

- determination of chlorophyll. *J. Cons. Cons. Int. Explor. Mer* **30**: 3–15.
- , AND B. RIEMANN. 1978. Chlorophyll *a* determination: Improvements in methodology. *Oikos* **30**: 438–447.
- JEFFREY, S. W. 1981. An improved thin-layer chromatography technique for marine phytoplankton pigments. *Limnol. Oceanogr.* **26**: 191–197.
- , AND G. M. HALLEGRAEFF. 1980. Studies of phytoplankton species and photosynthetic pigments in a warm core eddy of the East Australian Current. 2. A note on pigment methodology. *Mar. Ecol. Progr. Ser.* **3**: 295–301.
- , AND G. F. HUMPHREY. 1975. New spectrophotometric equations for determining chlorophylls *a*, *b*, *c*₁ and *c*₂ in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.* **167**: 191–194.
- JENSEN, A., AND E. SAKSHAUG. 1973. Studies on the phytoplankton ecology of the Trondheimfjord. 3. Chloroplast pigments in relation to abundance and physiological state of the phytoplankton. *J. Exp. Mar. Biol. Ecol.* **11**: 137–155.
- JOHNSON, P. W., AND J. MCN. SIEBURTH. 1979. Chroococcoid cyanobacteria in the sea: A ubiquitous and diverse phototrophic biomass. *Limnol. Oceanogr.* **24**: 928–935.
- KLEIN-BRETELER, W. C. 1980. Continuous breeding of marine pelagic copepods in the presence of heterotrophic dinoflagellates. *Mar. Ecol. Progr. Ser.* **2**: 229–233.
- LOFTUS, M. E., AND J. H. CARPENTER. 1971. A fluorometric method for determining chlorophylls *a*, *b* and *c*. *J. Mar. Res.* **29**: 319–338.
- LORENZEN, C. J. 1967. Determination of chlorophyll and pheopigments: Spectrophotometric equations. *Limnol. Oceanogr.* **12**: 343–346.
- , AND S. W. JEFFREY. 1980. Determination of chlorophyll in seawater. SCOR-UNESCO Tech. Pap. Mar. Sci. 35, p. 1–20.
- MARKER, A. H. 1972. The use of acetone and methanol in the estimation of chlorophyll in the presence of pheophytin. *Freshwater Biol.* **2**: 361–385.
- STRICKLAND, J. D., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Can.* 167.
- WATERBURY, J. B., S. W. WATSON, R. R. GUILLARD, AND L. E. BRAND. 1979. Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. *Nature* **277**: 293–294.

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Sinking rates of organic particles¹

Abstract—The flux of organic particles collected by sediment traps decreases in a nonlinear fashion with depth. This implies a loss of organic carbon with time as the particles sink. Samples of such particles held in the laboratory or left in situ do in fact decay, showing a significant loss of carbon.

Particles were collected in the upper 1,000 m of the water column with sediment traps south of the Hawaiian Islands. Aliquots from the traps were placed in combusted glass bottles and returned to the depths from which they were collected. After 5 days the bottles were recovered and the carbon content determined. On the average, about 30% of the particulate carbon was lost during the experiment.

With this knowledge of the decay rate, one can estimate the expected change in "apparent carbon flux" with time. This in combina-

tion with the measured vertical flux can be used to calculate the depth interval required for this change to occur. Average sinking rates of 92 m·d⁻¹ were thus estimated.

The flux of organic matter, measured as organic carbon, shows a nonlinear decrease with increasing depth (Suess 1980). The processes involved in this apparent loss of organic carbon have not been documented, but we will assume that the loss is related to decomposition rather than to solubilization or fragmentation because a summary of the published data (Menzel 1974) shows no marked increase in dissolved or particulate organic carbon with depth. Most likely this loss of carbon is the result of biological activity, either microbial or possibly via reingestion and repackaging by midwater animals.

We here report the results of an exper-

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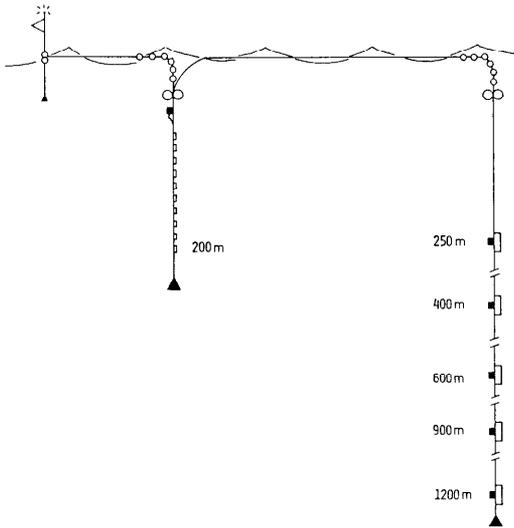


Fig. 1. Arrangement of floating sediment trap array (after Welschmeyer 1982).

iment conducted in the oligotrophic waters south of Oahu in which we investigated the sinking rates of organic particles (RV *Thomas G. Thompson* cruise TT-157).

Floating sediment trap arrays were deployed in two parts consisting of VLS Sampson braided rope (9.5 mm) and stainless steel wire (3.9 mm) (Fig. 1). The traps on the braided rope portion were PVC cylinders (15.2-cm diam \times 45.7 cm high: Lorenzen et al. 1981) placed at 250, 400, 600, and 900 m. The other traps, half as large, were placed on the wire at 20-m intervals starting at 20 m and going to a depth of 200 m. These traps were closed by a messenger at a predetermined time before the arrays were recovered. Previous comparisons showed that both traps captured and retained material with equal efficiency (Welschmeyer 1982). The arrays were deployed twice: the first time for 4 days and the second time for 5 days.

After the first deployment, each trap was sampled for particulate organic carbon, POC, and plant pigments. Samples were filtered either on combusted silver filters (0.45- μ m pore size) for POC determination by elemental analysis or Whatman GF/F glass-fiber filters for pigment

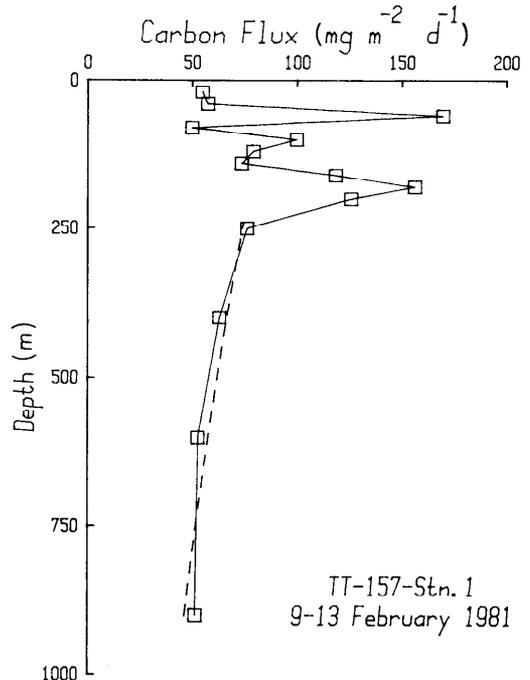


Fig. 2. Vertical distribution of carbon flux at 18°N, 156°W. Dashed line is statistically fitted curve for data between 250 and 900 m. Relationship is described by: $Z = 6,276 - 1,400 \times \ln(C_{flux})$ where $n = 4$ and $r^2 = 0.82$.

analysis (Lorenzen 1966). For the decay experiments, aliquots from the larger traps were placed in combusted glass bottles (1 liter) which were attached to the array when it was redeployed so that these samples were returned to the depths from which they were captured. After the second recovery, POC was measured in each bottle.

Primary production was measured in situ by the ^{14}C technique (Strickland and Parsons 1972). Exposure was for 24 h, sunrise to sunrise. Plant pigments were measured repeatedly in the water of the euphotic zone by a fluorometric technique; samples for those measurements were collected with 2.5-liter Niskin bottles.

Flux rates were calculated from the sediment trap samples for both POC (Fig. 2) and plant pigments (Fig. 3). Flux rates were maximum in the upper 250 m of the

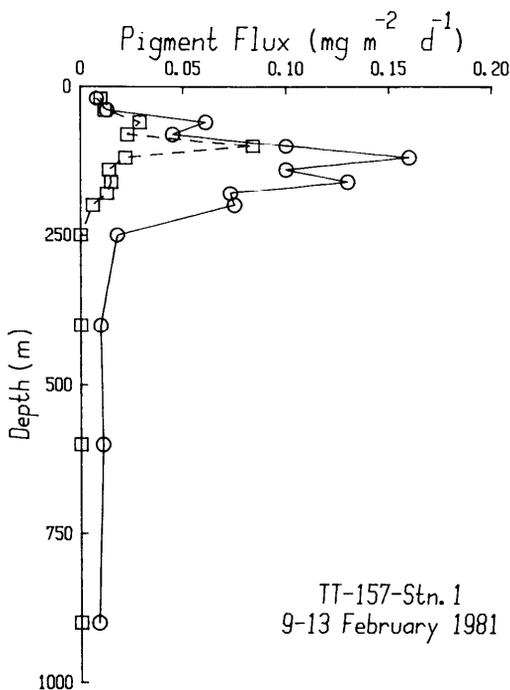


Fig. 3. Vertical distribution of pigment flux. Same experiment as shown in Fig. 2. ○—Pheopigment flux; □—chlorophyll flux.

water column. Below the euphotic zone, at the 250-m level, flux rates of both POC and pigments are markedly reduced; actual values are 45% (POC), 10% (pheopigments), and 0.1% (chlorophyll) of those at the maximum nearer the surface.

The change in POC $[C_t]/[C_0]$ over the course of the in situ "rotting" experiment was about 30% (Table 1).

The loss of POC during the in situ rotting experiments, the change measured in the glass bottles suspended on the second deployment, shows that some portion of the organic matter sinking out of the surface layers is labile. The pigmented portion of this material appears to be fecal pellets from herbivores, since the ratio of pheopigments to chlorophyll was 9.2 which is characteristic of fecal pellets of herbivores feeding on algae (Lorenzen unpubl.). On the other hand, the carbon : pheopigment ratio is entirely too high for herbivore fecal pellets (>400), suggesting that a relatively minor portion of the

Table 1. Carbon flux, change in carbon concentration during the rotting experiments, $[C_t]/[C_0]$, apparent carbon flux, depth interval necessary to account for change in carbon flux, and calculated sinking rates derived from rotting experiments.

Z (m)	C_{flux}	$[C_t]/[C_0]$	Apparent C flux	ΔZ	Sinking rate ($m \cdot d^{-1}$)
250	76.2	0.73	55.9	393	78
400	63.0	0.66	41.6	656	131
900	51.6	0.71	36.6	335	67
\bar{x}	—	0.70	—	—	92

sedimenting organic carbon has been recently associated with algae. Herbivory per se is a minor direct contributing factor to the vertical flux of organic matter in this particular area below the euphotic zone. At the same time, primary production and herbivory must be the primary source of organic particles and of the vertical flux of particulate organic carbon.

Below 120 m, pheopigment flux decreases markedly. Past experience in this laboratory shows that reingestion of pheopigments (in fecal pellets) by crustaceans brings about alterations in the pigments so that they are lost to our analytical technique. Coprophagy is probably of major significance in the upper layers of the water column. On the other hand, as pointed out below, coprophagy may only be a minor process in the deeper portions of the water column.

Chlorophyll flux is substantially lower than pheopigment flux below 50 m. At 100 and 400 m the daily flux of chlorophyll represents only 0.8 and 0.08% of the integrated standing crop of chlorophyll above these depths, suggesting that sinking of intact algae out of the euphotic

Table 2. Tabulation of carbon flux, apparent carbon utilization (ACU), and percentage change in carbon per meter with depth.

Z (m)	C_{flux}	ACU ($mg \cdot m^{-3} \cdot d^{-1}$)	$\Delta C \cdot m^{-1}$
250	76.2	0.088	0.11
400	63.0	0.051	0.081
600	52.8	0.004	0.0075
900	51.6	—	—

zone is of minor importance at this location.

Knowledge of the vertical distribution of organic carbon flux does not yield the information needed to estimate a sinking rate, but it does permit estimation of carbon utilization in the water column. In this case, the vertical distribution of organic carbon flux between 250 and 900 m (Fig. 2) is described by the statistically significant relationship ($n = 4$, $r^2 = 0.82$):

$$Z = 6,276 - 1,400 \times \ln(C_{\text{flux}}) \quad (1)$$

(where C_{flux} is carbon flux in $\text{mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, and Z is depth in meters).

The apparent carbon utilization over this depth range, ACU, calculated by

$$\text{ACU} = \frac{\text{flux}_1 - \text{flux}_2}{Z_2 - Z_1} \quad (2)$$

is tabulated for the sediment traps at 250 m and below (Table 2). The ACU decreases with depth both in absolute terms and as a percentage of the flux. In the first interval it is 0.088 and in the last interval $0.004 \text{ mg C} \cdot \text{m}^{-3} \cdot \text{d}^{-1}$. This is also reflected in the percentage loss. For the same intervals the values are 0.59 and 0.26 $\Delta\text{C}\% \cdot \text{m}^{-1}$, perhaps indicative of the material becoming more refractory deeper in the water column.

Deriving an estimate of the sinking rates of these particles is not straightforward. The results from the rotting experiments (Table 1) show that the collected material is indeed labile. The actual kinetics of the reactions involved are unknown, but a first-order chemical reaction may be assumed. If we use the measured change to reduce the flux at the level from which the material was collected and calculate the "apparent carbon flux" 5 days later, we can use Eq. 1 to calculate the depth at which this flux would be found. For example, in the case of the 400-m sample: $63.0(C_{\text{flux}}) \times 0.66(C_i/C_0) = 41.6$ (apparent carbon flux). The depth where a carbon flux of $41.6 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ would be found is 1,056 m. The interval 1,056 to 400 m, or 656 m covered in 5 days, would suggest an average sinking rate of $131 \text{ m} \cdot \text{d}^{-1}$. The calculations

yield sinking rates of 78, 131, and $67 \text{ m} \cdot \text{d}^{-1}$ for material collected at 250, 400, and 900 m. The average sinking rate is calculated as $92 \text{ m} \cdot \text{d}^{-1}$.

The fate of these organic particles as they sink is unclear and the mechanisms of their destruction may vary with depth. We suggest that in and just below the euphotic zone the major loss results from reingestion, i.e. coprophagy. At greater depths this seems less important: between 400 and 900 m, carbon flux decreases 18%, while pheopigment flux is unchanged. This suggests that coprophagy is relatively insignificant at these depths.

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References

- LORENZEN, C. J. 1966. A method for the continuous measurement of in vivo chlorophyll concentration. *Deep-Sea Res.* **14**: 735-745.
- , F. R. SHUMAN, AND J. T. BENNETT. 1981. In situ calibration of a sediment trap. *Limnol. Oceanogr.* **26**: 580-585.
- MENZEL, D. W. 1974. Primary productivity, dissolved and particulate organic matter and the sites of oxidation of organic matter, p. 659-678. In E. Goldberg [ed.], *The sea*, v. 5. Wiley-Interscience.
- STRICKLAND, J. D., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis, 2nd ed. *Bull. Fish. Res. Bd. Can.* 167.
- Suess, E. 1980. Particulate organic carbon flux in the oceans—surface productivity and oxygen utilization. *Nature* **288**: 260-263.
- WELSCHMEYER, N. A. 1982. The dynamics of phytoplankton pigment: Implications for zooplankton grazing and phytoplankton growth. Ph.D. thesis, Univ. Washington. 176 p.

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