Diel variations of marine snow concentration in surface waters and implications for particle flux in the sea

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Abstract

Successive measurements of the size distribution and abundance of marine snow in the upper 100 m of the Santa Barbara Channel, California, with an in situ still camera system following 11 tagged water masses revealed a consistent pattern of nighttime decreases in the abundance of large particles. A net nocturnal reduction in particulate flux from the upper 100 m as calculated from camera profiles occurred in 75% of the day–night comparisons, and nighttime aggregate carbon losses resulted in a 38% average reduction in camera-derived aggregate flux. Intensive investigation of three stations for 24–48 h each indicated that nighttime decreases in aggregate concentrations and derived aggregate flux could be registered throughout the observed water column. Nocturnal decreases in marine snow concentration are unlikely to result from diel variations in the production of marine snow either as feeding webs of zooplankton or through variations in aggregation rates of smaller particles. Moreover, measured diel variations in the intensity of surface mixing and convective overturn during one of the 24 h deployments were not intense enough to produce aggregate fragmentation and reduced aggregate flux. Nighttime increases in large crustacean zooplankton (i.e., euphausiids and the large copepod *Calanus pacificus*) could explain some or all of the reduction in aggregate abundance at most stations. Fragmentation and consumption of marine snow by migrating macrozooplankton could produce our observed synchronous diel cycles in marine snow concentration. This is the first empirical evidence of a diel pattern in the concentration and calculated particulate flux of large sinking particles in near-surface waters. The data presented here are consistent with the only other existing diel study, which also reported decreases in marine snow abundance at night at 270 m depths in the oceanic north Atlantic. Diel variations in the sizes and concentrations of

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marine snow may impact water column processes dependent upon particle availability and size, such as grazing and remineralization, and may generate a diel cycle of food availability to the benthos.

1. Introduction

The sinking of large amorphous aggregates, known as marine snow (Suzuki and Kato, 1953), largely mediates the transfer of organic matter from the sea surface to the sea floor (Fowler and Knauer, 1986). Therefore, considerable interest exists in processes that control the creation and fate of marine snow (e.g., Alldredge and Gotschalk, 1989; Riebesell, 1992; Passow and Wassmann, 1994; Tiselius and Kuylenstierna, 1996). Because many of these processes, including zooplankton feeding-web production, diatom bloom aggregation, and consumption of aggregates by vertically migrating zooplankton are biological in nature, we might expect marine snow abundances to vary on biologically relevant time-scales including scales less than one day (e.g., diel periods). However, current sediment trapping technologies are limited in their ability to accurately resolve variability in particulate flux on scales less than a few days (Knauer and Asper, 1989; Honjo, 1996). Possible higher frequency variations in the particle flux (time scales of less than a day and space scales of tens of meters) have gone largely undetected as 'noise' generated by non-uniform particle distributions.

A number of recent investigations using a variety of underwater video and still cameras have measured marine snow distributions at time and space scales smaller than those resolved by traditional sediment trapping techniques. These studies have identified a variety of small-scale patterns in the distribution of marine snow in both space (Gardner and Walsh, 1990; Asper et al., 1992; MacIntyre et al., 1995) and time (Lampitt et al., 1993a), suggesting that higher frequency variations in the particle flux previously treated as 'noise' may be ecologically significant and important to the production and fate of sedimenting particulate matter in the sea.

Lampitt et al. (1993a) presented the first evidence of a diel signal in marine snow abundance from a station 270 m deep in the mesotrophic north Atlantic Ocean. With no additional empirical data on the vertical distribution of this signal, Ruiz (1996) proposed that such a diel signal probably originated in the surface layer and was translated to depth through uniform aggregate sinking. Moreover, Ruiz (1997) used a simulation model to argue that surface origination of the diel flux signal was related to physical processes associated with coagulation theory, not to biological factors such as grazing by nocturnal migrators as originally proposed by Lampitt et al. (1993a). Ruiz's hypothesis is partially supported by Gardner et al. (1995), who attributed diel changes in sea surface beam attenuation, in part, to conservative losses of particles out of the mixed layer during nightly mixed layer deepening.

Prior to the present study, the only observational data of diel fluctuations in marine snow have been the observations of Lampitt et al. (1993a) in the meso-pelagic zone. Speculation of similar variations in the surface ocean (Ruiz, 1996, 1997) lacks supporting verification in nature. In the following study, conducted in the Santa Barbara Channel, California, we investigated diel changes in marine snow distribution in ocean surface waters for the first time. The aims of this study were two-fold: first, to characterize the extent and magnitude of temporal variations in marine snow abundance and calculated particle flux on scales of hours within and below the mixed layer, and second, to relate these variations to potential proximal causes.

2. Materials and methods

2.1. Field sampling strategy

Temporal variation in the vertical distributions of marine snow and concomitant hydrographic parameters were determined for the upper 80–150 m of the water column during 11 drifter deployments in the Santa Barbara Channel, California. These deployments ranged from 12 h (dusk-to-dawn) to 24 or 48 h (diel), and they consisted of multiple casts taken over time within 50–400 m of the drifter. All stations were located at $34°10'$ to $34°20'$N and $119°40'$ to $120°30'$W, near or over the Santa Barbara Basin (Fig. 1). The drogue was set at 10 m, and temperature-salinity (T–S) relationships over the course of each deployment matched very closely. We assume, therefore, that the drogue accurately tracked surface water movement and that sampling occurred in the same parcel of water over each deployment period.

Two types of sampling were conducted for this study. For three of the 11 drifter deployments (28–29 April 1991, 16–17 June 1996, and 4–6 April 1997), 24–48 h long time-series of repeated casts were made at approximately 4–6 h intervals. The other 8 drifter deployments (three on June 28–July 2, 1993, and five on September 21–26, 1993) were sampled only twice: once at dusk (usually 1–2 h prior to sunset) and again after dawn (usually 1 h after sunrise). These dusk–dawn comparisons were made to determine net changes in marine snow distribution and abundance overnight so as to verify generalities revealed by the three higher-resolution diel studies.

2.2. Marine snow abundance, size and vertical distribution

Vertical profiles of the abundance and size distribution of marine snow were obtained by photographing undisturbed particles in a collimated slab of light. The system, described in detail in MacIntyre et al. (1995), consists of a Photosea 5000 35-mm still camera synchronized with a Photosea 1500S strobe (150 W s^{-1}). An integrated Seabird SBE 19 CTD and Seatech fluorometer sampled hydrographic parameters and chlorophyll a fluorescence during these aggregate profiles. The instrument
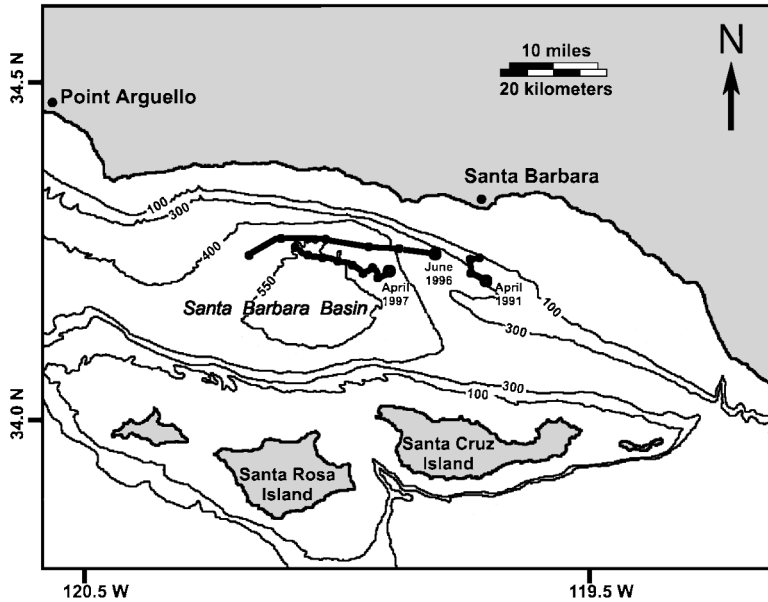
Fig. 1. Map of the study region in the Santa Barbara Channel, southern California Bight. Drifter tracks are shown for the 24–48 h studies of April 1991, June 1996 and April 1997. The large circle of each track indicates location of deployment.

package was lowered and raised continuously at 5 m min^{-1} yielding 250–300 photographs per profile with depth accuracy of $\pm$ 0.1 m and no overlap of imaged fields. In 1991 and 1993 a field $10.5 \times 14.7 \times 5$ cm in size (0.78 l per frame) was illuminated, in 1996 and 1997 a field $35 \times 25 \times 5$ cm (4.4 l) was illuminated. Both frame sizes yield particle resolution well below the size of marine snow.

Images were recorded on T-max 400 ASA black and white film (800 exposure rolls). All aggregates > 0.5 mm diameter (or 0.065 mm^3 equivalent spherical volume (ESV), i.e., 'marine snow' sized particles) contained in the central 70–75% portion of each image were counted and sized using computerized image analysis as described in MacIntyre et al. (1995). Aggregate concentration (number l^{-1}), average volume of individual aggregates (mm^3), and total aggregate volume (mm^3 l^{-1}) were determined for each frame. Oblique net tows (333 μm mesh) from 75 m to the surface during both night and day indicated that zooplankton in the marine snow size range constituted considerably less than 1% of the particles in each frame.

Vertical profiles of aggregate abundance, mean volume and cumulative volume were constructed for each cast. Profile construction was a three-step process. First, individual frames were combined into 1-m depth bins. Then, data gaps (likely due to pitch and roll of the ship during profiling) were filled by linear interpolation between nearest points. Finally, a 5-m running average was applied to the profile in order to smooth out very high frequency variability.

2.3. Conversion of size to mass and calculation of mass flux

The mass content of aggregates as a function of size was made using the conversion equation from Alldredge (1998):

$$M = 3.33V^{0.54}, \tag{1}$$

where M is the mass of an individual aggregate in μg and V is the equivalent spherical volume (ESV) of the aggregate in mm^3. Carbon content of aggregates was also calculated for later estimation of the impact of grazing on marine snow abundance using the conversion equation of Alldredge (1998):

$$C = 0.99V^{0.52}, \tag{2}$$

where C is the carbon content of an individual aggregate in μg. These conversions are based on the sizes and weights of hundreds of aggregates photographed and collected in situ in the Santa Barbara Channel over a 3-year period.

A profile of estimated mass flux was constructed for each aggregate profile using individual aggregate mass (obtained as described above) and size-specific sinking rates, calculated from the volume to sinking rate relationship in Alldredge and Gotschalk (1988). Mass flux was modeled for each profile by applying the mass conversion and sinking rate to individual aggregates > 0.065 mm^3 ESV within each analyzed image, after which mass accumulation in each frame was calculated. Further profile processing (i.e., binning, filling and smoothing) was as described earlier for aggregate profiling. The resulting profile of mass flux (what we term 'instantaneous flux') has units of mg m^{-2} d^{-1}.

2.4. Zooplankton abundance

Prior experience led us to recognize euphausiids, primarily the common pacific krill, *Euphausia pacifica*, and the copepod, *Calanus pacificus*, as the dominant vertical migrating zooplankters capable of consuming, or otherwise impacting, the abundance of marine snow in California waters (Dilling, 1997; Dilling et al., 1998). Therefore, the abundance of these vertically migrating species was measured in surface waters during the drifter deployments with a 333 μm mesh plankton net with a 1 m opening. The net containing a General Oceanics Model 2030 flow meter was towed obliquely to 75 m at a forward velocity of 1 m s^{-1} while being raised and lowered at 0.17 m s^{-1}. Zooplankton were preserved in 70% ethanol and animals enumerated using a dissecting microscope. In the April 1991 series, discrete depth tows at 20 m intervals from the surface to 80 m were made at 1200 and 2400 h (PST). The discrete samples were subsequently averaged over the entire 80 m. In the June 1996 and April 1997 series, oblique tows were made between the surface and 80 m. Tows were conducted at 1200 and 2300 h (PST) in 1996 and at 1430 and 2200 h (PST) in 1997.

2.5. Meteorological data

Wind data corresponding to the April 1991 series were taken from the shore meteorological station PTGC-1 at Pt. Arguello, CA. For the June 1996 and April 1997

series, we used the National Data Buoy Center meteorological buoy #46053 in the Santa Barbara Channel. All wind data presented here are hourly averages.

2.6. Temperature-gradient microstructure profiling

Measurements of the rate of turbulent kinetic energy dissipation were made over several days during the June 1996 study to determine variations in turbulence over diel time scales. Temperature, temperature gradients, conductivity, and pressure were measured at a frequency of 100 Hz using temperature-gradient microstructure profilers (Self-Contained Autonomous Microstructure Profiler or SCAMP, Precision Measurement Engineering) deployed from a Zodiac several hundred meters from the ship during the June 1996 diel study. The instruments are based on a modification of the design of Carter and Imberger (1986). Deployed in either rising or falling mode, they move at a speed of approximately 0.1 m s^{-1}; with a 100 Hz sampling rate their spatial resolution is 1 mm. Data are transmitted up an umbilical to a laptop computer. The sensors included two fast-response thermistors (FP07, time constant $\sim$ 10 ms) separated by about 1 mm with one paired with a micro-conductivity electrode (time constant $\sim$ 4 ms), which failed. A slower but more stable thermistor-conductivity sensor pair was located about 3 cm below the fast response sensors. Further details are in MacIntyre et al. (1999). Data from the fast response sensors were sharpened and smoothed digitally (Fozdar et al., 1985) before density and rates of energy dissipation were computed. The instrument was calibrated before and after sampling. Rates of turbulent kinetic energy dissipation, ε, were computed by a least-squares fit of the power spectral densities of the temperature-gradient signal to the Batchelor spectrum (Dillon and Caldwell, 1980; Imberger and Ivey, 1991). If spectra do not fit the theoretical Batchelor spectrum, the fluid is not turbulent; results were discarded for depth intervals where there was no fit. Power spectral densities were calculated in depth intervals known as segments in which the turbulence was determined to be statistically stationary using the procedure in Imberger and Ivey (1991) combined with an interactive step that relies on the fact that the distance function essentially separates depth intervals with different frequencies of fluctuations in the temperature-gradient signal (MacIntyre et al., 1999).

Because turbulence occurs intermittently, and because samples of ε are often lognormally distributed, we computed the maximum likelihood estimator X_{mle} for ε (Baker and Gibson, 1987). The arithmetic mean and sample variance of $\ln(\varepsilon)$ were obtained using 100 bootstrap samples. The bootstrap procedure is used to determine the statistics of a population whose underlying distribution is unknown (Dixon, 1993). We computed X_{mle} separately for profiles taken at night and in the day.

3. Results

3.1. April 28–29, 1991, 24-h diel study

Relatively weak surface currents in the Santa Barbara Channel caused the drifter to move northwestward at about 0.06 m s^{-1}, covering less than 5 km over the April 1991
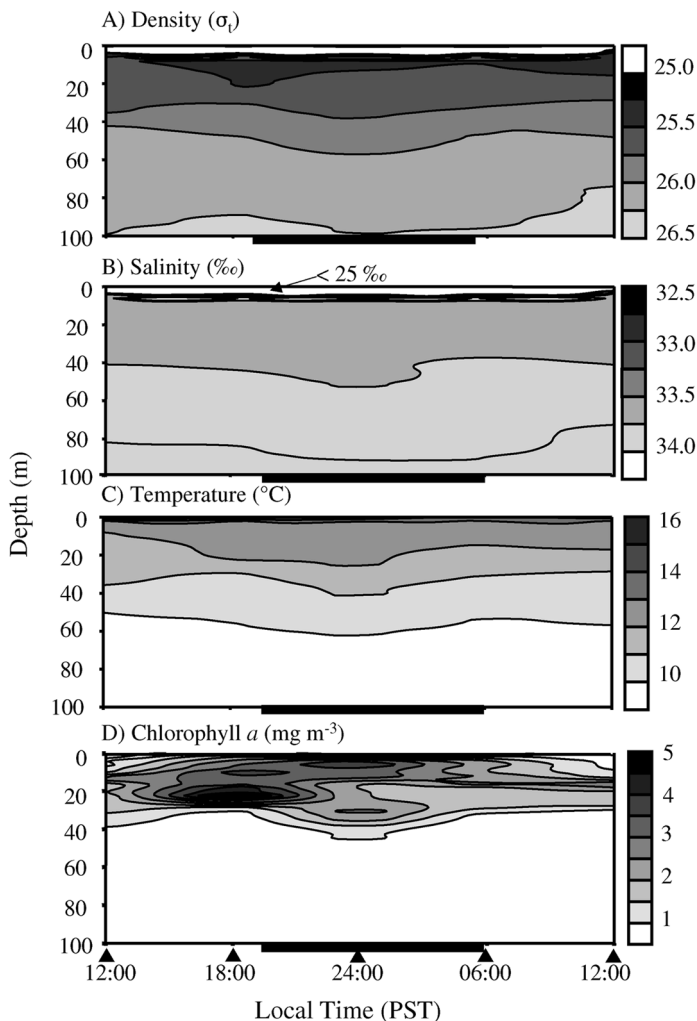
Fig. 2. Time–depth contours of physical and biological properties of the upper 100 m on 28–29 April, 1991. (a) density, (b) salinity and (c) temperature, and (d) chlorophyll *a* concentration at the drifter. Solid bar on time axis indicates nighttime and (▲) indicates where a profile was made.

study. The drifter remained over relatively shallow waters (less than 375 m) on the steep northeastern slope of the Santa Barbara Basin (Fig. 1). A thin (< 10 m) lens of lower salinity water was responsible for strong stratification in the extreme upper water column (Fig. 2a). Below the pycnocline, a semi-diurnal tidal component is apparent in all hydrographic contour plots (Fig. 2a–d). Winds remained relatively constant during both day and night at 8–10 m s^{-1} with only a slight rise at dawn (Fig. 3a).
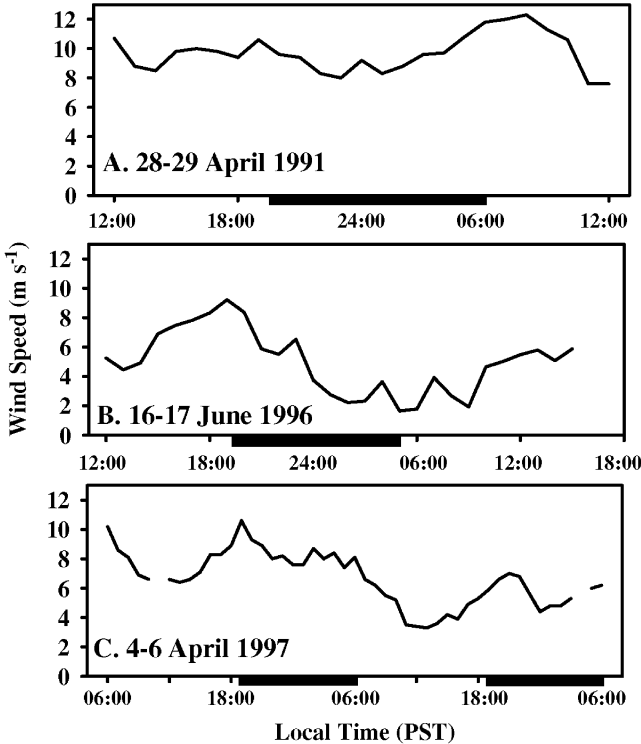
Fig. 3. Hourly averaged wind speeds from the Santa Barbara Channel: (a) 28–29 April 1991; data from National Data Buoy Center meteorological buoy at Pt. Arguello, California; (b) 16–17 June 1996 and (c) 4–6 April 1997; data from NDBC buoy in the east Santa Barbara Channel. Solid bar on time axis indicates nighttime.

A chlorophyll maximum, as indicated by a fluorescence peak, occurred at about 20–25 m with highest concentrations just prior to sunset (Fig. 2d). The location of this particular maximum coincided with a region of isopycnal 'squeezing' between the deepening surface layer (response to winds) and the shoaling deep layer (response to tides). By midnight, the single 'core' of chlorophyll was replaced with two discrete, albeit lesser-concentrated, maxima: one at < 10 m and the other at about 30 m (Fig. 2d). The shallow core tracked the shoaling pycnocline while the deeper core tracked the tide. After midnight, the fluorescence signal weakened and remained low until the study was terminated.

Marine snow was mostly concentrated, both volumetrically (Fig. 4a) and numerically (Fig. 4c), at depths shallower than 40 m during the April 1991 24-h study. Sixty percent of the total aggregate volume and 52% of the numerical distribution was above the pycnocline. We performed a Kruskal–Wallis ANOVA on both ranks of average volume and of numerical concentration for aggregates above the pycnocline (i.e., shallower than 20 m). Between-profile variance of both average volume and
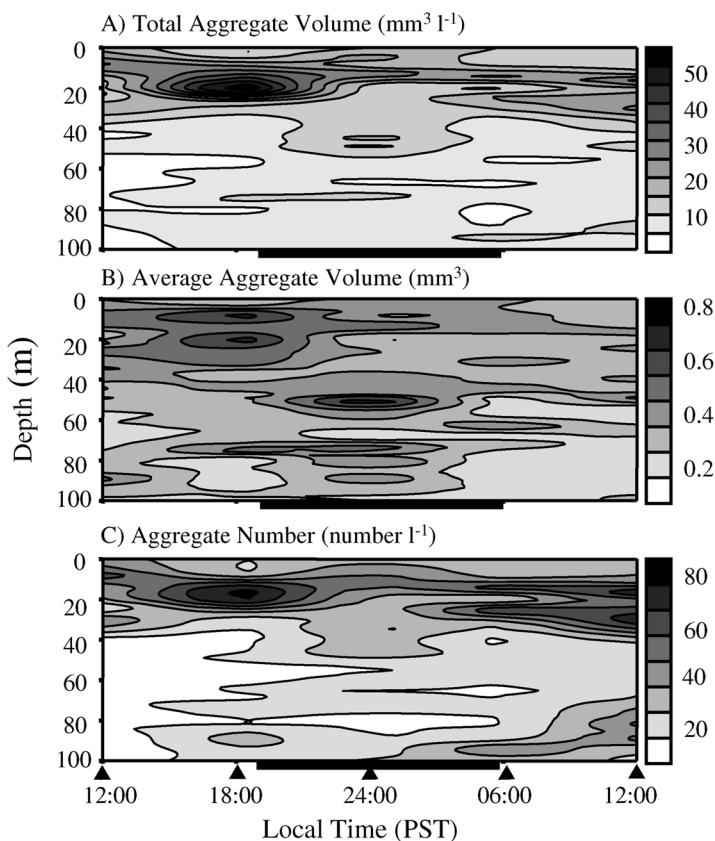
Fig. 4. Time–depth contours of the attributes of aggregates > 0.065 mm^3 equivalent spherical volume, ESV, in the upper 100 m during the 28–29 April 1991, 24 h study. (a) Total aggregate volume concentration (mm^3 l^{-1}); (b) average volume per aggregate (mm^3); (c) aggregate numerical concentration (number of aggregates l^{-1}). Solid bar on time axis indicates nighttime and (▲) indicates where a profile was made.

numerical concentration was significantly different from respective within-profile variance over the 24 h study (df $= 4$; $P < 0.05$). Largest aggregates (0.183 mm^{-3} median volume) occurred during the midday and decreased in volume (0.159 mm^{-3}) overnight and into the morning. Aggregates were numerically more abundant (79.4 aggregates l^{-1}) prior to sunset with a 38% nighttime decrease to 48.9 aggregates l^{-1}. Aggregate concentrations decreased further to 38.4 aggregates l^{-1} by the following morning profile. Thus, over the entire observed water column, this study showed a distinct decrease in size and concentration of aggregates at night as compared to the daytime values.

Vertical migration into surface waters was apparent during these studies (Fig. 5). Copepods, *C. pacificus*, and euphausiids (principally *Euphausia pacifica*) were more abundant in the upper 80 m water column at night than during the day. *Calanus*
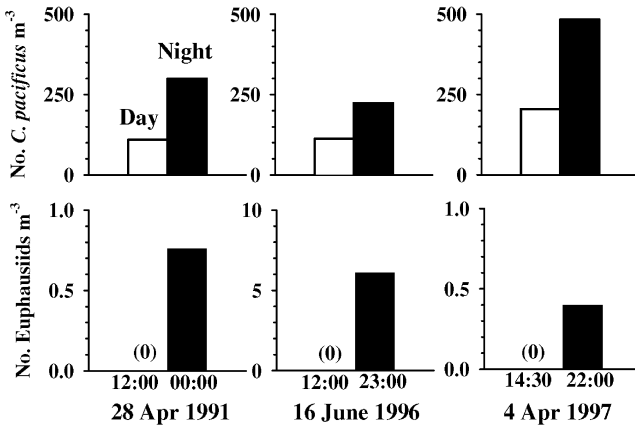
Fig. 5. Depth-averaged concentrations, from the surface to 80 m, of the dominant marine snow-consuming macrozooplankton during the three 24–48 h drifter studies: the copepod, *Calanus pacificus*, and euphausiids, primarily *Euphausia pacifica*. Open bars are daytime concentrations, solid bars are nighttime concentrations. Local time of collection is given; no adult euphausiids were collected during the daytime.

pacificus increased to about 300 animals m^{-3} at night from a daytime density of about 100 animals m^{-3}. Euphausiids were absent from the upper 80 m during the day, but present at densities of 0.75 animals m^{-3} at night.

3.2. June 17–18, 1996, 30-h diel study

Over the 30 h, 1996 deployment, prevailing westward surface currents carried the drifter rapidly along the northern portion of the Santa Barbara Basin and over water deeper than the previous 24 h deployment in April, 1991 (Fig. 1). Based on the $T-S$ characteristics of successive CTD casts (data not shown), the drifter remained within a single water mass up to the final cast. Data from the final cast indicates that the drifter encroached upon a region of mixing between westward flowing channel water and the southeastward flowing California Current jet. However, changes in salinity structure were subtle, no sharp fronts were encountered, and we do not believe that aggregate profiles were substantially influenced by this subtle shift at the end of the study.

The observed upper water column was highly stratified by temperature and had a poorly defined, shallow mixed layer over the duration of the study (Fig. 6a–c) as determined by CTD profiles. A chlorophyll maximum was observed at the base of this shallow pycnocline around 8 m with maximum concentration occurring just prior to sunset (Fig. 6d). In contrast to the 1991 deployment, local surface winds showed a diel pattern during the June 1996 study (Fig. 3b). Winds increased through the daylight hours of June 16, peaked at 9 m s^{-1} just prior to sunset and diminished through the night. Winds remained light during the early morning hours of 17 June, but increased in strength by late morning and early afternoon.
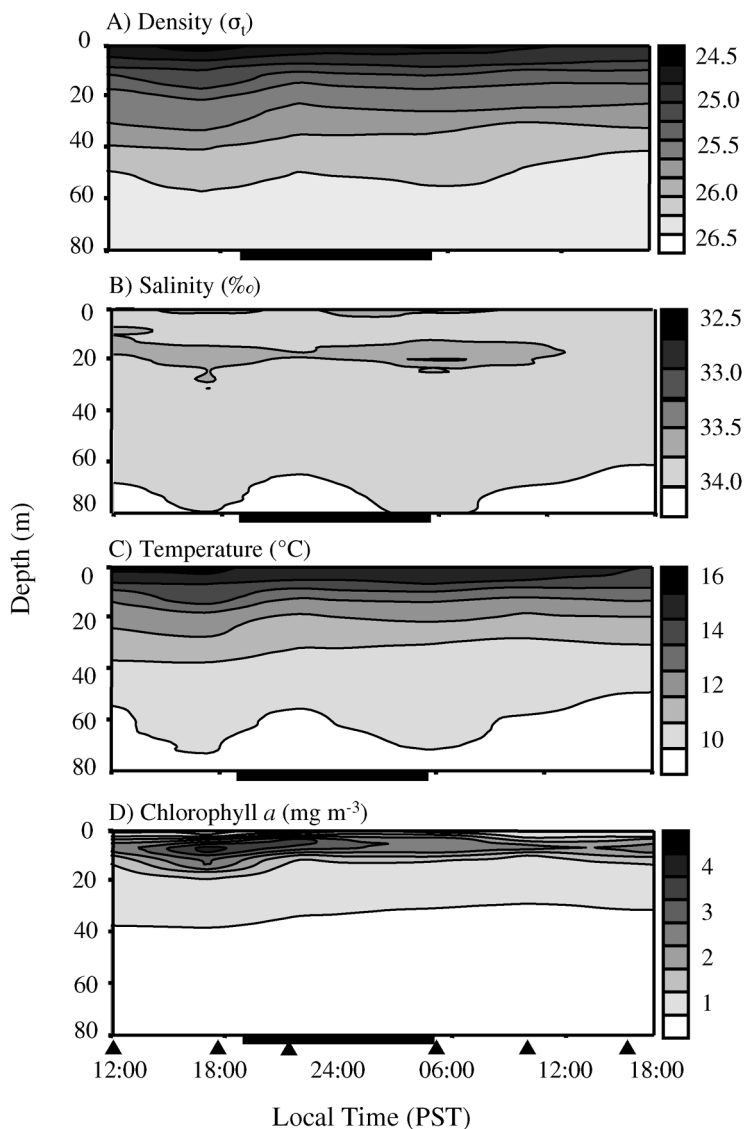
Fig. 6. Time–depth contours of physical and biological properties of the upper 80 m on 16–17 June 1996. (a) density, (b) salinity and (c) temperature; and (d) chlorophyll a concentration at the drifter. Solid bar on time axis indicates nighttime and (▲) indicates where a profile was made.

Data from the microstructure profiler shows the thermal stratification and the intensity and intermittency of turbulence in the upper 60 m. Fig. 7a is a profile with features typical of our sampling period in mid-June. The upper mixed layer tended to be 5 m deep or less, and profiles from early morning indicated minimal deepening at
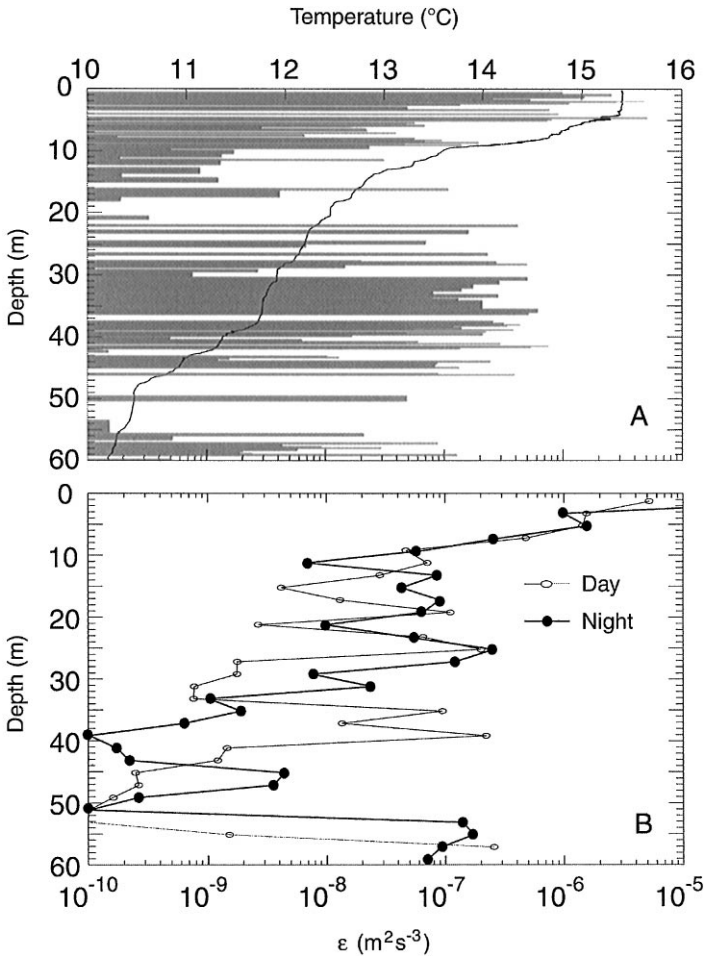
Fig. 7. Upper water column turbulence in the Santa Barbara Channel mid-June 1996. (a) Vertical profiles of temperature (solid line) and energy dissipation rate ε (shaded histogram) from 2245 h 15 June 1996. (b) Maximum likelihood estimator X_{mle} of ε in 2 m bins at night ($\bullet$) and in the day ($\circ$) for profiles taken on 16 and 17 June. Since most microstructure casts extended to only 20 m depth, and only 3 profiles in the day and 1 at night extended to 60 m, the robustness of the estimator varies with depth. In the upper 20 m, 120–224 values of ε were used to obtain X_{mle} in each 2 m bin; between 20 and 30 m, 26–116 values were used; between 30 and 40 m, 22–73 values were used, and below 40 m, 3–25 values were used.

night. (Differences between microstructure data and the Seabird CTD data are due to the much lower resolution of the CTD.) Consequently, turbulence due to heat loss would not have caused enhanced energy dissipation rates at night. Below the shallow upper mixed layer was a region of strong thermal stratification with temperature inversions suggestive of overturning eddies. Turbulence in this region was most likely induced by shear. Rates of energy dissipation were elevated in the shallow mixed layer ($\varepsilon = 10^{-6} \, \text{m}^2 \, \text{s}^{-3}$) and within some of the thermal inversions.

The upper 60 m was thermally stratified. Inversions often occurred where temperature gradients were strongest. For instance, 10 cm inversions were common between 4 and 10 m in the profile in Fig. 7a. A 1 m scale inversion occurred at 5 m depth. Throughout the upper 60 m, regions of strong thermal stratification were separated by regions with weaker stratification. Step-like structure such as we observed is typical of waters in which the thermal structure has been strained due to interactions of internal waves. The upper water column was intermittently turbulent, with some of the turbulence associated with the temperature inversions (e.g., the water column is turbulent within the inversion at 5 m depth (Fig. 7a), some with regions of high temperature gradient, and some with the layers with weaker temperature gradients. The step-like thermal structure and intermittent turbulence were found in all microstructure profiles taken during this study and in the days preceding it.

Rates of energy dissipation did not indicate a day–night difference in the intensity of turbulence in the upper 40 m (Fig. 7b). Maximum likelihood estimates X_{mle} of ε exceeded 10^{-6} m^2 s^{-3} near the surface, and decreased to 10^{-7} m^2 s^{-3} by 10 m depth. The large variations in ε reflect the intermittency of the turbulence made especially pronounced below 40 m due to undersampling. Such large excursions are not apparent when profiles are averaged from 14 to 17 June, 1996. Below 10 m, X_{mle} of $\varepsilon = 10^{-7}$ m^2 s^{-3} during both day and night, indicating that through much of the water column, aggregates are exposed to moderate to low strain, which depends upon ε.

Marine snow-sized particles were less abundant by about an order of magnitude in the June 1996 study (Fig. 8a and c) than in the April 1991 and 1997 studies. Analysis of variance on ranks (Kruskal–Wallis one-way ANOVA) of average aggregate volume did not show significant size changes over the 24 h study. However, ANOVA on ranks of numerical concentration did reveal a significant change in marine snow concentration (df = 5; $P < 0.001$). Pairwise analyses (Dunn's Test) of aggregate profiles showed that midday values of numerical aggregate concentration were always significantly greater than dusk, nighttime and morning values.

Zooplankton abundance increased dramatically in the upper 100 m at night (Fig. 5). Euphausiids, principally *Euphausia pacifica*, were absent from the upper 100 m during the day and increased to about 6 animals m^{-3} at night. In addition, the dominant copepod *Calanus pacificus* increased from about 100 animal m^{-3} during the day to 200 animal m^{-3} at night.

3.3. April 4–6, 1997, 48-h diel study

Drifter motion was toward the west at an average velocity of 0.11 m s^{-1}. This track caused the drifter to remain over the steep northern flank of the Santa Barbara Basin during most of this 48 h study (Fig. 1). The water column was thermally stratified over the upper 80 m with uniform temperature between 80 and 150 m (Fig. 9a and c). A strong thermocline between 17 and 22 m is apparent in Fig. 9c. Wind speed was higher during the first 24 h segment than in the second 24 h (Fig. 3). Diel variations in wind strength occurred in this study as wind speed increased through late afternoon to a pre-dusk maximum followed by nighttime subsidence during both 24 h segments.
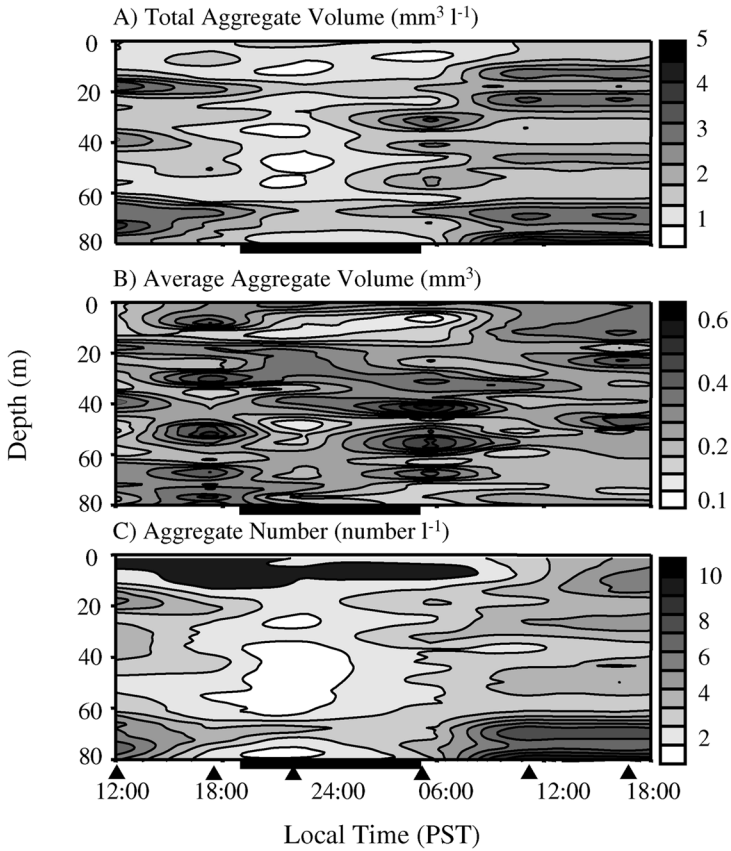
Fig. 8. Time–depth contours of the attributes of aggregates $> 0.065 \, \text{mm}^3$ equivalent spherical volume, ESV, in the upper 100 m during the 16–17 June, 1996, 30 h study. (a) Total aggregate volume concentration $(\text{mm}^3 \, \text{l}^{-1})$; (b) average volume per aggregate (mm^3); (c) aggregate numerical concentration (number of aggregates l^{-1}). Solid bar on time axis indicates nighttime and (▲) indicates where a profile was made.

Maximum chlorophyll *a* fluorescence was about an order of magnitude lower in April 1997 than in either April 1991 or June 1996 (Fig. 9d). Chlorophyll maxima occurred during the nighttime with greatest concentration during the second night, possibly suggesting that we were sampling the initial stages of a phytoplankton bloom. In addition to the strong diel surface chlorophyll variation, there was also a second nighttime chlorophyll maximum below 120 m.

Numerical and volumetric concentrations of marine snow were similar in magnitude to those observed in April 1991, but were an order of magnitude greater than in June 1996 (Fig. 10a and c). There was a striking nighttime reduction of marine snow-sized particles. Note that absence of particles during the daytime of April 5 is due to camera failure below 70 m. Analysis of variance on ranks (Kruskal–Wallis one-way ANOVA) for both numerical concentration and average aggregate volume
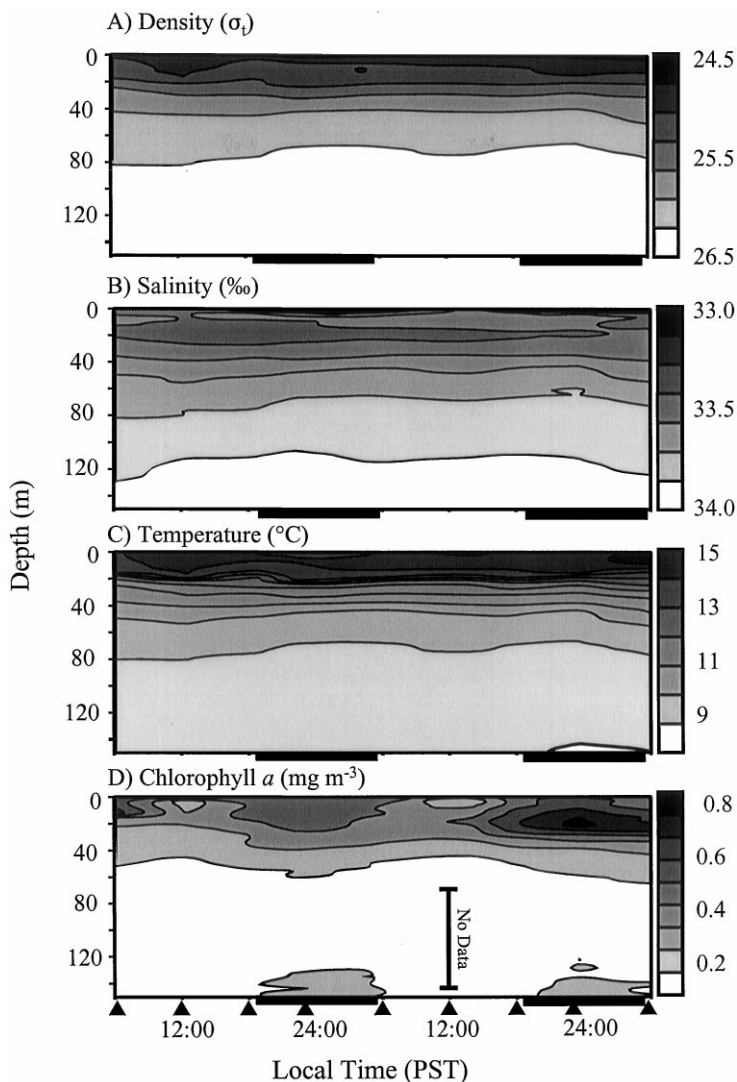
Fig. 9. Time–depth contours of physical and biological properties of the upper 150-m on 4–6 April 1997. (a) density, (b) salinity and (c) temperature; and (d) chlorophyll *a* concentration at the drifter. Solid bars on time axis indicate nighttime and (▲) indicates where a profile was made.

was performed for the two 24 h cycles on April 4–6. For both measures, between-profile variance exceeds the within-profile variance indicating significant changes in these properties over the study. Median aggregate concentration (number l^{-1}) decreased overnight by more than one order of magnitude during both 24 h cycles. Average aggregate volume was significantly larger at midday during both cycles but only by a factor of 0.5–1.5 (Dunn's Test; $P < 0.05$).
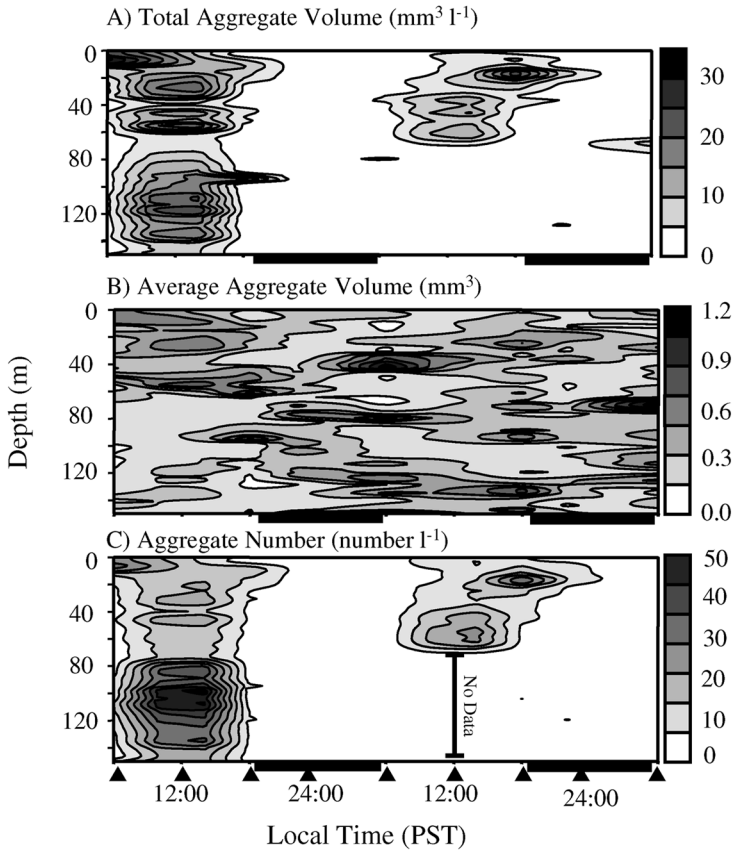
Fig. 10. Time–depth contours of the attributes of aggregates $> 0.065 \text{ mm}^3$ equivalent spherical volume, ESV, in the upper 150 m during the 4–6 April 1997, 48 h study. (a) Total aggregate volume concentration $(\text{mm}^3 \, \text{l}^{-1})$; (b) average volume per aggregate (mm^3); (c) aggregate numerical concentration (number of aggregates l^{-1}). Solid bars on time axis indicate nighttime and (▲) indicates where a profile was made.

Diel changes in zooplankton abundance were observed during the April 1997 study (Fig. 5). Average abundance of the copepod *Calanus pacificus* between the surface and 100 m showed a $> 2 \times$ increase in concentration at night from 200 animals m^{-3} during the day to 465 animals m^{-3} during the night. Euphausiids averaged 0.4 animals m^{-3} at night and were absent during the day.

3.4. Variations in camera-derived flux

Camera-derived fluxes using the aggregate characteristics determined above are presented in Fig. 11. These data are presented as 25th, 50th (median) and 75th percentiles for three 10-m intervals representing shallow (5–15 m), intermediate (40–50 m) and deep (65–75 m) depth strata. Derived flux in June 1997 was about an
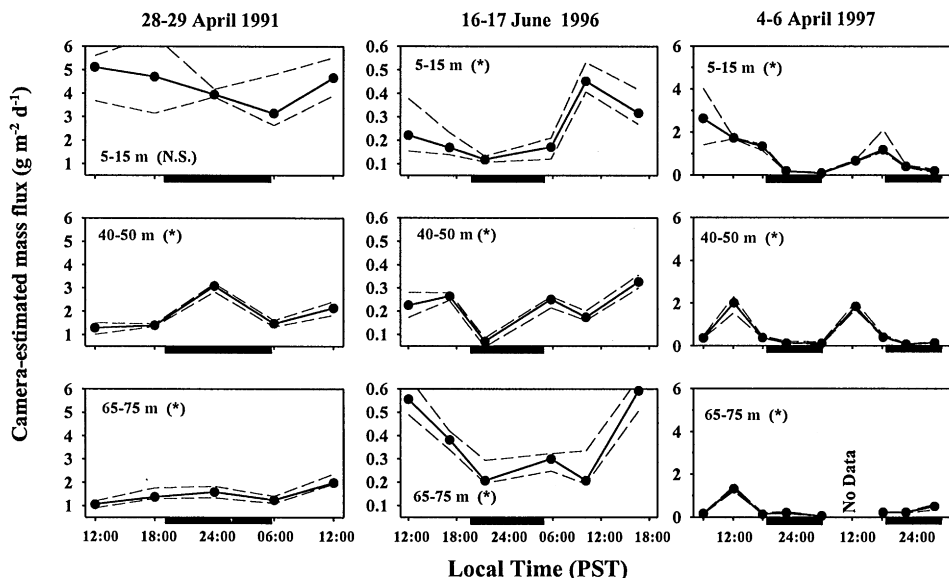
Fig. 11. Depth-stratified aggregate flux, as derived by imaged aggregate properties and in situ sinking rate models, during the three diel studies in April 1991, June 1996 and April 1997. Depth strata are 10-m intervals at the surface (5–15 m), intermediate (40–50 m) and deep (65–75 m). An (*) indicates that Kruskal–Wallis analysis of variance on ranks of fluxes showed significant change over time ($P < 0.05$) and significant differences between daytime and nighttime estimated flux by Dunn's Test ($P < 0.05$). No significance is indicated by (n.s.). Note that two analyses were made during the 48 h April 1997 study. Represented in each panel are median values (solid line) and the upper and lower quartiles (25 and 75% as dashed lines) of data pooled over the 10 m strata. Solid bars on axes indicate night. Note changes in scale between deployments.

order of magnitude lower than fluxes in April 1991 and 1997. These differences were due to the similar differences in numerical concentration and total aggregate volume over these sampling dates. Median fluxes at the surface in 1991 were 2–6 times greater than fluxes at intermediate and deeper strata. In June 1996 and April 1997, the magnitude of flux was relatively uniform over depth but not over time.

Diel changes in derived flux were compared within the three depth strata by non-parametric Kruskal–Wallis one-way analysis of variance. In situations where the between-profile variance was different from within-profile variance, pairwise compari-sons between daytime and nighttime fluxes were made using Dunn's method. The 48 h study of April 1997 allowed for two sets of comparisons within each stratum (except for the 65–75 m stratum, where camera failure occurred during the daytime profile on the second day). There were significant variations in derived flux (Kruskal–Wallis one-way ANOVA; $P < 0.001$) over time at all depths on all sampling dates except at the surface interval in April 1991. In June 1996 and again over both 24 h intervals of April 1997, these changes were significant between day and night with daytime fluxes being greater than nighttime fluxes. Below the surface layer in April 1991, day–night

changes were also significant; however, the pattern was reversed, with nighttime flux being greater than daytime flux.

3.5. Overnight deployments

A total of 12 dusk–dawn aggregate profile comparisons from 11 drifter deployments, summarized in Fig. 12, were made between 1991 and 1997. Table 1 summarizes day–night changes in both aggregate carbon and derived-flux for these profiles. The observed changes in aggregates, measured as particulate organic carbon (POC), ranged widely from increases of 4.2 µg C l^{-1} to dramatic losses of over 30 µg C l^{-1}. Overnight losses of aggregate carbon occurred in 9 of 12 comparisons (75% of our observations) indicating that nighttime losses of aggregate POC were typical. Nighttime reduction in aggregate carbon resulted in a 38% average reduction in camera-derived aggregate flux at night.
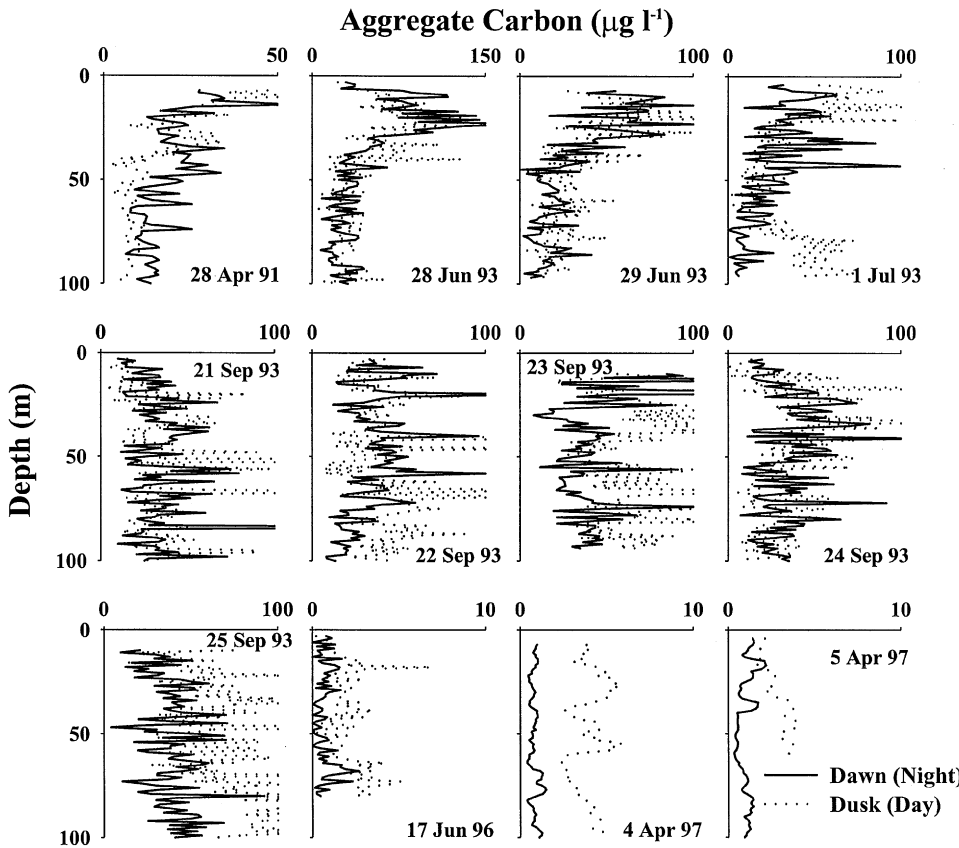

Fig. 12. Composite of 12 sets of aggregate carbon profiles (µg C l^{-1}) used in the analyses presented in Table 1. Dusk profiles are dashed lines and dawn profiles are solid lines; comparisons made with the April 1991, June 1996 and April 1997 studies are between midday and midnight profiles.

Table 1
Observed nighttime changes in aggregate carbon, camera-estimated mass flux, and abundances of the copepod *Calamus pacificus* and euphausiids, primarily *Euphausia pacifica*, at 8 dusk–dawn stations and three 24–48 h stations. The April 1997 study was split into two 24 h studies. The impact of the zooplankton feeding on marine snow for 8 h each night is calculated assuming that *C. pacificus* consumes 1.1 μg C as snow animal⁻¹ h⁻¹ and *E. pacifica* consumes 12 μg C of snow animal⁻¹ h⁻¹ based on mean values of snow consumption of these animals in the Santa Barbara Channel as measured by Dilling et al. (1998). When marine snow increased overnight (i.e., positive sign in that column), the 'change explained by feeding' was set at zero

Date	Observed change in snow overnight 0–100 m (μg C l^{-1})	Change in mass flux overnight 0–100 m (%)	*Calamus pacificus*		Euphausiids		Estimated total nocturnal snow consumption (μg C l^{-1})	Change explained by feeding (%)
			Nighttime abundance (#l^{-1})	Snow eaten (μg C l^{-1})	Nighttime abundance (# l^{-1})	Snow eaten (μg C l^{-1})		
28 June 1993	+ 2.5	+ 5.1	0.45	3.94	0.0054	0.52	4.46	0
29 June 1993	− 3.1	− 9.4	0.58	5.10	0.0052	0.50	5.60	181
1 July 1993	− 11.1	− 27.9	0.21	1.83	0.0001	0.01	1.84	17
21 Sept 1993	− 3.3	− 4.1	0.04	0.32	0.0030	0.29	0.61	18
22 Sept 1993	− 6.4	− 15.1	0.04	0.33	0.0036	0.35	0.68	11
23 Sept 1993	− 21.7	− 37.0	0.02	0.18	0.0023	0.22	0.40	2
24 Sept 1993	0	0	0.05	0.44	0.0045	0.43	0.87	0
25 Sept 1993	− 32.4	− 44.2	0.02	0.19	0.0013	0.13	0.31	1
28 April 1991	+ 4.2	+ 25.8	0.30	2.64	0.0008	0.08	2.72	0
17 June 1996	− 1.3	− 61.7	0.22	1.97	0.0061	0.59	2.56	197
4 April 1997	− 3.1	− 93.8	0.48	4.22	0.0004	0.04	4.26	137
5 April 1997	− 1.9	− 84.8	0.48	4.22	0.0004	0.04	4.26	224

Owing to heterogeneity of the Santa Barbara Channel, nighttime *C. pacificus* and euphausiid concentrations varied by an order of magnitude among the 11 drifter deployments (Table 1). Adult euphausiids never occurred in daytime plankton tows, and *C. pacificus* were less than 50% of their nighttime values during the day (daytime data not presented in Table 1). Using previously published estimates of aggregate grazing by *C. pacificus* and adult euphausiids (Dilling et al. 1999), we estimated the relative contribution of grazing to the disappearance of aggregate carbon overnight. The combined influence of the copepod *C. pacificus* and euphausiids grazing on marine snow could contribute from 1 to > 200% of the disappearance of aggregate carbon overnight.

4. Discussion

4.1. Comparisons with previous studies of marine snow distribution, variation and flux

The hydrography of the Santa Barbara Channel and surrounding Southern California Bight are complex and highly heterogeneous in both time and space. As such, direct comparisons of our camera-derived marine snow and flux data with data of other camera and sediment trap studies show that we are well within expected ranges given regional seasonality. Maximum numerical concentrations in this study ranged between 10 and 80 aggregates l^{-1} and varied greatly by season and phytoplankton bloom conditions with the April 1991 and 1997 marine snow concentrations exceeding the June 1997 concentrations by at least five-fold. The similar approach by MacIntyre et al. (1995) during April–May (1990–1992) in the same vicinity measured peak numerical concentrations of 80–100 aggregates l^{-1}, similar to our April 1991 and 1997 values. Aggregate concentrations over the Monterey Submarine Canyon, measured using a remotely operated submersible, varied seasonally from < 5 to 50 aggregates l^{-1} as a function of hydrographic season and depth (Pilskaln et al., 1998). Our cumulative marine snow volume also related well with the above studies and with camera-measured values of Walsh and Gardner (1992) from the northwestern Gulf of Mexico. Sediment trap measured particle fluxes in the Santa Barbara Basin are also highly seasonal (Thunell, 1998; Alldredge et al., Unpublished Data) and range from < 1 in winter to > 3.5 g dry mass $m^{-2} d^{-1}$ in spring below 500 m depth in the Santa Barbara Basin (Thunell, 1998). Our camera-estimated *instantaneous* mass fluxes from the upper 100 m ranged from about 1 to 10 g $m^{-2} d^{-1}$. Direct comparisons between our camera-derived fluxes and sediment trap measured fluxes have shown a reasonable similarity (Graham and Alldredge, Unpublished Data).

We have presented data indicating that diel variations in marine snow exist in coastal surface waters. These diel variations typically occur as nighttime reductions in aggregate concentration (Table 1). Except for the April 1991 study, when there were differences in aggregate concentrations and estimated flux across the pycnocline, we have documented that diel changes in aggregate concentration and flux extend throughout the entire upper water column in water above and below the pycnocline. Prior to our study, diel variations of marine snow in the upper 100 m were

undocumented. Only in the landmark paper by Lampitt et al. (1993a) was a diel signal in both total particle abundance and total particle volume previously described; however, this was at a depth of 270 m in the mesopelagic northeast Atlantic. Since both our data and the data of Lampitt et al. (1993a) show nighttime decreases in total particle volume and particle flux, we must consider the possibility that similar controlling mechanisms may be operating in these two different geographic regions. What are the mechanisms producing diel variations of marine snow throughout the water column? And, how can such diel signals be preserved at depths of hundreds of meters (i.e., equivalent to several days of sinking for aggregates originating near the surface)?

4.2. Possible causes of a diel signal in large particle abundance and flux

The distribution of marine snow in the upper ocean reflects not only seasonal and annual patterns of productivity (Wefer and Fischer, 1991; Lohrenz et al., 1992; Deuser, 1996; Fischer and Wefer, 1996), but also a variety of biological and physical processes operating over very short time-scales (Alldredge and Silver, 1988; Jackson, 1990). These processes can be categorized as either production or loss terms.

Two pathways of marine snow production are considered important over short time-scales: production of zooplankton feeding webs (e.g., pteropods) or houses (e.g., larvaceans), and coagulation of smaller, slower sinking particles into larger aggregates. Three pathways of marine snow losses are considered important over short time-scales: sinking out of the observed volume; consumption by zooplankton; and fragmentation into smaller, more slowly sinking forms, some smaller than marine snow (0.5 mm in diameter). Reduced marine snow concentration and flux at night requires that cumulative production (feeding web production + aggregation) is less than the cumulative loss (sinking + consumption + fragmentation). We discuss each of these five processes in terms of its potential to yield a diel cycle in marine snow abundance and particle flux.

Production of zooplankton feeding structures: While mucus feeding structures of zooplankton can, at times, dominate the composition of marine snow at the sea surface (Alldredge and Silver 1988), pteropods did not occur at our sites and larvaceans were rare. Dilling (1997) reported that larvaceans would contribute only 0.01–0.1 houses per liter over a 12-h period at our stations, a tiny fraction of the marine snow present. Moreover, larvaceans appear to feed continuously, generating houses at similar rates both day and night (Fenaux, 1985), precluding diel variations in the generation of marine snow as houses. Therefore, no evidence supports nighttime reduced production of mucus feeding structures as the cause of diel cycle of marine snow at our stations.

Aggregation of smaller particles: Formation of marine snow by aggregation processes may vary on a diel cycle under certain conditions. Rates of aggregation depend upon three factors: the intensity of the physical processes, particularly shear, which increase particle collision rates; the concentration of smaller particles available for aggregation; and the stickiness of the particle surfaces, which enhances adhesion (McCave, 1984). The last two factors are unlikely to generate a diel signal. The major classes of smaller particles available for aggregation are phytoplankton cells and fecal

pellets. While phytoplankton may show diel changes in abundance due either to cell division or to grazing by vertically migrating herbivores, diel changes in phytoplankton aggregation are unlikely. Healthy phytoplankton are usually not sticky (Kiørboe et al., 1990) and usually aggregate only near the end of blooms when both cell abundance and the abundance of transparent exopolymer particles, which facilitate aggregation, have reached critical levels (Jackson, 1990; Passow et al., 1994; Logan et al., 1995). Bloom aggregation produces a pulse of sedimenting particles on a scale of days to weeks. It is unlikely that diel variations in the abundance of healthy, non-sticky, non-aggregating phytoplankton, whether generated by growth or by grazing, would lead to the diel patterns observed in this study. This conclusion is further supported by Ruiz (1997), whose model of marine aggregation indicates that interactions between cell grazing and cell growth are not sufficient to yield a diel cycle in aggregate formation.

Nocturnally migrating zooplankton defecate within a few hours of the onset of feeding (Omori and Ikeda, 1984), potentially increasing the abundance of fecal pellets available for aggregation at night. However, increased abundance of aggregating fecal pellets would increase, rather than decrease, marine snow concentration and cannot account for the nighttime reduction we observed.

The principal factor controlling the collision rates, and thus the aggregation rates, of small particles at our study sites was most likely fluid shear (McCave, 1984; Jackson, 1990). Increased fluid shear in surface waters on a diel cycle would increase the collision rates of smaller particles thus increasing aggregation rates and generating a diel pattern in aggregate abundance and particulate flux (MacIntyre et al., 1995). Increased turbulence (i.e., higher energy dissipation rates and overturning throughout an extensive upper mixed layer) can be associated with nightly heat loss or with increased intensity of wind mixing (Brainerd and Gregg, 1993). During our study, we would expect these processes to be most important in late afternoon, evening or night. However, our combined hydrographic and microstructure data from June 1996 show limited increases in upper mixed-layer depth due to either of those forcing mechanisms. Highest dissipation rates were limited to the shallow upper mixed layer (<5 m) and to occasional overturning regions below it. Consequently, the decreases in abundance of marine snow at night were not associated with large, energetic convective motions that would have fragmented the aggregates and distributed them throughout a thick upper mixed layer.

Energy dissipation, from which shear is calculated in the water column, did not vary significantly between night and day when measured directly during the June 1996 diel study (Fig. 7). Nor was there evidence of diel variation in wind speed at the April 1991 station (Fig. 3). Thus we conclude that none of the factors altering aggregation rates, including diel variations in turbulent shear from wind and convective overturn, generated the diel cycles in marine snow abundance and flux observed in the April 1991 and June 1996 studies. However, this does not preclude the possibility that diel changes in wind-induced shear may impact diel patterns in aggregate abundances at other times and locations.

Increased sinking of marine snow at night: If the effective sinking rate of marine snow was greater at night than during the day, then a diel pattern similar to the one we

observed could be generated. Most models of the effects of mixing on particle sinking predict greater retention of particles due to entrainment and resuspension in layers where turbulence is higher both for slowly sinking particles ($1–10$ m d^{-1}) (Woods and Onken, 1982; Reynolds, 1984; Lande and Wood, 1987) and marine snow (Alldredge et al., 1987; MacIntyre et al., 1995). Generation of Langmuir cells by wind may also help retain particles near the surface (Denman and Gargett, 1983). It should be noted, however, that these aggregates would not have been lost from our system because they were not sinking rapidly enough. We would have noted a $35–40$ m downward shift in aggregates by morning given an average sinking rate of about 50 m d^{-1}. Such a shift was not observed (Figs. 4, 8 and 10). Moreover, as mentioned earlier, there is no evidence of convective overturns in the continuously stratified upper mixed layer during the June 1996 study. Therefore, reduction of marine snow abundance and flux throughout the upper 80 m water column during the June 1996 study cannot be attributed to a change in physics that might alter sinking rates of aggregates.

   Consumption of aggregates by vertically migrating zooplankton: Marine snow is consumed by many types of zooplankton including copepods (Dilling et al., 1998; Alldredge, 1972; Dagg, 1993), amphipods (Lampitt et al., 1993b) and euphausiids (Dilling et al., 1998; Dilling, 1997). *Euphausia pacifica* and *Calanus pacificus* are especially abundant and voracious consumers of marine snow in the Santa Barbara Channel (Dilling et al., 1998), and their vertical migration patterns (Fig. 5 and Table 1) could result in greater consumption of snow in the upper 100 m at night. We used mean animal abundances and average marine snow consumption rates measured by Dilling et al. (1998) of 1.1 µg C of snow animal^{-1} h^{-1} for *C. pacificus* and 12 µg C of snow animal^{-1} h^{-1} for *E. pacifica* to estimate the potential feeding impact of these taxa on marine snow. When potential consumption of marine snow is compared to the change in marine snow carbon overnight, it is apparent that grazing by vertical migrators could account for all the reduction in marine snow at some stations. The potential grazing impact of vertically migrating *C. pacificus* and euphausiids ranged from 1 to 224% and accounted for at least 15% of the aggregate carbon losses in more than half of the profile comparisons (Table 1).

   Interestingly, the magnitude of the potential impact of grazing by vertical migrators is inversely related to the amount of marine snow available for consumption in the water column (Fig. 13). When marine snow concentration is low (< 30 µg C l^{-1}), copepod and euphausiid grazing can explain virtually all of the overnight losses of snow from surface waters. However, high concentrations of marine snow (> 30 µg C l^{-1}) are less impacted directly by migrator grazing. The data presented in Fig. 13 suggest critical concentrations of marine snow above which a diel signal of grazing becomes swamped by other modes of variability such as fragmentation by macrozooplankton or changes in coagulation rates. Such a relationship between snow concentration and grazing impact can most likely be explained by a mismatch in scales where animal generation times of weeks far exceed the day-to-day variability of marine snow in surface waters. These results suggest that nocturnal grazing may be an important process generating diel cycles of sinking particles, but can only occasionally explain the entire observed pattern.
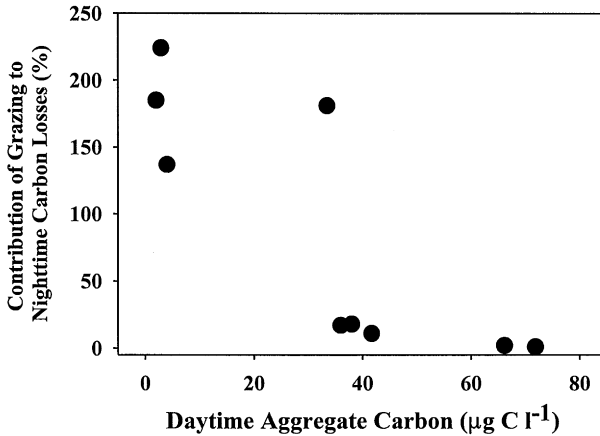
Fig. 13. The potential contribution of grazing by euphausiids and the copepod *Calanus pacificus* to the observed losses of aggregate carbon overnight relative to amount of aggregate carbon available during the daytime and prior to feeding. Only data reflecting decreases in carbon overnight (see Table 1) are presented.

Fragmentation of aggregates: Fragmentation of marine snow into smaller, more slowly sinking particles at night would reduce both particle flux and the concentration of marine snow, consistent with our observations. Owing to their high porosity, most aggregates appear fragile. This led Ruiz (1997) to assume that nighttime increases in turbulent energy, due to convective overturn, could cause fragmentation of marine snow, and thus alter particle fluxes with diel periodicity. Alldredge et al. (1990) directly measured the strength of natural marine snow collected in the Santa Barbara Channel. The maximum energy dissipation rates of 10^{-7} m^2 s^{-3} observed in our study and by Brainerd and Gregg (1993) are too low by several orders of magnitude to produce fragmentation of natural aggregates of marine snow. Alldredge et al. (1990) predict that energy levels required to fragment most aggregates occur only with extreme wind stress conditions and that even then, conditions of sufficient intensity would only occur close to the sea surface. Hill (1998) also presents evidence that natural aggregates are very strong. Our microstructure data clearly indicate that energy dissipation was too low by a factor of 100, both night and day, to disrupt marine snow in the June 1996 study. Furthermore, we conclude based upon our measurements here and upon the empirical data of Alldredge et al. (1990), and more recently Hill (1998), that levels of turbulence produced during nighttime convective overturn are not likely to contribute to aggregate fragmentation.

An alternative process producing disaggreation of marine snow is the swimming activities of large zooplankton. Dilling (1997) has shown that *E. pacifica* may be capable of fragmenting marine snow in situ into smaller, more slowly sinking particles through its swimming activities alone. Shear stresses sufficient to easily fragment marine snow can be generated near the body surfaces of large, rapidly swimming

macrocrustaceans such as *E. pacifica* (Dilling, 1997). *E. pacifica* often makes up more than 50% of the nighttime, near-surface zooplankton biomass in coastal California waters (Brooks and Mullin, 1983), and can swarm at high densities. *E. pacifica* migrates from daytime depths of around 400 m into the upper 100 m during the night to feed (Brinton, 1967), which can explain our relationship between total water depth and diel cycles of marine snow. A comparison of the April 1991 and June 1996 drifter series, and the 8 dusk–dawn series, makes a strong case that vertically migrating zooplankton (euphausiids and copepods) from the deeper Santa Barbara Basin (>375 m) contribute to diel variability of marine snow abundance in the overlying waters. When euphausiids are numerous, as was the case in June 1996, a strong diurnal signal can be generated throughout the water column. When euphausiid numbers are reduced, any diel signal will be limited to near-surface shear stresses (either wind induced or from convective overturn of surface waters). While our data supports Dilling's hypothesis that the fragmentation of sinking marine snow particles by vertically migrating macrozooplankton could reduce particulate flux and concentrations of sinking particles at night, considerable additional research will be needed to test this hypothesis.

While Ruiz (1997) included a grazing component in his model, he essentially discounted migrating zooplankton as significant contributors to diel variability of marine snow. We believe that his model's assumptions are incomplete. Ruiz (1997) only modeled the impact of grazers on the aggregation rates of 200 μm particles – smaller than the marine snow size-class. In addition, he did not know of the direct impact of zooplankton as either consumers of marine snow or sources of aggregate fragmentation. In summary, the nocturnal feeding and swimming activities of vertically migrating zooplankton appear to be the most likely processes contributing to the reduction in the concentration and calculated flux of large particles consistently observed at night in this study. While these processes do not explain all the reduction we observed at some stations, our calculations are limited to only two species and do not include quantitative estimates of the impact of zooplankton fragmentation. Additional consumption of marine snow by other vertical migrators needs to be considered and fragmentation quantitatively measured to fully evaluate the ability of migrating zooplankton to generate diel signals in marine snow concentration throughout the water column.

4.3. Diel signals of marine snow below the surface mixed layer

A surprising result of this study was that diel signals could be preserved over depths reflecting greater than 1 day's worth of sinking (i.e., down to 150 m, Fig. 10). Between our observations, and those of Lampitt et al. (1993a), we must consider factors that create synchronization in diel cycles throughout the water column from the mixed layer to 100 s of meters.

One possibility proposed by Ruiz (1997) is that aggregates sink uniformly as discrete layers, thus moving the diel signal through the water column. Ruiz (1997) used computer simulations to illustrate how daily pulses of aggregates could sink for several days (i.e., to Lampitt's depth of 270 m) with minimal smearing of the diel

signal. We know that particles undergo significant lateral advection when they sink; the angle of approach at sediment traps can be nearly horizontal (Siegel and Deuser, 1997). This creates a very large 'statistical funnel' of particle trajectories for an observational depth of 270 m, a funnel that may extend hundreds of kilometers (Siegel and Deuser, 1997). The spatial scale of this statistical funnel would exceed the scale associated with most biological processes involved with marine snow production. We believe that particle dynamics are unlikely to be uniform over this areal extent. Thus it is not reasonable to assume that particles produced at the surface over a very large area would be uniform in size distribution so as to produce a pulse of sinking particles maintaining coherence over a >250 m water column.

Our data do not indicate that a coherent core of particles can be followed through the water column over time, nor is there any indication of uniform spacing of particle maxima in aggregate profiles. Lateral processes and differential settling velocities appear to quickly smear any diel signal from the surface layer. A more likely scenario is that a diel signal is uniformly generated throughout the water column. This could be accomplished by vertically migrating zooplankton, including euphausiids and other macrocrustaceans, gelatinous species and fish, fragmenting and consuming aggregates as they ascend to the surface each evening. Based upon published ascent rates of about 100 m h^{-1} (Hardy and Bainbridge, 1954; Andersen and Nival, 1991), adult euphausiids would spend about 40 s swimming and feeding in each 1 m interval during their nightly migration. Such a scenario would result in a nearly uniform pattern with depth, excluding small time lags required for ascent time, and might explain both our coastal observations and those of Lampitt et al. (1993a) in the deep Atlantic. A time-dependent change over depth might be expected if our sampling resolution (in time) were shorter than the nightly ascent time of zooplankton. However, this was likely not the case here because our temporal resolution was 4–6 h between casts while vertically migrating crustaceans could ascend through the upper 150 m in about 1.5 h.

4.4. Impacts of diel patterns of aggregate abundance and particle flux on marine ecology

This study suggests that nighttime decreases in the flux of particles are common. Such diel patterns are likely to be significant for both midwater and benthic ecology. Diel pulses of detritus arriving at the seafloor may produce diel periodicity in the behaviors and interactions of benthic organisms as they scavenge detrital material. Such pulses of detritus may be an important diel signal for communities at depths where light–dark cycles are either reduced or absent. Since marine snow may act as focal points of reproduction and feeding for mid-water organisms (Steinberg et al., 1994), diel periodicity in marine snow abundance may influence cycles of reproduction and energy transformation rates in the mid-water. Finally, diel variations in the sinking of marine snow – especially when mediated by vertical migrators – may reflect very rapid remineralization of carbon before particles can penetrate the deep sea and supports the important role that macrozooplankton may play in altering the apparent vertical flux of particles as traditionally measured by sediment traps.

Acknowledgements

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