Daphnia distributions. Limnol. Oceanogr. **16:** 453–466.

STOMMEL, H. 1949. Trajectories of small bodies sinking slowly through convection cells. J. Mar. Res. **8:** 24–29.

WELLER, R. A., AND OTHERS. 1985. Three-dimensional flow in the upper ocean. Science **227:** 1552–1556.

WOODCOCK, A. H. 1944. A theory of surface water motion deduced from the wind-induced motion of the *Physalia*. J. Mar. Res. **5:** 196–205.

———. 1950. Subsurface pelagic *Sargassum*. J. Mar. Res. **9:** 77–92.

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Small, aloricate ciliates as a major component of the marine heterotrophic nanoplankton[1]

Abstract—Small, aloricate ciliates with equivalent spherical cell diameters <20 μm (biovolume <4,000 μm³) compose, on average, 4–57% of the total biomass of heterotrophic (apochlorotic) nanoplankton in diverse marine systems. Biomass production of nanoplanktonic ciliates in a southeastern U.S. estuary was also a significant part of the total production of heterotrophic microprotozoa. During summer in a salt marsh tidal creek, the production of small ciliates exceeded the production of heterotrophic microflagellates. Bacteria and coccoid cyanobacteria were frequently observed in the food vacuoles of the ciliates, while ingested nanoplanktonic algae were rarely seen. We suggest that small, aloricate ciliates can be an important component of the biomass of heterotrophic nanoplankton and deserve further attention as potential consumers of picoplanktonic cells in marine pelagic systems.

The smallest marine plankters are responsible for a large part of total production and respiration in the sea (Sieburth 1979; Pomeroy 1980; Williams 1981). It appears that most of the marine picoplankton, cells of 0.2–2 μm including heterotrophic bacteria, cyanobacteria, and small eucaryotic phytoplankton (Sieburth et al. 1978; Johnson and Sieburth 1979, 1982), grow rapidly (Azam et al. 1983; Platt et al. 1983) and that the relatively low and constant in situ abundances of these organisms are maintained by predation (Burney et al. 1981, 1982; Davis et al. 1985). Heterotrophic nanoplanktonic organisms, apochlorotic cells of 2–20 μm, have been identified as the dominant consumers of picoplankton, especially of bacteria (Fenchel 1982; Sieburth and Davis 1982; Azam et al. 1983). Marine heterotrophic nanoplanktonic organisms have been considered to consist predominantly of phagotrophic microflagellates (Fenchel 1982; Sieburth and Davis 1982), while marine pelagic ciliates have been generally recognized as important only in the microzooplankton, organisms 20–200 μm in size which graze nanoplanktonic cells (Sorokin 1981; Beers et al. 1980, 1982; Banse 1982). (Exceptions are Ibanez and Rassoulzadegan 1977; Johnson et al. 1982; Gast 1983, 1985.) Here we present evidence that small, aloricate ciliates with equivalent spherical cell diameters <20 μm are present in both eutrophic and oligotrophic marine waters and at times make up a large fraction of the total heterotrophic nanoplankton biomass. Indirect evidence also indicates that these ciliates may utilize the same food resources as do heterotrophic microflagellates, i.e. bacteria and other picoplanktonic microorganisms.

Ciliates in the nanoplanktonic size range have been reported in many parts of the world ocean, including coastal waters of southern California (Beers et al. 1980), the North Pacific central gyre (Beers et al. 1982), the northern Adriatic Sea (Revelante and Gilmartin 1983), the Chesapeake Bay (Haas

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1982), the Baltic Sea (Gast 1983), the northeastern Mediterranean Sea (Rassoulzadegan 1977), and coastal waters of southern England (Burkill 1982). Smetacek (1981) noted the presence of an 8-μm-diameter spherical ciliate in the Kiel Bight. Nanoplanktonic cililates also seem to be present in freshwater environments; 8–10-μm ciliates have been found in Lake Michigan (M. Boraas pers. comm.) and in a blackwater river in Georgia (L. Carlough pers. comm.). However, the quantitative occurrence and trophic significance of such small ciliates is poorly understood, owing mostly to methodological problems. Investigators studying microzooplankton populations using the Utermöhl inverted microscope technique have found that small, aloricate ciliates are not well preserved with the method and are not easily detected at low magnifications (<250×) (Beers et al. 1980, 1982; Burkill 1982; Revelante and Gilmartin 1983). Workers using most-probable-number culture techniques to evaluate the population of bacterivorous protozoa in marine systems have reported ciliate abundances two to three orders of magnitude lower than those estimated by direct counts (Lighthart 1969; Caron et al. 1982). Investigators studying heterotrophic microflagellates by recently developed epifluorescence techniques at high magnifications (>1,000×) (Haas 1982; Caron 1983; Sherr and Sherr 1983*a,b*) can easily miss the less numerous ciliates. We overcame many of these problems by using a double-staining epifluorescence method (Sherr and Sherr 1983*b*) and an intermediate magnification (500×).

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Water samples were collected in both winter and summer from a depth of 1 m at two sites in a Georgia estuary, the tidal creek and the open estuary, and at depths ranging from 5 to 45 m across the continental shelf off Georgia and South Carolina. In August 1984 water was also sampled in several habitats of Davies Reef on the Great Barrier Reef, Australia, including reef front, reef flat, and adjacent lagoon, at depths of 0–60 m. These various marine systems included eutrophic to oligotrophic conditions. In the estuary, concentrations of suspended bacteria range between 0.2 and 1.7 × 10^7 cells ml^{-1} (Newell unpubl. data, AODC) and Chl *a* between 0.2 and 8 μg $liter^{-1}$ (Pomeroy and Weigert 1981). In shelf waters of the Georgia Bight, the abundance of suspended bacteria ranges from 10^5 to 10^6 cells ml^{-1} and Chl *a* concentrations from 0.5 to 1.4 μg $liter^{-1}$, increasing from the outer to inner shelf (Pomeroy et al. 1983). In water over the Great Barrier Reef, bacterial populations are generally about 2–20 × 10^5 cells ml^{-1} (Moriarty 1979); over Davies Reef, bacterial abundance was within this range (B. Sherr unpubl. data, AODC), and Chl *a* ranged from 0.05 to 0.4 μg $liter^{-1}$ (Furnas unpubl. data).

Shelf and reef water samples were taken with 5-liter Niskin bottles. In the estuary, water samples were taken with a hand pump, during 17 low tides in August 1983 and 16 low tides in February 1984, at two sites in the Duplin River, a tidal embayment adjacent to Sapelo Island. The lower site was influenced by water from the open estuary; the upper site was a tertiary tidal creek draining a 35-ha *Spartina alterniflora* marsh (Imberger et al. 1983). Subsamples (5–20 ml) of Formalin-preserved water (final concn of 2%) were stained with the fluorescent dye 4,6-diamidino-2-phenylindole (DAPI), filtered gently onto Irgalan-black stained, 0.8-μm Nuclepore membrane filters, and stored at −20°C in individual Millipore Petri dishes. Samples treated this way can be preserved up to several months with negligible deterioration of nanoplanktonic cells and chlorophyll autofluorescence. The filters were subsequently stained with fluorescein isothiocyanate (FITC), mounted on glass slides, and examined with a Zeiss epifluorescence microscope (Sherr and Sherr 1983*b*).

On each filter, 200 fields were examined for ciliates at 500×, and 100 fields for heterotrophic microflagellates at 1,250×. Duplicate filters were counted for each water sample. A visual record of the numbers and cell dimensions of the ciliates and microflagellates counted on each filter with FITC fluorescence was used to calculate the num-

bers and biovolume ml^{-1}, with equations for a sphere, prolate spheroid, or cone, depending on cell shape. A factor of 0.08 pg C μm^{-3} was used to convert biovolume to biomass (Sherr and Sherr 1984). The presence of orange-fluorescing cyanobacteria or red-fluorescing eucaryotic phytoplankton in protozoan food vacuoles could be detected through the FITC fluorescence. Each ciliate was also inspected under DAPI fluorescence to assess the number and shape of nuclei and the presence of bacteria in food vacuoles (Sherr and Sherr 1983*b*). We identified cells as ciliates by shape, the presence of cilia, and the presence of multiple, dimorphic nuclei. We could also usually distinguish spirotrichous from hymenostome ciliates (Corliss 1979). Photosynthetic ciliates, probably *Mesodinium* spp., were in most samples and were easily identified by the abundant chloroplasts distributed throughout the cytoplasm. We presumed that these ciliates were primarily autotrophic (Sieburth 1979) and did not include them in our counts.

Aloricate ciliates with equivalent spherical cell diameters <20 μm (biovolume $\lesssim 4{,}000$ μm^3) were present in most samples examined (e.g. ciliates in Fig. 1A and B). The smallest ciliate we found was about 7 μm in diameter (Fig. 1A), and ciliates of 8–10 μm were commonly seen. Loricate ciliates, notably tintinnids, were also frequently encountered, but these organisms were generally >20 μm and were not counted. Many of the nanoplanktonic-size ciliates appeared to be in the order Oligotrichida, subclass Spirotricha (e.g. Fig. 1B). However, other types of small, aloricate ciliates, some of which looked like hymenostomes, were also abundant. Usually the ciliate fauna was diverse, but during summer in the tidal creek appeared to be mainly composed of two species: an oligotrich and a hymenostome that was probably in the order Scuticociliatida (Corliss 1979).

The average biomass of populations of naked ciliates with biovolumes $<4{,}000$ μm^3 in our study varied from 0.03 mg C m^{-3} in waters of the Great Barrier Reef to 12.2 in the salt marsh tidal creek in summer (Table 1). These biomass estimates are in line with the range of values reported for nanoplankton-size ciliates in southern California coastal waters (0.04–2.9 mg C m^{-3}: Beers et al. 1980) and in coastal waters of southern England (0.0–2.9 mg C m^{-3}: Burkill 1982). Although the numbers of heterotrophic flagellates in our samples were 100-fold those of ciliates, flagellate and ciliate biomasses were generally in the same order of magnitude (Table 1). The average relative proportion of ciliate biomass to total heterotrophic nanoplankton biomass varied from 4% in reef waters to 57% in tidal creek water

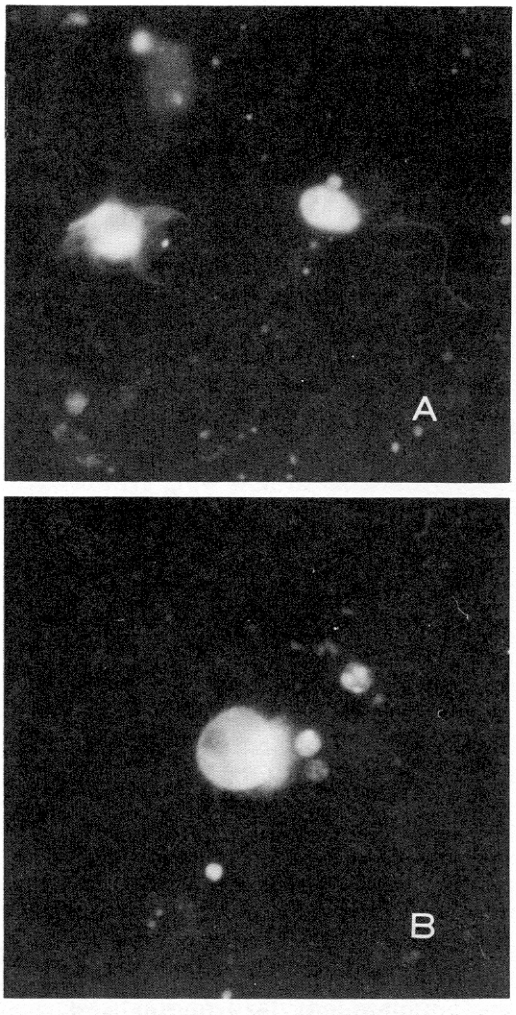

Fig. 1. Epifluorescence photomicrographs of two nanoplanktonic ciliates found in the Georgia estuary. A. Approximately 7-μm-diameter ciliate adjacent to 7-μm-long heterotrophic microflagellate. B. 13-μm-diameter oligotrichous ciliate.

Table 1. Abundance and biomass of small, aloricate ciliates (biovolume ≤4,000 m^3) and heterotrophic microflagellates in several marine pelagic systems. Mean ± 1 SD, range of values in parentheses; number of samples in brackets.

Location	Ciliates		Microflagellates	
	(No. ml^{-1})	(mg C m^{-3})	(No. ml^{-1})	(mg C m^{-3})
Georgia salt marsh				
Tidal creek, Aug 83 [17]	61±41 (16–185)	12.2±8.4 (3.0–36.8)	1,050±310 (460–1,710)	9.3±7.5 (2.3–31.3)
Tidal creek, Feb 84 [16]	28±14 (5–54)	2.8±1.5 (0.3–5.8)	1,950±720 (880–3,320)	10.7±3.3 (6.3–18.0)
Open estuary, Aug 83 [17]	16±22 (0–87)	1.8±2.2 (0.0–9.1)	2,340±920 (700–4,230)	6.4±2.9 (2.3–12.0)
Open estuary, Feb 84 [16]	29±14 (6–70)	3.1±1.6 (0.6–7.8)	3,970±570 (2,800–4,960)	15.9±6.3 (6.0–30.7)
Southeastern U.S. continental shelf				
Cross-shelf, Jun 83 [23]	0.9±1.3 (0.0–3.7)	0.1±0.2 (0.0–1.0)	380±140 (150–780)	0.6±0.2 (0.2–1.0)
Shelf edge, Jun 83 [18]	0.4±0.6 (0.0–1.8)	0.1±0.1 (0.0–0.3)	490±180 (210–790)	0.7±0.4 (0.2–1.2)
Inner shelf, Sep 83 [7]	5.7±5.5 (2.1–17.4)	0.7±0.7 (0.2–2.1)	820±360 (600–1,360)	5.5±3.4 (3.6–10.6)
Midshelf, Sep 83 [8]	4.8±2.4 (1.1–8.7)	0.6±0.3 (0.2–1.0)	530±270 (160–700)	2.1±2.1 (0.5–5.2)
Outer shelf, Sep 83 [9]	2.8±3.0 (0.5–8.7)	0.3±0.3 (0.1–0.8)	330±260 (170–710)	3.3±3.9 (0.3–8.7)
Shelf edge, Sep 83 [5]	0.9±0.4 (0.5–1.4)	0.1±0.1 (0.0–0.2)	270±60 (190–340)	0.5±0.2 (0.3–0.9)
Cross-shelf, Apr 84 [24]	1.4±1.9 (0.0–8.7)	0.2±0.3 (0.0–1.2)	670±240 (230–1,130)	2.3±1.8 (0.3–6.8)
Australia				
Great Barrier Reef, Aug 84 [25]	0.2±0.2 (0.0–0.7)	0.03±0.03 (0.0–0.10)	190±50 (100–300)	0.7±0.4 (0.1–1.4)

in summer. Ciliates usually made up about 10–20% of the total heterotrophic nanoplankton biomass in estuarine and shelf waters. However, in individual samples the ciliates sometimes composed >50% of the total biomass and in tidal creek waters up to 92% of the biomass of heterotrophic nanoplankton.

Pelagic ciliates have been characterized as inefficient grazers of picoplanktonic cells. From theoretical consideration of ciliate filtering capabilities as well as from results of laboratory feeding experiments, Fenchel (1980*a,b,* 1984) concluded that bacterivorous ciliates cannot maintain growth on suspensions of bacteria $\lesssim 5 \times 10^6$–5×10^8 cells ml^{-1}, assuming an average bacterial size of 0.1 μm^3, corresponding to 0.2–7 mg org. dry wt $liter^{-1}$. Similar conclusions have been drawn in field investigations of bacterivorous ciliates in Chesapeake Bay (Berk et al. 1976) and in the Baltic Sea (Gast 1985). In most of the waters we sampled, bacterial biomass concentrations were <0.2 mg org. dry wt $liter^{-1}$. Even in the salt marsh estuary, bacterial abundance was only of the order of 10^6–10^7 cells ml^{-1}, with an average cell size of 0.05 μm^3 (Newell unpubl. data), corresponding to 0.04–0.35 mg org. dry wt $liter^{-1}$ (calculated with the higher conversion factor of 0.22 pg C μm^{-3} bacterial biovolume suggested by Bratbak and Dundas 1984). When food vacuoles were observed in nanoplanktonic ciliates, however, they most often appeared to contain bacteria or coccoid cyanobacteria and only rarely had what looked like nanoplanktonic-size cells. (Ingested phytoplankton cells were commonly seen in ciliates >20 μm and in heterotrophic dinoflagellates.) In the estuary during summer, the nanoplanktonic ciliates seemed to be mostly bacterivorous. At the

Table 2. Biomass production (mg C m^{-3} h^{-1}, mean value with 1 SD in parentheses) of bacterioplankton, heterotrophic microflagellates, and small, aloricate ciliates at two sites in a salt marsh estuary, during 16-day periods in August and February.

	Tidal creek		Open estuary	
	Summer	Winter	Summer	Winter
Bacterioplankton	3.0(2.0)	2.4(1.3)	1.2(0.7)	1.0(0.4)
Microflagellates	1.0(1.0)	0.3(0.4)	0.1(0.2)	0.2(0.2)
Ciliates	1.2(0.8)	0.05(0.05)	0.03(0.06)	0.07(0.06)

open estuary site, an average of 55% of the ciliates counted contained bacteria in their food vacuoles, and in the tidal creek, up to 100% of the ciliates (avg 86%) in a given water sample had ingested bacteria. Among the ciliate assemblages in continental shelf waters, an average of only 5% of individual ciliates appeared to contain bacteria in their food vacuoles; however, up to 77% of shelf nanoplanktonic ciliates (avg 14.5%) in a given sample had photosynthetic cells, mostly cyanobacteria, in their food vacuoles. These estimates of the incidence of ingestion of bacteria and cyanobacteria are probably low because our epifluorescence method only detects recently ingested cells (Sherr and Sherr 1983*b*).

Protozoan biomass production was assessed in the estuary as described by Sherr et al. (1984) by holding 500-ml subsamples of water (screened through 17-μm Nitex netting to remove potential predators of nanoplanktonic protozoa) in the dark at the in situ temperature for 12–16 h and comparing initial and final biomass of microflagellates and ciliates. The results are compared to estimates of bacterial production in the same water samples via [^{3}H]thymidine uptake (Newell and Fallon 1982; Fallon et al. in press) in Table 2. Ciliate biomass production accounted for, on average, between 14 and 54% of total heterotrophic nanoplankton production. The productivity of suspended bacteria was sufficiently high to support the growth requirements of both apochlorotic microflagellates and ciliates, assuming a protozoan growth efficiency of about 33%, except in the tidal creek in summer. However, in that case the biomass of apochlorotic flagellates was dominated by 14–20-μm heterotrophic dinoflagellates which appeared to be ingesting small phytoplankton cells; on the basis of contents of food vacuoles, the ciliates seemed to be the dominant consumers of bacteria. The ciliate populations we observed in the tidal creek may have been resuspended from surface sediments, although the dynamics of growth suggested otherwise, i.e. the ciliate assemblage always grew well in laboratory-incubated water samples, with an average population generation time of 9 h.

In the other systems we investigated, it is less likely that the ciliates originated from the benthos. The presence of the ciliates, and the contents of their food vacuoles, suggested that they were at least maintaining stable populations at the expense of picoplanktonic cells. Fenchel's calculations of physical constraints to the maximum rate of filtration for hymenostome and oligotrichous ciliates (Fenchel 1980*b*, 1984) lead to the conclusion that bacterivorous ciliates cannot survive on the dilute suspensions of bacteria found in open marine waters. If suspended bacteria were not randomly dispersed, but aggregated in patches or around particles, it is more likely that bacterivorous ciliates could in fact exist in the open ocean (Sieburth 1984). Aloricate ciliates have routinely been observed associated with particles in even the most oligotrophic parts of the ocean (e.g. Caron et al. 1982; Silver et al. 1984). It has been suggested that microbial populations in the sea are in fact patchily distributed around microsites of higher organic matter concentration such as phytoplankton cells releasing DOM and organic detrital microaggregates (Azam and Ammerman 1984; Goldman 1984). Azam and Ammerman (1984) argued that bacterivorous ciliates would be able to survive under oligotrophic conditions if that were the case by swimming to microsites of higher bacterial abundance and productivity.

Our preliminary survey in several marine

pelagic systems, together with other published reports, suggests that nanoplanktonic-size ciliates are common in the ocean. Improved counting techniques have allowed us to quantify in situ populations of these ciliates. Laboratory incubations of estuarine water demonstrated that natural populations of apparently bacterivorous nanoplanktonic ciliates could grow when the total biovolume of suspended bacteria was <0.35 mg org. dry wt liter^{-1}. It has only recently been recognized that saprotrophic and autotrophic microbial populations in the sea are capable of rapid biomass production which is apparently immediately cropped by phagotrophic protozoa (*see* Sherr and Sherr 1984; Sieburth 1984). Nanoplanktonic ciliates may play a role in this microbial food web. Since ciliates are a known food for copepods and other metazooplankton (Berk et al. 1977; Porter et al. 1979; Robertson 1983), the presence of nanoplanktonic ciliates in the sea may represent a direct link in the marine food web between procaryotic microbes and metazoans.

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References

AZAM, F., AND J. W. AMMERMAN. 1984. Cycling of organic matter by bacterioplankton in pelagic marine ecosystems: Microenvironmental considerations, p. 345–360. *In* M. J. Fasham [ed.], Flows of energy and materials in marine ecosystems. Plenum.

———, AND OTHERS. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. **10:** 257–263.

BANSE, K. 1982. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnol. Oceanogr. **27:** 1059–1071.

BEERS, J. R., F. M. REID, AND G. L. STEWART. 1980. Microplankton population structure in southern California nearshore waters in late spring. Mar. Biol. **60:** 209–226.

———, ———, AND ———. 1982. Seasonal abundance of the microplankton population in the North Pacific central gyre. Deep-Sea Res. **29:** 227–245.

BERK, S. G., D. C. BROWNLEE, D. R. HEINLE, H. J. KLING, AND R. R. COLWELL. 1977. Ciliates as a food source for marine planktonic copepods. Microb. Ecol. **4:** 27–40.

———, R. R. COLWELL, AND E. B. SMALL. 1976. A study of feeding responses to bacterial prey by estuarine ciliates. Trans. Am. Microsc. Soc. **95:** 514–520.

BRATBAK, G., AND I. DUNDAS. 1984. Bacterial dry matter content and biomass estimations. Appl. Environ. Microbiol. **48:** 755–757.

BURKILL, P. H. 1982. Ciliates and other microplankton components of a near-shore food-web: Standing stocks and production processes. Ann. Inst. Oceanogr. Paris **58**(suppl.): 335–350.

BURNEY, C. M., P. G. DAVIS, K. M. JOHNSON, AND J. MCN. SIEBURTH. 1981. Dependence of dissolved carbohydrate concentrations upon small scale nanoplankton and bacterioplankton distributions in the western Sargasso Sea. Mar. Biol. **65:** 289–296.

———, ———, ———, AND ———. 1982. Diel relationships of microbial trophic groups and in situ dissolved carbohydrate dynamics in the Caribbean Sea. Mar. Biol. **67:** 311–322.

CARON, D. A. 1983. A technique for the enumeration of heterotrophic and phototrophic nanoplankton using epifluorescence microscopy, and a comparison with other procedures. Appl. Environ. Microbiol. **46:** 491–498.

———, P. G. DAVIS, L. P. MADIN, AND J. MCN. SIEBURTH. 1982. Heterotrophic bacteria and bacteriovorous protozoa in oceanic microaggregates. Science **218:** 795–797.

CORLISS, J. O. 1979. The ciliated protozoa. Pergamon.

DAVIS, P. G., D. A. CARON, P. W. JOHNSON, AND J. MCN. SIEBURTH. 1985. Phototrophic and apochlorotic components of the picoplankton and nanoplankton in the North Atlantic: Geographical, vertical, seasonal and diel distributions. Mar. Ecol. Prog. Ser. **21:** 15–26.

FALLON, R. D., S. Y. NEWELL, B. F. SHERR, AND E. B. SHERR. In press. Factors affecting growth in the Duplin River estuary and coastal Atlantic Ocean. Proc. 2nd Int. Colloq. Mar. Bacteriol. CNRS.

FENCHEL, T. 1980*a*. Suspension feeding in ciliated protozoa: Feeding rates and their ecological significance. Microb. Ecol. **6:** 13–25.

———. 1980*b*. Relation between particle size selection and clearance in suspension-feeding ciliates. Limnol. Oceanogr. **25:** 733–738.

———. 1982. Ecology of heterotrophic microflagellates. 4. Quantitative occurrence and importance as consumers of bacteria. Mar. Ecol. Prog. Ser. **9:** 35–42.

———. 1984. Suspended marine bacteria as a food source, p. 301–305. *In* M. J. Fasham [ed.], Flows of energy and materials in marine ecosystems. Plenum.

GAST, V. 1983. Untersuchen über die Bedeutung der Bakterien als Nahrungsquell für das Mikrozooplankton der Schlei und der Ostse unter besonderer Berucksichtigung der Ciliaten. Ph.D. thesis, Kiel Univ. 195 p.

———. 1985. Bacteria as a food source for microzooplankton in the Schlei Fjord and Baltic Sea with special reference to ciliates. Mar. Ecol. Prog. Ser. **22:** 107–120.

GOLDMAN, J. C. 1984. Oceanic nutrient cycles, p. 137–170. *In* M. J. Fasham [ed.], Flows of energy and materials in marine ecosystems. Plenum.

HAAS, L. W. 1982. Improved epifluorescent microscope technique for observing planktonic microorganisms. Ann. Inst. Oceanogr. Paris **58**(suppl.): 261–266.

IBANEZ, F., AND F. RASSOULZADEGAN. 1977. A study of the relationships between pelagic ciliates (Oligotrichina) and planktonic nanoflagellates of the neritic ecosystem of the bay of Villefranche-surmer. Analysis of chronological series. Ann. Inst. Oceanogr. Paris **53:** 17–30.

IMBERGER, J., AND OTHERS. 1983. The influence of water motion on the distribution and transport of materials in a salt marsh estuary. Limnol. Oceanogr. **28:** 201–214.

JOHNSON, P. W., AND J. MCN. SIEBURTH. 1979. Chroococcoid cyanobacteria in the sea: A ubiquitous and diverse phototrophic biomass. Limnol. Oceanogr. **24:** 928–935.

———, AND ———. 1982. In situ morphology and occurrence of eucaryotic phototrophs of bacterial size in the picoplankton of estuarine and oceanic waters. J. Phycol. **18:** 318–327.

———, H-S. XU, AND J. MCN. SIEBURTH. 1982. The utilization of chroococcoid cyanobacteria by marine protozooplankters but not by calanoid copepod. Ann. Inst. Oceanogr. Paris **58**(suppl): 297–308.

LIGHTHART, B. 1969. Planktonic and benthic bacterivorous protozoa at eleven stations in Puget Sound and adjacent Pacific Ocean. J. Fish. Res. Bd. Can. **26:** 299–304.

MORIARTY, D. J. W. 1979. Biomass of suspended bacteria over coral reefs. Mar. Biol. **53:** 193–200.

NEWELL, S. Y., AND R. D. FALLON. 1982. Bacterial productivity in the water column and sediments of the Georgia (USA) coastal zone: Estimates via direct counting and parallel measurement of thymidine incorporation. Microb. Ecol. **8:** 33–46.

PLATT, T., D. V. SUBBA RAO, AND B. IRWIN. 1983. Photosynthesis of picoplankton in the oligotrophic ocean. Nature **310:** 702–704.

POMEROY, L. R. 1980. Microbial roles in aquatic food webs, p. 85–109. *In* R. R. Colwell [ed.], Aquatic microbial ecology. Univ. Maryland.

———, AND OTHERS. 1983. Microbial distribution and abundance in response to physical and biological processes on the continental shelf of the southeastern U.S.A. Continental Shelf Res. **2:** 1–20.

———, AND R. G. WIEGERT [EDS.]. 1981. The ecology of a salt marsh. Springer.

PORTER, K. G., M. L. PACE, AND J. F. BATTEY. 1979. Ciliate protozoans as links in freshwater planktonic food chains. Nature **277:** 563–565.

RASSOULZADEGAN, F. 1977. Evolution annuelle des cilies pelagiques en Mediterranee nord-occidentale. Cilies Oligotriches "non-tintinnides" (Oligotrichina). Ann. Inst. Oceanogr. Paris **53:** 125–134.

REVELANTE, N., AND M. GILMARTIN. 1983. Microzooplankton distribution in the northern Adriatic Sea with emphasis on the relative abundance of ciliated protozoans. Oceanol. Acta **6:** 407–415.

ROBERTSON, J. R. 1983. Predation by estuarine zooplankton on tintinnid ciliates. Estuarine Coastal Shelf Sci. **16:** 27–36.

SHERR, B. F., AND E. B. SHERR. 1983*a*. Enumeration of heterotrophic microprotozoa by epifluorescence microscopy. Estuarine Coastal Shelf Sci. **16:** 1–7.

———, AND ———. 1984. Role of heterotrophic protozoa in carbon and energy flow in aquatic ecosystems, p. 412–423. *In* M. J. Klug and C. A. Reddy [eds.], Current perspectives in microbial ecology. Am. Soc. Microbiol.

———, ———, AND S. Y. NEWELL. 1984. Abundance and productivity of heterotrophic nanoplankton in Georgia coastal waters. J. Plankton Res. **6:** 195–202.

SHERR, E. B., AND B. F. SHERR. 1983*b*. Double-staining epifluorescence technique to assess frequency of dividing cells and bacteriovory in natural populations of heterotrophic microprotozoa. Appl. Environ. Microbiol. **46:** 1388–1393.

SIEBURTH, J. MCN. 1979. Sea microbes. Oxford.

———. 1984. Protozoan bacterivory in pelagic marine waters, p. 405–444. *In* J. E. Hobbie and P. J. Williams [eds.], Heterotrophic activity in the sea. Plenum.

———, AND P. G. DAVIS. 1982. The role of heterotrophic nanoplankton in the grazing and nurturing of planktonic bacteria in the Sargasso and Caribbean Sea. Ann. Inst. Oceanogr. Paris **58**(suppl.): 285–296.

———, V. SMETACEK, AND J. LENZ. 1978. Pelagic ecosystem structure: Heterotrophic compartments and their relationship to plankton size fractions. Limnol. Oceanogr. **23:** 1256–1263.

SILVER, M. W., M. M. GOWING, D. C. BROWNLEE, AND J. O. CORLISS. 1984. Ciliated protozoa associated with oceanic sinking detritus. Nature **309:** 246–248.

SMETACEK, V. 1981. The annual cycle of protozooplankton in the Kiel Bight. Mar. Biol. **63:** 1–11.

SOROKIN, Y. I. 1981. Microheterotrophic organisms in marine ecosystems, p. 293–342. *In* A. R. Longhurst [ed.], Analysis of marine ecosystems. Academic.

WILLIAMS, P. J. 1981. Incorporation of microheterotrophic processes into the classical paradigm of the planktonic food web. Kiel. Meeresforsch. **5:** 1–28.

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