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Predatory control of copepod seasonal cycles on Georges Bank

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Abstract

A stimulation model of copepod population dynamics (development rate, fecundity, and mortality) was used to compute the predatory consumption necessary to control population growth in three dominant copepod species (*Pseudocalanus* sp., *Paracalanus parvus,* and *Calanus finmarchicus*) on Georges Bank, given observed seasonal cycles of copepod and predator populations. The model also calculated secondary production of each species. Copepod development rate and fecundity were functions of temperature while mortality was a function of predator abundance and consumption rate. Daily inputs of temperature and predator abundance (chaetognaths, ctenophores, and *Centropages* spp.) were derived from equations fit to field data. Model runs were made with various consumption rates until the model output matched observed copepod seasonal cycles. Computed consumption rates were low compared with published values from field and laboratory studies indicating that, even at conservative estimates of consumption, predators are able to control these copepod populations. Combined annual secondary production by the small copepod species, *Pseudocalanus* sp. and *P. parvus,* was nearly twice that of the larger *C. finmarchicus* with *P. parvus* having the highest total annual production.

Introduction

Seasonality in zooplankton populations is a well-known feature of temperate marine environments. Studies of processes responsible for such fluctuations have involved descriptions of life cycles of dominant species in specific areas (cf. Marshall, 1949; Fulton, 1973) as well as energy/mass flow and other trophodynamic type analyses (Petipa *et al.,* 1970; Vinogradov *et al.,* 1972, 1973; Cohen *et al.,* 1982). Theoretical modeling studies have examined the roles of different trophic levels in structuring marine ecosystems (Steele, 1974; Steele and Frost, 1977), but it remains uncertain to what extent ecosystem structure is regulated by primary production, herbivory, or predation (Steele, 1976; Landry, 1976).

From population studies, it is evident that a wide variety of zooplankton life histories exists and that processes controlling ecosystem dynamics in any particular location depend on the biologies of the endemic species. A common problem with trophodynamic models is that too often individual species differences are overlooked by considering a trophic level in terms of total biomass of many species lumped together (Riley, 1946, 1947; Walsh *et al.,* 1981) or in terms of the biology of a single dominant species (Steele, 1974) i.e. the "black box" approach. For example, Riley (1946, 1947) explained the seasonal cycle of total zooplankton biomass, (from settled volumes) on Georges Bank as a function of phytoplankton biomass, respiration, predation, and natural mortality. By focusing on total zooplankton biomass, the seasonal cycle described by Riley was essentially that of the larger *Calanus finmarchicus* (Davis, 1982, in press). Importance of the other smaller species was not seen. It is becoming increasingly clear that such modeling approaches alone cannot provide the detailed information necessary for accurate assessment of zooplankton dynamics.

Alternatively, by modeling population dynamics of individual (dominant) species in relation to environmental parameters, life cycles and life histories of endemic species are dealt with directly while at the same time trophic interactions and production rates can be found.

On Georges Bank, small copepods are much more abundant than the larger *Calanus finmarchicus* (Davis, 1982, in press), contrary to earlier works (Riley and Bumpus, 1946; Sherman, 1980). Although biomass of the small copepod species is low in comparison with *C. finmarchicus,* laboratory rearing experiments indicate that

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two of the species, *Paracalanus parvus* and *Pseudocalanus* sp., have relatively short generation times and thus may contribute substantially to total secondary production (Vidal, 1980; Thompson, 1982; Davis, 1984a). In addition, processes controlling the seasonal cycle of *C. finmarchicus* as described by Riley (1946, 1947) may not be the same as those affecting the smaller species. Laboratory studies have shown that the larger copepods of the genus *Calanus* require more food for growth and reproduction than do the smaller *Pseudocalanus* spp. (cf. Vidal, 1980). Furthermore, the seasonal cycles of *Pseudocalanus* sp. and *P. parvus* appear to occur independently of food concentration on Georges Bank (Davis, 1984a). As discussed elsewhere (Davis, 1982), it is unlikely that temperature or physical processes are responsible for the seasonal declines in these populations either. Therefore, these declines must be due to behavioral factors or to predation.

In the present paper, a simulation model of copepod population dynamics was used to evaluate the role of predation in regulating the seasonal cycles of *Pseudocalanus* sp., *Paracalanus parvus,* and *Calanus finmarchicus* on Georges Bank. Specifically, the model was used to determine whether predation could be solely responsible for the observed seasonal cycles of the copepods, given: (1) observed seasonal cycles of predator populations and (2) predatory consumption rates that are realistic when compared with published values. The model was also used to estimate the secondary production of each copepod species in order to determine their contributions to total copepod production.

Material and methods

An empirical model of copepod population dynamics (development rate, fecundity, and mortality) was used to compute the predatory consumption rates necessary to control population growth in the three copepod species. Assumptions were that development rate and fecundity were functions of temperature but independent of food supply and that mortality was a function of predator abundance and consumption rates. Temperature and predator abundance (chaetognaths, ctenophores, and *Centropages* spp.) were entered into the model at a time step of one day and were based on field data from Davis (1982, in press) and Sherman (1979). Model runs were made with various consumption rates until the model output matched the observed seasonal cycles. The computed consumption rates were then compared with field and laboratory determined consumption rates reported in the literature for each predator.

Model formulation

The basic model equations are given in Davis (1984b). The model used here was the same except that spatial dimension was not considered and mortality was not constant but varied with predator abundance and temperature dependent consumption rates. Ignoring spatial dimension, as Riley (1946, 1947) did, assumes horizontal and vertical homogeneity. This is reasonable as a first approximation for zooplankton populations in the shallow well mixed region on Georges Bank (Butman and Beardsley, in press), where the seasonal samples were collected (Davis, 1982). Population parameters needed for the model are development rate, fecundity, and mortality.

Development rate

Mean duration of each life stage, D_i, was related to temperature through Belehradek's function (Corkett and McLaren, 1978):

$$D_i = a_i (T - \alpha)^b, \tag{1}$$

where D_i is the mean duration of stage i in days, T is temperature (°C), and a_i, α, and b are constants estimated from literature information and laboratory rearing experiments (Davis, 1984a). Values of the constants α and a_i used in this equation for each species are given in Table 1. b was constant between species at –2.05 and α was constant between life stages within species as suggested by Corkett and McLaren (1970, 1978).

For *Pseudocalanus* sp., the constants a_i varied with life stage as previously derived (Davis, 1984b). As a first approximation, *Paracalanus parvus* development was assumed to be isochronal (Miller *et al.,* 1977) through both copepodid (Davis, 1984a) and naupliar stages, thus the constant a_i was the same for all life stages N1-C5. α and a values for N1-C5 were computed from development times at 12 °C (Davis, 1984a) and 18 °C (Checkley, 1980b) (letting $b = -2.05$). Although, Landry (1983) found *P. parvus* to spend relatively less time in naupliar stages than as copepodids, data from Davis (1984a) indicate that these two developmental periods may be of the same duration. Using values of a_i given in Table 1, Eq. (1) gives a development time from hatching to adult at 15 °C of 21 d, which is quite close to the range (18 to 20 d) reported by Landry (1983). Adult females reproduce for approximately 10 d at 20 °C (Hoffman *et al.,* 1981). They were assumed to die at this point, so a_{12} was calculated from:

$$a_{12} = a \cdot 10/D, \tag{2}$$

where a is a_i for any stage N1-C5, and D is the duration of any stage N1-C5 at 20 °C. Embryonic duration, D_0, for *P. parvus* was taken from Checkley's (1980a) equation:

$$D_0 = 432 \cdot (T + 2.97)^{-2.25}. \tag{3}$$

Stage durations for *Calanus finmarchicus* at 14.5 °C were calculated from the generation time at that temperature (McLaren, 1978) by assuming isochronal growth for N1-C6. The relation of embryonic duration to temperature is given by McLaren (1966). Thus, the value of a for stages N1 to C5 was calculated from:

$$a = [D/D_0] \cdot a_0, \tag{4}$$

Table 1. Stage specific values of parameters used in Belehradek's equation for each copepod species (see text). Also given are length, width, and weight of each copepod stage, and the range of chaetognath size classes preying on each stage as used in the model

Copepod species	Copepod life stage	i	a_i	Length (mm)	Width (mm)	Weight (μgC)	a_j,b_j
Pseudocalanus sp.	Egg	0	2 312	0.127	–	0.06	–
$\alpha = -13.87$	N1	1	1 541	0.176	0.076	0.10	1,4
	N2	2	385	0.200	0.082	0.13	1,5
	N3	3	1 541	0.260	0.088	0.21	1,5
	N4	4	1 926	0.310	0.106	0.29	2,7
	N5	5	2 312	0.360	0.123	0.38	2,9
	N6	6	1 156	0.400	0.127	0.45	2,9
	C1	7	2 562	0.420	0.129	0.50	2,9
	C2	8	2 083	0.520	0.160	0.82	2,13
	C3	9	2 041	0.620	0.203	1.30	3,18
	C4	10	2 125	0.730	0.237	2.16	4,21
	C5	11	2 749	0.880	0.274	4.31	5,21
	C6	12	62 424	1.000	0.312	7.50	5,21
Paracalanus parvus	Egg	0	432	0.074	–	0.02	–
$\alpha = -30.7$	N1	1	4 712	0.090	0.030	0.03	1,1
	N2	2	4 712	0.110	0.035	0.04	1,1
	N3	3	4 712	0.160	0.053	0.09	1,2
	N4	4	4 712	0.210	0.070	0.14	1,4
	N5	5	4 712	0.240	0.080	0.18	1,5
	N6	6	4 712	0.250	0.083	0.20	1,5
	C1	7	4 712	0.280	0.092	0.23	1,6
	C2	8	4 712	0.360	0.118	0.37	2,8
	C3	9	4 712	0.410	0.135	0.46	2,10
	C4	10	4 712	0.520	0.173	0.82	3,14
	C5	11	4 712	0.620	0.207	1.30	4,18
	C6	12	31 284	0.740	0.252	2.26	4,21
Calanus finmarchicus	Egg	0	1 122	0.144	–	0.72	–
$\alpha = -14.1$	N1	1	2 773	0.220	0.073	0.16	1,4
	N2	2	2 773	0.270	0.090	0.22	1,6
	N3	3	2 773	0.400	0.133	0.45	2,11
	N4	4	2 773	0.480	0.160	0.68	3,13
	N5	5	2 773	0.550	0.183	0.94	3,16
	N6	6	2 773	0.610	0.203	1.24	3,19
	C1	7	2 773	0.700	0.238	1.88	4,21
	C2	8	2 773	0.950	0.322	5.96	6,21
	C3	9	2 773	1.350	0.458	10.41	8,21
	C4	10	2 773	1.750	0.594	28.64	11,21
	C5	11	2 773	2.250	0.763	76.31	14,21
	C6	12	85 931	2.550	0.865	124.33	16,21

where a_0 is 1 122 (McLaren, 1966), D_0 is embryonic duration at 14.5 °C, and D is the duration of any stage N1-C5 at 14.5 °C. The duration of adult life was taken to be 80 d at 16 °C (Marshall and Orr, 1952). The constant a for adults was found from Eq. (4) at 16 °C.

Fecundity

Daily egg production per adult female, E (t), was also related to temperature through Belehradek's function. *Pseudocalanus* sp. fecundity was described by (Davis, 1984 b):

$$E(t) = 0.00641 \cdot (T + 13.87)^{2.05}. \qquad (5)$$

Egg production in *Paracalanus parvus* was found from Checkley's (1980 a) equation:

$$E(t) = 115 \cdot L^3 \cdot [21/(T + 3.0)]^{-2.25}, \qquad (6)$$

where L is prosome length of adult females, 0.77 mm Checkley, 1980 a). Fecundity in *Calanus finmarchicus* was computed from data of Marshall and Orr (1952) by:

$$E(t) = (\text{total eggs produced per female lifetime}) / (\text{length of reproductive period})$$

$$E(t) = [600 \text{ eggs female}^{-1}] / [85\,931\,(T + 14.1)^{-2.05}]. \qquad (7)$$

These estimates of egg production for *C. finmarchicus* are time-averaged for the population as a whole (laying and nonlaying) and therefore are much lower than would be expected for an individual female during discrete bursts of reproductive activity (see Marshall and Orr, 1952, 1955).

Mortality

Mortality was assumed to occur from three component sources: (1) chaetognath predation, size selective, (2) ctenophore predation, non-selective, and (3) carnivorous copepod predation occurring on nauplii. Mortality from each predator was represented as the product of predator abundance (forcing function) and consumption rate (number copepods eaten predator^{-1} d^{-1}), which was assumed proportional to copepod abundance. In addition, consumption rates were related to temperature through a Q_{10} function with $Q_{10}=2$ (Kremer and Nixon, 1978). The resultant mortality equation is:

$$\mathrm{Mort}_i(t) = \mathrm{K1}\cdot\mathrm{Chaet}_i(t) + 2^{T/10}\cdot[\mathrm{K2}\cdot\mathrm{Cten}(t) + \mathrm{K3}\cdot\mathrm{Cent}(t)], \tag{8}$$

where $\mathrm{Mort}_i(t)$ is the fraction of the total number, N_i, of copepods in stage i which are preyed on during the time interval (1 d) (see Davis, 1984b, for equations describing population dynamics); T is temperature (°C); K1, K2, and K3 are coefficients of mortality for chaetognath, ctenophore, and *Centropages* spp. predation, respectively in units of predator^{-1} d^{-1}; Cten (t) and Cent (t) are forcing functions describing seasonal cycles in abundance (#/m^3) of ctenophores, and *Centropages* spp., respectively; and $\mathrm{Chaet}_i(t)$ is a forcing function (derived below) describing size selective chaetognath predation on copepod stage i. The predation coefficients K1, K2, K3 were adjusted so that the field data of *Pseudocalanus* sp. were simulated. These same values of K1, K2, and K3 were then used in simulations of the other species. Consumption rates by predators were determined from the values of these mortality coefficients (as described below), and compared to current published values.

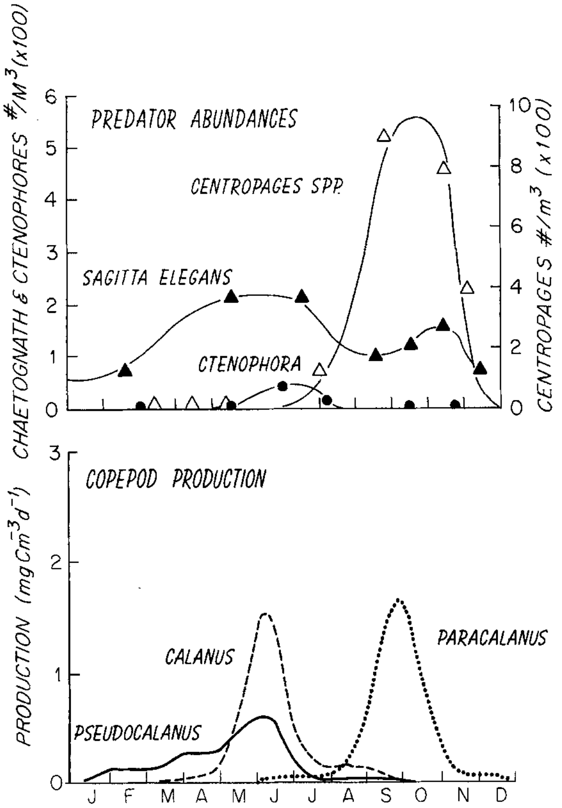

Fig. 1. (Top) Model forcing functions of predator abundances approximated from field data. Closed triangles = Chaetognatha, open triangles = *Centropages* spp. (both from fine mesh data), closed circles = Ctenophora (Sherman, 1979). (Bottom) Seasonal production curves for *Pseudocalanus* sp. (solid line); *Calanus finmarchicus* (dashed line); and *Paracalanus parvus* (dotted line) generated during model simulations

Predator abundance. Field data of predator abundances were approximated piece-wise with the logistic equation to obtain seasonal abundance curves for each predator (Fig. 1). Use of the logistic equation provides a more reasonable first approximation to actual seasonal curves than joining data points by straight lines. Data for chaetognaths and *Centropages* spp. abundances were obtained from fine mesh (0.165 mm) samples (Davis, 1982, in press), while ctenophore abundance was taken from Sherman (1979). The seasonal curves for ctenophores and *Centropages* spp. were used directly as Cten (t) and Cent (t), respectively, while the curve for chaetognaths was combined with size selective predation to give $\mathrm{Chaet}_i(t)$.

Chaetognath predation. The forcing function used to describe size-selective chaetognath predation on copepod stage i, $\mathrm{Chaet}_i(t)$, is:

$$\mathrm{Chaet}_i(t) = \sum_{j=a_i}^{b_i}\left[C_j(t)\cdot I_j\cdot 2^{(T/10)}\cdot B_i\Big/\sum_{n=c_j}^{d_j}B_n\right] \tag{9}$$

where $C_j(t)$ is abundance of chaetognath size class j in number m^{-3}, I_j is the normalized size-dependent ingestion rate for chaetognath size class j, T is temperature (°C), B_i is biomass of copepod stage i (mg C m^{-3}), a_i and b_i are lower and upper size classes, respectively, of chaetognaths preying on copepod stage i, and c_j and d_j are lower and upper life stages, respectively, of copepod preyed on by chaetognath size class j. This last biomass ratio term is used to impart "relative" biomass dependence on the stage specific mortality rate, (i.e. the greater the relative biomass of stage i, the greater Mort_i will be). The parameters in Eq. (9) were derived as follows.

To find the daily abundance of each chaetognath size class, $C_j(t)$, size-frequency distributions for *Sagitta elegans* were determined from Georges Bank winter (Dec.), spring (Feb., May), summer (July) and fall (Sept.) samples (Fig. 2; Davis, 1982). Measurements (2 to 5 samples per month) of total body length (excluding tail fin) were made on 30 to 200 chaetognaths per sample. These size frequency distributions were entered into the model according to season (Fig. 2) so that the absolute abundance of any one size class j, $C_j(t)$, could be calculated from the product of its frequency and total chaetognath abundance (Fig. 1).

Normalized size-dependent ingestion rates by *Sagitta elegans* size classes, I_j, were approximated from Reeve's

(1980) data for *S. hispida* at 21 °C. Although absolute ingestion between the two species may differ, the relative ingestion rates among size classes was assumed to be the same for the two species. The ingestion equation is:

$$I_j = 1.348 \cdot CHW_j^{0.285}, \tag{10}$$

where CHW_j is mean carbon weight per individual of chaetognath size class j and was calculated from Sameoto's (1971) length/dry weight regression for *S. elegans* and a carbon/dry weight ratio of 0.39 (Reeve, 1980).

Biomass of copepod stage i, B_i, was found from the product of abundance and mean individual body weight at stage i, w_i. Body weights of *Pseudocalanus* sp. (C1–C6), *Paracalanus parvus* (C4–C6), and *Calanus finmarchicus* (N4–C2) were obtained from a regression of freeze-dried weight on prosome length for *Pseudocalanus* sp. copepodids (Fig. 3, Table 1). Prosome length of 100 to 300 formalin preserved copepodids in each of stages C1–C6 was measured and each stage grouped, freeze-dried, and weighed. Weights of larger stages were found from the regression of Robertson (1968). Weights of all stages smaller than 0.42 mm were found from the power curve connecting length/weight data for *Pseudocalanus* sp. C1 (Fig. 3) and *P. parvus* egg (Checkley, 1980 a):

$$W = 4.69\,L^{1.79}$$

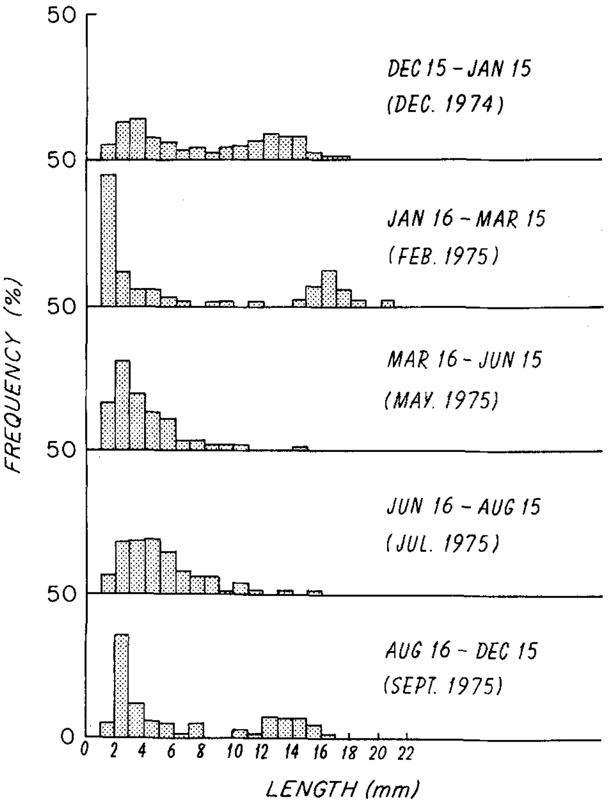

Fig. 2. *Sagitta elegans*. Seasonal shifts in size-frequency distribution of Georges Bank population. Distributions were used in the model according to the dates shown. Distributions were found from Georges Bank samples taken on dates shown in parentheses

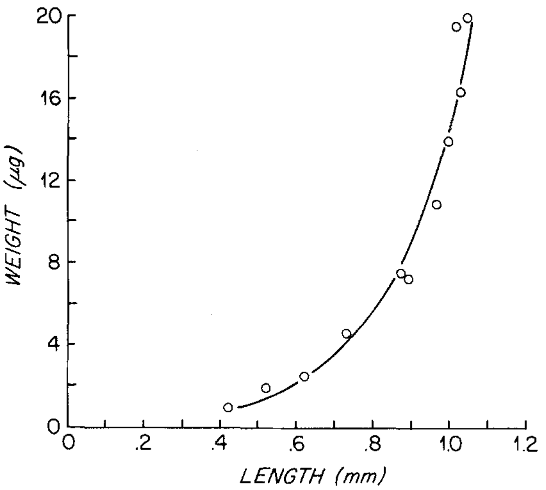

Fig. 3. *Pseudocalanus* sp. Length-weight regression for Georges Bank population. Freeze-dried weights and prosome lengths are used. Exponential equation fit to data: $W = 0.15^{4.612}$; ($r^2 = 0.99$)

Mean copepod size eaten by chaetognath size class j was determined from a regression of prey body width on *Sagitta elegans* head width (Pearre, 1980):

$$H_j = 0.494 \cdot P_j^{0.756}, \tag{11}$$

where H_j is mean prey body width (mm), and P_j is mean *S. elegans* head width (mm) in size class j. *S. elegans* head width/body length ratio used was 0.0517 (Pearre, 1980). Ranges of prey size eaten by *S. elegans*, size j, were approximated from the scatter about the regression curve of Pearre (1980) to be:

$$0.43\,H_j \leqq H_j \leqq 1.42\,H_j\,. \tag{12}$$

Body lengths and widths were measured for each *Pseudocalanus* sp. life stage. The length/width ratio obtained was used together with length measurements from Ogilvie (1953) and Conway and Minton (1975) to find width at stage estimates for *Paracalanus parvus* and *Calanus finmarchicus*. The range of copepod life stages eaten by chaetognath size class j, c_j to d_j, were found from Eq. (12) and the width at stage data for each copepod species (Tables 1, 2). These life stages were examined under the microscope together with the associated size-classes of *S. elegans* to check the plausibility of the computed limits.

Predatory consumption rates

Relative ingestion rates per predator (percent body weight consumed) were calculated daily during model simulations by the following equations:

For chaetognaths:

$$CHI_j = [(\sum_{i=c_j}^{d_j}(C_j \cdot I_j \cdot 2^{T/10} \cdot B_i/\sum_{n=c_j}^{d_j} B_n) \cdot K1 \cdot B_i)/ (C_j \cdot CHW_j)] \cdot 100, \tag{13}$$

where CHI_j is percent body weight ingested per day by chaetognaths size j.

For ctenophores:

$$CTI = [K2 \cdot 2^{T/10} \cdot CB/CTW] \cdot 100$$
$$Cten\,(t) > 0. \tag{14}$$

Table 2. Range of copepod life stages eaten by the different size classes of chaetognaths. Also shown is the body weight at each chaetognath size class and maximum % body weight consumed per day of each copepod species over the period of model simulation

Sagitta length class (mm)	*Sagitta* weight (μgC)	*Calanus* cj,dj	*Paracalanus* cj,dj	*Pseudocalanus* cj,dj	Maximum % body wt consumed per day per chaetognath of:		
					Calanus	*Pseudocalanus*	*Paracalanus*
1– 2	0.98	N1,N2	N1,C1	N1,N3	64	442	51
2– 3	3.30	N1,N3	N3,C3	N1,C2	25	100	26
3– 4	7.32	N1,N6	N4,C4	N1,C3	13	47	15
4– 5	13.3	N1,C1	N4,C6	N1,C4	8	35	10
5– 6	21.3	N2,C1	N5,C6	N2,C6	5	33	8
6– 7	31.6	N2,C2	C1,C6	N4,C6	4	27	10
7– 8	44.4	N3,C2	C2,C6	N4,C6	3	22	22
8– 9	59.7	N3,C3	C2,C6	N5,C6	3	10	18
9–10	77.7	N3,C3	C3,C6	N5,C6	2	8	15
10–11	98.4	N3,C3	C3,C6	C2,C6	2	14	15
11–12	122	N3,C4	C4,C6	C2,C6	2	13	11
12–13	148	N4,C4	C4,C6	C2,C6	1	11	1
13–14	178	N4,C4	C4,C6	C2,C6	3	10	9
14–15	211	N5,C5	C4,C6	C3,C6	1	8	9
15–16	247	N5,C5	C5,C6	C3,C6	2	8	7
16–17	286	N5,C6	C5,C6	C3,C6	1	8	1
17–18	329	N6,C6	C5,C6	C3,C6	1	1	1
18–19	376	N6,C6	C5,C6	C3,C6	1	1	1
19–20	425	N6,C6	C6,C6	C4,C6	1	1	1
20–21	479	C1,C6	C6,C6	C4,C6	1	1	1
21–22	535	C1,C6	C6,C6	C4,C6	1	1	1

For *Centropages* spp.:

$$\mathrm{CEI} = [\mathrm{K3} \cdot 2^{T/10} \cdot \mathrm{CB_n}/\mathrm{CEW}] \cdot 100$$
$$\mathrm{Cent}\,(t) > 0, \qquad (15)$$

where CTI is percent body weight consumed per day per ctenophore, CTW is carbon weight per individual ctenophore (estimated at 509 μg C for 12-mm *Pleurobrachia* sp., cf. Reeve, 1980), CB is total copepod biomass, $\mathrm{CB_n}$ is total naupliar biomass, CEI is percent body weight consumed per day per *Centropages* spp., and CEW is carbon weight per individual *Centropages* spp. (taken as 6.9 μg C for C4–C6).

Copepod production

Daily production estimates of the copepod populations were computed during model simulations from:

$$P = \sum_{i=1}^{12} (w_i - w_{i-1}) \cdot N_{i,0}(t) + w_0 \cdot N_{0,0}(t), \qquad (16)$$

where $N_{i,0}(t)$ is the number of individuals (m^{-3}) molted to stage i over the time interval, and $N_{0,0}(t)$ is the number of eggs (m^{-3}) produced over the time interval (see Davis, 1984b).

Initial conditions and model execution

The population dynamics of each copepod species was simulated in separate model runs. The model operated on a time step of one day during which temperature-dependent fecundity and molting probabilities were calculated, stage-specific mortalities were computed, and population dynamics were executed (Fig. 4). Starting dates and initial concentrations of each species were taken from fine mesh field data (Davis, 1982). *Pseudocalanus* sp. was simulated first, at an initial concentration of 100 adult females per m^3 on December 15 (Davis, 1984b). Predation coefficients, K1, K2, and K3, were chosen so that the simulated seasonal cycle fit (by eye) the field data for this species. The same values of K1, K2, and K3 were then used in simulations of *Calanus finmarchicus* and *Paracalanus parvus*, which were started at a concentration of 100 adult females per m^3 on March 15 and May 15, respectively (Davis, 1982). The seasonal temperature cycle was approximated as a sine wave fit to field data (Davis, 1984b).

Results

The model simulations indicate that predators, at observed concentrations, can control copepod population growth on Georges Bank at consumption rates which are low compared with published values. In addition, the combined annual secondary production by the small copepods *Pseudocalanus* sp. and *Paracalanus parvus* was over three times that of the larger *Calanus finmarchicus*, with *P. parvus* contributing the bulk of total production.

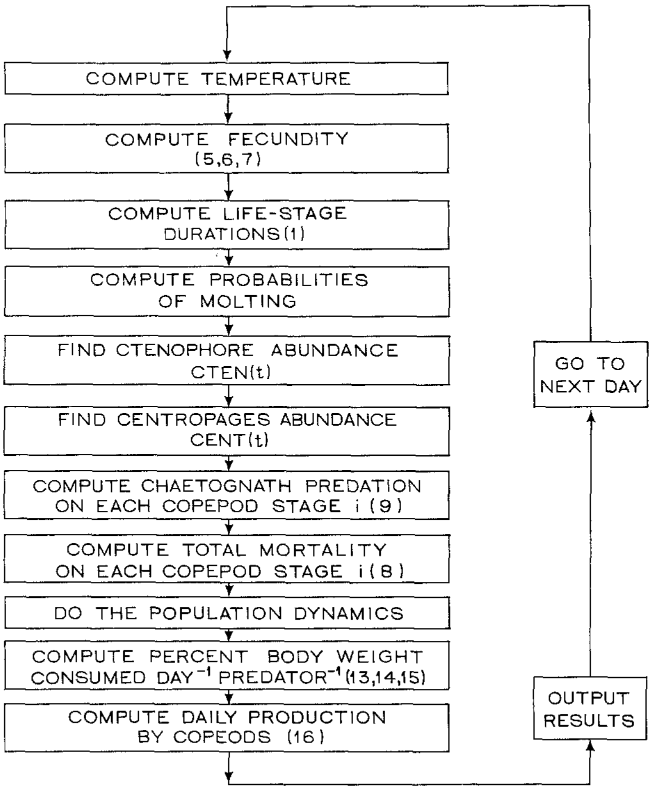

Fig. 4. Schematic of population model used in analysis of copepod seasonal cycles. Numbers in parentheses correspond to equations given in text. Temperature and population dynamics were calculated as in Davis (1984b)

Values of the predation constants, K1, K2, and K3, which gave the best fit to the observed seasonal cycle of *Pseudocalanus* sp. were: $K1=0.0095$, $K2=0.03$ and $K3=0.3$. Using these values the model output matched the *Pseudocalanus* sp. field data closely (Fig. 5). The large abundance peak in early June was preceded by two smaller peaks in January and March, with these corresponding to earlier cohorts. Given the variation in the field data it was not possible to distinguish the smaller peaks. The model shows, however, that four generations of *Pseudocalanus* sp. were produced between December 15 and August 15.

Using the same predation constants found for *Pseudocalanus* sp., the observed *Paracalanus parvus* and *Calanus finmarchicus* seasonal abundance cycles were also simulated closely (Fig. 5). *P. parvus* produced six generations between July 15 and December 15, while *C. finmarchicus* produced only one between March 15 and August 15.

Computed predatory consumption rates (expressed as % body weight consumed per predator per day) were low in comparison with published values (Tables 2, 3). Adult *Sagitta elegans* consumed a maximum of 8% of its body weight per day compared with field determined rates of 19% (Reeve, 1980). Ctenophores (*Pleurobrachia* sp. body weight used) consumed less than 10% whereas 20% is a conservative literature estimate (Reeve, 1980). Although published estimates of *Centropages* spp. consumption rates are lacking, the computed rates were low in comparison with the range of consumption rates found among other copepods (Table 3).

The annual cycle in carbon production was dominated by *Paracalanus parvus* (Fig. 1). Total annual production by *P. parvus* (85.9 mg C m^{-3}) was higher than that of either *Pseudocalanus* sp. (52.0 mg C m^{-3}) or *Calanus finmarchicus* (76.2 mg C m^{-3}). The daily production curve for *Pseudocalanus* sp. peaked near 0.6 mg C m^{-3} d^{-1} in early June while that for *P. parvus* attained a much larger daily

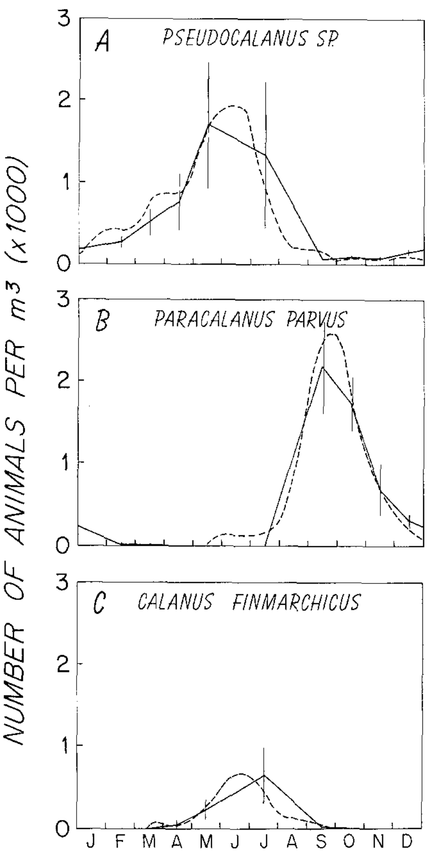

Fig. 5. Model simulations (dashed lines) fitted to observed seasonal cycles (solid lines) (from Davis, 1982) of three copepod species for estimation of predatory consumption rates necessary to control the copepod populations

Table 3. Maximum percent of body weight consumed per day by predators over the period of model simulation. Percentages calculated on carbon basis. Mean individual body weights of 509 μgC for *Pleurobrachia* sp. and 6.9 μgC for *Centropages* spp. were used. Weights and size-specific consumption rates by chaetognaths are given in Table 2

	Calanus	*Pseudocalanus*	*Paracalanus*	Literature
Sagitta elegans	2	8	7	19[a]
Pleurobrachia sp.	9	1	1	20[a]
Centropages spp.	2	1	21	75–148[b,c,d]

[a] Reeve, 1980
[b] Petipa, 1966 *Acartia* spp. (75%)
[c] Mullin, 1979 *Tortanus discaudatus* (120%)
[d] Paffenhofer and Harris, 1976 *Pseudocalanus* sp. (148%)

maximum near 1.8 mg C m^{-3} d^{-1} in September. Daily production by *C. finmarchicus* reached a peak at 1.6 mg C m^{-3} d^{-1} in June.

Discussion

Factors affecting copepod population cycles

In determining processes controlling seasonal abundance cycles of the dominant species, the model of copepod population dynamics presented here served as a basic and realistic method of analysis. In the model, Belehradek's equation relating fecundity and development rate to temperature has been shown to describe accurately these processes, assuming that food is nonlimiting (Corkett and McLaren, 1978; Checkley, 1980a). Evidence that this is the case on Georges Bank comes from many sources. O'Reilly *et al.* (1980, in press) found that the standing stock of phytoplankton on Georges Bank always remains higher than in adjacent water masses. Over their entire survey period (1976–1982), phytoplankton standing stock never dropped to the fecundity/growth limiting levels reported for *Paracalanus parvus* (Checkley, 1980a, b; Davis, 1984a) or *Pseudocalanus* sp. (Paffenhöfer and Harris, 1976; Corkett and McLaren, 1978; Davis, 1984a). Furthermore, at the times of year when population growth rates are inhibited (June/July for *Pseudocalanus* sp. and October/November for *P. parvus*, Fig. 5), phytoplankton levels on Georges Bank are still high ($>2.0\,\mu g$ Chl *a* l^{-1}; O'Reilly *et al.*, 1980, in press). In addition, Cohen *et al.* (1982) measured high primary production rates throughout the year on Georges Bank. Thus, it is apparent that Georges Bank, unlike surrounding waters, maintains a level of phytoplankton standing crop which is unlikely to limit growth and reproduction in *Pseudocalanus* sp. or *P. parvus*.

This being true, growth and reproduction must occur at physiologically determined temperature-dependent rates as has been suggested by McLaren (1978). Laboratory experiments with *Pseudocalanus* sp. have shown that reproduction and development rates are related to temperature by Belehradek's equations within the temperature range on Georges Bank (4° to 16 °C; Corkett and Zillioux, 1975; Corkett and McLaren, 1978). Temperature is never so high (or low) as to affect these processes abnormally (Davis, 1982). Such is not the case with *Paracalanus parvus*, which has considerable embryonic mortality below 10 °C (Checkley, 1980a). The upper temperature limit on Georges Bank is not critical for *P. parvus* either, however, as it is able to reproduce and grow normally at much higher temperatures, i.e. 18° and 20 °C (Checkley, 1980b; Hoffman *et al.*, 1981).

When population growth rates of *Paracalanus parvus* and *Pseudocalanus* sp. began to decline, just prior to reaching peak abundance (Fig. 5), neither food nor temperature was likely to have been limiting to normal growth and reproduction. Therefore, the reduction in these populations must have been due either to behavioral changes (changes in reproduction, development rate, migration in response to changing temperature, light, water stratification) or to changes in predation rate. The impact of predation components on population growth was investigated using the population model with fecundity and development rate described by Belehradek's temperature functions.

Predators

The three major predators of copepods on Georges Bank, from fine mesh (0.165 mm) samples, are chaetognaths, ctenophores, and the omnivorous copepod *Centropages* spp. (Davis, 1982). Larval fish predation was assumed to make a negligible contribution to total mortality. Published consumption rates for larval fish (Laurence, 1977) are similar to those for chaetognaths (Reeve, 1980), but larval fish abundance in the fine mesh samples (Davis, 1982) was always at least an order of magnitude lower than chaetognath abundance. Other predators were even less abundant. The impact of adult and juvenile fish predation could not be investigated since these were not sampled and there are no data available on their seasonal abundance cycles on Georges Bank. An argument against the control of the copepod populations by fish predation is that the numerical response (Holling, 1959) of a fish population is not rapid enough to control copepod population growth. Furthermore, it is unlikely that a functional response by fish predators to copepod increases is responsible since migratory circuits of fish are not precisely linked to production cycles (Cushing, 1975). On the other hand, the numerical responses of chaetognaths, ctenophores, and *Centropages* spp. are rapid enough so that control of copepod populations by the basic Lotka-Volterra relationship is entirely possible.

Predatory control of copepod seasonal cycles

It is unlikely that the summer decline of the *Pseudocalanus* sp. population was due to chaetognath predation alone because the abundance peaks of the two species coincide (Figs. 1, 5). This was also found by Riley and Bumpus (1946). A lag time of predator abundance would be expected if *Sagitta elegans* predation were responsible for the decline in *Pseudocalanus* sp. This was found to be the case in the model simulation of *Pseudocalanus* sp. With a fixed forcing function approximating observed *S. elegans* abundance, the *Pseudocalanus* sp. decline could not be effected by chaetognath predation alone. Sherman (1979) found that gelatinous zooplankton (assumed to be primarily ctenophores) on Georges Bank reached peak abundance (45.7 m^{-3}) in July and August and were not present in samples at other times of the year. (These values were based on net tows and are probably an underestimate of total ctenophore abundance.) In addition, the omnivorous copepods *Centropages typicus* and *C. hamatus* are present in large numbers from September to mid-December (Fig. 1) and prey on nauplii and free-floating eggs of other copepod species. Eggs of *Pseudocalanus* sp. are attached in sacs to the adult females and are unlikely to be exposed to *Centropages* spp. predation. In the model, the *Pseudocalanus* sp. population was brought down to observed August levels with the addition of ctenophore predation and was held to low levels through autumn and early winter by *Centropages* spp. predation on the nauplii (Figs. 1, 5).

Paracalanus parvus was introduced into the model in May when temperatures become favorable for its reproduction and growth (> 10 °C). The population was held at low levels through the summer by chaetognath and ctenophore predation (Figs. 1, 5). In August this predation subsided enough to permit *P. parvus* to increase its numbers rapidly. *P. parvus* can reproduce and grow much faster than *Pseudocalanus* sp., and had no trouble attaining high numbers by mid-September in spite of high naupliar (and egg) mortality. In the model, *P. parvus* declines in the fall as a result of *Centropages* spp. predation, with *Centropages* spp. peaking later in the season (Davis, 1982).

Calanus finmarchicus was input into the model in March at observed concentrations. The population at this point is primarily adults newly molted from overwintering C5 copepodids. Bigelow (1926) suggested that this species overwinters at depth in the Gulf of Maine as copepodid C5. In the spring, the C5s rise to the surface and molt to adult. Given the general circulation of the region, the new adults would be carried onto Georges Bank. Although the estimations of fecundity and growth in *C. finmarchicus* are less reliable than for the other species, and *C. finmarchicus* may become food limited even at high phytoplankton levels (Marshall and Orr, 1952), the model simulation agrees quite well with observed data for this species (Fig. 5). Again, the mortality coefficients used were the same as determined for *Pseudocalanus* sp.

Relative ingestion rates (% body weight consumed d^{-1}) for all three predators, calculated from their corresponding mortality rate constants, were low in comparison to published rates (Table 3), indicating that predatory control of the copepod populations can occur even at very modest consumption rates. These findings are in apparent contrast to the well-known model of Riley (1947) in which zooplankton biomass was dependent on phytoplankton concentration as well as on predation. This apparent discrepancy can be reconciled by considering two points: (1) The seasonal cycle of total zooplankton biomass, which Riley's model explained, was likely comprised almost entirely of the large copepod *Calanus finmarchicus* since this copepod dominates the seasonal cycle in biomass (Davis, 1982, in press). Furthermore, since smaller copepods were greatly undersampled by the coarse mesh (0.333 mm) net used by Riley, the relative biomass of *C. finmarchicus* would have appeared even larger. (2) *C. finmarchicus* may become food-limited on Georges Bank. As indicated earlier, laboratory studies have shown that *C. finmarchicus* requires more food for development and reproduction than do the smaller copepods. Thus, the seasonal cycle of total zooplankton biomass (i.e. *C. finmarchicus* biomass) may very well be influenced by phytoplankton concentration. The present model results indicate, however, that *C. finmarchicus* population growth even with nonlimiting food supply can be effectively controlled by predation. Thus, both predation and food availability can potentially limit *C. finmarchicus* population growth as suggested by Riley's (1947) model. On the other hand, population growth of *Pseudocalanus* sp. and *Paracalanus parvus,* unaffected by food on Georges Bank, may be controlled largely by predation as the present results indicate.

These small copepods, which contribute little in terms of biomass, are shown here to be important secondary producers on Georges Bank. Of the three species studied, *Paracalanus parvus* was found to be the major producer of copepod biomass. In the model, *Calanus finmarchicus* produced its annual biomass in the course of a single generation while it took *Pseudocalanus* sp. and *P. parvus* three and six generations per year, respectively. Shorter generation times of *Pseudocalanus* sp. and *P. parvus* compensate, in terms of secondary production, for their smaller body sizes (and lower biomass) so that the combined annual production of these small species is nearly twice that of *C. finmarchicus.* Production by other small species, *Centropages typicus* and *C. hamatus* (not estimated here because of lack of sufficient life-history information), may contribute somewhat more to total production. Thus, the combined production by small copepods is the major component of total copepod production on Georges Bank even though these species are not seen in the annual cycle of total zooplankton biomass as described by Riley (1947).

Fine mesh sample analysis (Davis, 1982, in press) has revealed that the smaller species of copepods on Georges Bank, especially *Paracalanus parvus,* are more abundant than previously thought. Production estimates presented here show that these small copepods contribute the bulk of total copepod production on Georges Bank. Even at conservative consumption rates, predators appear to be able to control these copepod populations.

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