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Control of marine bacterioplankton populations: Measurement and significance of grazing

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Abstract

A variety of methods have been used to estimate the degree of control exercised upon marine bacterioplankton by grazing organisms. These include filtration or dilution of samples to reduce grazers, the use of specific inhibitors to prevent growth or grazing, and the use of artificial particles or radio-labelled bacteria as tracers for the natural bacterioplankton. Each of these techniques has drawbacks which may lead to under- or overestimates of grazing. In addition, they tell us little about which organisms are doing the grazing or the degree to which viruses or lytic bacteria compete with grazers for bacterial production.

Because measurements of grazing and bacterioplankton growth rates are uncertain, exact comparisons are not presently possible. Thus measurements of bacterial and bacterivore abundance, concentrated on comparisons between seasons, on diel cycles and on spatial variations, have been used to evaluate mechanisms controlling bacterial populations. These give an idea of the degree of coupling between bacterial growth and bacterivore activity and of the time scales over which growth and grazing balance. Combined with laboratory studies of grazing, they currently provide the best insight into what controls populations of bacteria in the sea.

I. Introduction

Recently developed methods for the estimation of bacterial growth rates have shown that even if conservative assumptions are made, a large fraction of the bacterial cells are actively growing, and that bacterial production is a significant portion of primary production (Hagström *et al.*, 1979; Fuhrman & Azam, 1980, 1982; reviewed by Van Es & Meyer-Reil, 1982). Most estimates of the fraction of primary production passing through the bacterioplankton are in the 10–50% range (Andrews & Williams, 1971; Sieburth *et al.*, 1977; Hagström *et al.*, 1979; Williams, 1981; Fuhrman & Azam, 1982). At 50% growth efficiency, therefore, 5–25% of the primary production in coastal waters ends up as bacterial biomass. Bacterioplankton cells appear to be dividing on the order of 0.2–2 d^{-1} (reviewed by Ducklow, 1983; Williams, 1984), and the fate of this bacterial production has been the subject to many investigations in recent years.

The purpose of this review is to compare some of the methods that have been used to estimate bacterial mortality, especially grazing mortality, in the sea, and to examine: (a) to what extent grazing rate estimates obtained with different methods can be expected to be similar, and (b) how methodological problems are limiting our ability to study grazing with the same resolution as other biological processes in marine and aquatic environments. Although we will concentrate mainly on marine systems, some examples from the limnological literature will be discussed.

Four possibilities for the fate of bacterial produc-

tion have been suggested; these are: (1) spontaneous death and lysis of bacteria, (2) lysis due to infection by *Bdellovibrio* or other lytic bacteria, (3) lysis due to bacteriophage, or (4) grazing by larger organisms.

The possibility of spontaneous lysis has not been investigated, but it seems unlikely that rapid bacterial growth would be accompanied by sudden death. *Bdellovibrios* have been isolated from coastal and estuarine waters (Varon & Shilo, 1980; Shilo, 1984) and other lytic bacteria have also been found in natural waters (Guelin & Cabioch, 1972; Guerrero *et al.*, 1986), and much research remains to be done on these kinds of organisms before we can rule them out as important predators on heterotrophic bacteria. Currently, quantification of their abundance depends on obtaining suitable host bacteria and is subject to the same caveats that have accompanied all enrichment/plate count techniques (e.g., some forms may be unculturable). Accurate estimates of their impact will have to await the application of newer methods, such as immunofluorescent staining or electron microscopy.

Bacteriophages have been isolated from both coastal and open ocean ecosystems (Moebus, 1980) and have been observed by electron microscopy in samples from coastal waters (Sieburth, 1979; Torrella & Morita, 1979). Viruses have also been found in some species of eukaryotic marine algae (Mayer & Taylor, 1979; Johnson & Sieburth, 1982) and in freshwater cyanobacteria (Brown, 1972). It is not known what quantitative impact they may have on natural bacterioplankton populations although it has been suggested that bacterial abundance in most aquatic environments is too low to support their growth (Wiggins & Alexander, 1985). It is probably too early to make any broad generalizations, but phages most likely attain the highest importance under conditions of relatively high bacterial abundance. Present methods used to study them involve estimates of plaque-forming units on agar plates and at best only record their presence or absence.

II. Measurement of bacterial mortality

In recent years a variety of techniques have been employed to estimate overall mortality of bacteria in seawater samples. These techniques have involved selective filtration to eliminate predators, diluting out grazers with bacteria-free seawater, the addition of various inhibitors to prevent growth or grazing, and the measurement of DNA mineralization rates in bacteria pre-labelled with tritiated thymidine.

The filtration technique was introduced by Russian workers (Romanova & Zonow, 1964; Gak *et al.*, 1972) and has been applied to estuarine and coastal waters by Wright & Coffin (1984a, b) and to oligotrophic waters by Landry *et al.* (1984) and Ducklow & Hill (1985). Using this technique the investigator compares growth (as change in abundance of bacteria with time) in undisturbed seawater samples and in samples pre-screened through a 1.0 or 3.0 μm pore-size filter to remove potential predators. The samples are incubated for 6–24 hours and the change in bacterial abundance in the filtered samples is assumed to estimate growth, while that in the unfiltered sample is assumed to consist of the net result of growth minus grazing. This would represent a minimum estimate of both growth and grazing if some grazers make it through the filtration step (Wright & Coffin, 1984b). Kopylov & Moiseev (1980) suggested that 30% of the bacterivores can pass through even a 1.5 μm filter and Fuhrman & McManus (1984) presented indirect evidence that up to 50% of the grazing activity can pass 0.6 μm pore-size filters.

The dilution method for measuring grazing was developed by Landry & Hassett (1982) to measure microzooplankton grazing on phytoplankton, and applied by Landry *et al.* (1984) and Ducklow & Hill (1985) to the measurement of bacterivory. This technique involves measuring changes in bacterial abundance in undisturbed samples and in samples diluted with bacteria-free seawater, during 6–24 hour incubations. It is assumed that the intrinsic growth rate is the same for bacteria in both treatments, and that the difference in growth between treatments comes from lowered predation in the diluted sample, since predation is reduced by lowering the concentration of the grazers.

Filtration of seawater can result in significant increases of dissolved organic compounds in the filtrate relative to that originally present, presumably as a result of cell breakage (Fuhrman & Bell, 1985;

Goldman & Dennett, 1985). For the dilution method, this could result in increased growth in the diluted treatments. For the filtration method, bacteria in treatments rendered predator-free by pre-filtration through 1.0 or 3.0 μm pore-size filters would also experience increased substrate levels compared to those in unfiltered treatments. In both cases an overestimate of grazing would result. Also, care must be taken that the filtered seawater used for the dilution does not contain bacteria (Li & Dickie, 1985).

A third technique for the estimation of bacterial loss through grazing uses antibiotics to inhibit grazing and/or growth of bacterioplankton in otherwise undisturbed samples (Newell *etal.*, 1983; Fuhrman & McManus, 1984; B. F. Sherr *et al.*, 1986). One sample of seawater is treated with penicillin or another suitable prokaryote inhibitor of cell division; a second (control) sample receives the prokaryote inhibitor plus a eukaryote-specific inhibitor (either colchicine or cycloheximidine) to prevent grazing. In the penicillin-treated sample bacterial numbers decline, presumably due to grazing by eukaryotes. In the second treatment bacterial numbers remain approximately constant over 12–24 hours because, ideally, both growth and grazing are prevented. As with the dilution and filtration methods, caution is required when interpreting results because the separation of bacteria from grazers may itself affect bacterial growth rates (B. F. Sherr *et al.*, 1986) and the inhibitors may not be sufficiently selective (Oremland & Capone, in press; Taylor & Pace, 1987).

Servais *et al.* (1985) estimated bacterial mortality as the rate of loss of DNA from cells pre-labelled with tritiated thymidine. This technique provides an estimate of total mortality, which can then be compared to estimates of mortality in pre-screened, predator-free samples to estimate mortality due to grazing. With the current version of this technique, long incubations (up to 70 hours) are required, however, and questions about containment effects (Ferguson *et al.*, 1984) would seem to preclude its routine use. Wikner *et al.* (1986) recently described an analogous technique using radiolabelled minicells (non-growing daughter cells produced during asymmetric division in certain mutant strains of *Escherichia coli*) as a tracer for the natural bacterioplankton. This technique requires much shorter incubation times (a few hours or less).

The data from these different techniques support the idea that bacterial growth is often roughly balanced by losses on time scales of 12–24 hours, the length of most incubations (see Fig. 1). For example, in 17 out of 20 experiments, Wright & Coffin (1984b) found that grazing was within a factor of two of growth (per capita grazing rate, g, dimension of time^{-1}, compared to per capita growth rate, u; $0.5 < g/u < 2.0$).

Each of the techniques outlined above measures a slightly different aspect of bacterial mortality. The filtration technique measures bacterial mortality caused by organisms retained on a filter of a given pore size; dilution measures total predatory mortality (including that caused by viruses or lytic bacteria, unless they are present in the diluent); specific inhibitors, which can be combined with filtration (Fuhrman & McManus, 1984), measure mortality caused by eukaryotic organisms susceptible to the inhibitors; and the DNA turnover technique of Servais *et al.* (1985) measures total mortality, including any which might be caused by spontaneous cell lysis that is followed by DNA breakdown.

The long incubation times and considerable sample manipulations that are required for all of the techniques outlined above limit their usefullness with sensitive natural assemblages of bacterioplankton. In addition, the choice of models (exponential, linear or logistic) to be used in describing bacterial growth can affect estimates of grazing (see Ducklow & Hill, 1985).

III. Grazing by specific organisms or groups of organisms

Several investigators have attempted to quantify grazing by specific organisms using a combination of laboratory and field methods. These have included the use of radioisotopes or inert fluorescent particles as tracers for the bacterioplankton and the observation of changes in bacterial abundance in samples incubated with and without added grazers.

Tracer methods

DiSalvo (1971) showed that a variety of coral reef

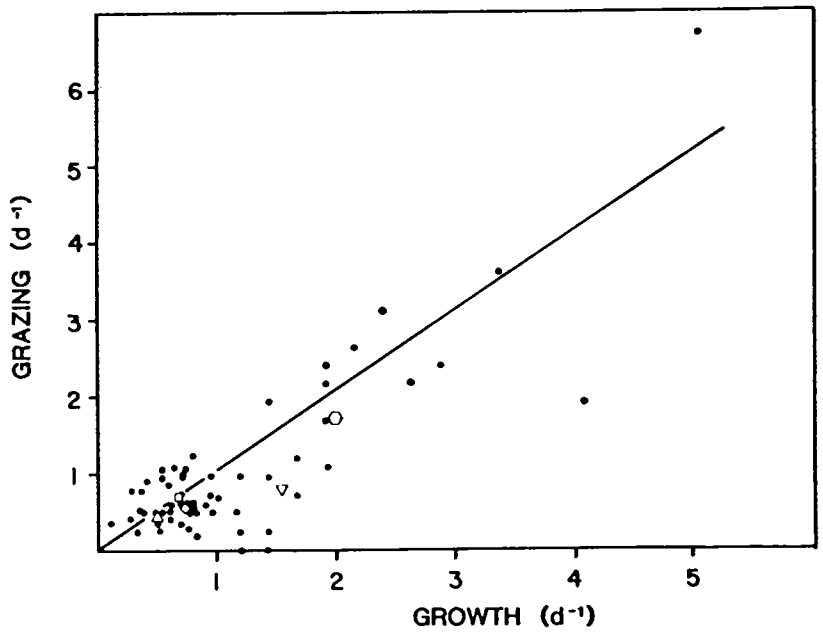

Fig. 1. Comparison of per capita growth and mortality estimates (units of d^{-1}). Symbols indicate averages for a given study: (○) Ducklow & Hill, 1985, n = 22; (▽) Landry *et al.*, 1984, n = 2; (◇) Fuhrman & McManus, 1984, n = 5; (□) Wright & Coffin, 1984a, n = 20; (△) Servais *et al.*, 1985, n = 14. Line represents x = y.

metazoans could remove radioactively-labelled suspended bacteria (cultures) in a laboratory microcosm. Sorokin (1973) confirmed this result with ^{14}C-labelled natural bacterioplankton. He identified gastropod veligers, hydroids, annelids, corals, sponges, tunicates, holothurians, gastropods and lamellibranchs as grazers on bacterioplankton, with daily rations ranging from 1.6 to 51% of body carbon. Bacteria associated with aggregates were reported to account for 20–30% of the total bacteria in that study so it is not known whether these animals grazed principally on the detrital particles or free bacteria, nor how much bacterial production was consumed by metazoan grazers. Earlier, Sorokin (1970, 1971), using ^{14}C-labelled natural bacteria, had found that coarse filterers, such as calanoid copepods and euphausiids, could feed on bacteria which were associated with aggregates, but showed very little uptake when the bacteria were first passed through a 4.0 μm pore-size filter. Fine filterers, like the cladoceran *Penilia* and the appendicularian *Oikopleura* could ingest 50–100% of their body weight per day in bacteria (including both free and attached bacteria). King *et al.* (1980) were the first to use radiolabelled free bacteria (0.2 μm < diameter < 1.0 μm) to study bacterivory by a metazoan, the larvacean *Oikopleura dioica*. They found that bacteria may form a substantial part (maximum 25–50%) of this animal's daily ration, but that its grazing had little impact on bacterial populations. A similar result was obtained by Boak & Goulder (1983) who fed ^{14}C-labelled bacterioplankton to the copepod *Eurytemora* sp. They found that grazing by this copepod had even less impact on bacterial populations than King *et al.* found for *Oikopleura*, and that bacteria could provide only 12% of the carbon required for respiration. Mullin (1983) used radiolabelled *Vibrio* sp. to measure bacterivory in the salp *Thalia democratica* in *in situ* feeding chambers. The use of the tracer allowed for short term incubations under natural conditions with this delicate animal. The same method was not suitable for the pteropod *Cavolina* sp., which did not feed normally when confined.

Using a technique for tritium labelling of natural assemblages of bacterioplankton, Hollibaugh *et al.*

(1980) picked out individual ciliates with a micropipette and measured grazing by *Helicostomella subulata* (a tintinnid) and *Strombidinopsis acuminata* (an oligotrich). A number of other recent studies have used similar applications of radiolabelled bacteria (Gast, 1985; Lessard & Swift, 1985; Riemann, 1985; Schoenberg & Maceubbin, 1985). This technique is labor intensive, especially for the microzooplankton, because it usually requires the investigator to pick out individual organisms with a micro-pipette before incubations.

Several investigators have labelled bacteria in water column enclosures and measured the appearance of radioactivity in larger size clases of plankton (Azam *et al.*, 1984; Ducklow *et al.*, 1986) but these longer-term studies do not quantify bacterivory alone, because the results are also influenced by multiple trophic transfers and transfer efficiency.

Caution has to be exercised in interpreting the results of radiotracer studies, especially if (a) they do not discriminate between free and attached bacteria, (b) they use large, cultured bacteria, which may form clumps or aggregates in suspension (see Mullin, 1983) or (c) they employ incubation times sufficiently long to result in significant respiratory loss of label from the grazers or multiple trophic transfers of label. The kinetics of particle uptake by small organisms are very rapid, and care must be taken that egestion and/or respiration of label does not result in underestimates of grazing.

Artificial particles of various kinds have been used as tracers in feeding studies with planktonic organisms. For example, Parke *et al.* (1955) used graphite particles to study phagotrophy among several species in the chrysophyte flagellate genus *Chrysochromulina*. More recently, fluorescent plastic pigment particles (McManus & Fuhrman, 1986) and fluorescent polystyrene latex beads (Børsheim, 1984; Bird & Kalff, 1986; Cynar & Sieburth, 1986) have been used to measure bacterivory in natural populations of protozoa. In this technique, one adds bacteria-sized fluorescent particles to a natural sample and observes uptake in short time courses using epifluorescence microscopy. Incubation times should be short enough to ensure that uptake will still be linear, and ideally particles should be added at low levels (<25% of the total food particles) to minimize the effect of increased particle concentration on grazing. The particles can be coated with protein or other substances to decrease hydrophobicity and (presumably) make them appear more like bacteria to the grazers.

Inert particles may be used in rapid assays with natural populations, require minimal handling of the sample, and can be manipulated in various ways to provide information on different aspects of grazing (e.g. size selection, chemosensory behavior, etc.). Their chief disadvantage is that grazers may be able to discriminate against the particles, preferentially ingesting real bacteria. Recent work has suggested that heat-killed, fluorescently labelled bacteria may be preferable to artificial particles for these kinds of experiments (Sherr & Sherr, 1987; Sherr *et al.*, in press). Care must also be taken to avoid fixation artifacts (Sieracki *et al.*, 1987).

Another disadvantage of fluorescent tracer experiments, whether they are performed with plastic particles or heat-killed bacteria, is that several hours of microscopy may be required to process a single sample, and even then the data are often inadequate to define grazing rates of individual species in a natural assemblage with any statistical confidence. For the future, alternate methods, such as flow cytometry, may help to automate the quantification of particle uptake.

Bacterioplankton incubated with added grazers

A method that has been used widely in freshwater, but not marine, grazing studies involves concentrating grazers (usually macrozooplankton) and measuring the decline in bacterial abundance in grazed and grazer-free treatments. Peterson *et al.* (1978) measured bacterivory by three *Daphnia* species using the acridine orange direct count method to compare the decline of bacterial numbers in vials containing grazers to those without grazers. They found that these cladocerans could graze on bacteria, although with a lower efficiency than on larger food, and that grazing could be an important source of mortality for the bacteria. They demonstrated that natural assemblages of bacterioplankton, dominated by small (~0.5 μm diameter) unattached cells,

could be subject to intense grazing pressure in nature. Pace *et al.* (1983), Porter *et al.* (1983), and Forsyth & James (1984) also used this technique to measure bacterivory among freshwater cladocerans and copepods. The latter found that grazing estimates using direct counts were unrealistically high when compared to estimates of bacterial growth, and obtained lower grazing rates using bacteria labelled with ^{3}H-thymidine. Porter *et al.* (1983) suggested that in short radiotracer incubations the animals may not have enough time to acclimate to experimental conditions, and therefore graze at reduced rates. They argued that the direct count method was more accurate. Riemann (1985) claimed just the opposite, that abnormally high concentration of the grazers, required by the direct count method, resulted in an underestimate of grazing. Certainly concentration, confinement and manipulation of grazers and long incubation times are drawbacks to the use of the direct count method.

In a marine system, Wright *et al.* (1982) measured grazing by the mussel, *Geukensia demissa*, with the AODC technique and suggested that this organism could have a significant impact on bacterioplankton populations in waters overlying salt marshes.

Laboratory estimates of grazing rates

Although microscopic observations by Lohman (1908) and other workers (e.g. Waksman & Carey, 1935) had implicated protozoa as bacterivores in the sea, early laboratory studies of bacterivory concentrated on metazoans. ZoBell & Feltham (1937–38), for example, maintained a variety of invertebrates on a diet consisting exclusively of suspended bacteria. The mussel *Mytilus californianus*, the sand crab, *Emerita asaloga* and the marine worms *Dendrostroma zostericola* (sipunculid) and *Urechis caupo* (echinoid) all showed growth on a diet of cultured bacteria. Uncertainty about the number of living bacteria in the sea, due to the discrepancy between estimates obtained with plate counts and direct microscopic counts, made it impossible to evaluate the importance of bacteria in the overall diet of these organisms in nature, but the authors did speculate that grazing might be responsible for keeping growing bacterial populations in steady state.

Luck *et al.* (1931) reviewed the early literature on bacterivory among the protozoa. Most of that work concentrated on microscopic observation and the manipulation of various monoxenic cultures of ciliates to define the nutritional requirements of these organisms. More recently, the ecological aspects of protozoan bacterivory have received more attention, and some quantitative estimates have been made. The scuticociliate *Uronema* sp., for example, has been much-studied in culture as a bacterivore. Hamilton & Preslan (1969), Berk *et al.* (1976), Gast (1985) and Taylor *et al.* (1985) have studied bacterivory in isolates of this genus feeding on bacteria. Fenchel (1984) has argued, however, that these organisms are opportunistic in nature and are selected for by enrichment techniques. Their quantitative importance as bacterivores in nature is probably greatest in eutrophic environments, and the relevance of these laboratory rates to coastal and open ocean environments is uncertain. However, the idea that small (<30 μm) planktonic ciliates can be as important as flagellates in bacterivory has recently been advanced (Rivier *et al.*, 1985; E. B. Sherr *et al.*, 1986; Sherr & Sherr, 1987). These organisms, consisting mainly of aloricate oligotrichs and small scuticociliates, are frequently overlooked in plankton enumerations. At times, their biomass may equal or exceed that of the flagellates (E. B. Sherr *et al.*, 1986).

The appearance of small ($2-20$ μm) colorless flagellates in bacterial enrichments of seawater was quantified by Lighthart (1969), who estimated the abundance of bacterivorous protozoa in the water column and sediments in Puget Sound and the adjacent Pacific Ocean. His dilution/enrichment technique probably underestimated the abundance of both bacteria and flagellates (Fenchel, 1982d; Caron, 1983), but his results allowed biological oceanographers to begin to appreciate the quantitative role of the latter as bacterial grazers.

Recent studies of bacterivory by these flagellates have supported the idea that they are important grazers on bacteria (Haas & Webb, 1979; Fenchel, 1982a, b, c; Sherr *et al.*, 1983; Davis & Sieburth, 1984; Caron *et al.*, 1985). Isolates of marine and freshwater heterotrophic flagellates have been studied in the laboratory and grazing rates on bacteria calculated in monoxenic or oligoxenic culture. There are several

ways to do this. Sherr *et al.* (1983) compared abundance of bacteria in control (no flagellate) and experimental (the flagellate *Monas* sp. added) treatments to calculate growth and growth minus grazing, respectively, with the grazing rate being the difference between the two. Caron *et al.* 61985) and Goldman & Caron (1985) also used this technique. One problem is that grazing per flagellate has to be corrected for exponential flagellate growth between successive sampling points. Heinbokel (1978) and Fenchel (1982b) have pointed out that this can lead to significant uncertainty in grazing rate estimates. To circumvent this difficulty, Fenchel (1982b) used a bacterial isolate that would not grow in unenriched seawater and calculated grazing rate as the inverse of cell yield (bacteria consumed divided by flagellates produced, in batch cultures) times the per capita growth rate of the flagellates.

Davis & Sieburth (1984) studied grazing rates of fourteen heterotrophic flagellate isolates fed cultures of a *Vibrio* sp. They estimated growth of the bacterium instantaneously, using a modification of the "frequency of dividing cells" method (Hagström *et al.*, 1979), and obtained grazing rates of flagellates fed actively growing bacteria.

Studies of decomposition and nutrient cycling have frequently employed enrichments of natural water with detritus or phytoplankton to estimate the role of bacterivory in these processes (Fenchel & Harrison, 1976; Linley *et al.*, 1981; Newell *et al.*, 1981; Sherr *et al.*, 1982; Grüde, 1985). For example, Linley *et al.* (1981) added dissolved organic matter in the form of kelp mucilage to a sample of seawater prescreened through a 62 μm mesh and studied the development of bacteria and bacterivore populations during incubations lasting up to several weeks. They found the bacterivorous protozoan biomass maximum to be 6–10% of the bacterial biomass maximum and that the increase in protozoa was correlated with a sharp decline in bacterial numbers. Changes in bacterial abundance with time are difficult to convert into grazing rates in these kinds of experiments unless bacterial growth rates are known. Andersen & Fenchel (1985), however, modeled bacterial and protozoan population dynamics in enriched and unenriched incubations of 8.0 μm pre-filtered seawater using Lotka-Volterra type predator prey equations and estimated growth and grazing directly from changes in abundance. Their values for clearance and cell yield were similar to those reported from laboratory studies, and when applied to field abundances indicated that flagellates could graze 5–250% of bacterial populations in marine waters, on a daily basis.

IV. Inferring grazing control of bacterioplankton from population dynamics

There is currently more confidence in measurements of the abundance of bacteria and protozoa than in measurements of growth and grazing rates. Thus efforts to model field population dynamics based on abundances of these two groups offers promise for evaluating the control of bacteria by grazing. One problem is that in open ocean environments, which are spatially more homogeneous than coastal areas, bacteria and their predators are closely coupled, and large temporal variations in abundance are not usually seen (Davis *et al.*, 1985). In coastal environments, these populations can become temporally uncoupled (Sorokin, 1977), and predator-prey cycles can be used to evaluate grazer control (Andersen & Sorensen, 1986). There, however, spatial inhomogeneity adds substantially to the variance of temporal abundance data and often makes them difficult to interpret.

Sorokin (1977) correlated oscillations in bacterioplankton populations with those of non-pigmented flagellates in the field. Sampling every 10 d at a coastal station in the Sea of Japan, he observed peaks of bacterial and heterotrophic flagellate abundance approximately two weeks apart in the summer and suggested that grazing by the flagellates could be controlling the bacteria. In coastal waters of the Limfjord, Denmark, Fenchel (1982d) and Andersen & Sorensen (1986) found peaks of bacteria and flagellates 3–8 d out phase, with population peaks about 1–3 weeks apart for both. Modelling the interaction of the two populations using predator-prey equations, Fenchel (1982b) demonstrated that stable oscillations in both populations could be reproduced when laboratory-derived values for ingestion, yield and growth rate

were used. Davis *et al.* (1985) sampled Narragansett Bay, USA, and 13 m^3 mesocosms used to simulate the bay, at 5–8 d intervals over the course of a year. In the mesocosms, they found flagellate abundance in a given sample to be correlated with bacterial abundance in the previous week's sample, suggesting coupled oscillations with a lag.

Variations in bacterial and flagellate abundances have been studied simultaneously on daily or shorter time scales in several studies (Burney *et al.*, 1981; Andersson *et al.*, 1985; Davis *et al.*, 1985; Fuhrman *et al.*, 1985; Sorokin *et al.*, 1985). Short term variations in populations of micro-organisms that are subject to mixing and advection in addition to biological influences are difficult to quantify, especially in coastal waters. Only Sorokin *et al.* (1985) reported a reasonably clear diel predator-prey cycle between bacteria and flagellates, with a peak in flagellate abundance lagging that in bacteria by about eight hours.

Comparing population dynamics of bacteria with those of organisms presumed to be their predators is a useful approach to the study of bacterivory, but there are a number of problems. The data sets available for such comparisons are often small, and poorly resolved on temporal scales commensurate with the generation times of bacteria and bacterivores. Evaluation of the statistical significance of peaks and valleys in abundance is often not possible, and comparisons of different populations are usually subjective. The use of automated sizing and counting instruments to generate the large data sets needed to overcome these problems is still experimental (cf. Yentsch & Yentsch, 1984), so this approach is currently mainly heuristic in value, indicating particular seasons or environments where different populations of grazers may be controlling bacterial abundance.

V. Conclusion

Recently, a number of authors have attempted to estimate the overall impact of protozoan bacterivory on bacterioplankton (Azam *et al.*, 1983; Ducklow, 1983; Linley *et al.*, 1983; Davis & Sieburth, 1984; Fenchel, 1984; Gray *et al.*, 1984; Newell & Linley, 1984; Newell, 1984; Sieburth, 1984; Sherr & Sherr, 1984; Williams, 1984). Mostly these efforts consist of combining clearance or ingestion rates of colorless flagellates which have been studied in the laboratory with field estimates of flagellate abundance. Often the greater part of bacterial production can be accounted for in this way, but there is an apparent shortfall in grazing during times when bacterial populations are very high, as in temperate coastal waters in the late spring and early summer (see Fig. 2). Caveats about the application of laboratory measured grazing rates to natural populations are in order. Natural populations of heterotrophic flagellates frequently contain very small forms; modal cell diameters may be less than 3 μm (Sherr & Sherr, 1983). Therefore, laboratory-measured clearance rates, often obtained for larger flagellates, should probably be applied to these organisms on a cell volume basis (body volumes cleared per unit time, or specific clearance; Fenchel, 1982b) rather than on a per cell basis. Even here there is some latitude available in choosing which laboratory clearance rates to apply to natural populations. For example, Davis & Sieburth (1984) measured maximum clearance rates of over 80×10^4 flagellate body volumes per hour for *Paraphysomonas imperforata* (recalculated from their Table 1, using an average cell volume of 180 μm^3), more than 40× higher than that measured by Caron *et al.* (1985) with the same organism.

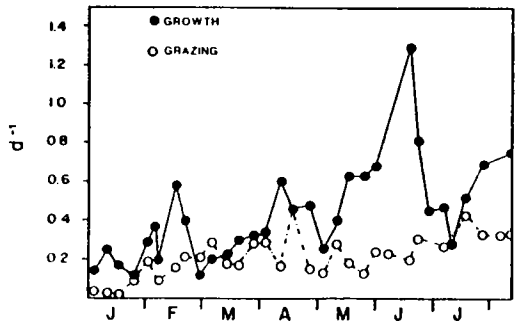

Fig. 2. Per capita growth (●) compared to grazing (○) in Long Island Sound during January to July, 1986. Growth rates are based on the thymidine incorporation technique of Fuhrman & Azam, 1982. Grazing is estimated as abundance of heterotrophic microflagellates times average body volume (45 μm^3 for this study) times 10^5 body volumes cleared per flagellate per hour. Unpublished data.

Since ingestion rate (bacteria consumed per flagellate per hour) is strongly dependent on bacterial concentration, the practice of applying maximum ingestion rates to field populations (e.g. Newell, 1984) should probably be avoided. In addition, bacterivory by nanoplanktonic ciliates (E. B. Sherr *et al.*, 1986) may have a significant impact and needs to be included in these models of the microbial food web.

While laboratory estimates of bacterivory by pure cultures of protozoans are useful in setting limits on the rates we may find in nature, and in allowing other aspects of bacterivory to be studied (conversion efficiency, respiration, temperature or concentration dependence, etc.) in a controlled fashion, we also need to develop new methods to measure bacterivory under conditions as close as possible to those in nature. This is particularly important because grazing rates on bacterial isolates may not be the same as those on the very small free bacterioplankton which comprise the bulk of the bacteria found in the water column (Ferguson & Rublee, 1976; Azam & Hodson, 1977; Maeda & Taga, 1983). Flagellate grazing can cause a shift in average bacterial size, presumably due to size-selective grazing (Andersson *et al.*, 1986), and it may be that some marine bacterioplankton obtain a refuge from predation because of their extremely small size. Also, bacterivorous protozoa in the environment may be adapted to additional food sources besides bacteria. They are frequently observed with ingested cyanobacteria and eukaryotic algae (Haas, 1982) and some may achieve higher clearance rates on the latter than they do on bacteria (Caron *et al.*, 1985).

The study of bacterial mortality rates and pathways for the utilization of bacterial production is limited by methodological difficulties. In particular, new methods are needed to evaluate the importance of viruses and lytic bacteria as agents of bacterial mortality. In addition, current methods for the measurement of both growth and grazing are not accurate enough to allow us to determine the time scales over which these processes balance in the sea. As a result, inferences about the interactions of bacteria and grazers have to be made from field population studies and models of the microbial food web (Pace *et al.*, 1984). For the future, it is hoped that estimates based on field abundances and models will converge with direct measurements of grazing based on new techniques.

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