Abstract.–The annual cycle of abundance and the monthly distributions of the copepod *Centropages hamatus* are described for U.S. northeast continental shelf waters from plankton samples collected approximately bimonthly from 1977 to 1987. The copepod was found distributed throughout the study area with a strong onshore–offshore abundance gradient. After its annual low, *C. hamatus* was found to increase in abundance slowly along the coast and to expand offshore following the northward progression of spring conditions. The highest monthly mean abundance estimates of *C. hamatus* were found on Georges Bank during the month of July. Distribution begins to constrict inshore following peak abundance periods.

Examination of environmental variables revealed that in general *Centropages hamatus* was prevalent when surface temperatures ranged from 12 to 17°C, when water-column chlorophyll levels were high, and where salinity was low on the shelf. The population in the Middle Atlantic Bight subarea declines sharply as water temperatures rise in summer and does not begin to recover until temperatures decline in the fall. In contrast, populations in the more northern regions decrease slowly from peak abundance and do not increase from their annual low until water temperatures rise in early spring. The pelagic population that survives through low abundance periods is concentrated in shoal or inshore (or both) waters where temperature is low and phytoplankton biomass high. There was no evidence from survey data that predation by ctenophores, chaetognaths, or the copepod *Centropages typicus* has a major effect on *C. hamatus* abundance.

Persistent spatial and temporal abundance patterns for late-stage copepodites of *Centropages hamatus* (Copepoda: Calanoida) in the U.S. northeast continental shelf ecosystem

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The calanoid copepod *Centropages hamatus* (Lilljeborg, 1853) is one of the dominant members of the zooplankton assemblage found within North Atlantic shelf waters (Davis, 1987; Sherman et al., 1987). The species has a wide latitudinal range that is reported to be as far north as Labrador (Pinhey, 1926) and southward to coastal waters off Florida in the Gulf of Mexico (Marcus, 1989). It occurs primarily in sheltered, coastal, and shoal regions of the continental shelf. This omnivorous copepod produces subitaneous eggs during the breeding season and also can produce diapausal ones in response to an environmental trigger (Pertzova, 1974; Marcus, 1989). McLaren (1978) estimated that generation period is comparatively short, 21–25 days at 12-13°C, and describes *C. hamatus* as a highly productive and ecologically efficient component of the zooplankton community. Sherman et al. (1987) reported that it is a major prey item of larval, juvenile, and adult fish stocks within continental shelf waters.

The National Marine Fisheries Service has monitored the zooplankton populations of the U.S. northeast shelf ecosystem with broadscale surveys since 1977 as part of the MARMAP (Marine Resources Monitoring, Assessment, and Pre-

diction) program (Sherman, 1980). The resulting historical data set provides the information needed to form a baseline for detection of future changes to the ecosystem. Previous reports on the annual abundance cycle of *Centropages hamatus* within the ecosystem have been limited to specific areas or to comparatively short periods (or both) (Bigelow, 1926; Deevey, 1956, 1960; Judkins et al., 1980; Davis, 1987; Sherman et al., 1987; Grant, 1988; Kane, 1993). No description of the monthly distribution of the copepod in this region has been published from collected data. This report uses information collected during MARMAP surveys from 1977 to 1987 to describe the persistent distribution and abundance patterns of *C. hamatus* throughout the ecosystem. Measurements of salinity, temperature, bottom depth, chlorophyll, and potential predator abundance were considered to gain insight into factors affecting the distribution and annual abundance cycle of *C. hamatus*.

Methods

Sample collection and analysis

The U.S. northeast shelf ecosystem extends from the Gulf of Maine to

Cape Hatteras (Sherman, 1994). Plankton samples were collected within the ecosystem at monthly or bimonthly intervals from 1977 to 1987. Plankton surveys occupied approximately 184 standard station locations that were relatively unchanged during the 11-yr period (Fig. 1). Samples were also collected on trawl and dredge cruises at randomly selected locations that varied yearly. Areal coverage and station spacing on these surveys were similar to broadscale plankton cruises.

Zooplankton were collected at each station from one side of a 61-cm bongo frame fitted with a 0.333-mm mesh net. The gear was lowered at 50 m/min to within 5 m of the bottom, or to a depth of 200 m maximum, and retrieved at 20 m/min. Ship speed was adjusted to maintain a 45° angle to the towing wire. A digital flowmeter was positioned in the center of the bongo frame to measure the volume of water filtered. All collections were preserved in 5% formalin. Samples were reduced to approximately 500 organisms in the laboratory by subsampling with a modified box splitter. Zooplankton were sorted, identified, and counted at the Plankton Sorting Center, Szczecin, Poland. The total number of samples analyzed for this report was 10,715. The abundance of *Centropages hamatus* is expressed here as numbers/100 m³ of water filtered and includes only advanced copepodite stages CV and CVI. Earlier copepodite stages were excluded because other copepods of similar size are undersampled by 0.333-mm mesh nets (Anderson and Warren, 1991).

The seasonal abundance cycles of known predators of copepods captured with the nets used during the surveys were examined to determine which might affect *Centropages hamatus* population levels. The three copepod predators examined in this study are: 1) ctenophores, 2) the copepod *Centropages typicus*, and 3) chaetognaths.

Sea-surface temperature was measured at each station to the nearest 0.1°C with a stem thermometer. During plankton surveys from 1977 to 1986,

Figure 1

Locations of standard MARMAP stations (•) in the U.S. northeast shelf ecosystem and subarea boundaries (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

water bottles with reversing thermometers were used to collect water samples at standard depths in order to measure salinity and temperature. Measurements of bottom temperature were determined by means of the deepest bottle or by means of a special bottom-tripped water-bottle sampler in water less than 75 m. Temperature and salinity data in 1987 were collected with a CTD (conductivity-temperature-depth) probe. Phytoplankton biomass was determined by measuring the concentration of chlorophyll *a* in the netplankton (>20 μmm) and the nanoplankton (<20 μmm) size fractions from water samples down to 100 m on plankton surveys from 1977 to 1984. These size fractions were summed to generate an estimate of total chlorophyll. The average water-column value of a variable for each station was calculated by arithmetically integrating measurements over depth.

More detailed accounts of sampling procedures and individual cruise tracks are given by Sibunka and Silverman (1984, 1989).
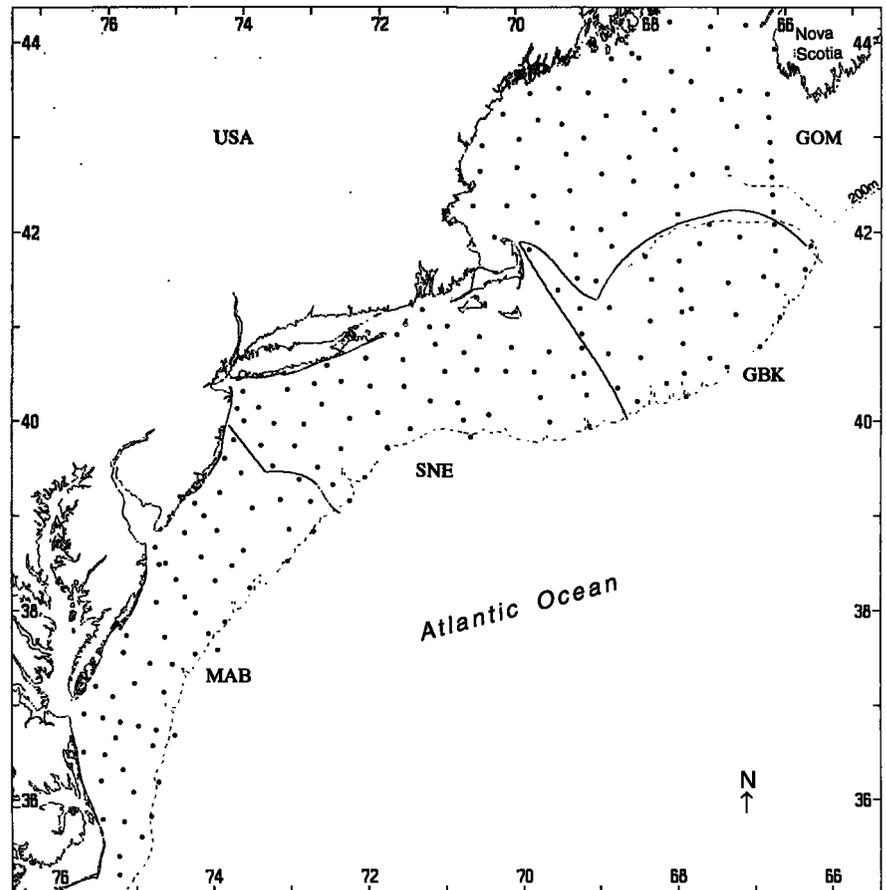
Statistical analysis

Estimates of *Centropages hamatus* and predator abundance were log transformed [log^{10}(no./100m^3 +1)] prior to contouring and data analysis. Contoured *C. hamatus* distribution maps were made by using Surface III software (Sampson, 1988) on station abundance data from the 11-yr data set grouped by monthly intervals.

Evaluation of species interannual abundance variability was facilitated by subdividing the ecosystem into four subareas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GBK), and Gulf of Maine (GOM) (Fig. 1). Each subarea is characterized by distinct patterns of circulation and bathymetry (Sherman et al., 1983). The average annual cycle of abundance and its variation was portrayed for each subarea by plotting the monthly mean abundance of all samples with its 95% confidence interval bar. Individual survey mean abundance and its 95% confidence interval bar were then superimposed on the latter plot. Surveys where the error bar did not overlap the one from the average cycle were judged to be situations where abundance departed substantially from the average cycle. Only surveys, except the one noted below, that covered 75% or more of a subarea were included in the analysis of interannual variability. Statistical analyses, comparing individual survey means with the time series monthly mean were not undertaken because they require the assumption of independence.

Several surveys (see Table 1) prior to 1981 were conducted by foreign vessels that did not have permission to sample east of the U.S.-Canada maritime boundary line in the GBK and GOM subareas. Although areal coverage in these surveys was reduced approximately 40% in relation to complete surveys, I included them in the analysis of this study because the area undersampled was consistent and our surveys still provided adequate coverage of the depth strata found within the two subareas.

Spearman's rank correlation coefficients were calculated for monthly subsets of station data to measure the strength of the relationship within individual months between *Centropages hamatus* abundance and the following variables: surface temperature, bottom depth, and the average water-column values of temperature, salinity, and total chlorophyll. Initial distribution plots of *C. hamatus* revealed that species abundance has a strong onshore–offshore gradient. Thus, to control the effect of depth on the calculation, Spearman's partial correlation coefficients were calculated for monthly subsets where both abundance and the other variable were significantly ($P<0.05$) correlated to depth.

Results

Distribution and abundance

The time-series mean distribution charts by month for *Centropages hamatus* are presented in Figure 2, A and B. Immediately apparent is the persistent onshore–offshore abundance gradient throughout the study area. There are high concentrations of the copepod inshore and within the shoal waters of GBK. Abundance in offshore waters is always much lower. *Centropages hamatus* is found throughout most of the ecosystem at some time during the year, the only exception being certain areas of the eastern offshore waters of the GOM where it is absent year round.

The timing of the annual abundance cycle of *Centropages hamatus* was not consistent throughout the ecosystem. The population in southern reaches of the study area declines through the summer, nearly disappearing from the water column during early autumn (Fig. 3). In December dense concentrations of *C. hamatus* begin to appear close to shore in the MAB subarea. These inshore centers of abundance slowly enlarge and expand along the coast and over the central shoals of GBK with the northward progression of spring (Fig. 2, A and B). Thus, peak times of abundance in the designated subareas vary with latitude (Fig. 3): May in the MAB, June in SNE, July on GBK, and September in the GOM. The population becomes distributed over nearly the entire shelf of each subarea during the annual peak period of abundance. The distribution and monthly abundance figures clearly show that GBK is the area of highest abundance for *C. hamatus* within the northeast shelf ecosystem.

Distribution begins to constrict towards the shore in each subarea during the months approaching the annual period of low abundance (Fig. 2). Abundance estimates in the SNE, GBK, and GOM subareas decline slowly through the autumn and, unlike the MAB region, do not reach the annual low until winter (Fig. 3).

Interannual variation in abundance of *Centropages hamatus* is shown in Figure 4 and individual survey statistics are given in Table 1. Although no long-term temporal trends in abundance were evident within any of the subareas, population estimates in certain years were exceptional. For example, the copepod's abundance in both the MAB and SNE subareas was high for an extended period in 1984 (Fig. 4). Both of these areas also had high abundance during the spring of 1987 and low population estimates in 1982. Departures from the average annual cycle of abundance were not always continuous across these subareas; *C. hamatus* density was low during early

Table 1

Centropages hamatus abundance data for each subarea by survey. The asterisk indicates where survey operations were not completed past the US-Canadian maritime boundary. Abbreviation Key: MAB = Middle Atlantic Bight; GBK = Georges Bank; SNE = Southern New England; GOM = Gulf of Maine; Yr = year; no. = number of samples, Mid-day = survey midpoint (jday), Log mean =log (10) mean abundance, SE = standard error of the mean.

MAB					SNE					GBK					GOM				
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
77	30	86	2.59	0.33	77	29	74	1.95	0.29	77	19	49	0.16	0.11	77	30	123	0.00	0.00
77	30	140	2.90	0.32	77	46	133	1.89	0.24	77	32	80	0.46	0.15	77	25	308	0.87	0.24
77	30	238	0.16	0.11	77	36	242	1.29	0.27	77	23	114	1.71	0.30	77	27	315	0.18	0.12
77	30	293	0.09	0.09	77	30	300	1.34	0.25	77	31	147	1.18	0.28	78*	25	139	0.09	0.09
78	29	49	1.16	0.27	78	31	60	1.07	0.20	77*	24	219	3.38	0.25	78*	31	193	0.44	0.17
78	28	112	2.00	0.29	78	30	131	1.38	0.25	77	19	307	2.58	0.45	78	29	240	0.46	0.18
78	29	177	2.43	0.30	78	34	188	2.12	0.27	77	22	333	2.47	0.32	78*	31	286	1.49	0.23
78	31	227	0.72	0.25	78	31	233	1.25	0.25	78	28	49	1.33	0.20	78*	31	322	0.44	0.17
79	46	59	1.74	0.24	78	31	294	1.62	0.28	78	29	137	0.46	0.19	79	40	114	0.06	0.06
79	30	129	3.06	0.29	79	40	64	1.64	0.20	78	19	241	3.04	0.42	79	32	147	0.19	0.11
79	49	172	2.74	0.22	79	27	107	1.12	0.29	78	32	287	2.84	0.25	79*	37	240	1.13	0.22
79	46	226	0.59	0.18	79	27	134	2.30	0.29	79	30	94	0.80	0.23	79	32	297	0.51	0.20
79	31	280	0.17	0.12	79	44	188	2.13	0.23	79	20	143	0.80	0.29	79	47	331	0.17	0.10
80	49	64	1.35	0.23	79	37	232	0.59	0.21	79*	18	192	2.38	0.50	80*	34	54	0.29	0.14
80	47	111	2.66	0.23	79	27	290	1.41	0.28	79*	17	238	3.15	0.43	80*	33	178	0.38	0.17
80	48	147	2.52	0.23	80	43	70	1.98	0.18	79	29	296	2.66	0.31	80*	37	217	1.06	0.23
80	45	201	0.97	0.23	80	41	117	2.21	0.21	79	33	349	2.19	0.32	80	51	296	0.34	0.12
80	47	273	0.11	0.08	80	43	157	2.28	0.26	80*	20	62	1.49	0.35	81	53	52	0.13	0.07
80	40	327	0.66	0.22	80	40	207	2.56	0.22	80	29	88	1.32	0.30	81	46	146	0.44	0.14
81	48	82	1.82	0.24	80	43	282	0.38	0.15	80	28	123	1.46	0.34	81	40	339	0.19	0.11
81	43	90	2.08	0.30	80	44	341	1.08	0.23	80*	21	163	3.05	0.40	82	35	49	0.04	0.04
81	42	222	0.99	0.25	81	43	77	1.25	0.18	80*	20	215	3.13	0.36	82	48	124	0.13	0.08
81	43	271	0.00	0.00	81	44	103	1.39	0.23	80	30	293	1.68	0.33	82	37	156	0	0
82	35	80	1.75	0.27	81	35	162	2.07	0.25	80	30	353	1.49	0.29	82	49	302	0.50	0.17
82	44	81	2.60	0.26	81	33	191	2.75	0.29	81	26	66	0.29	0.14	82	52	334	0.44	0.15
82	29	157	1.62	0.31	81	30	228	1.80	0.35	81	20	96	0.92	0.30	83	53	26	0.25	0.09
82	34	214	1.29	0.28	81	38	284	1.43	0.26	81	24	115	1.63	0.32	83	38	116	0.46	0.13
82	38	268	0.55	0.19	82	40	75	1.62	0.19	81	24	157	1.57	0.40	83	55	167	0.68	0.15
83	36	53	1.33	0.28	82	34	100	1.25	0.25	81	31	196	3.34	0.32	83	46	306	0.22	0.11
83	39	78	2.05	0.27	82	44	146	1.44	0.21	81	52	296	2.36	0.25	83	31	349	0	0
83	46	149	2.60	0.18	82	39	198	2.58	0.20	81	32	335	1.71	0.32	84	47	14	0.20	0.10
83	33	212	0.31	0.13	82	24	285	1.86	0.38	82	29	64	0.47	0.18	84	40	112	0.20	0.12
83	43	268	0.07	0.07	82	43	348	1.20	0.21	82	36	109	1.22	0.22	84	54	151	0.36	0.11

spring 1979 in SNE (Fig. 4) and above average in the MAB (Table 1). There were no substantial upward abundance departures recorded on surveys of GBK and only one in the GOM (1978). This is probably due to the limited coverage the areas received during the peak periods of abundance (Fig. 4). There were several years in three of the subareas where survey mean abundance had substantial downward departures from the average annual cycle when *C. hamatus* was at or near its annual low (Fig. 4). These anomalies are probably not significant because log transformation increases the amplitude of low values. Plots of untransformed data show little interannual variation between survey means during low periods of abundance.

Correlation of abundance with other variables

Bottom depth *Centropages hamatus* abundance is negatively correlated to depth in all the subareas for most or all of the entire year (Table 2). Exceptions occur and correlations weaken during low periods of abundance in the MAB and GOM subareas when the copepod is present only at a few inshore locations.
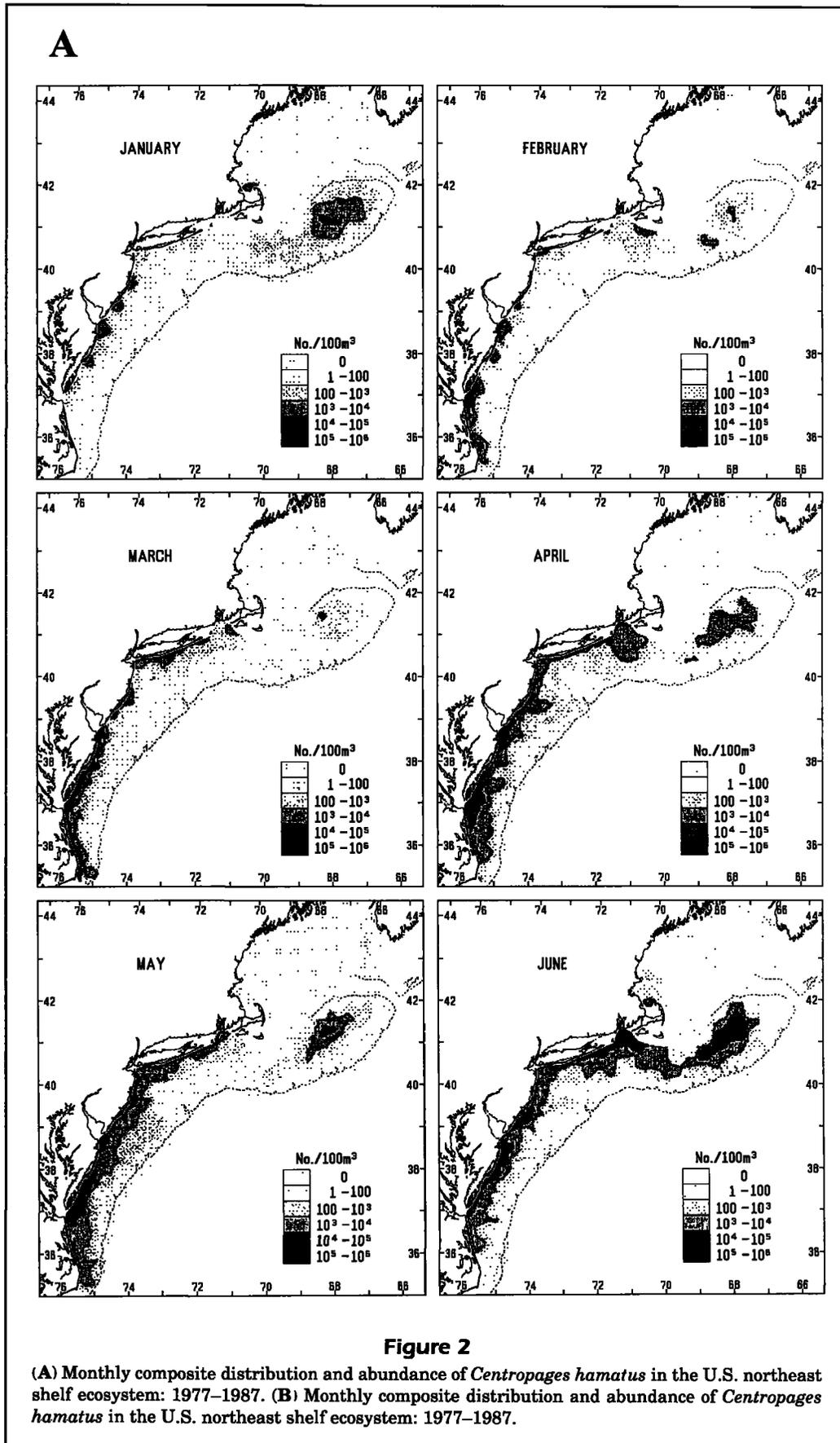
Table 1 (continued)

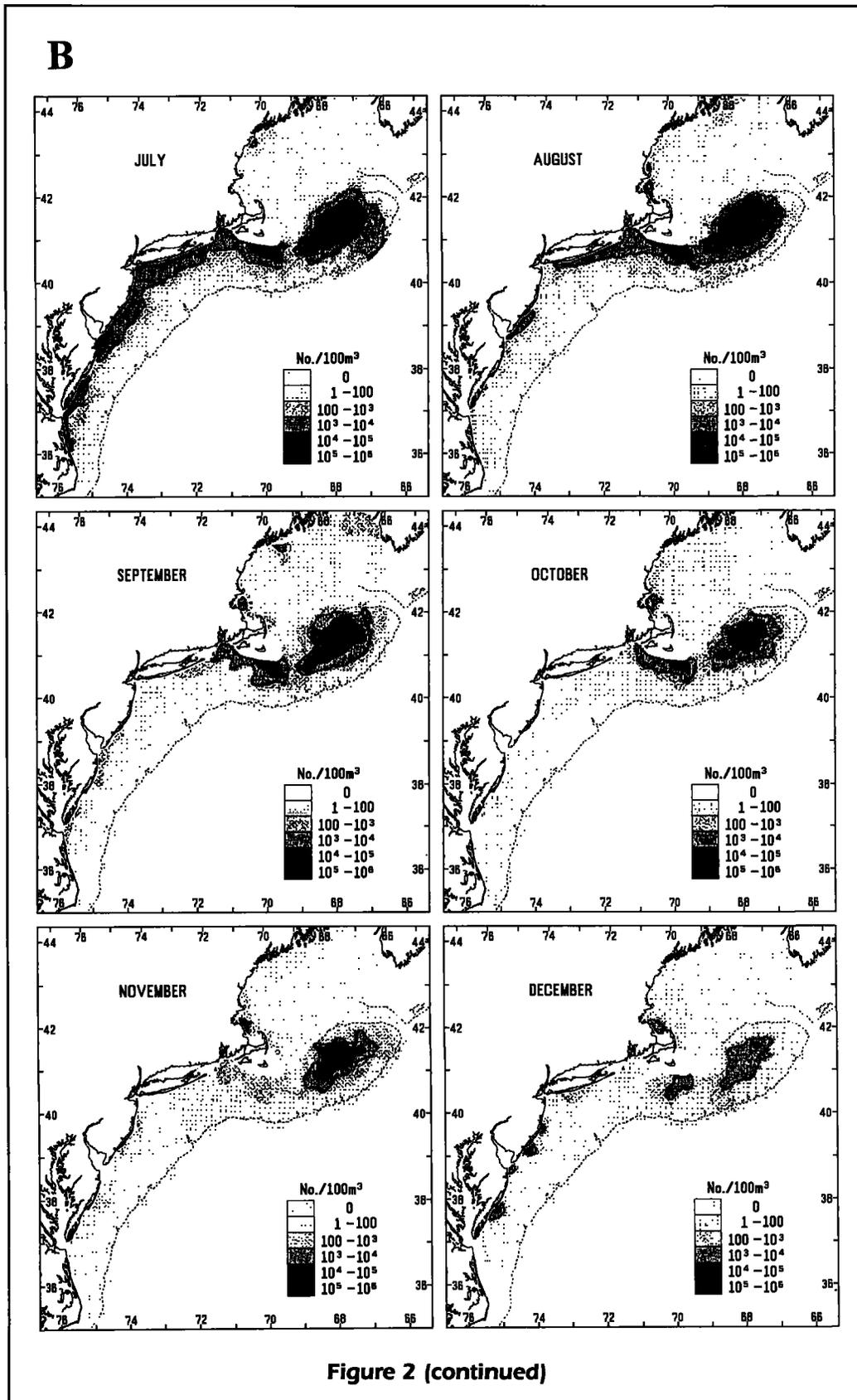|	MAB					SNE					GBK					GOM			
Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE	Yr	no.	Mid-day	Log mean	SE
83	48	323	0.75	0.19	83	29	41	1.44	0.27	82	29	140	0.66	0.23	84	50	298	0.59	0.15
84	40	37	1.31	0.26	83	29	91	2.14	0.24	82	34	208	2.82	0.30	85	29	99	0.21	0.13
84	41	71	1.96	0.30	83	41	158	2.84	0.26	82	31	295	2.57	0.29	85	44	260	0.97	0.20
84	48	133	3.32	0.16	83	38	222	2.74	0.28	82	29	323	2.52	0.30	85	37	306	0.29	0.14
84	38	193	2.12	0.31	83	38	278	0.96	0.27	83	28	21	1.55	0.32	85	56	340	0.21	0.09
84	51	198	2.39	0.28	83	42	334	1.28	0.20	83	32	104	1.70	0.33	86	50	39	0.18	0.08
84	31	211	1.24	0.29	84	43	26	1.07	0.20	83	30	163	2.37	0.32	86	44	112	0.23	0.11
84	37	264	0.51	0.20	84	38	83	1.55	0.23	83	36	233	2.69	0.36	86	39	154	0.49	0.17
84	47	309	0.46	0.17	84	42	138	2.75	0.19	83	37	292	1.95	0.29	86	32	262	1.21	0.27
85	38	35	1.22	0.28	84	31	189	3.19	0.23	83	28	340	2.10	0.26	86	45	303	0.59	0.16
85	36	66	1.69	0.30	84	31	205	3.28	0.25	84	29	21	1.88	0.24	87	42	115	0.48	0.14
85	51	110	2.50	0.26	84	35	221	2.07	0.25	84	37	95	0.90	0.21	87	56	155	0.57	0.15
85	51	142	2.64	0.26	84	34	272	0.83	0.26	84	32	146	1.73	0.32	87	55	259	0.92	0.18
85	32	209	0.34	0.14	84	42	318	0.48	0.16	84	25	210	4.95	0.11	87	40	295	0.85	0.21
85	51	245	0.30	0.09	85	50	29	1.00	0.20	84	37	227	3.33	0.27					
85	26	277	0.17	0.12	85	29	79	1.57	0.27	84	35	284	2.37	0.28					
85	47	314	0.21	0.12	85	42	100	1.55	0.24	84	31	334	2.12	0.30					
86	46	12	0.60	0.18	85	43	137	1.93	0.26	85	31	14	2.08	0.25					
86	42	68	1.99	0.27	85	48	214	2.37	0.26	85	27	86	1.56	0.29					
86	46	133	2.37	0.29	85	44	254	1.32	0.24	85	31	94	1.20	0.29					
86	45	175	2.40	0.28	85	33	289	0.97	0.24	85	32	132	2.01	0.35					
86	41	217	0.73	0.20	85	42	323	0.79	0.18	85	45	235	2.78	0.29					
86	47	243	0.15	0.08	86	43	22	0.85	0.17	85	36	258	2.02	0.35					
86	40	263	0.06	0.06	86	31	88	2.41	0.27	85	32	297	1.76	0.34					
86	47	311	0.11	0.08	86	41	138	2.48	0.24	85	29	328	2.00	0.35					
87	47	10	1.45	0.24	86	31	189	2.88	0.31	86	31	35	2.17	0.28					
87	46	87	2.74	0.25	86	37	213	1.51	0.27	86	25	102	1.75	0.37					
87	51	105	3.53	0.15	86	42	252	1.29	0.24	86	31	150	1.95	0.30					
87	58	129	2.90	0.20	86	36	278	0.96	0.24	86	24	197	4.63	0.20					
87	29	193	1.27	0.31	86	43	316	1.56	0.23	86	36	237	3.70	0.23					
87	48	234	0.79	0.19	87	42	28	1.68	0.20	86	31	260	2.62	0.31					
87	37	261	0.27	0.11	87	37	100	2.45	0.24	86	26	293	2.14	0.32					
87	46	311	0.35	0.13	87	38	110	2.97	0.19	86	31	328	1.68	0.29					
					87	53	134	1.55	0.24	87	30	37	1.74	0.24					
					87	46	149	1.84	0.23	87	26	113	1.31	0.29					
					87	37	199	1.23	0.24	87	30	140	1.48	0.30					
					87	43	239	0.98	0.21	87	37	217	2.70	0.31					
					87	36	273	1.39	0.27	87	29	248	3.05	0.35					
					87	43	323	0.75	0.18	87	31	280	1.86	0.30					
										87	29	342	1.17	0.27					

Temperature *Centropages hamatus* was found at station locations where surface temperatures ranged from −0.5°C to 28.7°C and where the average water column temperatures were between 0.2 and 24.6°C. Although the copepod can tolerate a wide range of temperatures, abundance was greatest at stations where surface temperature ranged from 12 to 17°C (Fig. 5A).

The relationship between surface temperature and the annual abundance cycle is shown in Figure 3. Rising temperatures in the MAB during summer may be responsible for a rapid decline of *Centropages hamatus* there. The population nearly disappears during late summer as surface temperature reaches annual maximums. The July correlation coefficient between variables indicates a strong inverse relationship ($P<0.01$). *Centropages hamatus* density remains low until the mean surface temperature falls below 15°C in December. Abundance in the more northern subareas slowly declines after the annual temperature high is reached. Unlike that for the population in the MAB, abundance in these subareas does not increase as temperatures decline in the fall, but only with spring warming (Fig. 3).

Monthly correlations between *Centropages hamatus* station abundance and temperature variables

Figure 2

(**A**) Monthly composite distribution and abundance of *Centropages hamatus* in the U.S. northeast shelf ecosystem: 1977–1987. (**B**) Monthly composite distribution and abundance of *Centropages hamatus* in the U.S. northeast shelf ecosystem: 1977–1987.

Figure 2 (continued)

were significant (*P*<0.05) during certain months in each of the subareas (Table 2). Significant relationships persisted between *C. hamatus* density and a temperature variable for several extended periods. Surface temperature was negatively correlated with abundance from November to March in the MAB subarea and also from June to February in SNE

waters. Abundance in the GBK subarea was positively correlated to average water-column temperatures from May to July and with bottom temperatures from September to December. In the GOM sub-
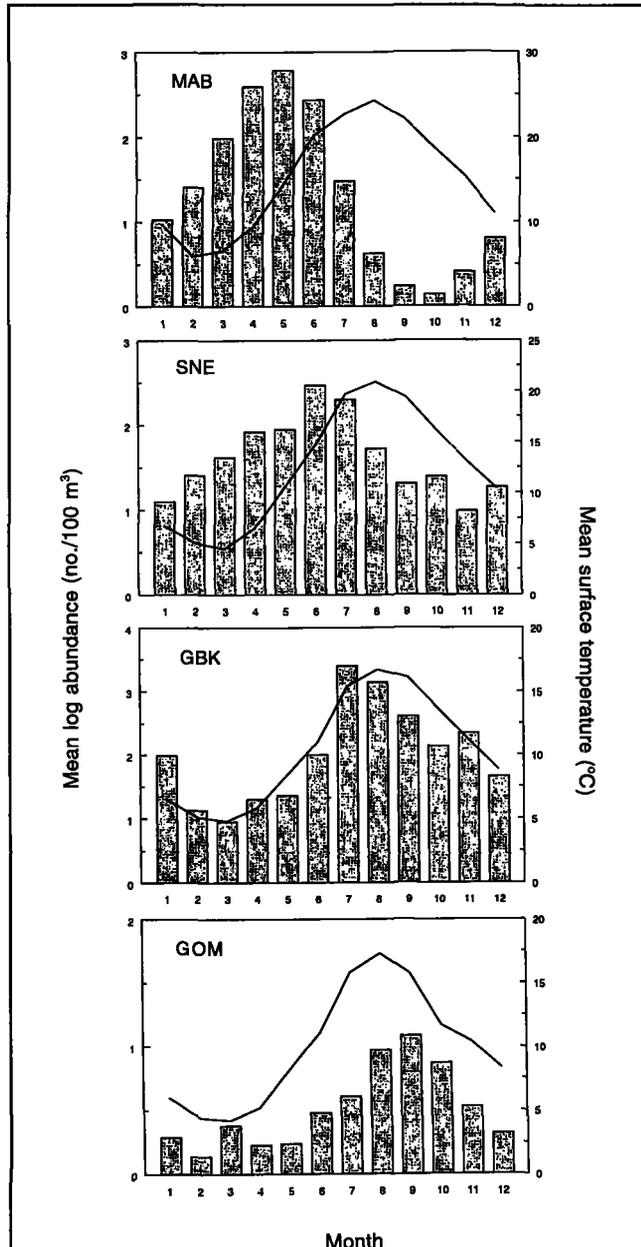
Figure 3

Bar graph of the monthly log mean abundance of *Centropages hamatus* with a line graph of the monthly mean surface water temperature for each subarea (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).
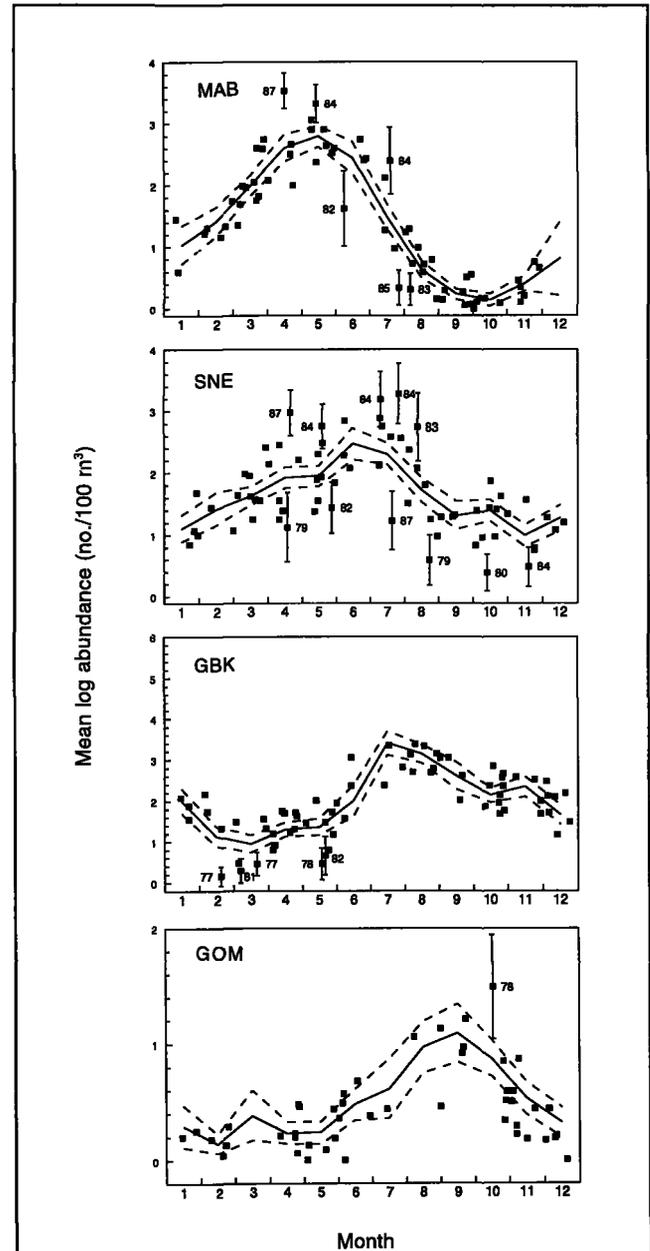
Figure 4

Time series monthly log mean abundance (solid line) of *Centropages hamatus* and the 95% confidence interval (dashed line) of the mean for each subarea. Single points are the log mean abundance of individual surveys. Surveys that departed substantially from the time series mean are labeled and the 95% confidence interval of the mean indicated with a error bar (MAB=Middle Atlantic Bight; SNE=Southern New England; GBK=Georges Bank; and GOM=Gulf of Maine).

area there were no strong correlations for extended periods between variables.

Chlorophyll Estimates of the abundance of *Centropages hamatus* were highest at locations where chlorophyll biomass was also high (Fig. 5B). Total chlorophyll and abundance measures at stations were significantly (*P*<0.01) correlated during certain times of the year in all subareas (Table 2). In the MAB, variables were posi-

Figure 5

Mean abundance of *Centropages hamatus* by (A) surface temperature, (B) chlorophyll, and (C) salinity interval. All time series data from the entire survey area was used.

tively correlated from May through July and, in SNE waters, during October and February. Variables on GBK were positively correlated from May through January, except for October. GOM correlations were significantly positive in August, November, and December.

Partitioning of total chlorophyll values into net-plankton and nanoplankton size fractions did not typically change the correlation coefficients between *Centropages hamatus* and phytoplankton abundance listed in Table 2. There were a few scattered months in the subareas where coefficients with netplankton were 0.1–0.2 units higher. The most substantial change occurred during October on GBK. The correlation coefficient with netplankton was 0.27 units above the value in Table 2 and was positively correlated (*P*=0.02).

Salinity *Centropages hamatus* was present at stations where integrated water-column salinity ranged from 27.09 to 36.00 psu. Maximum abundance occurred in the lower region of this range (Fig. 5C). Monthly correlation coefficients between station abundance and salinity were usually negative and oftentimes significant during the year (Table 2). Notable were the comparatively high negative correlations found during January in both the MAB and SNE subareas. Values in the MAB were also negatively correlated in February and again in August and September. SNE correlations were also significantly negatively correlated during April, July, and from September through December. GBK correlations, though not always significant, were positive from February through July and negative in the remaining six months. GOM coefficients were generally weak throughout the year.

Predation Pressure On average, *Centropages hamatus* and ctenophores both reach peak abundance during June in the SNE subarea (Figs. 3 and 6). During June and July of 1981 a large patch (9–12 stations) of ctenophores occupied inshore waters in the southern region of the subarea offshore of Long Island, New York. This concentration pushed overall mean abundance in the subarea to an 11-year high (Fig. 6). Predation on *C. hamatus* was apparently minimal; its mean abundance in late spring 1981 was slightly above the 11-year average (Table 1; Fig. 3). However, the abundance of *C. hamatus* in June within a ctenophore patch was much lower (611/100m^3) than outside (2,712/100m^3) it. Evidence for predation pressure was also found in the July survey; *C. hamatus* density was 8,138/100m^3 where it co-occured with ctenophores, 22,871/100m^3 where ctenophores were absent.

In the SNE subarea, the omnivorous copepod *Centropages typicus* is present at relatively high lev-
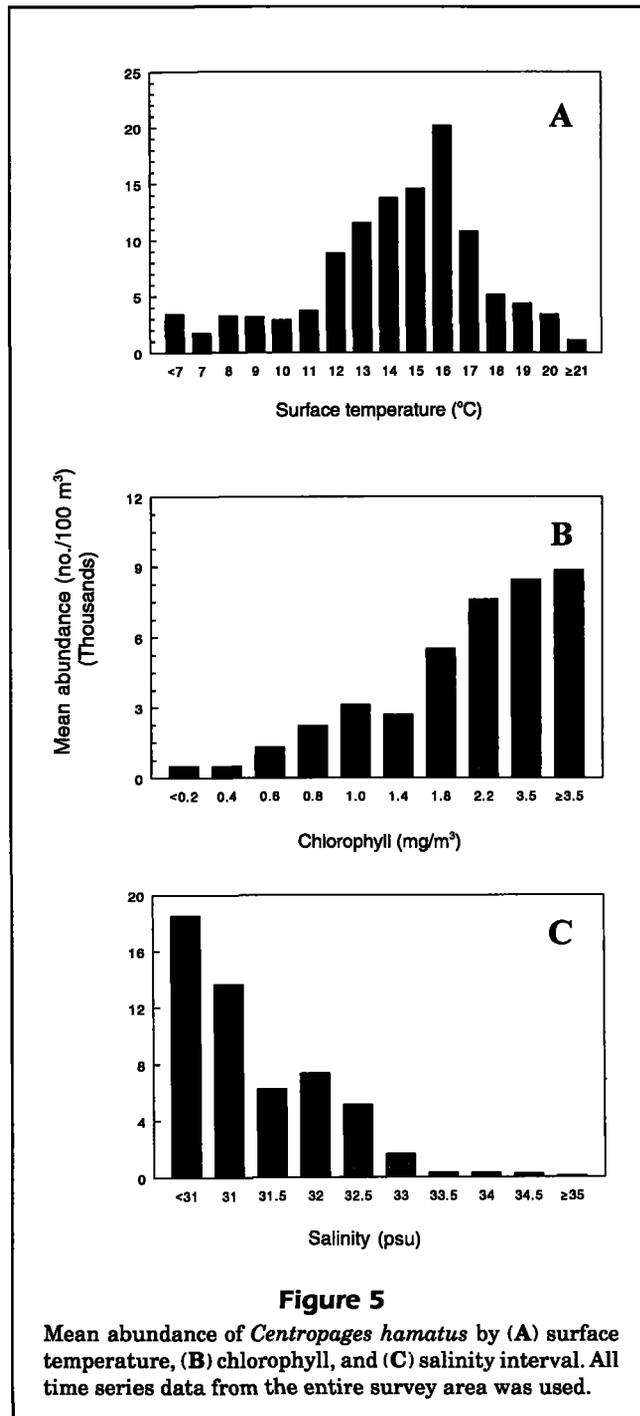
Table 2

Summary of correlation analysis between abundance and the different environmental variables. An asterisk indicates where partial correlation coefficients were used. Abbreviation key: temp. = temperature; chl. = chlorophyll; no. = number of observations; r = spearman correlation coefficient; P = probability that correlation is zero; MAB = Middle Atlantic Bight; SNE = Southern New England; GBK = Georges Bank; GOM = Gulf of Maine.

Area	Month	Bottom Depth			Surface temp.			Column temp.			Bottom temp.			Column salinity			Total chl.		
		no.	r	P	no.	r	P	no.	r	P	no.	r	P	no.	r	P	no.	r	P
MAB	1	93	−0.54	<0.01	89	−0.45	<0.01*	93	−0.47	<0.01*	90	−0.48	<0.01*	93	−0.54	<0.01*	0		
	2	190	−0.63	<0.01	190	−0.23	<0.01*	145	−0.33	<0.01*	139	−0.33	<0.01*	146	−0.40	<0.01*	146	−0.01	0.89*
	3	434	−0.65	<0.01	432	−0.11	0.03*	148	0.05	0.55*	139	0.05	0.60*	148	−0.18	0.03*	161	0.16	0.04
	4	223	−0.65	<0.01	218	−0.02	0.77	67	0.12	0.35	66	0.05	0.68	67	0.09	0.45*	75	0.05	0.64
	5	352	−0.68	<0.01	350	0.01	0.82	278	−0.05	0.41*	266	−0.02	0.78*	278	−0.21	<0.01*	197	0.24	<0.01*
	6	162	−0.64	<0.01	161	−0.03	0.75	75	−0.12	0.29*	73	−0.12	0.31*	75	−0.17	0.16*	79	0.25	0.03*
	7	290	−0.50	<0.01	287	−0.42	<0.01*	19	0.30	0.23*	19	0.30	0.21	19	−0.41	0.09*	70	0.38	<0.01*
	8	354	−0.22	<0.01	352	−0.01	0.98*	146	−0.18	0.04*	143	−0.18	0.04*	146	−0.30	<0.01*	77	0.18	0.12*
	9	313	−0.20	<0.01	306	0.01	0.89	93	−0.09	0.37*	86	−0.24	0.03*	93	−0.28	<0.01*	38	0.20	0.24*
	10	128	−0.04	0.70	127	0.12	0.19	73	0.18	0.14	69	0.17	0.16	73	−0.04	0.76	80	−0.02	0.84
	11	278	−0.36	<0.01	278	−0.24	<0.01	266	−0.23	<0.01	257	−0.20	<0.01	266	−0.08	0.17*	117	0.08	0.38*
	12	27	−0.69	<0.01	27	−0.31	0.12*	26	−0.21	0.32*	25	−0.22	0.31*	26	−0.23	0.27*	27	−0.12	0.56*
SNE	1	146	−0.34	<0.01	146	−0.41	<0.01*	145	−0.44	<0.01*	132	−0.43	0.01*	145	−0.52	<0.01*	64	−0.29	0.02*
	2	92	−0.39	<0.01	92	−0.29	<0.01*	63	0.08	0.56*	57	0.02	0.90*	63	−0.03	0.82*	66	0.25	0.05*
	3	339	−0.33	<0.01	336	−0.01	0.98*	175	−0.11	0.14*	165	−0.09	0.27*	175	−0.09	0.22*	205	−0.04	0.59*
	4	314	−0.42	<0.01	282	0.07	0.24*	61	−0.35	<0.01*	56	−0.35	0.01*	61	−0.49	<0.01*	58	−0.23	0.09*
	5	371	−0.51	<0.01	365	0.08	0.15	245	0.14	0.03*	230	0.23	<0.01*	241	−0.02	0.81*	167	0.17	0.03*
	6	146	−0.56	<0.01	146	−0.30	<0.01*	119	−0.07	0.46	110	0.06	0.55	119	−0.16	0.08*	123	0.01	0.95*
	7	343	−0.66	<0.01	343	−0.27	<0.01*	66	0.22	0.08*	63	0.24	0.06	66	−0.34	<0.01*	107	−0.05	0.63*
	8	289	−0.32	<0.01	286	−0.36	<0.01	89	−0.01	0.90*	89	0.09	0.39*	89	−0.14	0.21*	68	0.09	0.48*
	9	188	−0.33	<0.01	176	−0.44	<0.01*	104	−0.28	<0.01*	101	0.14	0.18*	104	0.28	<0.01*	14	0.52	0.06
	10	354	−0.27	<0.01	327	−0.58	<0.01*	113	−0.33	<0.01*	106	0.10	0.34*	113	−0.24	<0.01*	133	0.20	0.02*
	11	225	−0.15	0.03	224	−0.36	<0.01*	205	−0.31	<0.01*	191	−0.22	<0.01	205	−0.14	0.05*	76	0.11	0.37*
	12	160	−0.22	<0.01	158	−0.22	<0.01*	146	−0.16	0.06*	139	−0.02	0.78*	146	−0.37	<0.01*	141	0.01	0.91*
GBK	1	100	−0.69	<0.01	100	−0.14	0.17	71	0.24	0.05*	61	0.24	0.07*	71	−0.04	0.77*	72	0.28	0.02*
	2	104	−0.42	<0.01	103	0.38	<0.01*	54	0.52	<0.01*	45	0.50	<0.01*	54	0.24	0.08*	12	0	0
	3	152	−0.51	<0.01	148	0.03	0.70*	75	0.01	0.92*	66	−0.16	0.21	75	0.22	0.06*	92	−0.10	0.34*
	4	292	−0.53	<0.01	287	0.13	0.03	53	0.19	0.18*	46	0.22	0.15*	53	0.23	0.10*	28	0.31	0.10
	5	250	−0.61	<0.01	241	0.16	<0.01*	171	0.33	<0.01	153	0.30	<0.01	171	0.27	<0.01*	134	0.45	<0.01*
	6	97	−0.64	<0.01	93	−0.02	0.88*	69	0.40	<0.01*	58	0.45	<0.01*	69	0.14	0.26*	63	0.30	0.02*
	7	163	−0.64	<0.01	161	−0.29	<0.01*	31	0.47	<0.01*	30	0.37	0.05*	31	0.18	0.35*	42	0.36	0.02*
	8	250	−0.67	<0.01	242	−0.19	<0.01*	28	0.04	0.83*	25	0.03	0.91*	28	−0.55	<0.01*	48	0.33	0.03*
	9	124	−0.73	<0.01	108	−0.21	0.03	96	0.19	0.07*	87	0.33	<0.01*	96	−0.16	0.12*	23	0.47	0.03*
	10	393	−0.62	<0.01	388	0.21	<0.01	63	0.12	0.37*	55	0.42	<0.01*	63	−0.41	<0.01*	78	−0.01	0.99*
	11	194	−0.73	<0.01	194	0.11	0.14*	151	0.09	0.29	138	0.21	<0.01	151	−0.13	0.13*	94	0.21	0.04*
	12	165	−0.62	<0.01	152	0.36	<0.01	135	0.31	<0.01	114	0.30	<0.01	135	−0.12	0.16*	95	0.38	<0.01*
GOM	1	95	−0.12	0.26	95	0.01	0.95	59	−0.05	0.70	42	−0.13	0.40	59	−0.06	0.65	8	−0.25	0.55
	2	204	−0.23	<0.01	193	−0.01	0.95*	136	−0.04	0.62*	79	−0.05	0.64*	136	0.06	0.49*	99	0.18	0.07*
	3	70	−0.24	0.05	70	0.06	0.64	48	0.04	0.81	29	−0.05	0.80	48	−0.01	0.96	63	0.12	0.35
	4	288	−0.10	0.08	257	−0.01	0.97	19	−0.13	0.58	10	−0.12	0.74	19	−0.26	0.28	17	−0.22	0.40
	5	278	−0.22	<0.01	251	0.04	0.52*	136	0.17	0.54	84	0.36	<0.01*	136	0.06	0.46*	113	−0.01	0.91*
	6	245	−0.35	<0.01	244	0.10	0.11	189	0.10	0.17	105	−0.31	<0.01	149	−0.13	0.11*	52	−0.16	0.25
	7	75	−0.19	0.10	74	0.07	0.54	37	0.07	0.69	30	0.06	0.75	37	−0.11	0.52	45	0.19	0.20
	8	172	−0.40	<0.01	162	−0.06	0.45*	48	0.25	0.09*	46	0.21	0.17	48	−0.22	0.14*	93	0.25	0.01*
	9	155	−0.28	<0.01	145	<0.01	0.99*	135	−0.09	0.29*	114	−0.20	0.03*	135	−0.12	0.16*	23	−0.06	0.80
	10	307	−0.18	<0.01	302	0.10	0.09*	100	−0.01	0.89*	54	−0.02	0.91*	100	−0.15	0.13*	118	0.08	0.40
	11	274	−0.42	<0.01	272	0.18	0.01*	93	0.20	0.06*	65	0.10	0.42*	93	−0.27	<0.01*	93	0.29	<0.01
	12	274	−0.29	<0.01	269	0.05	0.42*	251	0.05	0.44	167	−0.07	0.38*	251	−0.02	0.72*	107	0.24	0.01

els year round and begins to increase inshore from its annual low in late spring-early summer (Fig. 6) when *Centropages hamatus* is at peak abundance. MARMAP data indicate that it is unlikely that the summer decline or the abundance levels reached by *C. hamatus* are controlled substantially by *C. typicus* predation. There was no strong inverse relationship

between the abundance trends of the two species. For example, in 1987 *C. hamatus* reached peak abundance earlier than usual, in late April, and declined rapidly to below average levels (Table 1). The abundance of *C. typicus* was average in late April 1987 and also declined through the summer to below average levels (Fig. 6). High levels of *C. hamatus* recorded in 1984 (Fig. 4) were not due to the absence of *C. typicus* predators; abundance was close to average for the copepod during spring and summer (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species during the time series were positive (0.07–0.24) from April through August, further evidence that predation by *C. typicus* is minimal.

Peaks of *Centropages hamatus* abundance and the presence of chaetognaths do coincide in the SNE subarea (Figs. 3 and 6). However, evidence that chaetognathan predation impacts *C. hamatus* abundance could not be found. All of the surveys that had exceptional high or low *C. hamatus* abundance, 1979, 1984, and 1987 (Fig. 4), had near average chaetognath density (Fig. 6). Conversely, *C. hamatus* abundance was close to average when chaetognath density was high in 1977 and low in 1985 (Fig. 6). Monthly partial correlation coefficients between station abundance values of the two species were not significant and very low (–0.10–0.25) throughout the year, indicating that chaetognath predation has little effect on *C. hamatus* abundance.
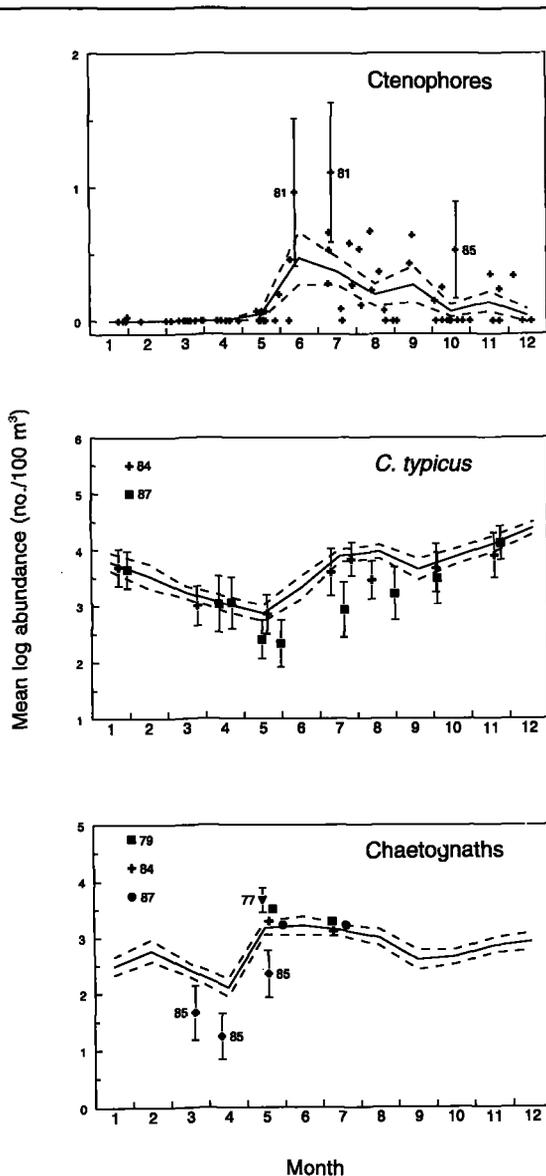
Figure 6

Time series monthly log mean abundance (solid line) and the 95% confidence interval (dashed line) of the mean for the following copepod predators in the Southern New England subarea: ctenophores, the copepod *Centropages typicus*, and chaetognaths. Single points are the log mean abundance of the taxon for individual surveys during certain years. The error bars indicate the 95% confidence interval of the mean.

Discussion

Temperature affects most processes in marine ecosystems and the life cycle of *Centropages hamatus* is no exception. Opposite extremes in temperature appear to limit the seasonal occurrence of the population at the southern and northern ends of the ecosystem. Warm summer temperatures in the MAB were correlated with the rapid decline of the copepod in this area as values approach or surpass the critical upper thermal level for the species. Similar relationships between temperature and *C. hamatus* were found by Deevey (1960) for the population present near and within Delaware Bay. She reported that the copepod disappears as temperatures rise in summer but is present year round in small numbers during cool summers. Grant (1988) also reported that *C. hamatus* abundance in the MAB declines with increasing temperature and is absent in some years during summer and fall seasons. The MAB population begins to reappear or increase close inshore in late autumn where waters cool faster than those offshore. Populations farther north decline slowly as

winter approaches until only small aggregations of cold-adapted individuals overwinter in the far eastern waters along the SNE coast, on the central shoals of GBK, and within inshore waters in the GOM. Abundance in these areas increase as temperatures rise in spring.

The life cycle of many marine copepods involves the production of resting eggs that allow the species to repopulate areas when environmental conditions again become favorable (Uye, 1985). Evidence that *Centropages hamatus* produce resting eggs has been found in the western North Atlantic (Lindley, 1990), the Gulf coast of Florida (Marcus, 1989), and in the MARMAP survey area on GBK (Davis, 1987). Although this report provides no direct evidence that *C. hamatus* produces resting eggs, it seems unlikely that the small pelagic population that overwinters, or oversummers, could produce the great abundance of the next generation without recruitment from benthic resting eggs. Marcus (1989) found that a *C. hamatus* population residing in a subtropical embayment area produces diapause eggs that allow the species to survive warm summer temperatures. This also likely occurs in the MAB when the population rapidly declines to a few individuals, or disappears entirely during summer, and begins to increase as temperatures decline in winter. Lower maximum temperatures observed on GBK are apparently not sufficiently high to impact populations there dramatically; abundance declines slowly during autumn after peak abundance is reached in summer and does not increase until temperatures rise in early spring. This slow decline in abundance may occur because success of egg hatching decreases as females gradually switch from subitaneous egg production to resting egg production owing to decreasing temperatures and daylengths, as was found for the copepod *Labidocera aestiva* in nearby waters (Marcus, 1982). The resting eggs hatch in the spring to supplement the production of overwintering late-stage copepodites and to ensure the success of the population. Such variation in egg production between well-separated populations has been reported for other species (Marcus, 1984; Uye, 1985). Somewhere in the SNE subarea there is probably a transition zone between adults that are "temperature shocked" to release quiescent eggs and those that slowly change their egg-laying strategy as autumn progresses. Egg-production strategy in the GOM is probably similar to that found in the GBK.

The strongly negative correlation of *Centropages hamatus* abundance to depth and its well-defined inshore–offshore abundance gradient confirm the importance of resting eggs in the life history of this species. Environmental conditions probably do not trigger the release of diapause eggs until after the population constricts inshore after peak abundance is reached. Evidence for this was found by Lindley (1990) in southern waters of Great Britain where *C. hamatus* eggs were found to be abundant only in depths of less than 50 m. When the eggs hatch, the prevailing westerly winds in the northwest Atlantic slowly spread the pelagic population and the new recruits offshore to establish the characteristic abundance gradient of this species.

Abundance of *Centropages hamatus* appears to be related strongly to the availability of phytoplankton. The copepod's abundance was highest at stations where chlorophyll values were high, and its distribution is similar to phytoplankton gradients in the study area (O'Reilly and Busch, 1984). However, correlation coefficients between variables were weak and inconsistent among subareas, indicating that the species is not particularly sensitive to phytoplankton availability. The low correlation may be because average water-column chlorophyll measurements are static measures that may not reflect the actual food concentrations that are, or were, available to the copepod over the previous 24 hours. Furthermore, it is also possible that late-stage copepodites of this omnivorous species may be more sensitive to zooplankton prey concentrations. Nonetheless, food availability is a key limiting factor throughout nature and certainly has a major role in shaping the life history of this copepod. The maximum mean abundance of *C. hamatus* is greatest on GBK, the ecosystem subarea with the largest estimate of annual primary production (O'Reilly et al., 1987). Conversely, population density is lowest in the GOM where average chlorophyll concentrations are also lowest.

Monthly correlation coefficients between salinity and abundance of *Centropages hamatus* were also weak even though both variables have a strong offshore gradient. Unlike chlorophyll correlations, these coefficients portray accurately the relationship between variables. *Centropages hamatus* is a coastal species with a wide latitudinal range and must tolerate wide environmental fluctuations. It has been reported in areas with salinity as low as 6 psu (Hernroth and Ackefors, 1977), as well as in Mediterranean waters where salinity exceeds 36 psu (Gaudy, 1971). The large numbers of *C. hamatus* associated with low salinity found in this study is probably an artifact of the high phytoplankton concentrations found in a narrow inshore band along the MAB and SNE coasts (O'Reilly et al., 1987). The annual spring increase in precipitation and subsequent river runoff that leads to lowered salinity in the MAB and SNE subareas (Manning, 1991) also introduces nutrient-enriched water that stimulates phytoplankton growth and zooplankton production. Further-

more, the highest mean abundance of *C. hamatus* is found over the central shoals of GBK where salinity usually ranges from 32.2 to 32.7 psu during peak abundance, well above the coastal areas where abundance, on average, is much lower. High salinity offshore may effect *C. hamatus* production there and restrict its distribution, but it is more likely that low offshore abundances are caused by low phytoplankton food stocks that cannot support an overwintering population or the generation that produces resting eggs after peak abundance is reached.

There was no strong evidence from survey data that predation affects interannual variability or causes the seasonal decline of the population in the SNE subarea. Ctenophores appear to lower *Centropages hamatus* abundance when they are plentiful, but this occurred only during one year and in a restricted area. Chaetognaths and the copepod *Centropages typicus* also appear to have little affect on *C. hamatus* density. Clearly, however, a dedicated study analyzing stomach contents and the vertical distribution of the predator-prey field is needed to define the actual food web. Potential predators such as squid, juvenile fish, and populations of planktiverous adult fish must also be considered in order to fully define the role predation has in controlling *C. hamatus* population levels.

Lindley and Hunt (1989) examined the distribution of *Centropages hamatus* to the north and across the Atlantic to the North Sea. They described a life cycle similar to the one reported in this paper and speculated that the autumn decline in abundance is caused by the pressure of competition with *Centropages typicus* for food resources. Dagg and Turner (1982) studied copepod populations in the SNE and GBK subareas during autumn and calculated that copepod grazers may consume entire phytoplankton stocks. If true, high abundance of *C. typicus* could impact population levels of *C. hamatus*. However, MARMAP survey data indicate that high *C. typicus* abundance does not lead to an early decline of *C. hamatus* in either subarea. For example, in 1985 on GBK, median *C. typicus* abundance was 2–3 orders of magnitude above the ten-year average, but *C. hamatus* was also above average and increased in late autumn (Kane, 1993). Data presented in this report also show that the abundance of the two species are not related in the SNE subarea. Although competition pressure between the two species does not appear to cause the decline of *C. hamatus*, laboratory feeding experiments are needed to measure the effect of low food levels on species abundance.

The copepod *Centropages hamatus* has evolved a unique life history to survive and reproduce within the waters of the northwestern Atlantic continental shelf. The population has a distinct seasonal cycle with peak abundance occurring in shallow areas where phytoplankton food stocks are rich and surface temperature ranges from 12 to 17°C. Predation pressure appears minimal, and *C. hamatus* abundance peaks between the annual maximum of early spring and autumn dominant copepod species (Sherman et al., 1983), thus reducing competition pressure for food resources. *Centropages hamatus* likely produces resting eggs that hatch and help repopulate the ecosystem when environmental conditions are favorable. Comprehensive laboratory and shipboard experiments are needed to distinguish how the above biotic and abiotic factors interact to determine the annual success of the population.

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