Estuarine and Coastal Marine Science (1978) **6**, 37–46

ROMAN, TENORE

Q

Tidal Resuspension in Buzzards Bay, Massachusetts

I. Seasonal Changes in the Resuspension of Organic Carbon and Chlorophyll *a*

Michael R. Roman[a]

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824, U.S.A.

and Kenneth R. Tenore[b]

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, U.S.A.

Received 24 June 1976

Keywords: tidal cycles, tidal currents, suspended particles, chlorophyll measurements, primary productivity, annual cycles, Massachusetts coast

Greater than 50% increases in the amount of particulate organic carbon and chlorophyll *a* per square meter occurred in a 13-m water column of Buzzards Bay during tidal cycles. The composition and quantity of the resuspended material varied seasonally. Greater percentages of the carbon in the water column were resuspended during the summer and winter months while more resuspension of chlorophyll *a* occurred during spring and summer. Increases in the amount of primary production in the water column occurred with the resuspension of chlorophyll *a*, indicating that the resuspended cells were viable. The contribution of this resuspended phytoplankton to the total yearly primary productivity can be significant.

The tidal resuspension of phytoplankton and detritus from the mud bottom of Buzzards Bay, if utilized by the zooplankton community, could provide significant food resources for secondary production.

Introduction

Rhoads & Young (1970) described how deposit-feeding bivalves such as *Yoldia limatula* and *Nucula annulata* that dominate the mud bottom of Buzzards Bay rework the sediment to make it unstable. Young (1971) first discussed the tidal resuspension phenomenon after finding sedimentation rates as high as 138 g m^{-2} day^{-1} in Buzzards Bay and attributed sediment instability to this biogenic reworking. Comparing this seston flux to Hough's (1940) estimated rate of sediment incorporation to the benthos of 2·3 mm year^{-1} for the same area, Young concluded that a maximum of 2% of the sediment remained as permanent deposits and 98% was resuspended. Steele & Baird (1972) placed sediment traps at various depths in a Scottish Loch and found that high sedimentation rates were due to resuspension of zooplankton fecal pellets from the bottom by tidal currents. Rhoads (1973) related tidal flow to turbidity cycles in bottom water above benthic deposit feeding communities.

[a]Present address: Rosenstiel School of Marine & Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A.

[b]Present address: Skidaway Institute of Oceanography, Savannah, Georgia 31406, U.S.A.

Looking more closely at the nutritive value of resuspended material, Rhoads *et al.* (1975) found that a turbid layer extends from the bottom to a height about 3 m in Buzzards Bay, and may extend to the surface in a 13-m water column during ebb and flood tides. They also found increases in amount of chlorophyll *a*, particulate organic carbon and particulate organic nitrogen in the water 1 m above the bottom during a tidal cycle. Monthly samples from 1 m above the bottom taken 1 h after mean ebb tide had higher concentrations of chlorophyll *a*, particulate organic carbon, and particulate organic nitrogen as compared to surface values over a year except during the spring phytoplankton bloom. Studying the photosynthetic activity of resuspended phytoplankton, Tenore (1976) found that primary productivity in the water column increased 40% during a tidal cycle in Buzzards Bay. He postulated that not only does tidal resuspension increase autotrophic activity but also heterotrophic activity on the resuspended detritus; both phenomena resulting in an increased food source for the benthic community by enhancing the nutritive value of the resuspended material. However, data were needed to assess the seasonal changes in the quality and quantity of suspended material.

Results of studies on the utilization of detritus by copepods are important in determining the significance of much of the resuspended particles for zooplankton. Heinle *et al.* (1974) demonstrated the nutritional value of detritus for zooplankton by the egg production of the calanoid copepod *Eurytemora affinis*, fed natural detritus in the laboratory. Poulet (1976) found that detritus composed the major fraction of the food ingested by *Pseudocalanus minutus*. The tidal resuspension of phytoplankton and detritus from the mud bottom of Buzzards Bay, if utilized by the zooplankton community could provide significant food resources for their annual energy budget. To determine the effect of these resuspended bottom muds upon the zooplankton community in Buzzards Bay, research was initiated to ascertain: (1) What is the carbon and chlorophyll composition as well as quantity of the material being resuspended ? (2) How much potential food is being resuspended in comparison to that already present in the water column ? (3) Does the amount of carbon, and chlorophyll in resuspended material vary over the year ?

Once the input of material from the bottom by resuspension is known, experimentation on the utilization of this material by copepods would determine its ecological significance for the zooplankton community.

Methods

The sampling station was located in Buzzards Bay in 13 m of water (Figure 1). This station, typical of the silt-clay mud bottom of Buzzards Bay, was the same used in Rhoads *et al.* (1975) study. At monthly intervals for 2 years water samples were taken every 2 m from surface to bottom with Niskin samplers. In addition to the seasonal sampling, every 2 months water samples were taken at 1, 5, 10 and 12 m at 2-h intervals over a tidal cycle.

Analysis of particulate organic carbon was determined with a Perkin-Elmer Model 240 Elemental Analyzer; chlorophyll *a* was determined by fluorescense (Yentsch & Menzel, 1963); and primary productivity determined by the '*in situ* 'C^{14} method (Steeman-Nielsen, 1952). Chorophyll in the sediment was determined from 5 cm diameter gravity core samples and extracted by the method outlined by Tietjen (1967). Inorganic nutrients were analyzed according to the methods outlined by Strickland & Parsons (1968).

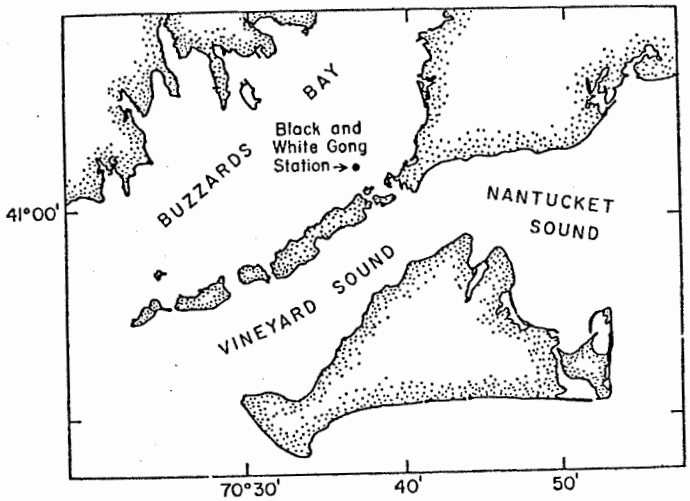

Figure 1. Sampling station (Black and White Gong Station) Buzzards Bay, Massachusetts.

Results

Seasonal cycles

The significance of the resuspended material will be assessed in the context of the yearly cycles of particulate organic carbon, chlorophyll *a* and primary productivity. The 1974–1975 cycles of standing crop of phytoplankton as measured by chlorophyll *a* m^{-2} showed a phytoplankton peak in winter and fall with a lesser bloom in mid-summer and agrees with Fish's (1925) original study of the area [Figure 2(a)]. The high amount of chlorophyll *a* m^{-2} in the sediment represents both endemic benthic diatoms and phytoplankton that have settled from the overlying water column [Figure 2(b)]. Young (1971) reported up to 1500 diatoms cm^{-2} in sediment of Buzzards Bay.

The yearly cycles of primary productivity for the water column [Figure 2(c)] show maxima during the summer and fall months. The amount of carbon fixed per m^2 per year is 89 g and 123 g for 1974 and 1975 respectively. The annual concentration of inorganic nutrients in the water column reflects the decomposition of plant and animal material in the fall and winter as well as the utilization of inorganic nutrients during phytoplankton blooms [Figure 2(d)]. No thermocline exists in Buzzards Bay because of tidal currents and hence nutrient concentrations tend to be homogeneous in the 13-m water column. Yearly cycles of particulate organic carbon [Figure 2(e)] reflects both the phytoplankton blooms as well as the build-up of organic detritus in the summer and winter months.

Tidal studies

In the context of these yearly cycles of particulate organic carbon and chlorophyll *a* several changes over tidal cycles were observed.

The distribution of chlorophyll *a* in the water column during May 1975; a period of low phytoplankton standing crop shows a threefold increase in the amount of chlorophyll *a* from the surface to 11 m, in the resuspension zone [Figure 3(a)]. Over a tidal cycle a 100% increase in the amount of chlorophyll *a* present in the water column is reflected in the change

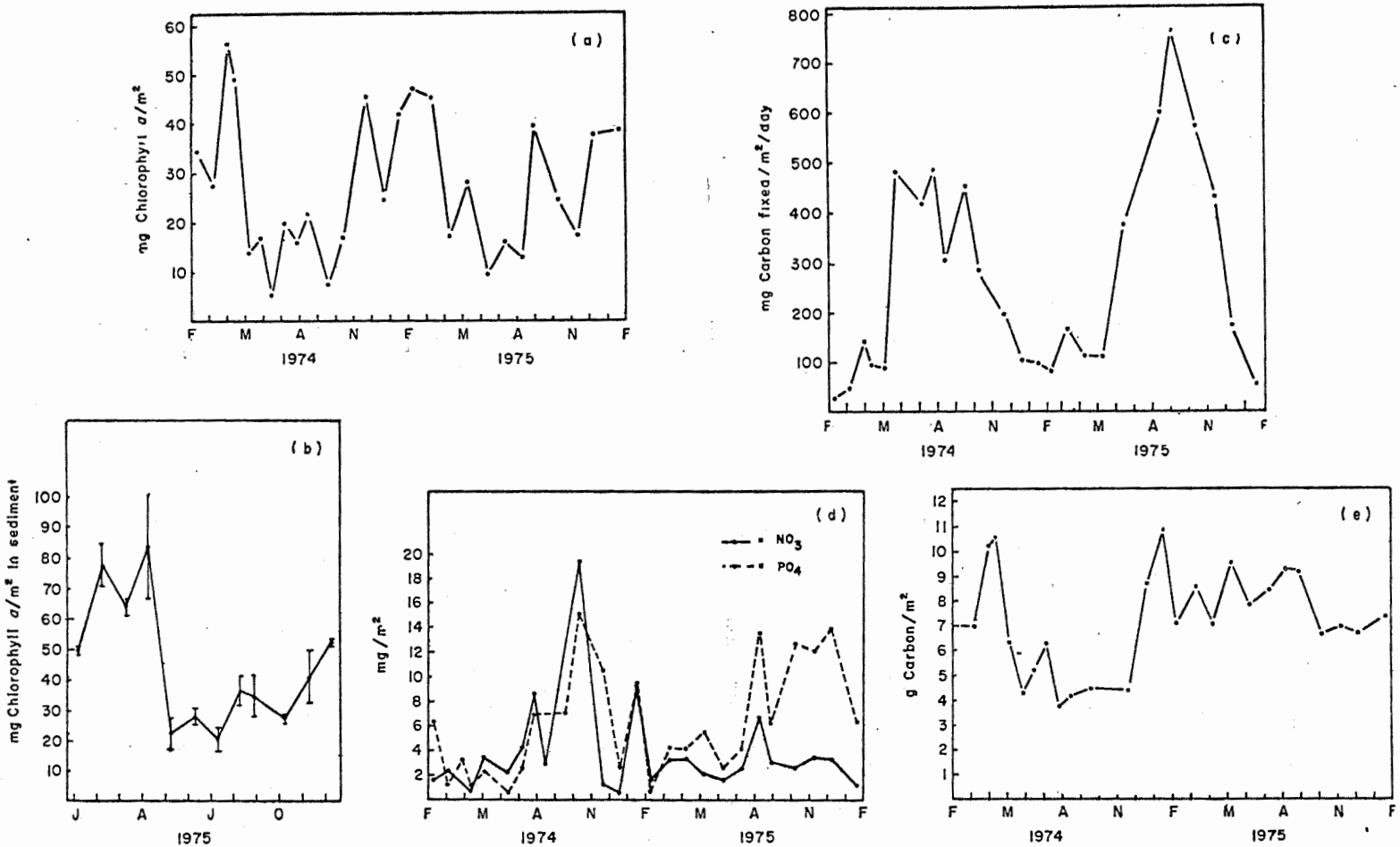

Figure 2. Seasonal hydrographic and biological data; 1974–75, Buzzards Bay, Massachusetts. (a) Phytoplankton biomass as mg chlorophyll *a* m^{-2}. (b) Sedimentary chlorophyll *a* as mg chlorophyll *a* $m^{-2} \pm 1$ standard deviation unit. (c) Primary production as mg carbon m^{-2} day^{-1}. (d) Nitrate and phosphate as mg m^{-2}. (e) Particulate organic carbon as g carbon m^{-2}.

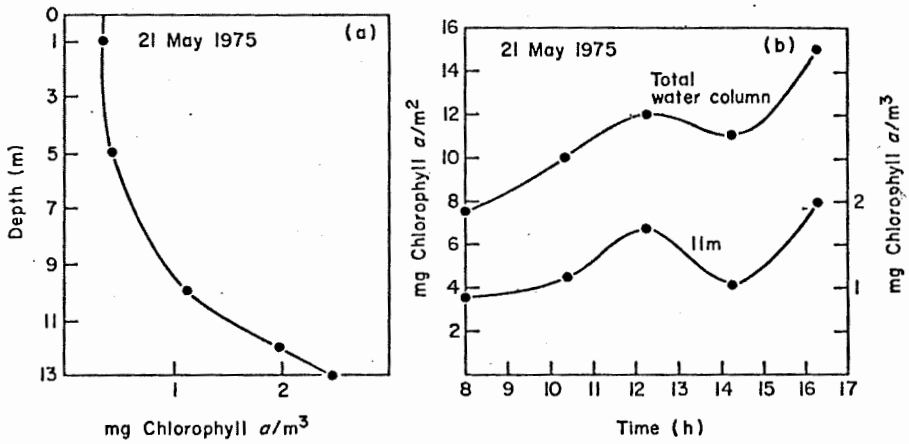

Figure 3. Chlorophyll *a*, 21 May 1975, Buzzards Bay, Massachusetts. High water at 1739. (a) Distribution of chlorophyll *a* (mg chlorophyll *a* m^{-2}) with depth (m) 0·124 before high water. (b) Change in chlorophyll *a* for the integrated water column (mg chlorophyll *a* m^{-2}) and the change at 11 m (mg chlorophyll *a* m^{-3}).

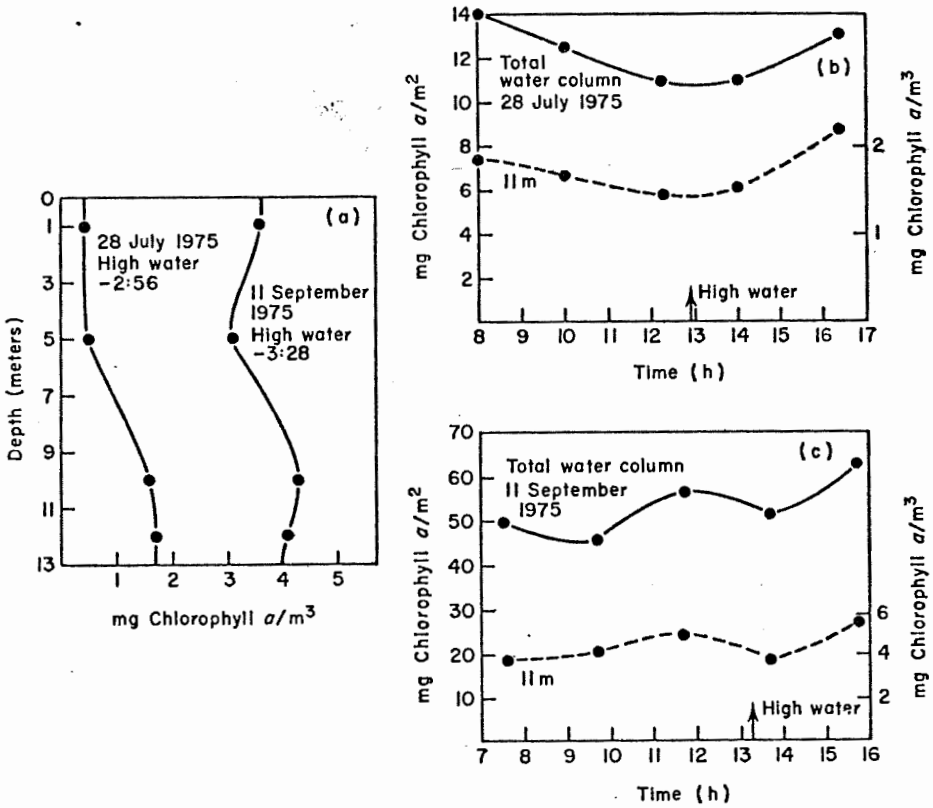

Figure 4. Depth distribution and tidal changes of chlorophyll *a*, Buzzards Bay, Massachusetts. (a) Distribution of chlorophyll *a* (mg chlorophyll *a* m^{-3}) with depth (m) for 28 July 1975 and 11 September 1975. (b) Change in chlorophyll *a*, 28 July 1975, for the integrated water column (mg chlorophyll *a* m^{-2}) and the change at 11 m (mg chlorophyll *a* m^{-3}) for a tidal cycle (high water at 10.55). (c) Change in chlorophyll *a*, 11 September 1975, for the integrated water column (mg chlorophyll *a* m^{-2}) and the change at 11 m (mg chlorophyll *a* m^{-3}) for a tidal cycle (high water at 13.13).

due to tidal resuspension at 11 m [Figure 3(b)]. The distribution of chlorophyll *a* in the water column during periods of high and low phytoplankton biomass is shown by comparing data for the July and September sampling [Figure 4(a)]. Both sampling times occurred during maximum flood tide, when resuspension is high. During September, at the onset of the fall bloom, a fairly homogeneous distribution of chlorophyll *a* was present. As the bottom current increased during flood tide additional phytoplankton cells were resuspended from the bottom into the water column. The distribution of chlorophyll *a* in July in the water column when the phytoplankton standing crop is low emphasizes the effect of tidal resuspension. The change in chlorophyll *a* in the water column is reflected in a 50% increase in the amount of chlorophyll *a* at 11 m [Figure 4(b)]. The phytoplankton in the bottom water are composed of numerous forms such as *Pleurosigma* spp., *Gyrosigma* spp. and *Nitzschia* spp. species, many of which are absent from surface waters.

In order to ascertain the effect of tidal resuspension on primary production, '*in situ*' C^{14} incubations were conducted during tidal cycle studies. For example on 22 July 1974 the

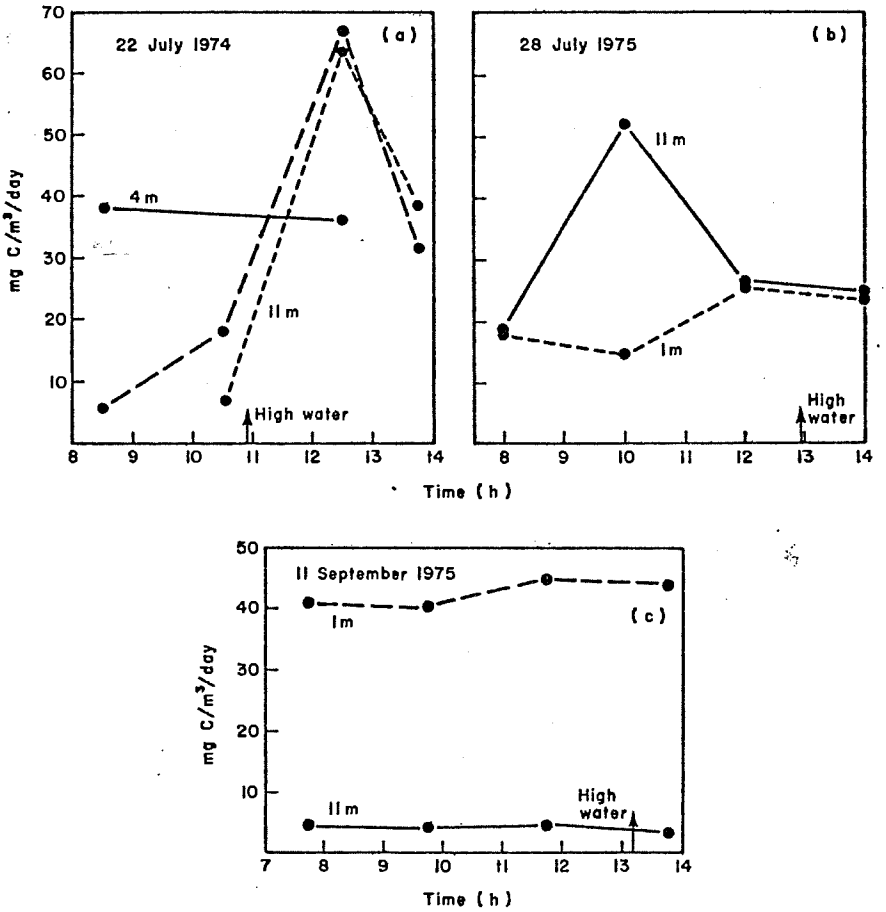

Figure 5. Tidal changes in primary production (mg carbon m^{-2} day $^{-1}$), Buzzards Bay, Massachusetts. (a) 22 July 1974, high water at 10.55. (b) 28 July 1975, high water at 12.56. (c) 11 September 1975, high water at 13.13.

change in primary productivity was compared at 4 and 11 m over a tidal cycle [Figure 5(a)]. As ebb tide proceeded and chlorophyll was resuspended from the bottom, the primary productivity at 11 m increased dramatically. To ascertain if light was limiting samples collected at 11 m were incubated at 4 m. No significant difference was seen comparing the two sets of 11 m water, indicating that there was sufficient light in the resuspension zone for enhanced primary productivity to occur. A July 1975 study revealed the same phenomenon, this time occurring during flood tide. With the 50% increase in chlorophyll *a* shown in Figure 4, the primary productivity at 11 m increased during mean flood tide [Figure 5(b)]. In contrast, tidal change in primary production in September 1975 during the fall bloom is different to that in the July study [Figure 5(c)]. Although concentrations of chlorophyll *a* at 11 m were higher than that of the July study [Figure 4(a)], the amount of primary production was markedly reduced. The distribution of chlorophyll *a* in the surface water during September was 6 times greater than in July. High surface productivity and cell biomass perhaps shades the phytoplankton in the resuspension zone resulting in lower primary production at these depths at various times of the year.

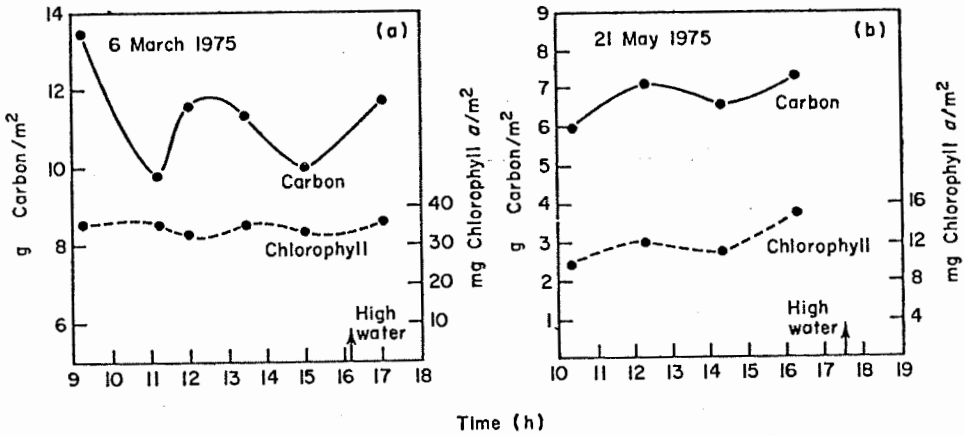

Figure 6. Tidal changes in particulate organic carbon (gm carbon m^{-2}) and change in chlorophyll *a* (mg chlorophyll *a* m^{-2}) for the integrated water column, Buzzards Bay, Massachusetts. (a) 6 March 1975, high water at 16.09. (b) 28 May 1975, high water at 17.39.

In March particulate organic carbon was high probably from the build-up of detrital material over the fall and winter. The spring bloom resulted in a homogeneous distribution of chlorophyll *a* in the water column. Tidal resuspension resulted in a 40% increase in the amount of particulate organic carbon in the water column during mean flood tide [Figure 6(a)]. Because no significant change in chlorophyll *a* occurred in the bottom water, most of the resuspended carbon was probably detrital. During May when the amount of particulate organic carbon in the water column was at a minimum, chlorophyll *a* resuspension accounted for the changes in the amount of carbon over a tidal cycle [Figure 6(b)]. Qualitative observations revealed that although much of the particulate material in the bottom water was still detrital, greater percentages of the material were benthic diatoms, due to the supposed higher benthic primary productivity during the preceeding spring months.

Discussion

Seasonal cycles

The seasonal cycle of particulate organic carbon in the 13-m water column of Buzzards Bay is influenced by benthic primary productivity and bioturbation by benthic animals. Although the highest pulses in the amount of organic carbon reflect phytoplankton blooms in the water column, subordinate peaks are measuring changes in energy from the benthos. One of these sources of carbon is resuspended benthic diatoms, most active in the summer months when the photoperiod is long and light penetration is great because of low cell densities in surface waters. The biomass and feeding activity of the benthic community is highest in the summer months and the high amount of feces and pseudofeces that these animals produce (Rhoads, 1974) is resuspended into the water column by tidal currents and contributes to the organic carbon measured in the water column.

Phytoplankton biomass as measured by chlorophyll *a* is highest in the winter and fall blooms. A subordinate bloom occurs during mid-summer of which resuspended diatoms are a major component. Although the biomass of phytoplankton cells is lower during the summer, photosynthetic activity is higher because of light intensity and the long photoperiod. The greater primary production during 1975 may be attributed to: higher nutrient concentrations, warmer water temperatures during 1975, and lower grazing pressure by zooplankton because of large numbers of predatory ctenophore species. Ctenophores decompose rapidly and their role in nutrient regeneration may also contribute to high algal productivity.

Tidal cycles

Tidal resuspension results in the infusion of several types of particulate material back into the water column. The resuspension of chlorophyll *a* represents both endemic benthic diatoms and phytoplankton that have sunk out of the water column. The tidal resuspension of phytoplankton cells, both viable and senescent, reintroduces those cells sunk and lost from the water column. The phytoplankton cells are resuspended up into two-thirds of the water column; the residence time in the upper water column allows greater photosynthetic activity and also utilization by the zooplankton community. In neritic waters phytoplankton blooms preceed maxima of zooplankton biomass, tidal resuspension is a means of conserving the algal food.

Benthic diatoms are also resuspended from the sediment into the water column where enhanced primary productivity can occur. Chlorophyll *a* concentrations are higher in the resuspension zone except during the winter and fall blooms when the distribution in the water column is homogeneous. In the context of yearly cycles of primary production and phytoplankton biomass, the impact of tidal resuspension is greatest during periods of low phytoplankton biomass in the water column. In late spring and summer primary productivity in the resuspension zone contributes the major percentage of the primary productivity in the water column. The standing stock of phytoplankton is low so that self-shading is minimal. One of the primary sources of nutrients is regeneration from the sediment (Hale *et al.*, 1975; Rowe *et al.*, 1975); so the benthic diatoms may utilize this nutrient source and when periodically resuspended into the upper water column where light intensity is greater, exhibit enhanced photosynthetic activity.

Rhoads (1974) identified much of the resuspended material in Buzzards Bay as fecal pellets from benthic deposit feeders. The nutritional value of fecal pellets for various organisms was discussed by Newell (1965) and Frankenberg *et al.* (1967), and suggested as an alternate food source for zooplankton by Jorgensen (1966).

Our own qualitative observations on particulate material from the resuspension zone revealed that a large percentage of the particles were macroalgae detritus with associated microfauna communities. Marshall (1970) has re-emphasized that adjacent saltmarshes have significant seasonal inputs of organic matter into coastal waters of New England. In addition, the submerged sea grasses and macroalgae such as *Zostera marina* and *Fucus* spp. are also highly productive in shallow coastal embayments. Harrison & Mann (1975) found that eel grass detritus decomposes slowly and Tenore (1975) determined eel grass detritus to be very slowly available to detrital feeders; therefore, a large detrital pool may exist in Buzzards Bay over the year.

The food sources for zooplankton available through tidal resuspension vary seasonally. Benthic primary productivity is highest during late spring and summer when the amount of chlorophyll *a* and primary productivity in the water column are greatest in the resuspension zone. The winter and fall phytoplankton blooms result in many cells sinking to the bottom and later being resuspended, often after phytoplankton in the surface waters have been grazed. Detritus, in the form of zooplankton fecal pellets as well as feces and pseudofeces from benthic organisms are highest in abundance in the resuspension zone during the summer months. Macroalgal detritus enters the bottom water of Buzzards Bay primarily in the fall and winter months. Because of its large particle size, high carbon : nitrogen ratio and slow decomposition rate, it may be a year before the detritus is a suitable food source for zooplankton. Therefore, because of the yearly cycles of particulate carbon and chlorophyll *a* measured in Buzzards Bay there is a possibility of seasonal changes in the food resources available to zooplankton through tidal resuspension.

The significance of much of the resuspended material for the zooplankton community awaits confirmation by feeding experiments. Benthic diatoms have not been used in grazing or incorporation studies with copepods, yet their contribution in the annual primary productivity of coastal waters may be significant. The work of Heinle *et al.* (1974) has shown utilization of detritus by a calanoid copepod. However, more work is needed on grazing rates and incorporation efficiencies of common calanoid copepod species on specific detrital sources.

Acknowledgements

We wish to thank Captain Richard Coburn of the R. V. *Asterias* for making sample collection a simple and pleasant task. Grateful acknowledgement is paid to Mr Philip Clarner for performing the carbon-nitrogen determinations, Mr Nathanial Corwin for analyzing inorganic nutrients and to Mr Ralph Vacarro and Ms Pamela Bowman for assistance in primary productivity data.

This research was conducted at the Woods Hole Oceanographic Institute with support from a Biological Oceanography NSF Doctoral Dissertation Fellowship, DES 75–10025 and grant GA–39911.

References

Fish, C. J. 1925 Seasonal distribution of plankton of the Woods Hole Region. *Fishery Bulletin Fishery Wildlife Service U.S.* **41**, 62–112.

Frankenberg, D., Coles, S. L. & Johannes, R. E. 1967 The potential trophic significance of *Callianassa* major fecal pellets. *Limnology and Oceanography* **12**, 113–120.

Hale, S. S., Nixon, S. W. & Oviatt, C. A. 1975 Benthic nutrient regeneration in Narragansett Bay. *American Society of Limnology and Oceanography Conference, Halifax, Nova Scotia, June 1975.*

Harrison, P. G. & Mann, K. H. 1975 Detritus formation from eelgrass (*Zostera marina.*): the relative effects of fragmentation, leeching and decay. *Limnology and Oceanography* **20**, 924–934.

Heinle, D. R., Flemer, D. A., Ustach, J. F., Murtagh, R. A. & Harris, R. P. 1974 The role of organic debris and associated micro-organisms in pelagic estuarine food chains. Final Report to OWRR U.S. Department of the Interior NRI Ref. 74–29.

Hough, J. L. 1940 Sediments of Buzzards Bay, Massachusetts. *Journal of Sedimentary Petrology* **10**, 19–32.

Jorgensen, C. B. 1966 *Biology of Suspension Feeding*. Pergamon Press, New York. 375 pp.

Marshall, N. 1970 Food transfer through the lower levels of the benthic environment. In *Marine Food Chains* (Steele, J. H., ed). University of California Press, Berkeley. pp. 52–66.

Newell R. 1965 The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proceedings of the Zoological Society of London* **144**, 24–45.

Poulet, S. A. 1976 Feeding of *Pseudocalanus minutus* on living and non-living particles. *Marine Biology* **34**, 117–125.

Rhoads, D. C. 1973 The influence of deposit-feeding benthos on water turbidity and nutrient recycling. *American Journal of Science* **273**, 1–22.

Rhoads, D. C. 1974 Organism-sediment relations on the muddy seal floor. *Oceanography and Marine Biology Annual review* **12**, 263–300.

Rhoads, D. C., Tenore, K. R. & Browne, M. 1975 The role of resuspended bottom muds in the food chain of shallow embayments. In *Estuarine Research* Vol. 1 (Cronin, L. E., ed.). Academic Press, New York. pp. 563–579.

Rhoads, D. C. & Young, D. K. 1970 The influence of deposit-feeding organisms on sediment stability and community trophic structure. *Journal of Marine Research* **28**, 150–178.

Rowe, G. T., Clifford, C. H., Smith, K. L. & Hamilton, P. L. 1975 Benthic nutrient regeneration and its coupling to primary productivity in coastal waters. *Nature* **255**, 215–217.

Steele, J. H. & Baird, I. E. 1972 Sedimentation of organic matter in a Scottish sea loch. *Memorie Dell Institute Italiano Di Idrobiologia* **29** (*Suppl.*), 73–88.

Steeman-Nielsen, E. 1952 The use of radioactive carbon (C^{14}) for measuring organic production in the sea. *Journal du Conseil* **18**, 117–140.

Stickland, J. D. H. & Parson, T. R. 1968 A practical handbook of seawater analysis. *Fisheries Research Board of Canada* **167**.

Tenore, K. R. 1975 Detritus utilization by the polychaete *Capitella capitata*. *Journal of Marine Research* **33**, 261–271.

Tenore, K. R. 1976 Food chain pathways in benthic communities: a review, with new observations on sediment resuspension and detrital recycling. In *Ecology of Marine Benthos* (Coull, B. C., ed.). Belle W. Baruch Library in Marine Science, No. 6, University of South Carolina Press, Columbia, S.C.

Tietjen, J. H. 1968 Chlorophyll and phaeopigments in estuarine sediments. *Limnology and Oceanography* **3**, 189–192.

Yentsch, C. S. & Menzel, D. W. 1963 A method for the determination of phytoplankton chlorophyll and phaeophtin by fluoresence. *Deep-Sea Research* **10**, 221–231.

Young, D. K. 1971 Effects of infauna on the sediment and seston of a subtidal environment. *Vie et Milieu* **22** (*Suppl.*), 557–571.

Estuarine and Coastal Marine Science (1978) 6, 47–53

ROMAN 1978

Tidal Resuspension in Buzzards Bay, Massachusetts

II. Seasonal changes in the size distribution of chlorophyll, particle concentration, carbon and nitrogen in resuspended particulate matter

Michael R. Roman[a]

Department of Zoology, University of New Hampshire, Durham, New Hampshire 03824, U.S.A.

Received 24 June 1976

Keywords: Seasonal variation, particle size distribution, suspended particles, nutrients, chlorophyll measurements, plankton blooms, Massachusetts coast

Seasonal changes in the particle size spectrum of suspended matter in near bottom water of Buzzards Bay was studied by fractional filtration. The greatest fraction of the total particulate organic carbon and particulate organic nitrogen throughout the year was less than 20 μm. The relative independence of the seasonal size distribution of particulate carbon to changes in the chlorophyll, as well as high carbon : nitrogen ratios during winter, suggest that large amounts of detritus are present in Buzzards Bay. Chlorophyll *a* distribution was dominated by nanoplankton in the spring and summer months when inorganic nutrients were low and zooplankton grazers abundant. The winter and fall phytoplankton blooms were dominated by individual and chain-forming diatoms greater than 53 μm. The dominance of nanoplankton and nanodetritus (<20 μm) in the suspended matter of Buzzards Bay suggests that the major source of nutrition for filter feeding zooplankton are small particles.

Introduction

The size distribution of particulate carbon, nitrogen and chlorophyll *a* reflect the composition of the seston community. Seasonal changes in the size distribution of suspended particles are related to community succession and, with species composition and production data, are a viable means of studying plankton trophic dynamics. Early phytoplankton studies were performed with nets; the species found and seasonal cycles of phytoplankton abundance described were for the larger net plankton. With the advent of whole water collection for phytoplankton study, size separation by screens and filters, and chlorophyll analysis, investigators found that nanoplankton (less than 20 μm) usually dominate both coastal and pelagic phytoplankton biomass and primary production (Yentsch & Ryther, 1959; Malone, 1971; Reynolds, 1973; McCarthy *et al.*, 1974; Bermen, 1975). The distribution of particulate organic carbon is also dominated by small particles. Riley (1963) and Sheldon *et al.* (1967) found that organic aggregates, usually less than 8 μm, form in seawater and are in great abundance in both neritic and pelagic seston. Analysing the size distribution of particulate

[a]Present-address Rosenstiel School of Marine & Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149, U.S.A.

carbon by fractional filtration, Mullin (1965) showed that over 50% of the total organic carbon in surface water from the Indian Ocean was less than 10 μm. Sutcliffe (1972) using ATP analysis, determined that over 60% of the living particulate organic matter in two Canadian Bays was less than 8 μm.

Tidal resuspension can result in significant inputs of biologically useable energy into the water column of shallow coastal embayments. Rhoads *et al.* (1975) found that organic material was resuspended up into two-thirds of a 13-m water column in Buzzards Bay. Hargrave (1976) showed that tidal resuspension increased the amount of particulate carbon in the bottom 20 m of a 70-m water column in St. Margaret's Bay. Roman & Tenore (1978) found that tidal resuspension can result in greater than 50% increases in particulate carbon, primary productivity and chlorophyll *a* m^{-2} in Buzzards Bay. Therefore, because tidal resuspension may be an important means of energy transfer in many coastal waters, resuspended matter in Buzzards Bay was studied by fractional filtration to determine the seasonal size distribution of particulate organic carbon, nitrogen, particle volume and chlorophyll *a*. The information would assess the seasonal patterns in the range of quality, size and quantity of the food resources available to zooplankton through tidal resuspension.

Methods

The sampling station in Buzzards Bay at a depth of 13 m was the same station used by Rhoads *et al.* (1975) and Roman & Tenore (1978) who showed that a turbid layer extends several meters from the bottom. Water samples were collected monthly from 1 m above the bottom with a 5-l Niskin sampler. Samples were collected during maximum tidal flow, either at mean ebb or flood tides, to insure sampling at a time of maximum resuspension (Roman & Tenore, 1978).

Seawater was poured through a series of Nitex screens to fractionate the particulate material. The technique described by Mullin (1965) and modified by Loder (1971), employed 250 ml Nalgene beakers with the bottom replaced by Nitex mesh. An array of stacked beakers with: 102 μm, 53 μm, 20 μm and 10 μm mesh over a 250-ml Millipore funnel, 0·5 μm GFC filter and vacuum flask was used to filter the seawater. Samples were filtered by gravity through the Nitex screens and by vacuum pressure of less than 500 mm through the 0·5-μm GFC filter. Particles remaining on the screens were removed by washing with filtered seawater. Seawater and the wash was refiltered on 0·5 μm GFC filters for carbon, nitrogen and chlorophyll *a* analyses. The per cent recovery of chlorophyll *a* between whole water samples and fractionated samples was equal to or less than the variation between whole water samples due to sample collection. Per cent recovery for particulate organic carbon and nitrogen in the fractionation process was always greater than 100%. The addition of carbon and nitrogen in the fractionation process was due to particles forming in the filtered seawater used to wash off the screens. To correct for this addition, 200 ml of filtered seawater was assayed for carbon and nitrogen and these values were subtracted from each sample fraction which was diluted by 200 ml of the filtered seawater wash. One liter of seawater was filtered for carbon and nitrogen samples and 0·5 l for chlorophyll *a* analyses. Particulate organic carbon and particulate organic nitrogen were determined with a Model 240 Perkin-Elmer Elemental Analyzer. Chlorophyll *a* was measured by fluorescence (Yentsch & Menzel, 1963). The particle distribution of seston expressed as concentration (parts/10^6) was determined with a Coulter Counter Model TAII.

Results

Nanoplankton and netplankton varied seasonally in their contribution to fluctuations in

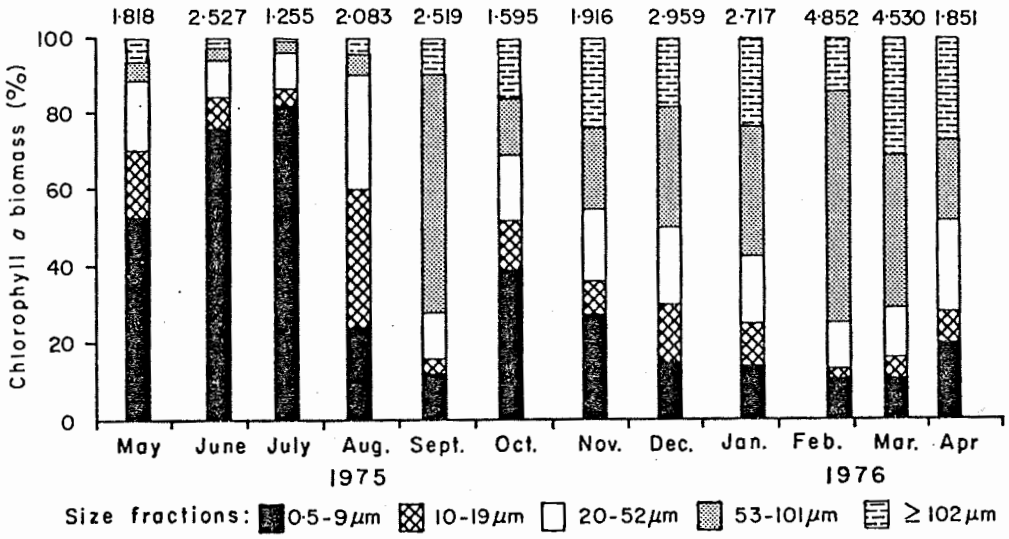

Figure 1. Size distribution of chlorophyll *a* (% of total) for 11 m Buzzards Bay, Massachusetts (5/75–4/76). Total chlorophyll *a* (mg chlorophyll *a* m^{-3}) for samples are written at the top of the histograms.

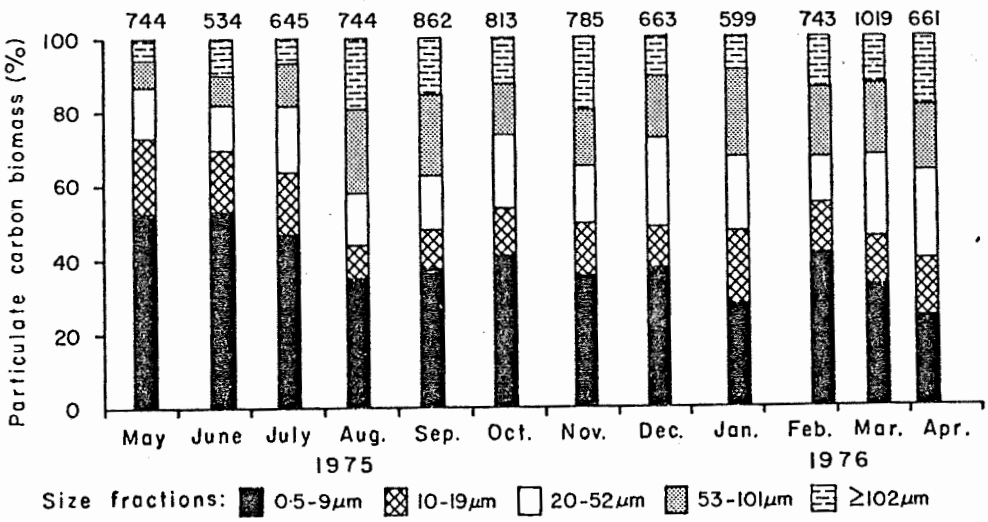

Figure 2. Size distribution of particulate organic carbon (% of total) for 11 m Buzzards Bay, Massachusetts (5/75–4/76). Total particulate organic carbon (mg carbon m^{-3}) for samples are written at the top of the histograms.

the total chlorophyll biomass. The amount of chlorophyll *a* measured in the resuspension zone (Figure 1) agrees with the seasonal data of Fish (1925) and Roman & Tenore (1978). A winter phytoplankton bloom occurred in March–February and a fall bloom in September. Over 75% of the phytoplankton biomass during the winter and fall blooms was dominated by cells greater than 53 μm. In contrast, spring and summer phytoplankton populations were predominantly cells less than 20 μm. In June and July, over 80% of the phytoplankton biomass was comprised of cells less than 10 μm.

The seasonal cycles of particulate organic carbon and nitrogen (Figures 2 and 3) in the

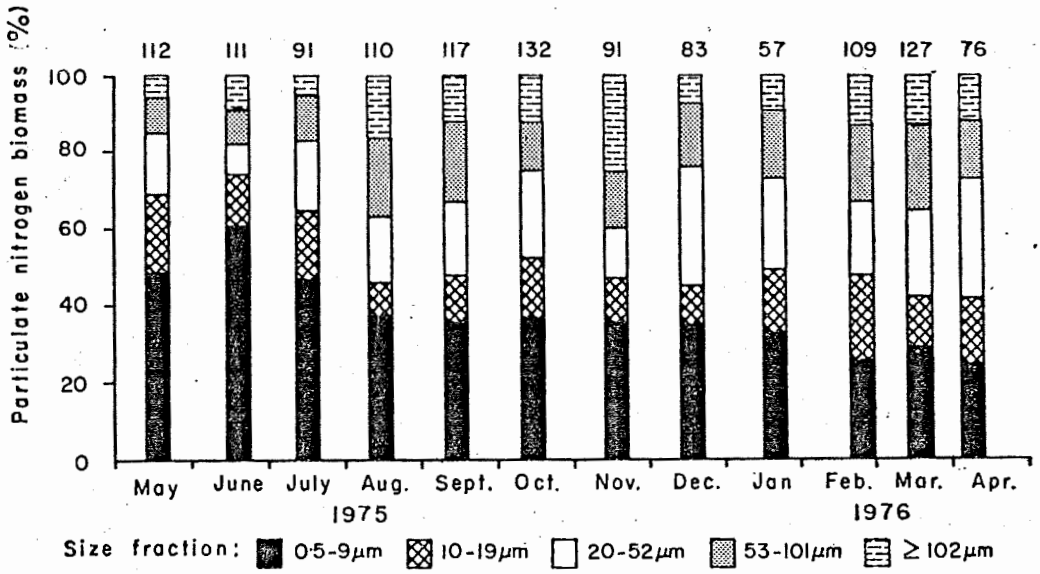

Figure 3. Size distribution of particulate organic nitrogen (% of total) for 11 m Buzzards Bay, Massachusetts (5/75–4/76). Total particulate organic nitrogen (mg nitrogen m^{-3}) for samples are written at the top of the histograms.

TABLE 1. Carbon:nitrogen ratios of particulates of various size fractions in water samples collected at 12 m in Buzzards Bay, Massachusetts

	Size divisions					
	0·5–9 μm	10–19 μm	20–52 μm	53–101 μm	>102 μm	Total
17 May 1976	7·2	6·5	6·0	5·8	5·5	6·6
18 June 1976	4·2	6·3	7·1	4·1	5·4	5·8
15 July 1976	7·2	6·6	6·9	7·1	9·0	8·1
14 August 1976	6·4	6·2	5·9	7·3	8·0	6·8
4 September 1976	7·8	6·3	5·8	7·9	8·8	7·4
14 October 1976	6·9	5·1	5·3	6·4	6·2	6·1
17 November 1976	8·6	11·2	10·9	8·7	6·5	8·6
16 December 1976	8·3	8·4	5·8	7·6	11·0	7·6
20 January 1976	9·0	13·0	8·7	14·1	9·4	10·4
26 February 1976	10·9	3·7	4·2	6·0	6·8	6·8
16 March 1976	9·3	7·4	7·8	7·4	7·2	8·0
1 April 1976	8·6	7·6	7·0	10·2	12·7	8·7

resuspension zone were influenced primarily by the amount of detritus in the water column. It is assumed that over the year the major fraction of particulate carbon was detritus (Parsons, 1963; Riley, 1970). Therefore, whereas 80% of the phytoplankton chlorophyll during March was due to cells greater than 53 μm, this fraction accounted for just 30% of the total particulate carbon. The carbon:nitrogen ratios of the various size fractions (Table 1) showed seasonal low values during spring and summer and the March and September phytoplankton blooms; and high values (up to 13) in November, December and January when the amount of chlorophyll in the water column was low.

The size distribution of particulates (Figure 4) is a measure of both organic and inorganic matter. One study in July on the weight of seston after ashing showed that less than 18% of the total particulate material was organic. Thus clays, quartz and silica frustules from

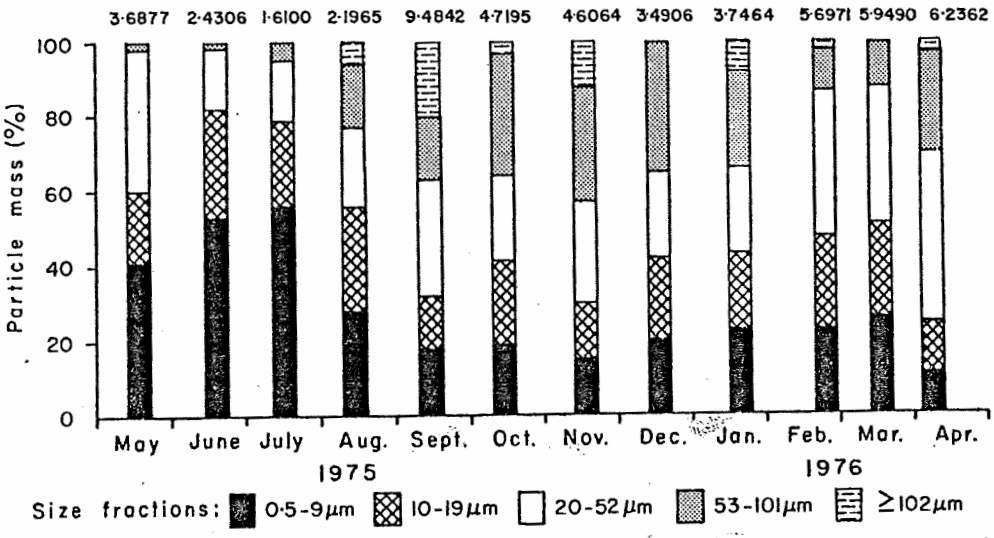

Figure 4. Size distribution of particle concentration (% of total) for 11 m, Buzzards Bay, Massachusetts (5/75–4/76). Total particle concentration (parts/10^8 by volume) for samples are written at the top of the histograms.

diatoms also contribute to particulate mass. Seasonal changes in particle concentration greater than 20 μm reflected the dynamics of the phytoplankton blooms. In general, however, the distribution of particle concentrations correlated with the distribution of the large particulate carbon pool rather than the chlorophyll *a* seasonal cycles. Because of the limit of sample size only 2-ml samples of seawater could be analysed in the Coulter Counter to determine the particle spectrum. Sheldon & Parsons (1967) suggested that larger sample sizes should be used when measuring the concentration of particles greater than 100 μm. Therefore the contribution of particulate material in the greater than the 102 μm fraction (Figure 4) may be underestimated.

Discussion

Nanoplankton may dominate the phytoplankton biomass in both neritic and pelagic environments. Looking at the seasonal size distribution of chlorophyll, Yentsch & Ryther (1959) found that nanoplankton were dominant in Vineyard Sound during June and July. The same seasonal pattern of nanoplankton biomass was found in this study. Inorganic nutrients in the water column were at a yearly minimum during June and July (Roman & Tenore, 1978). Nanoplankton, because of their high surface to volume ratio and high incorporation rate of inorganic nutrients, may be favored over the larger net plankton during summer oligotrophic conditions. Another possible reason for the greater abundance of nanoplankton is that net plankton are preferentially grazed over nanoplankton and are therefore in lower abundance (Malone, 1971).

Several studies have shown that primary productivity of various size fractions of phytoplankton, although not measured in this study, are dominated by nanoplankton in many coastal and pelagic areas. McCarthy *et al.* (1974) found that phytoplankton less than 3 μm accounted for 90% of the yearly primary productivity in the Chesapeake Bay. Berman (1975) working off California, showed that 13–83% of carbon fixed was by cells between 1 and 3 μm. Roman & Tenore (1978) found that yearly primary productivity in Buzzards Bay was highest in the summer, when nanoplankton comprised over 80% of the phytoplankton

biomass (Figure 1). Assuming rapid turnover rates because of small size and high photosynthetic rates, nanoplankton are probably the primary algal food source for zooplankton in Buzzards Bay during the spring and summer months.

Microscopic identification and particle distribution data showed that particles less than 20 μm—nanoplankton, broken fecal pellets, macrophyte detritus and organo-mineral complexes—comprised more than 50% of the total yearly particulate carbon biomass in Buzzards Bay. Roughly 80% of suspended particles in the resuspension zone were inorganic by ash weight analysis. Therefore, the organic carbon adsorbed to these minerals may be an important carbon fraction. Johnson (1974) found that particulate material at the sediment-water interface contained organic aggregates of 13–71% the total particle abundance. Nearly all clay and silt size particles were incorporated into an organic matrix. Poulet (1976) found that small detrital particles comprised over 70% of the annual particulate carbon biomass in the Bedford Basin. In addition to small detrital particles, the less than 20 μm fraction also contains dominant 'living carbon' material. For example, Sutcliffe (1972) working in two Canadian Bays found that 60% of the total living carbon, as measured by ATP, was less than 8 μm.

Seasonal changes in the nutritive quality of different particulate matter are difficult to assess because of the inability to accurately measure the amount of detritus in the water. Nanoplankton are highest in abundance during the spring and summer; net plankton are dominant in the fall and winter blooms. Zooplankton are most abundant in the water column in summer and fall, when bioturbation by the benthos is also highest. Therefore, the resuspension of fecal pellets from these two sources is significant during the summer and fall. Macrophyte detritus enters Buzzards Bay in large quantities in the fall (Marshall, 1970). The detritus is reduced in particle size by decomposition and wave action, and small macrophyte detritus, as supported by microscopic identification and high carbon:nitrogen ratios in the less than 20 μm fractions, is abundant in winter and spring. This seasonal trend was also observed by Flemer & Biggs (1971), Sutcliffe (1972) and Hargrave (1976), who all attributed yearly maxima of carbon:nitrogen ratios in the late winter to macrophytic detritus. As the carbon:nitrogen ratio and particle size spectrum of macrophyte detritus changes over the year, its nutritional quality changes for various zooplankton. Eel grass, a dominant macrophyte in temperate coastal waters, decomposes slowly (Harrison & Mann, 1975; Tenore, 1975). Because of this slow decomposition rate the residence time of the macrophyte detritus in the small carbon fractions may be considerable.

The quality, quantity and size distribution of the food resources available to zooplankton through tidal resuspension vary seasonally. Yearly changes in the size distribution of chlorophyll *a*, particulate carbon and nitrogen viewed in relation to the species composition and feeding strategies of zooplankton may explain their seasonal abundance and species succession. For example, in Buzzards Bay the copepods, *Centropages typicus* and *C. hamatus* reach their highest yearly abundance in the late winter and fall respectively (unpublished data). During these periods the amount of net phytoplankton in the water is greatest. Conversely, the smaller copepod *Acartia tonsa* is dominant in the summer when nanoplankton comprised over 80% of the phytoplankton chlorophyll in this study. My own preliminary laboratory results indicate that *A. tonsa* is able to filter and ingest particles as small as 2 μm. Perhaps the larger *C. typicus* and *C. hamatus* are not able to retain such small particles and thus do not dominate the zooplankton during spring and summer in Buzzards Bay. When additional data are available on the particle ingestion capabilities of copepods, ecological models might be constructed employing seasonal particle distribution data to predict the abundance and succession of zooplankton species.

Acknowledgements

Grateful acknowledgement is paid to Dr Kenneth Tenore for his help in criticizing the manuscript, Mr Philip Clarner for carbon–nitrogen determinations and to Captain Richard Coburn of the R.V. *Asterias* for aiding in sample collection. This research was conducted at the Woods Hole Oceanographic Institution with support from a Biological Oceanography NSF Doctoral Dissertation Fellowship, DES75-10025 and NSF Grant 39911.

References

Bermen, T. 1975 Size fractionation of natural aquatic populations associated with autotrophic and heterotrophic carbon uptake. *Marine Biology* **33**, 215–220.

Fish, C. J. 1925 Seasonal distribution of the plankton of the Woods Hole region. *Fishery Bulletin U.S. Wildlife Service* **41**, 91–179.

Flemer, D. A. & Biggs, R. B. 1971 Particulate carbon nitrogen relations in northern Chesapeake Bay. *Journal of the Fisheries Research Board of Canada* **28**, 911–918.

Hargrave, B. T. 1976 Short-term changes in suspended particulate carbon and nitrogen near the bottom of a marine bay. *Technical Report No. 602*, Research and Development Directorate, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, 20 pp.

Harrison, P. G. & Mann, K. H. 1975 Detritus formation from eel grass (*Zostera marina*): the relative effects of fragmentation, leeching and decay. *Limnology and Oceanography* **20**, 924–934.

Johnson, R. G. 1974 Particulate matter at the sediment-water interface in coastal environments. *Journal of Marine Research* **32**, 313–330.

Loder, T. C. 1971 Distribution of dissolved and particulate organic carbon in Alaskan polar, subpolar and estuarine waters. Ph.D. thesis, University of Alaska College, 236 pp.

Malone, T. C. 1971 The relative importance of netplankton and nanoplankton as primary producers in tropical oceanic and neritic phytoplankton communities. *Limnology and Oceanography* **16**, 633–639.

Marshall, N. 1970 Food transfer through the lower trophic levels of the benthic environment. pp. 52–56. In *Marine Food Chains* (J. H. Steele ed.). University of California Press, Berkeley, 551 pp.

McCarthy, J. J., Taylor, W. R. & Loftus, W. E. 1974 Significance of nanoplankton in the Chesapeake Bay estuary and problems associated with the measurement of nanoplankton productivity. *Marine Biology* **24**, 7–16.

Mullin, M. M. 1965 Size fractionation of particulate organic carbon in surface waters of the Western Indian Ocean. *Limnology and Oceanography* **10**, 459–462.

Parsons, T. R. 1963 Suspended matter in seawater, pp. 203–239. In *Progress in Oceanography* (M. Sears, ed.) Vol. I. Pergamon Press, Oxford.

Poulet, S. A. 1976 Feeding of *Pseudocalanus minutus* on living and non-living particles. *Marine Biology* **34**, 117–125.

Reynolds, N. 1973 The estimation of the abundance of ultraplankton. *British Phycological Journal* **8**, 135–146.

Riley, G. A. 1963 Organic aggregates in seawater and the dynamics of their formation and utilization. *Limnology and Oceanography* **8**, 372–381.

Riley, G. A. 1970 Particulate organic matter in seawater. *Advances in Marine Biology* **8**, 1–118.

Rhoads, D. C., Tenore, K. R. & Browne, M. 1975 The role of resuspended bottom muds on the food chain of shallow embayments. pp. 563–579. In *Estuarine Research* Vol. I (Cronin, L. E., ed.). Academic Press, New York, 738 pp.

Roman, M. R. & Tenore, K. R. 1978 Tidal resuspension in Buzzards Bay, Massachusetts. I. Seasonal changes in the tidal resuspension of organic carbon and chlorophyll *al Estuarine and Coastal Marine Science* **6**, 37–46.

Sheldon, R. W., Evelyn, T. P. & Parsons, T. R. 1967 On the occurrence and formation of small particles in seawater. *Limnology and Oceanography* **12**, 367–375.

Sheldon, R. W. & Parsons, T. R. 1967 A practical manual on the use of the coulter counter in marine science. Coulter Electronics, Toronto, 66 pp.

Sheldon, R. W. & Sutcliffe, W. H. 1969 Retention of marine particles by screens and filters. *Limnology and Oceanography* **14**, 441–444.

Sutcliffe, W. H. 1972 Some relations of land drainage, nutrients, particulate material and fish catch in two eastern Canadian Bays. *Journal of the Fisheries Research Board of Canada* **29**, 357–362.

Tenore, K. R. 1975 Detrital utilization by the polychaete, *Capitella capitata*. *Journal of Marine Research* **33**, 261–274.

Yentsch, C. S. & Ryther, J. H. 1959 Relative significance of net phytoplankton and nanoplankton in the water of Vineyard Sound. *Journal du Conseil, Conseil International poir l'Exploration de la Mer* **24**, 231–238.

Yentsch, C. S. & Menzel, D. W. 1963 A method for the determination of phytoplankton chlorophyll and phaeophytin by flourescence. *Deep-Sea Research* **10**, 221–231.