

# Food web interactions in the plankton of Long Island bays, with preliminary observations on brown tide effects

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**ABSTRACT:** We examined the relative importance of phytoplankton and ciliates as prey for metazoan zooplankton, and the role of predation in regulating ciliate populations in 2 Long Island (USA) bays. Depth-integrated primary production ( $\text{mg C m}^{-2} \text{ h}^{-1}$ ) was dominated by nanoplankton  $<5 \mu\text{m}$  in diameter throughout the year, ranging from  $>95\%$  of total production in mid-summer to an average of about  $60\%$  in winter and early spring. Predator exclusion and addition experiments conducted in microcosms showed that the mortality coefficient of ciliates ( $\text{d}^{-1}$ ) from zooplankton predation was higher when larger phytoplankton ( $>10 \mu\text{m}$ ) contributed less to total primary productivity. For adult copepods, an increase in the percentage ciliate contribution compared to phytoplankton contribution to total carbon intake also coincided with the higher percentages of small microalgal production. Egg production rates of *Acartia* spp. were positively correlated to the net growth coefficient of ciliates. In contrast, micrometazoa routinely obtained  $>70\%$  of their total carbon ration from phytoplankton, and at times during spring and summer, removed 23 to 52% of the total depth-integrated primary production. In addition to protozoa, we suggest that micrometazoa, particularly copepod nauplii, may serve as a trophic link between phytoplankton and mesozooplankton in Long Island bays.

**KEY WORDS:** Zooplankton grazing and production Primary production Ciliates

## INTRODUCTION

Temporal and spatial changes in phytoplankton abundance and composition reflect the dynamic nature of both physical and biological factors which contribute to the growth and loss of cells (reviewed in Frost 1980). In Long Island bays (New York, USA), diatoms are an important component of the late winter bloom, and are succeeded by smaller chrysophytes and chlorophytes in the summer months (Lively et al. 1983). Investigations of primary productivity in these bays (Great South Bay reviewed in Carpenter et al.

1991; Peconic Bays in Bruno et al. 1983, Coper et al. 1989) showed that nanoplankton was the major contributor to planktonic primary production in summer. Such shifts in the composition and size structure of the phytoplankton community can have important effects on the fecundity and survivorship of zooplankton. For example, Kleppel (1992, Kleppel et al. 1991) has questioned the role of diatoms as 'optimal' food for adult copepods in several locations (e.g. *Acartia tonsa* of the California coast), a hypothesis that has been supported recently in Long Island Sound studies (Jonasdottir 1994, Jonasdottir et al. 1995). Diatoms may also be an inferior food source compared to animal prey for some meroplankton (e.g. decapod larvae; Harms 1992). Exudates from diatoms in a stationary growth phase may actually inhibit copepod grazing (Malej & Harris 1993). Ciliates, dinoflagellates and other protists may provide a better nutritional source to fuel copepod egg production compared to diatoms because of chemical differ-

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ences in specific fatty acids and protein content (Stoecker & Capuzzo 1990 and references therein, Jonasdottir 1994)

The purpose of our study was to evaluate the relative importance of phytoplankton and ciliates in feeding and production of metazoan zooplankton in 2 Long Island bays. In recent years, the importance of protists, particularly phagotrophic ciliates and flagellates, in maintaining the coupling of phytoplankton productivity to zooplankton dynamics has become evident (Conover 1982, Landry & Lehner-Fournier 1988, Sherr et al. 1988). Because smaller algae, particularly those  $< 5 \mu\text{m}$ , are more likely to be efficiently utilized by protozoa compared to adult copepods (Azam et al. 1983), we hypothesized that predation on ciliates would be critical for copepod diets (as found for *Acartia tonsa*; Robertson 1983, Gifford & Dagg 1991) and production (Stoecker & Egloff 1987, reviewed in Stoecker & Capuzzo 1990), especially during summer when small nannoplankton dominate in Long Island bays. The specific objectives of this study were, firstly, to determine if there was seasonal variation in major food resources for mesozooplankton ( $> 202 \mu\text{m}$ ) and micrometazoa ( $> 64$  to  $202 \mu\text{m}$ ) in Long Island Bays. Secondly, we investigated whether prey productivity influenced copepod productivity. Thirdly, we evaluated the role of zooplankton predators on the population dynamics of ciliates. During the course of this investigation a 'brown tide' occurred. This algal species, *Aureococcus anophagefferens*, is  $\sim 2 \mu\text{m}$  in diameter (Sieburth et al. 1988), and has toxic properties that cause growth and feeding reduction in some marine organisms (e.g. bay scallop larvae; Gallagher et al. 1989). Dimethylsulfoniopropionate (DMSP), a precursor to dimethylsulfide (DMS) and acrylic acid, resides within the cell (Keller et al. 1989). The cell surface of *A. anophagefferens* contains a neurotransmitter-like,

bioactive compound that reduces gill ciliary beat frequency in some bivalve species (e.g. *Mercenaria mercenaria*; Gainey & Shumway 1991).

## METHODS

**Field sampling.** Our sampling sites during 1991 included 1 station (Blue Point on 2/12, 3/21, 4/16, 5/2, 7/25, 7/31, 11/25; dates expressed as month/day) in the Great South Bay (GSB) and 2 stations in the Peconic Bays (PB) (Reeves Bay on 5/20, 5/21, and West Neck Bay on 6/17, 6/20, 7/17, 7/22) (Fig. 1). Both primary productivity and zooplankton feeding experiments were conducted on each experimental date except on 5/2, 5/20, 6/20 when only the former was measured. Sampling was conducted from piers or docks at a 0.5 m depth for temperature and salinity measurements, zooplankton abundance, and ambient seawater collection. Strong vertical mixing of these shallow water bodies over large areas alleviated the necessity for water column depth profiles (Bruno et al. 1983, Lively et al. 1983).

**Zooplankton composition and abundance.** Larger zooplankton were collected and size fractionated by successively passing buckets of water (20 l) through Nitex sieves;  $202 \mu\text{m}$  and  $64 \mu\text{m}$  for mesozooplankton and micrometazoa, respectively ( $n = 2$  for each size fraction). Animals caught on the sieves were rinsed with  $0.22 \mu\text{m}$  filtered seawater into jars, preserved in 5% buffered formalin and enumerated under a dissecting microscope. Additional samples of whole seawater (400 ml,  $n = 2$ ) were collected and preserved in Lugol's fixative ( $\sim 10\%$ ) for enumeration of more delicate ciliates. Lugol's samples were allowed to settle for  $\sim 48$  h in the sampling jar, followed by removal of 300 to 350 ml of the overlying water. The remaining contents

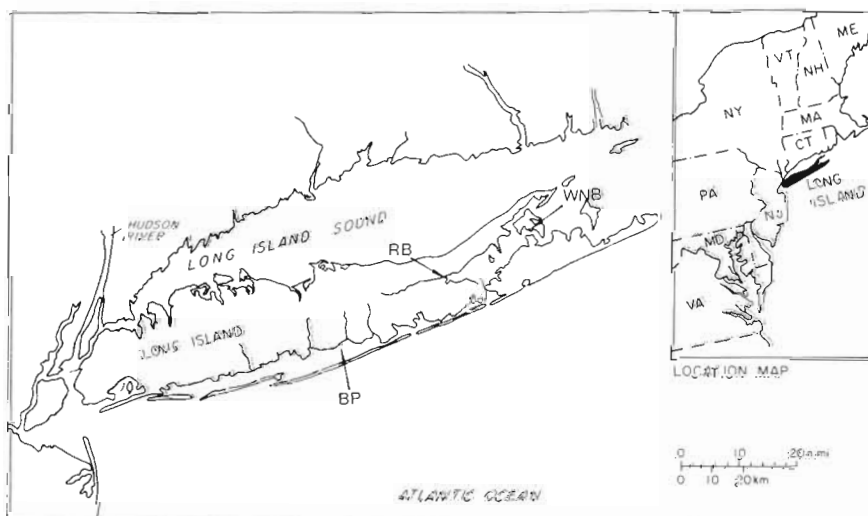


Fig. 1. Location of sampling sites in the Peconic Bays (RB: Reeves Bay; WNB: West Neck Bay) and Great South Bay (BP: Blue Point).

were then placed in a graduated cylinder, and allowed to settle for an additional 24 h. All but 5 ml of the overlying water was removed and protozoa were counted by 1 ml aliquots in a counting chamber until at least 100 ciliates were counted. A Zeiss compound microscope equipped with a micrometer was used for enumeration and measurement of ciliates  $>20\ \mu\text{m}$ .

**Primary productivity and phytoplankton biomass.** Phytoplankton biomass was estimated from 90% acetone-extracted chlorophyll *a* (chl *a*) by fluorometry using a Turner designs fluorometer (Strickland & Parsons 1972, Cosper et al. 1989). Ambient seawater samples (30 ml) were size fractionated to obtain  $<5$ ,  $<10$  and  $<20\ \mu\text{m}$  fractions using Nitex netting, as well as whole water samples ( $n = 3$  to 6 for each fraction). Total and size-fractionated primary productivity rates were obtained following simulated *in situ*, short-term incubations (2 to 4 h) with  $^{14}\text{C}$ - $\text{NaHCO}_3$  under a range of light intensities including 100, 33 and 2% ambient light using neutral screening and 0% in dark bottles (Cosper et al. 1989). The  $^{14}\text{C}$ - $\text{NaHCO}_3$  was added from a stock solution to a final concentration of  $\sim 0.2\ \mu\text{Ci ml}^{-1}$ . Whole seawater incubations were terminated by size fractionation and filtered onto  $0.22\ \mu\text{m}$  Millipore filters. Filters were placed in scintillation vials and dried in a desiccator overnight to volatilize any remaining inorganic  $^{14}\text{C}$ . The particulate  $^{14}\text{C}$  on the filters was counted in a Packard Tricarb 300C scintillation counter after the addition of 5 ml of opti-fluor scintillation liquid. Integral estimates of photic zone production were calculated based on field light extinction coefficients.

Cell counts of *Aureococcus anophagefferens* were conducted using the immunofluorescent detection method (Anderson et al. 1989), and at least 100 other larger species were identified from Lugol's samples using an inverted light microscope at  $600\times$  magnification.

**Zooplankton grazing on the natural phytoplankton community.** The algae *Nannochloris* sp. (chlorophyte;  $<5\ \mu\text{m}$  in diameter), *Thalassiosira pseudonana* (diatom; 5 to  $10\ \mu\text{m}$ ), *Thalassiosira weissflogii* (diatom; 10 to  $20\ \mu\text{m}$ ) and *Ditylum brightwellii* (diatom;  $>20\ \mu\text{m}$ ) were radiolabeled with  $^{14}\text{C}$ - $\text{NaHCO}_3$  and used as tracers of *in situ* zooplankton grazing on natural phytoplankton (modified from Lampert & Taylor 1985, Lampert et al. 1986). A 1 l, semi-continuous culture of each microalgal species was maintained in exponential growth throughout the duration of the project. Dilutions were performed aseptically in a sterile transfer hood. Stock cultures were grown in f/2 enriched Instant Ocean prepared at a salinity of 30 ppt (Guillard & Ryther 1962), and were maintained at  $20^\circ\text{C}$  on a 12:12 h light:dark cycle at a light intensity of  $\sim 100\ \mu\text{E m}^{-2}\text{ s}^{-1}$ .

Exponentially growing algae were dispensed aseptically from stock cultures into sterile, polystyrene flasks

for inoculations with radioactive sodium bicarbonate. These cultures were maintained under the same growth conditions as the stock cultures for 48 h prior to the experiment to ensure uniform radioactive labeling of cells.

Seawater for the grazing experiments was collected by bucket, placed into 20 l cubitainers, and transported to and held in the laboratory in coolers to maintain ambient temperature. Sampling was conducted in the morning, most often between 07:00 and 10:00 h. Grazing experiments generally began within 3 h after seawater collection. All experiments were conducted at ambient temperature ( $\pm 1.0^\circ\text{C}$ ). Cubitainers were rotated gently by hand prior to pouring into the grazing chambers (1.5 l glass or 2 l polycarbonate bottles wrapped in black plastic). The grazing chambers were then placed in coolers for temperature control, and the zooplankton allowed to 'recover' for approximately 15 to 30 min prior to the grazing experiment. Usually there were  $n = 4$  for each microalgal tracer species and for each sampling date.

The total amount of radiolabeled algal suspension added to the grazing chambers represented 5 to 20% of the carbon concentration ( $\mu\text{g C l}^{-1}$ ) of the representative phytoplankton size fraction determined just prior to experimentation by measuring chl *a* concentration of the sampled water and converting to carbon assuming a C:chl *a* ratio of 45, which is a reasonable conversion based on studies in waters with similar phytoplankton composition (i.e. Long Island Sound; Tanticodok 1990). The cell concentration of each culture of radiolabeled microalgae was determined just prior to experimentation, and estimates of cell carbon content were obtained using the Strathmann equation (Strathmann 1967).

Following inoculation with the microalgal suspension, the chamber was rotated gently by hand, and the experiment allowed to run for only 7 min to minimize error from recycling of dissolved organic carbon or coprophagy. Also, previous time-course grazing experiments using this technique showed no significant change or a decline in the estimate of zooplankton grazing with increased incubation time (Lonsdale & Cosper 1994). The chamber contents were sieved successively through  $>202\ \mu\text{m}$  and  $>64\ \mu\text{m}$  Nitex netting. Contents caught on the sieve were gently sprayed with  $0.45\ \mu\text{m}$  filtered seawater to remove unconsumed, radiolabeled cells, and then rinsed onto  $0.22\ \mu\text{m}$  Millipore filters. The contents were then prepared for scintillation counting as described above for primary productivity experiments. On each sampling date, 5 to 30 ml samples of the radiolabeled algae were prepared for scintillation counting ( $n = 3$ ) to convert radioactivity measurements to cell number. Thus, our grazing measurement technique accounted

for cell-size dependent differences in radiolabeling (Tackx & Daro 1993).

To account for radiolabel uptake by zooplankton not related to grazing (e.g. naupliar 'drinking'; Tester & Turner 1991), controls were conducted using the same amount of radiolabeled suspension as in the grazing experiments, but first passed through a 0.22  $\mu\text{m}$  Millipore filter, and then added to grazing chambers as above. Filtrate controls ( $n = 2$ ) were conducted for each microalgal tracer and experimental date. A second series of controls was conducted once to determine to what extent radiolabeled cells were retained successively on 202  $\mu\text{m}$  and 64  $\mu\text{m}$  sieves. Grazing chambers containing ambient filtered seawater (0.45  $\mu\text{m}$ ) were inoculated with algal suspension at 5 representative concentrations (cells  $\text{ml}^{-1}$ ;  $n = 4$  to 12 for each concentration), followed by size-fractionated sieving, and scintillation counting (see Lonsdale & Cosper 1994).

Zooplankton clearance rates were calculated from control-corrected data. Carbon ingestion rates ( $\mu\text{g C ind.}^{-1} \text{ h}^{-1}$ ) of the 4 size fractions of phytoplankton were calculated from clearance rates ( $\text{ml ind.}^{-1} \text{ h}^{-1}$ ) and phytoplankton carbon concentration ( $\mu\text{g C l}^{-1}$ ). Total carbon ingestion rate was determined from summation of the ingestion rates of the 4 size fractions. In several cases, no phytoplankton biomass was measured but minimal primary production was detected. Thus, carbon ingestion rates were obtained from zooplankton clearance and primary productivity rates ( $\mu\text{g C l}^{-1} \text{ h}^{-1}$ ).

**Zooplankton predation and population growth of ciliates.** Estimates of mesozooplankton and micrometazoan predation on ciliates were obtained using a predator removal/addition method. Incubation bottles (2 l polycarbonate bottles) were filled with whole seawater (WSW) or size-fractionated seawater to remove the  $>202$  or all  $>64$   $\mu\text{m}$  zooplankton predators ( $n = 2$  for each treatment). The latter treatment was used to estimate the net growth coefficient of ciliates  $\leq 64$   $\mu\text{m}$  ( $\text{d}^{-1}$ ; *sensu* Frost 1972, Stoecker et al. 1983), and the other treatments to assess the predatory impact on ciliates of all larger ( $>64$   $\mu\text{m}$ ) zooplankton (WSW control measured the realized rate of ciliate population increase), or only the micrometazoa ( $>64$  to 202  $\mu\text{m}$ ;  $>202$   $\mu\text{m}$  removal treatment). We use the term 'net growth' to describe ciliate production available to larger zooplankton, recognizing that cannibalism or parasitism may occur (e.g. Stoecker et al. 1983). Bottles were incubated for about 24 h outdoors in water tanks at 40% natural sunlight by using neutral density screening. Water temperature was maintained close to ambient with ice and/or running tap water. Initial microzooplankton samples (400 ml,  $n = 2$ ; Lugol's preserved) were taken from treatment and control waters, and again at the termination of the experiment for each incubation bottle. Ciliates were counted using the

same methods described above, including being counted in 1 ml aliquots of settled sample in a counting chamber until at least 100 individuals were counted.

The net growth coefficient of ciliates ( $\text{d}^{-1}$ ), zooplankton predation coefficient (or mortality coefficient of ciliates;  $\text{d}^{-1}$ ), and zooplankton predation rate (ciliates  $\text{ind.}^{-1} \text{ d}^{-1}$ ) were calculated using the equations of Frost (1972). Some error in the estimation of zooplankton predation may have occurred, however, if the net growth coefficient of ciliates in the sieved treatment did not match that in WSW. Carbon ingestion rates from ciliate prey were estimated by volume:carbon relationships for tintinnids (Verity & Langdon 1984) and aloricate ciliates (Putt & Stoecker 1989). Aloricate ciliates ( $n = 5$  on each date) were assumed to be ball shaped, and the diameter ( $d$ ) of the cell was measured and its volume assumed to be equal to  $\frac{4}{3}\pi(d/2)^3$ . Tintinnids ( $n = 5$ ) were assumed to approximate a cylinder and thus both the length ( $l$ ) and diameter of the lorica were measured and the volume of a cell was estimated by  $\pi(d/2)^2 l$ . Although zooplankton clearance rates ( $\text{ml ind.}^{-1} \text{ d}^{-1}$ ) were calculated for the total ciliate population, carbon ingestion rates were calculated separately from grazing rates on each ciliate type, and then totaled.

Adults and nauplii of the abundant copepod species were sorted from cod-end, 64  $\mu\text{m}$  net hauls to provide additional information on the predatory impact of mesozooplankton and micrometazoa, respectively, on population growth of ciliates. Ten adults or 50 nauplii were added to 2 l polycarbonate bottles containing unfiltered seawater ( $n = 2$  for each copepod treatment). Before being added to bottles, individual copepods were transferred 3 times to 0.22  $\mu\text{m}$  filtered seawater with a pipet to minimize the introduction of other plankton. Sampling protocols and incubation conditions were as described for predator removal studies. Zooplankton predation coefficients were calculated using the realized ciliate growth coefficient calculated from WSW incubations, rather than the net growth coefficient as in the removal experiments.

**Copepod egg production and hatching success.** To determine if egg production rates of the most common copepods were food-limited (*sensu* Durbin et al. 1983), or influenced by prey availability, 5 to 6 females of the most common species [i.e. *Acartia hudsonica* (Piley) and *Acartia tonsa* Dana] were put into each of 8 to 12 plexiglass cylinders with a 202  $\mu\text{m}$  Nitex mesh on the lower end, and hung inside 1 l beakers. The 202  $\mu\text{m}$  mesh in the inner containers allowed eggs to pass through, and kept females separate to minimize egg cannibalism. Half the beakers were filled with 800 ml of 64  $\mu\text{m}$  screened ambient water, and the remaining with 800 ml of enriched, screened ambient water. The screening was needed to remove any copepod eggs



and nauplii present in the water. Enrichment consisted of adding the flagellate *Rhodomonas lens* (7 to 8  $\mu\text{m}$  diameter) to achieve a minimum of  $2.0 \times 10^4$  cells  $\text{ml}^{-1}$ . This microalgal species has been found to be a good food source for *Acartia* spp., and the experimental density is above the critical concentration for growth (Jonasdottir 1994). Beakers were incubated at ambient temperatures (usually  $\pm 1^\circ\text{C}$ ) in dim light on a 14:10 h light:dark cycle. Egg production rates under ambient food conditions were determined after 24 h. Copepods in the enriched beakers were allowed to acclimate to the new food for 24 h. Following acclimation, the water was screened again through a 64  $\mu\text{m}$  mesh to remove eggs and nauplii, and animals were placed back in the same enriched water for another 24 h incubation. All eggs and nauplii were counted, and eggs were placed in culture plate wells (20 ml) to determine egg hatching success (%). Eggs were observed once a day for 2 to 4 d to measure hatching success. Hatching success for eggs produced under ambient food conditions was always determined, but not until 5/21 for eggs produced under enriched conditions. Percentage hatching of eggs under ambient conditions was not available on 7/17 because of their inadvertent loss following counting.

**Copepod development and survival with brown tide.** To evaluate further how *Aureococcus anophagefferens* impacts the growth of copepods, NI to NII nauplii of the meroplanktonic harpacticoid *Coullana canadensis* and mostly NVI of *Acartia hudsonica* were taken from laboratory batch cultures maintained at  $20^\circ\text{C}$  and  $16^\circ\text{C}$ , respectively, a salinity of 25‰ and under a 14:10 h light:dark cycle (see Lonsdale & Levinton 1985 for detail). *A. hudsonica* is common in Long Island bays from winter through late spring (e.g. Great South Bay; Duguay et al. 1989, this study), while *C. canadensis* nauplii have been found in summer (e.g. Quantuck Creek on the south shore; Lonsdale et al. 1993).

Five food treatments were utilized; ambient (non-bloom) seawater (26‰, sieved through 44  $\mu\text{m}$  mesh netting) or ambient-enriched with either a bloom concentration of *Aureococcus anophagefferens* ( $5 \times 10^5$  cells  $\text{ml}^{-1}$ ) or *Thalassiosira pseudonana* (3H) ( $1.22 \times 10^5$  cells  $\text{ml}^{-1}$ ). Both additions were equivalent to  $1100 \mu\text{g C l}^{-1}$  according to the equations of Strathmann (1967). Alternatively, copepods were reared in autoclaved, filtered (20  $\mu\text{m}$ ) seawater (25‰), with or without a suspension of *A. anophagefferens* cells ( $5 \times 10^5$  cells  $\text{ml}^{-1}$ ). Water temperature and the light cycle were the same as for batch culturing of copepods. The various copepod growth media were prepared fresh daily.

Nauplii and copepodites ( $n = 18$  for each food treatment and life stage) were placed individually in 1 ml wells of a multi-depression dish contained within an

airtight white plastic box. Distilled water in the bottom of the box served to reduce evaporation from the wells. Observations on copepod survival and molting were made twice daily. All of the copepod growth suspension was replaced during the day, and 50 % was replaced at night. Observations were made for 4.5 d. Percentage survival was calculated from the number of individuals surviving from NI to CI for *Coullana canadensis* and NVI to CIII for *Acartia hudsonica*, and included those surviving to the end of the experimental period if the final developmental stage had not been reached. Development times (h) used in the data analyses were from only those copepods which reached either CI (*C. canadensis*) or CIII (*A. hudsonica*).

**Statistical analyses.** Prior to analysis of variance and multiple regression, Bartlett's test or the  $F_{\text{max}}$  test was used to verify that variances around the mean, including those of transformed data, were homogeneous (Sokal & Rohlf 1981; pc statistical package). For multiple regression, a sample size of 1 was included in the data set (Sokal & Rohlf 1981). Statistical analyses were conducted using either SAS (Analysis of Variance) or the pc statistical package accompanying Sokal & Rohlf (1981; Linear Regression, Multiple Regression, Tukey-Kramer procedure and  $R \times C$  Test of Independence).

## RESULTS

### Primary productivity rates and biomass

The highest rates of depth-integrated primary production (Fig. 2) were measured in the summer months, and this can be attributed to increasing water temperature (Fig. 3). A multiple regression of the dependence of total primary productivity ( $\text{mg C m}^{-2} \text{h}^{-2}$ ,  $\log_{10}$  transformed) on water temperature ( $^\circ\text{C}$ ) and total chl *a* showed only water temperature to be significantly related ( $\text{df} = 1, 10$ ,  $F = 20.436$ ,  $p < 0.001$  and  $F = 1.156$ ,  $p > 0.25$ , respectively). The model explained 67.6 % of the variance and was significant at the 0.005 level ( $\text{df} = 2, 10$ ,  $F = 10.426$ ). The major contributor to the total depth-integrated rate of primary production on all sampling dates was phytoplankton  $< 5 \mu\text{m}$  in diameter. The range of contribution of these small phytoplankton to the total primary production was 45.8 to 95.7 %, being greatest in the summer months and lowest during winter and spring. The next-largest size fraction (5 to 10  $\mu\text{m}$ ) contributed nominally to phytoplankton community productivity (range = 0 to 6.7 %). The contribution to primary production by the larger phytoplankton ( $> 10 \mu\text{m}$ ) ranged from 5 to 47.9 %, and in general was greatest between February and early May.

Chl *a* concentration had a similar trend as found for primary productivity (Fig. 4). The 5  $\mu\text{m}$  fraction was

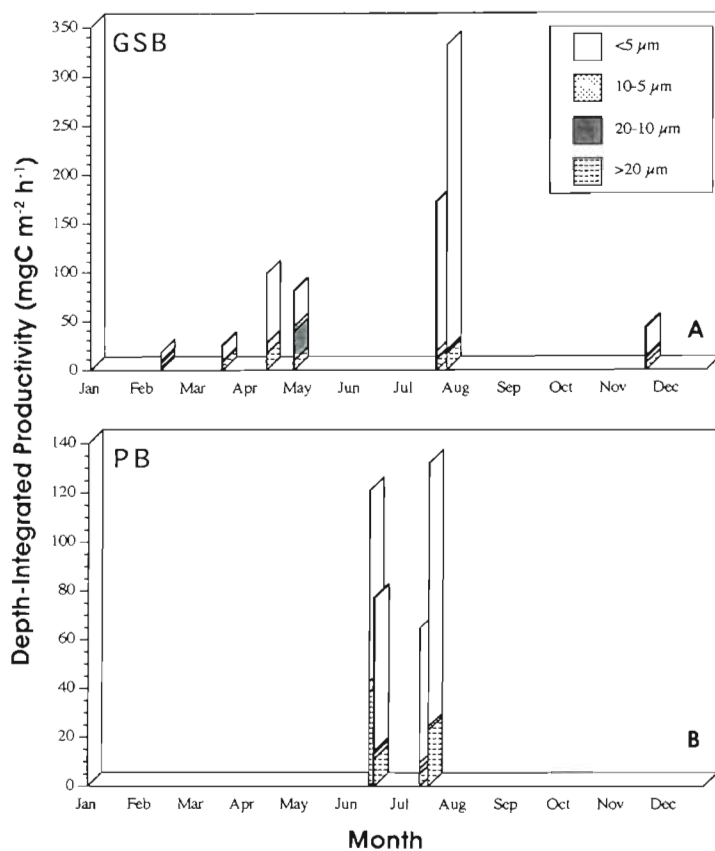


Fig. 2. Depth-integrated rate of primary productivity of 4 size fractions of phytoplankton in (A) Great South Bay, (B) Peconic Bays. Total depth-integrated rate of primary productivity is represented by the entire bar

ton, and the pennate diatom *Cylindrotheca closterium* was the most abundant component of the >20 μm size fraction. A few *Gymnodinium* spp. were also noted. During the early spring (3/21), the >20 μm size fraction was composed of the centric diatoms *Coscinodiscus* sp. (~70 to 100 μm), *Rhizosolenia setigera*, and *Rhizosolenia* sp., and the dinoflagellates *Prorocentrum* sp., *Gymnodinium* spp., and *Protoperidinium bipes*.

### Zooplankton abundances

Late-stage copepodites and adult copepods, primarily *Acartia* spp. (*A. hudsonica* from February through May, and *A. tonsa* in June and July), comprised most of the mesozooplankton size fraction (>202 μm; Fig. 6). The micrometazoan size fraction (>64 μm to 202 μm) was com-

always the major component, ranging from 50 to 99.3% of the total phytoplankton biomass. Chl *a* concentration also was related to water temperature (linear regression;  $\log_{10} y = 0.853 + 0.015x$ ;  $df = 1, 49$ ,  $F = 10.321$ ,  $0.001 < p < 0.005$ ).

A bloom of *Aureococcus anophagefferens* occurred in West Neck Bay of the Peconic Bays system during June and July, and reached a peak concentration of  $1.43 \times 10^6$  cells ml<sup>-1</sup> on 6/17 (Fig. 5). By 7/22, the bloom had dissipated, and the concentration of this picoplankter was only  $2.74 \times 10^4$  cells ml<sup>-1</sup>. Dinoflagellates were also abundant during the brown tide peak, including *Dinophysis acuminata* (30 to 40 μm, 'red tide'), *Gymnodinium* spp. (>20 μm, 'red tide'), and *Polykrikos kofoidi* (60 to 80 μm, a heterotrophic dinoflagellate). During the decline of the brown tide (7/22), *Gymnodinium* spp. (≥20 μm) and *Protoperidinium* sp. (≥20 μm, a heterotroph) were noted. In GSB during the same summer period (7/25), a *Nannochloris*-like sp. (chlorophyte ~2 μm in diameter) was the major component of the <5 μm size fraction of planktonic phytoplank-

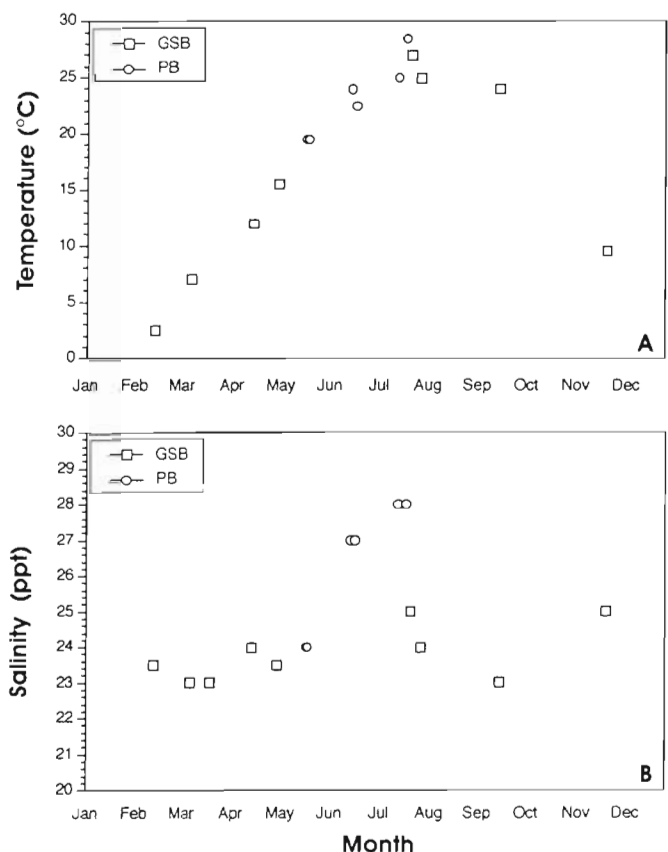


Fig. 3. (A) Water temperature and (B) salinity in Great South Bay (GSB) and the Peconic Bays (PB)

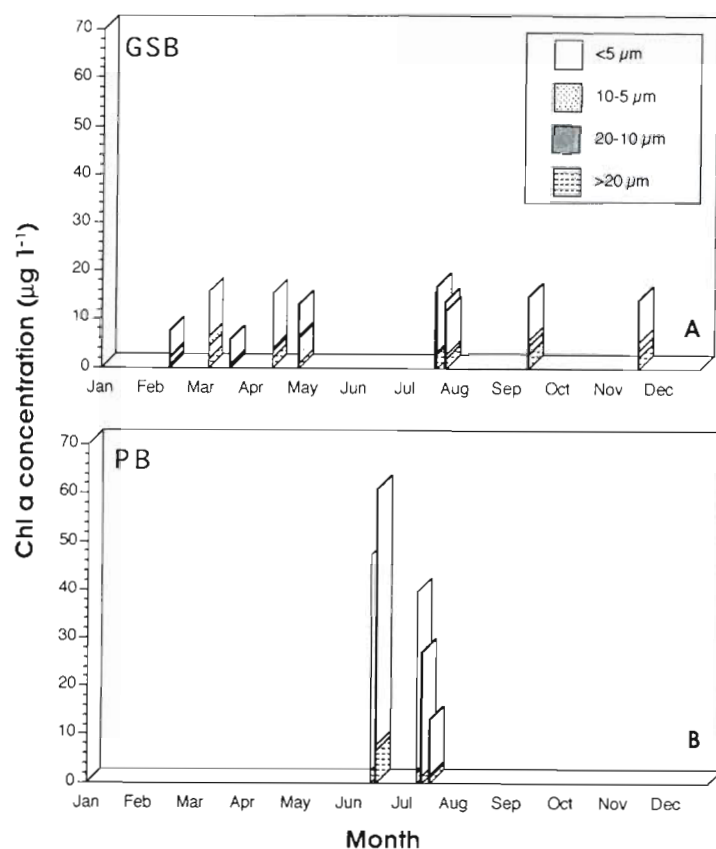


Fig. 4. Chlorophyll *a* concentration of 4 size fractions of phytoplankton in (A) Great South Bay, (B) Peconic Bays. Total chl *a* concentration is represented by the entire bar

prised mostly of copepod nauplii and meroplanktonic larvae (Fig. 6, Table 1) except on 7/25 and 7/31 when large tintinnids were also abundant. The mean density of total metazoan zooplankton was substantially lower in PB compared to GSB not only during the brown tide (27.1 vs 671.2  $l^{-1}$ , respectively, June and July comparison), but also in the spring (147.7 vs 729.5  $l^{-1}$ , May and April comparison)

Ciliates were most abundant in the ~20 to ≤64  $\mu m$  size fraction (Fig. 7), and throughout the year were

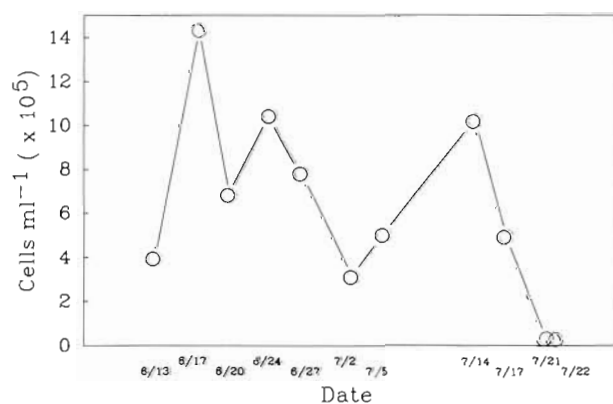


Fig. 5. Concentration of *Aureococcus anophagefferens* in West Neck Bay, PB during 1991. Dates given as Month/Day

represented by tintinnids and aloricate ciliates. The latter group were primarily oligotrichs in the family Strombidiidae. Scuticociliates were also frequently found. Following the decline of the brown tide in PB (7/22), however, the population was composed almost exclusively of small (~30 to 40  $\mu m$ ), aloricate ciliates at a density > 20 000  $l^{-1}$ .

### Population dynamics of ciliates

Multiple regression analysis revealed that the net growth coefficient of ciliate populations ( $d^{-1}$ ; Fig. 8) determined from grazer removal experiments was significantly correlated with water temperature (Table 2). Net growth coefficients were positive throughout the sampling period except in February in GSB when water temperature was the lowest (2.5°C), and during the peak of brown tide in PB (6/17). The highest rate of population increase was 1.24  $d^{-1}$  in PB during May. This analysis also showed a significant negative effect of cell concentration of *Aureococcus anophagefferens* on ciliate population growth. Salinity (‰) and total and <10  $\mu m$  depth-integrated primary productivity ( $mg\ C\ m^{-2}\ h^{-1}$ ) were not significant variables that explained variation in the net growth coefficient of ciliates (Table 2). These results suggest that growth of ciliates is not limited

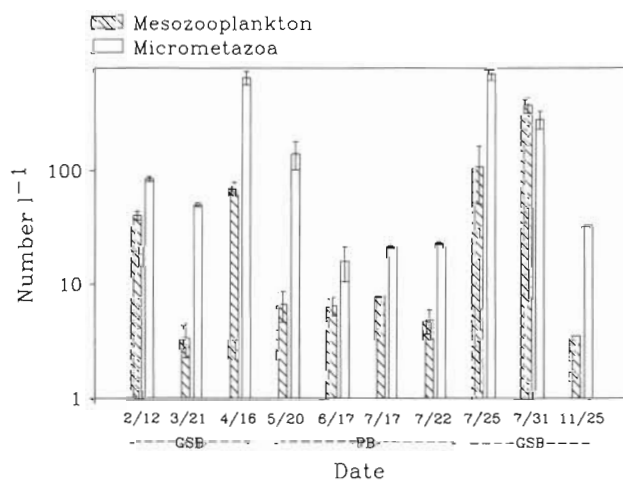


Fig. 6. Abundance (mean  $\pm$  range,  $n = 2$ ) of mesozooplankton and micrometazoa

Table 1. Abundance (number  $l^{-1}$ ) of the most common zooplankton taxa >64 to 202  $\mu m$  in Great South Bay (GSB) and the Peconic Bays (PB) during 1991

Taxon	Date (Month/Day)					
	2/12	3/21	4/16	7/25	7/31	11/25
<b>GSB</b>						
Copepod nauplii	83.5	48.1	617.8	423.8	163.5	31.1
Polychaete larvae	0.0	0.0	38.8	35.8	8.5	0.2
Barnacle larvae	0.0	0.0	1.8	1.0	0.0	0.0
Tintinnids	0.2	0.0	0.0	236.0	110.5	0.8
	5/20	6/17	7/17	7/22		
<b>PB</b>						
Copepod nauplii	49.5	14.2	19.9	18.0		
Polychaete larvae	3.4	0.3	0.6	4.2		
Barnacle larvae	57.4	1.3	0.0	0.1		
Tintinnids	0.2	0.0	0.0	0.0		

Table 2. Dependence of the net growth coefficient of ciliate populations ( $d^{-1}$ ) on ambient physical factors ( $^{\circ}C$  and ‰), primary productivity ( $mg\ C\ m^{-2}\ h^{-1}$ ), and brown tide concentration ( $\times 10^3\ cells\ ml^{-1}$ ) in Long Island bays determined from multiple regression analysis. The model was significant ( $df = 5, 14$ ;  $F = 15.047$ ;  $p < 0.001$ ), and explained 68.0% of the variance in the net growth coefficient

Variable	Partial regression coefficient	F (df = 1, 14)	p
Intercept	0.807		
Temperature	0.077	10.914	$0.005 < p < 0.01$
Salinity	-0.051	0.291	$0.5 < p < 0.75$
Primary productivity			
Total	0.012	1.547	$0.1 < p < 0.25$
<10 $\mu m$	-0.017	3.099	$0.1 < p < 0.25$
Brown tide concentration	-0.192	49.792	$p < 0.001$

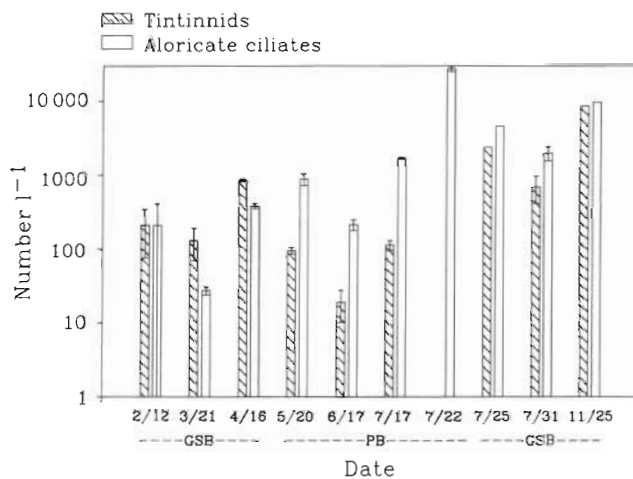


Fig. 7. Abundance (mean  $\pm$  range,  $n = 2$ ) of tintinnids and aloricate ciliates 20 to 64  $\mu m$

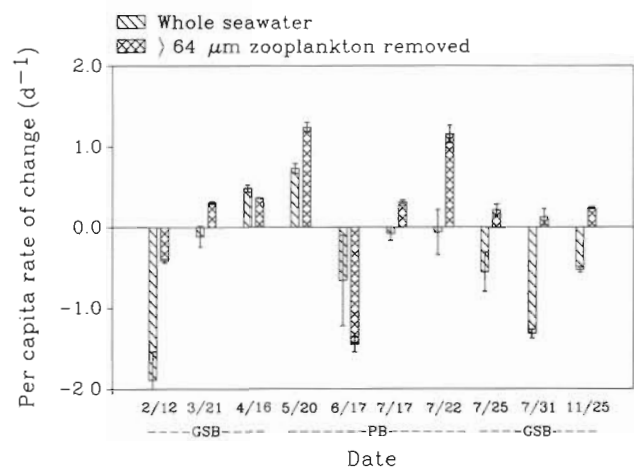


Fig. 8. Per capita rate of change (mean  $\pm$  range,  $n = 2$ ) of ciliate populations determined in microcosm experiments. The net growth coefficient of the ciliate population is shown as the >64  $\mu m$  zooplankton removal treatment

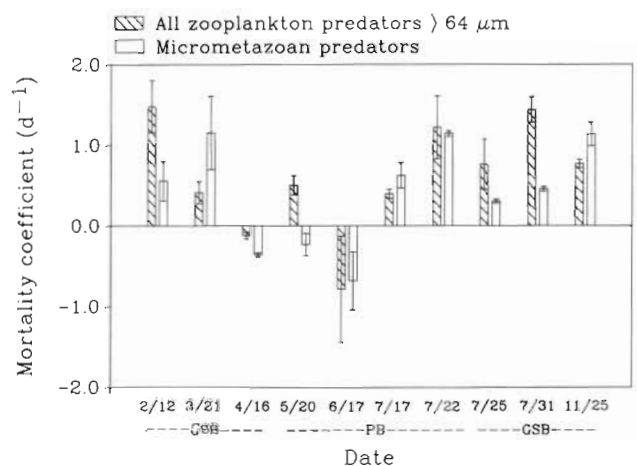


Fig. 9. Mortality coefficient of ciliate populations (mean  $\pm$  range,  $n = 2$ ) from all larger zooplankton (>64  $\mu m$ ) or only micrometazoa determined in microcosm experiments

by phytoplankton food resources under non-bloom conditions.

The mortality coefficient of ciliates ( $d^{-1}$ ; i.e. zooplankton predation coefficient) from total metazoan zooplankton was positive on all sampling dates, except in April in GSB (mean =  $-0.12\ d^{-1}$ ), and during the peak of the brown tide in PB ( $-1.445\ d^{-1}$ ; Fig. 9). However, the presence of *Aureococcus anophagefferens* cells was shown not to be a significant factor in contributing to variation in mortality rate (Table 3). Mortality rates were negatively correlated with >10  $\mu m$  primary production, and positively related to total primary production, the majority of which is mostly <5  $\mu m$ . During April, when a negative mortality rate



Table 3. Dependence of the mortality coefficient of ciliates ( $\text{d}^{-1}$ ) on water temperature ( $^{\circ}\text{C}$ ), total zooplankton abundance (number  $\text{l}^{-1}$ ), primary productivity ( $\text{mg C m}^{-2} \text{h}^{-1}$ ), brown tide concentration ( $\times 10^5$  cells  $\text{ml}^{-1}$ ), and the initial concentration of ciliates (number  $\text{l}^{-1}$ ) determined from multiple regression analysis. The model was significant ( $\text{df} = 6, 13$ ;  $F = 7.496$ ;  $0.001 < p < 0.005$ ), and explained 77.6% of the variance in the mortality coefficient

Variable	Partial regression coefficient	F (df = 1, 13)	p
Intercept	1.535		
Temperature	-0.062	5.591	$0.025 < p < 0.05$
Zooplank. abund.	-0.001	1.641	$0.50 < p < 0.75$
Primary productivity			
Total	0.007	11.693	$0.001 < p < 0.005$
$> 10 \mu\text{m}$	-0.046	8.873	$0.01 < p < 0.025$
Brown tide concentration	0.019	0.122	$0.50 < p < 0.75$
Initial ciliate abundance	0.055	6.662	$0.01 < p < 0.025$

Table 4. Dependence of the mortality coefficient of ciliates ( $\text{d}^{-1}$ ) on physical and biological variables as in Table 3, but excluding data during the peak of the brown tide on 6/17. The model was significant ( $\text{df} = 6, 11$ ;  $F = 4.723$ ;  $0.01 < p < 0.025$ ), and explained 72.0% of the variance in the mortality coefficient

Variable	Partial regression coefficient	F (df = 1, 11)	p
Intercept	1.531		
Temperature	-0.065	5.351	$0.025 < p < 0.05$
Zooplank. abund.	-0.001	2.075	$0.10 < p < 0.25$
Primary productivity			
Total	0.007	11.980	$0.005 < p < 0.010$
$> 10 \mu\text{m}$	-0.045	8.663	$0.01 < p < 0.025$
Brown tide concentration	0.034	0.102	$p > 0.75$
Initial ciliate abundance	0.057	8.059	$0.01 < p < 0.025$

was measured, the rate of primary production in the  $> 10 \mu\text{m}$  size fraction was higher than at any other time in GSB, and the same was also true in PB during the peak of the brown tide. Other variables that also explained variation in ciliate mortality rate included water temperature and the initial concentration of ciliates. The negative correlation between mortality and primary productivity by larger phytoplankton was not a spurious result due to the inclusion of data during the brown tide peak. An additional multiple regression analysis that excluded these data did not significantly change the statistical outcome for any independent variables (Table 4).

Our results indicate that both mesozooplankton and micrometazoa exert a significant impact on ciliate pop-

ulation growth. The average mortality coefficient of ciliates due to micrometazoa was on average 67.8% of the total mortality from all zooplankton. There was no significant difference among the mortality coefficients from the 2 zooplankton treatments ( $t$ -test for paired comparisons of mortality coefficients on each date;  $\text{df} = 19$ ,  $t = 1.23$ ,  $0.2 < p < 0.4$ ).

### Zooplankton grazing and predation

In general, mesozooplankton had a higher average carbon consumption rate per individual in winter/spring than in summer (Table 5), although averages were not significantly different ( $0.408 \pm 0.537$  95% confidence interval, CI, and  $0.036 \pm 0.061 \mu\text{g C ind.}^{-1} \text{h}^{-1}$  including brown tide dates, respectively). The highest phytoplankton carbon consumption by mesozooplankton in summer occurred on 7/17 during the brown tide,  $0.161 \mu\text{g C ind.}^{-1} \text{h}^{-1}$ , and in winter/spring on 3/21 ( $1.449 \mu\text{g C ind.}^{-1} \text{h}^{-1}$ ). In contrast, a seasonally based trend in phytoplankton carbon consumption by micrometazoa was not evident ( $0.056 \pm 0.051$  and  $0.028 \pm 0.028 \mu\text{g C ind.}^{-1} \text{h}^{-1}$  for winter/spring and summer, respectively).

Dietary trends in carbon ingestion showed that mesozooplankton obtained a smaller percentage of their diet from phytoplankton and more from ciliates (Table 6) during summer compared to winter and spring, the 2 exceptions being during the decline of brown tide. In contrast, micrometazoa routinely obtained  $> 70\%$  of their carbon intake from phytoplankton except during the decline of the brown tide. On two dates in spring and summer, the micrometazoan community grazed  $> 40\%$  of the total primary productivity ( $\% = \text{mg C ingested m}^{-2} \text{h}^{-1} / \text{mg C produced m}^{-2} \text{h}^{-1}$ , depth-integrated rates  $\times 100$ ; Table 7), and this occurred when copepod nauplii were an abundant taxon (Table 1). The greatest grazing pressure by mesozooplankton was found in winter and spring when  $\geq 15\%$  of total depth-integrated primary productivity was consumed.

Throughout the year, adult copepods had a higher clearance rate ( $\text{ml ind.}^{-1} \text{d}^{-1}$  determined from addition experiments; Fig. 10) on ciliates compared to the average rate on phytoplankton (Fig. 11; paired  $t$ -test for differences between means on each sampling date;  $\text{df} = 9$ ,  $t = 2.425$ ,  $0.02 < p < 0.05$ ). For a conservative comparison, we calculated zooplankton clearance rates on phytoplankton by assuming that negative rates were equal to 0 (Fig. 11). Two points for micrometazoan clearance were excluded from the data because they were more than an order of magnitude higher than other rates and were deemed to be outliers (Dixon-Massey test; Sokal & Rohlf 1981;  $427.1 \text{ ml ind.}^{-1} \text{d}^{-1}$

Table 5. Carbon ingested ( $\mu\text{g C ind.}^{-1} \text{ h}^{-1}$ ; mean  $\pm$  1 SE,  $n = 4$ ) by mesozooplankton (M) and micrometazoa (m) from 4 size fractions of the phytoplankton community. Total carbon ingestion does not always equal the summation of all fractions due to rounding errors. Radiolabeled, laboratory cultured microalgae were used as tracers of size-selective grazing;  $< 5 \mu\text{m}$  diameter: *Nannochloris* sp.;  $5\text{--}10 \mu\text{m}$ : *Thalassiosira pseudonana*;  $10\text{--}20 \mu\text{m}$ : *Thalassiosira weissflogii*;  $> 20 \mu\text{m}$ : *Ditylum brightwellii*.

Negative ingestion rates are shown as 0. Brown tide dates in West Neck Bay, Peconic Bays system are noted by \*

Date		Phytoplankton size-fraction ( $\mu\text{m}$ diameter)				Total
		$< 5$	$5\text{--}10$	$10\text{--}20$	$> 20$	
2/12	M	0.026 (0.012)	0.009 (0.003)	0.004 (0.005)	0.005 (0.003)	0.043
	m	0.005 (0.003)	0.002 (0.003)	0.003 (0.001)	$< 0.001$ (0.003)	0.011
3/21	M	1.339 (0.293)	0.075 (0.027)	0.030 (0.010)	0.005 (0.006)	1.449
	m	0.067 (0.017)	0.004 ( $< 0.001$ )	0.003 ( $< 0.001$ )	0.001 ( $< 0.001$ )	0.075
4/16	M	0.023 (0.017)	0.009 (0.008)	0.017 (0.010)	0.011 (0.007)	0.060
	m	0.024 (0.024)	$< 0.001$ ( $< 0.001$ )	0.017 (0.011)	0.009 (0.005)	0.051
5/21	M	0.002 (0.001)	0	0.004 (0.002)	0	0.007
	m	$< 0.001$ ( $< 0.001$ )	0	$< 0.001$ ( $< 0.001$ )	0	$< 0.001$
*6/17	M	0	0	$< 0.001$ ( $< 0.001$ )	0	$< 0.001$
	m	0	$< 0.001$ ( $< 0.001$ )	0	0	$< 0.001$
*7/17	M	0.159 (0.169)	$< 0.001$ ( $< 0.001$ )	$< 0.001$ ( $< 0.001$ )	0.001 (0.008)	0.161
	m	0	$< 0.001$ ( $< 0.001$ )	0.001 ( $< 0.001$ )	0.002 (0.001)	0.002
*7/22	M	0	0	$< 0.001$ ( $< 0.001$ )	0	$< 0.001$
	m	0	0.011 (0.009)	0	0.025 (0.021)	0.036
7/25	M	0.007 (0.063)	$< 0.001$ ( $< 0.001$ )	$< 0.001$ ( $< 0.001$ )	0	0.007
	m	0.047 (0.046)	0.006 (0.001)	$< 0.001$ ( $< 0.001$ )	0.025 (0.003)	0.078
7/31	M	0.003 (0.003)	$< 0.001$ ( $< 0.001$ )	0.002 (0.001)	0.006 (0.003)	0.012
	m	0.002 (0.001)	$< 0.001$ ( $< 0.001$ )	0.004 ( $< 0.001$ )	0.018 (0.004)	0.023
11/25	M	0.465 (0.211)	0.005 (0.003)	0.011 (0.003)	0	0.480
	m	0.054 (0.078)	0.004 (0.002)	0.004 (0.001)	0.084 (0.090)	0.145

with *Thalassiosira pseudonana* as a tracer on 3/21 and  $458.7 \text{ ml ind.}^{-1} \text{ d}^{-1}$  with *Nannochloris* sp. on 7/22). On only 1 sampling date (7/22) was the clearance rate on ciliates less than that on phytoplankton for adult copepods. For micrometazoa, however, the dietary importance of the larger ciliates is less certain. In the grazer

addition experiments, naupliar clearance rates on ciliates were positive for only 50% of the experimental dates (Fig. 10). Clearance rates of micrometazoa were not effected by prey type (paired  $t$ -test;  $df = 9$ ,  $t = 0.910$ ,  $p > 0.2$ ).

Table 6. Total carbon ingested ( $\mu\text{g C ind.}^{-1} \text{ h}^{-1}$ ) (I) and percentage carbon intake from phytoplankton (PP) and ciliates (C) for total mesozooplankton and micrometazoa

Bay	Date	Mesozooplankton			Micrometazoa		
		I	PP	C	I	PP	C
GSB	2/12	0.047	92.1	7.2	0.011	97.6	2.4
	3/21	1.451	99.9	0.1	0.075	99.4	0.6
	4/16	0.085	70.7	29.3	0.051	100.0	0.0
PB	5/20	0.015	43.7	56.3	$< 0.001$	63.4	36.6
	6/17	0.004	8.6	91.4	$< 0.001$	100.0	0.0
	7/17	0.171	93.6	5.4	0.007	37.3	62.7
	7/22	$< 0.001$	100.0	0.0	0.400	9.0	91.0
GSB	7/25	0.071	10.1	89.9	0.109	71.1	28.9
	7/31	0.037	32.7	67.3	0.024	98.3	1.7
	11/25	0.550	87.5	12.5	0.266	54.6	45.4

### Copepod egg production and hatching success

Copepod egg production during summer (i.e. by *Acartia tonsa*) was limited by food, but this was not true in winter or spring (i.e. by *A. hudsonica*; Fig. 12). This was shown by the significant effect of sampling date  $\times$  food treatment (ambient or enriched) on egg production rate [ $\log(\text{number} + 1) \text{ female}^{-1} \text{ d}^{-1}$ ; 2-way ANOVA;  $df = 6, 48$ ,  $F = 4.74$ ,  $p < 0.001$ ]. Egg production rate also increased significantly during the summer ( $df = 6, 48$ ,  $F = 60.44$ ,  $p < 0.0001$  for sampling date effect;  $df = 1, 48$ ,  $F = 2.29$ ,  $p = 0.14$  for food treatment effect).

Under ambient food conditions, water temperature did not correlate with egg produc-

Table 7. Total depth-integrated carbon ingested ( $\text{mg C m}^{-2} \text{ h}^{-1}$ ) (I) and percentage of total depth-integrated primary production consumed by mesozooplankton and micrometazoa

Bay	Date	Mesozooplankton		Micrometazoa	
		I	%	I	%
GSB	2/12	2.638	14.9	2.197	12.4
	3/21	6.086	24.5	5.627	22.6
	4/16	4.952	5.1	50.371	52.3
PB	5/20	0.047	<0.1	0.051	<0.1
	6/17	0.003	<0.01	<0.001	<0.001
	7/17	1.697	2.8	0.074	0.1
	7/22	<0.001	<0.001	2.570	2.0
GSB	7/25	6.529	3.9	73.865	44.2
	7/31	4.525	1.4	9.974	3.1
	11/25	12.524	29.5	7.227	17.0

tion rate (Multiple Regression analysis; Table 8). However, the production of ciliate food resources, as measured by their net growth coefficient, was directly related to copepod reproduction. The cell concentration of *Aureococcus anophagefferens* was negatively correlated to egg production rate, and likely reflected the fact that ciliate growth and *A. anophagefferens* cell concentration were negatively correlated (Table 2). All remaining environmental variables, including copepod species and total and  $>10 \mu\text{m}$  depth-integrated primary productivity, did not correlate to egg production rate.

Egg hatching success of copepod eggs produced under ambient food conditions remained high throughout the study ( $>75\%$ ; Fig. 13), although there was an effect of sampling date ( $R \times C$  test of independence,  $df = 5$ ,  $G = 50.081$ ,  $p > 0.001$ . Variances in the

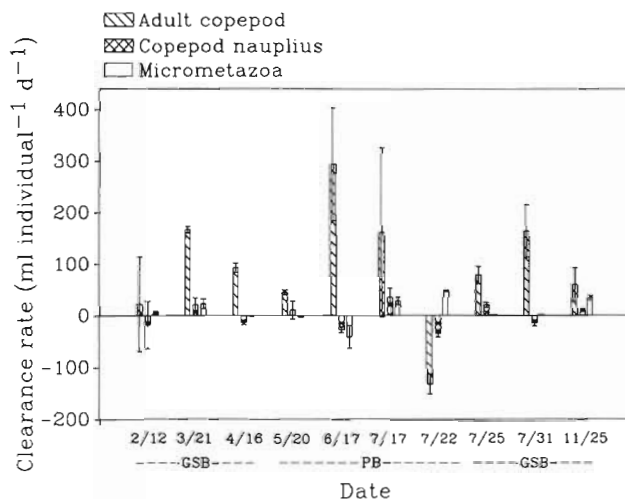


Fig. 10. Clearance rate (mean  $\pm$  range,  $n = 2$ ) of zooplankton predators (copepod adults, copepod nauplii, and natural assemblages of micrometazoa) on ciliates  $\leq 64 \mu\text{m}$

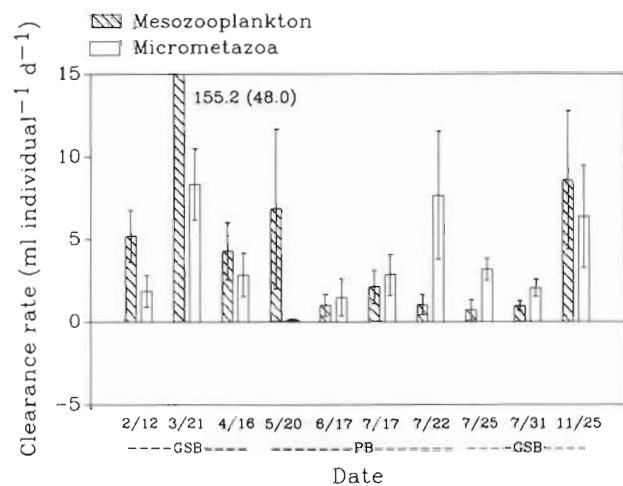


Fig. 11. Average clearance rate ( $\pm 1$  SE, generally,  $n = 16$  for all size fraction clearance rates) of mesozooplankton and micrometazoa on the total phytoplankton community

data sets were not normally distributed with an arcsine transformation, and thus a non-parametric test was necessary; Sokal & Rohlf 1981). The lowest success occurred during the winter months.

#### Copepod development rate and survival with brown tide

Naupliar and copepodite survival were not affected by the addition of either *Thalassiosira pseudonana* or brown tide cells to ambient seawater compared to ambient conditions. Survival of copepods with only brown tide cells for food was the same as in autoclaved seawater (Fig. 14). In suspension of only brown tide

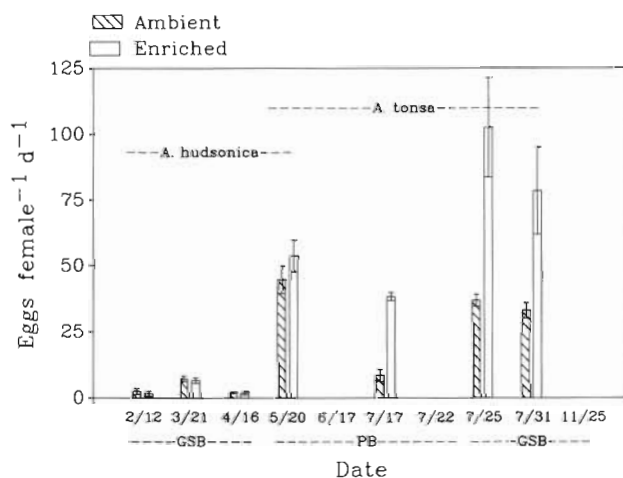


Fig. 12. Mean egg production rate ( $\pm 1$  SE,  $n = 3$  to 6) of *Acartia* spp. under ambient and enriched food conditions. Experiments were not conducted on 6/17, 7/22 or 11/25

Table 8. Dependence of ambient egg production rate (log number + 1 copepod<sup>-1</sup> d<sup>-1</sup>) on water temperature (°C), copepod species composition, primary productivity (mg C m<sup>-2</sup> h<sup>-1</sup>), brown tide concentration ( $\times 10^5$  cells ml<sup>-1</sup>), and the net growth coefficient of ciliates (d<sup>-1</sup>) determined from multiple regression analysis. The model was significant (df = 6, 27;  $F = 28.660$ ;  $p < 0.001$ ) and explained 86.4% of the variance in egg production rate

Variable	Partial regression coefficient	$F$ (df = 1, 27)	$p$
Intercept	0.521		
Temperature	0.047	0.633	0.25 < $p$ < 0.50
Copepod species	0.306	0.169	0.50 < $p$ < 0.75
Primary productivity			
Total	0.002	1.256	0.25 < $p$ < 0.50
>10 $\mu$ m	-0.048	3.088	0.05 < $p$ < 0.10
Brown tide concentration	-0.115	4.392	0.025 < $p$ < 0.05
Net growth coefficient of ciliates	0.528	12.223	0.001 < $p$ < 0.005

Table 9. Mean ( $\pm 1$  SE) development time (h) of *Acartia hudsonica* copepodites (CI to CIII) and *Coullana canadensis* nauplii (NI to CI) reared under 3 food treatments (AMB: ambient seawater; AMB + 3H: ambient seawater enriched with *Thalassiosira pseudonana* cells; and AMB + BT: ambient seawater enriched with *Aureococcus anophagefferens* cells). Copepods did not complete development with only filtered seawater or brown tide cells

Species	AMB	Treatment	
		AMB + 3H	AMB + BT
<i>A. hudsonica</i>			
n	8	10	12
x	67.5	61.3	72.7
SE	3.3	1.5	5.5
<i>C. canadensis</i>			
n	13	15	14
x	112.1	105.2	116.2
SE	1.8	1.7	1.7

cells or filtered seawater, nauplii and copepodites did not molt past NII or CII, respectively. Copepodite development rates were not significantly different among the 3 other food treatments (ambient, ambient + brown tide cells, ambient + *T. pseudonana* cells; 1-way ANOVA, df = 2, 27,  $F = 1.33$ ,  $p = 0.28$ ; Table 9), but naupliar development rate was faster with 3H additions compared to ambient or brown tide addition treatments (ANOVA, df = 2, 39,  $F = 10.95$ ,  $p = 0.0002$ , and Tukey-Kramer unplanned comparisons among means at 0.05 level of significance). Thus, the brown tide did not contribute to or hinder growth and survival of copepods at lower bloom concentrations (i.e.  $5 \times 10^5$  cells ml<sup>-1</sup>) in the presence of alternate food sources.

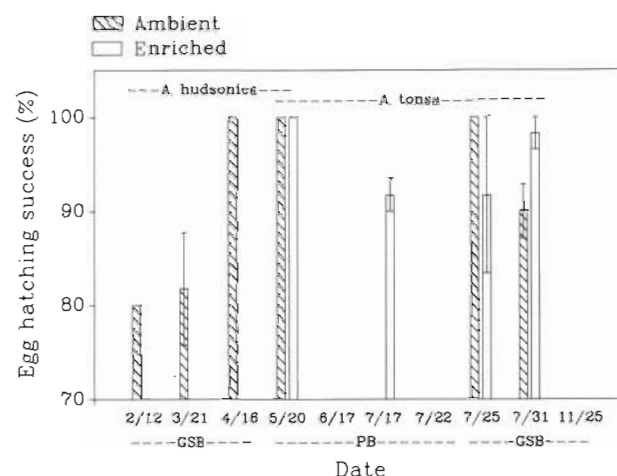


Fig. 13. Mean hatching success ( $\pm 1$  SE,  $n = 3$  to 6) of copepod eggs produced under ambient and enriched food conditions by *Acartia* spp.

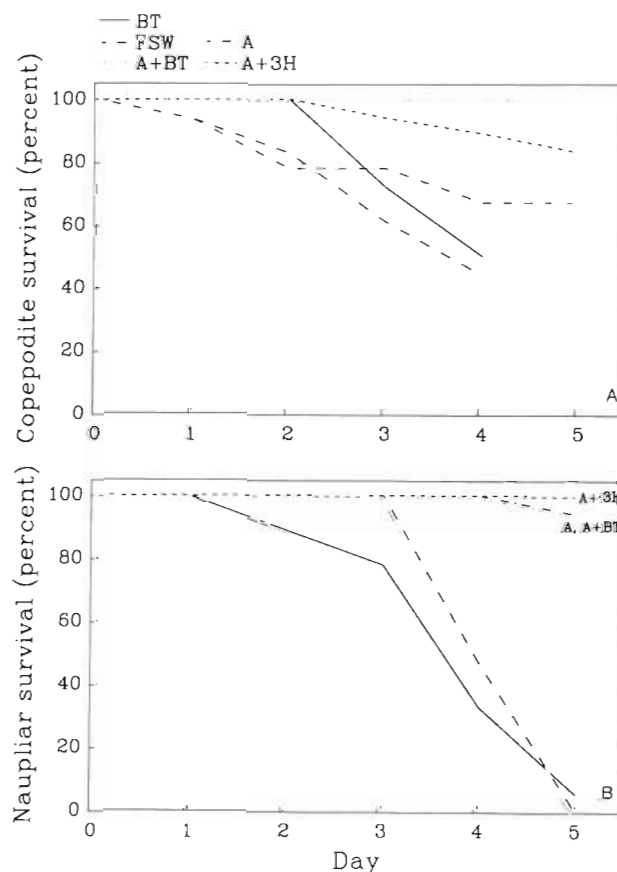


Fig. 14. Percentage survival of laboratory-reared copepods, (A) *Acartia hudsonica* (NVI to CIII) and (B) *Coullana canadensis* (NI to CI), reared under 16 and 20°C, respectively, and 5 food treatments (BT: brown tide cells only; FSW: filtered seawater; A: ambient seawater; A + BT: ambient plus brown tide cells; A + 3H: ambient plus *Thalassiosira pseudonana* cells).



## DISCUSSION

This study supports the idea that predation on protozoa is critical for copepod production in summer when nanoplankton  $<5\ \mu\text{m}$  dominate the phytoplankton. Although larger nanoplankton and netplankton ( $>20\ \mu\text{m}$ ) never dominated the plankton in terms of either productivity or biomass, phytoplankton was a major source of carbon nutrition for copepods in winter and spring. Holoplanktonic and meroplanktonic larvae, however, almost always utilized phytoplankton to obtain the majority of their carbon ration. The carbon ration accrued from ciliates by micrometazoa may be a passive consequence of feeding on phytoplankton as no prey-dependent difference in clearance rates was found. In contrast, adult copepods routinely had a higher clearance rate on ciliates compared to phytoplankton throughout the year.

Laboratory studies by Jonsson & Tiselius (1990) showed that *Acartia tonsa* adults switched between suspension and raptorial feeding depending on the concentration of phytoplankton. *Acartia* spent more time in suspension feeding under high concentrations of the flagellate *Rhodomonas baltica* ( $\sim 8\ \mu\text{m}$  width,  $13\ \mu\text{m}$  length) compared to low or moderate concentrations. Such a switch in feeding behavior could explain our field results which indicated that the mortality coefficient of ciliates from all zooplankton was inversely correlated with  $>10\ \mu\text{m}$  primary productivity and positively related to total depth-integrated primary productivity (Fig. 9, Table 2). Necessary for this explanation would be the lack of response (detection?) by copepods to the high productivity rates of the  $<5\ \mu\text{m}$  phytoplankton in summer, and hence raptorial feeding may predominate. However, a concomitant increase in adult copepod clearance rates (per individual) on ciliates in the summer was not obvious in our study (Fig. 10), except during the peak of the brown tide. Increased ciliate concentrations during the summer may have negated the necessity for increased time spent in raptorial feeding for copepods to increase their ration.

Our finding that in GSB in summer, ciliates were more important than phytoplankton in mesozooplankton diets does not match studies in Chesapeake Bay. For *Acartia tonsa*, at least, over 80% of the carbon ingested was from phytoplankton in August compared to only 19% in May in Chesapeake Bay (White & Roman 1992a). These differences could be due to variation among locations in the composition of phytoplankton, although a seasonal shift from diatoms to flagellates is also characteristic of Chesapeake Bay (Malone et al. 1988, cited by White & Roman 1992b).

Few studies have measured feeding rates of meroplanktonic and holoplanktonic larvae and other

micrometazoa on natural plankton despite the fact that their weight-specific ingestion rates may be 3 to 4 times higher than adults, and that numerically they are usually very important (e.g. Lonsdale & Coull 1977, Turner 1982). Using other  $^{14}\text{C}$  tracer techniques (i.e. Daro 1978, Roman & Rublee 1981), Kim (1993) found that the micrometazoan community in the Peconic Bays system graze on average 0.3 to 10.0% of total depth-integrated primary productivity compared with 0.2 to 4.3% for mesozooplankton. In GSB in summer, we found that micrometazoa consume the greatest percentage of total depth-integrated primary productivity compared to mesozooplankton (Table 6). The impact of micrometazoan grazing was greatest when copepod nauplii were an abundant taxon (i.e. 4/16 and 7/25; Table 1). Thus, these results agree with studies in the Chesapeake Bay (White & Roman 1992b) that showed copepod nauplii often accounted for a large proportion of the total zooplankton grazing, and removed up to 50% of the total depth-integrated primary production in summer.

Zooplankton predation on a major nanoplankton consumer, the ciliates (Capriulo & Carpenter 1980, Verity 1985, Sherr et al. 1991, Pierce & Turner 1992 and references therein, Turner & Granéli 1992), may contribute to the dominance of small phytoplankton in GSB, particularly in summer (Kim 1993). And although not specifically studied herein, we propose that mesozooplankton predation on micrometazoa, especially copepod nauplii (Lonsdale et al. 1979), could at times also have a 'cascading' (sensu Carpenter et al. 1987) influence on the phytoplankton community. We have shown herein that micrometazoa are important grazers of phytoplankton in Long Island bays, and it is known that copepod nauplii are prey for some adult copepods (e.g. Landry 1981). Thus, copepod nauplii likely serve as an additional link between primary productivity and mesozooplankton productivity in Long Island bays. As an example, depending on naupliar species and stage, adult *Acartia tonsa* may consume between 1.4 to 8.4 nauplii  $\text{d}^{-1}$  at a concentration ranging from  $\sim 50$  to 300 prey  $\text{l}^{-1}$  (Lonsdale et al. 1979). Thus, it is possible that mesozooplankton could obtain up to an additional  $0.015\ \mu\text{g C ind.}^{-1}\ \text{h}^{-1}$  from copepod nauplii, which is about 11 to 29% of that obtained from ciliate predation in summer (i.e. 7/25 and 7/31). [We used the dry weight of *Acartia clausi* NV and NVI,  $0.1\ \mu\text{g}$  (Marshall 1973), and assumed a carbon equivalent of 41.6% of the dry weight (Beers 1966) to estimate naupliar carbon content.] Naupliar predation by mesozooplankton may also be an important trophic link between primary productivity and copepod productivity in the Chesapeake Bay because nauplii also consume a significant fraction of the primary productivity (White & Roman 1992b).

Our grazing experiments were conducted for 7 min to minimize error from carbon recycling processes. Extrapolation of these short-term experiments to daily rates may not be appropriate given that zooplankton can exhibit diel variation in grazing activity. Roman et al. (1988) found that coastal copepods often showed higher feeding at night and that oceanic forms sometimes had higher feeding rates during the day. Mesozooplankton clearance rates on phytoplankton that we measured using radiolabeled algae were similar to Louisiana (USA) field populations of *Acartia tonsa* determined from gut pigment analysis (Gifford & Dagg 1991) when the exceptionally high mean for 3/21 (155.2 ml ind.<sup>-1</sup> d<sup>-1</sup>; Fig. 11) is excluded from the data set [yearly average on all algal species = 3.4 (±1.9 95% CI) ml ind.<sup>-1</sup> d<sup>-1</sup> compared to 3.6 ml ind.<sup>-1</sup> d<sup>-1</sup>, respectively]. Including the 3/21 clearance rate data also resulted in no significant difference among the studies (18.6 ± 29.8 95% CI). Also, total carbon ingestion rates of phytoplankton had similar seasonally based trends. For Long Island bays, ingestion rates averaged 0.9 µg C ind.<sup>-1</sup> d<sup>-1</sup> in summer (i.e. primarily *A. tonsa*) and 9.8 µg C ind.<sup>-1</sup> d<sup>-1</sup> in winter/spring (*A. hudsonica*), and in Louisiana, 1.9 and 4.7 µg C copepod<sup>-1</sup> d<sup>-1</sup>, respectively (*A. tonsa* year-round). Limitations of the radiotracer technique for measuring zooplankton grazing, however, became apparent during the experiments conducted in PB during the brown tide. The negative clearance rates of micrometazoa on <5 µm microalgae at this time are attributed to an experimental artifact due to the large number of *Nannochloris* sp. tracer cells retained on the 64 µm sieve at the high experimental concentrations (20% of the <5 µm biomass; Lonsdale & Coper 1994) that masked any detectable feeding by the few micrometazoa (16.5 to 23.7 l<sup>-1</sup>). Occasionally, relatively high values for the filtrate control were also obtained, and we can only speculate as to the cause. Variation in grazing rate estimates within a sampling date was likely due to variation in zooplankton density in the grazing chambers, especially when density was low (e.g. on 3/21 when the average mesozooplankton concentration was lowest, 2.8 l<sup>-1</sup>).

In Long Island bays, mesozooplankton clearance rates on ciliates when *Acartia tonsa* was abundant were mostly comparable to other studies of copepods preying on natural assemblages of ciliates and/or other protists such as *Euglenoid* sp. (average = 25.2 and 23.8 ml copepod<sup>-1</sup> d<sup>-1</sup>; Gifford & Dagg 1991, Kim & Chang 1992, respectively). The clearance rates on ciliates in Long Island bays when *A. hudsonica* was dominant, however, were on average higher than those in a natural prey assemblage during a dinoflagellate bloom in another temperate bay (4.8 to 9.6 ml copepod d<sup>-1</sup>; Turner & Anderson 1983). Mesozooplankton carbon

ingestion rates of ciliates in Long Island bays match closely that found by Gifford & Dagg (1991); average = 0.4 µg C ind.<sup>-1</sup> d<sup>-1</sup> in winter/spring, and 2.5 µg C ind.<sup>-1</sup> d<sup>-1</sup> in summer/fall compared with 0.1 and 2.1 µg C copepod<sup>-1</sup> d<sup>-1</sup>, respectively, for *A. tonsa* in Louisiana.

Mesozooplankton were found to have high ingestion rates on phytoplankton in the spring in Long Island bays and copepod egg production was not food limited, at least as measured by our food enrichment studies. Over the course of spring and summer, however, we found that egg production was not related to either total or >10 µm depth-integrated primary production, but to the net growth coefficient of ciliates. In Chesapeake Bay following the spring bloom, egg production by *Acartia tonsa* was also positively related to microzooplankton (>10 µm) (measured as carbon concentration), while no relationship to chl *a* concentration (total or >10 µm size fraction) was found despite substantial ingestion of phytoplankton (White & Roman 1992a).

There have been numerous field studies that conclude that water temperature is a major factor controlling egg production rate in copepods (e.g. Durbin et al. 1992). Our result showing no relationship of copepod egg production to temperature is not particularly strong because we have limited data for each copepod species (i.e. *Acartia hudsonica* and *A. tonsa*). However, a significant positive effect of temperature on egg production rate was calculated when the net growth rate of ciliates was not included as an independent variable in the multiple regression analysis (df = 1,28, *F* = 18.080, *p* < 0.001). White & Roman (1992a) found that both water temperature and carbon concentration of microzooplankton, and not phytoplankton abundance, were 'the best indicators of *A. tonsa* reproductive potential in Chesapeake Bay'. Perhaps the correlation between water temperature and egg production rate found in some field studies may partially reflect the underlying relationship of water temperature effects on the production rate of ciliate populations (Table 2).

### Ciliate population dynamics

Robertson (1983) suggested that tintinnid population growth would only be suppressed when adult copepod densities exceeded 10 l<sup>-1</sup> (also see Pierce & Turner 1992). In GSB, at least, adult copepod populations routinely exceeded this concentration, ranging from 2.8 to 248 l<sup>-1</sup> (Fig. 6). Ciliate population growth, however, was also suppressed by micrometazoa predation that contributed on average 67.8% to the total daily mortality from all zooplankton. This substantial influence on ciliate population growth was found despite the fact that ciliates contributed only a small percentage, usu-

ally <30%, to the daily carbon ration of micrometazoa. It is possible, however, that our measures of ciliate mortality from predation deviated from nature. For example, small-scale turbulence impacts the detection and/or contact rates of some predators and prey (e.g. Rothschild & Osborn 1988), and turbulence effects may have been altered in the microcosms.

The net growth coefficient of ciliate populations that we measured in Long Island bays (Fig. 8) was always lower than during spring in a Massachusetts bay; 1.55 and 0.77 d<sup>-1</sup> for an aloricate and large tintinnid, respectively (Stoecker et al. 1983). During the spring and summer in Long Island bays, however, the net growth coefficient of aloricate ciliates reached 1.17 to 1.31 d<sup>-1</sup> (7/22 and 5/20, respectively). Tintinnid growth rates, on the other hand, reached a maximum rate of only 0.35 d<sup>-1</sup> found in early spring (3/21).

### Brown tide effects on plankton trophic interactions

This investigation shows the importance of ciliates in the diets of metazoan zooplankton, and provides insight into the manner in which blooms of *Aureococcus anophagefferens* may alter plankton dynamics. Previous studies on plankton dynamics in Long Island bays during brown tides have shown that grazing, measured with fluorescently labeled algae and bacteria, and growth of some species of protozoa were not suppressed in the presence of a brown tide (PB and GSB; Caron et al. 1989), yet we found ciliate population growth to be negatively affected. It is noteworthy that the cell concentrations of *A. anophagefferens* under which Caron et al. conducted their laboratory and field investigations were lower ( $1 \times 10^6$  cells ml<sup>-1</sup> and  $\sim 1 \times 10^4$  to  $4 \times 10^5$  cells ml<sup>-1</sup>, respectively) than during our study on 6/17 ( $1.46 \times 10^6$  cells ml<sup>-1</sup>) when a negative growth rate of the ciliate population occurred (Fig. 8). We also found that the density of aloricate ciliates increased substantially from 6/17 to 7/22 (230 to 27400 l<sup>-1</sup>) during the decline of the brown tide (to  $3 \times 10^4$  cells ml<sup>-1</sup>). Thus, these 2 studies are not inconsistent, but rather suggest a 'threshold' phenomenon in which microbial processes, especially protozoan grazing and production, continue over a wide range of cell concentrations of *A. anophagefferens*, and are disrupted only during peak bloom conditions (i.e.  $>1 \times 10^6$  cells ml<sup>-1</sup>). This hypothesis is further supported by our laboratory findings on copepod growth and survival, which showed that at  $5 \times 10^5$  cells ml<sup>-1</sup> there were no detrimental effects of the brown tide if alternate food sources were available.

During 1985 and 1986, the bloom of *Aureococcus anophagefferens* did not appear to be associated with reduced copepod abundances in GSB (Duguay et al.

1989), and abundances were not unlike those we found during the 1991 non-bloom year. For 1986, when extensive monitoring of the brown tide was conducted in GSB, the average concentration was  $1.4 \times 10^5$  cells ml<sup>-1</sup>, and reached a peak of only 6 to  $7 \times 10^5$  cells ml<sup>-1</sup> (Nuzzi & Waters 1989). Other phytoplankton such as *Nannochloris* sp., a likely food resource for many protozoa, also outnumbered *A. anophagefferens*. Thus, microbial processes likely remained intact, and allowed for normal levels of zooplankton productivity. Durbin & Durbin (1989) also provide evidence that lower concentrations of brown tide cells are not especially detrimental to zooplankton production. They reported that *Acartia tonsa* weight, 'condition factor', and egg production rate during a brown tide ( $7.6 \times 10^5$  cells ml<sup>-1</sup>) in Narragansett Bay (Rhode Island, USA) were low, but not unlike those sometimes found in other non-bloom years. We found that egg production rates were significantly affected by the brown tide, but this observation (7/17) was made just after the brown tide had reached over  $1 \times 10^6$  cells ml<sup>-1</sup> on 7/14 (Fig. 5). However, we cannot conclude from our limited sampling in 1991 that the lower summer density of PB zooplankton compared to GSB was due to brown tide cell concentration on 6/17 because these differences may be due to local differences, and we do not have estimates for West Neck Bay (PB) prior to the bloom.

### Conclusion

This study has shown that the relative importance of phytoplankton and ciliates as prey differs among mesozooplankton and micrometazoa in Long Island bays. But, because their food resource niches are not mutually exclusive, and because micrometazoa comprise a major component all larger zooplankton, exploitative competition for ciliates is likely intense, particularly in the summer. During summer, the mortality coefficient often exceeds the net growth coefficient of ciliates, and thus ciliates may be in short supply. The effects of competition for ciliates may be especially acute for mesozooplankton, and this hypothesis is supported by our finding that ambient food resources limited the production rate of copepod eggs during the summer months. We do not have similar evidence to determine the impact of food limitation on growth of micrometazoa. However, it is probable that food limitation effects under non-bloom conditions would be minimal on copepod naupliar or polychaete larval growth, as also found for ciliates, because phytoplankton is not in short supply, at least as measured by rates of primary productivity in Long Island bays. Future studies on the role of food limitation on zooplankton growth and survival rates will provide insight



into the biological processes controlling recruitment in coastal bays. Measurements of food limitation in zooplankton will also enhance our understanding of the evolution and significance of life-history variation among marine invertebrate populations.

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#### LITERATURE CITED

- Anderson DM, Kulis DM, Cetta CM, Cosper EM (1989) Immunofluorescent detection of the brown tide organism, *Aureococcus anophagefferens*. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 213–228
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Mar Ecol Prog Ser* 10:257–263
- Beers JR (1966) Studies on the chemical composition of the major zooplankton groups in the Sargasso Sea. *Limnol Oceanogr* 11:520–528
- Bruno SF, Staker RD, Sharma GM, Turner JT (1983) Primary productivity and phytoplankton size fraction dominance in a temperate North Atlantic estuary. *Estuaries* 6:200–211
- Capriulo GM, Carpenter EJ (1980) Grazing by 35 to 202  $\mu\text{m}$  microzooplankton in Long Island Sound. *Mar Biol* 56:319–326
- Caron DA, Lim EL, Kunze H, Cosper EM, Anderson DM (1989) Trophic interactions between nano- and microzooplankton and the 'brown tide'. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 265–294
- Carpenter EJ, Brinkhuis BM, Capone DG (1991) Primary production and nitrogenous nutrients in Great South Bay. In: Schubel JR, Bell TM, Carter HH (eds) The Great South Bay. State University of New York Press, Albany, p 33–42
- Carpenter SR, Kitchell JF, Hodgson JR, Cochran PA, Elser JJ, Elser MM, Lodge DM, Kretchmer D, He X (1987) Regulation of lake primary productivity by food web structure. *Ecology* 68:1863–1876
- Conover RJ (1982) Interrelationships between microzooplankton and other plankton organisms. *Ann Inst Oceanogr*, Paris 58(S):3146
- Cosper EM, Carpenter EJ, Cottrell M (1989) Primary productivity and growth dynamics of the 'brown tide' in Long Island embayments. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 139–158
- Daro MH (1978) A simplified  $^{14}\text{C}$  method for grazing measurements on natural planktonic populations. *Helgoländer Wiss Meeresunters* 31:241–243
- Duguay LE, Monteleone DM, Quaglietta C (1989) Abundance and distribution of zooplankton and ichthyoplankton in Great South Bay, New York during the brown tide outbreaks of 1985 and 1986. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 599–623
- Durbin AG, Durbin EG (1989) Effect of the 'brown tide' on feeding, size and egg laying rate of adult female *Acartia tonsa*. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 625–645
- Durbin EG, Durbin AG, Campbell RG (1992) Body size and egg production in the marine copepod *Acartia hudsonica* during a winter-spring bloom in Narragansett Bay. *Limnol Oceanogr* 37:342–360
- Durbin EG, Durbin AG, Smayda TJ, Ventry PC (1983) Food limitation of production by adult *Acartia tonsa* in Narragansett Bay, Rhode Island. *Limnol Oceanogr* 28:1199–1213
- Frost BW (1972) Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. *Limnol Oceanogr* 17:805–815
- Frost BW (1990) Grazing. In: Morris I (ed) The physiological ecology of phytoplankton. University of California Press, Berkeley, p 465–491
- Gainey LF Jr, Shumway SE (1991) The physiological effect of *Aureococcus anophagefferens* ('brown tide') on the lateral cilia of bivalve mollusks. *Biol Bull* 181:298–306
- Gallager SM, Stoecker DK, Bricelj VM (1989) Effects of the brown tide alga on growth, feeding physiology and locomotory behavior of scallop larvae (*Argopecten irradians*). In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 511–541
- Gifford DJ, Dagg MJ (1991) The microzooplankton-mesozooplankton link: consumption of planktonic protozoa by the calanoid copepods *Acartia tonsa* Dana and *Neocalanus plumchrus* Murukawa. *Mar Microb Food Webs* 5:161–177
- Guillard RRL, Ryther JH (1962) Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt, and *Detonula confervacea* (Cleve) Gran. *Can J Microbiol* 8:229–239
- Harms J (1992) Effects of nutrition (herbivore vs carnivore) on energy charge and nucleotide composition in *Hyas araneus* larvae. *Helgoländer Meeresunters* 46:29–44
- Jonasdottir SH (1994) Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar Biol* 121(1):67–81
- Jonasdottir SH, Fields D, Pantoja S (1995) Copepod egg production in Long Island Sound, USA, as a function of the chemical composition of seston. *Mar Ecol Prog Ser* 119:87–98
- Jonsson PR, Tiselius P (1990) Feeding behavior, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar Ecol Prog Ser* 60:35–44
- Keller MD, Bellows WK, Guillard RRL (1989) Dimethylsulfide production and marine phytoplankton: an additional impact of unusual blooms. In: Cosper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 101–115



- Kim WS (1993) Zooplankton community effects on the phytoplankton community in Long Island bays. PhD dissertation, State University of New York at Stony Brook
- Kim WS, Chang M (1992) Zooplankton grazing during an euglenoid bloom in Reeves Bay, New York, USA. *Ocean Res* 14:25–34
- Kleppel GS (1992) Environmental regulation of feeding and egg production by *Acartia tonsa* off southern California. *Mar Biol* 112:57–65
- Kleppel GS, Holliday DV, Peiper RE (1991) Trophic interactions between copepods and microplankton: a question about the role of diatoms. *Limnol Oceanogr* 36:172–178
- Lampert W, Fleckner W, Rae H, Taylor BE (1986) Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. *Limnol Oceanogr* 31:478–490
- Lampert W, Taylor BE (1985) Zooplankton grazing in a eutrophic lake: implications of diel vertical migration. *Ecology* 66:68–82
- Landry MR (1981) Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Mar Biol* 65:77–82
- Landry MR, Lehner-Fournier JM (1988) Grazing rates and behaviors of *Neocalanus plumchrus*: implications for phytoplankton control in the subarctic Pacific. *Hydrobiologia* 167/168:9–19
- Lively JS, Kaufman Z, Carpenter EJ (1983) Phytoplankton ecology of a barrier island estuary: Great South Bay, New York. *Estuar Coast Shelf Sci* 16:51–68
- Lonsdale DJ, Coper EM (1994) Phytoplankton productivity and zooplankton feeding and productivity in the lower Hudson River estuary. Final Report to the Hudson River Foundation. Hudson River Foundation, New York
- Lonsdale DJ, Coull BC (1977) Composition and seasonality of zooplankton of North Inlet, South Carolina. *Chesapeake Sci* 18:272–283
- Lonsdale DJ, Heinle DR, Siegfried C (1979) Carnivorous feeding behavior of the adult calanoid copepod *Acartia tonsa* Dana. *J Exp Mar Biol Ecol* 36:235–248
- Lonsdale DJ, Levinton JS (1985) Latitudinal differentiation in copepod growth: an adaptation to temperature. *Ecology* 66:1397–1407
- Lonsdale DJ, Weissman P, Dobbs FC (1993) A reproductive-resting stage in an harpacticoid copepod, and the significance of genetically based differences among populations. *Bull Mar Sci* 53:180–193
- Malej A, Harris RP (1993) Inhibition of copepod grazing by diatom exudates: a factor in the development of mucus aggregates. *Mar Ecol Prog Ser* 96:33–42
- Marshall SM (1973) Respiration and feeding in copepods. *Adv Mar Biol* 11:57–120
- Nuzzi R, Waters RM (1989) The spatial and temporal distribution of 'brown tide' in eastern Long Island Sound. In: Coper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 117–138
- Pierce RW, Turner JT (1992) Ecology of planktonic ciliates in marine food webs. *Rev Aquat Sci* 6:139–181
- Putt M, Stoecker DK (1989) An experimentally determined carbon:volume ratio for marine 'oligotrichous' ciliates from estuarine and coastal waters. *Limnol Oceanogr* 34:1097–1103
- Robertson JR (1983) Predation by estuarine zooplankton on tintinnid ciliates. *Estuar Coast Shelf Sci* 16:27–35
- Roman MR, Ashton KA, Gauzens AL (1988) Day/night differences in the grazing impact of marine copepods. *Hydrobiologia* 167/168:21–30
- Roman MR, Rublee PA (1981) A method to determine *in situ* zooplankton grazing rates on natural particle assemblages. *Mar Biol* 65:303–309
- Rothschild BJ, Osborn TR (1988) Small-scale turbulence and plankton contact rates. *J Plankton Res* 10:465–474
- Sherr BF, Sherr EB, Hopkinson CS (1988) Trophic interactions within pelagic microbial communities: indications of feedback regulation of carbon flow. *Hydrobiologia* 159:19–26
- Sherr EB, Sherr BF, McDaniel J (1991) Clearance rates of <6 µm fluorescently labeled algae (FLA) by estuarine protozoa: potential grazing impact of flagellates and ciliates. *Mar Ecol Prog Ser* 69:81–92
- Sieburth J McN, Johnson PW, Hargraves PE (1989) Pico-plankton ultrastructure: a decade of preparation of the brown tide alga, *Aureococcus anophagefferens*. In: Coper EM, Bricelj VM, Carpenter EJ (eds) Novel phytoplankton blooms: causes and impacts of recurrent brown tides and other unusual blooms. Lecture notes on coastal and estuarine studies. Springer-Verlag, Berlin, p 1–22
- Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman, San Francisco
- Stoecker DK, Capuzzo JM (1990) Predation on protozoa: its importance to zooplankton. *J Plankton Res* 12:891–908
- Stoecker DK, Davis LH, Provan A (1983) Growth of *Favella* sp. (Ciliata: Tintinnina) and other microzooplankters in cages incubated *in situ* and comparison to growth *in vitro*. *Mar Biol* 75:293–302
- Stoecker DK, Egloff DA (1987) Predation by *Acartia tonsa* Dana on planktonic ciliates and rotifers. *J Exp Mar Biol Ecol* 110:53–68
- Strathmann RR (1967) Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. *Limnol Oceanogr* 12:411–418
- Strickland JD, Parsons TR (1972) A practical handbook of seawater analysis. Bull Fish Res Bd Can 167
- Tackx MLM, Daro MH (1993) Influence of size dependent <sup>14</sup>C uptake rates by phytoplankton cells in zooplankton grazing measurements. *Cah Biol Mar* 34:253–260
- Tandichodok P (1990) Relative importance of phytoplankton and organic detritus as food resources for the suspension-feeding bivalve *Mytilus edulis* L. in Long Island Sound. PhD dissertation, State University of New York at Stony Brook
- Tester PA, Turner JT (1991) Why is *Acartia tonsa* restricted to estuarine habitats? In: Proceedings of the Fourth International Conference on Copepoda, Karuizawa, Japan. Bull Plank Soc Jap Spec Vol, p 603–611
- Turner JT (1982) The annual cycle of zooplankton in a Long Island estuary. *Estuaries* 5:261–274
- Turner JT, Anderson DM (1983) Zooplankton grazing during dinoflagellate blooms in a Cape Cod embayment, with observations of predation upon tintinnids by copepods. *PSZN I: Mar Ecol* 4:359–374
- Turner JT, Granéli E (1992) Zooplankton feeding ecology: grazing during enclosure studies of phytoplankton blooms from the west coast of Sweden. *J Exp Mar Biol Ecol* 157:19–31
- Verity PG (1985) Grazing, respiration, excretion, and growth rates of tintinnids. *Limnol Oceanogr* 30:1268–1282
- Verity PG, Langdon C (1984) Relationships between lorica volume, carbon, nitrogen, and ATP content of tintinnids in Narragansett Bay. *J Plankton Res* 6:859–868
- White JR, Roman MR (1992a) Egg production by the calanoid copepod *Acartia tonsa* in the mesohaline Chesapeake Bay: the importance of food resources and temperature. *Mar Ecol Prog Ser* 86:239–249
- White JR, Roman MR (1992b) Seasonal study of grazing by metazoan zooplankton in the mesohaline Chesapeake Bay. *Mar Ecol Prog Ser* 86:251–261