Seasonal particulate carbon flux in the coastal northwestern Mediterranean Sea, and the role of zooplankton fecal matter

Particulate carbon flux
Fecal pellets
Sediment traps
Seasonal particles flux

Flux de carbone particulaire
Pelotes fécales
Pièges à sédiments
Flux particulaire saisonnier

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ABSTRACT

During a six-year (1978-1984) sediment trap study in the northwestern Mediterranean off the coast of Monaco, large variations in mass flux and carbon flux through 100 and 150 m were observed with maximum flux values occurring in late winter or early spring and minimum flux in late summer. Total particulate carbon flux was linearly related to mass flux. During March through October total particulate carbon flux represented, on average, approximately 7 % of the mass flux, whereas from November through February it averaged about 4.7 %. From recent organic carbon content data collected in the same region, it was estimated that approximately 5 % of the total mass flux through 100 and 150 m in calm seas was organic carbon (calm seas were prevalent during March through October). Organic carbon export out of the euphotic zone ("new production") ranged from 17 to 42 % of primary production.

Zooplankton fecal pellets were always an abundant component of the sinking particles and the pellet carbon flux was linearly related to the total carbon flux at the three depths (50, 150 and 250 m) examined. Higher pellet fluxes were always observed at the greater depths. Pellet carbon fluxes were calculated to be roughly 25, 29 and 33 % of total particulate carbon fluxes through 50, 150 and 250 m, respectively. These estimates suggested that zooplankton fecal pellet deposition is a significant contributor to the downward particulate carbon flux in this region of the northwestern Mediterranean Sea.

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RÉSUMÉ

Flux saisonnier de carbone particulaire et rôle de la matière fécale planctonique près des côtes dans le bassin nord-occidental de la Méditerranée

Le flux de carbone particulaire a été étudié à l'aide de pièges à particules ancrés au large de Monaco pendant six années (1978-1984) ; d'importantes variations ont été observées sur les flux de masse et de carbone total entre 100 et 150 m, avec des maxima en fin d'hiver ou au début du printemps et un minimum en fin d'été. Les deux flux sont proportionnels : de mars à octobre, le flux moyen de carbone total particulaire représente approximativement 7 % du flux de masse, contre 4,7 % de novembre à février. Des données obtenues récemment dans la même région indiquent que par mer calme (c'est-à-dire de mars à octobre), le carbone organique représente environ 5 % du flux de masse total entre 100 et 150 m. Au-delà de la zone euphotique, le flux de carbone organique («production nouvelle» représente 17 à 42 % de la production primaire.

Les pelotes fécales zooplanctoniques ont toujours constitué une part importante de la sédimentation des particules et le flux de carbone fécal est proportionnel au flux de carbone total aux trois profondeurs considérées (50, 150 et 250 m). Les flux les plus importants de pelotes fécales sont observés aux plus grandes profondeurs. Les flux de carbone fécal sont évalués à 25, 29 et 33 % des flux de carbone particulaire total à 50, 150 et 250 m de profondeur respectivement. Ces estimations suggèrent que la déposition des fèces zooplanctoniques contribue de manière significative aux flux verticaux de carbone particulaire dans cette région de la Méditerranée nord-occidentale.

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INTRODUCTION

The northwestern Mediterranean Sea has generally been classified as oligotrophic, although there is evidence that primary productivity is very patchy, reaching values as high as 2gC m^{-2} d^{-1} in some regions during spring (Jacques *et al.*, 1973). Productivity and the appearance of phytoplankton blooms also vary with time (Jacques *et al.*, 1973; Nival *et al.*, 1975; Jacques, 1988; Minas *et al.*, 1988). Export of particulate carbon out of the euphotic zone would be expected to follow spatial and temporal patterns similar to euphotic-zone production; however, very little information exists at present on carbon flux in the Mediterranean, particularly in nearshore waters.

Since 1978 we have been measuring the flux of particulate matter and associated materials using sediment traps at a nearshore station off Monaco (Fowler *et al.*, 1979; Burns and Villeneuve, 1983; Burns *et al.*, 1985). From mid-1978 through mid-1984 our temporal coverage appeared good enough to extract a six-year seasonal record which could be compared with historical primary productivity measurements from the same area (Brouardel, 1971). In addition, the record appeared consistent enough to allow us to assess the potential contributions of zooplankton fecal pellets to the vertical particulate carbon flux in this region.

MATERIALS AND METHODS

Sediment traps were moored at a site (43°42.57'N, 7°27.30'E) approximately two nautical miles off the coast of Monaco (Fig. 1). The traps are of cylindrical design (H/D = 2.5; collecting area = 0.076 m^2) with a conical device attached at the bottom to funnel the sample into detachable polyethylene cups. The trap itself is made of polyester resin fiberglass covered with gel-coat. The collection cup is opened and closed manually with nylon cords when the trap is just beneath the surface.

From June 1978 through July 1982, the traps were deployed at 100 m depth in a water column approximately 200 m deep. During these deployments, the duration of which ranged between 5 and 20 days, no poisons or preservatives were used in the traps. After July 1982, the mooring was moved slightly further offshore to a depth of 300 m, so that a series of three traps could be deployed on a single mooring at 50, 100 or 150 m, and 250 m to measure variation in particle flux with depth.

The 100 or 150 m depths were chosen to be below the photic zone and mixed layer during all sampling periods (Brouardel, 1971; M. Boisson, pers. comm.). In subsequent analyses we could measure no significant differences ($p = 0.05$) between the 100 and 150 m traps under similar conditions, so that data from these two trap depths were pooled in order to extend the temporal coverage of fluxes below the photic zone. For these deployments, the collection cups were filled with filtered sea water containing a 4 % buffered formalin solution. In some cases, paired traps were moored at the same depth to increase the amount of material collected.

During the entire study, 85 trap deployments were made. Due to problems with weather, ship availability and trap losses, the seasonal record for any given year was incomplete. Unfortunately, these gaps resulted in fewer data being obtained for the winter months. Nevertheless, the flux record represents the longest such record in the Mediterranean to date.

Upon recovery of the traps, the samples were returned to the laboratory within one hour and either immediately processed or stored in the dark at 4°C until processing could begin. The methods for preparing and processing trap samples have been described in detail elsewhere (Monaco *et al.*, 1987; Heussner *et al.*, 1987; 1988). Briefly, each sample was sieved and carefully hand-picked to remove zooplankton "swimmers" which often entered the traps. Aliquots of the remaining particulate samples were removed and oven-dried to constant weight at 60°C to determine mass flux. Dried aliquots of most of the samples were subsequently ground in a mortar and analyzed for total carbon using a Perkin Elmer Model 140C CHN analyzer. On selected dates between March and September 1983, and February to August 1984, aliquots of wet sample from all trap depths were transferred to a gridded Petri dish and intact zooplankton fecal pellets were enumerated using a dissecting microscope. Carbon contents of fecal pellets were determined in the CHN analyzer so that fecal pellet carbon fluxes could be calculated.

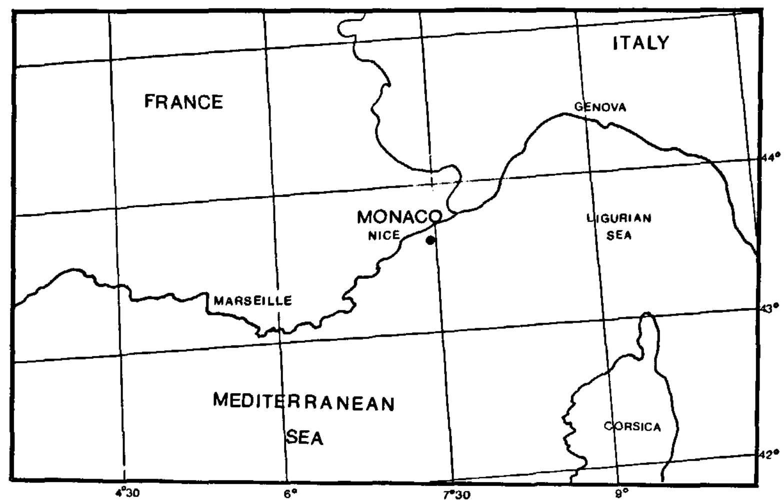

Figure 1

Location of the sediment trap mooring (●) in the northwestern Mediterranean.

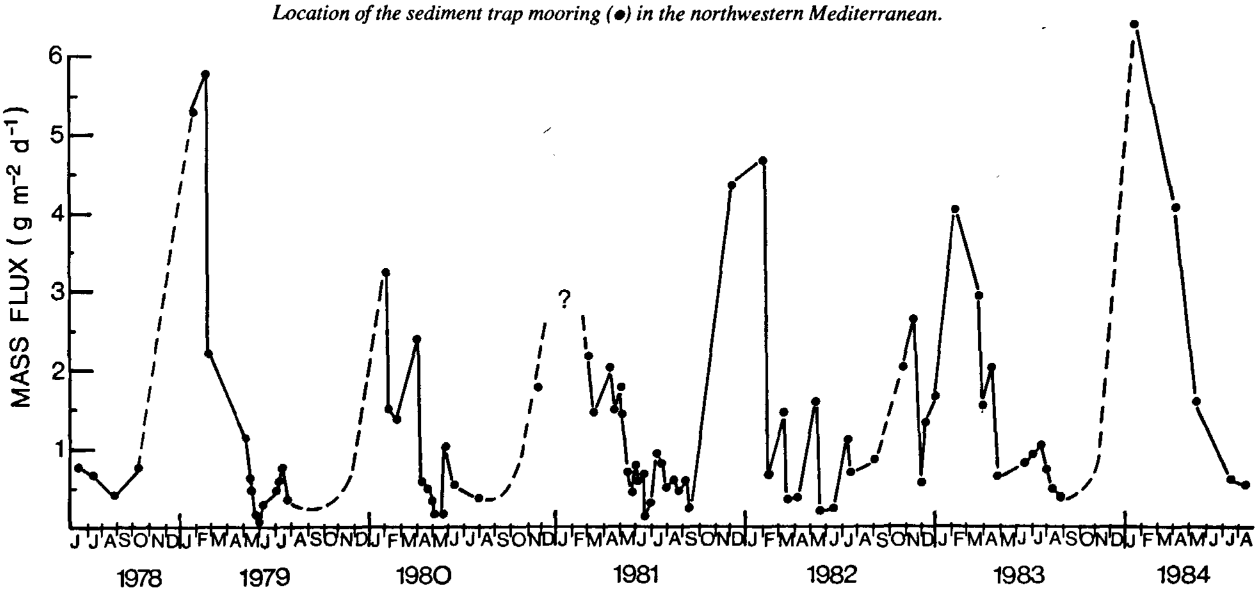

Figure 2

Temporal variation in particulate mass flux (g dry m^{-2} d^{-1}) through 100 m (June 1978 - December 1982) and 150 m (January 1983 - August 1984) depths at a station off the coast of Monaco in the northwestern Mediterranean. The dashed lines represent major gaps in the record and are drawn to approximate assumed fluxes for those months based on data from the same period in other years.

RESULTS AND DISCUSSION

Total mass flux

Particulate mass flux through the 100 m (or 150 m in some cases) depth horizon showed definite seasonality (Fig. 2). Every year from 1979 to 1984, maximum flux values were recorded in late winter or early spring, with minimum flux tending to occur in late summer.

Although the frequency of data points was low in winter, those fluxes that were obtained showed order-of-magnitude increases compared to summer fluxes. The late winter-spring peaks in particle flux in these nearshore waters were similar to those observed during recent years in offshore waters between Monaco and Corsica (Buat-Ménard *et al.*, 1989), and were related to the presence of the spring bloom and resultant grazing activity in this region of the Mediterranean. No water-column biomass data were obtained concurrently with our sediment trap deployments; however, long-term studies of primary productivity and zooplankton biomass in these waters have shown seasonal maxima of these parameters in late winter and spring and seasonal minima in late summer (*e.g.*, Brouardel, 1971; Fenaux and Quelart, 1977; Seguin, 1981; Andersen and Nival, 1988 *a*).

Superimposed on the effects of enhanced primary productivity, increased wind velocities and storm events during winter, combined with elevated riverine and non-point-source land runoff, undoubtedly contributed to the increased winter particle fluxes at our coastal site.

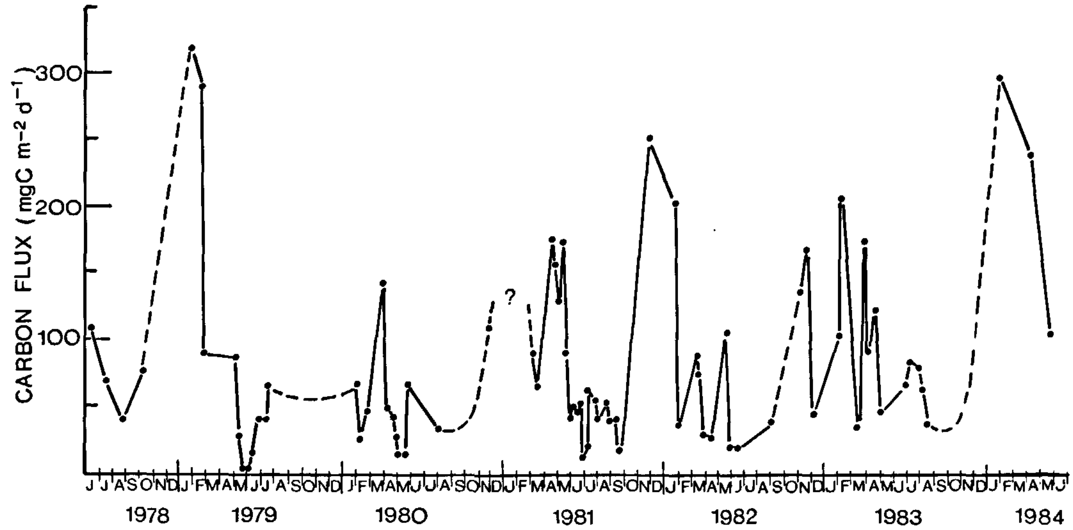

Figure 3

Temporal variation in total carbon flux (mg C m^{-2} d^{-1}) through 100 m (June 1978 - December 1982) and 150 m (January 1983 - June 1984) depths at a station off the coast of Monaco in the northwestern Mediterranean. The dashed lines represent major gaps in the record and are drawn to approximate assumed fluxes for those months based on data from the same period in other years. Note that carbon values are not available for all samples depicted in Figure 1.

Total carbon flux

Total particulate carbon flux showed similar seasonal trends (Fig. 3) and was linearly related to the mass flux at 100 and 150 m (Fig. 4). Although the regression lines in Figure 4 were not statistically different ($p = 0.05$) between winter months and the rest of the year, we have nonetheless shown the two lines to highlight the trend of lower carbon content per unit of mass flux during winter. During spring, summer and fall (March through October) the linear relationship accounted for 88 % of the variability, indicating that the total particulate carbon flux through 100 or 150 m represented, on average, about 7 % of the mass flux. In winter (November through February) the mass flux averaged about 4.7 % carbon content, 85 % of the variability being accounted for by the linear relationship. The highest mass and carbon fluxes through 100 or 150 m during non-winter periods occurred in spring.

Total carbon flux estimates at 100 or 150 m, when grouped by two-month intervals throughout the years of sampling, further demonstrated the high fluxes associated with the winter months and the low fluxes in summer (C_T in the Tab.). The standard deviations about the means were high, as expected from this type of data assembled in this manner, so that the apparent progression from the highest mean fluxes in January-February to the lowest in September-October may be somewhat artifactual. When only those fluxes measured under calm sea conditions (sea state ≤3) were considered [C_T (c), Tab.], winter fluxes were similar to summer fluxes (although there was only one calm sampling interval each in the January-February and November-December periods). The highest mean particulate carbon flux through 100 or 150 m in calm seas (133.9 mg C m^{-2} d^{-1}) occurred during the March-April period. The mean particulate carbon fluxes shown in theTable were higher than those which have been measured at 200 m in open northwestern Mediterranean waters (Miquel and Fowler, unpublished results), primarily due to the much lower mass fluxes (*e.g.*, 8-335 mg m^{-2} d^{-1}) typically observed at those stations (Buat-Ménard *et al.*, 1989).

Organic carbon flux and new production

From other data taken from sediment trap samples in the same region as our samples (Miquel and Fowler, unpublished results), we determined that the organic carbon content averaged 70.0 ± 10.3 % (range 60-96, n = 10) of the total carbon content during calm periods [C org (c), Tab.]; *i.e.* approximately 4.9% of the total mass flux through 100 or 150 m in calm seas was organic carbon. Our mean organic carbon flux values (26-94 mg C m^{-2} d^{-1}) were similar to those (44-86 mg C m^{-2} d^{-1}) reported for short-term (35-48 hr), drifting sediment trap deployments at a 200 m depth off the coast near Nice (Copin-Montégut, 1988).

Under calm weather conditions we might presume that the upper waters of the northwestern Mediterranean approach steady state conditions, so that the flux of organic carbon out of the euphotic zone can be considered equivalent to new production in terms of carbon (Eppley and Peterson, 1979) ; thus, [C org (c)/PP] x 100 in the Table might be equivalent to the percentage of mean integral primary production (PP) that is new production. If the above presumption is correct, then new production in our coastal waters during calm weather was approximately 20 % of primary production throughout most of the year, but increased to 42 % during early spring (Tab.). These estimates, in fact, would have to be considered as minimum values if indeed any carbon was lost from the trapped particles

Table

Mean total carbon flux (C_T ± 1 s.d.) and mean total carbon flux during calm periods only ($C_{T(c)}$ ± 1 s.d.), through 100 and 150 m depth horizons. Number of samples are given in parentheses for successive two-month periods. Also given are the estimated mean organic carbon flux for calm periods [C org (c)], and [C org (c)] as a percentage of primary production (PP), for the two-month periods.

Period	C_T (mgC m^{-2} d^{-1})	$C_{T(C)}$ (mgC m^{-2} d^{-1})	C org (c)* (mgC m^{-2} d^{-1})	PP** (mgC m^{-2} d^{-1})	$\frac{\text{C org (c)}}{\text{PP}} \times 100$
January/February	160.4 ± 111.7 (12)	37.7 (1)	26.4	155	17
March/April	100.7 ± 64.1 (15)	133.9 ± 70.0 (10)	93.7	223	42
May/June	53.6 ± 45.1 (30)	56.1 ± 45.7 (25)	39.3	216	18
July/August	50.9 ± 22.4 (20)	50.9 ± 22.4 (20)	35.6	180	20
September/October	42.0 ± 24.5 (4)	42.0 ± 24.5 (4)	29.4	149	20
November/December	141.2 ± 77.3 (5)	41.9 (1)	29.4	121	24

* C org (c) = 70.0 ± 10.3 % $C_{T(c)}$, based on data from the same area.
** from Brouardel (1971), weighted by the number of flux samples in each month of the two-month period.

between the time of sedimentation and the recovery of the sediment traps (*e.g.*, Gardner *et al.*, 1983; Knauer *et al.*, 1984).

The March-April period in this part of the Mediterranean Sea is often characterized by phytoplankton blooms (Brouardel, 1971; Jacques *et al.*, 1973; Jacques, 1988; Andersen and Nival, 1988 *a*, *b*; Minas *et al.*, 1988), so that enhanced sinking of particulate organic carbon through 100 or 150 m might be expected, regardless of the ultimate form of the sinking material as phytodetritus (Smetacek, 1985; Rice *et al.*, 1986) or as large particles (Fowler and Knauer, 1986; Alldredge and Silver, 1988). Based on nutrient utilization data from the open waters off Marseille together with appropriate conversion factors, Jacques (1988) computed a mean organic carbon

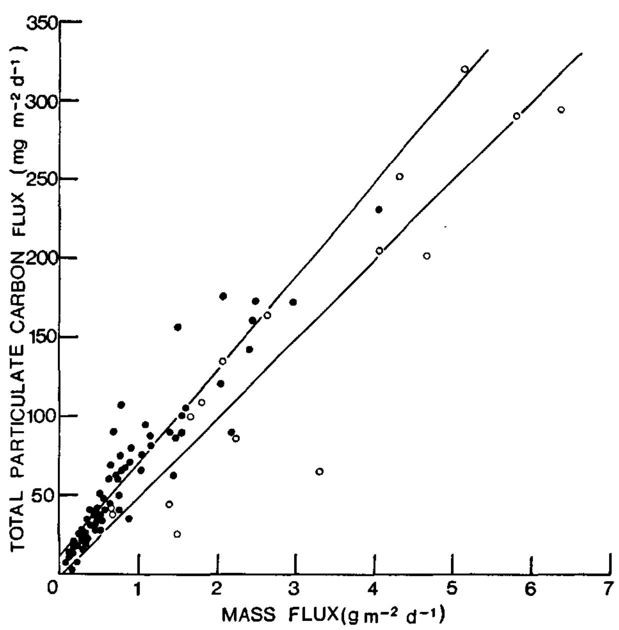

Figure 4

Relationship between total carbon flux (mg m^{-2} d^{-1}) and mass flux (g m^{-2} d^{-1}) through 100 and 150 m at a station off Monaco. Regression equations have been calculated for two separate periods of the year: March - October (•, Y = 58.78X + 11.11, r = 0.94, n = 68) and November - February (o, Y = 50.22X - 3.29, r = 0.92, n = 16).

flux through the 100 m horizon of 170 mg C m^{-2} d^{-1} during a 30-day period from mid-March to mid-April. His estimate was 1.8 times higher than the mean value we found for calm periods off Monaco during those months (Tab.). However, from Jacques' (1988) data we calculated that the organic carbon flux out of the euphotic zone accounted for approximately 37 % of the primary production within the euphotic zone at that time. This percentage agreed favorably with the 42 % we measured during March-April at our station. In addition, Minas *et al.* (1988) reviewed estimates of new production based on seasonal nutrient and oxygen data in the northwestern Mediterranean, and reported that these estimates, as percentages of total primary production, were relatively high in spring (typically between 25 and 50 %) but low by the end of summer. The yearly average was 25 % (our annual average was almost 24 %). The northwestern Mediterranean thus appeared to be similar to other coastal regions in which new and total production have been measured (Eppley and Peterson, 1979; Knauer *et al.*, 1984), and therefore should not be considered oligotrophic.

Particle flux with depth

During late 1982 and through most of 1983 and 1984, trap fluxes were determined at 50 and 250 m depths as well as at 100 or 150 m. Significantly, the 50 m traps did not record the large winter fluxes as prominently as the 100, 150 or 250 m traps (Fig. 5), suggesting that resuspension and subsurface lateral advection were important contributors to mass flux during periods of significant mixing of the water column. In winter, the particulate carbon flux generally followed the same pattern as the mass flux. When only the calm-weather data for the March-April periods in 1983 and 1984 were examined, mass fluxes at 100, 150 and 250 m were still larger than those at 50 m, but carbon fluxes at 50 m were greater on two out of four occasions than the 150 m C fluxes (not illustrated); thus, the enhanced upper-water phytoplankton production anticipated at this time of year began to show itself in the carbon fluxes, but was completely hidden in the mass fluxes which were

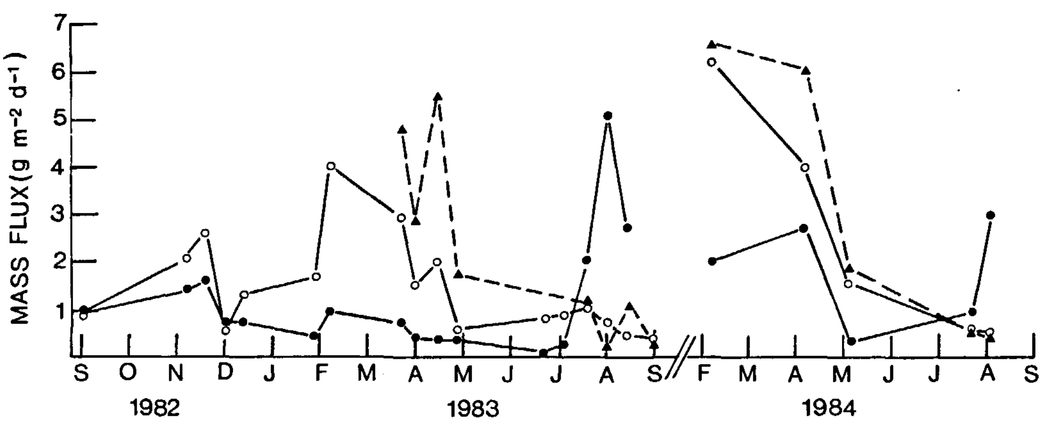

Figure 5

Temporal variation in particulate mass flux (g dry m^{-2} d^{-1}) through three depths at a station off Monaco (●-● 50 m, o-o 100 and 150 m, ▲-▲ 250 m). The 100 m data were collected through December 1982 ; 150 m data were collected thereafter.

composed of a greater proportion of inorganic material at this time. The high mean total carbon flux (C_T) at 100 or 150 m during March-April, and the presumed high particulate organic carbon flux at the same depth range for the same period (Tab.), undoubtedly had some contribution from particles sinking directly from surface waters; however, much of the 100 or 150 m flux could have been the result of high production of organic carbon elsewhere in the area rather than immediately over the trap mooring. A similar situation of increased mass flux with depth had been observed in the Lacaze-Duthiers canyon in the Golfe du Lion, and was attributed primarily to lateral advection of particles from the shelf region (Monaco *et al.*, 1987; Heussner *et al.*, 1987). If lateral advection was a major influence on the particulate carbon caught in traps, then our presumption of steady state for the calculation of new production would not hold, and our calculation of new production as a percentage of total production (see Tab.) would be suspect (at least for the winter and March/April periods). However, the basic agreement between our percentages and those of Jacques (1988) and Minas *et al.* (1988), calculated by independent methods, suggested that the net effect of lateral advection on the relationship between new and total production was minimal for this region.

The 50 m mass fluxes in late summer (mid-July and August) were the only mass fluxes greater than the corresponding deeper fluxes, in both 1983 and 1984 (Fig. 5). At this time of year the 50 m traps filled with fish fecal matter principally from the horse mackerel (*Trachurus trachurus*) and round sardinella (*Sardinella aurita*), two species common in near-surface waters at this time (Heussner *et al.*, 1987). Because the carbon and nitrogen contents of this fecal matter were so high, the total 50 m trap contents in late summer were as high as 35 % carbon and 6 % nitrogen, compared to winter percentages in the 50 m trap of about 5 %C and 0.3 %N, and spring percentages of approximately 12 %C and 2 %N. The particulate C/N weight ratios in the 50 m trap remained a rather consistent 5.7 ± 0.5 from early spring through fall; thus, although sinking fish fecal material greatly increased the fluxes of total mass, carbon and nitrogen in late summer at 50 m, it did not alter the C/N ratio of the 50 m trap material.

It is significant that the sinking fish fecal matter did not carry into the 100, 150 or 250 m traps. Inspection of the deeper trap contents revealed almost no fish feces at any time, and the percentages of carbon and nitrogen in this trapped material were approximately 6-8 % and 0.4-0.7 %, respectively (compared to 35 %C and 6 %N in the 50 m traps loaded with fish feces). The very gelatinous fish fecal material obviously was rapidly consumed or remineralized in the upper waters. A similar observation was noted from sediment trap studies during the summer in the Golfe du Lion, not far from our own sampling site (Heussner *et al.*, 1987). The mean spring-through-fall C/N weight ratio for our 100, 150 and 250 m trap material was 12.8 ± 4.6, over twice the mean ratio in the 50 m traps and with much greater variation about the mean. This suggested rapid remineralization of N in the particles sinking from 50 m to depth, in addition to the possibility of lateral advection of particles with variable C/N ratios into the deeper traps. In winter, the few C/N ratios available ranged between 15.2 and 45.9, with no apparent distinction among the different trap depths.

Fecal pellet carbon flux

From March to September 1983 and February to August 1984, fecal pellets were enumerated in the 50, 150 and 250 m traps. Numerical fecal pellet fluxes ranged from approximately 1 x 10^5 to 7 x 10^6 pellets m^{-2} d^{-1} and were generally lower at 50 m than at the two other depths. Numerical fluxes were converted to mass fluxes of fecal pellets after the method of Heussner *et al.* (1987)

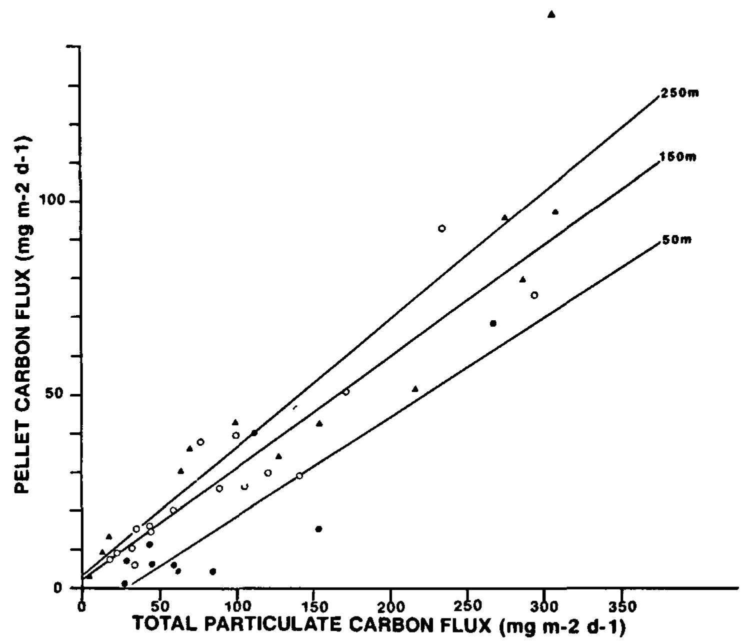

Figure 6

Relationship between fecal pellet carbon flux and total particulate carbon flux at three depths in the northwestern Mediterranean Sea (●-● 50 m, o-o 100 and 150 m, ▲▲ 250 m). Regression equations for each depth : 50 m, Y = 0.25X - 6.2, r = 0.88, n = 11; 150 m, Y = 0.29 + 1.9, r = 0.93, n = 17; 250 m, Y = 0.33X + 2.9, r = 0.92, n= 13.

assuming that the types and size distributions of pellets they determined during September 1983 were similar to those in the same general region off Monaco. Consequently, the mean pellet dry weights derived from this comparison were 0.068, 0.079 and 0.090 µg pellet^{-1} at 50, 150 and 250 m, respectively. We then used the measured mean carbon value (27.4 ± 7.1 %) of 13 fecal pellet samples from our 100 m traps to convert to fecal pellet carbon content; *viz.*, 0.019, 0.022 and 0.025 µg C pellet^{-1} at the same depths. Computed carbon fluxes due to small fecal pellets were well correlated with total particulate carbon fluxes at the 50, 150 and 250 m trap depths (Fig. 6). The 50 m trap on average yielded the smallest amount of pellet carbon per unit of carbon flux, and the 150 and 250 m traps yielded the most. Furthermore, all but one of the highest pellet fluxes (those pellet carbon fluxes associated with total particulate carbon fluxes greater than 200 mg m^{-2} d^{-1}) were either from the 150 or 250 m trap depths (Fig. 6).

Unfortunately we had no distributional data on zooplankton populations in the near vicinity of our traps; however, other studies (Jacques *et al.*, 1973; Razouls and Thiriot, 1973; Nival *et al.*, 1975; Franqueville, 1975) have shown that zooplankton populations in the northwestern Mediterranean are not skewed toward large numbers at mid-depths and smaller numbers near the surface, either when averaged over a 24-hour day or when only the night-time distributions are considered. Thus, we suggest that the greater pellet carbon fluxes at 150 and 250 m did not result from greater numbers of zooplankton voiding fecal pellets at depth. It is more likely that the mesozooplankton community was fairly evenly distributed in the upper 200 m and that the lower traps integrated sinking pellets over a greater depth range than the trap at 50 m which only caught pellets released by organisms living above it. Heussner *et al.* (1987; 1988) came to the same conclusions at their sites in the northwestern Mediterranean. Alternatively, some fecal pellets might have been advected laterally into the site at depth during periods of higher mass flux, as suggested earlier.

Because the 95 % confidence intervals about the mean pellet carbon fluxes bracketed the origin for all three depths (not shown in Figure 6 for clarity), we assumed all Y-intercept values were zero and ignored them. The average fecal C fluxes thus were estimated at 25, 29 and 33 % of total particulate C fluxes through 50, 150 and 250 m, respectively. However, given the number of assumptions made in this approach, and the fact that pellets from deeper traps may contain less carbon than we measured in those from 100 m, the small differences between these percentages with depth are probably not significant. Nevertheless, we conclude that fecal carbon deposition by zooplankton is a primary contributor to total particulate carbon flux in the northwestern Mediterranean. The significant role of fecal pellets in the vertical flux of various chlorinated and petroleum hydrocarbon compounds has also been observed in this region (Fowler *et al.*, 1979; Burns and Villeneuve, 1983; Burns *et al.*, 1985). Moreover, our data support the model predictions of Andersen and Nival (1988 *b*) that fecal pellets of small-particle feeders in the northwestern Mediterranean account for a large fraction of the particulate organic material sedimenting through 200 m. Although Andersen and Nival (1988 *b*) suggested that salps are far more important contributors to the particle flux than copepods, it is perhaps noteworthy that only very few, intact salp fecal pellets (recognizable as rectangular flakes or ribbons) were observed in our trap samples, and that the majority of the recognizable fecal pellets collected were either cylindrical or ellipsoidal in shape; *i.e.* similar to those commonly produced by copepods.

CONCLUSIONS

It is evident from our long-term sediment trap study that particle flux is highly variable, even in the short term, in the upper layers of coastal northwest Mediterranean waters. Mass and carbon flux maxima generally coincided with maximum phytoplankton production and zooplankton grazing activity in this region of the Mediterranean. Particle flux minima were noted primarily in late summer and were up to an order of magnitude lower than those occurring during winter and spring.

Total particulate carbon flux also exhibited strong seasonal variations and was linearly related to mass flux. It was estimated that organic carbon flux represented roughly 5 % of the mass flux through 100 and 150 m in calm seas. By comparing organic carbon fluxes with primary production measurements made previously at the same site, it was found that carbon export out of the euphotic zone averaged 24 % (range 17 to 42 %) of primary production on an annual basis. Such relatively high new production values are more typical of coastal eutrophic waters than an oligotrophic system, a term often used to characterize the Mediterranean. Moreover, a relatively high fraction (≈ 30 %) of total carbon flux through 50, 150 and 250 m was carried by zooplankton fecal pellets, suggesting that fecal pellets are a primary contributor to the downward particulate carbon flux in these coastal waters.

Acknowledgements

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