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## Estimating the impact of invertebrate predation on target species of copepods on Georges Bank

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### ABSTRACT

Large zooplankton including pelagic hydroids, hyperiid amphipods, decapod shrimp, chaetognaths, medusae and ctenophores can affect survival and recruitment of larval cod and haddock on Georges Bank through direct predation, and through competition with the larvae for copepod prey. As part of the GLOBEC Georges Bank program, we plan to estimate the magnitude of these effects with information on the co-distribution of predators and prey, and the specific feeding rates for each predator-prey pair. Distributional data for predators and prey comes from 1m<sup>2</sup> and 10m<sup>2</sup> MOCNESS net hauls made during Process and Broad Scale Survey cruises in 1994-97. Feeding rates and prey selection of the main predator species are estimated by several methods depending on the predator, including analysis of gut contents, feeding experiments, and energetic calculations. Because prey are sometimes unidentifiable in gut contents, we are developing an immunological assay for the specific detection of Calanus remains in predators. Results for predation impact on copepods will be presented in this paper.

Estimates of predation impact at well-mixed ("crest") and stratified ("flank") sites on Georges Bank in May, 1995 indicate the relative importance of predator and prey abundances. Estimated impacts for predators such as floating hydroid colonies (Clytia gracilis), chaetognaths (Sagitta), and amphipods (Themisto) range from less than 1% to 400% of prey stock per day. We will use time- and site-specific estimates of removal to compare predation mortality with other losses of target species over the entire Bank, throughout the winter-spring sampling season.

## INTRODUCTION

The US GLOBEC Northwest Atlantic Program on Georges Bank seeks to understand the biological and physical processes that control the abundance of target species of copepods and fish on the Bank. Among several hypotheses proposed for the field program is: "Predation rather than starvation is the dominant source of mortality of fish larvae; predation rather than advective loss is the dominant source of mortality of copepods" (p. 3, US GLOBEC, 1992). During the first two Phases of the GLOBEC Georges Bank Program, we have been working to determine the distributions, abundances, and feeding rates of the invertebrate predators of the target species of copepod (*Calanus finmarchicus* and *Pseudocalanus* spp.) and fish (*Gadus morhua* and *Melanogrammus aeglefinus*), both on the Bank and across its margins. This work has involved a combination of broad-scale surveys and process-oriented cruises on the bank in 1994 through 1997, as well as ship-board and shore-based laboratory experiments. With renewed funding, we hope to continue the research through 2000. Our ultimate goal is the direct measurement of predation mortality on the target species on Georges Bank, and the comparison of this source of mortality to all other loss and gain terms (i.e., growth, reproduction, starvation, immigration, emigration) in the population dynamics of the target species.

Preliminary sampling conducted in 1994 and 1995 showed that invertebrate predators were quite variable in abundance and species composition from one month and one site to another. Common predators included expected forms such as chaetognaths, decapod crustaceans and hydromedusae, under-sampled forms such as lobate ctenophores, physonect siphonophores and scyphomedusae (Sullivan and Meise 1996), and quite unexpected forms, such as the suspended hydroids of *Clytia gracilis* (Madin et al. 1996). Large variations in abundance between day and night suggested that predation mortality in the water column varies on a diel cycle, due to vertical migration of many of the predators.

Some predator species (e.g. hydroids, chaetognaths, *Cirolana*, *Themisto*, *Crangon*) appear to be resident on the Bank, but others predators may be advected (or move actively) onto the Bank from external source regions at various times of year. Perhaps the most striking examples are the migrant populations of herring and mackerel that cross Georges in the spring and summer, but euphausiids, siphonophores, ctenophores and some amphipods appear to be among invertebrates which also enter Bank waters from surrounding regions. For example, large populations of the ctenophore *Bolinopsis* and the siphonophore *Nanomia cara* have been reported from both net collections (Bigelow, 1924) and submersible observations (Bailey et al. 1994; Rogers et al. 1978; Youngbluth, 1996) in the Gulf of Maine; we have seen both of these in great abundance on Georges Bank. Dense populations of the ctenophore *Pleurobrachia pileus* occur in coastal waters of the Scotian Shelf southwest of Nova Scotia, where their feeding may be responsible for a drastic decrease in copepod abundance (Suthers and Frank, 1990). This species also occurs on Georges, and may in part be advected on by flow off the Scotian Shelf. Intrusions of Slope water onto the southern flank of the Bank occur fairly frequently forced by Gulf Stream rings or meanders.

Our approach to estimation of predation mortality requires 1) measuring rates of predation by specific predators on specific target species prey and 2) determining the co-distribution in time and space (annual, seasonal, horizontal and vertical) of these predators and the prey. Rate determinations are made in several ways depending on the species, as described below. Data on abundance and distribution of predators and prey is derived mainly from the Broad Scale Survey, which samples a grid of stations on the Bank (and selected off Bank sites) on monthly cruise from January to June, every year from 1995 through 2000 (projected). As soon as sufficient distribution data are available, we expect to be able to map predation intensity, as daily percent removal of target species, over the entire Bank, month by month, from 1995-2000. In this paper we describe methods used to date for estimation of predation rates, variation in species composition and abundance of the main invertebrate predators, and examples of estimated predation impacts for two samples sites in 1995 and 1996.

## METHODS

### Predator and prey distributions.

Information on the distribution of target species and of invertebrate predators comes mainly from collections made on the Broad Scale Survey. This program includes cruises every month from January through June from 1995 through 1999. Sampling is done on a standard grid of 38 stations divided into 4 priority groups, and includes use of 1 m<sup>2</sup> and 10m<sup>2</sup> MOCNESS nets, as well as CTD casts, plankton pump lowerings and Bongo net tows. MOC-10 samples are scheduled at a total of 18 Priority 1 and 2 stations. Additional samples using both net systems were taken during Process cruises in 1994, 1995 and 1997, and visual estimates of the abundance of *Bolinopsis infundibulum* were made by divers on most of these cruises.

Broad Scale samples from the 1 m<sup>2</sup> MOCNESS are sorted and identified by the GLOBEC Zooplankton Sorting Group at the Graduate School of Oceanography, University of Rhode Island. Samples selected for analysis are split with a Folsom splitter to provide a subsample of about 1000-1200 total animals. *Calanus finmarchicus* and *Pseudocalanus* spp. copepodites are identified to stage. Adults of other copepods are identified to species, while copepodites were grouped and identified to species where possible (e.g. *Temora longicornis*), or to genus where it was not possible to identify the younger copepodite stages of individual species (e.g. *Centropages hamatus*, *C. typicus* and *C. bradyi*). Other zooplankton taxa are identified to the lowest possible taxon and enumerated. Nauplii present in MOCNESS samples are not counted since most were not quantitatively sampled. Data on naupliar abundance are from the plankton pump samples instead. Results of the 1m<sup>2</sup> MOCNESS analyses are made available to us and other investigators in a database maintained on the GSO GLOBEC web site (<http://globec.gso.uri.edu:81/>). Additional samples from the 1 m<sup>2</sup> MOCNESS collected on Process cruises were analyzed in a similar way by Sullivan.

Samples from the 10 m<sup>2</sup> nets from both Broad Scale and Process cruises are sorted by our group at Woods Hole or San Francisco State. For these samples, we record total displacement volume, and then usually sort and count the entire sample; appropriate subsamples are taken from particularly dense samples. All invertebrates are identified to species (and sex or stage where possible), counted and measured. Measurements are used to estimate biomass as carbon weight, using published or newly derived relationships. Results are expressed as numbers and C biomass of animals per m<sup>3</sup> and per m<sup>2</sup>, for 3 depth ranges at each station site and time. In some cases, size distribution data are also included. Data are to be added to the GLOBEC database (<http://globec.who.edu/globec.html>).

#### Estimation of feeding rates.

The second element we are determining is the specific feeding rate of each predator species on the target species of prey. In general, we aim to express this as numbers or biomass of prey consumed per day under field conditions. We have had to use different methods to estimate these rates, depending on the feeding biology and tractability of the particular predator. Where possible, we have examined gut contents microscopically to identify and count prey items. To determine feeding rates from these data, we have measured digestion or gut passage times (depending on the type of gut) in shipboard experiments, for use in the expression:

$$\text{Prey ingested } d^{-1} = \text{number of prey in gut/gut passage time (d)}$$

In other cases we have relied on literature data to make provisional estimates. Methods used for the five predator species considered here include:

#### *Clytia gracilis*

The types of prey ingested by the floating hydroid colonies of *Clytia gracilis* and related species were determined from examination of gut contents of freshly caught hydranths. Estimates of field feeding rates were based on counts of copepod nauplii and eggs in the guts, together with digestion rates measured in laboratory incubations. In addition, feeding experiments with the hydroids were conducted both on shipboard and on shore (with cultured hydroids), using copepod eggs and nauplii, and cod larvae as prey. These methods and results are described in Madin et al. (1996). All feeding rates for *Clytia* are expressed as prey consumed hydranth<sup>-1</sup> d<sup>-1</sup>.

#### *Sagitta elegans*

Prey types and numbers per chaetognath were again determined by microscopic examination of gut contents. Temperature dependent gut passage rates for copepod prey have been reported previously (Stuart and Verheye 1991), and we used these values to calculate in situ ingestion rates.

#### *Pleurobrachia pileus* and *Bolinopsis infundibulum*

The types and numbers of prey in these ctenophores were also determined by

examination of the gut contents. *Pleurobrachia* for this purpose were collected in the 1 and 10 m<sup>2</sup> MOCNESS nets, and also by divers. *Bolinopsis* were only collected by divers (in individual jars) because they are destroyed by the nets. Digestion times for typical prey were determined in shipboard experiments using diver-collected ctenophores and known prey. Digestion was monitored at intervals and considered complete when no exoskeletal remains were visible in the stomodeum.

### *Themisto gaudichaudii*

This hyperiid amphipod grinds its food in the foregut, making microscopic identification of gut contents difficult or impossible. We have conducted shipboard feeding experiments to demonstrate that *Themisto* do eat *Calanus* and larval cod, and to determine gut passage times for these prey. Gut passage was monitored by feeding the amphipods prey organisms stained with carmine dye and then timing the appearance of dyed fecal pellets. It is our intention to identify *Calanus* in the guts of *Themisto* using a polyclonal antibody probe currently being developed, but for the present, we have used an indirect method to estimate feeding on copepods by this predator, based on data from the North Sea (Sheader and Evans, 1975). These workers found that the diet of smaller *Themisto* (<8 mm) was almost entirely copepods, while for larger individuals the diet was about 25% copepods, 25% fish larvae, 25% chaetognaths and 25% other. We estimated ingestion from values for daily ration (as mg dry weight) of *Themisto* as a function of size and temperature (Sheader and Evans, 1975). Using the reported distribution of prey types for small and large amphipods, and equivalent dry weight values for *Calanus* CV stage (0.17 mg), we converted the daily ration figures to numbers of copepods eaten per day. For small *Themisto* we chose a median length of 4 mm, which would have a daily ration at 9.8° C of 0.1 mg dw; large *Themisto* with a median length of 11 mm have a daily ration of 0.4 mg dw, of which 25% is assumed to be copepods. These figures represent 0.6 *Calanus* CV day<sup>-1</sup>.

## RESULTS

### Distribution of predator species

Distributional information for predators and target prey species are derived mainly from the Broad Scale survey collections described above. A complete data set for all stations and dates is not yet available, so for the purposes of this paper, we have focussed on a small number of sites and times. It is clear that the qualitative and quantitative distribution of predators collected by both MOCNESS systems varies considerably from one region of the Bank to another, as well as interannually. This is illustrated in Figure 1, which shows the main predator groups collected with the 1 m<sup>2</sup> and 10 m<sup>2</sup> nets at two stations in 1994, 1995 and 1996. The region designated "crest" is in the central well-mixed region inside the 60 m isobath. The "flank" region is between the 60 m and 100 m isobaths, south of the crest (Fig. 2).

There is a large difference in abundance between the smaller species collected with the 1 m<sup>2</sup> net and the larger ones sampled with the 10 m<sup>2</sup> trawl. Data in Fig. 1 are expressed in numbers of individuals, which in the case of hydroids means single hydranths. Although

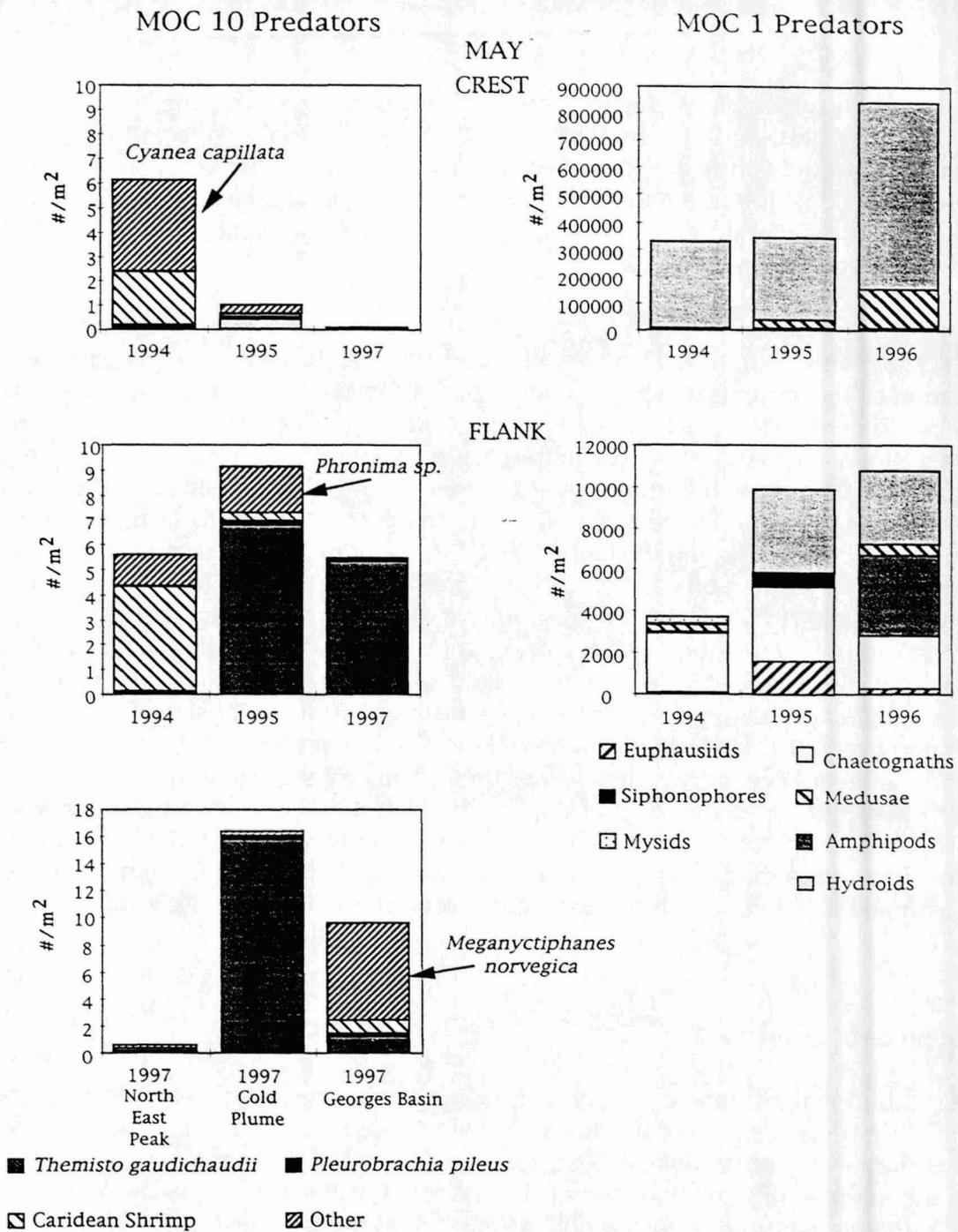


Figure 1. Variation in occurrence and abundance of the main species of invertebrate predators in 1994, 1995 and 1997, expressed as numbers of individuals  $m^{-2}$  (integrated over sampling depth). "Crest" and "flank" regions and three 1997 stations in lower left panel are also located in Fig. 2. MOC-10 predators are those collected with the 10  $m^2$  MOCNESS trawl, 3.0 mm mesh; MOC-1 Predators are those collected in the 1  $m^2$  MOCNESS nets, 300  $\mu m$  mesh. Principal constituents of "other" category for MOC-10 samples are indicated on the figure.

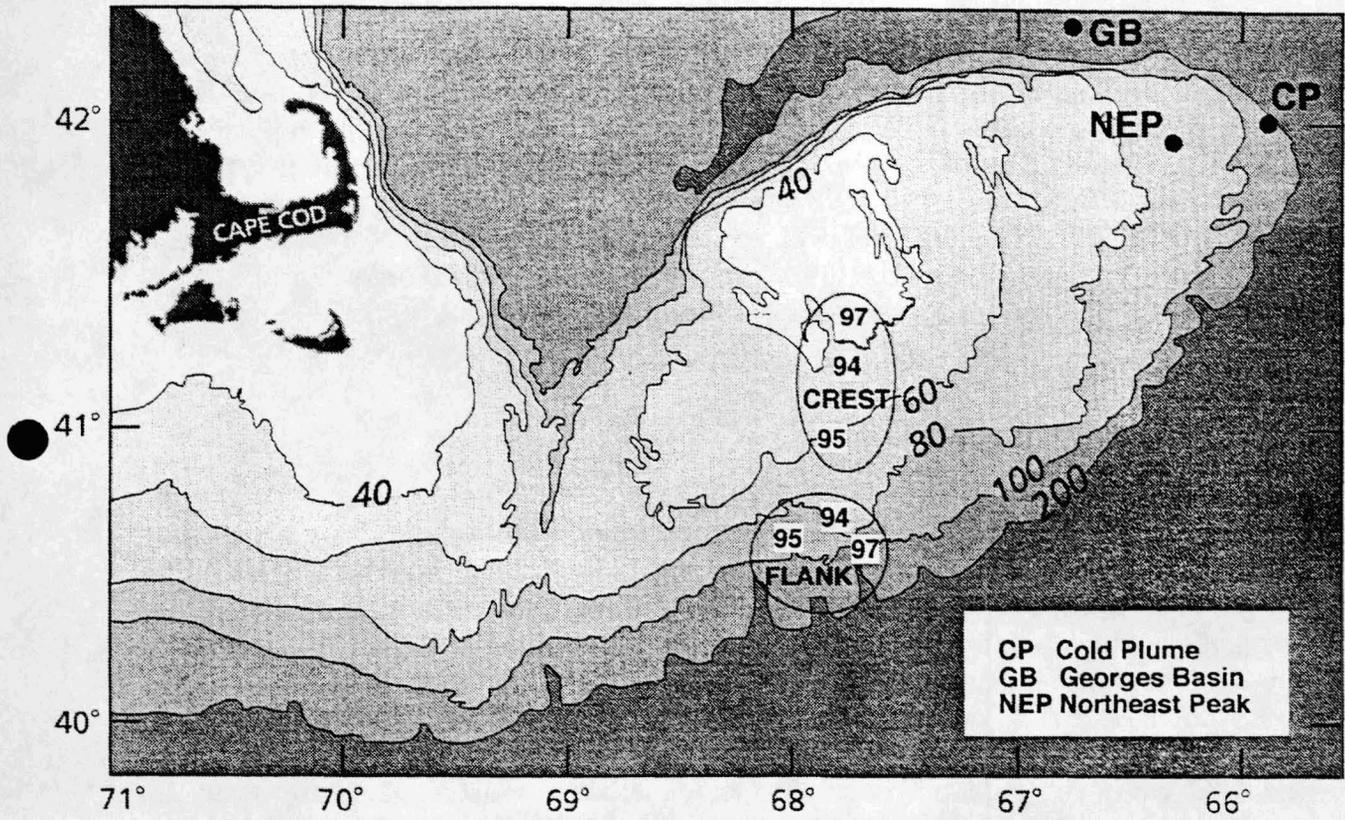


Figure 2. Map of Georges Bank, showing location of "crest" and "flank" regions sampled in 1994, 1995 and 1997. Station locations for each years indicated by numbers within the ovals. Also shown are 3 stations sampled in 1997, from which predator distribution data are given in Figure 1.

biomass data have not yet been calculated for these tows, the contrast in biomass between the large and small animals caught in the two nets should be substantially less than the contrast in numbers. Among small predators, the crest site was dominated by hydroids in all three years, with large numbers of the medusa stage also present in 1996. Composition of the large predator fauna varied considerably, dominated by *Cyanea* and caridean shrimp in 1994, then very few organisms in 1995 and 1996. At the flank site, the composition of the small predators had a consistent fraction of chaetognaths in each year, but varying proportions of amphipods, hydroids, euphausiids, medusae and siphonophores. Large animals at the flank station included numerous carideans in 1994, largely replaced by *Themisto* in 1995 and 1996. The presence of *Phronima*, a slope water species, in 1995 was due to slope water intrusion onto the Bank. For 1997 we have only analyzed 10 m MOCNESS samples from three stations occupied in May (Fig. 2): at the Northeast Peak, in a plume of cold water coming from the Scotian Shelf, and in Georges Basin slightly northeast of the Bank. *Themisto* was the most constant component, but large numbers of the euphausiid *Meganyctiphanes norvegica* and some caridean shrimps were also found in the Basin.

### Feeding rates

Estimates of daily ingestion for the 5 predator species considered here were made with the methods described above, and are summarized in Table 1. In general these values are averages for the entire water column. It was not always possible to identify *Calanus* or *Pseudocalanus* in gut contents, so predation rates are for total copepods, nauplii or eggs  $d^{-1}$ . Similarly, indirect estimates from energetic calculations (*Themisto*) refer only to total copepods. In these cases, our estimates of the impact on *Calanus* and *Pseudocalanus* assume that these species will be consumed in proportion to their abundance among all copepods. As we develop better information about selectivity for or against these species by particular predators, this default assumption of neutral selection will be modified.

### Estimated Predation Impacts

We have made preliminary calculations of predation effects in two ways. In the first case we used data on predator abundance from samples collected during a Process cruise at the crest and flank stations in May, 1995. Many of the samples and measurements that were used to estimate individual feeding rates (Table 1) were also taken during this cruise. Prey abundance data for *Calanus finmarchicus* and *Pseudocalanus* spp. at the same time and regions (but sampled on different cruises) were taken from the Broad Scale Survey zooplankton database. These estimates (Tables 2 and 3) are for night predator abundances, and express the expected predation loss (as percent of prey  $m^{-2} d^{-1}$ ) for *Calanus* and *Pseudocalanus*, based on alternative assumptions about their selection by the various predators. The first case (not shown in the tables) is an electivity of -1, in which case 0% of the target species are removed daily by the predators. The middle situation is an electivity of 0, indicating no selection for or against those species, a reasonable default assumption in the absence of other information. In this case prey species are consumed in

Table 1. Summary of prey types, gut contents, digestion times and estimated daily consumption for five predator species. Data pertain to May 1995, except as noted.

	Prey types	Number of prey in guts	Gut passage times, h	Ingestion rates prey predator <sup>-1</sup> d <sup>-1</sup>
<i>Clytia gracilis</i>	copepod eggs and nauplii	n.a.	eggs 33 nauplii 0.25	eggs 0.11 nauplii 0.24
<i>Pleurobrachia pileus</i>	copepods 75% ( <i>Calanus</i> 32%) other 25%	copepods 5.5 <i>Calanus</i> 2.4	copepods 4.8 @10° C	copepods 27 <i>Calanus</i> 9
<i>Bolinopsis infundibulum</i>	copepods 78% ( <i>Calanus</i> 0%) pteropods 17% other 5%	copepods 4.5 <i>Calanus</i> 0	copepods 3.4 @9° C	copepods 31 <i>Calanus</i> 0
<i>Sagitta elegans</i>	copepods 84% nauplii 11% chaetognaths 5%	copepods 0.35 (June 1995)	copepods 7.6 @10° C	copepods 1.1
<i>Themisto gaudichaudii</i>	4 mm amphipod: copepods 100%  11 mm amphipod: copepods 25% fish larvae 25% chaetognaths 25% other 25%	daily ration: 4 mm amphipod: 0.1 mg dw  11 mm amphipod: 0.4 mg dw (Sheader & Evans 1975)	3.8 @ 10° C	4 mm amphipod: 0.6  11 mm amphipod: 0.6

Table 2. Georges Bank, Crest region. Estimates of nighttime predation impact from 5 predator species in May 1995. Predator feeding rates derived as described in text and Table 1. Predator abundance from Process cruise samples (cruise SJ9507, Sta. 12). Prey numbers from Broad Scale Survey samples at same stations. Prey are nauplii for *Clytia*, copepodites and adults for other predators. Prey densities were *Calanus*: 753 nauplii and 2475 copepodites/adults m<sup>-2</sup>; *Pseudocalanus*: 1065 nauplii and 13,600 copepodites/adults m<sup>-2</sup>, all values integrated over depth sampled.

Predator	Feeding Rate prey m <sup>-2</sup> d <sup>-1</sup>	Predators m <sup>-2</sup>	Prey eaten m <sup>-2</sup> d <sup>-1</sup>	% <i>Calanus</i> eaten d <sup>-1</sup> if E=0	% <i>Calanus</i> eaten d <sup>-1</sup> if E=1	% <i>Pseudo-calanus</i> eaten d <sup>-1</sup> if E=0	% <i>Pseudo-calanus</i> eaten d <sup>-1</sup> if E=1
<i>Clytia</i>	0.24	1140	274	1.2	36.4	1.2	25.7
<i>Bolinopsis</i>	31	20	620	1.3	25.0	1.3	4.6
<i>Pleurobrachia</i>	27	0.1	2.7	<<1	0.1	<<1	<<1
<i>Sagitta</i>	0.6	1770	1062	2.2	42.9	2.2	7.8
<i>Themisto</i>	0.6	159	95	0.2	3.8	0.2	0.7
Total		3089	2054	4.9	108.2	4.9	38.8

Table 3. Georges Bank, Flank region. Estimates of nighttime predation impact from 5 predator species in May 1995. Predator feeding rates derived as described in text and Table 1. Predator abundance from Process cruise samples (cruise SJ9507, Sta. 9). Prey numbers from Broad Scale Survey samples at same stations. Prey are nauplii for *Clytia*, copepodites and adults for other predators. Prey densities were *Calanus*: 27,430 nauplii and 39,344 copepodites/adults m<sup>-2</sup>; *Pseudocalanus*: 30,567 nauplii and 19,030 copepodites/adults m<sup>-2</sup>, all values integrated over depth sampled.

Predator	Feeding Rate prey m <sup>-2</sup> d <sup>-1</sup>	Predators m <sup>-2</sup>	Prey eaten m <sup>-2</sup> d <sup>-1</sup>	% <i>Calanus</i> eaten d <sup>-1</sup> if E=0	% <i>Calanus</i> eaten d <sup>-1</sup> if E=1	% <i>Pseudo-</i> <i>calanus</i> eaten d <sup>-1</sup> if E=0	% <i>Pseudo-</i> <i>calanus</i> eaten d <sup>-1</sup> if E=1
<i>Clytia</i>	0.24	1250	300	0.1	1.1	0.1	1.0
<i>Bolinopsis</i>	31	0	0	0	0	0	0
<i>Pleurobrachia</i>	27	0.2	5.4	<<1	<<1	<<1	<<1
<i>Sagitta</i>	1.1	2330	2563	1.5	6.5	1.5	13.5
<i>Themisto</i>	0.6	513	308	0.2	0.8	0.2	1.6
Total		4093	3176	1.8	8.4	1.8	16.1

proportion to their occurrence, and the percent of target species removed per day is the same as it is for total copepods. The third is an electivity of 1, meaning that only *Calanus* or *Pseudocalanus* are consumed. Of course, the true values for any given station or time will fall somewhere in this range, depending on the actual station-specific composition of gut contents of the predators. For example, in May 1995 we know that *Calanus* and *Pseudocalanus* made up 32% of the gut contents of *Pleurobrachia*, yielding an estimated feeding rate on these species of 9 *Calanus/Pseudocalanus* d<sup>-1</sup>. At the Crest station, this would be 0.04% and 0.007% respectively of the *Calanus* and *Pseudocalanus* stocks d<sup>-1</sup>. We do not expect to be able to obtain ad-hoc values for all predators and all stations, but will use these data as much as possible to modify the default assumption of neutral selection (E=0).

Our second method to estimate predation impact uses the same values for feeding rates of the different predators (Table 1), and applies these to abundance values for both predators and prey derived from the Broad Scale Survey samples. This is the approach we expect to use ultimately to map estimates of total predation mortality on the Bank over several years. Results of a sample calculation for Crest and Flank regions in May, 1996, are shown in Figure 3. In this case predation impacts of three predators, *Clytia*, *Sagitta* and *Themisto*, have been calculated, with nauplii as the prey of *Clytia*, and copepodites/adults as prey of the others. For these estimates, we have assumed the default value of E=0, so that copepodites and nauplii of *Calanus* or *Pseudocalanus* are consumed in proportion to their availability in the plankton.

At the crest station, no *Calanus* nauplii were found, and copepodites composed only 0.8% of the total copepods. *Pseudocalanus* composed 12 and 13% respectively, of nauplii and copepodites present. Hydranths of *Clytia* were extremely abundant, at over 300,000 m<sup>-2</sup>, and their potential consumption of nauplii exceeded the stock of total nauplii by a factor of 4. Presumably under these circumstances the hydroids are catching alternative prey, possibly including copepod or fish eggs (Madin et al. 1996). *Sagitta* and *Themisto* were present at 4061 and 765 individuals m<sup>-2</sup>, and their predation impact was considerably less, a little over 2% of *Calanus* and *Pseudocalanus* per day.

At the flank station, *Clytia* were about 100 times less abundant, at 3563 m<sup>-2</sup>, and their impact on the more numerous nauplii (1100 *Calanus*, 30,600 *Pseudocalanus* m<sup>-2</sup>) essentially nil. *Themisto* were much more numerous on the flank (3888 m<sup>-2</sup>), and together with *Sagitta* (2500 m<sup>-2</sup>) could consume about 3% of the *Calanus* and *Pseudocalanus* stocks daily.

## DISCUSSION

Mortality of target species of copepods and larval fish due to predation will depend on the feeding rates and selectivities of the predators, the ability of the prey to avoid the predators, and the co-distribution of predator and prey at particular locations and times. We are attempting to understand the combined effects of predator feeding rate, selectivity and prey avoidance success by examining the end result of these processes, namely the numbers and distribution of prey articles in the guts of the predators. Because of difficulties in the identification of gut contents and the unpredictable occurrence of different predators, it may not always be possible to quantify feeding impact by this method for all predators, stations or seasons. Determinations of rates and selectivity need to be tailored to each species, and repeated with collections from different times and locations to get realistic estimates of variation in feeding behavior.

Even with the best estimates we can make for behavior of particular predator species, it is apparent that the greatest factor controlling the impact of any one predator is its abundance relative to its prey. The large variations in abundance of the hydroids, for example, make the difference between a potential for 400% daily removal of prey at the crest region and 1% removal in the flank region a few km away (Fig. 3). In contrast, *Sagitta* has a relatively uniform distribution over wide areas of the Bank,

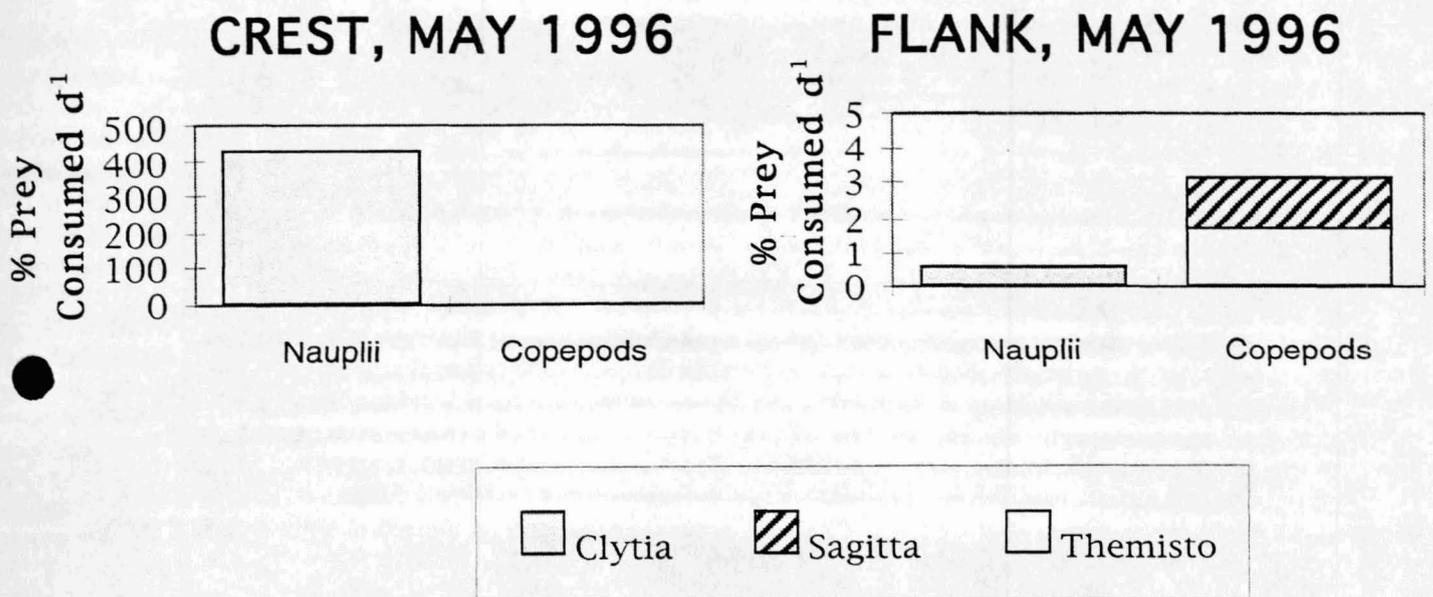


Figure 3. Estimates of predation impact by 3 predators, *Clytia*, *Sagitta* and *Themisto*, based on feeding rates and abundances of predators and prey from Broad Scale Survey samples. Impact is expressed as percent of the stocks of *Calanus* and *Pseudocalanus* removed daily, assuming that the predators are non-selective ( $E=0$ ), and consume these species in the same proportions as they occur. Prey of *Clytia* are nauplii, prey of the other predators are copepodites and adults.

with little seasonal or interannual variation (Sullivan and Meise 1996). Compared to the range of variation in predator type and abundance (Fig. 1), differences in predation rate among different predator species, or of a single species from one time or place to another, are minor factors. Selectivity is probably more important than predation rate, but neither will change total predation mortality by more than a factor of about 5. Changes in predator abundance may vary by up to 1000 times from one station, month or year to another. Assuming that we have identified the predator species which are consuming target species, and have a reasonable estimates of their selectivity and feeding rates, the critical parameter for accurate prediction of predation mortality will be their co-occurrence in space and time and relative abundance with the target species. For this reason, we believe that the Broad Scale Survey data for copepods, larval fish and predators will permit an estimate of predation mortality that is within acceptable limits.

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