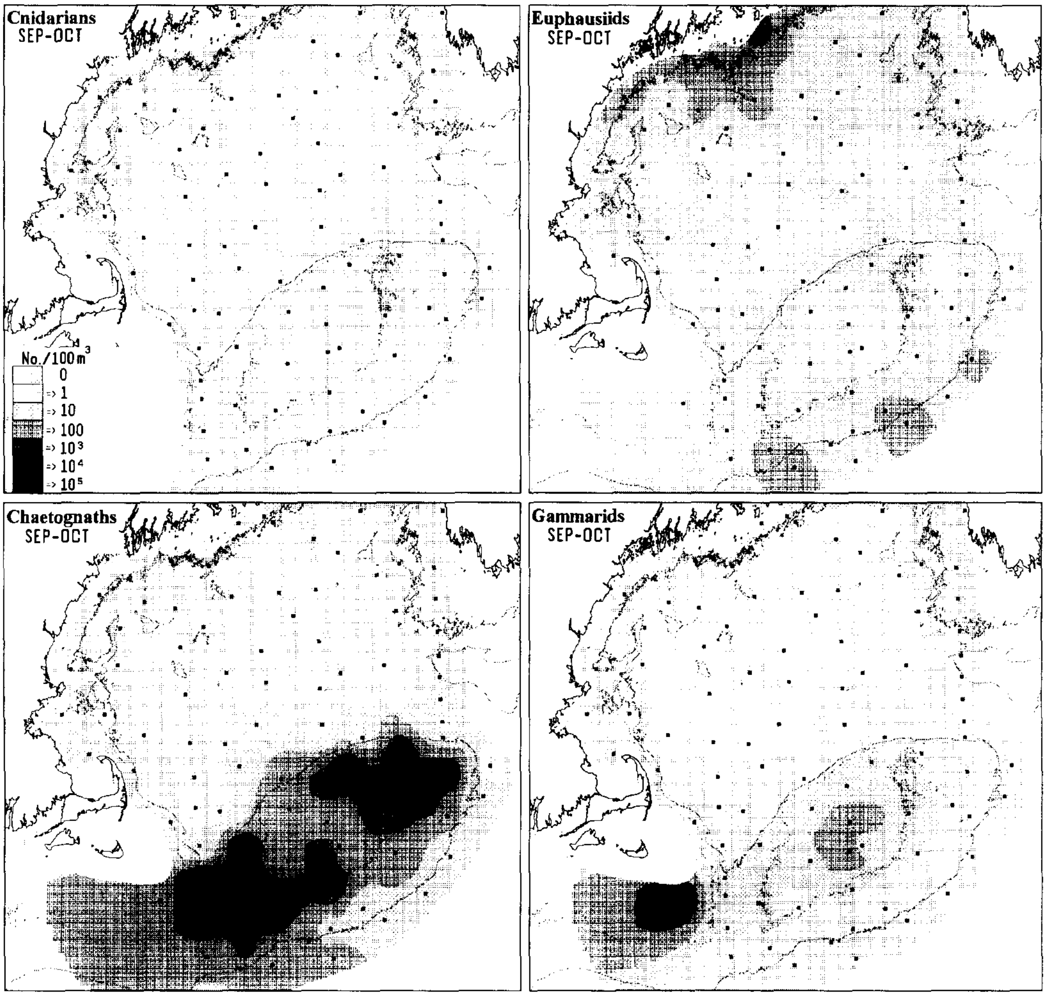

Cnidarians
SEP-OCT
No./100 m³
0
=> 1
=> 10
=> 100
=> 10³
=> 10⁴
=> 10⁵
Euphausiids
SEP-OCT
Chaetognaths
SEP-OCT
Gammarids
SEP-OCT

Fig. 2(e).

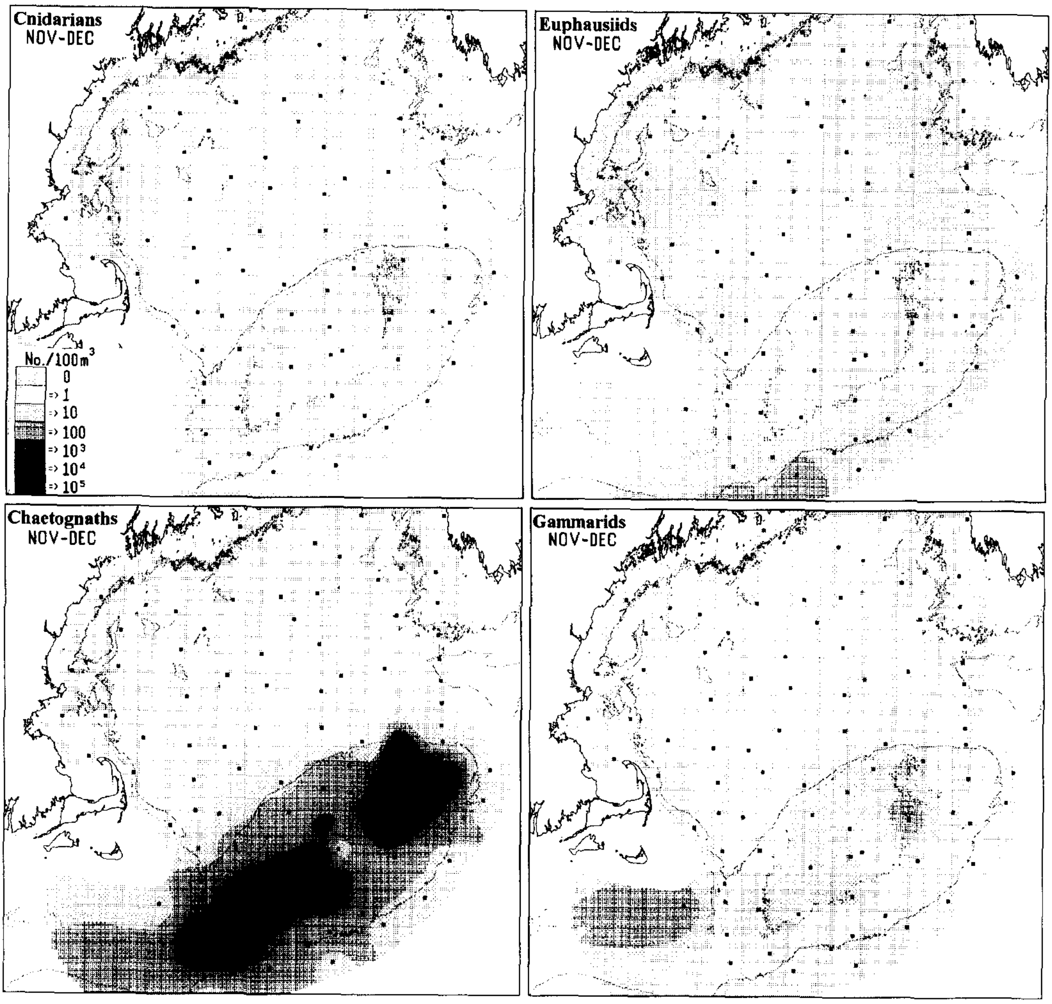

Cnidarians
NOV-DEC
No./100m^3
0
=> 1
=> 10
=> 100
=> 10^3
=> 10^4
=> 10^5
Euphausiids
NOV-DEC
Chaetognaths
NOV-DEC
Gammarids
NOV-DEC

Fig. 2(f).

Table 3. *Invertebrate predators collected on Georges Bank in nighttime net tows during* 1977–1987

Predator category	Night (%)
Sagitta elegans	55.5
Sagitta enflata	69.9
Sagitta serrodentata	53.8
Sagitta spp.	44.7
Coelenterates	47.4
Meganyctiphanes norvegica	96.4
Euphausia krohnii	96.1
Euphausiacea	57.9
Gammarid amphipods	55.7
Hyperid amphipods	45.7
Mysid shrimp	53.1
Euchaeta spp.	55.1

more animals were collected during the day were immature chaetognaths (*Sagitta* spp.) and coelenterates.

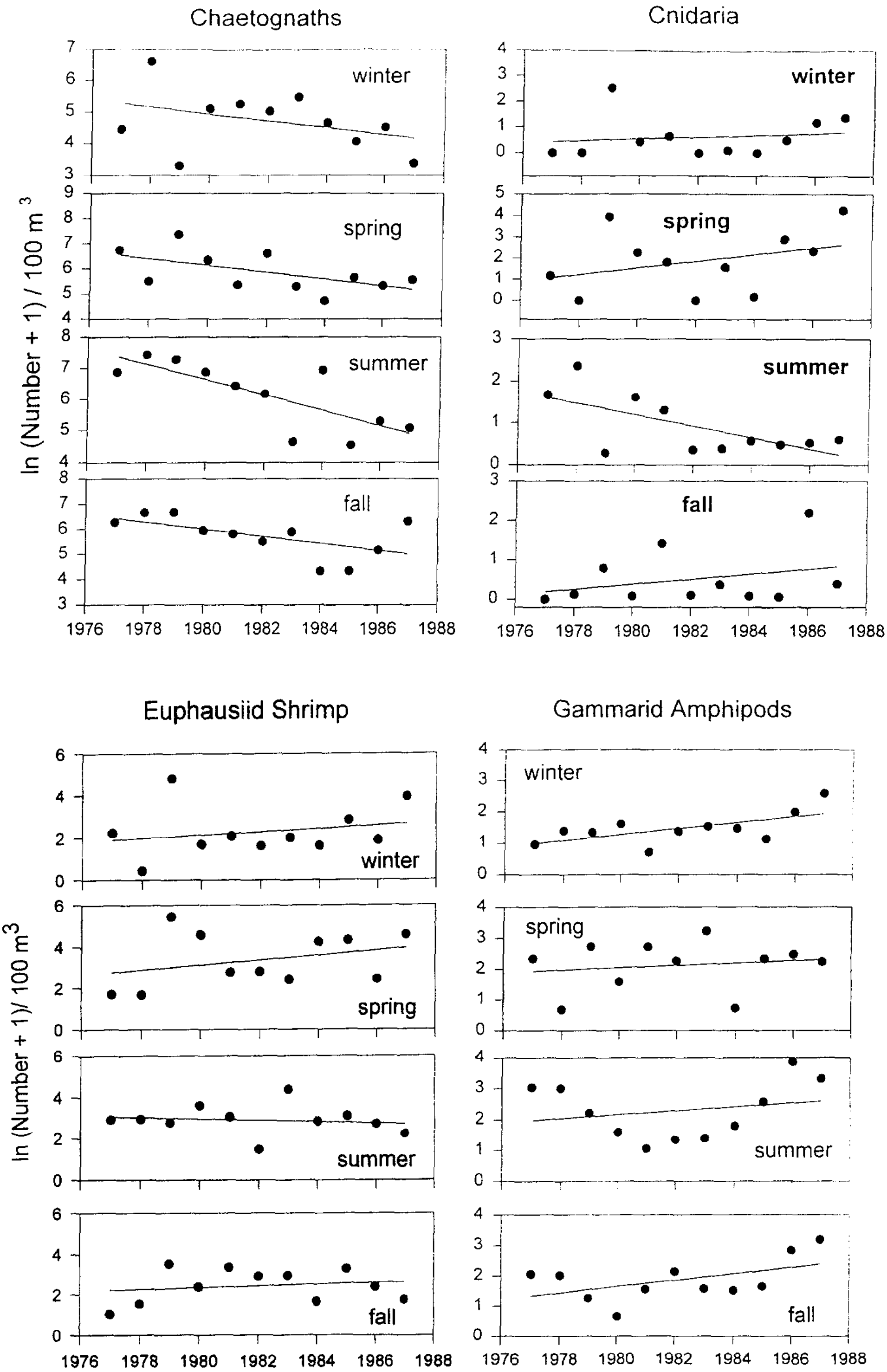
III. Annual trends and temperature

Seasonal mean abundances (ln + 1 transformed data) of the dominant groups of predators were examined for temporal trends during the 10-year time period (Fig. 3). Chaetognaths were very abundant during 1978; high concentrations of *Sagitta elegans* observed in late October and early November on the northeast peak of Georges Bank have previously been reported (Lough and Trites, 1989). Chaetognaths decreased in abundance over the period 1977–1987; this decrease was evident during all seasons (Fig. 3) but was most pronounced and statistically significant in summer (Spearman Rank Correlation Coefficient = -0.727; $p = 0.009$). Average abundance in summer was negatively correlated with average temperature during the previous winter (Spearman Rank Correlation Coefficient = -0.745; $p = 0.007$). This relationship was slightly improved by using the temperature anomalies calculated for the years 1980–1987 (Spearman Rank Correlation Coefficient = -0.810; $p = 0.009$).

Cnidaria were most abundant in 1979 and again in 1987 (Fig. 3). No statistically significant patterns in seasonal abundance versus year (1977–1987) were evident for cnidaria, but abundance in summer was inversely correlated with average summer temperature (Spearman Rank Correlation Coefficient = -0.609; $p = 0.043$).

Euphausiids were most abundant in winter and spring 1979 (Fig. 3). There were no significant temporal trends in abundance and no correlation of abundance with temperature in any season.

Numbers of Gammarid amphipods were highest during 1986–1987 (Fig. 3); no significant correlations with time were observed. There were no significant correlations of seasonal average abundance with temperature.


Chaetognaths
Cnidaria
Euphausiid Shrimp
Gammarid Amphipods
winter
spring
summer
fall
ln (Number + 1) / 100 m 3
ln (Number + 1)/ 100 m3
1976
1978
1980
1982
1984
1986
1988

DISCUSSION

General patterns of abundance and distribution described here are consistent with patterns observed in earlier studies. The chaetognath *Sagitta elegans* has been described by both Clarke *et al.* (1943) and Cohen and Lough (1982) as the most common invertebrate predator on Georges Bank. Despite decreasing abundance recorded here for the MARMAP decade, *S. elegans* remained the numerical dominant throughout the period 1977–1987. *S. elegans* also has been found consistently in greatest abundance in the shallow, well-mixed areas of the Bank (Clarke *et al.*, 1943; Davis, 1987).

Gelatinous zooplankton, including medusae and ctenophores, have received little attention in this and most previous studies, probably because they are difficult to collect, preserve and quantify. When encountered in this survey, "cnidaria" tended to be very abundant; at certain locations they were the second most abundant predator. Moreover, abundances reported are almost certainly underestimates. More recent reports indicate extensive populations of hydromedusae (Gallager *et al.*, 1996) and hydroids (Madin *et al.*, 1996). Populations of this magnitude could have important impacts on prey when they occur and argue for increased emphasis on the study of these predators.

Amphipods and euphausiid shrimp were also abundant predators in the system. The prevalence of euphausiids in deeper waters surrounding Georges Bank, in contrast with the distribution of gammarid amphipods in shallow waters, is also consistent with previous reports (Cohen and Lough, 1982; Davis, 1987). However, it should be noted that euphausiids do occur on the Bank between the 60 and 100 m isobaths as well (Table 2).

Gammarid amphipods, while often considered benthic (Bigelow, 1926), were found in the water column of the shallow Bank both day and night. A similar peak distribution within the 60 m isobath has been described previously (summarized by Davis, 1987). It may be that an even larger population is resident on the bottom. The potential importance of gammarids to production and predation on the Bank has been investigated by Avery (1993) who demonstrated their reliance on predation to meet metabolic needs. Avery *et al.* (1996) examined MARMAP data for patterns in abundance and distribution with results similar to those reported here. Highest densities were found in the Nantucket shoals region (evident here in Fig. 2) in 1984. This region was not included in our analysis of seasonal abundances, which indicated that 1986–1987 were peak years for amphipods on the Bank proper when Nantucket shoals are excluded from the analysis.

Our synthesis of MARMAP data clearly indicates a greater abundance of predators in the central shoal area of Georges Bank and out to the 100 m isobath compared to deeper waters (Table 2). The central shoal area is also characterized by a more diverse community of predators than elsewhere. Clearly, the well-mixed waters support a high biomass and production of predators. An important role for predators in this region has been suggested by Davis (1984), who concluded that chaetognaths, ctenophores and *Centropages* spp. together could control copepod production on Georges Bank.

Fig. 3. Seasonal mean abundances of natural log (+1) transformed MARMAP data for the most abundant invertebrate predator taxa during the decade 1977–1987. Regression lines are plotted as an aid to the eye; significance of trends were determined with nonparametric statistics (reported in the text) because of the small number of data points.

We performed an analysis with results consistent with the idea that *Calanus finmarchicus* can be an important prey species for invertebrate predators in the shoal region of Georges Bank. We noted that Kane (1993) reported significantly higher median abundance of *Calanus finmarchicus* during the period 1977–1979 and, in contrast to other years, this species was uncharacteristically abundant in the central shoals during this period. Years during which *C. finmarchicus* was most abundant correspond to peak years for chaetognaths and cnidaria (in summer) as reported in this study. We investigated this apparent correlation more formally and found it to be statistically significant for populations of chaetognaths, cnidaria and *C. finmarchicus* residing within the 60 m isobath. Moreover, correlations that were slightly negative become strongly positive over time, with increases in predators following increases in herbivores. There are two possible interpretations of this result. First, predator abundances responded to the increased supply of their prey resource, or second, mechanisms which enhance the abundance of *Calanus finmarchicus* on the central Bank also do so for the predator species.

Kane (1993) noted that it was during cold years that herbivorous copepods including *Calanus finmarchicus* were abundant on the shallow Bank, while *Centropages hamatus* was the more abundant copepod in warm years. We found that *Sagitta* spp. were more numerous in years with cold winters. Temperature may have an indirect effect on chaetognath abundance by increasing the supply of herbivorous copepod prey in cold years. Future studies could focus on whether *C. hamatus* is a less suitable prey for *Sagitta elegans* than the herbivorous copepods.

However, a more direct effect of temperature on the decadal decline in numbers of chaetognaths is also possible. Georges Bank and latitude 41°N mark the southern extent of endemic populations of *Sagitta elegans* (Alvariño, 1965). While *S. elegans* ranges into warmer waters, temperatures for breeding and maintaining an endemic population are more restrictive (Russell, 1932). Body size and egg number at maturity are inversely correlated with temperature experienced during development. On Georges Bank a cohort of juveniles develops during winter, maturing by April (Clarke *et al.*, 1943). *S. elegans* may achieve a smaller body size and lower reproductive potential while maturing during warm winters, a condition leading to smaller populations the following summer.

Maps of chaetognath abundance are clearly inverse images of maps showing *Calanus finmarchicus* inhabiting only waters offshore of the 100 m isobath (Meise and O'Reilly, 1996). This inverse correlation on the broader geographic scale is so striking that it is tempting to invoke a predatory control mechanism of chaetognaths excluding *C. finmarchicus* from shoal areas as suggested by Clarke *et al.* (1943). Alternatively, physical processes or life history characteristics may be more important to maintaining chaetognaths on the Bank and *Calanus finmarchicus* in deeper waters. For example, Lough and Trites (1989) showed that vertical migration patterns of *Sagitta elegans* were apparently important to increased residence time on the Bank. By remaining deeper in the water column migrating adults reduce their rate of advection offshore by surface currents. In contrast, migration patterns of *Calanus finmarchicus*, if different from chaetognaths, could exclude them from the shallow areas of the bank.

Without further information it is difficult to determine the relative importance of physical processes, behavior, food limitation and predation to population dynamics of predators and herbivores on Georges Bank. A clearer understanding should result from intensive studies of hydrography, herbivore feeding and production, and predation rates by the GLOBEC program.

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REFERENCES

Alvariño A. (1965) Chaetognaths. In: *Oceanography and marine biology annual review*, Vol. 1, H. Barnes, editor, George Allen and Unwin Ltd, London.

Avery D. E. (1993) Amphipods in the Georges Bank ecosystem. M.S. Thesis, University of Rhode Island, RI, 152 pp.

Avery D. E., J. Green and E. G. Durbin (1996) The distribution and abundance of pelagic gammarid amphipods on Georges Bank and Nantucket Shoals. *Deep-Sea Research II*, **43**, 1521–1532.

Bigelow H. B. (1926) Plankton of the offshore waters of the Gulf of Maine. *Bulletin of the Bureau of Fisheries*, **40**, 1–509.

Clarke G. L., E. L. Pierce and D. F. Bumpus (1943) The distribution of *Sagitta elegans* on Georges Bank in relation to hydrographic condition. *Biological Bulletin*, **85**, 201–226.

Cohen R. E. and R. G. Lough (1982) Zooplankton distribution and abundance in the Georges Bank–Nantucket Shoals area during the autumn winter larval herring surveys (1973–1977). Lab. Ref. 82–12, Northeast Fisheries Center, Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA, 533 pp.

Davis C. S. (1984) Predatory control of copepod seasonal cycles on Georges Bank. *Marine Biology*, **82**, 31–40.

Davis C. S. (1987) Zooplankton life cycles. In: *Georges Bank*, R. A. Backus and D. E. Bourne, editors, MIT Press, Cambridge, pp. 256–267.

Gallager S. M., C. S. Davis, A. W. Epstein, A. Solow and R. C. Beardsley (1996) High-resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. *Deep-Sea Research II*, **43**, 1627–1663.

Kane J. (1993) Variability of zooplankton biomass and dominant species abundance on Georges Bank: 1977–1986. *Fisheries Bulletin*, **91**, 464–474.

Lough R. G. and R. W. Trites (1989) Chaetognaths and oceanography on Georges Bank. *Journal of Marine Research*, **47**, 343–369.

Madin L. P., S. M. Bollens, E. Horgan, M. Butler, J. Runge, B. K. Sullivan, G. Klein-MacPhee, E. Durbin, A. G. Durbin, D. van Keuren, S. Plourde, A. Bucklin and M. E. Clarke (1996) Voracious planktonic hydroids: unexpected predatory impact on a coastal marine ecosystem. *Deep-Sea Research II*, **43**, 1823–1829.

Meise C. J. and J. E. O'Reilly (1996) Spatial and seasonal patterns in abundance and age-composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank: 1977–1987. *Deep-Sea Research II*, **43**, 1473–1501.

Meise-Munns C., J. Green, M. Ingham and D. Mountain (1990) Interannual variability in the copepod populations of Georges Bank and the western Gulf of Maine. *Marine Ecology Progress Series*, **65**, 225–232.

Russell F. S. (1932) On the biology of *Sagitta*. The breeding and growth of *Sagitta elegans* Verrill in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom*, **18**, 131–146.

Sampson R. J. (1988) *Surface III Users Manual*. Kansas Geological Survey, Lawrence, Kansas. Interactive Concepts Incorporated, Lawerence, KS, 277 pp.

Sherman K., W. G. Smith, J. R. Green, E. B. Cohen, M. S. Berman, K. A. Marti and J. R. Goulet (1987) Zooplankton production and the fisheries of the Northeastern Shelf. In: *Georges Bank*, R. A. Backus, editor, MIT Press, Cambridge, pp. 268–282.

Sibunka J. D. and M. J. Silverman (1984) MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1983), Atlas No. 1, Summary of Operations. NOAA Technical Memorandum. NMFS–F/NEC–33.

Sibunka J. D. and M. J. Silverman (1989) MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1984–1987), Atlas No. 3, Summary of Operations. NOAA Technical Memorandum. NMFS–F/NEC–68.

Snyder J. P. (1987) Map Projections—A Working Manual. US Geological Survey Professional Paper 1395, United States Government Printing Office, Washington, DC, 383 pp.