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The distribution and abundance of pelagic gammarid amphipods on Georges Bank and Nantucket Shoals

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Abstract—In this study, long-term, broad-scale zooplankton survey data were used to estimate the temporal and spatial distribution and abundance of gammarid amphipods present in the water column on Georges Bank. Delta-mean abundances computed from 10 years of data showed that gammarid amphipod abundances peaked in summer and again in fall. The amphipods were also most numerous in water less than 50 m deep. The statistical tests employed revealed no conclusive evidence for diurnal vertical migration. Interannual delta-mean abundances fluctuated approximately 5-fold between 1977 and 1986, ranging from 217 to 1181 amphipods 100 m^{-3}. Peak amphipod biomass occurred in July and was estimated to be 2.8 kcal m^{-2}. Using production-to-biomass ratios from the literature, mean annual production of amphipods in these samples was estimated to be between 1.6 and 9.8 kcal m^{-2}. Production in shallow areas was especially high, 22 kcal m^{-2} $year^{-1}$. Copyright © 1996 Elsevier Science Ltd

INTRODUCTION

Georges Bank is an area of high fish production and high primary production, but relatively low zooplankton production (Cohen and Grosslein, 1987; Sissenwine, 1987). Zooplankton production may appear to be paradoxically low for several reasons: microbial oxidation of a large part of the primary production; migration of fish onto the bank from adjacent areas; advective loss of zooplankton originating on Georges Bank; underestimation of zooplankton production (Bourne, 1987); and subsidy of Georges Bank fish populations by surrounding deep-water zooplankton (Greene *et al.*, 1988).

Copepods account for a large portion of the zooplankton production in the Georges Bank ecosystem and have been studied extensively (Davis, 1982,1987a, 1987b). Therefore, any increases in zooplankton production estimates will probably result from including the production by invertebrates not traditionally considered to be secondary producers. These include mysids, euphausiids, and amphipods. The relatively large size and good swimming ability of these crustaceans probably cause them to be underrepresented in most sampling programs. As a result, our understanding of the distribution, abundance, and ecological function of some of these animals is limited. For example, experiments with *Gammarus annulatus*, a gammarid amphipod that is occasionally abundant in the water column on Georges Bank (Harding *et al.*, 1991; Perry *et al.*, 1993), have shown that it is capable of filtering phytoplankton from the water (Avery, 1993). Thus, this species of gammarid amphipod, a member of a group normally considered benthic-dwelling detritivores, may contribute to the secondary production total.

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Amphipod production on Georges Bank is virtually unstudied. Collie (1985) made the only attempt to quantify the production of any amphipod species on Georges Bank, and no estimates of the production of the entire amphipod community exist. Amphipods, however, may contribute much to fish production. Considerable numbers of gammarid amphipods at times are swimming in the water column (Sherman *et al.*, 1987; Whiteley, 1948) and may therefore be vulnerable to a wide variety of fish predators. Our study uses the frequency of occurrence and relative abundances of gammarid amphipods as reflected in zooplankton samples collected as part of the long-term Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program to assess the distribution in time and space and the potential contribution of gammarids to fish production on Georges Bank.

METHODS

Data

Ten years of data from the National Oceanic and Atmospheric Administration MARMAP program were made available by the National Marine Fisheries Service Laboratory, Narragansett, RI. The broad-scale surveys of the MARMAP program were designed to assess the seasonal and annual variations in phytoplankton, zooplankton, ichthyoplankton and hydrography over a large section of the east coast of the United States. The surveys covered the continental shelf from Cape Sable, Nova Scotia, to Cape Hatteras, North Carolina (Sibunka and Silverman, 1984). The data used for the following analyses were collected between 1977 and 1986. The sampling procedures for the zooplankton portion of these surveys are given in Jossi and Marak (1983). In general, zooplankton were sampled with a 61-cm bongo sampler (Posgay and Marak, 1980) with 333 μm mesh net. Oblique hauls from the surface to 200 m or within 5 m of the bottom to the surface were made. A flow-meter was employed to measure the volume of water passing through the net. Towing speed was 1–2 knots.

Samples were preserved in formalin onboard ship and later sent to the Morski Instytut Rybacki (MIR), Szczecin, Poland, for sorting, identification, and enumeration according to Jossi and Marak (1983). One-half of the original sample was archived, and one-half subsampled to approximately 500 organisms. Animals were identified to the lowest taxon possible and counted. Amphipods were identified only to the suborder Gammaridea. Therefore, the analysis here represents all gammarid amphipods.

The present analysis includes only data from Georges Bank and Nantucket Shoals. The boundaries of this region are 39°92′N to 42°10′N and 65°93′W to 71°00′W. This subset of the larger MARMAP dataset included 2385 records.

Statistical analyses

The chi-square test (Snedecor and Cochran, 1980) was used to test for patterns in the frequency of occurrence of amphipoods in the MARMAP data. The data set used contained two kinds of records relative to amphipods: those with amphipods and those without. For each test the number of samples containing amphipods within some defined class was compared to the proportion of total samples in that class. For example, Table 1 shows a test for diurnal differences in frequency of occurrence. Of 2385 total samples, 1213 (51%) were obtained during the day. Therefore, of the 744 samples containing amphipods, the same

Table 1. *Summary statistics of delta-mean calculation of abundance (number* 100 m^{-3}*) and chi-square frequency test for day and night samples*

	Mean	s^2	m	n	**Delta-mean**	o	e	**Chi-square**
Day	5.79	3.90	317	1213	**591**±222	317	378.39	9.96
Night	5.69	3.12	427	1172	**507**±139	427	365.61	10.31
Totals			744	2385		744	744	**20.27**

The delta-means are accompanied by 95% confidence intervals. The chi-square test statistic = 20.27; degrees of freedom = 1; chi-square$_{0.95}$ = 8.84; mean is the mean of log-transformed non-zero data; s^2 = variance of log-transformed non-zero data; m = number of non-zero observations; n = total number of samples; o = observed frequency of occurrence; e = expected frequency of occurrence.

proportion, 378, are expected to have been taken during the day. Deviations from this proportional equality are tested for significance ($p = 0.05$) with the chi-square test.

The data set used for this analysis is nearly 70 percent "zeros". In such a case the arithmetic mean of the data or the median cannot estimate "average" abundance adequately. This problem is common in broad-scale surveys. The delta-mean may be used in these cases to give a better estimate of the mean abundance, and to estimate the variance of this mean estimator (Pennington, 1983; Northeast Utilities Environmental Laboratory, 1988). The delta-mean is given by Pennington (1983) as

$$\text{delta-mean} = (m/n)e^{x}Gm(y) \tag{1}$$

where m is the number of non-zero occurrences, n is the number of zero observations, x is the arithmetic mean of the log-transformed, non-zero data, and $Gm(y)$ is a Bessel function computed as

$$\begin{aligned} Gm(y) &= 1 + (m-1)y/m \\ &+ (m-1)^3y^2/m^2(2!)(m+1) + (m-1)^5y^3/m^3(3!)(m+1)(m+3)\ldots \end{aligned} \tag{2}$$

where $y = s^2/2$ and s^2 is the variance of the log-transformed, non-zero data. Nine terms in this series were used to approximate $Gm(y)$ for Equation (2). The delta-mean variance is given as

$$\text{delta-variance} = (1/n)e^{(2x+s^2)}[\delta(1-\delta) + 1/2(1-\delta)(2s^2 + s^4)] \tag{3}$$

where $\delta = 1 - m/n$ and the other symbols are as described previously. The 95% confidence intervals reported are assumed to be normal for the delta-mean and therefore are computed as,

$$95\%CI = \text{delta-mean} \pm 1.96(\text{delta-variance})^{1/2} \tag{4}$$

for samples of large n (>100). For smaller samples the appropriate two-tailed t-value ($p = 0.05$) is substituted for 1.96.

RESULTS

The frequency of occurrence and delta-mean analyses sometimes showed different trends. Chi-square test results showed that the amphipods were captured more frequently at night

Table 2. Seasonal delta-means and chi-square test

	Mean	s^2	m	n	**Delta-mean**	o	e	**Chi-square**
Spring	5.98	2.95	210	691	**517**±192	210	215.56	0.14
Summer	6.26	3.61	151	471	**987**±490	151	146.93	0.11
Autumn	5.69	3.40	250	819	**486**±182	250	255.49	0.12
Winter	4.83	2.97	133	404	**177**±80	133	126.03	0.39
Totals			744	2385		744	744	**0.76**

Winter was defined as January–March; spring, April–June; summer, July–September; autumn, October–December. The chi-square value of 0.76 is less than chi-square$_{0.95}$ = 7.82. Degrees of freedom = 3.

Table 3. Delta-mean and chi-square tests by month

	Mean	s^2	m	n	**Delta-mean**	o	e	**Chi-square**
January	4.19	1.61	19	49	**54**±39	19	15.29	0.90
February	4.56	3.66	18	53	**160**±176	18	16.53	0.13
March	5.05	2.90	96	302	**204**±106	96	94.21	0.03
April	5.49	3.32	78	284	**333**±208	78	88.59	1.27
May	6.29	2.24	87	304	**461**±214	87	94.83	0.64
June	6.22	3.17	45	103	**988**±741	45	32.13	5.15
July	6.85	3.22	60	181	**1469**±1000	60	56.46	0.22
August	5.73	3.67	76	245	**559**±376	76	76.42	0.002
September	6.60	2.28	15	45	**666**±633	15	14.04	0.07
October	5.99	4.36	127	414	**1036**±633	127	129.15	0.04
November	5.51	1.91	67	210	**199**±94	67	65.51	0.03
December	5.22	2.62	56	195	**188**±118	56	60.83	0.38
Totals			744	2385		744	744	**8.87**

Chi-square = 8.87; chi-square$_{0.95}$ = 19.68.

than during the day (Table 1), but were equally likely to be caught in all seasons (Table 2) and all months (Table 3). Delta-mean abundances, on the other hand, showed the amphipods to be equally abundant by day and by night (Table 1). The delta-mean also showed a distinct peak in abundance in summer and a low in winter (Fig. 1 and Table 1). When examined by month, a more detailed pattern of abundance emerged with two peaks of delta-mean abundance, one in July and one in October (Fig. 2).

Tests for interannual differences in delta-mean abundances and frequency of occurrence were conducted for the 10 years of survey data. The relative abundances (Fig. 2 and Table 4) indicated long-term changes in gammarid densities on Georges Bank and Nantucket Shoals. Delta-mean abundances ranged from 217 to 1181 amphipods 100 m^{-3}. The variability of the data within each year was high (Table 4), causing the 95% confidence intervals to widen for years in which they were most abundant. Nonetheless, the numbers caught in 1984 were significantly greater than those caught in 1980 or 1981 (by comparison of 95% confidence intervals). Despite these interannual trends in delta-mean abundance, gammarid amphipods were equally likely to be caught in all years (Table 4). Between 1977

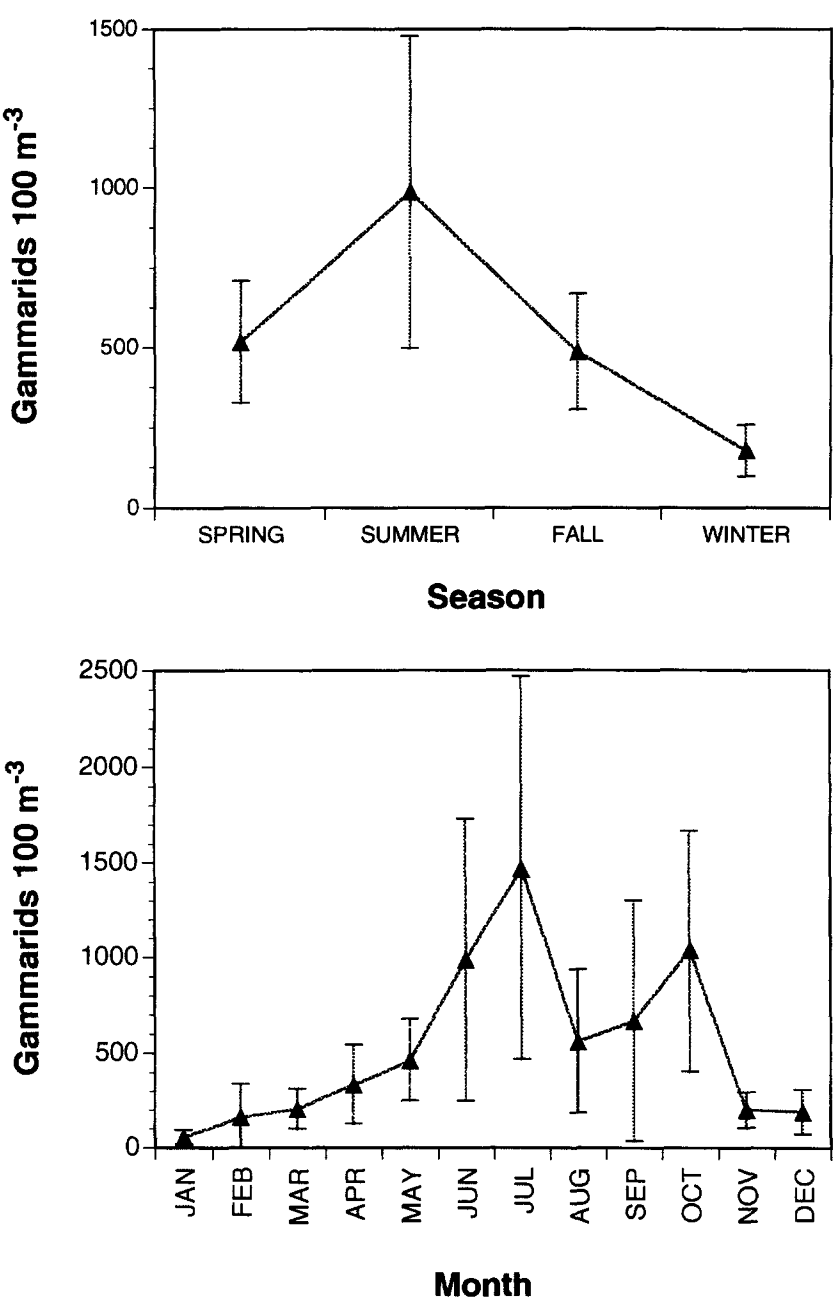

Fig. 1. Delta-mean abundances of gammarid amphipods on Georges Bank. Error bars represent 95% confidence intervals. Winter was defined as January–March, spring as April–June, summer as July–September, and autumn as October–December.

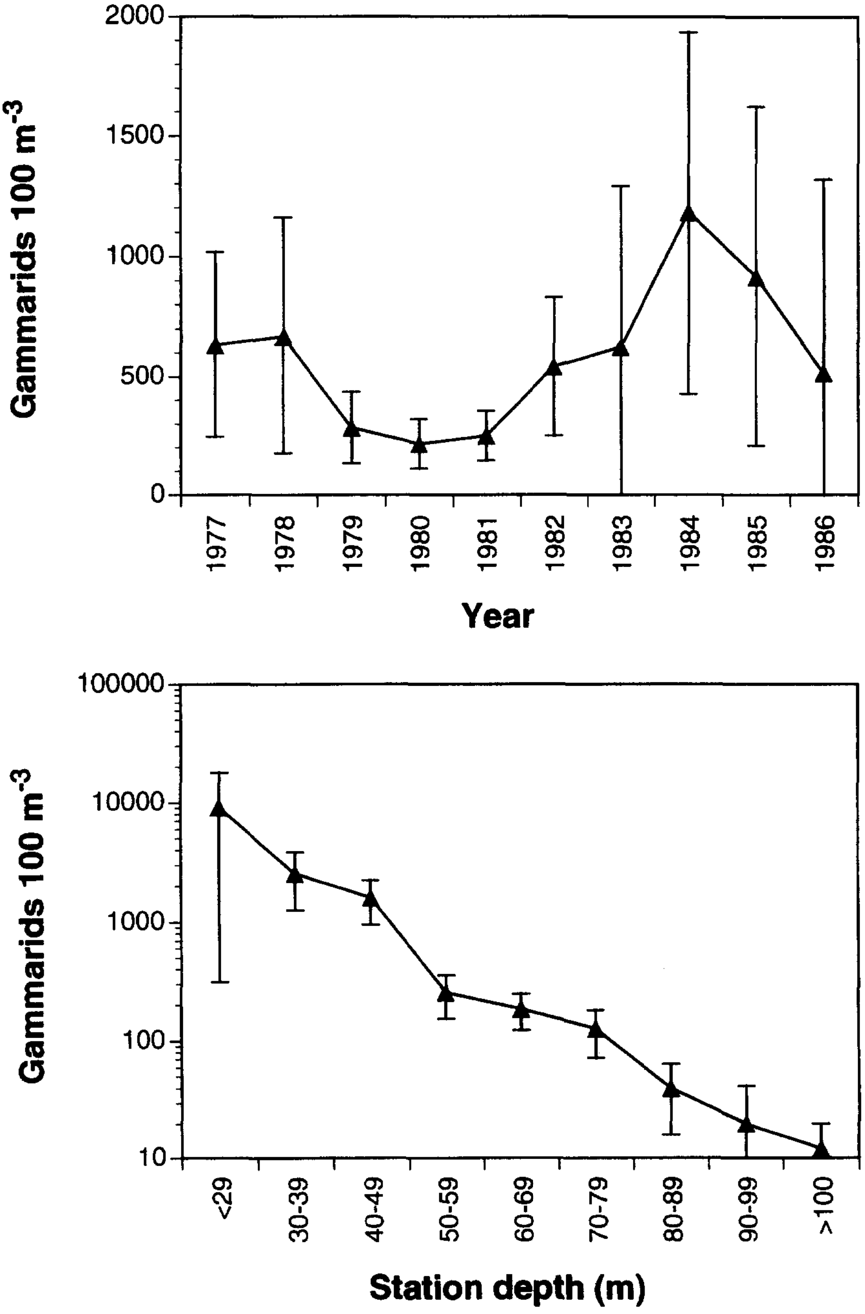

Fig. 2. Delta-mean abundances of gammarid amphipods by year and station depth. Error bars indicate 95% confidence intervals.

Table 4. Delta-mean and chi-square statistics by year, 1977–1986

	Mean	s^2	m	n	**Delta-mean**	o	e	**Chi-square**
1977	5.72	3.45	87	271	**633**±386	87	84.54	0.07
1978	6.66	2.85	42	189	**669**±492	42	58.96	4.88
1979	5.75	2.44	73	263	**285**±151	73	82.04	1.00
1980	5.41	2.50	93	325	**217**±105	93	101.38	0.60
1981	5.73	2.11	100	346	**250**±106	100	107.93	0.58
1982	5.82	3.14	102	295	**541**±290	102	92.03	1.08
1983	5.14	5.02	36	98	**625**±664	36	30.57	0.96
1984	5.96	4.48	119	345	**1181**±755	119	107.62	1.20
1985	5.49	4.87	86	239	**916**±707	86	74.56	1.76
1986	5.42	4.96	6	14	**516**±802	6	4.37	0.61
Totals			744	2385		744	744	**12.84**

Chi-square statistic = 12.84; chi-square$_{0.95}$ = 16.92; degrees of freedom = 9.

Table 5. Delta-mean and chi-square test results by station depth (m)

Depth	Mean	s^2	m	n	**Delta-mean**	o	e	**Chi-square**
≥ 29	6.93	5.40	54	76	**9184**±8868	54	23.71	38.70
30–39	6.52	3.69	143	231	**2563**±1304	143	72.68	69.84
40–49	6.55	2.69	143	233	**1601**±650	143	72.68	68.02
50–59	5.53	1.83	92	222	**256**±102	92	69.25	7.47
60–69	5.46	1.57	109	299	**186**±63	109	93.27	2.65
70–79	5.26	1.72	72	252	**127**±55	72	78.61	0.55
80–89	4.61	1.63	55	253	**40**±24	55	78.92	7.25
90–99	3.44	2.72	24	195	**20**±22	24	60.83	22.30
> 100	3.94	2.14	52	624	**12**±8	52	194.65	104.55
Totals			744	2385		744	744	**321.34**

Chi-square = 321.34; chi-square$_{0.95}$ = 15.51; degrees of freedom = 8.

and 1986 the annual observed frequency of capture did not differ significantly from the expected frequency.

Both the delta-mean and the chi-square show that gammarids occurred in greater numbers and more frequently at stations in shallower water (Fig. 2 and Table 5). The confidence intervals around the delta-mean of the ≤29 m stratum were very wide, reflecting high variability ($s^2 = 5.4$) even though the proportion of zero samples from this stratum was relatively low.

DISCUSSION

The MARMAP bongo tows no doubt include many species of gammarid amphipods: 95% of all amphipods belong to the suborder Gammaridea (Bousfield, 1973). Because the samples were not identified to the species level, we do not know which species are represented here nor in what proportions.

Amphipod biomass estimates

The July peak abundance of this study, 15 amphipods m^{-3}, can be conservatively estimated to be 2.8 kcal m^{-2} by using a 50 m water column, an assumed average length of 6 mm (= 1.2 mg dry weight) and an assumed carbon content of 31% (Avery, 1993). The total mean benthic biomass on Georges Bank is 82.8 kcal m^{-2} (Steimle, 1987), of which amphipods account for 2.1% or approximately 1.7 kcal m^{-2} (Theroux and Grosslein, 1987). In comparison to these amphipod biomass estimates, the July peak total planktonic copepod biomass (most of which is due to *Calanus finmarchicus*) is about 2.5 gC m^{-2} (Davis, 1987b), which is equivalent to 25 kcal m^{-2} (using 1 gC = 10 kcal (Sherman *et al.*, 1987)). Sherman *et al.* (1987) determined the 5-year (1977–1981) mean annual total zooplankton biomass (including amphipods caught in bongo tows) to be 4.7 g dry weight m^{-2}. If approximately one-third is carbon (Parsons *et al.*, 1984), this biomass is equivalent to 1.6 gC m^{-2} or 16 kcal m^{-2}. The mean annual estimates of between 2 and 12 amphipods m^{-3} of this study amount to between 2% and 14% of the mean annual zooplankton biomass.

Amphipod production estimate

Collie (1985) estimated the production of three benthic amphipod species on Georges Bank. He found that the production of these amphipods was comparable to that of related species in near-shore environments. He also speculated that the gradient of production to biomass ratios he saw was related to the life history and adult mortality risk of each species (as in Van Dolah and Bird, 1980). The biennial infaunal species *Ampelisca agassizi* had the lowest P:B ratio, 1.5, whereas the epibenthic semi-annual *Ericthonius fasciatus* had the highest, 4.4. By assuming that most of the species present in the MARMAP samples were more epibenthic than infaunal and using a corresponding P:B ratio of 4.4, we calculated a production estimate of between 1.6 kcal m^{-2} $year^{-1}$ and 9.8 kcal m^{-2} $year^{-1}$ for the amphipods captured by bongo nets. This range of values amounts to between 0.8% and 4.9% of the annual macrozooplankton production on Georges Bank reported by Sherman *et al.* (1987). By comparison, Davis (1987b) estimated *Calanus finmarchicus* production to be 32 kcal m^{-2} $year^{-1}$ or 15.8% of macrozooplankton production. Amphipod production is probably most important in shallower water, where they appear to be most numerous. If 5 kcal m^{-2} is the average biomass in waters less than 50 m, amphipod production there could be as high as 22 kcal m^{-2} $year^{-1}$.

Temporal distribution

The analysis undertaken in this study does little to show clear diurnal patterns in amphipod abundance. While the chi-square test results sometimes show that gammarids tend to be captured more often at night, the delta-mean results indicate that they may be more numerous during the day. Thus, although others have shown diurnal vertical migration in gammarid amphipods (e.g. Harding *et al.*, 1991), and the negative phototaxis is well known (Holmes, 1901; Kaestner, 1970), there is no clear evidence of either from the present study. However, the MARMAP sampling program was not designed to resolve time to this fine a scale.

There is, however, a seasonal signal in amphipod abundance with peaks in July and October. Such a bimodal pattern could indicate that a large portion of the animals represented in the MARMAP data have a semiannual life-history pattern with the October peak reflecting the birth and recruitment of a second generation. Other factors, such as the annual dispersal of pelagic young by benthic species, may contribute to the bimodal pattern also. Further, the chi-square results indicate that this pelagic gammarid community is a permanent feature of the Georges Bank ecosystem. It is not, for example, the result of a seasonal intrusion from the south. The timing of the summer peak in amphipods may be important to juvenile fishes. Summer is when recently metamorphosed young of many demersal fish species settle to the bottom (Lough *et al.*, 1989), and this amphipod biomass would provide a ready supply of food for them.

Sullivan and Miese (1996) also explored the distribution and abundance of gammarids on Georges Bank. They found similar patterns of distribution in space and time, but their annual abundance estimates differed from ours primarily because they used a more narrowly defined geographic space for their analysis.

Comparison with fish consumption

Although amphipods make up a relatively small proportion of the benthic biomass on Georges Bank, they constitute nearly half of the benthic animals numerically (Theroux and Grosslein, 1987). Their numerical dominance may make amphipods especially important as prey of fishes feeding near the bottom. Furthermore, the amphipods caught in bongo nets, whether truly pelagic or not, spend a portion of their time in the water column and are therefore vulnerable to fish predation. Amphipods are the principal prey of young cod (Bowman, 1981). The diet of juvenile haddock in the southern New England area includes 75% amphipods by weight (Langton and Bowman, 1981). Yellowtail flounder (Collie, 1987; Langton, 1981) and silver hake (Bowman and Bowman, 1980) also are major predators of near-bottom dwelling amphipods.

To compare amphipod production with fish consumption on Georges Bank over years corresponding to the MARMAP survey, consumption estimates for each fish species were made as follows. First, biomass-at-age results, derived from virtual population analysis (NOAA/NMFS, 1990, 1991), were converted to kilocalories according to the relation 1 g wet weight = 1 kcal (Sissenwine *et al.*, 1984). This value was normalized over the area of Georges Bank, 53,000 km^2 (Sissenwine *et al.*, 1984). Then consumption-to-biomass ratios for each age class (Sissenwine, 1987) were applied to arrive at an annual consumption by age for each species. Consumptions of the first three age classes were totaled.

The correlations between annual amphipod production and annual fish consumption are the covariance of amphipod production and fish consumption divided by the product of their standard deviations (Snedecor and Cochran, 1980). A -1.0 correlation indicates a perfect negative relationship, while a 0 correlation indicates no relationship. Amphipod production appears to vary negatively with yellowtail consumption (Fig. 3). Amphipods are known to constitute a major portion of the diet of this flatfish (Collie, 1987). Young cod also prey on amphipods (Bowman, 1981). However, the correlation is not as pronounced as the correlation for yellowtail flounder.

Other species also may prey on amphipods. The near-bottom-dwelling silver hake preys

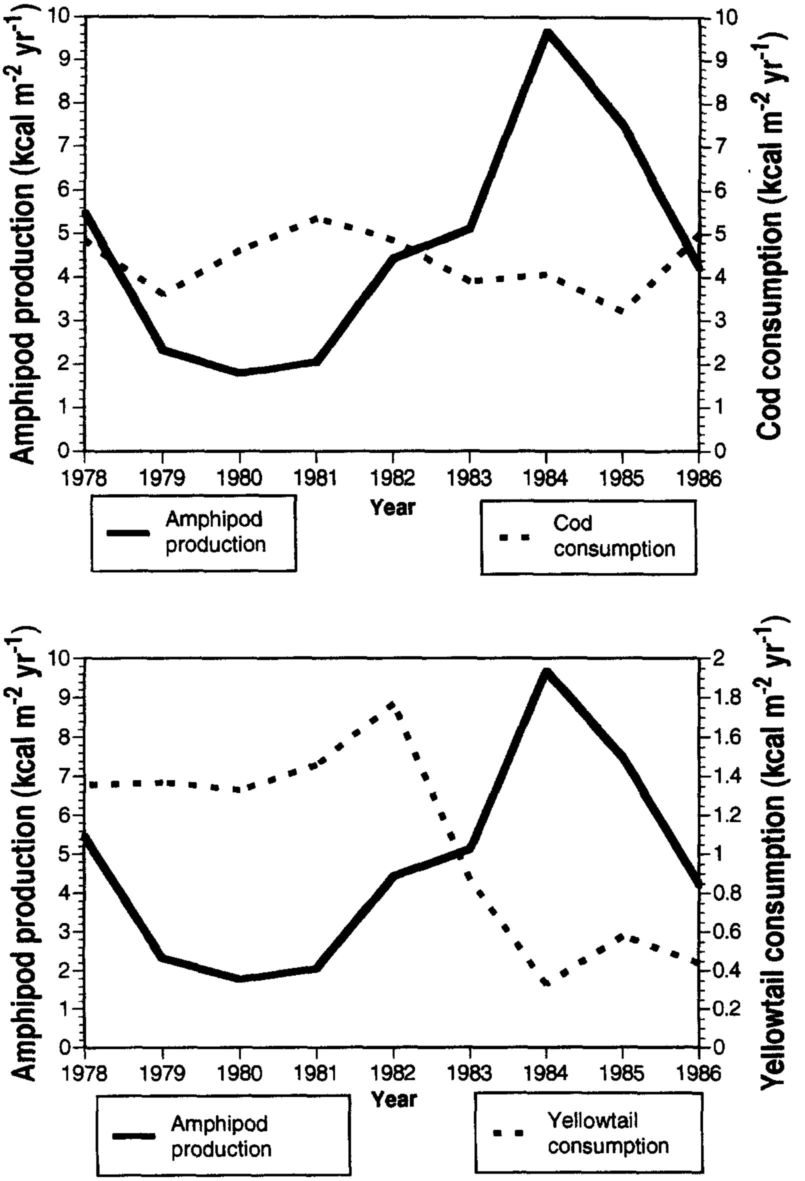

Fig. 3. Comparison of amphipod production with consumption by first three age classes of cod and yellowtail flounder on Georges Bank. The correlation between ages 1 and 3 cod consumption and amphipod production was −0.43. For yellowtail consumption the correlation was −0.68.

heavily on large free-swimming crustaceans such as decapods and amphipods (Bowman and Bowman, 1980). In addition, some guts of Atlantic mackerel taken from waters just south of Georges Bank contained numerous gammarid amphipods (NMFS, unpublished data), indicating that these amphipods were up in the pelagic zone and densely packed. Thus, amphipod production on Georges Bank may represent a significant and available food resource that is readily exploited by many demersal and pelagic fishes.

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