Continental Shelf Research, Vol. 10, No. 8, pp. 795–806, 1990.
Printed in Great Britain.

0278-4343/90 $3.00 + 0.00

Size-fractionated sedimentation in a tropical neritic ecosystem near Kingston, Jamaica

RUSSELL R. HOPCROFT,* JOHN C. ROFF* and JOHN A. BERGES*

(*Received* 3 *May* 1989; *accepted* 29 *September* 1989)

Abstract—Particles collected at a tropical neritic station by 24 h sediment trap deployment were size fractionated and analysed for chlorophyll *a* and phaeopigment. Under calm conditions, picoparticles (<2 μm) did not settle out and therefore must be grazed within the water column; the data also indicate that 12–18% of the nanoplankton (2–20 μm) and >30% of the netplankton (>20 μm) daily primary production were exported to the benthos. Assuming that the annual pattern of net sedimentation can be predicted from a knowledge of the size structure and production of the phytoplankton, our calculations indicate a flux to the benthos of 36 g C m^{-2} y^{-1} or ~15% of the annual primary production.

INTRODUCTION

THE size spectrum of the biomass, the rate of primary production and the rate of sedimentation of phytoplankton are fundamental attributes of marine ecosystems (TAKAHASHI and BIENFANG, 1983), influencing the overall structure and dynamics of all other trophic levels (MICHAELS and SILVER, 1988; FENCHEL, 1988). One of the underlying purposes of separating phytoplankton into size fractions, is to determine how the energy produced is used by (or lost to) higher trophic levels. At present, we lack a perspective on the relative importance and fate of the various phytoplankton size fractions in aquatic ecosystems.

The pattern of phytoplankton sedimentation (ignoring resuspension) may be predicted from a knowledge of the relative settling velocities of the particles of each size fraction. It has been demonstrated, both by theory (Stokes Law) and by observation (SMAYDA, 1969, 1971; TAKAHASHI and BIENFANG, 1983; BIENFANG, 1985), that small particles have negligible settling velocities while larger particles may settle several metres per day. Therefore, sedimentary material should be dominated by large cells, prepackaged and/or agglomerated material (i.e. fecal pellets; FOWLER and KNAUER, 1986; EMERSON and ROFF, 1987), independent of the overlying size distribution of biomass or production. The seasonal pattern of sedimentation is thus expected to be determined primarily by the patterns of biomass and production of the netplankton, being greatest when netplankton dominates, and negligible when picoplankton dominates.

To better understand these processes a study was undertaken to explore the magnitude of sedimentation and determine the annual cycle of size-fractionated phytoplankton

*Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1.

biomass and production in a typical neritic tropical environment. Details of the annual patterns of phytoplankton biomass and production are presented elsewhere (HOPCROFT and ROFF, 1990).

METHODS

The study area was located on the shallow shelf to the south of Kingston, Jamaica, an extensive area (~250 km^2) of mean depth ~20 m. Sampling was conducted near Lime Cay (17°56'N, 76°49W) in 30 m of water within a slightly deeper basin of water (depth 25–30 m) partially sheltered by the numerous reefs and shoals which form a protective barrier from rough seas and oceanic swells. Water temperature and salinity in the study area varied between 27 and 29°C, and 35 and 36‰, respectively (D. SHURLAND, personal communication). The average annual concentrations of chlorophyll and phaeopigment at Lime Cay were 0.35 (0.09–0.80) and 0.21 (0.06–0.58) mg m^3, respectively, partitioned as 42, 30 and 28% between the net-, nano- and picoplankton (HOPCROFT and ROFF, 1990). The euphotic zone (1% incident PAR) generally exceeded the depth of the Lime Cay station (HOPCROFT and ROFF, unpublished data), inferring that photo-oxidation of pigments may be a factor requiring consideration.

On four occasions sediment trap arrays of the design used by EMERSON and ROFF (1987) [a modification of STARESINIC *et al.* (1978), but used here as a moored array], were deployed for 24 h, without preservatives, at the Lime Cay station. On the first occasion, 1 August, an array of three traps was moored at 25 m supported by a surface float. On the remaining occasions, 23 October, 19 November and 10 December, two arrays of three traps each were deployed at 10 and 20 m on a single line supported by a subsurface float at 5 m. A general Oceanics mechanical flowmeter, equipped with a low velocity rotor (model 2030), was attached approximately 1 m above the upper array to estimate current speed. Water samples were collected for the determination of ambient chlorophyll concentrations at the time of deployment and 24 h later when the traps were retrieved. Concurrent estimates of primary production were obtained by carbon-14 technique with 4 h *in situ* incubations commencing at ~1000 h.

Upon retrieval, traps were emptied and rinsed into plastic containers and held in near darkness during transport to the laboratory. From each trap 1 or 2 litres of gently mixed sample were subsampled for cell counts (preserved in Lugol's solution) and chlorophyll determination approximately 1–2 h after retrieval. The contents of the traps as well as whole water samples were later analysed employing an image analysis system as described by ROFF and HOPCROFT (1986). Particle measurements were converted to volume by approximation of the geometric shape of the particle. The carbon content of particles was calculated as described by EMERSON and ROFF (1987). No attempt was made to quantify the amorphous material in the traps (i.e. disintegrated fecal pellets or aggregated "empty" phytoplankton cells), which could have either entered the traps as such or have resulted from the decomposition of fecal pellets prior to preservation, and/or subsequent disruption during handling prior to analysis.

All unfixed water samples were size fractionated into >20 and 2–20 and <2 μm by serial filtration. Within the phytoplankton these categories are equivalent to the net-, nano- and picoplankton (SIEBURTH *et al.*, 1978), but because the particles in this study consist of fecal pellets, algal cells and unidentifiable material, for convenience we shall adopt the terms net-, nano- and picoparticles. For chlorophyll fractionation, 20 μm Nitex, GF/D and GF/F

glass filters were employed; for primary production 20 μm Nitex, 2.0 and 0.2 μm Nuclepore Polycarbonate filters were employed. Filtration was completed under reduced lighting at pressure <15 kPa. Pigment concentration was estimated by fluorometric techniques (PARSONS *et al.*, 1984). Details of these methodologies are discussed elsewhere (HOPCROFT and ROFF, 1990).

To estimate carbon flux, pigment capture by the traps was determined by the subtraction of background concentrations at the time of deployment from the concentration within the traps at the time of retrieval. It was then assumed that all phaeopigment entering the traps was as phaeophorbide *a* in the form of fecal material (WELSCHMEYER and LORENZEN, 1985). It had until recently been believed that phaeopigment should be converted to chlorophyll *a* equivalents through multiplication by 1.51 (the molar ratio of the two molecules, e.g. WELSCHMEYER and LORENZEN, 1985; DOWNS and LORENZEN, 1985), because the molarity of pigments was thought to be conserved during gut passage (SHUMAN and LORENZEN, 1975). This has been shown to be incorrect (CONOVER *et al.*, 1986); our methodology estimates phaeopigment directly as "chlorophyll *a* equivalents". What is unclear is the extent to which Chl *a* and its equivalents are destroyed during gut passage (CONOVER *et al.*, 1986; PASTERNAK and DRITS, 1988); we have assumed that 40% is destroyed but also present estimates assuming 0 and 80% destruction.

It was assumed that all phaeopigment was associated with fecal chlorophyll in the ratio of 19:1 because 90–100% of Chl *a* is degraded to phaeopigment during gut passage through copepods (DOWNS and LORENZEN, 1985). Assuming a carbon to Chl *a* ratio of 40:1 (ZEITZSCHEL, 1970), the total carbon flux and the percentage of flux attributable to fecal material vs viable algal cells was estimated. It must be stressed that these estimates of fecal flux are for the herbivores only, and will underestimate the actual carbon flux depending on the extent of omnivory, carnivory and coprophagy within the water column during trap deployment.

RESULTS

During all deployments, a significantly greater concentration of pigment was observed inside the traps than in the ambient waters outside (Fig. 1). The amount of size-fractionated material collected by the traps varied directly with particle size. Of the four occasions on which sediment traps were deployed, the first and last were rough sea periods when notable resuspension occurred; the other two deployments were during calm sea conditions. For all occasions the estimated horizontal water velocity was under 3 cm^{-1}.

On the first occasion, 1 August 1986, the average wind speed during the deployment was ~10–15 kn (1 kn = 0.52 m s^{-1}), with seas 1 m by mid-morning. At the time of collection a notable amount of material was visible on the trap bottoms, accumulated while the average horizontal water velocity was approximately 3 cm s^{-1}. The traps at 25 m captured 30 and 40 times the background concentration of chlorophyll and phaeopigment, respectively, in netparticles (Fig. 1). Only 3.7 and 8.3 times the background concentration of chlorophyll and phaeopigment in nanoparticles, and 1.1 and 2.9 times the background concentrations of chlorophyll and phaeopigment in picoparticles were captured. A comparison of netparticle carbon flux to netplankton production on this date (Table 2) indicates that a substantial amount of the material captured by the traps was resuspended netparticles. In contrast, sedimentation represented only 31 and 5% of the rates of nano- and picoplankton production, respectively, suggesting much lower (if any) contributions

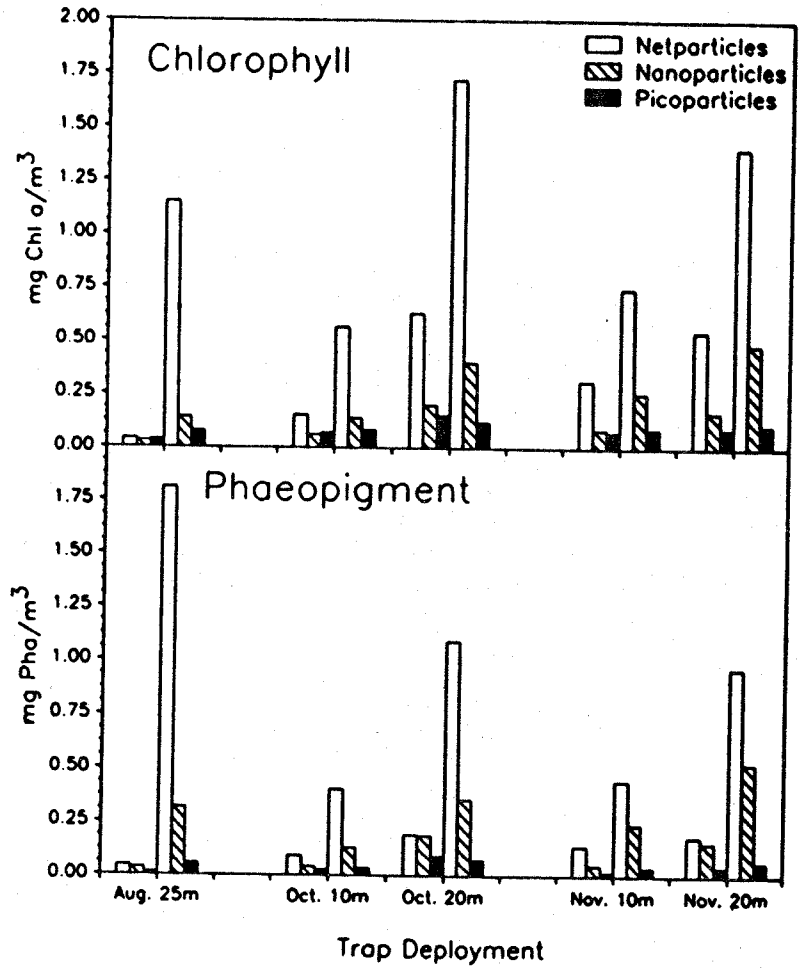

Fig. 1. Sedimentation of pigment at Lime Cay, Jamaica, 1986. Water column pigment concentrations at time of deployment presented to left of *X*-axis data label, trap concentrations (unadjusted for background) presented to right of label.

of resuspended material in these size fractions. The relatively low percentage of chlorophyll in the water column at the time of deployment and the even lower percentage of chlorophyll inside the traps (Table 1, $P < 0.01$, all size fractions) further suggests a predominance of resuspended material on this occasion.

Table 1. *Percentage of chlorophyll* a *present in total pigments (chlorophyll* a + *phaeopigments) for the water column and inside the sediment traps deployed at Lime Cay, Jamaica*, 1986

	Water column			Inside traps		
Deployment	Net	Nano	Pico	Net	Nano	Pico
Aug. 25 m	47	47	72	39	31	58
Oct. 10 m	63	60	72	58	52	71
Oct. 20 m	77	52	62	61	53	62
Nov. 10 m	69	64	81	63	51	69
Nov. 20 m	75	52	68	59	48	62
Annual mean	67	52	70			

On the second and third occasions, 23 October and 19 November 1986, the winds were weak at 3–4 kn, with calm seas (CTD profile indicated weak density stratification starting at ~10 m) and average horizontal current speeds were under 1 cm s^{-1}. At the time of collection there was little material visible on the trap bottoms. Quantitatively, 2–3 times more net- and nanoparticle chlorophyll (Fig. 1) was collected inside the traps than was observed outside at the time of deployment (1-tailed t-test, $P < 0.001$, with the exception of the nanoparticles at 20 m on 23 October for which $P > 0.1$), suggesting little, if any, resuspension on these dates. In November, there were minor (17–18%) increases in the concentration of picoparticle chlorophyll inside the traps which were not significant ($P > 0.24$); however, in October changes in picoparticle concentration were significant ($P < 0.05$), but of opposite sign (+23% at 10 m and −21% at 20 m). Therefore it appears that only particles larger than 2 μm show significant accumulation in the traps, and that particles larger than 20 μm show greater accumulation than the 2–20 μm particles (Fig. 1). It should also be noted that the proportion of Chl *a* in the water column was comparable to the annual mean on both dates (Table 1). Furthermore, although the pigment collected in the traps contained a lower proportion of chlorophyll than the surrounding water (Table 1, $P < 0.01$ for net- and nanoparticles), the proportionate decrease was not to the extent observed for the August deployment.

Table 2. Estimates of carbon (mg C m^{-2} day^{-1}) *due to ungrazed algal cells plus herbivore grazing* (mg C m^{-2} day^{-1}) *as collected by sediment traps at Lime Cay, Jamaica, 1986. Data are presented for the cases where 0, 40 or 80% of the pigment is destroyed during gut passage. Values in parentheses represent the percentage of overhead primary production which is captured. Also presented is the percentage of flux attributable to fecal pellets as estimated by pigment flux (– flux not significant)*

		Carbon sedimentation			% fecal pellet	
	Deployment	Net	Nano	Pico	Net	Nano
0% Degradation						
	Aug. 25 m	103.0 (280)	14.1 (21)	2.9 (4)	64	75
	Oct. 10 m	25.9 (62)	6.0 (9)	–	45	56
	Oct. 20 m	71.2 (132)	13.3 (13)	–	47	49
	Nov. 10 m	26.5 (34)	13.0 (14)	–	44	56
	Nov. 20 m	58.6 (23)	24.6 (13)	–	50	56
40% Degradation						
	Aug. 25 m	145.1 (394)	20.8 (31)	3.9 (5)	75	83
	Oct. 10 m	33.4 (80)	8.2 (12)	–	58	68
	Oct. 20 m	92.6 (171)	17.4 (18)	–	60	61
	Nov. 10 m	33.8 (43)	17.6 (18)	–	56	68
	Nov. 20 m	77.2 (30)	33.4 (17)	–	62	68
80% Degradation						
	Aug. 25 m	355.7 (967)	54.6 (82)	8.9 (11)	90	94
	Oct. 10 m	70.6 (169)	18.9 (29)	–	80	86
	Oct. 20 m	199.7 (369)	37.8 (38)	–	81	82
	Nov. 10 m	70.4 (90)	40.6 (43)	–	79	86
	Nov. 20 m	170.3 (67)	77.7 (41)	–	83	86

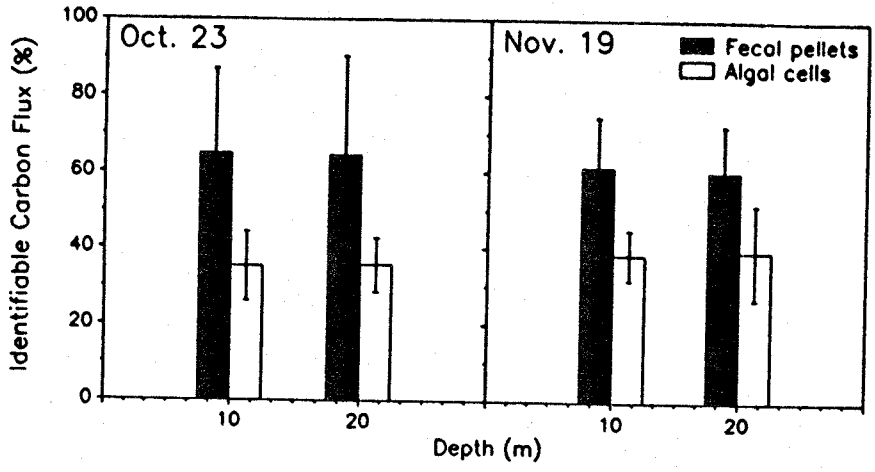

Fig. 2. Carbon flux estimated from particle volumes obtained by microscopic examination of sediment trap contents from Lime Cay, Jamaica, 1986. Standard error bars of each estimate included.

On 23 October, the netparticle sedimentation at 20 m of 1.7 times the estimated primary production (Table 2) suggests some degree of resuspension at depth. Ignoring this high value, the remaining data suggest that 80% of the netplankton, 12–18% of the nanoplankton and a negligible percentage of the picoplankton daily primary production are lost to sedimentation under calm conditions. On 19 November, the data suggest that a more conservative estimate of 30–43% of the netplankton, a comparable estimate of 17–18% of the nanoplankton, and again a negligible percentage of the picoplankton daily production are lost to sedimentation under calm conditions.

On the fourth deployment, 10 December 1986, rough seas prevented the retrieval of the traps until 48 h after deployment. At the time of retrieval the trap bottoms were completely covered with silt-like material which rendered the otherwise transparent trap bottoms opaque. In light of the results of the first deployment which also experienced resuspension, and because of the expected degradation of pigments after 48 h at the water temperature of 28°C, the contents of these traps were not analysed.

Microscopic examination of trap contents indicated that during the two calm periods, fecal pellets represented 60–70% of the identifiable carbon flux in traps (Fig. 2), values which are in close agreement with the estimates of percentage flux as fecal pigments when assuming 40% pigment destruction (Table 2). The flux of both fecal pellets and algal cells increased ~2 fold between 10 and 20 m, consistent with the observations for chlorophyll biomass. Furthermore, the mean size of fecal pellets collected by the traps was greater than that observed as background from bottle casts (Fig. 3). However, owing to the high variance in the size of sedimenting particles, these differences were not always statistically definable.

Although water samples collected from outside the traps contained primarily identifiable algal cells and fecal pellets bound by intact peritrophic membranes, the traps contained a large and unquantified amount of unidentifiable material. Of the identifiable fecal pellets within the traps, less than 1% possessed a peritrophic membrane, suggesting rapid decomposition of pellets in the traps.

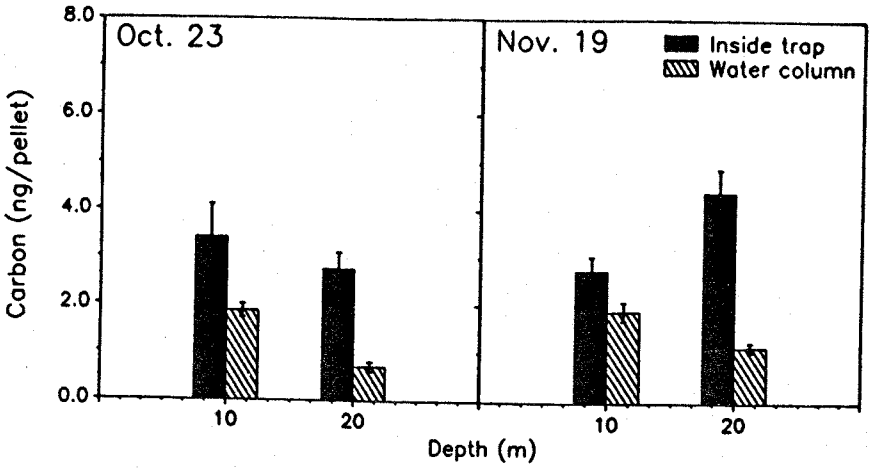

Fig. 3. Mean carbon content of fecal pellets in traps and water column during trap deployment at Lime Cay, Jamaica, 1986. Standard error bars of each estimate included ($n > 50$).

DISCUSSION

It is generally difficult to accurately estimate sedimentation rates in shallow coastal waters (HARGRAVE and TAGUCHI, 1978; PARMENTER *et al.*, 1983). While it seems certain that for much of the year a considerble amount of material is resuspended and/or horizontally transported into our study area, under periods of calm conditions it was possible to derive estimates of direct losses of primary production, and those via herbivory. At the current velocities observed during deployment, there is no evidence to suggest the traps employed were inefficient in the capture or retention of small particles (ROFF and HOPCROFT, 1985). The particles which do sediment are primarily the larger cells and fecal pellets, with upwards of 30% of the netplankton and 12–18% of the nanoplankton daily primary production being exported to the benthos. Picoplankton sedimentation was negligible, suggesting that the picoplankton production must be entirely "turned over" within the pelagos (AZAM *et al.*, 1983; DUCKLOW *et al.*, 1986; MICHAELS and SILVER, 1988).

The sedimentation rate clearly diminished in smaller size fractions, and hence with decreased settling velocity, as predicted from Stokes Law. Natural settling velocities of living cells in tropical waters, as determined by direct experimentation, are 0.29–1.65, 0.09–0.83 and 0.00 m day^{-1} for the net-, nano- and picoplankton size fractions, respectively (TAKAHASHI and BIENFANG, 1983; BIENFANG, 1985). Therefore, the pattern of sedimentation observed is related to particle size. Applying the *highest* settling velocities from these studies (which are in good agreement with calculations based on Stokes Law) to our estimates of pigment concentration in October and November, yielded predicted particle fluxes comparable to actual observations. The ratios of captured to predicted flux ranged from 0.76 to 2.57 (mean 1.5) for net particles, and from 1.08 to 4.35 (mean 2.13) for nanoparticles. However, *actual* settling velocities of individual cells can be substantially less than these upper values (e.g. by as much as 10 fold, see above), and we cannot discount the operation of other sedimentation processes. Two plausible mechanisms are: the transport by fecal pellets of high chlorophyll content and the flocculation of particles (e.g. from Appendicularian houses or "marine snow", FOWLER and KNAUER, 1986), both of

Table 3. Biomass (kJ m^{-2}) of major fecal pellet producers at Lime Cay, Jamaica, at the time of sediment trap deployment

Deployment	Copepods	Salps
Aug.	3.1	0.00
Oct.	3.6	0.28
Nov.	4.4	4.95
Annual mean	4.1	1.18

which involve particles with settling velocities greater than algal cells (LORENZEN *et al.*, 1983; FOWLER and KNAUER, 1986).

The fact that, under calm conditions, captured particles greater than 2 μm contain 50–60% of their pigments as Chl *a* indicates that the traps are capturing viable cells. We have estimated that viable cells account for ~30–40% of the flux based on pigments; however this conclusion is subject to a number of biases. For example, if other non-crustacean, pellet-producing herbivores (e.g. salps, which are periodically abundant in the area, Table 3) degrade chlorophyll less completely than copepods (D. DEIBEL, personal communication), then our calculations would overestimate cellular flux and underestimate fecal flux. Similarly, if there is a significant flux of fecal pellets from carnivorous zooplankters, or if during gut passage a larger percentage of pigment is degraded to a non-fluorescing form, then our calculations will have underestimated the fecal flux.

Microscopic examination of traps deployed under calm conditions indicated a dominance of relatively intact fecal pellets, compared to algal cells, for the material which could be identified. It is likely that a still higher flux of fecal pellets entered the traps but that a proportion were destroyed by loss of integrity from decomposition in the warm water (HONJO and ROMAN, 1978; LAUTENSCHLAGER *et al.*, 1978). This supposition is supported by the relatively low percentage of fecal pellets which possessed a peritrophic membrane and the greater proportion of amorphous material in the traps than in the water column. The fact that we estimate similar percentages of pigment flux attributable to fecal pellets for both the net- and nanoparticles (Table 2), also suggests that nanoparticles represent fragments of former netparticles. Thus, it would appear that under calm conditions the majority of the vertical carbon flux is as fecal pellets produced by grazers in the water column.

In contrast, under turbulent conditions the traps were dominated by an even larger proportion of amorphous material, undoubtedly from the resuspension of sediments in shallower waters on the shelf (B. GREENWOOD, personal communication). Because the site of trap deployment was in a deeper basin than the surrounding waters, the annual sedimentation (both organic and inorganic) may exceed that predicted on the basis of the annual primary production measured at the station due to the "focusing" of particles from shallower areas (HARGRAVE and TAGUCHI, 1978; CARPENTER *et al.*, 1986). Because of such possible complications, the use of pigments as an index of sedimentation rates is preferable to carbon, because they have relatively short half lives within the euphotic zone (see below) and therefore tend not to accumulate in shallow benthic sediments. Had sedimentation during these periods been measured directly as carbon instead of plant pigments, it is likely that the discrepancy between production and sedimentation would be pronounced, because carbon estimates include refractile detrital material of unknown age.

Two important sources of biases in estimating pigment flux due to herbivory are the extent to which pigments are destroyed during gut passage (CONOVER *et al.*, 1986; PASTERNAK and DRITS, 1988) and the effects of photodegradation on the pigments, neither of which were directly assessed in this study. Our estimates of particle flux by microscopic examination appear most consistent with estimates of pigment flux assuming 40% destruction during gut passage and/or bacterial degradation within the traps. However, because it is likely that a significant proportion of the unidentifiable material observed in the traps was formerly fecal pellets, it is likely that microscopic estimates underestimate the relative flux from pellets. If these fecal pellet fragments are of nanoparticle size, then estimates derived from pigments will underestimate the flux from netparticles and overestimate that from nanoparticles. In either case, higher destruction rates (e.g. 80%) of pigments and/or greater contribution of fecal pellets to overall flux can "fit" within the constraints of our data.

Attempts to compensate for the effects of photodegradation on pigments captured by the traps are also beset with uncertainty, including the magnitude of the photodegradation constant itself (i.e. ranges from ~0.01 to 0.08 m^2 Ein^{-1} from SooHoo and KIEFER, 1982; WELSCHMEYER and LORENZEN, 1985; CARPENTER *et al.*, 1986). Chlorophyll *a* sedimentation should be reliable because it occurs primarily as viable cells, for which synthesis of new chlorophyll and photodegradation should be in equilibrium. For phaeopigment, photodegradation is difficult to estimate as it will depend on the time of day and depth of production, the settling velocity of particles and the time spent in the trap (where shading of particles may be significant). Assuming a photodegradation constant of 0.0373 m^2 Ein^{-1} (SooHoo and KIEFER, 1982), we estimate that ~80, 35 and 10% of the phaeopigments at 0, 10 and 20 m, respectively, would be destroyed if present at these depths for the full daylight period. However, if most of the phaeopigment captured occurs as netparticles, then photodegradation may be minimal if most of this flux occurs at night [e.g. estimates of 90% by EMERSON and ROFF (1987) and 80% by LORENZEN and WELSCHMEYER (1983)]. On balance, we believe this effect to be minimal (probably <15%) in our system.

No attempt will be made to quantitatively compare the results of this study to the work of others. Sedimentation estimates in shallow waters are, for the most part, excessively biased by resuspension. Furthermore, traps are generally deployed for such long periods that pigments are excessively degraded when collected. Therefore, most workers measure and report carbon sedimentation which, as indicated, may be severely biased. Sedimentation rates from deeper waters are also difficult to compare to our study due to effects of depth (SUESS, 1980), differences in surface productivity and constant grazing and repackaging in deeper water which alters the concentration and composition of the sedimenting material (LORENZEN *et al.*, 1983; SMALL *et al.*, 1987).

On a qualitative basis, comparisons can be made to other studies. Foremost, is the fact that, in agreement with most studies, most of the observed flux (ignoring resuspension) is in the form of fecal material (BISHOP *et al.*, 1977; HONJO, 1978; HOFFMAN *et al.*, 1981; FOWLER and KNAUER, 1986; SMALL *et al.*, 1987) which experiences high settling velocities (SMALL *et al.*, 1979; KOMAR *et al.*, 1981; LORENZEN and WELSCHMEYER, 1983); furthermore, algal material which does settle is only the relatively large cells, or cell parts of high density (FOWLER and KNAUER, 1986). Finally, the observations by EMERSON and ROFF (1987) were confirmed, in that the mean size of fecal pellets inside the traps was greater than those collected in bottle casts. This suggests that either the bottles are biased against large

particles (cf. WELSCHMEYER and LORENZEN, 1985), or that the diurnal migration of larger epibenthic organisms (which produce bigger pellets, KOMAR *et al.*, 1981) has a measurable impact on the export of material from the pelagos as suggested by EMERSON and ROFF (1987).

Although the temporal coverage of trap deployment is limited, it is possible to speculate on the annual flux of pelagic production which reaches the benthos. The lowest estimate of sedimentation obtained under calm conditions was ~35 and 18% of the daily primary production of the net- and nanoplankton, respectively. The lowest estimates of sedimentation are employed because they represent the estimates least biased by resuspension. These estimates of relative flux compare favourably with estimates of 35% of the total primary production measured in the spring diatom bloom by DAVIS and PAYNE (1984), and 29% measured in a eutrophic coastal area by KNAUER *et al.* (1984). Assuming that these relative rates of sedimentation are representative, then sedimentation can be predicted simply from the observed patterns of net- and nanoplankton production.

Annual primary production at Lime Cay was estimated as 240 g C m^{-2} y^{-1} or 13,100 kJ m^{-2} y^{-1}, with the net-, nano- and picoplankton contributing 27, 30 and 43% of the production, respectively (HOPCROFT and ROFF, 1990). Thus, on an annual basis sedimentation would represent a flux of 22.7 g C m^{-2} y^{-1} for the netparticles and 12.9 g C m^{-2} y^{-1} for the nanoparticles. This represents a total flux of 35.6 g C m^{-2} y^{-1} (=1960 kJ m^{-1} y^{-1}) or ~15% of the annual primary production at Lime Cay. However, total flux could be as low as 27.5 g C m^{-2} y^{-1} (11% of annual) or as high as 52.0 g C m^{-2} y^{-1} (34% of annual), corresponding to 0 and 80% destruction of pigment during gut passage, respectively.

It is possible that this is an overestimate of carbon flux because the measurements were obtained during periods of higher than average phytoplankton biomass (cf. values in Fig. 1 to annual means of 0.149, 0.105 and 0.101 mg Chl *a* m^{-2} for the net-, nano- and picoplankton, respectively), at which time flux may be at a maximum (e.g. DAVIES and PAYNE, 1984). In contrast, estimates of sedimentation obtained when small cells dominate (and biomass is low) may actually approach zero (SMALL *et al.*, 1987), causing an underestimation of the relative carbon flux. However, if loss of phytoplankton cells is a simple function of biomass or production, then these estimates should be reasonable as an annual rate. Grazing by zooplankton will clearly influence the rate of production and hence sedimentation rate of fecal pellets. It is unlikely that the flux as fecal pellets was excessively biased in our observations because the biomass of the major pellet producers during the calm deployments, was representative of their annual mean biomass, particularly for the copepods (Table 3). Thus, by obtaining estimates of sedimentation during a calm period of high phytoplankton biomass, and typical grazing pressure, an upper limit should have been placed on the annual carbon flux attributable to herbivory. The conclusion of a relatively minor export of pelagic production to the benthos is consistent with the generalization of PETERSON and CURTIS (1980) and LONGHURST (1983), that increasingly toward low latitudes, or in systems which experience low seasonal "pulsing", energy is cycled predominantly within the pelagic realm.

Acknowledgements—This work was supported by an NSERC operating grant to J. C. Roff, a CIDA Award to R. R. Hopcroft, and an NSERC summer fellowship to J. A. Berges. We thank C. Clarke for technical assistance and I. M. Goodbody for access to facilities at the Port Royal Marine Lab, University of the West Indies.

REFERENCES

AZAM F., T. FENCHEL, J. G. FIELD, J. S. GRAY, L. A. MEYER-REIL and F. THINGSTAD (1983) The ecological role of water column microbes in the sea. *Marine Ecology Progress Series*, **10**, 257–263.

BIENFANG P. K. (1985) Size structure and sinking rates of various microparticulate constituents in oligotrophic Hawaiian waters. *Marine Ecology Progress Series*, **23**, 143–151.

BISHOP J. K. B., J. M. EDMOND, D. R. KETTEN, W. B. SILKER and M. P. BACON (1977) The chemistry, biology and vertical flux of particulate matter from the upper 400 m of the equatorial Atlantic Ocean. *Deep-Sea Research*, **24**, 511–548.

CARPENTER S. R., M. M. ELSER and J. J. ELSER (1986) Chlorophyll production, degradation, and sedimentation: implications for paleolimnology. *Limnology and Oceanography*, **31**, 112–124.

CONOVER R. J., R. DURVASULA, S. ROY and R. WANG (1986) Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton, and some consequences. *Limnology and Oceanography*, **31**, 878–887.

DAVIES J. M. and R. PAYNE (1984) Supply of organic matter to the sediment in the northern North Sea during a spring phytoplankton bloom. *Marine Biology*, **78**, 315–324.

DOWNS J. N. and C. J. LORENSEN (1985) Carbon: pheopigment ratios of zooplankton fecal pellets as an index of herbivorous feeding. *Limnology and Oceanography*, **30**, 1024–1036.

DUCKLOW H. W., D. A. PURDIE, P. J. LEB. WILLIAMS and J. M. DAVIES (1986) Bacterioplankton: a sink for carbon in a coastal marine plankton community. *Science*, **232**, 865–867.

EMERSON C. W. and J. C. ROFF (1987) Implications of fecal pellet size and zooplankton behaviour to estimates of pelagic–benthic carbon flux. *Marine Ecology Progress Series*, **35**, 251–257.

FENCHEL T. (1988) Marine plankton food chains. *Annual Review of Ecology and Systematics*, **19**, 19–38.

FOWLER S. W. and G. A. KNAUER (1986) Role of large particles in the transport of elements and organic compounds through the oceanic water column. *Progress in Oceanography*, **16**, 147–194.

HARGRAVE B. T. and S. TAGUCHI (1978) Origin of deposited material sedimented in a marine bay. *Journal of the Fisheries Research Board of Canada*, **35**, 1604–1613.

HOFFMAN E. E., J. M. KLINCK and G. A. PAFFENHOFER (1981) Concentrations and vertical fluxes of zooplankton fecal pellets on a continental shelf. *Marine Biology*, **61**, 327–335.

HONJO S. (1978) Sedimentation of materials in the Sargasso Sea at a 5367 m deep station. *Journal of Marine Research*, **36**, 469–492.

HONJO S. and M. R. ROMAN (1978) Marine copepod fecal pellets: production, preservation and sedimentation. *Journal of Marine Research*, **36**, 45–57.

HOPCROFT R. R. and J. C. ROFF (1990) Phytoplankton size fractions in a tropical neritic ecosystem near Kingston, Jamaica. *Journal of Plankton Research*, **12**, in press.

KNAUER G. A., J. H. MARTIN and D. M. KARL (1984) The flux of particulate organic matter out of the euphotic zone. In: *Global ocean flux study, proceedings of a workshop*, National Academy Press, pp. 136–150.

KOMAR P. D., A. P. MORSE, L. F. SMALL and S. W. FOWLER (1981) An analysis of sinking rates of natural copepod and euphausid fecal pellets. *Limnology and Oceanography*, **26**, 172–180.

LAUTENSCHLAGER K. P., N. K. KAUSHIK and J. B. ROBINSON (1978) The peritrophic membrane and faecal pellets of *Gammarus lacustris limnaeus* Smith. *Freshwater Biology*, **8**, 207–211.

LONGHURST A. (1983) Benthic–pelagic coupling and export of organic carbon from a tropical Atlantic continental shelf—Sierra Leone. *Estuarine, Coastal and Shelf Science*, **17**, 261–285.

LORENZEN C. J. and N. A. WELSCHMEYER (1983) The *in situ* sinking rates of herbivore fecal pellets. *Journal of Plankton Research*, **5**, 929–933.

LORENZEN C. J., N. A. WELSCHMEYER, A. E. COPPING and M. VERNET (1983) Sinking rates of organic particles. *Limnology and Oceanography*, **28**, 766–769.

MICHAELS A. F. and M. W. SILVER (1988) Primary production, sinking fluxes and the microbial food web. *Deep-Sea Research*, **4**, 473–490.

PARMENTER C. M., M. H. BOTHNER and B. BUTMAN (1983) Characteristics of resuspended sediment from Georges Bank collected with a sediment trap. *Estuarine and Coastal Shelf Science*, **17**, 521–533.

PARSONS T. R., Y. MAITA and C. M. LALLI (1984) *A manual for chemical and biological methods in seawater*. Pergamon Press, Toronto, p. 173.

PASTERNAK A. F. and A. V. DRITS (1988) Possible degradation of chlorophyll-derived pigments during passage through the gut of herbivorous copepods. *Marine Ecology Progress Series*, **49**, 187–190.

PETERSON G. H. and M. A. CURTIS (1980) Differences in energy flow through major components of the subarctic, temperate and tropical marine shelf ecosystems. *Dana*, **1**, 53–64.

ROFF J. C. and R. R. HOPCROFT (1985) Determination of efficiency of sediment traps with respect to their size and aspect ratio, and water velocity and particle size. Final report for Department of Supply and Services, Government of Canada, contract KW405-4-0039.

ROFF J. C. and R. R. HOPCROFT (1986) High precision microcomputer based measuring system for ecological research. *Canadian Journal of Fisheries and Aquatic Science*, **43**, 2044–2048.

SHUMAN F. R. and C. J. LORENZEN (1975) Quantitative degradation of chlorophyll by a marine herbivore. *Limnology and Oceanography*, **20**, 580–586.

SIEBURTH J. MCN., V. SMETACEK and J. LENZ (1978) Pelagic ecosystem structure: Heterotrophic compartments of the plankton and their relationship to the plankton size fractions. *Limnology and Oceanography*, **23**, 1256–1263.

SMALL L. F., S. W. FOWLER and M. Y. UNLU (1979) Sinking rates of natural copepod fecal pellets. *Marine Biology*, **51**, 233–241.

SMALL L. F., G. A. KNAUER and M. D. TUEL (1987) The role of sinking fecal pellets in stratified euphotic zones. *Deep-Sea Research*, **34**, 1705–1712.

SMAYDA T. J. (1969) Some measurements of the sinking rates of fecal pellets. *Limnology and Oceanography*, **14**, 621–625.

SMAYDA T. J. (1971) Normal and accelerated sinking of phytoplankton in the sea. *Marine Geology*, **11**, 105–122.

SOOHOO J. B. and D. A. KIEFER (1982) Vertical distribution of phaeopigments—II. Rates of production and kinetics of photooxidation. *Deep-Sea Research*, **29**, 1553–1563.

STARESINIC N., G. Y. ROWE, D. SHAUGHNESSEY and A. J. WILLIAMS II (1978) Measurements of the vertical flux of particulate organic matter with a free-drifting sediment trap. *Limnology and Oceanography*, **23**, 559–563.

SUESS E. (1980) Particulate organic carbon flux in the oceans-surface productivity and oxygen utilization. *Nature*, **288**, 260–263.

TAKAHASHI M. and P. K. BIENFANG (1983) Size structure of phytoplankton biomass and photosynthesis in subtropical Hawaiian waters. *Marine Biology*, **76**, 203–211.

WELSCHMEYER N. A. and C. L. LORENZEN (1985) Chlorophyll budgets: zooplankton grazing and phytoplankton growth in a temperature fjord and the Central Pacific Gyres. *Limnology and Oceanography*, **30**, 1–21.

ZEITZSCHEL B. (1970) The quantity, composition and distribution of suspended particulate matter in the Gulf of California. *Marine Biology*, **7**, 305–318.