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Predation by gelatinous zooplankton and resource limitation as potential controls of *Acartia tonsa* copepod populations in Chesapeake Bay

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Abstract

Gelatinous zooplankton are conspicuous predators during summer in Chesapeake Bay. Inverse correlations of the abundances of gelatinous predators and their zooplankton prey have led to speculation that these predators may control their prey populations. We measured predation on copepods by hydromedusae, scyphomedusae, and ctenophores in the mesohaline region of the bay in May–October 1987 and 1988. We simultaneously assessed the possibility of food limitation in *Acartia tonsa* by measuring its phyto- and microzooplankton food resources and rates of adult female egg production. We conclude that *A. tonsa* populations are not limited by gelatinous zooplankton predation and rarely by food. Other predators (e.g. fish, adult copepods) and environmental limitations (e.g. temperature, hypoxic bottom waters) probably affect *A. tonsa* abundances in this region.

Variations in copepod populations are caused by physical conditions in the environment, food abundance and nutritional quality, and predation intensity. The importance of predation on the structure of pelagic communities has been well documented in lake ecosystems (e.g. Brooks and Dodson 1965; Carpenter and Kitchell 1988). The effects of predation on complex estuarine and marine communities have been studied much less than they have in lakes.

Predator control of estuarine copepod populations has been implicated in some earlier studies. For example, predation rates of *Acartia tonsa* copepods and *Mnemiopsis leidyi* ctenophores frequently exceeded the abilities of two harpacticoid and cyclopoid copepod species to increase (Lonsdale 1981). Reduced abundances of copepods in a North Carolina estuary were associated with low temperatures and increased predation by mysids in winter and with increased abundances of planktivorous fish in summer (Fulton 1982).

Chesapeake Bay is well known for large populations of gelatinous zooplankton. In their recent modeling study of energy flows, Baird and Ulanowicz (1989) emphasized the potential importance of gelatinous predators there. Feigenbaum and Kelly (1984) showed inverse patterns of abundance that suggested control of ctenophore populations by *Chrysaora quinquecirrha,* resulting in increased copepods and reduced phytoplankton. However, these studies did not measure feeding rates of the gelatinous predators.

Several previous studies, in which predation rates were measured, concluded that the predation effects of gelatinous zooplankton (<10% d^{-1}) cannot reduce standing stocks of the crustacean zooplankton (Kremer 1979; Larson 1987; Purcell and Nemazie 1992 and references therein). Other studies indicate much higher predation (>20% d^{-1}) that suggests possible reduction of zooplankton standing stocks (Deason 1982; Matsakis and Conover 1991; Purcell 1992). None of these studies measured production rates of the prey populations.

The dominant copepod species in the mesohaline portion of Chesapeake Bay from April through October is *A. tonsa* (Brownlee and Jacobs 1987; Olson 1987). Egg production of *A. tonsa* is closely linked to its food supply (Dagg

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1977; Durbin et al. 1983) and depends on food quality (Kiørboe 1989) as well as quantity. Above a critical food concentration, copepod growth is constant (Kiørboe et al. 1985) and weight-specific growth rate of juveniles is equal to reproductive effort of adults (Berggreen et al. 1988). The ability of *A. tonsa* to feed on various food types (including phytoplankton, microzooplankton, and detritus) may enable it to maintain a high production rate under widely different food conditions (White and Roman 1992*a*). Here we use egg production rates to determine whether *A. tonsa* populations were limited by food in Chesapeake Bay.

In studies where food limitation of copepod growth has been rejected, predation has usually been invoked as the mechanism controlling populations (Landry 1978; Ohman 1985). In Dabob Bay, Ohman (1985) found that production of the copepod *Pseudocalanus* is not resource limited, suggesting that predation may control populations, In other studies it is less clear whether food limitation or predation is more important in controlling copepod population growth, since both forces seem to act in concert (Daan 1989; Kimmerer and McKinnon 1989).

A rigorous analysis of biological factors that potentially control copepod populations demands that the growth potential of the prey copepod populations be quantified. Here, we present a series of instantaneous rate and biomass measurements ("snapshots") of the combined impacts of gelatinous predators on copepod populations in Chesapeake Bay, together with food availability and estimated production of *A. tonsa* from April through October 1987 and 1988, in order to determine whether predation by gelatinous zooplankton or food limitation could have controlled copepod populations.

Materials and methods

Sampling dates and locations—We sampled during May through August on eight dates in 1987 and during May through October on 11 dates in 1988 at five stations on a transect across Chesapeake Bay (38°33′N, 76°22′–76°30′W; Sta. 5–Sta. 1). Bottom depths at each station were: Sta. 1, 5 m; Sta. 2, 10 m; Sta. 3, 12 m; Sta. 4, 20 m; Sta. 5, 5 m. Sampling began ~0630 hours and was completed by 1200 or 1300 hours. On selected dates, sampling took place at 6-h intervals during day and night at the deep station (Sta. 4).

Zooplankton densities and biomass—Copepods were collected with a submersible pump and 2.5-cm-diameter hose by pumping water (20–40 liters min^{-1}) from 1-m intervals above the pycnocline. The water was filtered through a 64-μm-mesh net on deck, and the samples preserved in 5% buffered Formalin. Copepod densities were determined by counting three 5-ml subsamples. Whole samples were counted for rare taxa. Adult copepods and later stage copepodites were identified to species. Copepod biomass (μg C) was determined with a computer image analysis system and a length-weight regression for each species and developmental stage (White and Roman 1992*b*).

Medusae and ctenophores were collected in a 1-m-diameter, 1.6-mm-mesh plankton net with flowmeter in double-oblique tows from the surface to the pycnocline (<11-m depth). These samples were drained in a colander and the water again filtered through a 200-μm sieve to retrieve small specimens. The species were separated gently by hand, and the volumes of each species were measured in a 250-ml or 1-liter graduated cylinder. These samples then were preserved in 5% Formalin and specimens counted in the laboratory. Numbers and sizes of ctenophores were determined by counting and measuring preserved tentacle bulbs (Purcell 1988).

Clearance rates of gelatinous predators eating copepods—At each station where *C. quinquecirrha* medusae were present, we collected them individually by dip net and immediately preserved them in 5% Formalin for identification of prey in the guts with a dissecting microscope. Digestion times (D) were calculated from temperatures of the mixed layer (T) and the number of copepods (adults + copepodites) in the guts (Cp) according to the equation $D = 10.86 - 0.31\ T + 0.001\ Cp$ ($r^2 = 0.53$; Purcell 1992).

Ingestion of copepods by *C. quinquecirrha* was calculated for each field sample according to the equation

$$I = Cp/D \times M \times 24\ \text{h}\ \text{d}^{-1}.$$

I is the number of copepods ingested $m^{-3}\ d^{-1}$, Cp the average number of copepods in medusae, D the digestion time in hours, and M the number of medusae m^{-3}. Ingestion rates

were converted to clearance rates (liters cleared m^{-3} d^{-1}) by dividing by the number of copepods $liter^{-1}$. Predation rates (μg copepod C removed m^{-3} d^{-1}, analogous units to carbon production) were estimated by multiplying I by the average carbon content per copepod which varied with time of collection (range, 0.59–1.0 μg $copepod^{-1}$).

Ingestion rates (copepods m^{-3} d^{-1}) of *Nemopsis bachei* were calculated from medusa densities and a regression of copepod densities (X) and feeding rates (Y, copepods $medusa^{-1}$ d^{-1}) measured in 1989 and 1990 by the gut content method as described above ($Y = 4.24X^{0.44}$, $r^2 = 0.72$; Purcell and Nemazie 1992). Ingestion rates were converted to clearance rates (liters m^{-3} d^{-1}) and then to predation rates (μg C m^{-3} d^{-1}), as above.

The clearance rates of *M. leidyi* were determined by first calculating ctenophore live wet weights (W) by counting and measuring the preserved ctenophore tentacle bulb lengths (B) in the above plankton tows and entering these into the equation $W = 0.81\ B^{1.913}$ ($r^2 = 0.98$; Purcell 1988). Then clearance rates were calculated from the wet weights according to the equations Clearance = $0.84\ W^{-0.53}$ at 5–10°C and Clearance = $0.113\ W^{-0.44}$ at 20–25°C (Kremer 1979). Clearance of all ctenophores in each sample was divided by the volume filtered by the net to determine total clearance m^{-3}. Predation rates (μg C m^{-3} d^{-1}) were estimated by multiplying clearance rates by the biomass of copepods in the water column (μg copepod C m^{-3}).

Potential foods for copepods and environmental data—Depth profiles of chlorophyll *a*, temperature, and dissolved oxygen were determined over 1-m intervals at each station with a pump-CTD-fluorometer system (Malone and Ducklow 1990). To convert in vivo fluorescence measurements to Chl *a*, we collected samples from surface and bottom waters on Whatman GF/F glass-fiber filters (0.8-μm pore size) and analyzed them for Chl *a* by fluorometer after acetone extraction (Parsons et al. 1984). Particulate organic C (POC) was determined by filtering pump water on precombusted GF/F filters that were then dried and measured in a Control Data 240 HA analyzer. Phytoplankton C (μg) was estimated from Chl *a* by multiplying values by 51, the slope of a regression of POC against Chl *a* (POC = 235 + 51 × Chl *a*, $n = 13$, $r^2 = 0.48$, SE = ±16; White and Roman 1992*a*). For this estimation, the y-intercept was assumed to equal nonphytoplankton C and was not included in the calculation of phytoplankton POC. Unfortunately, attempts to size fractionate chlorophyll with 10-μm screens proved unreliable compared with random counts of screened phytoplankton fixed with acid-Lugol's solution (T. C. Malone pers. comm.). Therefore, only data for whole chlorophyll (collected on GF/F filters) are reported here.

Whole-water samples were collected by Niskin bottle and preserved in 2% glutaraldehyde. Microzooplankton (oligotrich and tintinnid ciliates and heterotrophic dinoflagellates >10 μm) were enumerated from these samples in a Zeiss inverted microscope. Abundances were converted to biomass (μg C) by using taxon-specific geometric shapes and carbon-to-volume ratios (Lessard 1991).

Copepod egg production—Egg production experiments were carried out at the deep mid-bay Sta. 4 on many of the same cruises as the above predation estimates. Copepods used in the experiments were collected in a 200-μm-mesh, 0.5-m-diameter plankton net fitted with a closed codend towed obliquely through the surface mixed layer. *A. tonsa* adult females were identified under a stereoscopic microscope (dim light for nighttime incubations) and 3–4 animals gently picked by pipet into flow-through, polycarbonate egg production chambers pre-filled with 200-μm-screened surface water. Chambers were then placed in an incubator system containing flowing surface water (White and Roman 1992*a*) for two consecutive 12-h (night and day) or one 24-h incubation. Chambers containing only 200-μm-screened water were incubated along with treatment chambers to correct for eggs and small nauplii added with the water.

At the end of the experimental period, both copepods and eggs were washed into sample jars with filtered bay water and the samples preserved in 5% buffered Formalin. In the laboratory, adult females and eggs were measured and their C determined from length-carbon weight regressions (White and Roman 1992*a*). Carbon-specific daily egg production [EP = μg egg C (μg female C)$^{-1}$ d^{-1}] was determined by dividing the total egg C produced per chamber over a 24-h period by the total C of living

females in the chamber and averaging over three replicate chambers.

To determine whether egg production was limited by food during the study, we compared the measured production rates with potential egg production rates derived as a function of temperature using two separate functions. A polynomial model derived by White and Roman (1992*a*) was used above 20°C to account for the decrease in egg production found at high temperatures. The nonlinear Bělehrádek's equation modified from Uye (1981) was used for temperatures <20°C because it gives a better fit to egg production data at low temperatures. Under abundant food conditions, egg production of adult *A. tonsa* equals somatic growth of earlier stages (Berggreen et al. 1988). Therefore, the in situ production rate (*P*, μg C m^{-3} d^{-1}) of the copepod population (dominated by *A. tonsa* in Chesapeake Bay in summer) was estimated by multiplying *EP* (*G* = growth) by copepod biomass (*B*, μg copepod C m^{-3}) to give production.

Results

Zooplankton densities and biomass—Few gelatinous predators were present at the beginning of May (Figs. 1, 2). During the second and third weeks of May, both ctenophores and hydromedusae were present. Biomass in spring was low, but hydromedusae had the highest densities of any species with maxima of 10.5 and 11.2 m^{-3} in 1987 and 1988. Hydromedusae declined through June and July and were not present in August. In late May to early June, many small ctenophores were present. Biomass peaked in mid-August, and ctenophore biomass declined through October. Greatest densities and biomasses of ctenophores were in midbay stations. Scyphomedusae first appeared at flank Sta. 1 in June 1987. Their numbers and biomass increased through July and August in both years. Scyphomedusae were most abundant at flank Sta. 1 and 5. The general pattern for both years was high densities of small hydromedusae and ctenophores in spring and high biomasses of ctenophores and scyphomedusae in August.

Overall, the pattern of gelatinous zooplankton abundance was similar in 1987 and 1988 (Figs. 1, 2). Densities of hydromedusae were comparable in both years, but they persisted longer in 1987. Densities and biomasses of ctenophores were somewhat greater in 1988 (max, 8.4 m^{-3}, 90.0 ml m^{-3}) than in 1987 (max, 4.4 m^{-3}, 71.9 ml m^{-3}). In contrast, there were more scyphomedusae in 1987 (max, 2.4 m^{-3}, 21.6 ml m^{-3}) than in 1988 (max, 2.3 m^{-3}, 14.4 ml m^{-3}).

Copepod densities were low (<11 $liter^{-1}$) in surface waters in May and June and decreased during that period (Fig. 3). Their densities increased in July and August and were generally much higher than in May. Densities were more similar throughout spring and summer in 1988 than they were in 1987. The numbers of copepods were much greater in August 1987 (max, 92.5 $liter^{-1}$) than in 1988 (max, 43.3 $liter^{-1}$), but their densities had decreased by mid-October in 1988.

Clearance rates of gelatinous predators eating copepods—The seasonal pattern of copepod clearance by predators resembled the pattern of gelatinous zooplankton biomass. Clearance rates (liters m^{-3} d^{-1}) were very low in early to mid-May, but increased due to hydromedusae and ctenophores in late May to early June (Fig. 4). Ctenophores were the main predators in the midbay stations, but scyphomedusae were most important at the flank Sta. 1 and 5. Clearance peaked in mid-August in both years and was much greater in 1987 (total, 234 liters cleared m^{-3}) than in 1988 (70 liters cleared m^{-3}), even though copepod densities were greater in 1987 and predator volume (mostly ctenophores) was greater in 1988. The greatest clearance was by scyphomedusae in 1987.

Potential food for copepods—Chl *a* concentrations measured in surface waters were con-

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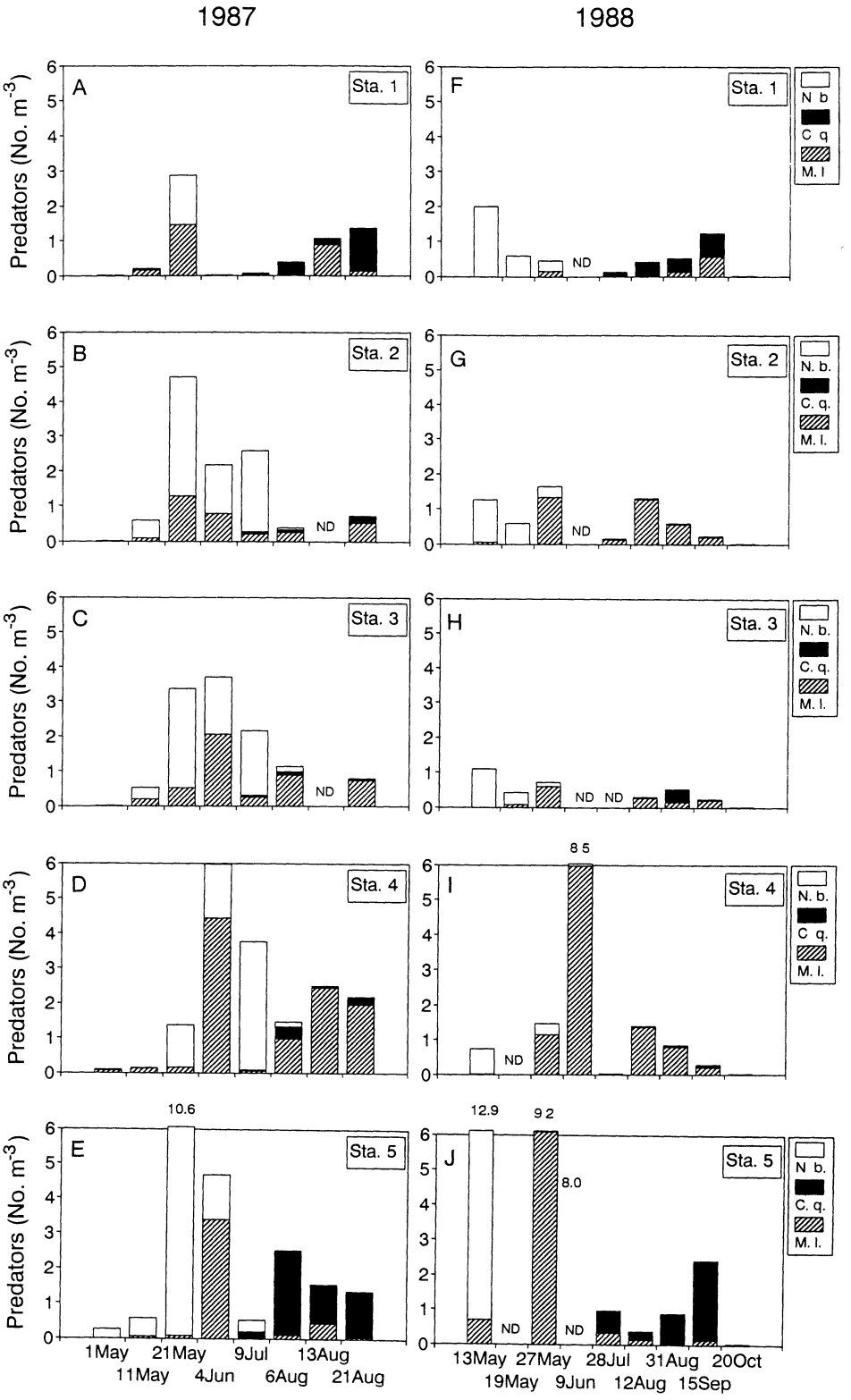
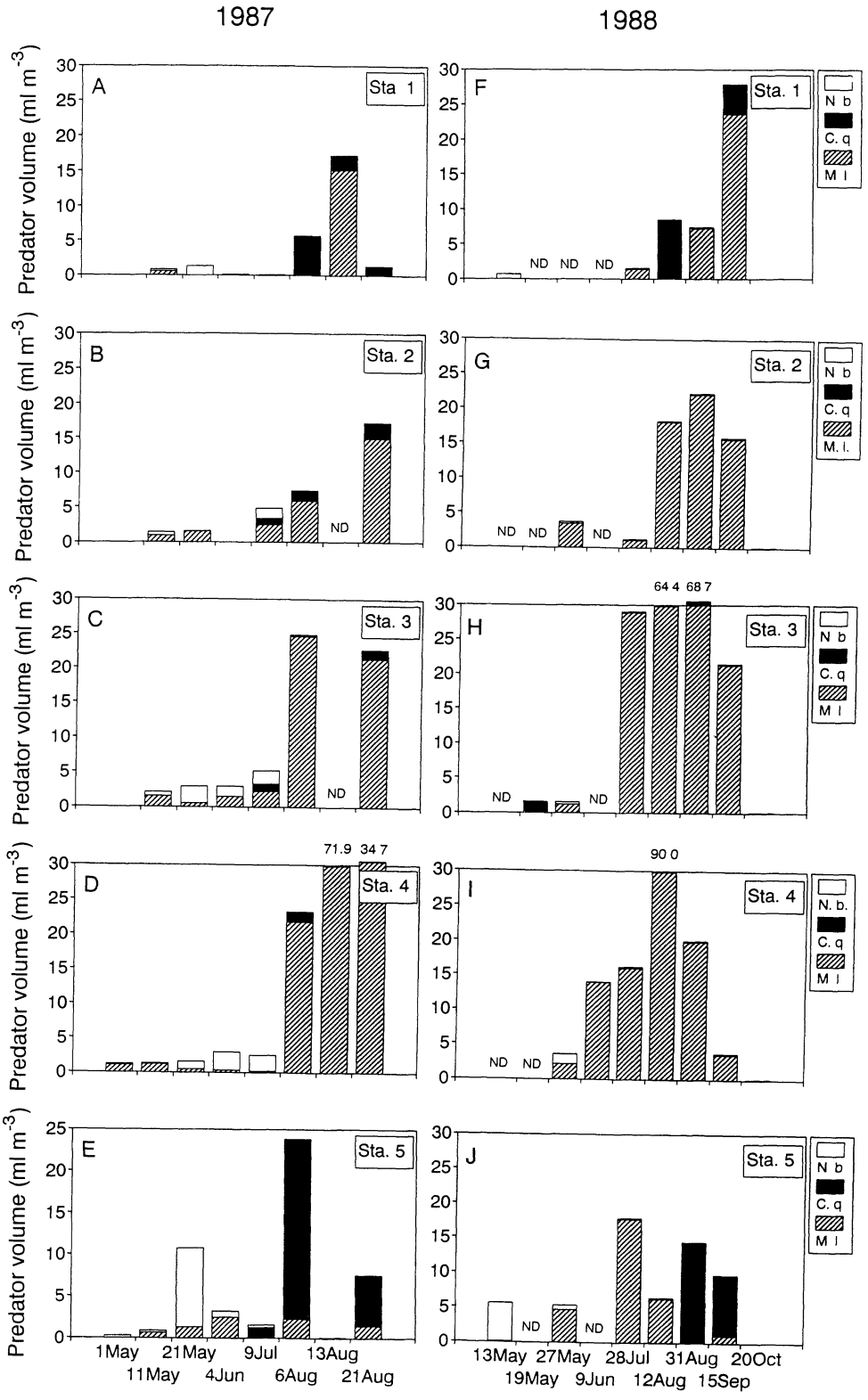
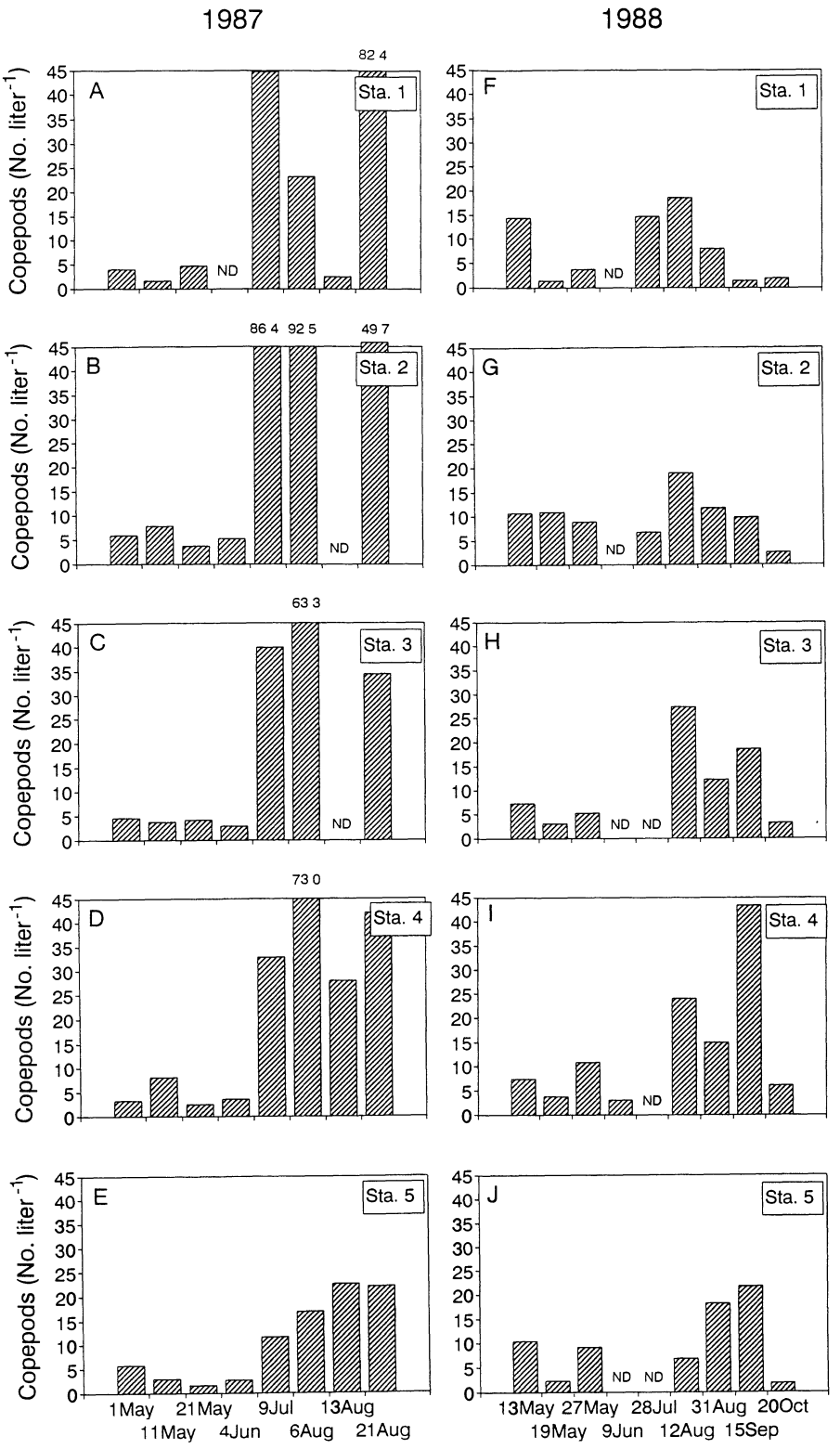
Fig. 1. Numbers of gelatinous zooplankton in surface waters on sampling dates in 1987 and 1988. N.b.—*Nemopsis bachei* hydromedusae, C.q.—*Chrysaora quinquecirrha* scyphomedusae, M.l.—*Mnemiopsis leidyi* ctenophores. Numbers above the bars are total numbers m^{-3}; numbers beside the bars refer to only one species. (ND—no data.)

Fig. 2. Live biomass of gelatinous zooplankton in surface waters on sampling dates in 1987 and 1988. Abbreviations and notations as in Fig. 1.

Fig. 3. Numbers of copepods (>200 μm) in surface waters on sampling dates in 1987 and 1988. Notations as in Fig. 1.


1987
1988
Predators (No. m-3)
A
Sta. 1
F
Sta. 1
N b
C q
M. l
B
Sta. 2
G
Sta. 2
N. b.
C. q.
M. l.
C
Sta. 3
H
Sta. 3
D
Sta. 4
I
Sta. 4
8 5
E
Sta. 5
10.6
J
Sta. 5
12.9
9 2
8.0
ND
1May 21May 9Jul 13Aug
11May 4Jun 6Aug 21Aug
13May 27May 28Jul 31Aug 20Oct
19May 9Jun 12Aug 15Sep


1987
1988
Predator volume (ml m-3)
A
Sta 1
B
Sta. 2
C
Sta. 3
D
Sta. 4
E
Sta. 5
F
Sta. 1
G
Sta. 2
H
Sta. 3
I
Sta. 4
J
Sta. 5
N b
C. q
M l
M. l.
N. b.
ND
71.9 34 7
64 4 68 7
90 0
1May 21May 9Jul 13Aug
11May 4Jun 6Aug 21Aug
13May 27May 28Jul 31Aug 20Oct
19May 9Jun 12Aug 15Sep


1987
1988
Copepods (No. liter^{-1})
A
Sta. 1
82 4
ND
F
Sta. 1
ND
B
Sta. 2
86 4
92 5
49 7
ND
G
Sta. 2
ND
C
Sta. 3
63 3
ND
H
Sta. 3
ND ND
D
Sta. 4
73 0
I
Sta. 4
ND
E
Sta. 5
J
Sta. 5
ND ND
1May 21May 9Jul 13Aug
11May 4Jun 6Aug 21Aug
13May 27May 28Jul 31Aug 20Oct
19May 9Jun 12Aug 15Sep

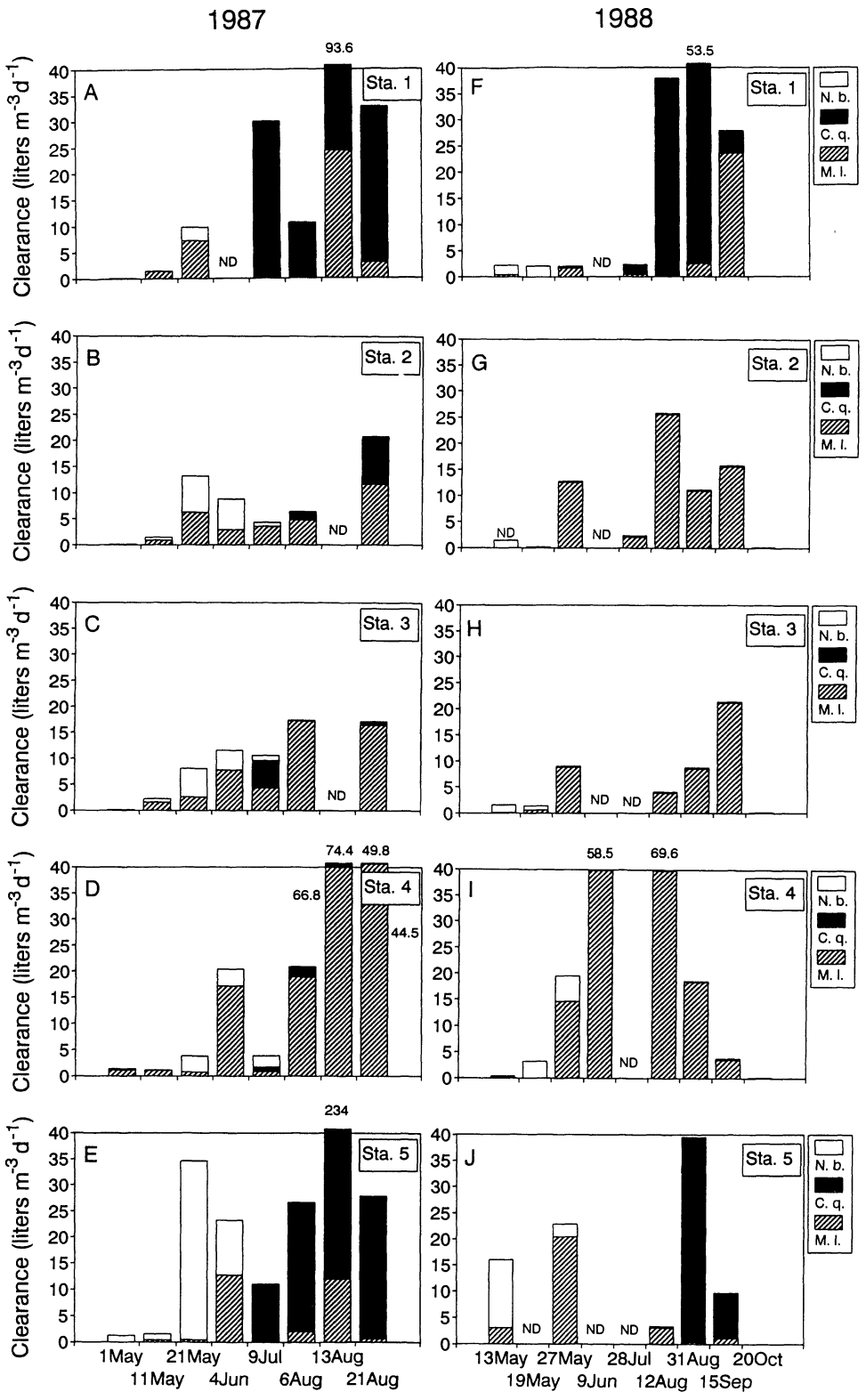

1987
1988
Clearance (liters m-3 d-1)
A
B
C
D
E
F
G
H
I
J
Sta. 1
Sta. 2
Sta. 3
Sta. 4
Sta. 5
N. b.
C. q.
M. l.
ND
93.6
53.5
74.4
49.8
66.8
44.5
58.5
69.6
234
1May 21May 9Jul 13Aug
11May 4Jun 6Aug 21Aug
13May 27May 28Jul 31Aug 20Oct
19May 9Jun 12Aug 15Sep

Table 1. Data collected in 1987 and 1988 at midbay Sta. 4 for temperature, weight-specific *Acartia tonsa* egg production [μg C (μg C)$^{-1}$ d^{-1}] both measured (EP_m) and predicted from temperature (EP_t), and the difference between them ($EP_m - EP_t$). Also shown are phytoplankton and microzooplankton C (μg C liter^{-1}) and their total.

	Temp. (°C)	Phyto. C	Microz C	Phyto + Microz C	EP_m	EP_t	$EP_m - EP_t$
1987							
1 May	12.5	1,095	—	—	—	0.11*	—
11 May	16.5	390	—	—	0.54	0.41*	0.13
21 May	17.2	1,533	—	—	—	0.50*	—
4 Jun	23.0	1,708	—	—	0.32	1.07†	−0.75‡
9 Jul	26.4	278	—	—	—	0.91†	—
6 Aug	27.5	194	—	—	—	0.78†	—
13 Aug	26.3	367	—	—	1.22	0.92†	0.30
20 Aug	27.3	198	—	—	0.39	0.81†	−0.42
1988							
13 May	15.7	725	49	774	0.30	0.32*	−0.03
19 May	17.8	855	90	945	0.73	0.59*	0.14
27 May	18.7	600	171	771	0.89	0.74*	0.15
9 Jun	20.2	1,140	237	1,377	0.93	0.94†	−0.01
28 Jul	26.6	385	104	489	0.51	0.89†	−0.38
12 Aug	28.6	490	132	622	0.60	0.62†	−0.02
31 Aug	25.9	250	65	315	1.03	0.96†	0.07
15 Sep	23.2	215	74	289	1.22	1.07†	0.15
20 Oct	16.1	260	33	293	0.37	0.36*	0.07

* Bělehrádek's equation modified from Uye (1981) used to predict egg production from temperature (below 20°C). $EP = 0.0000011(T - 0.5)^{4.623}$

† Polynomial equation from White and Roman (1992*a*) used to predict egg production from temperature (above 20°C): $EP = -7.29 + 0.72T - 0.015T^2$

‡ Significant difference between measured and predicted egg production (EP_t outside 95% confidence interval for EP_m, one-tailed t-test)

sistently >5.0 μg liter^{-1} and occasionally were much higher (>30 μg liter^{-1}; Fig. 5). The seasonal pattern of Chl *a* was similar for both 1987 and 1988; values were relatively high in early May, dropping some in mid- to late May, increasing to a peak in June and July, but remaining generally low throughout August (Fig. 5). The only consistent spatial pattern was elevated Chl *a* values in shallow water at Sta. 1 during August.

Particulate phytoplankton and microzooplankton C were estimated for Sta. 4 in midbay for the 1988 sampling season. Phytoplankton C was estimated from Chl *a* and therefore tracked the seasonal variation in Chl *a*, peaking in June (Figs. 5, 6A). In general, microzooplankton C at Sta. 4 was <25% of phytoplankton C (Fig. 6A, Table 1). Unlike phytoplankton biomass, which was relatively high throughout May at Sta. 4, microzooplankton biomass was low in early May and increased steadily until it peaked in June (Fig. 6A, Table 1). Phytoplankton and microzooplankton C were both relatively low from late summer to early fall.

Egg production and food limitation—Egg production rates measured for *A. tonsa* were between 30 and 120% of female C per day at Sta. 4 (Fig. 6B, Table 1). During 1988, egg production rates did not closely follow seasonal changes in phytoplankton or total C but did increase with microzooplankton C through May (Fig. 6A). Egg production of *A. tonsa* increased with temperature to a value near 27°C and then decreased at higher temperatures (Table 1). Egg production was significantly correlated with temperature and protozoan biomass but not with phytoplankton biomass or production (White and Roman 1992*a*).

Measured rates of egg production were significantly below (outside the 95% C.I.) rates predicted from the models on only 1 of 13 dates, suggesting that egg production was not food limited on most of our sampling dates (Table 1). The reason for low egg production on 4 June 1987 is not clear, since temperature

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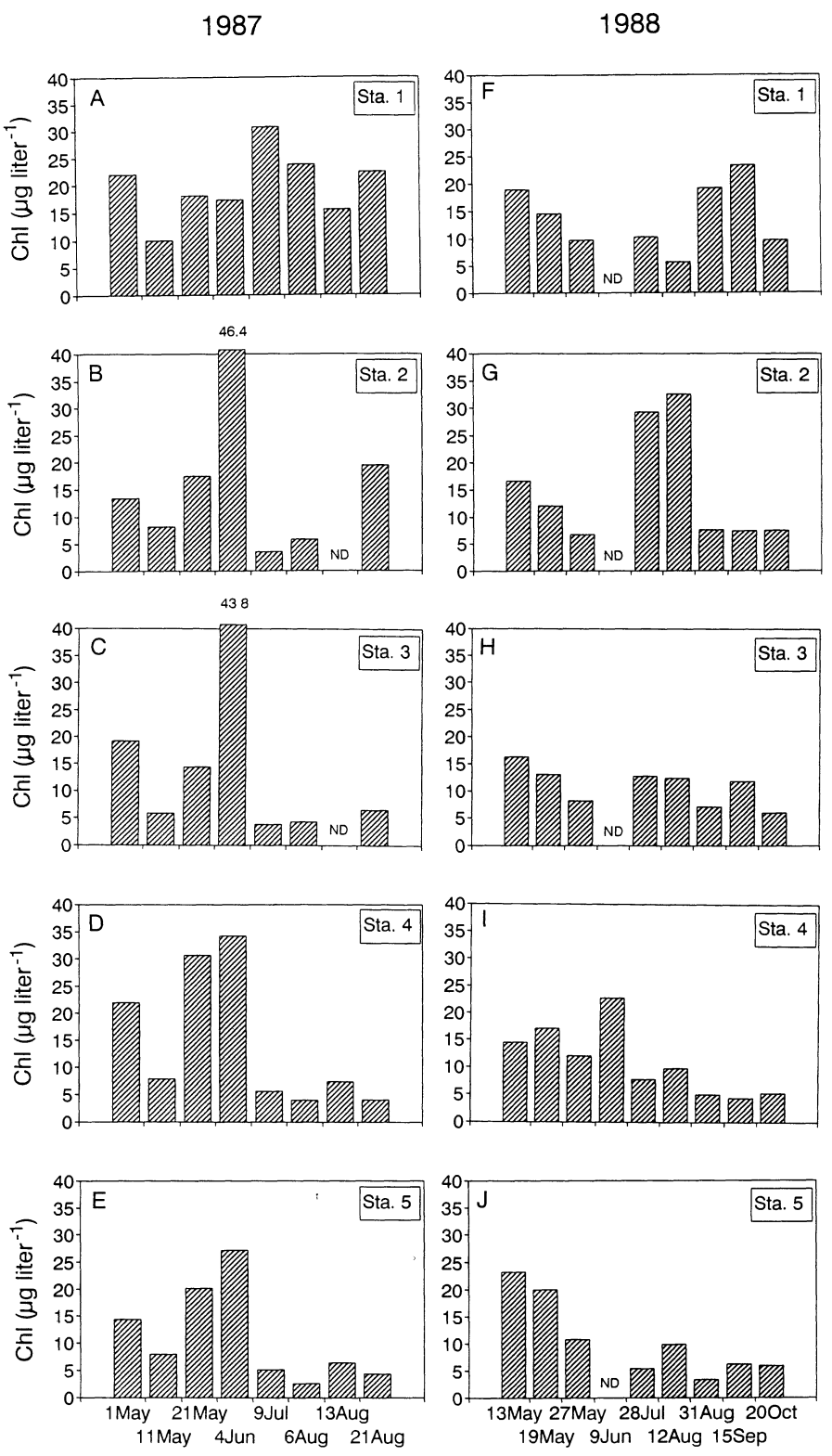
Fig. 4. Clearance rates of gelatinous zooplankton feeding on copepods (>200 μm) in surface waters on sampling dates in 1987 and 1988. Abbreviations and notations as in Fig. 1.


1987
1988
A
Sta. 1
F
Sta. 1
B
Sta. 2
46.4
G
Sta. 2
C
Sta. 3
43 8
H
Sta. 3
D
Sta. 4
I
Sta. 4
E
Sta. 5
J
Sta. 5
ND
Chl (µg liter^{-1})
0
5
10
15
20
25
30
35
40
1May 21May 9Jul 13Aug
11May 4Jun 6Aug 21Aug
13May 27May 28Jul 31Aug 20Oct
19May 9Jun 12Aug 15Sep

was moderate and phytoplankton C was the highest measured.

Production and predation—Most predation on copepods by gelatinous zooplankton at Sta. 4 was due to the ctenophore *M. leidyi* in both years (Table 2). However, total predation was high late in summer 1987 at Sta. 4 due to the combined effects of *M. leidyi* and *C. quinquecirrha,* and predation was high early in the season in 1988 due to greatest feeding by *N. bachei. C. quinquechirra* had little effect in 1988.

Because of a combination of high C-specific growth rates (egg production, Table 1) and large copepod biomass, copepod production was always at least one order of magnitude higher than predation for both 1987 and 1988 (Table 2). Predation by gelatinous zooplankton removed at most 7% of copepod standing stock and 12% of copepod production per day at Sta. 4. Production rate ($G \times B$) of *A. tonsa* (Table 2) was more variable than egg production rate (Table 1) due to high variation in biomass between sampling dates.

Discussion

Food limitation of copepods can be common in oceanic environments (Huntley and Boyd 1984), but there is also evidence of it in coastal and estuarine populations (Checkley 1980; Durbin et al. 1983). For example, Durbin et al. (1983) showed that egg production by *A. tonsa* in Narragansett Bay can be enhanced by adding cultured phytoplankton to ambient seston, indicating food limitation.

However, the mesohaline Chesapeake Bay is characterized by high rates of primary production, ranging from 80 to 5,300 mg C m^{-2} d^{-1} or ~4–265 mg C m^{-3} d^{-1} (Malone et al. 1986), and high but variable standing stocks of Chl *a,* microzooplankton, and particulate C. Our estimate of phytoplankton C from regression of POC against chlorophyll (C = 51 × Chl *a,* $r^2 = 0.48$) accounts for about half the variation in POC and has a low slope compared with values found by Malone and Ducklow (1990) for Chesapeake Bay and its coastal plume (range, 48–115). Although we do not have data on the size spectra of phytoplankton present, our conservative estimates indicate that total phytoplankton C available to copepods is generally high. Consistent with our view that food resources rarely limit copepods in Chesapeake Bay, White and Roman (1992*a*) found that phytoplankton C ingested by *A. tonsa* copepodites and adults exceeded requirements for growth and respiration in summer and that ingestion of microzooplankton supplemented phytoplankton in the copepods' diet.

Under high food conditions, copepod growth rate should not be food limited but should

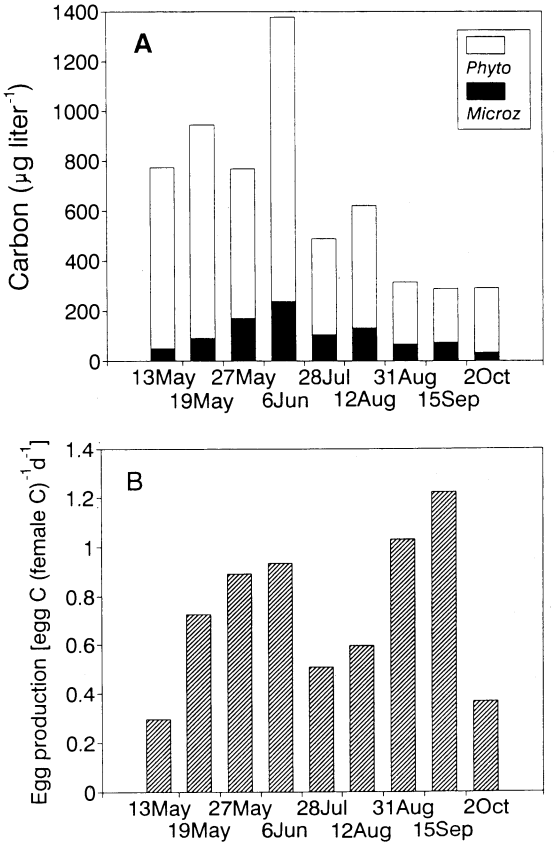


Fig. 6. Phytoplankton C and microzooplankton C (A) and daily weight-specific egg production by *Acartia tonsa* females (B). All were measured in surface water collected at Sta. 4 in 1988.

←

Fig. 5. Chlorophyll concentrations in surface waters at five stations in 1987 and 1988. Notations as in Fig. 1.

Table 2. Data collected in 1987 and 1988 at midbay Sta. 4 for copepod (>200 μm) biomass, production (estimated from egg production and biomass), and predation by gelatinous predators *Nemopsis bachei* (*N.b.*), *Mnemiopsis leidyi* (*M.l.*), and *Chrysaora quinquecirrha* (*C.q.*) (both volume-specific and % biomass and production removed).

	Copepod biomass (μg C m^{-3})	Copepod prod (μg C m^{-3} d^{-1})	Predation (μg C m^{-3} d^{-1})				Biomass removed	Prod removed
			N b	*M b*	*C q*	Total	(% d^{-1})	
1987								
1 May	3,420	—	0	4.48	0	4.48	0.13	—
11 May	5,000	2,715	0.05	5.50	0	5.55	0.11	0.20
21 May	900	—	2.79	0.77	0	3.55	0.40	—
4 Jun	880	279	2.85	15.19	0	18.04	2.05	6.45
9 Jul	16,870	—	37.28	14.51	16.36	68.15	0.40	—
6 Aug	13,980	—	0.70	265.06	28.94	294.70	2.11	—
13 Aug	7,480	9,133	0	499.51	57.07	556.58	7.44	6.09
20 Aug	20,910	8,113	0	930.91	111.03	1,041.94	4.98	12.84
1988								
13 May	3,940	1,162	0.94	0.87	0	1.81	0.05	0.16
19 May	2,680	1,943	8.59	0	0	8.59	0.32	0.44
27 May	5,500	4,911	27.22	81.29	0	108.51	1.97	2.21
9 Jun	1,750	1,632	0.09	102.25	0	102.34	5.85	6.27
28 Jul	3,830	1,941	0	9.50	3.56	13.06	0.34	0.67
12 Aug	13,860	8,246	0	964.93	0	964.93	6.96	11.70
31 Aug	8,440	8,701	0	156.65	0	156.64	1.86	1.80
15 Sep	20,830	25,454	0	77.90	0	77.90	0.37	0.31
20 Oct	2,800	1,024	0	0.01	0	0.01	<0.01	<0.01

reflect changes in ambient temperature (Uye 1981). We found that measured egg production fell below rates predicted based on temperature alone on only 1 of 13 occasions. This finding indicates that copepod growth rates (measured as egg production) should rarely be food limited in the mesohaline Chesapeake Bay during summer. If copepods are occasionally food limited in the bay in summer, it is probably because the food is unsatisfactory due to small size or poor biochemical composition rather than to the quantity of available particulate matter (e.g. Verity 1988; Kiørboe 1989; White and Roman 1992*a*).

The copepod production rates derived here are lower than potential production calculated for *A. tonsa* by Durbin and Durbin (1981) in Narragansett Bay and Heinle (1966) in the Patuxent River, a subestuary of Chesapeake Bay. The higher average production rates in those studies were due to greater copepod biomass and the methods of calculation, not to higher instantaneous growth rate (Table 3). Application of our method for calculating production ($P = G \times B$) to the data for Narragansett Bay and for the Patuxent River gives lower values of P (16.66±5.25 and 25.14±3.07 mg C m^{-3} d^{-1}, respectively) than those the investigators obtained with population dynamics approaches (Table 3). Therefore, if the egg production rate of adult female *A. tonsa* is representative of somatic growth in earlier stages, then the production rates given here for Chesapeake Bay probably are conservative.

The lower copepod biomass found in our study can be explained in part by the fact that we only included copepods >200 μm; the other studies used all stages of *A. tonsa* in production calculations. Nauplii and early stage copepodites (<200 μm) of *A. tonsa* commonly account for >50% of copepod biomass in the mesohaline Chesapeake Bay during summer (White and Roman 1992*b*), and including this size group in our calculation would roughly double our estimate of production. Production rates of copepods in the Patuxent River were similar to those in our study, even though copepod biomass there was greater due to lower growth rates (Table 3).

Our estimates of predation by *M. leidyi* ctenophores (0–11.2% d^{-1} of copepod standing stock) are lower than estimates in other studies. Higher predation effects were estimated in the Patuxent River and York River tributaries of Chesapeake Bay: 31% d^{-1} of *A. tonsa* standing stocks (Bishop 1967) and 73%

Table 3. Values for *Acartia tonsa* biomass (*B*), instantaneous growth rate (*G*), and production (*P*) averaged over the growing season for different estuarine systems (±95% C.L.).

Study area	Size fraction	*n*	*B* (mg C m^{-3})	*G* (d^{-1})	*P* (mg C m^{-3} d^{-1})
Mesohaline Chesapeake Bay (present study)	>200 μm	13	7.83(2.96)	0.69(0.16)	5.79(3.35)
Upper Narragansett Bay (Durbin and Durbin 1981)	total	13	23.72(12.88)	0.69(0.05)	24.24(13.70)
Patuxent River (Heinle 1966)	copepodids	7	19.12(2.78)	0.42(0.27)	7.68(2.23)
	total	7	51.04(8.94)	0.48(0.04)	26.50(5.79)

of total zooplankton mortality (Burrell 1968). These early studies were not as comprehensive as the later ones. In Narragansett Bay, Kremer (1979) estimated average predation of 5–10% d^{-1} of the copepod standing stocks, with maxima of >30% d^{-1}, and Deason (1982) reported mean predation by *M. leidyi* in August 1975–1979 to be from 0.04 to 54.0% d^{-1} of the copepod standing stocks.

Scyphomedusae (*C. quinquecirrha*) may reduce the predation effects of ctenophores on copepods in Chesapeake Bay in comparison with Narragansett Bay where the medusae are not present. Maximum measured volumes of ctenophores were similar in Narragansett Bay (20 to >100 ml m^{-3}, Kremer and Nixon 1978) and at the middle stations in Chesapeake Bay (72 and 90 ml m^{-3} in 1987 and 1988) where medusae were not abundant (Figs. 1 and 2). However, at the flank stations, ctenophore biomass was much lower (maxima of 6 and 15 ml m^{-3} in 1987 and 1988), probably due to predation on them by the abundant medusae.

The predation rates on copepods by medusae in the present study can be compared with rates estimated previously. We estimated that *N. bachei* medusae removed 0–3.3% d^{-1} of the copepod standing stocks, and *C. quinquecirrha* removed 0–5.1% d^{-1}. These rates for *N. bachei* in 1987 and 1988 were similar to those in 1989 and 1990 along the same transect but are somewhat lower than rates estimated along a more southern transect (0–30% d^{-1}; Purcell and Nemazie 1992). Predation by *C. quinquecirrha* in two tributaries of Chesapeake Bay during 1987 was much greater (maxima of 42 and 94% d^{-1}; Purcell 1992) than that reported here in the main bay.

Inverse correlations led some investigators to conclude that ctenophore predation controlled the standing stock of copepods. Several studies in Chesapeake Bay and other U.S. East Coast estuaries reported an inverse correlation between densities of crustacean zooplankton and *M. leidyi* (e.g. Kremer 1979; Mountford 1980; Lonsdale 1981; Deason 1982; Feigenbaum and Kelly 1984). However, in our study, both gelatinous zooplankton biomass and grazing and copepod densities were low in spring and high in summer.

We also could not attribute seasonal declines in copepod densities to predation or to food limitation. A spring decline in copepod abundance has been found repeatedly in Chesapeake Bay (e.g. Brownlee and Jacobs 1987; Olson 1987), and its possible causes are subject to active speculation (Bradley 1991). In our study, although copepod densities did decrease in May to June 1987 and 1988 when predation pressure increased (Figs. 3, 4, Table 2), direct predation by gelatinous predators on copepods could not have caused the observed decline in either year. Less than 0.5% d^{-1} of biomass and production was consumed in early to mid-May and only ~6% d^{-1} in late May to early June. Food also was not limiting copepod production at that time, and egg production was increasing (Fig. 6A,B, Table 1). The causes of the decline in copepod stocks in spring remain unclear.

Copepod densities also decreased between 15 September and 20 October 1988 (Fig. 3), but predation effects by gelatinous zooplankton were low then (<1.7 and <0.001% d^{-1}, respectively; Fig. 4). Food levels were lower then than in spring, but egg production was not significantly different than predicted from temperature, suggesting that lower temperatures, and not food, reduced production in fall (Fig. 6A,B, Table 1).

Although predation by gelatinous zooplankton was usually an order of magnitude less than measured *A. tonsa* production, the cumulative effect of all predator species could act to limit copepod populations. Other potentially important predators include the menhaden (*Brevortia tyrannus*), bay anchovy (*Anchoa mitchilli*), and *A. tonsa* adults. Kremer and Nixon (1978) included predation by ctenophores, fish larvae, and menhaden and carnivory by adult copepods to balance juvenile copepod growth in their simulation model of the Narragansett Bay ecosystem. Fulton (1982) showed that predation by bay anchovy was important in the seasonal decline of *A. tonsa* in North Carolina estuaries, and Klebasko (1991) estimated from fish densities in situ that 22% d^{-1} of *A. tonsa* standing stocks could be consumed by *A. mitchilli* in October in the mesohaline region of Chesapeake Bay.

Cannibalism has been reported for *Acartia* spp. living in culture and in situ (Landry 1978; Lonsdale et al. 1979), and its importance is positively correlated with copepod density (Ohno et al. 1990). In laboratory cultures, mortality rates of *Acartia tsuensis* nauplii exceeded 50% d^{-1} in the presence of copepodite stages (Ohno et al. 1990). When densities of copepods are high in Chesapeake Bay in August (Fig. 3), cannibalism may be an important cause of mortality.

Physical as well as biological factors could be important in limiting copepod populations. Dissolved oxygen levels began to fall as the water column became stratified in late April of both 1987 and 1988 (T. C. Malone unpubl. data). Waters below the pycnocline were hypoxic (<1 ppm O_2) from 21 May through 15 August 1987 and from 28 July through 15 September 1988 (T. C. Malone unpubl. data).

Such low dissolved oxygen levels may be detrimental to copepods. No adult *A. tonsa* survived after 24 h of exposure to 1 ppm O_2, and copepods and nauplii were absent or in low abundance in bottom waters of <1 ppm O_2 (Roman et al. 1993). After 30 h of exposure to 1 ppm O_2, 12.5–62.5% of *A. tonsa* eggs hatched, but no eggs hatched at <0.5 ppm O_2 (Roman et al. 1993). *Acartia* eggs did not hatch at 0.21–0.24 ppm O_2, while at 0.37–0.67 ppm O_2, eggs hatched but nauplii did not survive (Uye and Fleminger 1976). Therefore, copepod eggs that sank into anoxic water during our study may not have hatched, or the nauplii may not have survived, reducing copepod production as a consequence.

Hairston et al. (1960) argued that when resources are abundant, organisms are primarily regulated by predation, and when resources are rare, organisms are regulated by food. Chesapeake Bay is characterized by high inputs of nutrients during the spring freshet (Malone et al. 1988), which results in high standing stocks of phytoplankton and microzooplankton throughout summer (Fig. 6 and Table 1). Under these conditions, the theory of Hairston et al. (1960) would suggest limitation of copepod populations in the bay by predation rather than food. Although our data indicate infrequent food limitation, predation by gelatinous zooplankton alone was insufficient to hold copepod populations in check at the observed production rates.

The relative importance of predation and resource limitation may be clearer in whole-lake or enclosure experiments, where predator populations and nutrient inputs can be manipulated (Vanni 1987; Carpenter and Kitchell 1988; McQueen et al. 1989), than in marine and estuarine environments, where advection and vertical migration of prey and predators make it difficult to repeatedly sample the same populations. We used the technique of taking a series of "snapshot" measurements of carbon flow (biomass, egg production, and ingestion rates) to estimate whether predation or resources are limiting estuarine populations at any given time. This method does not assume sampling of single populations and offers an alternative to population dynamics approaches. In our study, numerous measurements taken throughout two growing seasons suggest that neither predation by gelatinous zooplankton nor resource limitation were sufficient to control copepod populations in Chesapeake Bay.

As more evidence is compiled on predation and resource limitation of organisms in nature, it is apparent that both processes work in concert (McQueen et al. 1989; Hunter and Price 1992). In the mesohaline Chesapeake Bay, populations of *A. tonsa* are likely controlled by a number of factors simultaneously, including predation from gelatinous zooplankton, fish, adult copepods, and others, physical characteristics such as temperature and hypoxia, and occasional food limitation.

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