

# Size structure and sinking rates of various microparticulate constituents in oligotrophic Hawaiian waters

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**ABSTRACT:** In subtropical Hawaiian waters, about 80 % of total chlorophyll and about 60 % of C, N, P, and Si occur in the  $<5 \mu\text{m}$  fraction. This predominance of chlorophyll in the  $<5 \mu\text{m}$  fraction prevails throughout the photic zone in extensive areas of the North Central Pacific Ocean. Sinking rates of various constituents reveal vertical, size-related, and day:night differences. In the deep chlorophyll layer, sinking rates were lower than those in the upper mixed layer. Flux estimates indicated that sedimentation accounted for about 7 % of daily photosynthetic carbon production, and that particles  $>20 \mu\text{m}$  accounted for most of the microparticulate C, N, P, and Si flux. Calculations showed that constituent turnover rates from sedimentary loss alone are  $<1\%$  of other biological rate processes influencing the concentrations of these constituents (e.g. growth rate). These findings indicate that sedimentation losses from the photic zone resulting from the sinking of intact phytoplankton and/or suspended microparticulates are of comparatively minor importance to the time-dependent changes of phytoplankton biomass in subtropical waters.

## INTRODUCTION

Oligotrophic waters represent some of the most extensive yet least understood oceanic ecosystems in the world. Persistent stratification constrains the vertical supply of essential plant nutrients to the photic zone (Dugdale 1967, Eppley et al. 1973). This results in low ambient nutrient concentrations, and resident phytoplankton consequently depend largely on regenerated nutrients. The predominance of small cells in the phytoplankton biomass distinguishes oligotrophic environments (Beers et al. 1975, Fryxell et al. 1979, Bienfang & Szyper 1981, Platt et al. 1983, Takahashi & Bienfang 1983). The quantitative importance of both regenerated nutrients and small autotrophs suggests that the sedimentation loss of suspended microparticulate material from the photic zone (= 'new' production) would be low (Eppley & Peterson 1979). There have been very few observations of sedimentation rates in oligotrophic waters. Bienfang (1980b) measured vertical variations of photosynthetically-active particulates in 2 size fractions, and there are some sediment trap data (Honjo 1978, Knauer et al. 1979, Lorenzen et al. 1983).

To date, there is no information descriptive of the size structure and settling rates of the various chemical constituents of suspended microparticulate matter in subtropical waters. In this paper, the term 'suspended microparticulates' refers to the particulate material collected using conventional Niskin samplers; Karl & Knauer (1984) use the term 'suspended particulate organic carbon (S-POC)' when referring to the carbon content of this material. The purpose of this work was to describe the size structure, sinking rates and flux values of various chemical constituents of the suspended microparticulates, and to examine their vertical, diurnal, and size-related variability. Work was conducted leeward of Oahu, Hawaii, in an area that was previously the focus of an intensive survey (Bienfang et al. 1984b). Phytoplankton populations in the region are nutrient-limited, have low standing stocks, and temporal changes in primary productivity are related to variations in the physical system. This area is in the trade wind zone of the subtropical Pacific, where seasonal changes in oceanic properties are relatively small. The water column has persistently low nutrients in the surface, a deep chlorophyll maximum ( $z = 90 \text{ m}$ ), and a deep (i.e. 150 m) photic zone.

## MATERIALS AND METHODS

Sinking rates were measured over 3 cruises (Aug 1982, Jan 1983, Jun 1983) aboard RV 'Kana Keoki'. All 3 cruises examined a station (21°20'N, 158°13'W) located about 10 km off the leeward coast of Oahu, Hawaii. Chlorophyll size-structure information (from stations between 18°N 153°W and 6°S 153°W) was collected during a cruise in January 1982. Water samples were collected with 12 and 30 l Niskin samplers. The size structure of particulate chlorophyll, carbon (pC), nitrogen (pN), phosphorus (pP), and silica (pSi) were determined by filtrations through Nuclepore polycarbonate filters (0.4, 3, 5, and 10  $\mu\text{m}$  pore sizes) and Nitex screens (20, 35, and 100  $\mu\text{m}$  pore sizes). Gravity pressure alone was used for all filtrations involving pore sizes  $>0.4 \mu\text{m}$ , and triplicate determinations were made for each size interval. The percent concentration occurring above a given pore size was calculated by comparison with total concentration data given by filtrations using 0.4  $\mu\text{m}$  Nuclepore filters. Previous works involving microscopic examination of material retained by filters of various pore sizes have shown that such fractionation procedures adequately

describe particle size structure, and separate particulates into size classes available to suspension-feeding herbivores (Runge & Ohman 1982, Takahashi & Bienfang 1983). The  $>20 \mu\text{m}$  material was collected with an opening-closing net (20  $\mu\text{m}$  mesh) pulled through the water at  $5 \text{ m min}^{-1}$ . Daytime samples were taken at 1000 h and night-time samples were taken at 2200 h.

The homogeneous sample approach (Bienfang et al. 1977) called SETCOL (Bienfang 1981a) was used for sinking rate measurements. For use at sea, the SETCOL was mounted on a 2-dimensional gimble which was vibration-dampened to attenuate ship motion and propeller beat. The columns were surrounded by a thermostatically-controlled water jacket to maintain a hydrostatic environment. All samples were pre-screened through 202  $\mu\text{m}$  mesh to remove large zooplankton whose mobility could compromise hydrostatic conditions. Triplicate standing-stock determinations of each biomass parameter under inspection were made both at the beginning and end of each sinking rate trial. These determinations were made to evaluate any biomass changes caused by processes other than sinking. In no cases were the means of the biomass levels before and after the trial significantly ( $p > 0.05$ )

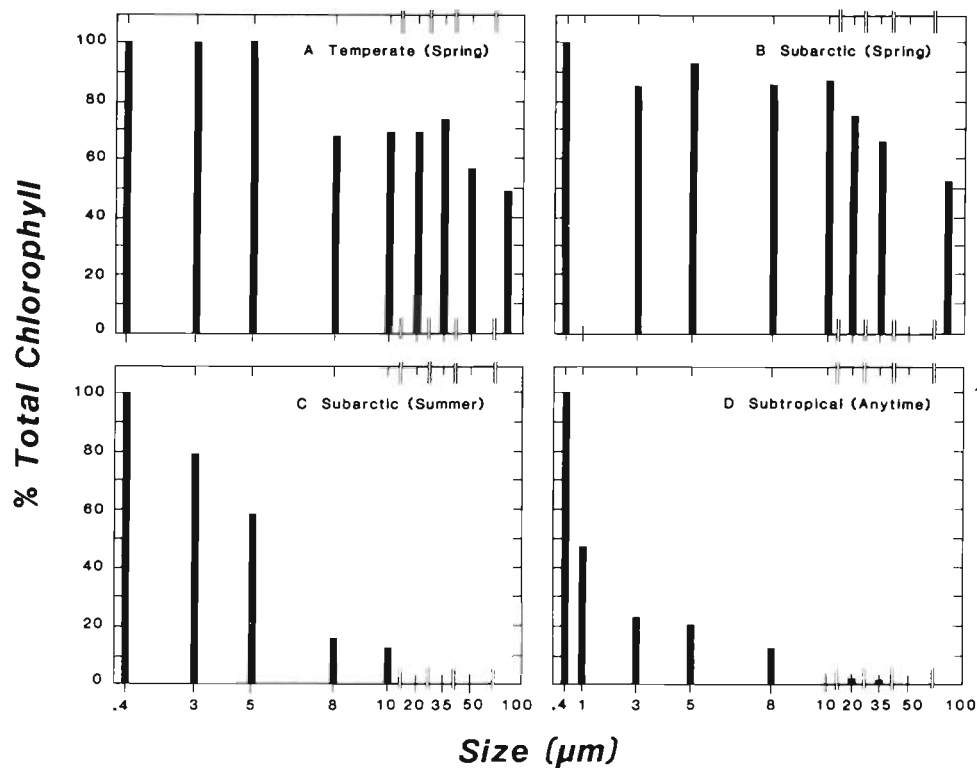


Fig. 1. Chlorophyll size structure in several marine environments. Plots illustrate the percentage of total chlorophyll represented by various size fractions of natural phytoplankton assemblages from (A) temperate (spring); (B) and (C) subarctic (spring and summer); (D) subtropical ecosystems. Samples representing temperate waters were collected from Washington State, adjacent the Friday Harbor Laboratory; subarctic samples, from Resurrection Bay, Alaska; subtropical samples, from waters off Hawaii. Values indicate percentage of total biomass greater than various pore sizes and are based on triplicate analyses in each case ( $cv \leq 15\%$ )

different. Chlorophyll was measured according to the fluorometric methods for extracted samples (Strickland & Parsons 1972). The procedures of Solorzano & Sharp (1980) and Paasche (1980) were used to measure pP and pSi while pC and pN were measured by gas chromatographic analyses (Sharp 1974).

## RESULTS AND DISCUSSION

### Particulate size structure

Fig. 1 contrasts the size structure of chlorophyll in subtropical Hawaiian waters (Fig. 1 D) with those found in other marine environments. Most of the total population chlorophyll in subtropical seas occurs in the  $<5 \mu\text{m}$  fraction, which consists primarily of small flagellates and coccoid cells (Takahashi & Bienfang 1983). This size distribution is very different from those found in temperate waters (Fig. 1 A) or in a subarctic fjord (Fig. 1 A) during spring when populations are mostly comprised of large centric diatoms (Bienfang 1984, Bienfang & Harrison 1984). Other works have shown that the size structure depicted in Figure 1 D prevails in Hawaiian waters (Bienfang & Szyper 1981, Bienfang et al. 1984a). Fig. 2 presents data taken from both the surface and 100 m depth (near the chlorophyll

maximum) at 13 stations between  $18^\circ\text{N}$   $153^\circ\text{W}$  and  $6^\circ\text{S}$   $153^\circ\text{W}$ . These data show that about 80% of total chlorophyll occurs in cells  $<5 \mu\text{m}$  throughout the photic zone and over extensive areas of the Pacific. The persistence of small-celled phytoplankton biomass appears to be a signature of warm, well-stratified oligotrophic ecosystems where low ambient nutrient levels prevail. The high surface area:volume ratio of small cells promotes diffusive nutrient uptake, which together with reduced sinking losses, are advantageous mechanisms in low nutrient environments. The change in phytoplankton size structure in the subarctic coastal environment (Fig. 1 B, C) coincided with changes in the nutrient field (Bienfang 1984). In summer, when stratification restricts vertical nutrient supply and phytoplankton uptake and sinking depletes ambient nutrients, the population size structure shifts to a pattern similar to that observed in permanently stratified subtropical waters (Fig. 1 D).

Other microparticulate constituents display size distributions similar to that of chlorophyll, although the decrease in concentration with increasing size is less pronounced (Table 1). In subtropical waters, 57 to 66% of the pC, pN, and pP occurs in the  $<5 \mu\text{m}$  fraction. In the subarctic or the temperate environments, the total concentrations of pC, pN, pP, and pS are much higher and relative contributions are at a size threshold considerably greater than that found in subtropical waters. Together these data illustrate that the total concentration of various particulate constituents in oligotrophic waters is not only lower but occurs in particles of generally smaller size than those found in higher latitude systems.

### Sinking rates

Fig. 3 presents the mean sinking rates and standard deviations of the various chemical constituents for several size classes of particulates. The mean values represent ensemble averages of samples collected over the year at various times of day and at various depths throughout the photic zone. Mean sinking rates of total ( $>0.4 \mu\text{m}$ ) particulates were low overall, ranging from  $0.06 \pm 0.02 \text{ m d}^{-1}$  for chlorophyll to  $0.23 \pm 0.08 \text{ m d}^{-1}$  for silica. Size-related differences in the sinking rates of all constituents are evident. A systematic increase in sinking rate with increasing particle size is particularly apparent for rates based on chlorophyll. A higher chlorophyll quota for the predominant small-celled phytoplankton lowers the sinking rate value calculated on the basis of this constituent. Average sinking rates for the  $>20 \mu\text{m}$  fraction with respect to all constituents were distinctly higher than rates for total particulates; the degree of difference was most pronounced for chlorophyll ( $\psi_{>20 \mu\text{m}}/\psi_{>0.4 \mu\text{m}} = 7\times$ ) and

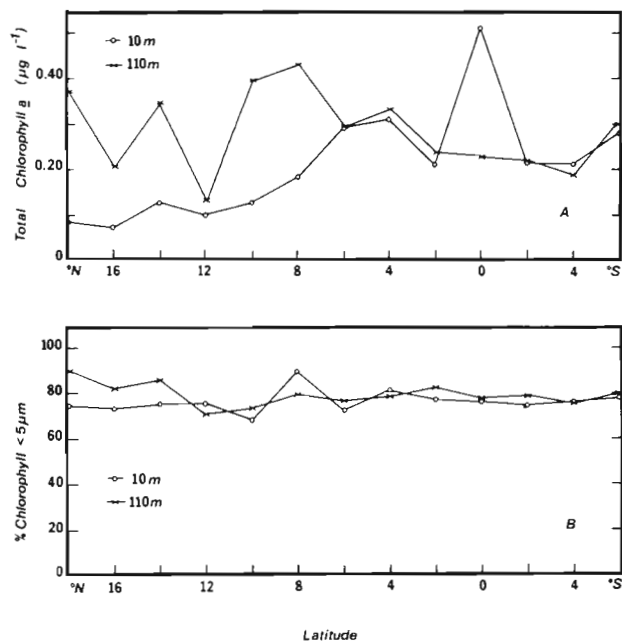


Fig. 2. Chlorophyll size distribution across the Central Pacific Ocean. (A) Total chlorophyll concentrations at surface (10 m) and near deep chlorophyll maximum (110 m) at 13 stations between  $18^\circ\text{N}$   $153^\circ\text{W}$  and  $6^\circ\text{S}$   $153^\circ\text{W}$ ; means of triplicate analyses ( $cv \leq 15\%$ ). (B) Percentage of total chlorophyll in the  $<5 \mu\text{m}$  fraction, indicating predominance of this size fraction throughout the photic zone over an extensive range of subtropical and tropical waters

Table 1. Size structure of particulate C, N, P, and Si in 3 marine environments. Data give average concentration values ( $\mu\text{g l}^{-1}$ ) and percent of total concentrations due to particulates greater than the various size thresholds. Standard deviations based on triplicate analyses except for the  $0.4 \mu\text{m}$  C and N data where  $n = 36$

Ecosystem	Season	Size fraction ( $\mu\text{m}$ )	Particulate parameters ( $\mu\text{g l}^{-1}$ )					
			Carbon			Nitrogen		
			Mean	SD	%	Mean	SD	%
Subtropical	Anytime	0.4	54.78	9.45	100	7.69	2.55	100
		5	35.33	0.74	65	4.34	0.13	57
		10	23.32	1.72	42	4.28	0.22	56
		20	10.96	1.89	20	1.54	0.41	20
Subartic	Summer	0.4	491.50	34.80	100	55.90	4.50	100
		8	153.40	2.50	31	17.40	0.60	31
		20	325.60	4.90	66	33.00	0.70	59
		35	216.40	38.70	44	15.70	1.00	28
Temperate	Spring	0.4	359.60	10.40	100	44.80	4.30	100
		5	360.50	30.10	100	42.60	1.80	95
		10	289.30	22.50	80	36.90	2.70	82
		20	274.70	7.50	76	32.40	4.30	72
		100	105.00	6.50	29	13.70	0.60	30
			<b>Phosphorus</b>			<b>Silica</b>		
Subtropical	Anytime	0.4	0.42	0.028	100	2.61	1.04	100
		5	0.28	0.050	66	-	-	-
		10	-	-	-	1.11	0.13	42
		20	0.11	0.01	25	0.57	0.13	22
Subartic	Summer	0.4	9.34	1.99	100	56.50	6.00	100
		8	2.99	0.03	32	31.00	9.50	55
		20	1.72	-	18	28.30	2.40	50
		35	1.16	0.22	12	7.60	5.50	13
Temperate	Spring	0.4	106.40	26.00	100	243.40	3.20	100
		5	63.20	5.70	59	221.60	0.20	91
		10	69.20	36.80	65	235.00	0.00	97
		20	63.40	12.20	60	57.50	17.20	24
		100	12.70	2.70	12	26.50	14.30	11

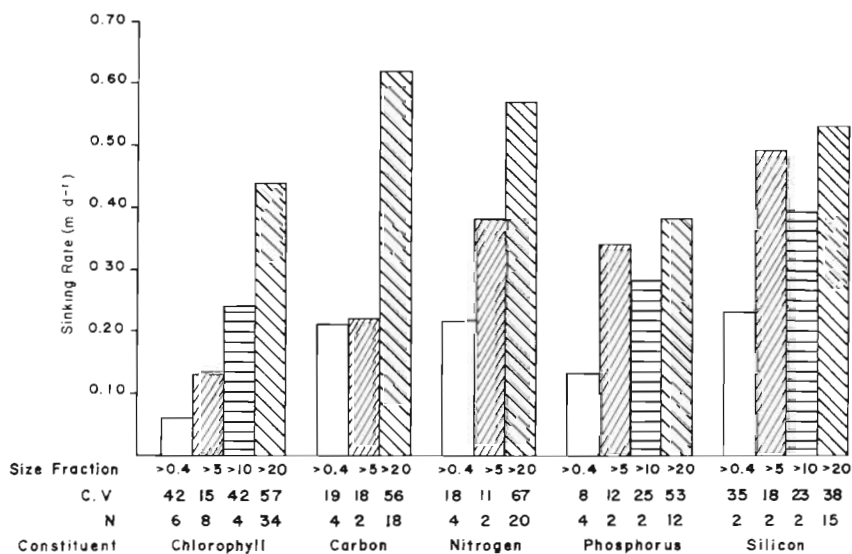


Fig. 3. Summary of size-related sinking rate differences for various constituents of suspended microparticulates in subtropical ocean waters. Mean values represent ensemble averages of samples collected throughout the year at various times of day and at various depths throughout the photic zone. Coefficient of variation (c.v.) is based on N determinations and embraces vertical, temporal, and analytical variability

ranged between 2 and 3× for the other parameters examined. The floristic composition of phytoplankton in the >20 μm fraction was dinoflagellates > coccolithophorids > diatoms on the basis of numerical abundance. Pennate diatoms outnumbered centrics by ca 3:1; other studies (Bienfang & Harrison 1984) have indicated that pennate diatoms have generally lower sinking rates than centric forms. The most common genera for the dinoflagellates were *Peridinium* spp. and *Prorocentrum* spp.; for the coccolithophorids, *Discoisphaera* spp.; and for the pennate diatoms, *Navicula* spp. and *Nitzschia* spp.

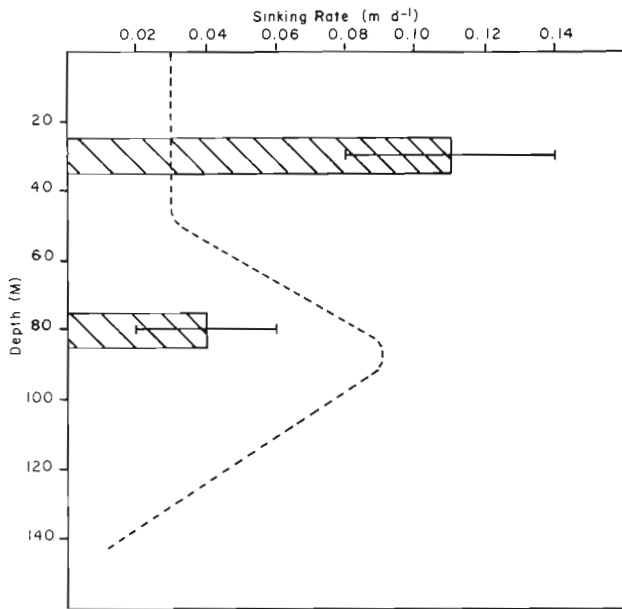


Fig. 4. Variation in sinking rate of total particulate chlorophyll between upper mixed layer and subsurface chlorophyll maximum layer. All samples collected during the day. Mixed layer samples (n = 6) came from 20, 30, and 50 m; deep samples (n = 4), from 80 m. Error bars: standard deviation; dashed line: qualitative vertical chlorophyll distribution typical of the area

Vertical differences in sinking rates were also apparent. Fig. 4 illustrates a comparison of the mean sinking rates of total particulate chlorophyll found in samples from the upper mixed layer (z = 10 to 50 m) and from the region near the deep chlorophyll maximum (z = 90 m). These results indicate that sinking rates in these 2 areas differ by more than a factor of 2. The lower sinking rates in the region of the chlorophyll maximum are consistent with findings from a study of larger particulates conducted in another subtropical locale (Bienfang 1980b), using a method which focused only on the photosynthetically-active components of the population. As explained in Bienfang et al. (1983), in subtropical waters, the appearance of reduced sinking rates in this layer is thought to coincide with rather than cause the increased chlorophyll concentrations. Observation indicates physiological adjustments to the region do produce lower sinking rates, but, given the prevailing particle size structure and the degree of chlorophyll increases common in such areas, shade-adaptation alone can account for the subsurface chlorophyll maximum in oligotrophic waters (Venrick et al. 1973, Kiefer et al. 1976, Bienfang et al. 1983).

Day:night differences were evident in the sinking rates of the various constituents in the >20 μm fraction (Fig. 5). For chlorophyll, day:night differences appeared in samples taken from both the 0 to 100 m and 100 to 200 m depth interval. Other analyses, based on separate sampling over the 0 to 150 m range, also indicated higher sinking rates for the different constituents during the evening period. Only particulate phosphorus failed to show appreciable day:night differences in sinking rate. Data from all constituents, depth intervals, and samplings suggest that sinking rates in the evening were about twice what was measured during the day in this subtropical system. In the field samples, the nature of diurnal sinking rate variability parallels that observed in laboratory cultures (Eppley et al. 1967a, b, Boleyn 1972, Smayda 1975,

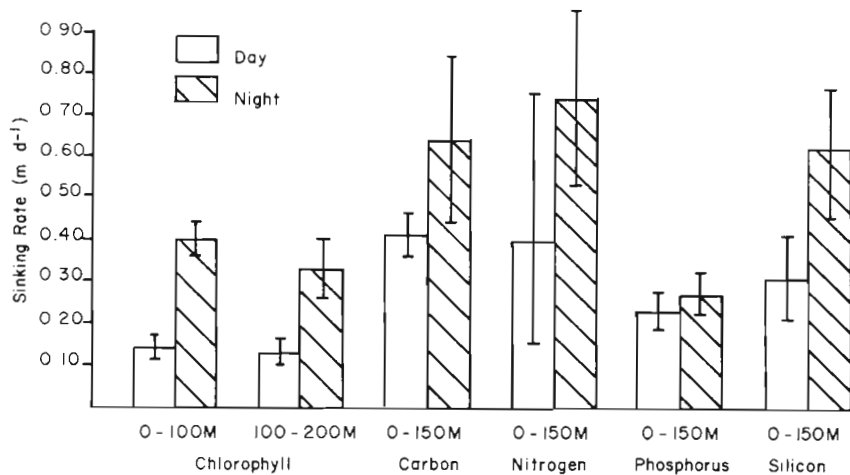


Fig. 5. Day:night differences in sinking rates of various constituents in the >20 μm fraction of suspended particulate material in subtropical Hawaiian waters. Samples collected by net tows over the depth range indicated. Error bars: standard deviation for n = 4 replicate determinations in each case

Bienfang 1981b). Such diurnal variability suggests a close association of the energy-requiring mechanism of buoyancy regulation with photosynthetic activity.

### Microparticulate fluxes

Table 2 summarizes the downward flux (F) calculated for various constituents of the suspended microparticulates in subtropical waters. F values are the products of the concentration (B) and sinking rate ( $\psi$ ) values. The B and  $\psi$  values listed represent ensemble averages from samplings at a variety of times and depths throughout the photic zone, and are used to describe the system's general synoptic condition. Note that all analyses are based on discrete samples, and it is therefore improbable that the particulate material collected would include large particles (e.g. fecal pellets, marine snow, or large aggregates which are not numerically abundant). The implication of sediment trap studies (McCave 1975, Stephens et al. 1976, Honjo 1978, Knauer et al. 1979) is that such particles, despite their low abundance, are important contributors to total particulate flux, especially deep in the ocean. The sinking rates of fecal pellets are 2 to 3 orders of magnitude greater than these rates for microparticulates (Smayda 1969, 1971, Fowler & Small 1972, Turner 1977, Honjo & Roman 1978, Small et al. 1979, Bienfang 1980a). The term 'total microparticulates', as used here, is operationally defined to mean the particulates collected by discrete samples.

Some useful information can be derived from these results. First, Table 2 contains flux estimates for a

variety of particulate constituents (e.g. pC, pN, pP, pSi) which have both ecological and geochemical importance. Small particles constitute most of the suspended particulate material (McCave 1975, Honjo 1978) in such systems. The flux estimates for these elements have a wide range; carbon is highest ( $11.50 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and phosphorus lowest ( $0.055 \text{ mg P m}^{-2} \text{ d}^{-1}$ ). The C:N:Si:P ratio of the microparticulate fluxes is 209:31:11:1 (by weight) and 544:69:12:1 (by atoms). The higher value for carbon is caused partly by the substantial content of detrital carbon in the total particulate material, and reflects the high degree of re-ingestion and regeneration of suspended particulate material occurring in subtropical ecosystems. Carbon flux estimates for subtropical Hawaiian waters have recently been collected using floating sediment trap arrays which would include contributions of large particulates (Lorenzen et al. 1983). The flux estimates found for carbon were also much higher than those for chlorophyll, and indicated that a comparatively small fraction of the sedimentary pC was recently associated with phytoplankton. Comparison of the carbon flux value from this study ( $F_c = 11.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) with Lorenzen et al.'s (1983) value using sediment traps ( $F_c = 55.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) suggests that about 21% of the total carbon flux is due to the type of suspended microparticulate material collected via Niskin samplings.

Secondly, chlorophyll flux is very low, probably because of the size structure of phytoplankton in oligotrophic ecosystems (Fig. 1 & 2). Nearly all the chlorophyll is present in very small cells which have negligible settling rates, so very little sedimentary loss

Table 2. Summary of sinking rate and flux data for various constituents in 2 size classes of particulate material in an oligotrophic ecosystem. Concentration (B) and sinking rate ( $\psi$ ) data are averages from samples taken at various times and depths throughout the photic zone. Calculated flux (F) is the product of  $B \times \psi$ ; F' gives the percentage of total flux due to particles  $> 20 \mu\text{m}$  [ $F' = 100 (F_{>20\mu\text{m}}/F_{>0.4\mu\text{m}})$ ]. The term B\* gives depth-integrated values for the photic zone where the limits of integration are  $z = 0$  to 150 m. Turnover time (t) based only on direct sedimentation of microparticulates is given by  $t = F/B^*$

Size fraction	Chlorophyll	Carbon	Constituent Nitrogen	Phosphorus	Silica
<b>&gt;0.4 <math>\mu\text{m}</math></b>					
B ( $\text{mg m}^{-3}$ )	0.11	54.78	7.69	0.421	2.610
$\psi$ ( $\text{m d}^{-1}$ )	0.06	0.21	0.22	0.13	0.23
F ( $\text{mg m}^{-2} \text{ d}^{-1}$ )	0.0066	11.50	1.69	0.055	0.600
B* ( $\text{mg m}^{-2}$ )	19.90	8217	1154	63.2	391.5
t ( $\text{d}^{-1}$ )	.0003	.0014	.0015	.0009	.0015
<b>&gt;20 <math>\mu\text{m}</math></b>					
B ( $\text{mg m}^{-3}$ )	0.0033	10.956	1.538	0.084	0.522
$\psi$ ( $\text{m d}^{-1}$ )	0.44	0.55	0.57	0.38	0.57
F ( $\text{mg m}^{-2} \text{ d}^{-1}$ )	0.0015	6.026	0.877	0.032	0.277
F' (%)	22	52	52	58	46
B* ( $\text{mg m}^{-2}$ )	0.60	1643	230.8	12.64	78.30
t ( $\text{d}^{-1}$ )	.0025	.0037	.0038	.0025	.0035

of phytoplankton directly results from sinking. Third, the proportion of total flux due to larger (i.e.  $>20\ \mu\text{m}$ ) particles can be calculated from the flux data for both total microparticulates and the  $>20\ \mu\text{m}$  fraction. The relative amount of total flux attributable to particles in the  $>20\ \mu\text{m}$  fraction was similar for most constituents (pC, pN, pP, pSi) and ranged from 46 to 58%; the low value (22%) for chlorophyll results from the very low chlorophyll concentrations in the  $>20\ \mu\text{m}$  fraction.

Fourth, the photosynthesis and carbon flux data can be used to generate estimates of the percentage of daily primary production leaving the subtropical photic zone via sedimentation. Annual primary production in this area is  $60.4\ \text{g C m}^{-2}$  (Bienfang et al. 1984b). Given the average sinking flux value for carbon (pC =  $11.5\ \text{mg C m}^{-2}\ \text{d}^{-1}$ ) and an estimate for average photosynthesis ( $165.5\ \text{mg C m}^{-2}\ \text{d}^{-1}$ ), I estimate that about 7% of daily primary production is lost as a result of the sinking of microparticulate material. This percentage is in general agreement with percentage values calculated from sediment trap data collected in subtropical waters (Eppley & Peterson 1979, Lorenzen et al. 1983).

Comparison of the SETCOL results with those of Lorenzen et al. (1983) also reveals an inconsistency: (a) similar values for the percentage of total carbon production represented by sedimentary loss, but (b) carbon flux values for suspended microparticulates (i.e. SETCOL results) about a fifth those for total particulates (i.e. sediment trap results). For both (a) and (b) to be true would imply that, in this system, total carbon flux is about 33% (i.e.  $0.07/0.21$ ) of total primary production; this is an inordinately high fraction for an oligotrophic area. There are two possible explanations for the apparent contradiction: either the primary production value used by Lorenzen et al. is higher than the one used here or the 7% value derived in this work overestimates the actual carbon flux out of the photic zone which is due to suspended microparticulate material. First, the Lorenzen et al. (1983) study does not give a value for total primary production applied. For the carbon flux estimate ( $55.9\ \text{mg C m}^{-2}\ \text{d}^{-1}$ ) to be 10 to 15% (Lorenzen pers. comm.) of total primary production would require a daily integrated carbon production of 375 to  $550\ \text{mg C m}^{-2}\ \text{d}^{-1}$ , which is considerably greater than the value for photosynthetic carbon production (Bienfang et al. 1984b) which was used to derive the 7% value in this study. The increased carbon production might be due to production by components of the microbial community other than the photoautotrophs. Based on nucleic acid synthesis, Winn & Karl (1984) showed a total microbial production in Hawaiian oceanic waters equivalent to  $400\ \text{mg C m}^{-2}\ \text{d}^{-1}$ . Secondly, the values which led to the 7% estimate in this work were based on water samples taken from a

variety of depths within the photic zone. If the suspended material examined with these samplings was subjected to substantial regeneration/reworking prior to leaving the photic zone, then the 7% value derived would overestimate the fraction of suspended microparticulate flux which actually exits the photic zone.

Finally, turnover times for the various particulate constituents can be calculated solely on the basis of sedimentation (Table 2). The values  $B^*(x)$  represent the vertically-integrated values, giving total photic zone concentrations for each constituent (x); division of the flux values by the  $B^*(x)$  values yields turnover rates (t) in units of inverse time. For all constituents, the t values for the  $>20\ \mu\text{m}$  fraction are considerably larger than those for total microparticulates ( $>0.4\ \mu\text{m}$ ). For pC, pN, pP, and pSi, the t values for the  $>20\ \mu\text{m}$  fraction are about 2 to  $3\times$  those for the  $>0.4\ \mu\text{m}$  particulates. Considerably larger (about  $8\times$ ) size-related differences are indicated for chlorophyll, despite the small amount of material in the  $>20\ \mu\text{m}$  fraction. The magnitude of this difference results primarily from the extremely low sinking velocities of the total picoplankton-dominated assemblage. More importantly, the absolute values for turnover rate resulting from sedimentary loss are at least 2 orders of magnitude lower than the biological rate processes (e.g. specific growth rate) which influence concentrations of these constituents. Although sinking may affect the fate and/or vertical distribution of certain floristic components, the nature of phytoplankton assemblages in oligotrophic ecosystems lends conservative properties to the environment. These values indicate that the sinking of intact phytoplankton from the photic zone in subtropical waters is of comparatively minor importance to the time-dependent changes of photoautotrophic biomass. Another way of expressing this result is to state that the downward flux of (microparticulate) chlorophyll accounts for 0.03% of the total depth-integrated standing stock, or 0.25% of the depth-integrated standing stock of the  $>20\ \mu\text{m}$  fraction. Lorenzen et al. (1983) derived a value of 0.8%; this value represents an upper bound for the relative chlorophyll loss due to sedimentation because their sampling scheme would include ingested/excreted chlorophyll.

The large differences between the calculated t values and rates of other biological processes influencing biomass affect modelling efforts seeking to describe time-dependent changes in the biomass of subtropical assemblages. Models do not need to incorporate a term to account for biomass loss resulting from direct phytoplankton sinking until the precision of such efforts would be influenced by rate processes less than 1% those of phytoplankton growth. The modest importance of sinking losses is probably unique to subtropi-

cal environments which display comparatively little climatic, chemical or biological seasonality.

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