REVIEW

Benthic Filter Feeding: A Natural Eutrophication Control

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ABSTRACT: The importance of the benthic filter feeding community as a natural control on eutrophication is considered. The important environmental factors favorable for such a control are relatively shallow water depths and a dense benthic filter feeding community of small animals. The criteria are summarized in the equivalence of the water recycling time, τ_f, for the benthic community and the time constant, τ_p, for phytoplankton growth. The criteria are applied specifically to the conditions that exist in South San Francisco bay.

INTRODUCTION

The causes and natural controls for eutrophication have received considerable attention over the past several years, largely related to the increased anthropogenic inputs of nutrients to limnological, estuarine and coastal regions. The importance of a variety of controls on the quantity and quality of the phytoplankton populations have been considered including light and temperature, turbidity and phytoplankton selfshading, nutrient concentrations and limitations, trace elements and chemicals, initial seed populations, phytoplankton sinking and motility, zooplankton grazing, and hydrodynamic effects.

The interest of the present investigations are focussed on an additional control, specifically that related to suspension feeding, benthic animals. In this control the benthic filter feeding population, in many cases clams and mussels, removes planktonic particulate matter from the system. The possibility and importance of this type of control has been recognized by several investigators including Kuenzler (1961), Hobbie (1976) and Smayda (1976) as well as others. More recently, Boynton et al. (1980) and Dame et al. (1980) have investigated various aspects of interactions among benthic filter feeding communities as well as those with the water column. Depending on the depth of water and the density of the benthic population, the benthic community can filter, or recycle, the volume of water in the region under consideration with a time constant much smaller than the hydrodynamic residence time and comparable with the time constant for phytoplankton growth. Under such conditions filter feeding communities may have a considerable effect on the seston content of the water column and thus may exert a significant control on the phytoplankton population, which forms a part of this seston.

Our interest in this type of control was stimulated by the thorough and definitive investigations by Cloern (1981a, b,) in South San Francisco bay. This bay receives the bulk of the sewage nutrient effluents from the greater San Francisco metropolitan area. The bay is relatively shallow, well mixed vertically, and has a hydrodynamic residence time of a few months. There are no obvious light, temperature, turbidity or nutrient limiting conditions and the zooplankton population is small. Consequently, it would be expected from these considerations alone that South San Francisco bay would represent a large eutrophication pond or, at least, would be characterized by substantial seasonal phytoplankton blooms. This, however, is not the case. The phytoplankton populations remain at a low level of a few μg chlorophyll l^{-1} throughout the year with the exception of a brief period during spring related to change in the hydrodynamic regime which is caused by an inflow of brackish, riverine water from North San

Francisco bay producing a vertically stratified condition in the South bay channels. The benthic population in this area, dominated by clams and mussels, is large with values of around several hundred g total weight m^{-2}; Cloern (1981a, b) has demonstrated that the filter feeding activity of this population effectively prevents the occurrence of phytoplankton blooms.

CONCEPTUAL RELATIONS

Following Di Toro et al. (1971), Winter et al. (1975) and Kremer and Nixon (1978), the defining equations for the various constituents interacting in a chemostat, or well mixed, marine ecosystem may be written in the form

$$\frac{dc_m}{dt} = \left(k_m - \sum_{n=1}^{N} k_{mn}\, c_n - k_h \right) c_m + k_h c_{mo} \qquad (1)$$

where c_m = concentration of any constituent of the system; N = total number of constituents or dependent variables; c_{mo} = influent constituent concentration to the system; t = time; k_m = net internal production rate of the constituent over natural decay, respiration or sinking out of the system; k_{mn} = rate coefficients for uptake of c_m by other constituents c_n; and k_h = reciprocal to the hydrodynamic residence time. These equations form a set of coupled, nonlinear differential equations which can be evaluated by computer procedures. Unfortunately they include a large number of coefficients, many of which are not well understood or are functions of c_n as well as passive variables such as light, temperature and turbidity.

If, fortuitously, there is a s i n g l e control, the benthos, on a particular component, the phytoplankton, and vice versa for the control of phytoplankton on benthos growth, the equations reduce for these two components to the familiar prey-predator, or Lotka-Volterra, equations. For our purposes these equations may be written in the form

$$h\frac{dP}{dt} = k_p h P - 24 \times 10^{-3}\, FBP \qquad (2)$$

$$\frac{dB_n}{dt} = k_b B_n + 24 \times 10^{-6}\, \alpha\beta_1\, FBP \qquad (3)$$

or

$$\frac{dP}{dt} = k_p P - 24 \times 10^{-3}\, \frac{F}{h}\, BP \qquad (2a)$$

$$\frac{dB}{dt} = -k_b B + 24 \times 10^{-6}\, \alpha\beta_1\beta_2\, FPB \qquad (3a)$$

where P = phytoplankton population, µg chlorophyll l^{-1}; B = benthic filter feeding population, g total weight m^{-2}; B_n = nitrogen content of benthic population, g N m^{-2}; $k_p = 1/\tau_p$ = plankton growth rate, d^{-1};

$k_b = 1/\tau_b$ = benthic mortality rate, d^{-1}; F = specific filtration rate for a given benthic animal, l h^{-1} g total weight of animal^{-1}; h = water depth, m; α = conversion coefficient, plankton nitrogen: plankton chlorophyll by weight; β_1 = benthic population feeding efficiency, food intake: filtering intake; β_2 = conversion coefficient, total weight of benthic animal: nitrogen weight of animal.

Equation (2) expresses the continuity relation that the time rate of increase of phytoplankton in a column of water is equal to the rate of production of plankton through photosynthesis in the column minus the rate of removal through the benthic filter feeding population. Correspondingly, Equation (3) expresses the continuity relation that the time rate of increase of the benthic population nitrogen is equal to the rate of increase of population nitrogen through plankton feeding minus the rate of decrease of population nitrogen through mortality. For constant coefficients the solutions of Equations (2a) and (3a) will oscillate about mean values for P and B given by

$$P = \frac{k_b}{\alpha\beta_1\beta_2 F} \times \frac{10^6}{24} \qquad (4)$$

$$B = \frac{k_p h}{F} \times \frac{10^3}{24} \qquad (5)$$

Before discussing the implications of Relations (4) and (5), it is useful to delinate the values of the parameters α, β_1, β_2, k_p, k_d and F. From Kremer and Nixon (1978), $\alpha = 5$. The values and dependencies for k_p have been studied in some detail for various phytoplankters and are summarized in Di Toro et al. (1971) and Kremer and Nixon (1978). For a relatively rapid growth rate of 1.5 divisions d^{-1}, $k_p = 1$ d^{-1}.

The β_1 and β_2 coefficients relate to the benthic population. One of the more thorough studies of the dynamics of a benthic filter feeding population has been given by Kuenzler (1961). He studied the phosphorus budget for a natural population of *Modiolus demissus* dominated by larger animals. For a filter intake of 5,480 µg P m^{-2}, 780 are used as food and 4,700 rejected as pseudofeces, giving a β_1 value of $\beta_1 = 780/5,480 = 0.14$. For the same population the body fraction comprised 67 % of the total animal phosphorus. According to Mann (1979) around 8 % of the dry meat weight of the clam *Tapes philippinarum* is nitrogen and the dry meat weight represents 6 % of the total animal weight. Presuming that the nitrogen and phosphorus fractionations are the same, the β_2 value is given by $\beta_2 = .67/.08 \times .06 = 140$ and $\beta = \beta_1\,\beta_2 = 140 \times .14 = 20$. From aquaculture experiments using secondary treated sewage effluent as a nutrient source Tenore et al. (1973) obtained values for β_1 of 0.10 for the mussel *Mytilus edulis*, 0.18 for the oyster *Cras-*

sostrea virginica, and 0.24 for the clam *Mercenaria mercenaria*. It may be reasonably anticipated that both the β_1 and β_2 values will vary from one ecological condition to another, depending on the quantity and quality of the phytoplankton food supply and the particulars of the benthic filter feeding population.

A value for the mortality rate coefficient, k_b, for a natural clam population can be obtained from the study by Ohba (1959) of a *Tapes japonica* community. Fig. 1 is a plot of the population density of clams versus age in months for 3 year classes. The distribution follows a reasonable first order, or exponential, decay with a time constant of $\tau_b = 170$ d or $k_b = 6 \times 10^{-3}$ d^{-1}. The average weight of a clam in this community varied seasonally with the introduction of new spat and their

growth from around 0.6 g to 2.2 g with an average value of 1.6 g.

Table 1 is a compilation of τ_b and k_b values for other species. The sampling and control techniques varied substantially among these studies, and the emphasis for several was on the larger size animals of commercial importance. Generally such adult animals have a lower mortality rate than the corresponding juveniles.

The filtration rate for a suspension feeding animal is defined as the volume of water filtered free of particles per unit time. The specific filtration rate, F, used here is the filtration rate per unit total weight of the animal, W. Generally, F is related to W by an empirical relation of the form, $F = aW^{-b}$. If the filtration rate is proportional to a surface area of the animal and the weight proportional to its volume, $F \alpha W^{-1/3}$. If filtration rate is proportional to a linear dimension, $F \alpha W^{-2/3}$; and if filtration rate is proportional to the volume, F will be a constant.

Winter (1978) has summarized observations of filtration rates for a variety of suspension feeding animals. For our purposes we have taken from his summary observations which were (1) of smaller animals less than 8 g total weight to correspond to a natural community, (2) within a temperature range of 10 to 20 °C corresponding to limited temperature effects on filtration rate, and (3) not affected by large food supplies to correspond again to a natural condition. Winter's data are tabulated in terms of dry meat weight, W_d; we have converted to total weight, W using a ratio $W_d/W = 0.06$ from Mann (1979). The resulting data are graphed in Fig. 2. They can be reasonably fit with the relation

$$F = .53 \, W^{-.42} \qquad (6)$$

In addition, Møhlenberg and Riisgård (1979) have presented regression lines of filtration rate versus dry meat weight for 5 species of suspension feeding animals. An average curve of F versus W from their data for animals less than 8 g has also been included in Fig. 2 defined by the relation

$$F = .97 \, W^{-.38} \qquad (7)$$
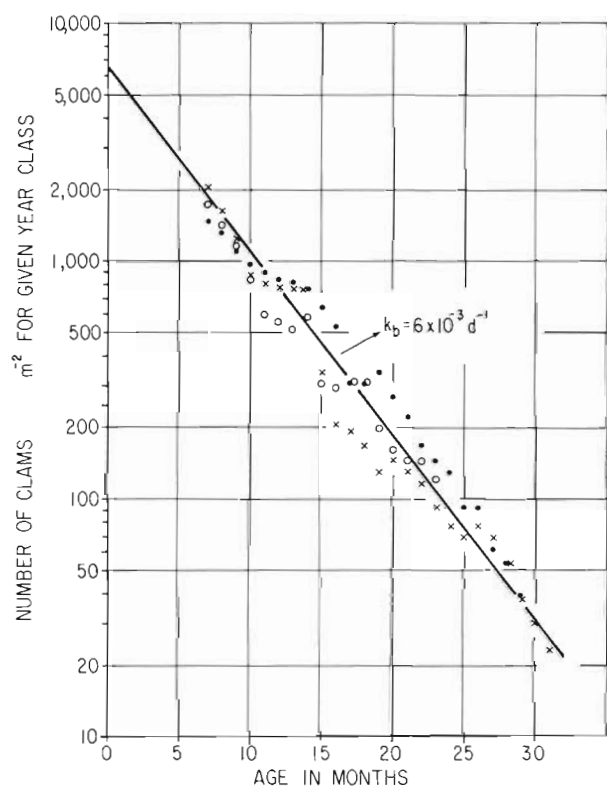
For subsequent calculations we have used values of F

Fig. 1. *Tapes japonica*. Graph of number of individuals m^{-2} for given year class versus age in months. Data from Ohba (1959). ● Year class 1954; × Year class 1955; ○ Year class 1956

Table 1. Time constants, τ_b, and mortality rates, k_b, for various benthic suspension feeding species

| Species	Age, yr	τ_b, d	k_b, d^{-1}	Source
Tapes japonica	0–3	170	5.9×10^{-3}	Ohba (1959)
Cardium edule	0–1	120	8.3×10^{-3}	Franklin & Pickett (1979)
Cardium edule	1–2	250	4.0×10^{-3}	Franklin & Pickett (1979)
Mya arenaria	0–1	110	9.1×10^{-3}	Brousseau (1978)
Mya arenaria	1–3	880	1.1×10^{-3}	Brousseau (1978)
Choromytilus meridionalis	1–4	470	2.1×10^{-3}	Griffiths (1981)
Venerupis decussata	2–3	1400	0.7×10^{-3}	Walne (1976)
Mercenaria mercenaria	4–7	280	3.5×10^{-3}	Hibbert (1977)
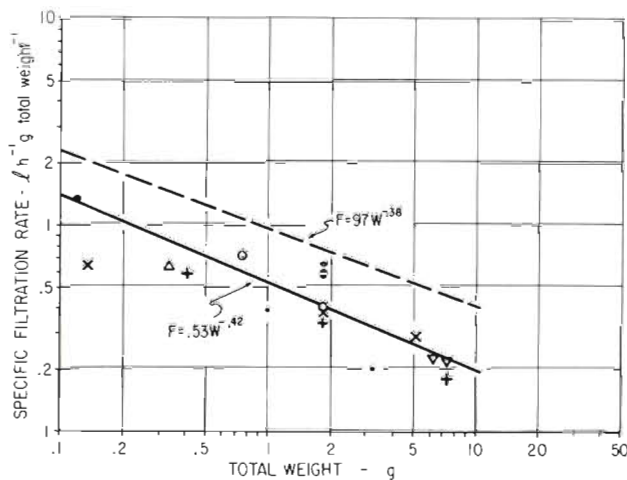
Fig. 2. Graph of specific filtration rate (1 h^{-1} g^{-1} total weight of animal) versus total weight of animal (g). ● Willemsen (1952), *Mytilus edulis;* ○ Vahl (1973b), *M. edulis;* ● Theede (1963), *M. edulis;* ○ Winter (1973), *M. edulis;* + Vahl (1973a), *Cerastoderma edule;* × Kuenzler (1961), *Modiolus dimissus;* △ Sanina (1976), *Cerastoderma lamarcki;* ▽ Coughlan and Ansell (1964), *Mercenaria mercenaria.* Solid line: Average curve through data points; broken line: average curve from Møhlenberg and Riisgård (1979)

midway between these 2 regression lines. It is to be noted that with either relation F decreases with increasing animal size.

To return to the Relations (4) and (5), P is directly proportional to k_b and inversely proportional to F. For k_b small, or average life span large, P will be small; and for F large, P will be small. The quantities k_b and F have offsetting effects on the determination of P. For a decrease in k_b, the implication is that the average size of an animal in the community will increase with a corresponding decrease in F and vice versa. Approximate calculations of these offsetting effects may be made along the following lines. Ohba (1959) states that after 1, 2 and 3 yr the average weight of an animal is 1.75, 4.25 and 7.5 g, respectively. From Fig. 2 these correspond to F values of 0.56, 0.40 and 0.30 1 h^{-1} g total weight^{-1}. The corresponding values for a k_b parameter for a population dominated by 1, 2 and 3 yr animals are 3.8, 1.9 and 1.3×10^{-3} d^{-1}. From Equation (4) the related values for P are 3, 2, and 2 µg chlorophyll l^{-1}. We may, then, anticipate that if the benthos is the control of the phytoplankton population, the plankton concentrations will be in the range of a few µg chlorophyll l^{-1}.

The important criteria in all of the above is whether, indeed, the benthos is the control. This is summarized in Relation (5). The required benthic population density, B, will decrease with decreasing depth, d, and increasing specific filtration rate, F. The opportunity for a given benthic community to be the principal control on the phytoplankton population is enhanced

by shallow depths and by a community with small size animals.

Illustrative calculations may be made from the data of Ohba (1959) and a depth, $h = 2$ m, using $\alpha = 5$, $\beta = 20$, $k_p = 1$ d^{-1}, $k_b = 6 \times 10^{-3}$ d^{-1}, $W = 1.6$ g and $F = 0.6$ 1 h^{-1} g total weight^{-1} from Fig. 2. From Relations (4) and (5) we obtain

$$P = \frac{6 \times 10^{-3}}{5 \times 20 \times .6} \times \frac{10^{-6}}{24} = 4 \text{ µg chlorophyll } l^{-1} \qquad (8)$$

$$B = \frac{1 \times 2}{.6} \times \frac{10^3}{24} = 140 \text{ g total weight m}^{-2} \qquad (9)$$

In other words, for shallow water depths a benthic, filter feeding community of a few hundred g m^{-2} will act as a control on the phytoplankton population, and the plankton concentrations will be a few µg chlorophyll l^{-1}.

The recycling time, τ_f, for a given benthic community is also of interest as an index of its importance with respect to other time constants of the system. It is given by the relation

$$\tau_f = \frac{h}{FB} \times \frac{10^3}{24} \qquad (10)$$

For the example cited above, $\tau_f = 1$ d. For the equilibrium conditions implied by this formulation we have from Equation (5) that

$$\tau_p = \frac{1}{k_p} = \tau_f \qquad (11)$$

as expected. The Relations (10) and (11) provide convenient criteria for assessing whether a given benthic communitiy is the control within a particular region.

It is of importance to note that the small value of k_b, or relatively long life span, of a benthic, filter feeding community is critical in the determination of the phytoplankton population. For example, if one were to postulate the zooplankton as a single limiting control, the relation corresponding to Equation (4) would be

$$P = \frac{k_z}{\gamma \delta F_z} \times 10^3 \qquad (12)$$

where k_z = zooplankton respiration rate, d^{-1}; F_z = zooplankton grazing rate, 1 d^{-1} mg C zooplankton^{-1}; γ = zooplankton conversion efficieny; δ = conversion coefficient, phytoplankton carbon: chlorophyll.

Taking characteristic values of $k_z = 4$ d^{-1}, $\gamma = 0.6$, $\delta = 50$ and $F = 0.13$ 1 d^{-1} mg C zooplankton^{-1}, we obtain

$$P = \frac{4}{.6 \times 50 \times .13} \times 10^3 = 1,000 \text{ µg chlorophyll } l^{-1} \quad (13)$$

Presumably such a large value for P would not be reached with nutrient supply, selfshading or other effects acting as a control on the population.

SOUTH SAN FRANCISCO BAY

The biology, chemistry, geology and physics of the San Francisco bay estuarine system are among the better known estuarine system, related in substantial part to the continuing studies by the U.S. Geological Survey. Much of this information is summarized in the volume edited by Conomos (1979a). The southern arm of the system, or South San Francisco bay, has an area, A, of approximately 500×10^6 m^2 and an average depth, h, of 2 m, or a volume, V, of $1,000 \times 10^6$ m^3. The South bay receives approximately 70 % of the sewage effluents from the San Francisco metropolitan area. This amounts to an imput of 37 tonnes d^{-1} of total nitrogen of which 26 tonnes d^{-1} is in an inorganic form, Conomos et al. (1979). There is a negligible river flow into the South bay and the hydrodynamic residence time, τ_h, is of the order of a few months increasing to several months during the summer, Conomos (1979b). With these values of waste loading and hydrodynamic residence time the South bay has a strong eutrophication potential, Officer and Ryther (1977). However, as discussed below, no eutrophication occurs.

The phytoplankton levels in the South bay remain at 2 to 5 µg chlorophyll l^{-1} year around with the exception of a brief period of a week or so during early spring when they rise to 10 to 40 µg chlorophyll l^{-1}, Cloern (1979, 1981b). As discussed by Cloern (1979), this modest bloom is related to a change in the hydrodynamic regime in the channels of the South bay from their normally well mixed condition to a stratified condition; the hydrodynamic change is caused by the increased flow of spring, river runoff water from the North bay into the South bay. From Cloern (1981a) the plankton productivity in the summer is 1 to 1.5 divisions d^{-1}, or $k_p = 0.7$ to 1.0 d^{-1}. As discussed by Nichols (1979), the benthic biomass in the South bay is large. The individual biomass values vary considerably from station to station with an average of around 300 g m^{-2}. The benthic biomass is dominated by bivalves, approximately 60 % or 180 g m^{-2}. For the 4 stations with the largest biomass 3 are dominated by the Japanese clam, *Tapes japonica*, and the fourth by the Japanese mussel, *Musculus senhousia*. The numbers of benthic macrofauna are around 200 m^{-2}, or an average weight of 1.5 g. The benthic population would appear to be similar to that studied by Ohba (1959).

The Calculations (8) and (9) apply to the conditions of South San Francisco bay. The benthic recycling time, τ_f, is comparable with the phytoplankton growth constant, τ_p. We conclude, as did Cloern (1981a, b), that the benthic bivalve population in South San Francisco bay is controlling the level of the phytoplankton standing stock.

It is possible to continue the analysis further to examine the flux of nitrogen through the system. The flux of nitrogen, F_b, in tonnes d^{-1} taken out of the system by the benthic filter feeding population, presuming no nitrogen regeneration from the bottom, is given by

$$F_b = \alpha\text{PAFB} \times 24 \times 10^{-12} \tag{14}$$

or for the South bay

$$F_b = 5 \times 4 \times 500 \times 10^6 \times .6 \times 140 \times 24 \times 10^{-12}$$
$$= 20 \text{ tonnes d}^{-1} \tag{15}$$

The hydrodynamic flux of inorganic nitrogen, F_h, in tonnes d^{-1} exiting out of the South bay is given by

$$F_h = \frac{NV}{\tau_h} \times 10^{-6} \tag{16}$$

where N = average concentration of inorganic nitrogen in mg l^{-1}. From Conomos et al. (1979) N has a value of around 1.4 mg l^{-1} (100 µg at l^{-1}) for the South bay, giving

$$F_h = \frac{1.4 \times 1,000 \times 10^6}{90} \times 10^{-6} = 16 \text{ tonnes d}^{-1} \tag{17}$$

The fluxes of nitrogen are approximately equally divided between that going to the bottom through benthic feeding processes excluding benthic recycling and that exiting out of the South bay through the hydrodynamic, tidal exchange processes. Ideally, our general equations should include a term for the recycling of nutrients by benthic excretion. Studies in Narragansett Bay have shown that the rate of benthic nutrient release is temperature-dependent, and varies with benthic community structure, Hale (1975) and Nixon et al. (1976). Similar studies on other benthic communities are needed before general nutrient excretions terms can be generated for our purpose. For the natural system studied by Kuenzler (1961) only 5 % of the total phosphorus intake by the *Modiolus* population is rejected as phosphate; for the laboratory system studied by Mann (1979) 50 % of the total nitrogen intake by the *Tapes* population is rejected as ammonia.

It is also of interest to note that both the dominant clam and mussel, *Tapes japonica* and *Musculus senhousia* are exotic, or introduced, species to the region. As discussed by Carlton (1979), both were first observed in the bay system in 1946. This particular feature raises an interesting question as to what conditions might exist today in South San Francisco bay if these species had not been introduced. Would the indigenous species have taken over as a control in the absence of the introduced species? In turn this raises the question as to whether some benthic species thrive better than others in regions such as the South bay where there is a substantial sewage and sewage nutrient input.

OTHER POSSIBLE EXAMPLES

We have searched the literature for other examples in which the benthic filter feeding population may exert a control, or be an important constituent, in the delineation of the phytoplankton population. Important criteria for identifying such possible regimes are (1) shallow water depths in the range of 2 to 10 m; (2) a large and widespread benthic filter feeding population dominated by small animals as contrasted with more localized regions dominated by larger animals of commercial size; (3) partially enclosed regions of substantial size with relatively poor hydrodynamic exchange characteristics with adjacent water bodies in order to eliminate from consideration regions in which the hydrodynamics is also a control; (4) regions with adequate nutrient supplies, often from sewage sources; and (5) regions which show relatively constant and low phytoplankton levels year around or modest bloom periods. Only 2 regions are discussed below. We suggest that there may be other examples of the same control, but it has been difficult for us to ascertain from the published literature the requisite combination of nutrient, phytoplankton, benthos and hydrodynamic information for an assessment of other possible regions.

Pamlico Estuary, North Carolina. The Pamlico estuary has been studied in detail by personnel associated with the Water Resources Research Institute of North Carolina State University. Much of the results are summarized in Copeland et al. (1974) and Hobbie et al. (1975). The estuary is unusually shallow, averaging 1.5 m with channel depths of 5 m. The estuary is protected by Pamlico sound and the outer banks so that the tidal amplitude averages 20 cm, and the flushing rate is correspondingly low. Nutrients are abundant year around with values of 5 to 50 μg at l^{-1} for nitrogen and 2 to 20 μg at l^{-1} for phosphorus; the nitrate component of the inorganic nitrogen concentration has values of less than 1 μg at l^{-1} in the middle to lower reaches of the estuary during the summer. The phytoplankton is dominated by motile dinoflagellates with normal values of 5 to 10 μg chl l^{-1} except during a bloom of 25 to 50 μg chl l^{-1} in January, February, March and a smaller bloom in late summer, both occurring in the middle to lower reaches of the estuary. Tenore (1972) has studied the macrobenthos of the estuary. It is dominated by a large population of small-sized molluscs: *Rangia cuneata*, a suspension feeding bivalve, in the upper reaches with seasonal averaged population densities of 275 ind. m^{-2}, and *Macoma balthica*, a deposit feeding bivalve, in the middle to lower reaches with comparable population densities. During fall the deep water, channel, stations contained no benthic organisms as a result of the anoxic condi-

tions occurring at these depths in late summer. It is difficult to understand why there is not a more extensive algal bloom in the estuary throughout the year in consideration of the existing light, turbidity and nutrient (particularly ammonium) conditions. We suggest that the large *R. cuneata* and, to a lesser degree, *M. balthica* populations may be the important control preventing this condition from occurring.

Core and Bogue Sounds, North Carolina. Core and Bogue sounds are geographically located between the North Carolina mainland and the outer banks. They encompass an area of around 400 km², and the water depths throughout most of the region do not exceed 2 m. There is little tidal flushing with the adjacent ocean and low river flow into the region. As discussed by Thayer (1971), nutrients are low and are a determining factor in the phytoplankton growth coefficient, k_p. Dissolved inorganic phosphorus averages 0.2 to 0.3 μg at l^{-1} and available nitrogen 0.5 to 1.2 μg at l^{-1}. Nevertheless, the net phytoplankton production of 53 g C m^{-2} yr^{-1} is comparable with that of open ocean areas, Williams et al. (1968). The standing crop of phytoplankton is low with values of 2 to 4 μg chl l^{-1} during most of the year increasing to 8 to 10 μg chl l^{-1} during the summer, Williams and Murdoch (1966) and Thayer (1971). Williams et al. (1968) studied the zooplankton population, which is scarce in the region, and concluded that it is a relatively unimportant in the food chain of this shallow water area. They also concluded that the benthic animals contribute most of the herbivore link in the food chain, a conclusion with which we agree. Brett (1963) has studied the invertebrate infauna in Bogue sound. It is substantial with values of 2 to 200 g total weight m^{-2} for the filter feeding portion of the benthic community. The filter feeding population is dominated by the clam, *Mercenaria mercenaria*, over most of the region and by the bay scallop *Aequipecten irradians* over portions of the region. Both the phytoplankton and benthic filter feeding community levels are in accord with the calculations given herein for the benthic population to be a control of the phytoplankton standing stock.

SUMMARY AND DISCUSSION

We have considered the importance of the benthic filter feeding community as a natural control on eutrophication. The environmental conditions that are favorable for such a control are shallow water depths, an abundant nutrient supply with no critical light, temperature or turbidity limitations, poor hydrodynamic water exchange characteristics, and a dense benthic filter feeding community of small animals. The

criteria are summarized in the Relations (10) and (11), specifically that the water recycling time, τ_f, for the benthic community is equivalent to the time constant, τ_p, for phytoplankton growth.

Following Smayda (1976) we suggest that any ecosystem modeling of phytoplankton or nutrients in relatively shallow water regions examine closely the quantity and quality of the benthos. In regions for which the benthic filter feeding population is not as dense as that in South San Francisco bay, the benthos may still play an important role in defining phytoplankton and nutrient levels during part of the annual cycle.

Following Ryther (1954) and Ryther and Officer (1981) we further suggest that an environment with a large sewage nutrient input consisting of nitrate and nitrite as well as ammonia and organic nitrogen compounds is conducive to the growth of smaller planktonic forms, some of which might be characterized as 'weed' species, as contrasted with a natural environment dominated by nitrate, which is conducive to the growth of larger planktonic forms. Further, following Tenore and Dunstan (1973), Tenore et al. (1973), Grassle and Grassle (1974), and Mann and Ryther (1977) we suggest that such a planktonic environment is in turn conducive to the propagation of small, opportunistic or 'weed' species of benthos, such as those belonging to the genera Tapes, Venerupis, and Rangia.

We acknowledge, however, that sewage nutrient input a priori does not lead to predominance of microflagellates (Eppley and Weiler, 1979). Indeed, such eutrophication may favor diatom-dominated natural assemblages (Thomas et al., 1980), and lead to only slight increases in microflagellate abundance (Parsons et al., 1977). As Braarud (1945) pointed out, environmental factors other than elevated nutrients regulate species occurrence and predominance in eutrophied areas. Significant among these factors regulating species responses is the hydrodynamic residence time. Our hypothesis is not conditional on a phytoplankton response similar to that found in Moriches bay (Ryther, 1954). Increased nutrient fertility can also stimulate the growth of representative coastal diatoms, including Skeletonema costatum and Thalassiosira nordenskioeldii (Dunstan and Menzel, 1971). Pratt and Campbell (1956) found a strong positive correlation between the growth of Mercenaria mercenaria and abundance of small planktonic diatoms (Skeletonema costatum and Thalassiosira nordenskioeldii) in Narrangansett bay. This clam is the most abundant animal of its size living in or on the bottom, and constitutes a significant fraction of the total benthic community in Narragansett bay (Pratt, 1953), a region which also appears to have its phytoplankton dynamics strongly coupled to benthic processes (Nixon, 1981).

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