Marine Biology 83, 263–270 (1984)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Diel fluctuation in zooplankton grazing rate as determined from the downward vertical flux of pheopigments *

N. A. Welschmeyer **, A. E. Copping, M. Vernet and C. J. Lorenzen

School of Oceanography, University of Washington; Seattle, Washington 98195, USA

Abstract

The diel grazing activity of zooplankton was measured at a single study site in a temperate fjord, Dabob Bay, Washington, USA at several periods during spring, summer and fall of 1979–1981. Pheopigments were used as an indicator of herbivorous zooplankton activity. The downward vertical flux of pheopigment-containing fecal pellets was measured with sediment traps deployed over repetitive 4 h periods. Experiments were run for 24 to 36 h. A maximum in the flux of pheopigments was consistently noted within the euphotic zone during hours of darkness. Diel fluctuations in pheopigment flux showed amplitudes up to 29-fold. Nightly grazing activity accounted for 41 to 82% of the daily (24 h) grazing and was indirectly related to seasonal changes in daylength.

Introduction

The grazing activity of zooplankton is usually determined by placing animals in a suspension of food and measuring the decrease in food concentration over time. Attempts to calculate community grazing rates in nature have met with limited success since they require knowledge of the grazing activity of all species in the water column, their life stages, the abundance of all species, the distribution of the animals through space and time, and diel variations (if any) in *per capita* feeding activities. A considerable degree of uncertainty is inherent in grazing rates calculated from feeding experiments, primarily due to the large data base required for the calculations.

Considering the time involved, and the number of experiments that must be conducted, it is not surprising that quantitative estimates of diel grazing activity within the euphotic zone have been rare. Diel variations in feeding rates of individual species have been reported (Haney, 1973; Duval and Green, 1976; Mackas and Bohrer, 1976; Starkweather, 1975, 1978); however, a measurement of diel variation in total community grazing pressure, as a result of the combined effects of diel feeding and migratory pattern, is unknown.

It is well documented that maximum zooplankton concentrations occur within the euphotic layer during night. The assumption that maximum herbivorous grazing activity occurs at night, follows from this observation. However, reverse diel migrations of grazers have been observed (Dumont, 1972; Ohman *et al.*, 1983) and daytime maximum feeding rates of some zooplankton have been measured (Gauld, 1953; Nauwerck, 1959; Starkweather, 1978). These conditions would tend to negate the effect of normal diel migrations, resulting in a possible dampening of the diel rhythm of community herbivorous grazing within the euphotic layer. The assumption that community grazing rates are highest at night is not trivial. This assumption forms an integral component of theories regarding the temporal nature of phytoplankton-zooplankton trophic interactions (McAllister, 1969; Petipa and Makarova, 1969; Kerfoot, 1970) and the adaptive significance of vertical migration (McLaren, 1963, 1974; Enright, 1977).

We present here a new approach to estimating zooplankton grazing activity in nature, with emphasis on the measurement of diel fluctuations. The method used here for measuring grazing is based on the dynamics of chlorophyll *a* in nature. An inherent feature of the technique is that the experiments are free from bottle incubations and require no manipulation of either the phytoplankton or the zooplankton.

It was previously suggested that chlorophyll degradation products, pheopigments, sampled in the water column were produced from chlorophyll *a* by grazing (Lorenzen, 1965, 1967a, b). It has also been noted that degraded chlorophylls were associated with zooplankton fecal pellets

* Contribution No. 1405 from the School of Oceanography, University of Washington
** Present address: The Biological Laboratories, Harvard University, 16 Divinity Avenue, Cambridge, Massachusetts 02138, USA

(Currie, 1962). Nemoto (1968, 1972) and Nemoto and Saijo (1968) measured pheopigments within the guts of several genera of zooplankton. Daley (1973) noted that pheopigments accumulated concurrently as chlorophyll disappeared when phytoplankton were grazed by either the cladoceran *Daphnia pulex*, or the phagotrophic chrysophyte *Ochromonas sp.*, The conversion of chlorophyll to pheopigments due to the grazing activity of red crabs (Longhurst *et al.*, 1967) and rotifers (Levi and Wyatt, 1971) has also been observed. More recently, diel variations have been noted in the quantity of pheopigments per animal in the gut contents of several species of copepods captured in the field (Mackas and Bohrer, 1976; Boyd *et al.*, 1980; Dagg and Grill, 1980; Welschmeyer, 1982).

The acidification techniques used to measure pheopigments either fluorometrically (Lorenzen, 1966) or spectrophotometrically (Lorenzen, 1967a) do not distinguish between pheophytin *a* and pheophorbide *a*. However, Shuman and Lorenzen (1975) quantified the production of pheopigments by the grazing of copepods in the laboratory. For every mole of chlorophyll *a* ingested, one mole of pheophorbide *a* appeared in the form of fecal pellets. Thus, the porphyrin structure of the chlorophyll *a* molecule appears to be conserved during the passage of plant food through the guts of herbivores.

Patterson and Parsons (1963), Jeffrey (1965, 1974), Lorenzen (1967a, b) and Yentsch (1967) used thin-layer chromatography for the separation and isolation of water-column pigments and noted that the dominant degraded form of chlorophyll *a* in nature is pheophorbide *a*. The same results have been found for suspended water-column material and naturally occurring fecal pellets in our study site (Shuman, 1978; Welschmeyer, 1982). This suggests that the quantity of chlorophyll *a* that was ingested by grazers can be determined by capturing zooplankton fecal material and analyzing for pheopigments.

Here, we have employed sediment traps to measure the downward flux of pheopigment-containing fecal pellets. The traps were exposed repetitively for short periods of time (4 h) so that diel variations in pheopigment flux could be determined. This technique quantifies the phytoplankton-zooplankton grazing interaction by measuring the fecal material produced by that interaction. The experiments are thus passive in design and require no manipulation of either the food source (phytoplankton) or the grazers. *In situ* variations in grazing due to migration, diel feeding and even changes in food abundance are measured. Further, since the technique is based on the analysis of phytoplankton pigments, grazing rates for those organisms capable of both herbivorous and omnivorous activity are included.

Collection site

The experiments were conducted at a single station in Dabob Bay (Latitude 47°N; Longitude 123°W), Washington State, USA in the spring, summer and fall of 1979–1981. The station was in the middle of the fjord, approximately 1.2 km from both shores in an east-west direction. Water column depth was 110 m. The bay is a moderately productive fjord, with about 200 g C m^{-2} yr^{-1} primary production. Spring and fall algal blooms occur each year, although the timing is quite variable. Blooms have been observed as early as February and as late as November (Lorenzen *et al.*, 1981; Welschmeyer, 1982). Maximum euphotic zone depths are about 30 m, with a characteristic subsurface chlorophyll maximum during the summer months. Horizontal advection is small due to the lack of significant river input and the presence of a sill at the mouth of the bay. Horizontal excursions as low as 100 m d^{-1} have been noted at the sampling station (Ebbesmeyer, 1973). The bay is dominated by planktonic crustacean grazers of the copepod genera *Calanus, Pseudocalanus, Metridia* and *Acartia*, as well as the euphausiid *Euphausia pacificus* (Damkaer, 1964; Shuman, 1978; Runge, 1981; Welschmeyer, 1982).

Materials and methods

Messenger-operated sediment traps were used to measure the flux of pheopigments through the water column (Welschmeyer, 1982; Lorenzen and Welschmeyer, 1983). The traps were small PVC cylinders with a height:width ratio of 3:1 (mouth area was 40.7 cm^2). The small size of the traps facilitated rapid recovery and sampling so that turnaround time between deployments could be minimized. Prior to deployment, the traps were filled with filtered seawater and solid NaCl (ca. 10 g) was added. NaCl was used to provide a density gradient to prevent the captured trap material from washing out. A circular grate with 1 cm × 1 cm openings (fluorescent light diffuser) was fitted in the mouth of each trap to reduce turbulence at the opening. The deployments were made anchor-first. Eight to ten traps were fastened at 10 m intervals onto a 100 m length of hydrowire and suspended over the side while the ship was on anchor. A 70 kg weight, terminating the hydrowire, was suspended off the bottom to keep the sediment trap array taut. In all, eight experiments were attempted, one of which was aborted due to foul weather. The seven successful experiments reported here were conducted during periods of flat calm seas.

The traps were left in place for 4 h, closed with a messenger, and then recovered. After sampling, the traps were prepared again, as above, and redeployed. Turnaround time for each retrieval was ca. 30 min (exact times were noted for each exposure period). The experiments were continued for 24 to 36 h, yielding the variation in flux rates versus time of day for each of 8 to 10 depths.

On retrieval, the entire content of each trap was resuspended, and aliquots were taken for pigment determination (2 to 3 replicates). The samples were filtered onto glass-fiber filters (Gelman Type A/E) which were covered with $MgCO_3$. These were then extracted in 90% acetone either by tissue-grinding or sonication (7 min with a

Megason ultrasonicator, Model PG-200-20-1). No difference between grinding or sonicating could be detected. Pigments were determined immediately on board ship by fluorometry (Lorenzen, 1966). Sediment trap material was also saved for later analysis in the laboratory by either thin-layer or high-pressure liquid chromatography. The filtered material was stored in liquid N_2. The chlorophyll-like pigments found in the trap material, ranked in decreasing abundance, were pheophorbide *a*, pheophytin *a*, and chlorophyll *a*. The relative mass abundance, determined by HPLC, was 20:4:1, respectively (Vernet and Lorenzen, unpublished data).

Pigments were sampled in the water column with Niskin bottles while the sediment traps were in place. Pigment samples were filtered as above and analyzed immediately by fluorometry. Sampling was always made through the full extent of the euphotic zone so that areal standing crops (mg m^{-2}) could be calculated. Primary production was measured by the ^{14}C technique. Tethered *in situ* incubation moorings were used (24 h, sunrise to sunrise).

Results

Concentrations of pheopigments inside the traps were always two to ten times higher than the ambient concentrations in the water column. Pheopigment concentrations in the traps were also higher than the chlorophyll concentrations in the traps, often by factors of 10. The size composition of the pigmented material inside and outside the traps was also markedly different. While >50% of the pheopigments suspended in the water column would pass through a 5 μm nylon mesh, > 50% of the pheopigments from the sediment traps were retained on a 20 μm mesh. This is consistent with the idea that the phytoplankton chlorophyll is converted to pheophorbide by grazers and voided as larger particles, fecal pellets, which sink to the bottom. Fecal pellets from the sediment traps could easily be seen after filtration onto the glass-fiber filters. Microscopic examination showed that the material in the traps consisted largely of fecal pellets or debris of broken pellets which may have been produced during the sampling procedure (Shuman, 1978; Prahl and Carpenter, 1979; Bennett, 1980).

The experiments showed that diel variations in pheopigment flux were always evident at sampling depths corresponding to the euphotic layer, i.e., the upper 30 m. However, at the deeper sampling depths (50 to 100 m) the amplitudes of the diel fluctuations were greatly dampened, or altogether undetectable. Examples of these observations are given in Fig. 1 for experiments made on 3–4 June 1980 and 9–11 September 1980. A diel variation in pheopigment flux is clearly evident at each depth in the upper 30 m for these two dates (Fig. 1). The maximum flux of pheopigments occurs during periods of darkness for those depths nearest the surface. At depths greater than 50 m in Fig. 1, the amplitude of the flux variation becomes reduced, and the time of maximum flux is shifted with respect to the time it was noted at the surface. For

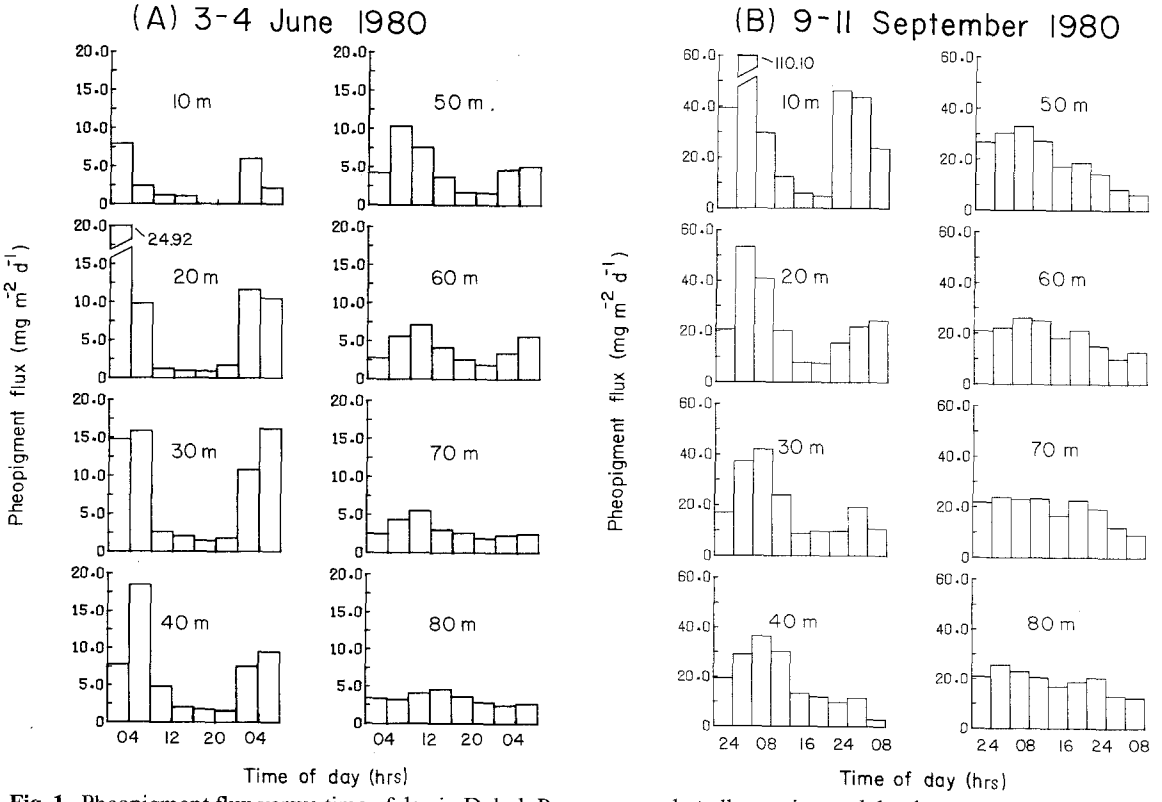

Fig. 1. Pheopigment flux versus time of day in Dabob Bay, measured at all experimental depths

instance, on 3–4 June 1980 (Fig. 1 A), the maximum flux at 20 m occurred during the exposure beginning at 24.00 hrs, whereas, at 60 m the maximum flux occurred at the exposure beginning at 08.00 hrs. The delayed maximum at 60 m, with respect to the surface, is presumably due to the lag it takes for surface-produced fecal pellets to sink to 60 m. Calculations of *in situ* fecal pellet sinking rates based on these data have been given by Lorenzen and Welschmeyer (1983). The average sinking rate was 87 m d^{-1}. If fecal pellets produced near the surface sink to the bottom, we would expect the average 24 h flux of pheopigments near the surface to be equivalent to the 24 h pheopigment flux at depth, i.e., the mass of pheopigments should be conserved.

In order to test this, the weighted 24 h flux of pheopigments at each depth was calculated for all experiments (Fig. 2). A 24 h summation period was chosen so that one day-time period and one night-time period would be included at each depth. The results in Fig. 2 show that in most cases the flux of pheopigments is uniform with depth below 30 m; that is, the pigment is conserved. Reduced fluxes at the shallowest depths (3 June 1980 and 29 April 1981, Fig. 2) suggest those traps did not sample all the fecal pellets, i.e., appreciable fecal pellet production occurred below the shallowest trap, but still within the euphotic zone.

On two occasions (3 June 1980 and 9 September 1980) the flux of pheopigments near the surface could not be accounted for by an equivalent flux at depth (Fig. 2). This is probably the result of day-to-day variability in herbivorous grazing pressure. In other words, given that fecal pellets sink at a rate of ca. 90 m d^{-1} (Lorenzen and Welschmeyer, 1983), it follows that material caught at depth (90 m) was produced 24 h previous to material caught at the surface, within the same 24 h experimental period. Thus, reduced or elevated grazing pressure on the day before commencement of a diel experiment would result in an imbalance between surface and bottom fluxes. We have indeed found that longer trap deployments (weeks) smooth the effects of daily variability, and yield equivalent pheopigment fluxes at depths in excess of 30 m, i.e., below the euphotic zone (Welschmeyer, 1982; Lorenzen and Welschmeyer, 1983). Therefore, pheopigments produced within the euphotic zone appear to be conserved during their transit to the bottom in Dabob Bay. However, the short-term variations in pheopigment flux, measured with shallow (< 30 m) and deep (> 50 m) traps, can be quite different (Fig. 1).

It is apparent that diel variations in grazing activity are best represented by pheopigment flux measurements made as close to the surface as possible. This minimizes the lag that occurs from the time the fecal pellets are egested to the time they are finally sampled by the sediment traps. Thus, the actual time of the onset of grazing is more accurately represented by traps positioned near the surface. Also, the absolute magnitude of grazing rate fluctuation is more accurately measured by shallow traps, since dampening of flux variations, as a result of particle sinking-rate variability, is avoided (Lorenzen and Welschmeyer, 1983). We have therefore used pheopigment flux data from the shallowest available trap depths to show diel variations in zooplankton grazing activity. Pheopigment flux rates measured at the three shallowest trap depths within the upper 35 m are displayed in Fig. 3 for all experiments. Diel variations in pheopigment flux were always evident, with higher fluxes noted during hours of darkness (Fig. 3). On occasion, there was a noticeable lag in the timing of the maximum flux at the deeper of the three depths, i.e., 3–4 June 1980 and 12–14 August 1980. Not too surprisingly, Lorenzen and Welschmeyer (1983) calculated fecal pellet sinking rates of only 31 m d^{-1} on 12 August 1980, where the lag was most pronounced.

Pheopigment fluxes at the shallowest trap depths were used to calculate the relative amplitude and net impact of diel grazing activity. These data are marked by heavy lines in Fig. 3 and the calculations are summarized in Table 1.

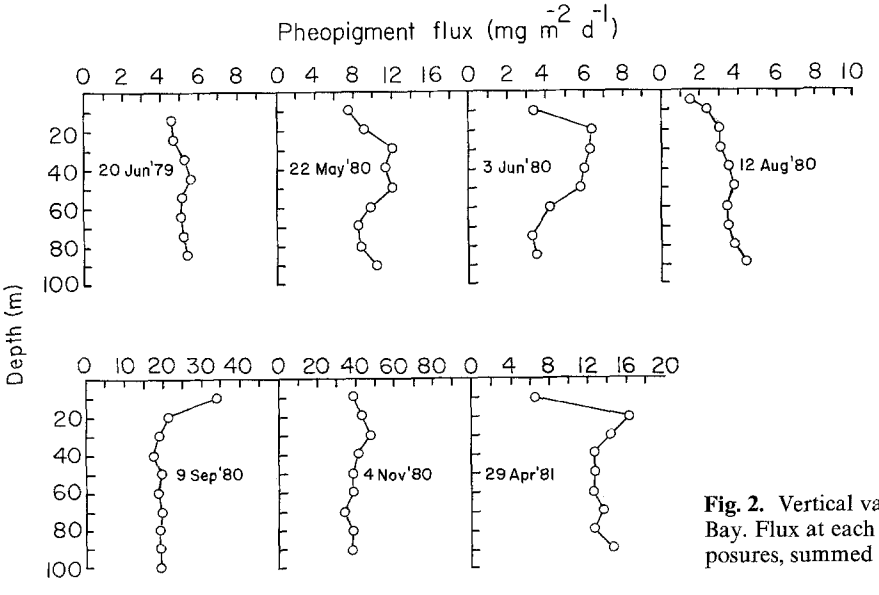

Fig. 2. Vertical variation of pheopigment flux over 24 h in Dabob Bay. Flux at each depth was calculated from 4 h sediment trap exposures, summed over 24 h

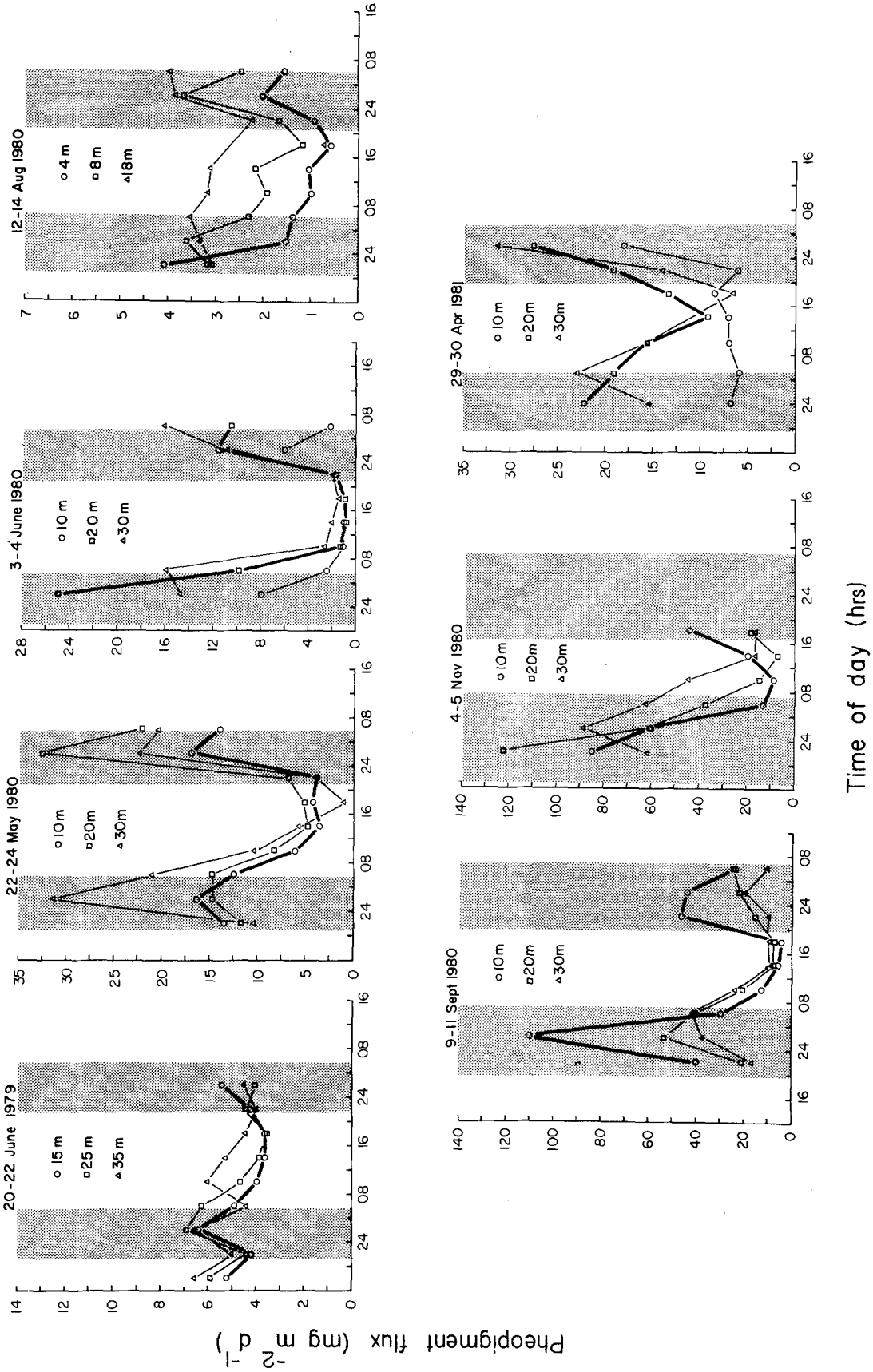

Fig. 3. *Diel variation of pheopigment flux at three depths within the euphotic zone (upper 35 m) in Dabob Bay.* Data marked by heavy lines were used in the calculation of diel grazing effects in Table 1 (see "Results"). Shaded areas represent periods of darkness, calculated from times of sunset and sunrise (civil time)

Table 1. Summary of diel pheopigment flux experiments in Dabob Bay. Ratio of 4 h maximum:minimum pheopigment fluxes were taken from sediment trap depths marked by heavy lines in Fig. 3 (see "Results"). Σ night flux was obtained from integration of areas below heavy curves in Fig. 3; when data from two complete nightly intervals were available (22 May 1980 and 9 September 1980), the average of the two nights was used. Chlorophyll grazed (% d^{-1}) is the ratio of (chlorophyll-equivalent flux:chlorophyll crop) × 100 (see "Discussion"). C:chl was calculated as (primary production:chlorophyll-equivalent flux).

Date	Day-light hours	Maximum 4 h night flux / Minimum 4 h day flux	Σ night flux (as % of 24 h flux)	Pheopigment flux at depths > 30 m (mg pheo m^{-2} d^{-1})	Primary production (mg C m^{-2} d^{-2})	Chlorophyll crop (mg chl m^{-2})	Chlorophyll grazed (% d^{-1})	C:chl (wt wt^{-1})
20–22 June 1979	16.1	1.8	41	5.3	331	51.8	15	41
22–24 May 1980	15.5	4.7	56	10.2	978	62.5	25	64
3– 4 June 1980	15.8	29.0	65	4.6	445	21.9	32	64
12–14 Aug. 1980	14.5	7.4	59	3.8	262	21.5	27	46
9–11 Sep. 1980	12.9	23.2	78	19.0	1 672	64.4	45	58
4– 5 Nov. 1980	9.7	9.6	82	38.2	1 160	55.9	103	20
29–30 Apr. 1981	14.4	3.0	49	13.4	1 417	60.7	33	70

[On two occasions, the next shallowest depths (20 m) were used because of lost samples at 10 m on 3–4 June 1980, and because the 10 m trap depth apparently missed the diel flux increase on 29–30 April 1981.] The maximum daily variation in day/night flux, based on 4 h sampling intervals, was 29 x, and the minimum was 1.8 x (Table 1). However, pheopigment flux, integrated through the full dark period, was not necessarily higher than the flux measured through the full daylight period. Dabob Bay, Latitude 47°43'N, experiences large variations in daylight hours through the year. On 21 June, the longest, and on 21 December, the shortest daylight day of the year, there are 16.1 and 8.3 h of daylight, respectively. Night-time pheopigment flux, as a percentage of daily (24 h) pheopigment flux, is listed in Table 1 (percentages were obtained by integrating the areas below the heavy curves in Fig. 3). Although night-time grazing comprised as much as 82% of the total daily grazing, several of the experiments showed that night-time grazing was comparable to day-time grazing and, in two cases, actually less.

Discussion

The flux of pheopigments in Dabob Bay reflects the grazing activity which might be expected in a temperate fjord dominated by large crustacean grazers. During the course of 24 h, a characteristic pattern in the flux of pheopigments could be seen, with a consistent pulse of pheopigments introduced into the euphotic zone during hours of darkness.

The increase in pheopigment flux at night presumably results from increased grazing activity which may be due to the combined effects of both diel vertical migration of animals into the euphotic zone and an increased feeding activity of non-migratory animals (Haney, 1973; Haney and Hall, 1975; Duval and Geen, 1976; Starkweather, 1978). The grazing activity at night may comprise as much as 82% of total daily grazing, but generally was somewhat less, despite the fact that night-time grazing rates, determined over short 4-h periods, were higher than the day-time rates (Fig. 3). This is due to the relative length of the day/night. For example, night-time rates (over 4 h) were greater than day-time rates (over 4 h) on both 20–22 June 1979 and 29–30 April 1981 (Fig. 3) but, because of the relatively short night, night-time grazing accounted for less than 50% of the daily (24 h) grazing (Table 1).

Several theories concerning the adaptive significance of zooplankton vertical migration have included the assumption that the transit of grazers out of the euphotic zone during the day-time allows photosynthetic production by phytoplankton to proceed at maximal rates, unimpeded by grazing (McAllister, 1969; Petipa and Makarova, 1969; Kerfoot, 1970; Enright, 1977). Our results show that grazing proceeds throughout the day-time at moderate rates, and that the integrated day-time grazing pressure can equal or exceed night-time grazing (Table 1). This occurs in spite of the fact that Dabob Bay is dominated by copepod species which are known to be strong nocturnal vertical migrators, i.e., the genera *Calanus, Pseudocalanus,* and *Metridia* (Shuman, 1978; Runge, 1981; Ohman *et al.,* 1983). One theory on vertical migration has predicted that the time of onset of the increase of night-time grazing is critical in supporting the tenet that energetic benefits are accrued by vertical migrators (Enright, 1977; Enright and Honneger, 1977). In this case, vertically migrating animals would be required to start feeding in the surface layers as much as 3 h before sunset. Further, the net mass of phytoplankton grazed is assumed to be maximal at that time due to elevated zooplankton filtration rates caused by starvation effects (Enright, 1977). The data show that, in Dabob Bay at least, increased grazing rates are not usually seen until the second full sampling period after sunset (Fig. 3). For example, on 22–24 May 1980, maximal flux rates of pheopigments occurred between 24.00 and 04.00 hrs. Sunset was at 20.50 hrs. These results suggest that the magnitude and timing of increased night-time grazing rates should be questioned as possible factors in the adaptive significance of vertical migration.

Grazing rates of fecal pellet-producing zooplankton can be estimated by converting the flux of pheopigments into the equivalent mass of chlorophyll grazed. Here we assume that pheopigments measured by the standard fluorometric procedure are predominantly pheophorbide *a*. Standard fluorometric equations calculate pheopigment concentration (mg m^{-3}) as if it were pheophytin *a* (Holm-Hansen *et al.*, 1965; Lorenzen, 1966, 1967 b; Shuman and Lorenzen, 1975). The molecular weight of chlorophyll *a* is 894 and that of pheophorbide *a* is 593. Thus, the mass of pheopigments in chlorophyll-equivalents is:

$$\text{mg chlorophyll-equivalents} = \text{mg pheopigments} \times (894/593).$$

This assumes the conversion of chlorophyll to pheophorbide by grazers is 100% efficient on a molar basis (Shuman and Lorenzen, 1975).

A first-order approximation of the grazing rates can be made by comparing the flux of chlorophyll-equivalents to the standing crop of chlorophyll. For this purpose we have used the average flux of pheopigments measured at depths in excess of the euphotic zone (> 30 m) to represent the daily loss of pigments (Fig. 2). This smooths the effects of diel fluctuations and avoids the possibility that shallow traps may miss fecal material egested at deeper depths. The data are included in Table 1. As an example, on 22–24 May 1980 the flux of pheopigments out of the euphotic zone was 10.2 mg m^{-2} d^{-1} or 15.4 mg chl-equiv m^{-2} d^{-1}. The standing crop of chlorophyll was 62.5 mg m^{-2}. Approximately 25% of the algal standing crop was grazed. This grazing rate represents the activity of only the fecal pellet-producing zooplankton. The total grazing rate may be higher since microzooplankton grazers are likely to produce pheopigments in the form of debris with negligible sinking rates. This material would not be sampled by sediment traps, and would contribute to the pool of suspended pheopigments which are sampled with conventional water bottles (Lorenzen, 1967 a; Shuman, 1978; SooHoo and Kiefer, 1982 a, b; Welschmeyer, 1982).

The fraction of the algal standing crop grazed each day is variable and is affected by a number of factors. The grazing calculations summarized in Table 1 assume a steady state, and that the primary grazers were fecal pellet-producing herbivores. If the experiments were conducted while the algal populations were increasing, one would expect grazing losses to be small. The converse would be true if the phytoplankton levels were decreasing. Grazing losses could be higher than that tabulated if microzooplankton grazing activity comprised a significant fraction of total grazing. The assumption that the system is in steady state, and that the primary grazers are the larger fecal pellet-producing herbivores, can be tested indirectly. For example, a carbon to chlorophyll ratio, C:chl, can be calculated from the data in Table 1. That is, each day's primary production and its associated chlorophyll is grazed and the residue, pheopigments, finds its way into the sediment trap. C:chl then would be:

$$\text{C:chl} = (\text{primary production})/(\text{chlorophyll-equivalent flux}).$$

The calculated C:chl values are tabulated in Table 1. The range of values are within those that might normally be expected in coastal areas (Welschmeyer and Lorenzen, 1984), suggesting that the assumptions used may be appropriate.

The experiments in Dabob Bay demonstrate that sediment traps can be useful in characterizing the grazing activity of macrozooplankton that feed as herbivores, i.e., animals that produce pigmented fecal pellets. Using the appropriate scale of space and time, one can detect both the spatial and temporal variability of grazing, as well as measure the magnitude of the daily losses sustained by the phytoplankton crop. The results were qualitatively in agreement with conventional assumptions regarding diel grazing activity. However, quantitative estimates showed that grazing losses sustained by phytoplankton through the full dark period may not necessarily be higher than those through the day. The two dates of greatest nightly grazing losses were the two dates of shortest daylength (9–11 September and 4–5 November). It appears that sunset and sunrise serve as cues for the increase and decrease in herbivore activity, but a unifying principle, that the majority of the daily (24 h) grazing activity occurs at night, is not supported. If the nightly influx of migrators to the surface is the major cause of the measured increase in pheopigment flux, the data lend support to the notion that migration is an adaptive mechanism of avoidance from visual predators (Zaret and Suffern, 1976), since the measured increases in pheopigment flux were confined largely to the limits of darkness.

Acknowledgements. This research was supported by Grants Nos. OCE 77-06066 and OCE 79-18838 from the Oceanography Section, National Science Foundation, Washington, D.C. 20550, USA.

Literature cited

Bennett, J. T.: The biogeochemical significance of zooplankton fecal material in a biologically productive, temperate fjord, 258 pp. Ph.D. thesis, University of Washington, Seattle, Washington 1980

Boyd, C. M., S. L. Smith and T. J. Cowles: Grazing patterns of copepods in the upwelling system off Peru. Limnol. Oceanogr. *25*, 583–596 (1980)

Currie, R. I.: Pigments in zooplankton faeces. Nature, Lond. *193*, 956–957 (1962)

Dagg, M. J. and D. W. Grill: Natural feeding rates of *Centropages typicus* females in the New York Bight. Limnol. Oceanogr. *25*, 597–609 (1980)

Damkaer, D. M.: Vertical distribution of copepods in Dabob Bay, December, 1960, 84 pp. M.S. thesis, University of Washington, Seattle, Washington 1964

Daley, R. T.: Experimental characterization of lacustrine chlorophyll diagenesis. II. Bacterial, viral and herbivore grazing effects. Arch. Hydrobiol. *72,* 409–439 (1973)

Dumont, H. J.: A competition-based approach of the reverse vertical migration in zooplankton and its implications, chiefly based on a study of the interactions of the rotifer *Asplanchna priodonta* (Gosse) with several Crustacea Entomostrara. Int. Revue ges. Hydrobiol. *57,* 1–38 (1972)

Duval, W. S. and G. H. Geen: Diel feeding and respiration rhythms in zooplankton. Limnol. Oceanogr. *21,* 823–829 (1976)

Ebbesmeyer, C. C.: Some observations of medium scale water parcels in a fjord: Dabob Bay, Washington, 111 pp. Ph.D. thesis, University of Washington, Seattle, Washington 1973

Enright, J. T.: Diurnal vertical migration: adaptive significance and timing. Part 1. Selective advantage: a metabolic model. Limnol. Oceanogr. *22,* 856–872 (1977)

Enright, J. T. and H. W. Honegger: Diurnal vertical migration: adaptive significance and timing. Part 2. Test of the model: details of timing. Limnol. Oceanogr. *22,* 873–886 (1977)

Gauld D. T.: Diurnal variations in the grazing planktonic copepods. J. mar. biol. Ass. U.K. *31,* 456–474 (1953)

Haney, J. F.: An *in situ* examination of the grazing activities of natural zooplankton communities. Arch. Hydrobiol. *72,* 87–132 (1973)

Haney, J. F. and D. J. Hall: Diel vertical migration and filter-feeding activities of *Daphnia.* Arch. Hydrobiol. *75,* 413–441 (1975)

Holm-Hansen, O., C. J. Lorenzen, R. W. Holmes and J. D. H. Strickland: Fluorometric determination of chlorophyll. J. Cons. perm. int. Explor. Mer *30,* 3–15 (1965)

Jeffrey, S. W.: Paper chromatographic separation of pigments in marine phytoplankton. Aust. J. mar. Freshwat. Res. *16,* 307–313 (1965)

Jeffrey, S. W.: Profiles of photosynthetic pigments in the ocean using thin-layer chromatography. Mar. Biol. *26,* 101–110 (1974)

Kerfoot, W. B.: Bioenergetics of vertical migration. Am. Nat. *104,* 529–546 (1970)

Levi, D. and T. Wyatt: On the dependence of pheopigment abundance on grazing by herbivores. Thalassia jugosl. *7,* 181–183 (1971)

Longhurst, A. R., C. J. Lorenzen and W. H. Thomas: The role of pelagic crabs in the grazing of phytoplankton. Ecology *48,* 190–200 (1967)

Lorenzen, C. J.: A note on the chlorophyll and phaeophytin content of the chlorophyll maximum. Limnol. Oceanogr. *10,* 482–483 (1965)

Lorenzen, C. J.: A method for the continuous measurement of in vivo chlorophyll concentration. Deep-Sea Res. *13,* 223–227 (1966)

Lorenzen, C. J.: Vertical distribution of chlorophyll and phaeopigments: Baja California. Deep-Sea Res. *14,* 735–745 (1967 a)

Lorenzen, C. J.: Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. Limnol. Oceanogr. *12,* 343–346 (1967 b)

Lorenzen, C. J., F. R. Shuman and J. T. Bennett: *In situ* calibration of a sediment trap. Limnol. Oceanogr. *26,* 580–584 (1981)

Lorenzen, C. J. and N. A. Welschmeyer: The *in situ* sinking rates of herbivore fecal pellets. J. Plankton Res. *5,* 929–933 (1983)

Mackas, D. and R. Bohrer: Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J. exp. mar. Biol. Ecol. *25,* 77–85 (1976)

McAllister, C. D.: Aspects of estimating zooplankton production from phytoplankton production. J. Fish. Res. Bd Can. *26,* 199–220 (1969)

McLaren, I.: Effects of temperatures on the growth of zooplankton, and the adaptive value of vertical migration. J. Fish. Res. Bd Can. *20,* 685–727 (1963)

McLaren, I.: Demographic strategy of vertical migration by a marine copepod. Am. Nat. *108,* 91–102 (1974)

Nauwerck, A.: Zur Bestimmung der Filtrierrate limniischer Planktontiere. Arch. Hydrobiol. (Suppl.) *25,* 83–101 (1959)

Nemoto, T.: Chlorophyll pigments in the stomach of euphausiids. J. oceanogr. Soc. Japan *24,* 253–260 (1968)

Nemoto, T.: Chlorophyll pigments in the stomach and gut of some macrozooplankton species. *In:* Biological oceanography of the Northern North Pacific Ocean, pp 411–418. Ed. by A. Y. Takennonti. Tokyo: Idemitsu Shoten 1972

Nemoto, T. and Y. Saijo: Trace of chlorophyll pigments in stomachs of deep-sea zooplankton. J. oceanogr. Soc. Japan *24,* 310–312 (1968)

Ohman, M. D., B. W. Frost and E. B. Cohen: Reverse diel vertical migration: an escape from invertebrate predators. Science, N.Y. *220,* 1404–1407 (1983)

Patterson, J. and T. R. Parsons: Distribution of chlorophyll *a* and degradation products in various marine materials. Limnol. Oceanogr. *8,* 355–356 (1963)

Petipa, T. S. and N. P. Makarova: Dependence of phytoplankton production on rhythm and rate of elimination. Mar. Biol. *3,* 191–195 (1969)

Prahl, G. F. and R. Carpenter: The role of zooplankton fecal pellets in the sedimentation of polycyclic aromatic hydrocarbons in Dabob Bay, Washington. Geochim. cosmochim. Acta *43,* 1959–1972 (1979)

Runge, J. A.: Egg production of *Calanus pacificus* Brodsky and its relationship to seasonal changes in phytoplankton availability, 110 pp. Ph.D. thesis, University of Washington, Seattle, Washington 1981

Shuman, F. R.: The fate of phytoplankton chlorophyll in the euphotic zone: Washington coastal waters, 250 pp. Ph.D. thesis, University of Washington, Seattle, Washington 1978

Shuman, F. R. and C. J. Lorenzen: Quantitative degradation of chlorophyll by a marine herbivore. Limnol. Oceanogr. *20,* 580–586 (1975)

SooHoo, J. B. and D. A. Kiefer: Vertical distribution of phaeopigments – I. A simple grazing and photooxidative scheme for small particles. Deep-Sea Res. *29,* 1539–1552 (1982 a)

SooHoo, J. B. and D. A. Kiefer: Vertical distribution of phaeopigments – II. Rates of production and kinetics of photooxidation. Deep-Sea Res. *29,* 1553–1564 (1982 b)

Starkweather, P. L.: Diel patterns of grazing in *Daphnia pulex.* Ver. int. Verein. theor. angew. Limnol. *19,* 2851–2857 (1975)

Starkweather, P. L.: Diel variation in feeding behavior of *Daphnia pulex.* Influence of food density and nutritional history of mandibular activity. Limnol. Oceanogr. *23,* 307–317 (1978)

Welschmeyer, N. A.: The dynamics of phytoplankton pigments: implications for zooplankton grazing and phytoplankton growth, 176 pp. Ph.D. thesis, University of Washington, Seattle, Washington 1982

Welschmeyer, N. A. and C. J. Lorenzen: Carbon-14 labeling in phytoplankton carbon and chlorophyll *a* carbon: determination of specific growth rates. Limnol. Oceanogr. *29,* 135–145 (1984)

Yentsch, C. S.: The measurement of chloroplastic pigments – thirty years of progress? *In:* Chemical environment in the aquatic habitat, pp 225–270. Ed. by H. C. Golterman and R. S. Clymo. Amsterdam: North-Holland 1967

Zaret, T. M. and J. S. Suffern: Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. *21,* 804–813 (1976)

Date of final manuscript acceptance: July 6, 1984.
Communicated by N. D. Holland, La Jolla