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Zooplankton grazers as transformers of ocean optics: A dynamic model

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ABSTRACT

A model was developed, based on data collected in the Southern California Bight region, to assess the effect of zooplankton grazing on the attenuation of light due to suspended particles. Diel vertical distribution and grazing activity of the principal zooplankton grazers in the coastal waters of southern California were studied during mid-March, 1986. *Calanus pacificus* exhibited vertical migration, but *Acartia* spp. and *Paracalanus* spp. did not. All species had a diel feeding rhythm, whether or not they migrated; grazing activity, measured by the gut fluorescence method, increased at night. Model parameters are temperature, particle doubling rate, particle size-frequency distribution, zooplankton grazing efficiency and zooplankton size-frequency distribution. With parameters at their standard values, the diffuse attenuation coefficient, K_p, remains approximately constant, decreasing by only 3.5% in one 24-h cycle. The model is most sensitive to changes in temperature and, secondly, to changes in the abundance of grazers. Without grazers, and at the reference value for particle doubling rate, K_p is expected to increase by 8.2% d^{-1}. At the upper limit of zooplankton abundance grazing produces a decrease in K_p of 63.5% d^{-1}; at the upper limit of particle growth rate, K_p increases by $\geq$50% d^{-1}. We conclude that macrozooplankton can have a major effect on the optical characteristics of sea water.

1. Introduction

a. The role of zooplankton in ocean optics. One of the most widely accepted methods to describe the optical quality of sea water is to measure the rate at which light is attenuated vertically (Jerlov, 1968, 1976). As it passes through the water column, light is reduced by processes of diffusion, absorption and scattering due to three components: the water itself, dissolved matter and suspended particles. Most *in situ* measurements yield an apparent property, K, the "diffuse attenuation coefficient" (usually called the "extinction coefficient" by marine biologists), which integrates the many factors attenuating light.

What controls optical variability in the ocean? Jerlov (1968), in his comprehensive text on optical oceanography stated at the outset (p. 1) that "The subject is chiefly physical. . . ." However, in the euphotic zone of the coastal ocean, the primary

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contribution to light attenuation is from suspended particles (Clarke and James, 1939; Kishino, 1980), for which particles in the size range 1–40 μm diameter are chiefly responsible (Morel and Bricaud, 1981). It is therefore not surprising that phytoplankton have been recognized to have a key influence on light extinction in the ocean (Lorenzen, 1972; Kirk, 1975a,b; Atlas and Bannister, 1980).

Thus, the factors controlling light attenuation in the ocean are identical to those which control the distribution and standing stocks of suspended particulates (Marra and Hartwig, 1984). Ignoring advective processes, the standing stock of phytoplankton at any given time is determined by the balance between phytoplankton growth and death. It has long been recognized that the principal cause of phytoplankton death is predation by zooplankton (Riley, 1946). The impact of zooplankton grazing on particulate dynamics has been the subject of numerous field studies and mathematical models (*e.g.* Steele and Mullin, 1977; Wroblewski, 1977; Frost *et al.*, 1983; Herman and Platt, 1983), but the effects of grazing on light attenuation have not been considered in optical oceanography.

Our fundamental assertion is that zooplankton grazing affects the attenuation of light in sea water. In this paper we attempt to quantify this phenomenon. We first report on a series of *in situ* measurements of zooplankton diel vertical distribution and grazing. We then proceed to model the effect of zooplankton grazing on natural particulate populations, and consider the consequent change in light attenuation. The output of the model is the diffuse attenuation coefficient, K. The terms in the model include temperature, the standing stock and growth rate of particulates, their size-frequency distribution, the weight-frequency distribution of zooplankton, their size-selective feeding behavior, and their grazing rates.

b. Diel changes in zooplankton grazing. It is generally accepted that many marine and freshwater zooplankton feed at night. Many recent studies have inferred the presence of a distinct nocturnal feeding rhythm, associated with diel migration, from visual observations of gut fullness. Such observations have been made for a number of zooplankton species, including *Pseudocalanus elongatus* (Zagorodnyaya, 1975), *Pseudodiaptomus hessei* (Hart, 1977), *Mysis relicta* (Grossnickle, 1979), *Euphausia diomedeae* (Ponomareva, 1971), *Thysanopoda* sp. (Hu, 1978), *Calanus glacialis* (Peruyeva, 1978), *Calanus helgolandicus* (Gauld, 1953), *Calanus finmarchicus* (Gauld, 1953), and many copepods from the Pacific Central Gyre (Hayward, 1980). In one of the few attempts to make simultaneous *in situ* measurements of grazing and vertical migration, Haney and Hall (1975) showed that *Daphnia* spp. fed by night, at a time corresponding to their residence period in surface waters.

Head *et al.* (1985) measured daily rhythms in the *in situ* grazing rates of Arctic copepods, and suggested that these might be due to daily changes in light intensity, even though the copepods did not migrate vertically. Pronounced nocturnal grazing activity has been observed in the arctic copepods *Calanus hyperboreus* and *Calanus*

glacialis (Head, 1986), as well as in several species of North Sea copepods (Baars and Oosterhuis, 1984). However, diel periodicity in zooplankton grazing activity has not always been observed. For example, Boyd *et al.* (1980) observed no diel periodicity in grazing activity of *Calanus chilensis* or *Centropages brachiatus* at onshore stations near Peru, but offshore they found increasing grazing activity either during the day (*C. chilensis*) or during the night (*C. brachiatus*).

In summary, zooplankton sometimes migrate on a diel basis, and sometimes they do not. Similarly, their grazing activity may or may not fluctuate with regular diel periodicity. Therefore, before we could proceed to model particle dynamics in local waters during spring, we required certain field measurements. First, we observed diel changes in vertical distribution of the entire zooplankton community, defined as all zooplankton trapped by 100-μm mesh. Second, we estimated diel changes in the *in situ* grazing rates of the principal species in the community using the gut fluorescence method. In the model presented here, we have used simple discrete-time equations to apply zooplankton grazing pressure to natural particulate assemblages comprised of particles 1–20 μm radius, and have calculated the hourly change in the diffuse attenuation coefficient, K, over a 24-h cycle. We demonstrate that, in a range of conditions which prevail in the coastal waters of southern California, zooplankton grazing can have a significant effect on the optical quality of sea water.

2. Methods

a. Sample collection. Zooplankton samples were collected from aboard a 17-ft. Boston Whaler in La Jolla Bay (32°50′N: 117°10′W) at a station located over 80 m of water near the head of a submarine canyon, Scripps Canyon, approximately 1 km offshore. We used a pumping system to collect samples at a series of six discrete depths (3, 8, 13, 22, 28 and 37 m). Each series constituted a "station." We collected samples from 13 such stations at roughly 3-h intervals from 1700 h, March 19 to 0700 h, March 21, 1986.

The pumping system was operated as follows. Water was pumped through a 7.5-cm diameter flexible hose from the sampling depth to a double-diaphragm, gas-powered Mud-Hog® pump, and from there into a 200-liter polyethylene tub on the deck of the skiff. Inflow was diverted over the side of the skiff when the tub was filled to an overflow port at the 180-liter mark. The tub contents were then drained by opening a valve in the base and allowing water to flow out through a quick-disconnect fitting covered with 10-μm mesh. Once the tub was empty the quick-disconnect fitting was removed, inverted over a sample jar, and material on the filter was backwashed into the jar with filtered sea water. Formalin was added to bring the final concentration to approximately 5%, and the sample was stored for later taxonomic analysis. The pump intake was then lowered to the next sampling depth and the procedure repeated until all station depths had been sampled.

b. Taxonomic analyses. Formalin preserved samples were subsampled, using a Stempel pipet, to obtain three equal aliquots of 1/10 each. Counts for a given species and stage generally exceeded 20 in each aliquot, but when the total count was less than 10, we counted the entire sample. Zooplankton were sorted into the following categories: small nauplii (100–300 μm), large nauplii (300–500 μm), *Corycaeus* spp. copepodites CI–CV, *Corycaeus* spp. adults, and copepodite stages CI–CIII, CIV–CV, and CVI adults of *Calanus pacificus, Acartia* spp. and *Paracalanus* spp. Together, these accounted for >90% of the total zooplankton numbers. The remainder included larvaceans, harpacticoid copepods, pteropods, and larvae of decapods and euphausiids.

c. In situ gut pigment content of zooplankton. One of the most popular methods for estimating grazing rates of zooplankton is the "gut fluorescence" method (Mackas and Bohrer, 1976), which purportedly provides an *in situ* rate. As the gut fluorescence method for estimating *in situ* grazing rates has come into common use, certain problems have appeared. The method is usually applied by capturing zooplankton from the field, sorting them to species or stage, then allowing them to defecate in filtered sea water for a period of several hours (e.g. Boyd *et al.*, 1980; Dagg and Grill, 1980; Dagg *et al.*, 1980; Dagg and Wyman, 1983; Tande and Båmstedt, 1985). During this incubation period animals are removed and their gut contents measured with a fluorometer. The decline in gut pigment, P, has been described as a negative exponential function of time, t from the equation

$$P = P_{\max} e^{-kt} \tag{1}$$

where $P_{\max}$ is the initial gut pigment content and k is the defecation rate constant. Calculation of the ingestion rate, I, from the equation

$$I = kP_f \tag{2}$$

where P_f is the gut pigment content of an animal freshly collected from the field, requires the assumption that rates of defecation and ingestion are equal.

Three main problems have arisen with this method. First, most experiments have required sorting zooplankton before placing them in filtered sea water. This procedure takes enough time that the initial gut content, $P_{\max}$, may be underestimated; furthermore, time constrains one to use relatively few animals, thus reducing potential statistical significance of the results. Second, several authors have suggested that the defecation rate, k, is not constant but rather decreases with time (Mackas and Bohrer, 1976; Baars and Oosterhuis, 1984; Wang and Conover, 1986). This is a more serious problem, since it suggests that the exponential equation (1)—which requires a constant k—is the wrong mathematical formulation of the process. Finally, there is mounting evidence that ingestion and defecation rates are not simultaneously equal; a number of studies suggest that ingestion exceeds defecation during periods of initial feeding, and

vice-versa once a feeding period ceases (e.g. Dagg and Wyman, 1983; Head *et al.*, 1984, 1985).

In our study, samples of zooplankton for *in situ* pigment analysis were collected using the same general procedure used for preserved samples, However we generally filtered three samples of >250 liters from each depth, and preserved them by freezing rather than by adding formalin. Instead of rinsing the sample into a sample jar, we rinsed into a 200-ml filtration manifold and removed the zooplankton on a 45-mm Whatman GF/D filter using gravity, a process which required <20 sec. The filter was then placed immediately in a plastic petri dish on dry ice. Once we returned to the laboratory (within several hours) the samples were placed in a −100°C freezer until fluorometric analyses could be performed.

For fluorometric analysis we used a Turner Designs® fluorometer. From frozen filters placed on a −25°C cold stage under a dissecting microscope, zooplankton were sorted and placed directly into test tubes containing 5 ml of 100% methanol. Gaseous nitrogen was passed over the frozen filter to prevent condensation and subsequent freezing of atmospheric H_2O. We restricted our analyses to CV and adult females of *Acartia* spp., *Paracalanus* spp. and *Calanus pacificus*. For each sample we generally used no more than five *Acartia* spp., eight *Paracalanus* spp. or two *C. pacificus*. For each time and depth we obtained 15–20 replicate measurements when possible. Samples were not homogenized (cf. Mackas and Bohrer, 1976), but were permitted to extract passively for at least 120 min, a procedure which has been shown to be equally effective (Huntley *et al.*, 1987).

d. Gut evacuation experiments. For these experiments we collected live zooplankton in a 333-μm mesh net towed obliquely from 30 m to the surface near our sampling station at approximately midnight of March 19, 1986. As soon as the net was brought to the surface we placed the codend contents in approximately 60 liters of Whatman GF/C-filtered sea water. We then removed samples of about 100 ml at time intervals of 3–5 min over an initial period of 30 min, and at least every 20 min for the next two hours. Each sample was treated in the same manner as the field samples, i.e. gravity filtered onto Whatman GF/D filter paper and placed in petri dish on dry ice. Zooplankton were sorted and analyzed using the same procedure we used for measurements of *in situ* pigment content.

3. Results

a. Diel vertical distribution of zooplankton. More than 95% of the numerical abundance of zooplankton >100 μm was accounted for by copepods. Of these, four taxa—*Calanus pacificus, Acartia* spp., *Paracalanus* spp. and *Corycaeus*—comprised more than 90%. With the exception of *Calanus pacificus* and large nauplii, all copepods exhibited the same pattern of diel vertical distribution, with abundances

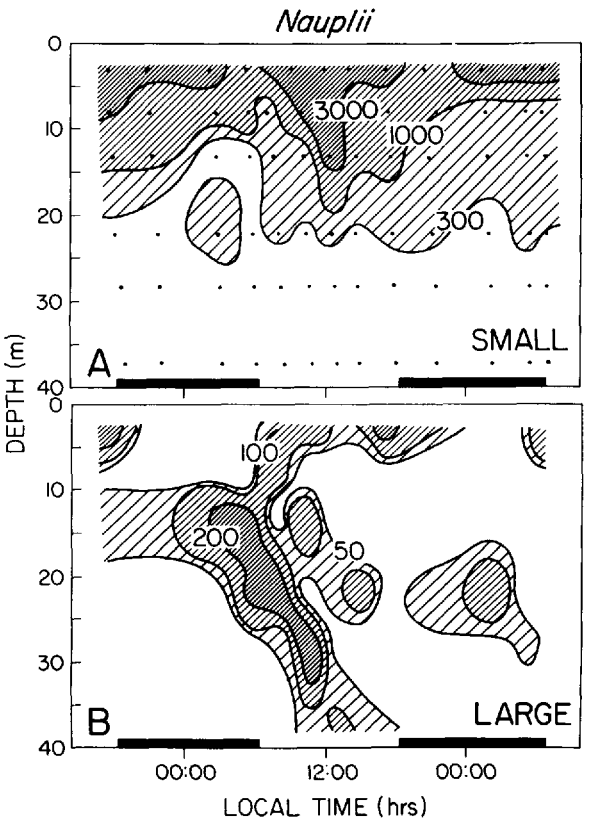

Figure 1. Abundance of small nauplii, 100–300 μm (a), and large nauplii, 300–500 μm (b), in numbers m^{-3}, as a function of depth and time. Nighttime is indicated by the two dark horizontal bars at the base of the graph. Dots indicate the time and depth of sampling, which is identical for Figs. 2–6. Figures 2–6 use the same conventions, with contours at increasing levels of darkness representing at least successive doublings of abundance.

being greatest in the upper 15 to 20 m (Figs. 1–5). Small nauplii were most abundant in the upper 5 m, attaining >3,000 m^{-3}, while below 20 m their abundance was generally <300 m^{-3} (Fig. 1a). Large nauplii were less abundant by an order of magnitude and displayed no distinct distributional pattern, though they tended to be more abundant in the upper 25 m (Fig. 1b).

Of all the copepods, *Acartia* spp. had the most restricted vertical range. Early copepodites (CI–CIII) were concentrated at >1,000 m^{-3} in a subsurface layer between 5 and 15 m (Fig. 2a), and were virtually absent below 20 m. Mid-copepodites (CIV–CV) and adults were concentrated in the upper 10 m (>400 m^{-3}); abundances below 15 m were consistently <30 m^{-3} (Figs. 2b, c). Nocturnal abundances of mid-copepodites and adults were slightly greater.

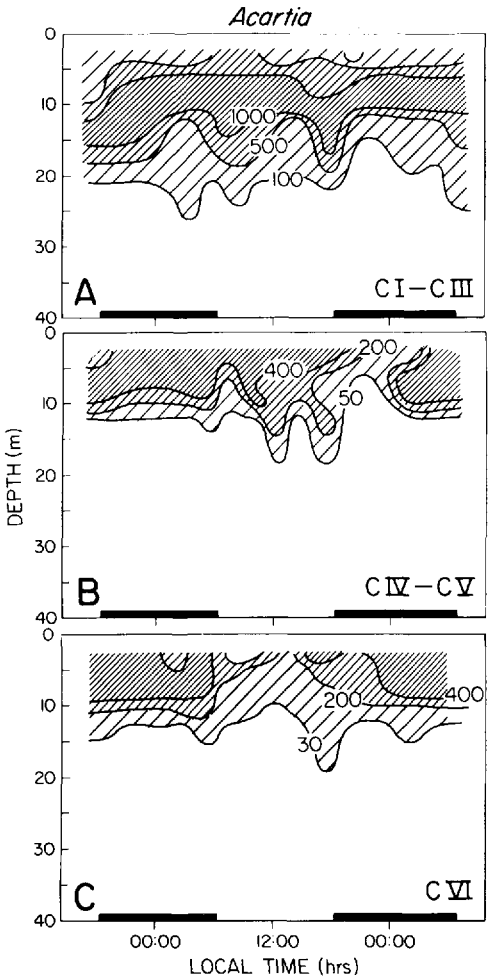

Figure 2. Abundance of *Acartia* spp. CI–CIII copepodites (a), CIV–CV copepodites (b) and adults (c) in numbers m^{-3}, as a function of depth and time.

Paracalanus spp. early copepodites were also concentrated in a subsurface layer, between 5 and 15 m, at >1,000 m^{-3} (Fig. 3a); they were present in low abundance (<200 m^{-3}) below 25 m. Mid-copepodites and adults were similarly distributed, with subsurface maxima >300 m^{-3}, and declining to <50 m^{-3} below 25 m (Figs. 3b, c).

Calanus pacificus was distributed differently than the other copepods. Early copepodites (CI–CIII) were found at abundances >20 m^{-3} in a layer between 10 to 25 m (Fig. 4a). Mid-copepodites exhibited no clear pattern (Fig. 4b). However, adults appeared to exhibit diel vertical migration, with maximum abundances (>30 m^{-3}) above 25 m during the night, and below 25 m during the day (Figs. 4c).

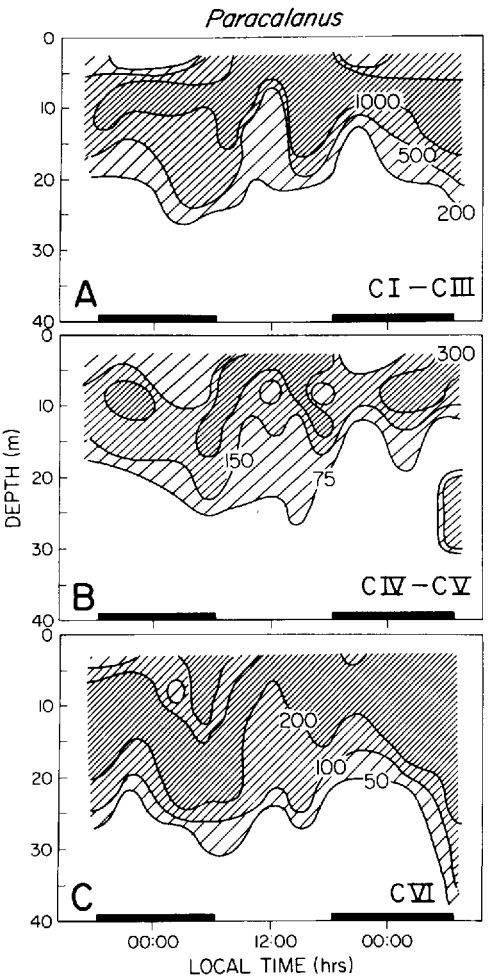

Figure 3. Abundance of *Paracalanus* spp. CI–CIII copepodites (a), CIV–CV copepodites (b) and adults (c) in numbers m^{-3}, as a function of depth and time.

Corycaeus spp. were most abundant in the upper water column. Copepodites reached abundances of >400 m^{-3} above 15 m, but were virtually absent below 20 m (Fig. 5a). Adults were most abundant (>800 m^{-3}) at mid-depths, from 10 to 20 m, and were distributed more deeply, with abundances <200 m^{-3} occurring down to 30 m (Fig. 5b).

b. In situ gut pigment content of copepods. Acartia spp., *Paracalanus* spp. and *Calanus pacificus* clearly had more pigment in their guts during the night than during the day (Fig. 6). For *Acartia* spp., gut pigment contents ranged over almost an order of

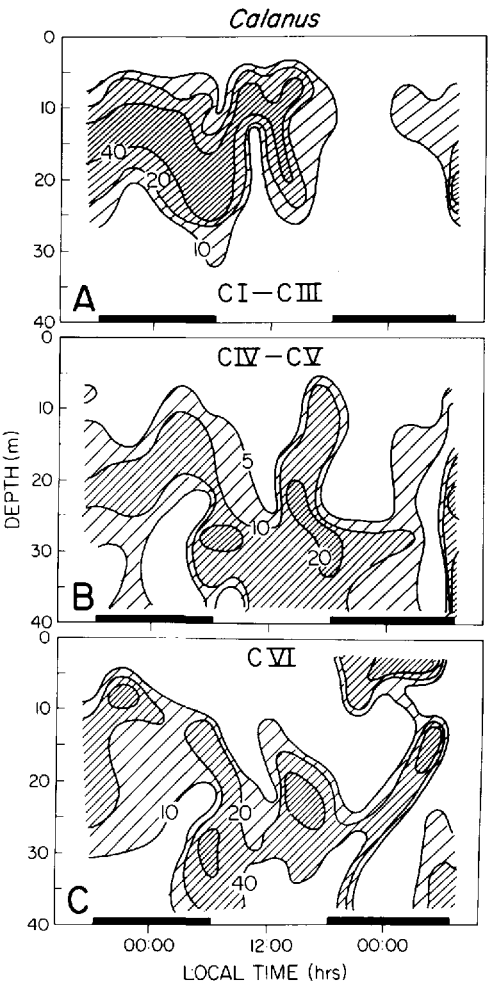

Figure 4. Abundance of *Calanus pacificus* CI–CIII copepodites (a), CIV–CV copepodites (b) and adults (c) in numbers m^{-3}, as a function of depth and time.

magnitude, from <0.15 ng individual^{-1} during the day to >0.75 ng individual^{-1} in the upper 10 m at night (Fig. 6a). High values of gut pigment tended to coincide with high abundances (Fig. 2). The mean gut pigment content for *Acartia* spp. was 0.48 (S.D. = 0.18) at night and 0.29 (S.D. = 0.11) during the day (Table 1). Gut pigment contents of *Paracalanus* spp. were low during the day (<0.10 ng individual^{-1}), but increased at all depths at night (>0.20 ng individual^{-1}; Fig. 6b). The mean value during the day (0.080 ± 0.026) almost doubled at night (0.153 ± 0.037; Table 1). For *Calanus pacificus* the diel changes in pigment content were even more striking, being <1.0 ng individual^{-1} during the day at all depths, and increasing to >5 ng individual^{-1}

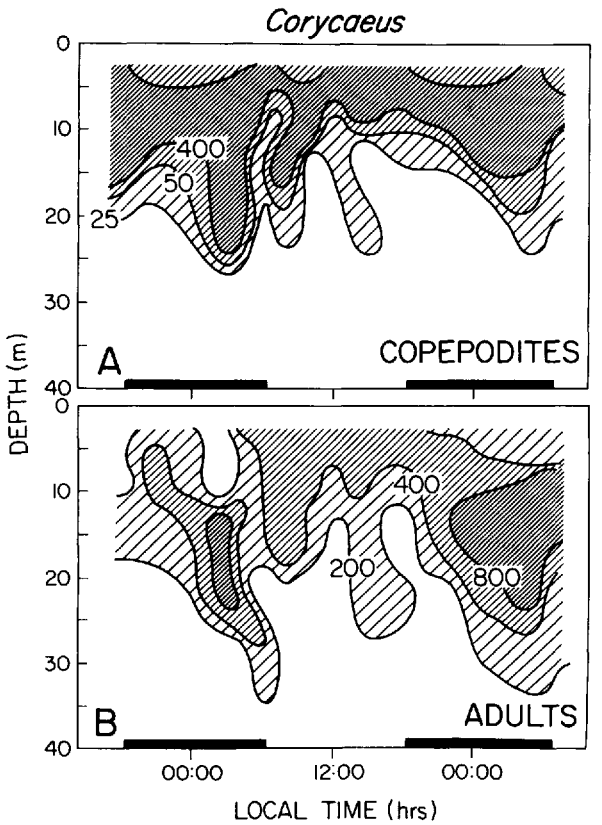

Figure 5. Abundance of *Corycaeus* copepodites (a) and adults (b) in numbers m^{-3}, as a function of depth and time.

in the upper 15 m at night (Fig. 6c). The mean night value for *C. pacificus* (4.23 ± 1.81) was more than five times greater than during the day (0.80 ± 0.41; Table 1).

c. Gut evacuation rates. We found that the exponential model of gut evacuation, using Eq. 1, gave a very poor fit to our data (Fig. 7), yielding lower coefficients of determination (Table 2), than those obtained by fitting a power model of the form:

$$P = P_{max}\, t^{-\phi} \tag{3}$$

where t is time (min) since maximum gut fullness, and where ϕ is the dimensionless constant from which we can obtain the gut evacuation rate, k, by:

$$k = \phi/t. \tag{4}$$

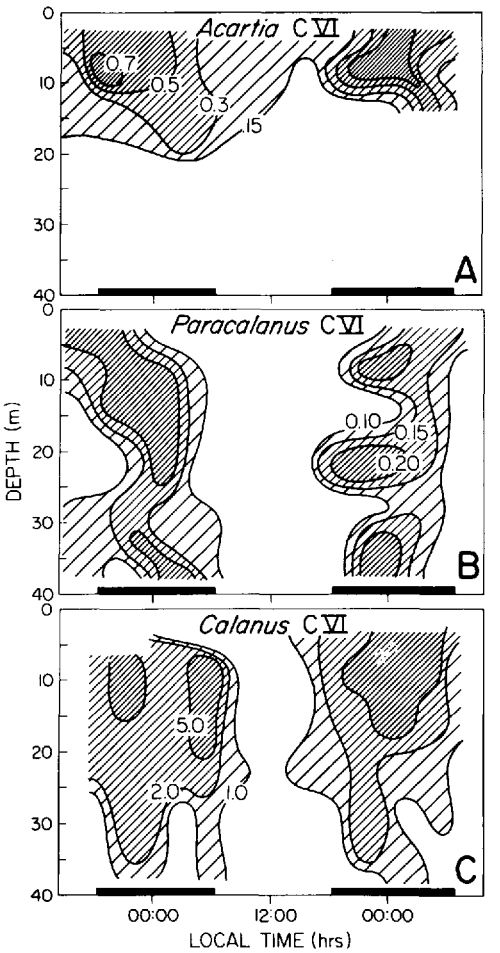

Figure 6. Gut pigment content (ng chlorophyll equivalents) of individual late copepodites of *Acartia* spp. (a), *Paracalanus* spp. (b) and *Calanus pacificus* (c). Contours at increasing levels of darkness representing at least successive doublings of gut pigment content. Highest contents were in surface waters (0–20 m) at night.

There is compelling biological justification for accepting the power model over the exponential one (Jobling, 1981). It incorporates the assumption that defecation rate, k, is an inverse function of residence time in the gut. This accounts for the frequent observation that k decreases with time since feeding (*e.g.* Mackas and Bohrer, 1976; Baars and Oosterhuis, 1984; Wang and Conover, 1986; Head, 1986). The exponential model, on the other hand, assumes that k is constant. It was suggested to us independently by both L. Quetin (pers. comm.) and E. Head (pers. comm.) that we

Table 1. Copepod gut pigment contents (ng chlorophyll equivalents individual^{-1}) of late stage copepodites (CV-CVI) of *Acartia* spp., *Paracalanus* spp. and *Calanus pacificus* at different times of night and day. Shown also are mean values and standard deviations. (*nd* = no data)

	Local time (h)	*Acartia* spp.	*Paracalanus* spp.	*Calanus pacificus*
Day	06:30	0.43	0.103	1.48
	07:45	0.15	0.053	1.25
	10:15	0.42	0.063	0.68
	12:30	0.26	0.064	0.59
	14:20	*nd*	0.128	0.52
	17:30	0.20	0.070	0.40
Mean:		0.29	0.080	0.80
S.D.:		0.11	0.026	0.41
Night	18:00	0.25	0.130	1.70
	21:00	0.40	0.214	3.52
	21:20	0.67	0.175	4.38
	01:45	0.79	0.152	6.70
	02:45	0.51	0.182	2.00
	05:00	0.37	0.097	4.98
	05:40	0.37	0.121	6.30
Mean:		0.48	0.153	4.23
S.D.:		0.18	0.037	1.81

could use the exponential model if we assume that only the initial data are relevant (e.g. data from the first 30 min of a 3-h experiment), and that we then fit the model only to those initial data. This approach has the effect of increasing the coefficient of determination but it ignores the acknowledged observation that gut evacuation rate decreases with time. Furthermore, the k value which results is strongly related to the amount of data one chooses to accept for the analysis.

If the gut pigment method for estimating evacuation rate has been used so widely, then why has the power model never been applied to copepods? We suggest the reason is purely statistical. Our measurements of the disappearance of gut pigment over time, particularly for *Acartia* spp. and *Paracalanus* spp., were much more numerous and frequent than those typically made in this type of experiment. For example, Dagg and Wyman (1983) made their measurements at invervals $\geq$20 min on $\leq$3 replicate samples of *Neocalanus plumchrus;* Head's (1986) measurements on *Calanus hyperboreus* and *C. glacialis* were made at 30-min intervals; Wang and Conover's (1986) measurements on *Temora longicornis* were made at invervals $\geq$15 min. By contrast, our measurements were made every 3–5 min during the first half hour, and every 10–20 min for the remainder of the experiment, on as many as 8 replicates. We would argue that the sheer difference in number and frequency of measurements permitted

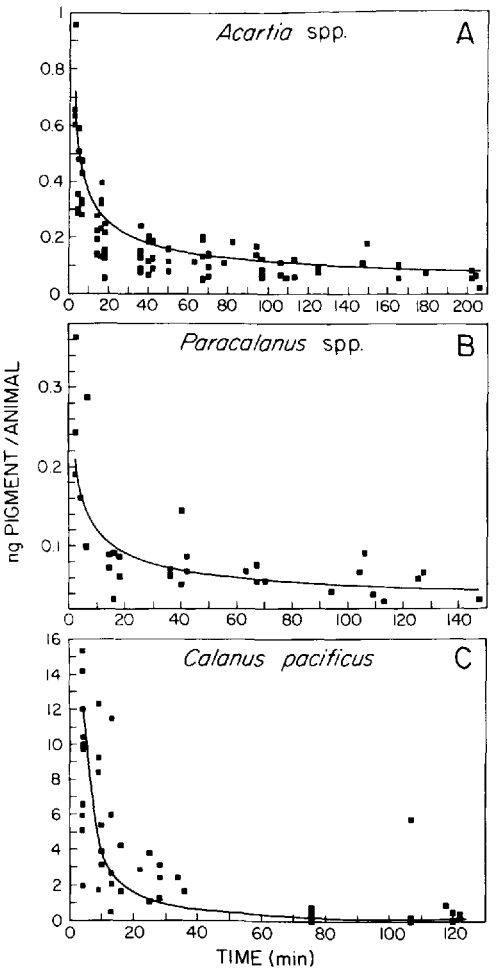

Figure 7. Gut evacuation experiments. Late-stage copepodites of *Acartia* spp. (a), *Paracalanus* spp. (b) and *Calanus pacificus* (c) were collected at night, placed in filtered sea water, and allowed to defecate for at least 2 h. The data were best fit by a negative power function; statistics are presented in Table 2.

us to better fit a relationship which was not a negative exponential function, and to differentiate it statistically (i.e. as a power function of time).

d. Ingestion and clearance rate estimates. The use of the power model to estimate ingestion rate from the gut pigment content of field-collected grazers requires assumptions which are different than those used in applying the exponential model. The basic equation for ingestion rate remains the same (i.e., $I = kP_f$), but the

Table 2. Gut evacuation rates of *Arcartia* spp., *Paracalanus* spp. and *Calanus pacificus*. Linear regression statistics for goodness of fit to both exponential and power models. P_{max} is the initial gut content estimated from gut evacuation experiments conducted at night. $P_{max,f}$ is the maximum gut content measured in separate individuals collected from the field at night. Number of measurements = n.

Model	Equation	Species	r^2	ϕ	k ($\cdot 10^3$ min^{-1})	P_{max} (ng pigment)	$P_{max,f}$ (ng pigment)	n
Exponential	$P = P_{max}e^{-kt}$	*Acartia*	0.44		8.57	0.249		
		Paracalanus	0.41		8.96	0.124		
		Calanus	0.50		36.70	6.228		
Power	$P = P_{max}t^{-\phi}$	*Acartia*	0.68	0.467	ϕ/t	0.762	0.79	83
		Paracalanus	0.62	0.372	ϕ/t	0.272	0.21	30
		Calanus	0.56	1.274	ϕ/t	68.85	6.70	49

dependence of k on the time since maximum gut fullness (Eq. 4), requires that we estimate it.

The principal assumption we require is that maximum gut fullness is equal to the initial value of gut pigment we measured in our nighttime gut evacuation experiments. This assumption may come close to the truth, since our estimates of maximum gut fullness are derived from measurements made at night—when all grazer species attained their greatest gut pigment content. Maximum gut pigment values of field-collected grazers, $P_{max,f}$, are comparable to estimated values of P_{max} from gut evacuation experiments (Table 2). In all cases, P_{max} is approximately equal to or greater than in field-collected individuals ($P_{max,f}$). Values of P_{max} estimated by the exponential model are significantly lower—yet another indication of the inadequacy of the exponential model (Table 2).

We now assume that field-collected grazers are actively defecating (i.e. $P_f = P$). Substituting into Eq. (3), we can now write:

$$P_f = P_{max}t^{-\phi} \tag{5}$$

which simply states that the gut pigment content of a field-collected grazer (P_f) is a negative power function ($-\phi$) of the time (t) since maximum gut fullness (P_{max}). We can now estimate the time, t, elapsed since a field-collected grazer had maximum gut fullness by rearranging Eq. (5) as follows:

$$\log t = \{\log P_{max} - \log P_f\}/\phi. \tag{6}$$

Ingestion rate is then calculated from:

$$I = \phi P_f/t \tag{7}$$

where all variables are as previously defined.

The clearance rate, F (ml h^{-1}), can then be calculated from:

$$F = I/C \tag{8}$$

(Frost 1972; Marin *et al.*, 1986), where C is the ambient concentration of pigment-containing food particles in the field (ng chl-*a* ml^{-1}), and I is given in units of ng chl-*a* h^{-1}. On the days we conducted our studies, concentrations of chlorophyll at 6 depths from 3 to 40 m ranged from 1.69 to 1.81 $\mu g\ L^{-1}$ ($\bar{x} = 1.75$; O. Holm-Hansen and B. G. Mitchell, unpubl. data).

We calculated the clearance rates, using Eq. (8), for all samples of late copepodite stages of each copepod species in our day and night field collections. Then, pooling all day and night data separately as in Table 2, we determined the fraction of the population which had estimated clearance rates, in 1-ml h^{-1} intervals, ranging from 0–20 ml h^{-1}. The results are presented in Figure 8.

There were distinct day-night differences in all three species, with clearance rates being significantly greater at night. For *Acartia* spp., >70% of the day population had clearance rates of <2 ml h^{-1}, whereas >75% of the night population had clearance rates of >2 ml h^{-1} (Fig. 8a). Similarly, >69% of the *Paracalanus* spp. day population had clearance rates of <2 ml h^{-1}, but >65% of the night population had clearance rates of >2 ml h^{-1} (Fig. 8b). A similar trend was evident for *Calanus pacificus* late stage copepodites (Fig. 8c).

It follows that the mean clearance rate of each copepod species was significantly greater during the day than during the night. We calculated a weighted mean clearance rate, F, from

$$\bar{F} = \sum_{i=1}^{j} \rho_i F_i \tag{9}$$

where ρ_i is the proportion of the population having a clearance rate F_i for the i'th category of clearance rate, considering a total of j categories of clearance rate in intervals of 1 ml h^{-1}. Mean clearance rates calculated by this method are presented in Table 3, and compared to reference estimates of clearance rate for pelagic grazers of similar weight using equations given by Huntley and Boyd (1984), which were based on approximately 1,000 experimental measurements of zooplankton clearance rates reported in the literature. The reference estimates were made assuming a temperature of 13°C, which is the approximate sea-surface temperature in La Jolla Bay during March (Huntley *et al.*, 1986). For all three species the clearance rates calculated from gut content were greater, particularly at night, than those estimated from the historical database of experimental measurements.

4. Model equations

a. Diffuse attenuation coefficient. In this model, we consider the diffuse attenuation coefficient due to suspended particulates at time t ($K_{p,t}$). In the euphotic zone of the

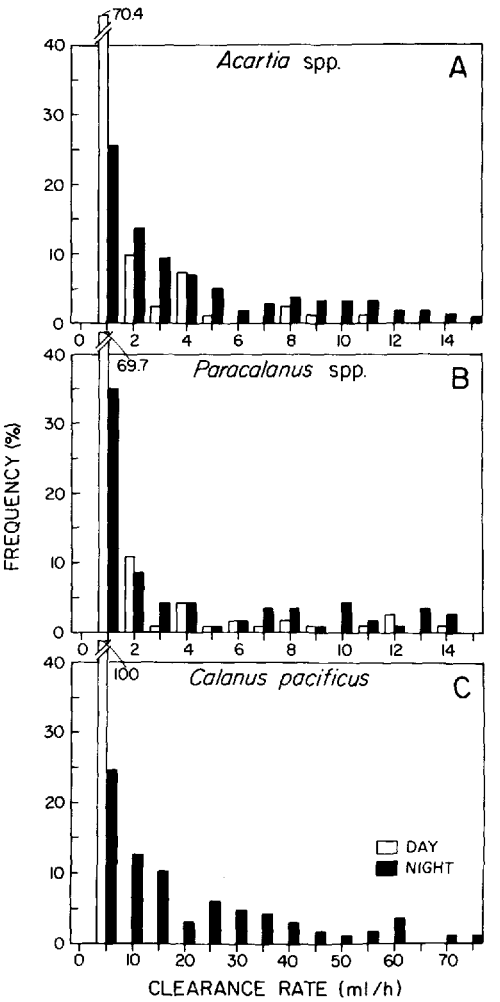

Figure 8. Frequency distribution of clearance rates of *Acartia* spp. (a), *Paracalanus* spp. (b) and *Calanus pacificus* (c), estimated from the power model of gut evacuation rate. Calculated frequencies are based on 81 to 249 samples, depending on the species. Without exception, a greater portion of the population had lower clearance rates during the day than during the night.

ocean it is suspended particles which are primarily responsible for the attenuation of light, as opposed to contributions from either dissolved matter or sea water itself, and therefore $K_{p,t}$ in this region closely approximates K (Jerlov, 1968). We chose to evaluate $K_{p,t}$ only at 435 nm, since it is at this wavelength that phytoplankton-derived pigments (Morel and Bricaud, 1981) and natural particulates (Kishino, 1980) have their maximum absorbance. In our model, the assemblage is composed of particles

Table 3. Copepod clearance rates: a comparison of mean rates estimated from the power model of gut evacuation rate (Eq. 9) to those estimated from traditional grazing experiments. The "traditional" estimate is based on equations given by Huntley and Boyd (1984), and assumes a temperature of 13°C; we used dry weights of 8 μg for both *Acartia* and *Paracalanus* spp., and 100 μg for *Calanus pacificus* CV/CVI copepodites (see Table 4).

		Clearance Rate (ml h^{-1})		
Method	Time	*Acartia* spp.	*Paracalanus* spp.	*Calanus pacificus*
Power Model:	Day	2.62	3.39	4.81
	Night	7.92	9.74	45.24
Traditional Estimate:		0.53	0.53	4.89

which range in size from 1 to 20 μm radius. $K_{p,t}$ is calculated as the sum of the diffuse attenuation coefficients for each particle size class, at intervals of 1 μm radius, from:

$$K_{p,t} = \sum_{i=1}^{20} a_{i,t} \tag{10}$$

where $a_{i,t}$ is the diffuse attenuation coefficient (m^{-1}) of a suspension of particles of radius i (μm) at time t (h).

Morel and Bricaud (1981) proposed a theoretical approach for evaluating the specific absorption of phytoplankton cells, from which their contribution to light attenuation can be determined. Here we make the simplifying assumption that their model can be extended to include all suspended particulates. We would certainly prefer to distinguish between the absorption and scattering characteristics of living and nonliving particles, but experimental and theoretical studies appear generally not to have advanced sufficiently (Jerlov, 1976). Furthermore, even if we would differentiate between the optical characteristics of living and nonliving particles, their proportionate contributions to categories of natural size-spectra are known only in bandwidths which are much broader (O. Holm-Hansen, pers. comm.) than required for the evaluation of optical effects. Therefore, following Morel and Bricaud (1981), we express the attenuation coefficient for a given size class of particles of radius i ($a_{i,t}$) in terms of their abundance, absorption efficiency and cross-sectional area:

$$a_{i,t} = B_{i,t}\ Q_{a,i}\ s_i \tag{11}$$

where $B_{i,t}$ is the abundance of particles (particles m^{-3}) of radius i at time t, $Q_{a,i}$ is the absorption efficiency (dimensionless) of particles of radius i, and s_i is the cross-sectional area (m^2) of a particle of radius i. $Q_{a,i}$ was calculated using Eq. (1) from Morel and Bricaud (1981) and increases with particle size (Fig. 9).

b. Particulate abundance. Changes in $K_{p,t}$ depend upon changes in particulate abundance (Eqs. 10 and 11). We used a discrete-time equation to model hourly

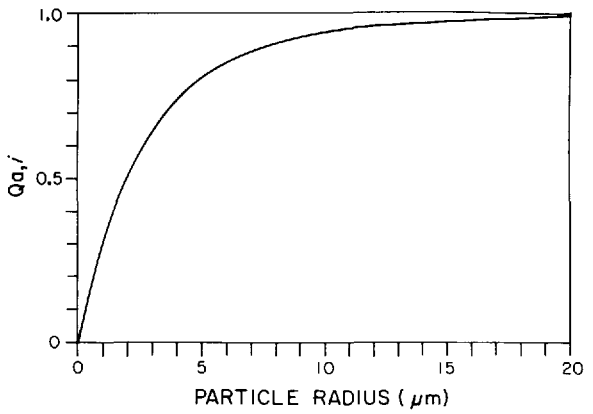

Figure 9. Absorption efficiency ($Q_{a,i}$) for particles of radius 1 to 20 μm. $Q_{a,i}$ was evaluated at a wavelength of 435 nm using Eq (1) from Morel and Bricaud (1981).

changes in the abundance of each particle size category ($B_{i,t}$) as a function of its doubling rate and the grazing pressure upon it by zooplankton:

$$B_{i,t} = (\mu_i - g_{i,t})\, B_{i,t-1} \tag{12}$$

where μ_i is the doubling rate (h^{-1}) of a particle of radius i, $g_{i,t}$ is the grazing coefficient (h^{-1}) of zooplankton on particles of radius i at time t, and $B_{i,t-1}$ is the abundance of particles of radius i one hour prior to time t.

The model considers only the upper 40 m of the water column, and further considers this region to be physically homogeneous. This depth was chosen because (1) it represents the approximate depth of the 1% light level in the Southern California Bight (Eppley and Holm-Hansen, 1986) and (2) it was the maximum depth of sampling in our field study. We assume that changes in phytoplankton abundance are not affected by the physical environment (e.g. horizontal advection, vertical mixing).

The initial abundance of each particle size class was based on the mean of >30 Coulter Counter measurements of natural particulate matter in samples collected from the euphotic zone in La Jolla Bay during the period of our study (O. Holm-Hansen and B. G. Mitchell, unpubl. data). These data indicated that the abundance of particles is a negative power function of size; the abundance in a given size class can be specified from the abundance of 1-μm radius particles from the equation:

$$B_i = B_1\, r_i^{-3.25} \tag{13}$$

where B_1 is the abundance of 1-μm radius particles (30,000 particles ml^{-1}) and r_i is particle radius (μm).

c. Particle doubling rate. We assume in this model that the only growing particles in natural assemblages are phytoplankton. It is generally accepted that the doubling rate

of a phytoplankton cell can be expressed as a function of both its size and temperature. The mathematical expressions proposed for these relationships are exponential (Banse, 1982; Eppley, 1972). Although our model conserves the size and temperature exponents, we have modified the intercept to account for (1) the combined effect of both size and temperature and (2) the relative contribution of nonliving particles to natural particulate assemblages. To begin with, we produced a combined coefficient by evaluating the equations of both Banse (1982) and Eppley (1972) at 20°C. We then corrected this coefficient to produce an effective doubling rate based on the ratio of ^{14}C productivity:POC concentration measured at 14 stations in the Southern California Bight (Eppley *et al.*, 1983). This yielded the equation:

$$\mu_i = 0.045\ \mu_1\ T^{0.00275}\ [1.333\ \pi\ r_i^3]^{-0.11} \tag{14}$$

where μ_i is the doubling rate of a particle of radius i (h^{-1}), μ_1 is the doubling rate of a 1-μm radius particle and T is temperature (°C).

In this model the doubling rate is assumed to be constant during the day-night cycle. There are several reasons for this assumption. Doubling rate should not be confused with growth rate or the rate of carbon incorporation, which clearly is greater during the day during photosynthesis. Doubling rate, *per se,* has a distinct diel rhythm in some dinoflagellate species (e.g. Weiler and Eppley, 1979; Sweeney, 1959), but not in others (Hall, 1925; Nozawa, 1940). In those dinoflagellates where phased cell division occurs, it generally occurs at night. In marine diatoms, however, division occurs throughout the 24-h cycle (Subramanyan, 1945; Jorgensen, 1966; Paasche, 1968). Given this broad variability, we have no reason to incorporate phased cell division into the model. Furthermore, the effect of cell division on diel particle dynamics will be diminished in proportion to the amount of nonliving particulate matter, which can be considerable in southern California waters (Beers *et al.*, 1980).

d. Zooplankton grazing rate. Many factors influence the grazing rate of a pelagic herbivore (Steele and Mullin, 1977; Steele and Frost, 1977). In the grazing equation that follows, we have incorporated the effects of zooplankton body weight and temperature (Huntley and Boyd, 1984), cell size (Bartram, 1980) and observed diel variability:

$$g_{i,t} = \sum_{j=1}^{5} g_{i,j,t} \tag{15}$$

where $g_{i,t}$ is the grazing coefficient (h^{-1}) and where j denotes the zooplankton dry weight class W_j (mg). We considered that all grazing could be accounted for by nauplii, copepodites and adults of *Acartia* spp., *Paracalanus* spp. and *Calanus pacificus*. Together, these species and stages accounted for >90% of the total zooplankton observed in our field study. We assigned these to the weight categories shown in Table 4.

Table 4. Distribution of the most common species and stages of epipelagic zooplankton herbivores in the La Jolla Bight according to dry weight categories assigned in the model. Dry weights (μg) for *Acartia* spp. and *Calanus pacificus* are approximations from published sources (Mullin and Brooks, 1970; Landry, 1978; Durbin and Durbin, 1981; Huntley, 1985b); dry weights for *Paracalanus* spp. are assumed to be identical to those of *Acartia* spp., since both are the same size.

Dry weight category (W_j)	Weight (μg)	Species & stage
W_1	0.5	*Acartia* spp. nauplii
		Paracalanus spp. nauplii
W_2	1.0	*Acartia* spp. CI-CIII
		Paracalanus spp. CI-CIII
		Calanus pacificus nauplii
W_3	3.0	*Acartia* spp. CIV-CV
		Paracalanus spp. CIV-CV
		C. pacificus CI-CIII
W_4	8.0	*Acartia* spp. adults
		Paracalanus spp. adults
W_5	20.0	*C. pacificus* CIV-CV
W_6	150.0	*C. pacificus* adults

Huntley and Boyd (1984) conceived a model which expressed zooplankton clearance rate as a function of dry body weight, W, and temperature, T. To their model we have added the effect of size-selective feeding, based on measurements and a mathematical model presented by Bartram (1980). We have combined the appropriate equations to express the grazing coefficient as follows:

$$g_{i,j,t} = N_j \, [b_{1,t} \, W_j^n] \, [1 - e^{b_2(r_i - r_o)}] \tag{16}$$

where N_j is the abundance of zooplankton (individuals L^{-1}) in weight class W_j (mg dry weight), $b_{1,t}$ is the clearance rate coefficient, evaluated as:

$$b_{1,t} = f_t e^{0.234T} \tag{17}$$

where T is temperature (°C), as given in Huntley and Boyd (1984), where n is the clearance rate ceofficient, evaluated as:

$$n = 0.681 \, e^{0.0199T} \tag{18}$$

also as given by Huntley and Boyd (1984), and where b_2 is the slope of the grazing efficiency equation (Bartram, 1980) and r_o is the radius of the smallest particle which can be grazed with measurable efficiency (Bartram, 1980).

The second term in Eq. (16), $[b_{1,t} \, W_j^n]$, represents the maximum clearance rate of a zooplankter of weight W_j. Huntley and Boyd (1984), basing their model of zooplankton grazing on classical measurements of clearance rate, evaluated f_t in Eq. (17) at f_t= 1.78. We have used this value in one run of the model presented here. However,

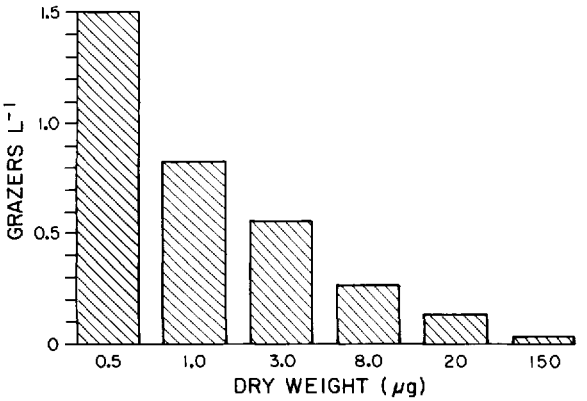

Figure 10. Abundance of grazers per dry weight class (μg) used for the standard run of the model. Both the absolute values and the relative abundances between weight classes are based on a compilation of data from our own field study in La Jolla Bay (78 samples) and those of Mullin *et al.* (1985) in nearby Del Mar, California during spring (44 samples).

estimates of clearance rate based on gut fluorescence measurements of zooplankton collected during our field study were much higher than those estimated using $f_t = 1.78$. Furthermore, clearance rates were even greater during the night than during the day. The day/night difference ranged from 1–9.2 times greater for *Calanus pacificus,* to 5.0–15.0 times greater for *Acartia* spp., to 6.4–18.5 times greater for *Paracalanus* spp. To account for the mean difference in clearance rate estimates, which we believe may be real, we have modeled the grazing rate as a step function by increasing the value of f_t such that during the day (i.e. for $6 < t < 18$), $f_t = 7.4$, and at night $f_t = 25.4$. At the same time, however, we have preserved the value of the exponent, n, given by Huntley and Boyd (1984), since we have no reason to doubt the weight-dependence of clearance rate which they evaluated.

The abundance of zooplankton in each weight category approximately follows an exponential decrease (Fig. 10), where the abundance of weight class (j) is defined as a proportion of the previous ($j - 1$) weight class from:

$$N_j = k_j N_{j-1} \text{ (for } j = 2 \text{ to } 6) \tag{19}$$

where $N_1 = 1.5$ (zooplankton L^{-1}, standard run), $k_2 = 0.55$, $k_3 = 0.67$, $k_4 = 0.48$, $k_5 = 0.50$ and $k_6 = 0.24$. The values for N_1 and k_j were obtained from mean values of zooplankton abundance in the respective size categories from both our field data and that of Mullin *et al.* (1985).

5. Model parameters

Five parameters (*i.e.* temperature, μ_1, N_1, b_2, and r_o) were analyzed in the sensitivity analysis (Jörgensen, 1986). Their standard values and ranges are given in Table 5. The standard value for temperature (17°C), and its range, were taken from Scripps Pier

Table 5. Standard values, and the range of values, of the five parameters used in the model. All values were obtained from published reports for studies from the Southern California Bight. For sources of values please see text.

Parameter	Range of values: Lower	Standard	Upper	Units
Temperature	12	17	22	°C
Particle doubling rate	0.04	0.10	0.60	d^{-1}
Naupliar abundance	0.15	1.5	40	L^{-1}
Grazing efficiency slope	0.05	0.55	1.05	μm^{-1}
Size of smallest particle grazed	0.25	2.25	4.0	μm

data (Huntley *et al.*, 1986). The range and standard value for effective particle doubling rate was calculated as the ratio of ^{14}C productivity:POC concentration at representative stations in the Southern California Bight (Eppley *et al.*, 1983). Using the value of $\mu_1 = 0.005$ (h^{-1}) at 17°C, the combined doubling rate of all particles from 1 to 20 μm radius is 0.1 (d^{-1}), which falls in the middle of the range of effective doubling rates reported by Eppley *et al.* (1983). The effect of doubling rate on $K_{p,t}$ was studied by adjusting the value of μ_1.

Since the total abundance of zooplankton is a function of the abundance in the first weight category (N_1; Eq. 19), we studied the effects of zooplankton abundance on $K_{p,t}$ by changing the value of N_1. The standard value and range were based on our own field data and that of Mullin *et al.* (1985).

Values for the grazing efficiency slope (b_2) and the size of the smallest particle grazed (r_o) were taken from Bartram (1980). In both cases the range was chosen to reflect a 90% change in the value of the parameter.

6. Model results

a. Runs of the model. With all parameters at their standard values (Table 5) there is a 3.5% decrease in K_p after 24 h (Fig. 14). Changes in the abundance of particles in all size classes control the changes in the attenuation coefficient (see Eqs. 10 and 11). Analysis of the percent change in the abundance of every particle size class after 24 h shows a decrease in the abundance of particles >3.5 μm radius and an increase in particles <3.5 μm radius (Fig. 11). This result is due to the inefficient grazing by zooplankton on small particles (Fig. 12). The relative contribution of each particle size class to the total (3.5%) decrease in K_p after 24 h shows that the attenuation due to particles <3.5 μm increased over 24 h (Fig. 13). On the contrary, the attenuation due to particles >3.5 μm decreased over 24 h.

The total effect of the zooplankton on K_p was then studied by running the model without zooplankton and with the remaining parameters at their standard values. Under these conditions, there was an increase of 8.22% in K_p after 24 h (Fig. 3). In the

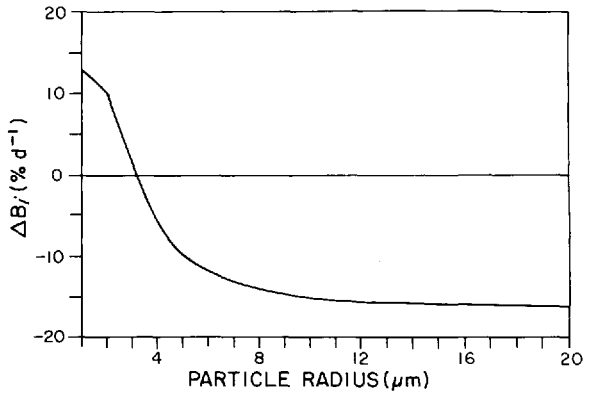

Figure 11. Percent change in the abundance of particles in each size category, from 1 to 20 μm radius, after running the model for 24 h, with all parameters at their standard values (Table 5).

standard run, $K_{p,6}$ had a value of 0.1466 m^{-1}, whereas in the run without zooplankton $K_{p,6}$ was 0.1645 m^{-1}. Thus, relative to the standard run, in the absence of zooplankton the attenuation coefficient may increase by 12% per day. Using maximum observed particle doubling rates in combination with standard zooplankton abundance resulted in an increase in K_p of 53% per day.

We also ran the model using the original equations of Huntley and Boyd (1984), which are based on a summary of classically measured clearance rates, and we assumed no diel variability (i.e. $f_t = 1.78$ for all t). Under these conditions we obtained

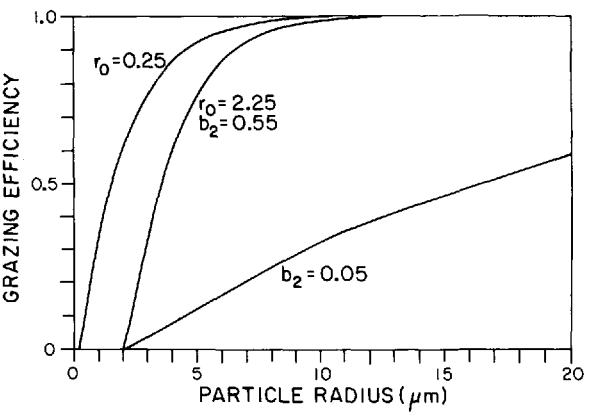

Figure 12. Size-selective grazing efficiency of copepod grazers, based on the experimental data of Bartram (1980). In general, small particles are grazed less efficiently than large ones. Figure shows the standard values ($r_o = 2.25$; $b_2 = 0.55$), as well as the lower limits (−90% of standard value) for both r_o (0.025) and b_2 (0.05), which illustrate the approximate range of grazing efficiency.

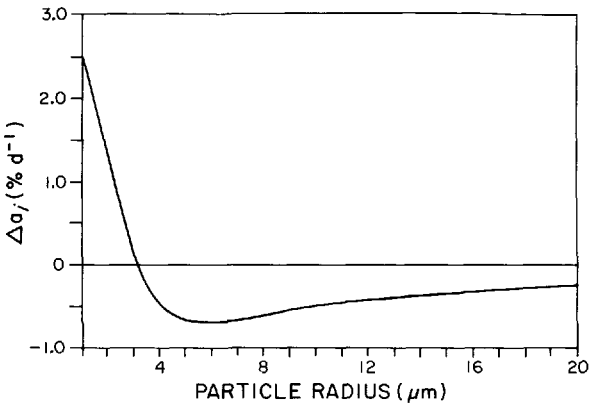

Figure 13. Percent change in the attenuation coefficient (a_i) for each size class of particles in each size category, from 1 to 20 μm radius, after running the model for 24 h, with all parameters at their standard values (Table 5). The cumulative change in diffuse attenuation coefficient, K_p, was 3.5%.

a result ($K_{p,6} = 0.1624$ m^{-1}) that was virtually equivalent to that produced by the total absence of zooplankton ($K_{p,6} = 0.1645$ m^{-1}). Consequently, there is an increase in K_p of 11% per day.

b. Sensitivity analysis. The value of the attenuation coefficient of the particulate assemblage at $t = 0600$ h (i.e. $K_{p,6}$; after running the model for one full 24-h cycle) was used as the variable on which the sensitivity analysis was conducted. The sensitivity of the model was analyzed as the change in $K_{p,6}$ relative to the change in the value of a

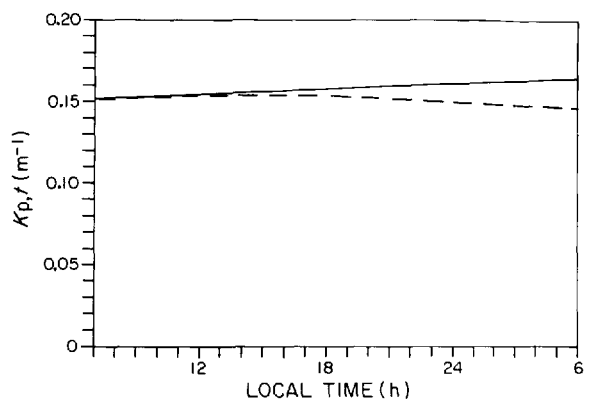

Figure 14. Hourly changes in model output (diffuse attenuation coefficient, K_p) over a 24-h cycle. Under standard conditions, but with no grazers (solid line), K_p increased steadily from 0.1510 m^{-1} to 0.1645 m^{-1}. Under standard conditions with grazers (dashed line) K_p increased during the day, but decreased at night to a value of 0.1466 m^{-1}.

Table 6. Sensitivity analysis results. Parameter values were varied in the range from −90% to +2500% of the standard value (Table 5), and sensitivity of the model output ($K_{p,6}$) was calculated using Eq. (20). The most sensitive parameter was temperature, followed by naupliar abundance.

	Sensitivity ($\times 10^3$) of $K_{p,6}$ at:					
Parameter	−90%	−30%	+30%	+90%	+500%	+2500%
Temperature		−213	−670			
μ_1	65	61	63	71	86	
Naupliar abundance	−121	−114	−107	−101	−71	−24
Grazing efficiency slope	−87	−33	−20	−15		
Size of smallest grazed particle	61	52	44	37		

given parameter P_x (where x = 1 to 5; Table 5), and sensitivity (S_x) was calculated as follows:

$$S_x = \frac{\{K_{t,x} - K_s\}/K_s}{\{P_{t,x} - P_{s,x}\}/P_{s,x}} \tag{20}$$

where $K_{t,x}$ is the value of $K_{p,6}$ after a change in the parameter x, K_s is the standard value of $K_{p,6}$, $P_{t,x}$ is the test value of parameter P_x (all other parameters kept at standard value during test), and $P_{s,x}$ is the standard value of parameter P_x.

The most sensitive parameter in the model is temperature (Table 6). This means that small changes in temperature will have a greater effect on the value of $K_{p,6}$ than small changes in the other four parameters. Temperature has an exponential effect on both particle doubling rate (Eq. 14) and zooplankton clearance rate coefficients (Eqs. 17 and 18). Thus, if temperature increases, both particle growth and grazing will increase exponentially. The negative sign in the values of temperature sensitivity, however, indicates that grazing prevails over particle growth (Table 6). This is because the temperature dependence of the grazing rate coefficients is more acute than that of particle doubling rate.

Given a ±90% change in parameter value, the second most sensitive parameter is zooplankton abundance (Table 6). The sensitivity of the model to changes in zooplankton abundance decreases at high abundances (+500% and +2500%). However, the greatest abundances (N_1 = 40 L^{-1}) cause a decrease in K_p of >60% per day (Fig. 15).

The model is not highly sensitive to changes in the grazing efficiency parameters b_2 and r_o, except at −90% of their respective standard values (Table 6). Only a decrease in r_o to 0.25 (−90%), meaning that zooplankton could graze particles smaller than 2.0 μm radius, which in the standard run are not grazed, can cause a significant

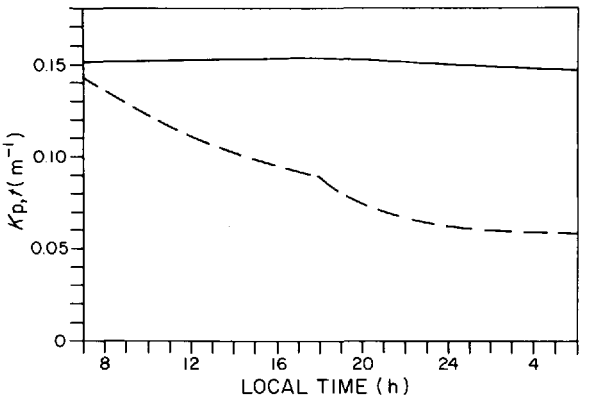

Figure 15. Hourly changes in model output (diffuse attenuation coefficient K_p) over a 24-h cycle, under both standard conditions (solid line), and with the upper limit of grazer abundance (+2500%, dashed line). Grazing during the day is great enough to reduce K_p significantly. The inflection point at 1800 h is due to the onset of increased nocturnal grazing, considered a step function in the model. After a 24-h run of the model with maximum grazing pressure, K_p is reduced by 63.5%, to 0.0551 m^{-1}.

decrease in K_p (Fig. 12). A decrease in the grazing efficiency slope, b_2, to 0.05 (−90%) substantially reduces the efficiency of zooplankton grazing in all particle size categories (Fig. 12), causing an increase in K_p.

7. Discussion

a. Diel vertical migration. Calanus pacificus adults exhibited diel migration behavior during our study in La Jolla Bay, but *Acartia* spp. and *Paracalanus* spp. did not. Diel vertical migration by *Calanus pacificus* has been observed previously (Esterly, 1912; Enright and Honegger, 1977; Mullin *et al.*, 1985), however, in our study the adults appeared to have more pronounced migration behavior than copepodites. This is similar to the experimental results of Huntley and Brooks (1982), who observed greater migration amplitude of the later copepodite stages of *C. pacificus* maintained in a 10-m deep tank.

By contrast, both *Acartia* spp. and *Paracalanus* spp. showed no signs of diel vertical migration. Both were concentrated near the surface, with *Acartia* spp. being abundant to a depth of ≈20 m, and *Paracalanus* spp. to a depth of ≈25 m. This observation is contrary to some reports, such as those of distinct migrations in *Acartia clausii* (Petipa, 1958; Johnson, 1938). However, Mullin *et al.* (1985) did not observe vertical migration in either *Acartia* spp. or *Paracalanus* spp. in coastal waters <10 km from our study site.

Vertical migration is a complex behavior, effectuated by a combination of many stimuli. We know from both experimental and field studies that the principal stimuli

include light, pressure, gravitation, temperature and feeding behavior (Cushing, 1951; Bainbridge, 1960; Rudjakov, 1970; Huntley, 1985a). However, it is rarely possible to interpret natural migrations, if only because most field studies neglect to measure at least one of the critical variables. In this regard, the present study is no exception. Our goal was simply to observe changes in both vertical distribution and feeding behavior of the dominant zooplankton grazers in the upper water column of La Jolla Bay. Observations of vertical migration are inevitable in such a study, but we cannot explain why one species (*Calanus pacificus*) migrated and the others did not. However, we do conclude that vertical distribution and grazing activity were strongly correlated. Individuals of each species fed most actively in the upper 15 m, regardless of migratory behavior. Feeding intensity did not reflect the vertical distribution of chlorophyll, which was virtually uniform throughout the upper 40 m.

b. Diel changes in zooplankton grazing. All species had a diel feeding rhythm, whether or not they migrated. Diel feeding rhythms have been observed in many migrating zooplankton species (e.g. Gauld, 1953; Haney and Hall, 1975; Zagorodnyaya, 1975; Peruyeva, 1978). Diel feeding rhythms in nonmigrating zooplankton species, though more rare, have been observed in *Centropages hamatus* (Nicolajsen *et al.*, 1983; Head *et al.*, 1984), *Temora longicornis* (Head *et al.*, 1984), *Pseudocalanus* sp., and several copepod species from the Pacific Central Gyre (Hayward, 1980). Although there are exceptions (Boyd *et al.*, 1980) the common pattern is a nocturnal increase in grazing activity.

It is not clear why any grazer located in the upper 20 m of the water column, in the midst of relatively abundant food, should not feed continuously. Head *et al.* (1985) suggested that diurnal variations in light intensity may trigger feeding rhythms in copepods, even when they do not vertically migrate. Feeding experiments with *Calanus glacialis* support this hypothesis, but suggest that there is also an interaction with an endogenous feeding rhythm. Head (1986) collected *C. glacialis* during both the day and night, and performed feeding experiments in both the light and the dark; *C. glacialis* feeding at night in the dark had the greatest ingestion rates, whereas those feeding during the daytime had very low ingestion rates, regardless of the light conditions.

c. Rates of gut evacuation and ingestion. The method of estimating *in situ* ingestion rates of zooplankton based on gut evacuation rate measurements was introduced by Mackas and Bohrer (1976) and popularized by a number of authors (e.g. Dagg and Grill, 1980; Boyd *et al.*, 1980; Nicolajsen *et al.*, 1983; Tande and Båmstedt, 1985; Head, 1986). In routine practice, application of the method assumes that the pigment content of the gut at any time is a negative exponential function of the initial pigment content, i.e., that the gut evacuation rate (k) is constant. From this it follows that the ingestion rate of a grazer *in situ* is a linear function of its gut pigment content.

Table 7. Comparison of ingestion rates of *Acartia* spp. late copepodites estimated from both power and exponential models of gut evacuation. Values of the necessary variables are those used in this paper. Maximum gut capacity, P_{max}, is 0.79 ng; the exponential evacuation rate, k_{exp}, is 0.00857 min^{-1}; and the dimensionless evacuation constant, ϕ, for the power model is 0.467. Ingestion rate estimated from the exponential model (I_{exp}), estimated using Eq. (2), is lower than that estimated from the power model (I_{pwr}), using Eq. (7), for approximately 55 min after maximum gut capacity.

Time (min)	P_f (ng)	k_{pwr}	I_{exp} (ng h^{-1})	I_{pwr} (ng h^{-1})
5	0.37	0.093	0.192	2.088
10	0.27	0.047	0.139	0.755
15	0.22	0.031	0.115	0.417
20	0.20	0.023	0.100	0.273
25	0.18	0.019	0.090	0.197
30	0.16	0.016	0.083	0.151
35	0.15	0.013	0.077	0.120
40	0.14	0.012	0.073	0.099
45	0.13	0.010	0.069	0.083
50	0.13	0.009	0.065	0.071
55	0.12	0.008	0.063	0.062

By contrast, our results indicate that gut evacuation rate is not constant, but rather that it is an inverse function of the time since the grazer had a full gut. Our analysis suggests that the appropriate model for this phenomenon is a negative power function—not a negative exponential. Our method of sampling (i.e., quick-freezing mixed zooplankton, and subsequent sorting on a frozen microscope stage) allowed us to take a greater number of samples at shorter time intervals than has been the usual practice (e.g. Dagg and Wyman, 1983; Wang and Conover, 1986). The result—a data set with high resolution in time—permitted greater statistical power than might otherwise have been possible and, we believe, allowed us to obtain a better fit to the power model.

The ramifications of applying the power model to estimates of ingestion rate are not trivial. For individuals which have recently fed, the estimated ingestion rate will be greater than that obtained by applying the exponential model. This is because the value of the gut evacuation rate estimated from an exponential model (k_{exp}) is lower than that estimated from the power model (k_{pwr}). For the species examined in the present study, $I_{pwr} > I_{exp}$ for at least 55 min after maximum gut fullness (Table 7). However, individuals which have not fed for 55 min may not be feeding at all, since the amount of pigment in the gut after 55 min is not significantly different from the amount found in an empty gut (Fig. 7). We therefore conclude that, for animals which are actively feeding, the power model should yield an estimate of ingestion rate which is consistently greater than that estimated from the exponential model. This may explain why Wang and Conover (1986; Fig. 5, p. 873) found that estimates of ingestion rate of

Temora longicornis based on the exponential model consistently *under*estimated ingestion rates measured by traditional methods. They attributed this to the loss of chlorophyll and related pigments during digestion, which was established in separate species, *Calanus hyperboreus* and *C. glacialis* (Conover *et al.*, 1986). However, in that paper, the authors state (p. 882) "We do not suggest that pigment loss in the guts of herbivores is always >90–99%," implying that this phenomenon may not occur in *Temora longicornis*. We suggest that the discrepancy between gut pigment and traditional measures of ingestion noted by Wang and Conover (1986) for *T. longicornis* could be corrected simply by applying the power model.

We suggest that traditional methods may underestimate true zooplankton grazing rates. The true ingestion and clearance rates may be more closely approximated by applying the power model to *in situ* gut pigment data, as we have done in this paper. We arrive at this conclusion by two independent approaches. First, by comparison to mean clearance rates estimated from traditional methods, the power model yields values which, at least at night, are almost one order of magnitude greater. The second approach is to consider the clearance rates which would be necessary to maintain observed levels of the standing stock of particulate matter in nature. Even the greatest total zooplankton abundances in the Southern California Bight (e.g. Mullin *et al.*, 1985) could not keep particulate standing stocks in check unless individual clearance rates were up to one order of magnitude greater than measured by traditional methods. This assessment included nauplii and other zooplankton down to 100 μm in length. The standing stock of other microzooplankton, such as ciliates, appears too small to make up the difference (Beers *et al.*, 1980), even considering their greater size-specific rates of grazing (Heinbokel, 1978; Capriulo, 1982; Taniguchi and Kawakami, 1985).

Thus, by both inductive and deductive reasoning we arrive at the conclusion that traditional methods may underestimate zooplankton grazing rates. We can offer two suggestions as to why this may be so. First, most published measurements of zooplankton grazing rates are derived either from short-term experiments conducted during the day, or from 24-h experiments; both approaches would lead to underestimating greater nighttime rates. Second, most traditional methods involve considerable handling of the animals, which may damage them or cause abnormal behavior. Copepods are subject, in the initial net capture, to antennular damage which produces significant mortality during molting (Miller *et al.*, 1984). In addition, they may be subjected to changes in temperature and light intensity, and a host of mechanical insults ranging from being sucked into a pipet to swimming in a rotating bottle. The effect of such manipulations is difficult to assess quantitatively, but we are not the first to suggest that they might compromise the experimental results (Mullin, 1963; Anraku, 1964; Roman and Rublee, 1980).

Given the potential problems of traditional methods, one can appreciate the attraction of an *in situ* approach to measuring grazing rates of zooplankton. It is not surprising that the gut pigment method pioneered by Mackas and Bohrer (1976) has

achieved widespread use. In contrast to earlier reports (Shuman and Lorenzen, 1975; Kiörboe *et al.*, 1982), some recent studies have seriously criticized the gut pigment method (Conover *et al.*, 1986; Wang and Conover, 1986). We hope those criticisms, as well as our own, may eventually serve to improve the method.

d. Effects of zooplankton grazing on ocean optics. Results of the model show that, under the standard conditions specified, K_p remains approximately constant over a 24-h cycle, decreasing by only 3.5%. In the absence of zooplankton, K_p may increase by 12% per day due to the lack of grazing. When the model was run using the greatest zooplankton abundances typically observed in southern California coastal waters (Mullin *et al.*, 1985), K_p decreased by >60% per day. On the other hand, given the greatest observed particulate doubling rates in the Southern California Bight (Eppley *et al.*, 1983), K_p increased by 53% per day. Thus, the results of the model suggest that zooplankton grazing may play a major role in the variability of the diffuse attenuation coefficient, K_p.

Temperature was the most sensitive of all five parameters analyzed. Small changes in temperature produce a comparatively greater change in K_p than small changes in the other four parameters. This high sensitivity is due to the relative differences between the temperature dependence of the grazing rate of pelagic herbivores (Huntley and Boyd, 1984) and that of the doubling rate of phytoplankton (Eppley, 1972). As a result of this exercise we predict that ΔK_p will be comparatively greater in areas of high temperature and/or high zooplankton abundance.

The model incorporated, for all parameters, values which have been reported in the literature. Assuming that our parameterization was correct, we should expect the output of the model to be in good agreement with measurements in the real ocean. However, there are two principal points at which the model output diverges from reality. The first concerns zooplankton grazing rates, and the second concerns the role of very small particles, <1–5 μm radius. In the first case, the model suggests that classical measurements of zooplankton grazing may seriously underestimate true rates. When we used the equations of Huntley and Boyd (1984)—which are based on classical measurement—to estimate grazing rates we obtained, assuming standard conditions (Table 5), an increase in K_p of 11% per day. At this rate, one would expect K_p to increase, due to the imbalance between particle production and grazing, at the rate of >100% per week. Grazing could balance mean productivity only by invoking the greatest abundances of zooplankton observed in coastal California waters—a result which stretches one's imagination.

Indeed, other models have encountered similar problems. For example, to balance carbon production and zooplankton grazing in their model of particulate dynamics on the Scotian Shelf, Herman and Platt (1983) were forced to invoke grazing rates which implied zooplankton daily rations in the range 25–50% per day. Herman and Platt (1983) cited two reports of rations in this range (Hargrave and Geen, 1970; Gamble,

1978), however, these are atypically high (please see review by Conover, 1978). It may be that the atypical measurements are real. Our *in situ* measurements of zooplankton clearance rates conducted during the present study yielded estimates which are almost one order of magnitude greater than would be predicted from most classical measurements. When the model was run with these measurements, and assuming standard conditions (Table 5), we obtained an approximate balance between zooplankton grazing and particulate production, and a consequently small change (3.5%) in the diffuse attenuation coefficient.

The second important issue addressed by model output concerns the role of small particles. In the model, zooplankton do not graze efficiently on particles smaller than $\simeq 3$ μ radius, which reflects many reports of size-selective grazing (e.g. Mullin, 1963; Frost, 1972). Therefore, in the standard run the 3.5% decrease in K_p was the net result of the increase in attenuation (a_i) due to growth of particles <3 μm, and the decrease of attenuation due to grazing of particles >3 μm. While this result may reflect the real impact of zooplankton grazing, it cannot be the complete story. If it were, the model predicts an ocean dominated by very small particles, which we know to be untrue. A more realistic model should account for grazing on picoplankton (<1–5 μm radius), which might be accomplished by microzooplankton grazers. The data available on microzooplankton grazing is so much less complete than that available for macrozooplankton that to incorporate it in the present model would, in our opinion, be premature. However, we emphasize that even in the absence of small particle grazers macrozooplankton grazing can account for significant changes in the optical characteristics of sea water.

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REFERENCES

Anraku, M. 1964. Some technical problems encountered in quantitative studies of grazing and predation by marine planktonic copepods. J. Oceanogr. Soc. Japan, *19*, 19–29.

Atlas, D. and T. T. Bannister. 1980. Dependence of mean spectral extinction coefficient of phytoplankton on depth, water color and species. Limnol. Oceanogr., *25*, 157–159.

Baars, M. A. and S. S. Oosterhuis. 1984. Diurnal feeding rhythms in North Sea copepods measured by gut fluorescence, digestive enzyme activity and grazing on labelled food. Neth. J. Sea Res., *18*, 97–119.

Bainbridge, R. 1960. Migrations, *in* The Physiology of Crustacea, Vol. 2, T. H. Waterman, ed., Academic Press, 431–463.

Banse, K. 1982. Cell volumes, maximal growth rates of unicellular algae and ciliates, and the role of ciliates in the marine pelagial. Limnol. Oceanogr., *27*, 1059–1071.

Bartram, W. C. 1980. Experimental development of a model for the feeding of neritic copepods on phytoplankton. J. Plankton Res., *3*, 25–51.

Beers, J. R., F. M. H. Reid and G. L. Stewart. 1980. Microplankton population structure in Southern California nearshore waters in late spring. Mar. Biol., *60*, 209–226.

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

Capriulo, G. M. 1982. Feeding of field collected tintinnid micro-zooplankton on natural food. Mar. Biol., *71*, 73–86.

Clarke, G. L. and H. R. James. 1939. Laboratory analysis of the selective absorption of light by seawater. J. Opt. Soc. America, *29*, 43–55.

Conover, R. J. 1978. Transformation of organic matter, *in* Marine Ecology, Dynamics, Vol. 4, O. Kinne, ed., Wiley, 221–499.

Conover, R. J., R. Durvasula, S. Roy and R. Wang. 1986. Probable loss of chlorophyll-derived pigments during passage through the gut of zooplankton and some of the consequences. Limnol. Oceanogr., *31*, 878–887.

Cushing, D. H. 1951. The vertical migration of planktonic crustacea. Biol. Rev., *26*, 158–192.

Dagg, M. J., T. Cowles, T. Whitledge, S. Smith, S. Howe and D. Judkins. 1980. Grazing and excretion by zooplankton in the Peru upwelling system during April 1977. Deep-Sea Res., *27*, 43–59.

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

Dagg, M. J. and K. D. Wyman. 1983. Natural ingestion rates of the copepods *Neocalanus plumchrus* and *N. cristatus*, calculated from gut contents. Mar. Ecol Prog. Ser., *13*, 37–46.

Durbin A. G. and E. G. Durbin. 1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries, *4*, 24–41.

Enright, J. T. and H.-W. Honegger. 1977. Diel vertical migration: adaptive significance and timing. II. Test of the model: details of the timing. Limnol. Oceanogr., *22*, 873–886.

Eppley, R. W. 1972. Temperature and phytoplankton growth in the sea. Fish. Bull., *70*, 1063–1085.

Eppley, R. W. and O. Holm-Hansen. 1986. Primary production in the Southern California Bight, *in* Plankton Dynamics of the Southern California Bight, R. W. Eppley, ed., Springer-Verlag, 176–215.

Eppley, R. W., E. H. Renger and P. Betzer. 1983. The residence time of particulate organic carbon in the surface layer of the ocean. Deep-Sea Res., *30*, 311–323.

Esterly, C. O. 1912. The occurrence and vertical distribution of the Copepoda of the San Diego region, with particular reference to nineteen species. Univ. Calif. Publ. Zool., *9*, 253–340.

Frost, B. W. 1972. Effects of the size and concentration of food particles on the feeding behavior of the marine planktonic copepod, *Calanus pacificus*. Limnol. Oceanogr., *17*, 805–817.

Frost, B. W., M. R. Landry and R. P. Hassett. 1983. Feeding behavior of large calanoid copepods *Neocalanus cristatus* and *N. plumcrhus* from the subarctic Pacific Ocean. Deep-Sea Res., *30*, 1–13.

Gamble, J. 1978. Copepod grazing during a declining spring bloom in the northern North Sea. Mar. Biol., *49*, 303–315.

Gauld, D. T. 1953. Diurnal variations in the grazing of planktonic copepods. J. Mar. Biol. Ass. U.K., *31*, 461–474.

Grossnickle, N. E. 1979. Nocturnal feeding patterns of *Mysis relicta* in Lake Michigan, based on gut fluorescence. Limnol. Oceanogr., *27*, 777–780.

Hall, R. P. 1925. Binary fission in *Oxyrrhis marina* Dujardin. Univ. Calif. Publs Zool., *26*, 281–324.

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

Hargrave, B. T. and C. H. Geen. 1970. Effects of copepod grazing on two natural phytoplankton populations. J. Fish. Res. Bd. Canada, *27*, 1395–1403.

Hart, R. C. 1977. Feeding rhythmicity in a migratory copepod, *Pseudodiaptomus hessei* (Mrazek). Freshwater Biol., *7*, 108.

Hayward, T. C. 1980. Spatial and temporal feeding patterns of copepods from the North Pacific Central Gyre. Mar. Biol., *58*, 295–309.

Head, E. J. H. 1986. Estimation of arctic copepod grazing rates *in vivo* and comparison with *in vitro* methods. Mar. Biol., *92*, 371–379.

Head, E. J. H., L. R. Harris and C. Abou-Debs. 1985. Effect of day-length and food concentration on *in situ* diurnal feeding rhythms in arctic copepods. Mar. Ecol. Prog. Ser., *24*, 281–288.

Head, E. J. H., R. Wang and R. J. Conover. 1984. Comparison of diurnal feeding rhythms in *Temora longicornis* and *Centropages hamatus* with digestive enzyme activity. J. Plankton Res., *6*, 543–551.

Heinbokel, J. 1978. Studies on the functional role of tintinnids in the Southern California Bight, I. Grazing and growth rates in laboratory cultures. Mar. Biol., *47*, 177–189.

Herman, A. W. and T. Platt. 1983. Numerical modelling of diel carbon production and zooplankton grazing on the Scotia shelf based on observational data. Ecological Modelling, *18*, 55–72.

Hu, V. J. H. 1978. Relationships between vertical migration and diet in four species of euphausiids. Limnol. Oceanogr., *23*, 296–306.

Huntley, M. E. 1985a. Experimental approaches to the study of vertical migration of zooplankton. Contr. Mar. Sci., *27*, 71–90.

—— 1985b. A method for estimating food-limitation and potential production of zooplankton communities. Arch. Hydrobiol. Beih. Ergebn. Limnol., *21*, 41–55.

Huntley, M. E. and C. M. Boyd. 1984. Food-limited growth of marine zooplankton. Am. Nat., *124*, 455–478.

Huntley, M. E. and E. R. Brooks. 1982. Effects of age and food availablility on diel vertical migration behavior of *Calanus pacificus*. Mar. Biol., *71*, 23–31.

Huntley, M. E., P. Sykes, S. Rohan and V. Marin. 1986. Chemically-mediated rejection of dinoflagellate prey by the copepods *Calanus pacificus* and *Paracalanus parvus*: mechanism, occurrence and significance. Mar. Ecol. Prog. Ser., *28*, 105–120.

Huntley, M. E., K. Tande and H. C. Eilertsen. 1987. On the trophic fate of *Phaeocystis pouchetii*. II. Grazing rates of *Calanus hyperboreus* on diatoms and different size categories of *P. pouchetii*. J. Exp. Mar. Biol. Ecol., *110*, 197–212.

Jerlov, N. G. 1968. Optical Oceanography. Elsevier, 194 pp.

—— 1976. Marine Optics. Elsvier Scientific Publ., 231 pp.

Jobling, M. 1981. Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J. Fish Biol., *19*, 245–257.

Johnson, W. H. 1938. The effect of light on vertical movement of *Acartia clausi* (Giesbrecht). Biol. Bull., *75*, 106–118.

Jörgensen, E. G. 1966. Photosynthetic activity during the life cycle of synchronous *Skeletonema* cells. Physiologia Pl., *19*, 789–799.

Jörgensen, S. E. 1986. Fundamentals of Ecological Modelling. Elsevier, 389 pp.

Kiörboe, T., F. Möhlenberg and N. Nicolajsen. 1982. Ingestion rate and gut clearance in the planktonic copepod *Centropages hamatus* (Lilljeborg) in relation to food concentration and temperature. Ophelia, *21*, 181–194.

Kirk, J. T. O. 1975a. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. I. General treatment of suspensions of living cells. The New Phytol., *75*, 11–20.

—— 1975b. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. II. Spherical cells. The New Phytol., *75*, 21–36.

Kishino, M. 1980. Energy balance of underwater radiation related to marine photosynthesis, *in* Biological and Chemical Utilization of Solar Energy, K. Shibata, A. Iwamura and A. Ikagami, eds., Japan Sci. Soc. Press, (in Japanese), 59–69.

Landry, M. R. 1978. Population dynamics and production of a planktonic copepod, *Acartia clausii,* in a small temperate lagoon on San Juan Island, Washington. Int. Rev. Gesamten. Hydrobiol., *63*, 77–119.

Lorenzen, C. J. 1972. Extinction of light in the ocean. J. Cons. Perm. Int. Explor. Mer, *34*, 262–267.

Mackas, D. L. and R. Bohrer. 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. J. Exp. Mar. Biol. Ecol., *25*, 77–85.

Marin, V., M. E. Huntley and B. W. Frost. 1986. Measuring feeding rates of pelagic herbivores: analysis of experimental design and methods. Mar. Biol., *93*, 49–58.

Marra, J. and E. O. Hartwig. 1984. Biowatt: A study of bioluminescence and optical variability in the sea. EOS, *65*, 722–732.

Miller, C. B., M. E. Huntley and E. R. Brooks. 1984. Post-collection molting rates of planktonic, marine copepods: Measurement, applications and problems. Limnol. Oceanogr., *29*, 1274–1290.

Morel, A. and A. Bricaud. 1981. Theoretical results concerning light absorption in a discrete medium, and application to specific absorption of phytoplankton. Deep-Sea Res., *28*, 1375–1398.

Mullin, M. M. 1963. Some factors affecting the feeding of marine copepods of the genus *Calanus*. Limnol. Oceanogr., *8*, 239–250.

Mullin, M. M. and E. R. Brooks. 1970. Growth and metabolism of two planktonic, marine copepods as influenced by temperature and the type of food, *in* Marine Food Chains, J. Steele, ed., Oliver & Boyd, 74–95.

Mullin, M. M., E. R. Brooks, F. M. H. Reid, J. Napp and E. F. Stewart. 1985. Vertical structure of nearshore plankton off Southern California: A storm and a larval fish food web. Fish. Bull., *83*, 151–170.

Nicolajsen, H., F. Möhlenberg and T. Kiörboe. 1983. Algal grazing by the planktonic copepods *Centropages hamatus* and *Pseudocalanus* sp.: Diurnal and seasonal variation during the spring phytoplankton bloom in the Oresund. Ophelia, *22*, 15–31.

Nozawa, K. 1940. Problem of the diurnal rhythm in the cell division of *Oxyrrhis marina*. Annotnes Zool. Jap., *19*, 170–174.

Paasche, E. 1968. Marine plankton algae grown with light-dark cycles. II. *Ditylum brightwelli* and *Nitzschia turgidula*. Physiologia Pl., *21*, 66–77.

Peruyeva, Y. G. 1978. Diurnal feeding rhythm of IV copepodite stage of *Calanus glacialis* Jaschnov. Oceanology, *17*, 719–721.

Petipa, T. S. 1958. The diurnal feeding rhythm of the copepod crustacean *Acartia clausi*. Dokl. Akad. Nauk. SSSR, *120*, 435–437.

Ponomareva, L. A. 1971. Circadian migrations and feeding rhythms of some Indian Ocean euphausiid species. Oceanology, *11*, 226–231.

Riley, G. A. 1946. Factors controlling phytoplankton population on Georges Bank. J. Mar. Res., *6*, 54–73.

Roman, M. R. and P. A. Rublee. 1980. Containment effects in copepod grazing experiments: a plea to end the black box approach. Limnol. Oceanogr., *25*, 982–990

Rudjakov, J. A. 1970. The possible causes of diel vertical migrations of planktonic animals. Mar. Biol., *6*, 98–105.

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

Steele, J. H. and B. W. Frost. 1977. The structure of plankton communities. Proc. R. Soc. (Ser. B), *280*, 485–535.

Steele, J. H. and M. M. Mullin. 1977. Zooplankton dynamics, *in* The Sea, Vol. 6, E. D. Goldberg, ed., Wiley-Interscience, 857–890.

Steemann-Nielsen, E. 1972. Light and primary production, pp 361–388, *in* Optical Aspects of Oceanography, N. G. Jerlov and E. Steemann-Nielsen, eds., Academic Press, 494 pp.

Subrahmanyan, R. 1945. On the cell division and mitosis in some south Indian diatoms. Proc. Indian Acad. Sci., Section B, *22*, 331–334.

Sweeney, B. M. 1959. Endogenous diurnal rhythms in marine dinoflagellates, pp. 204–207, *in* Int. Oceanogr. Congr. Preprints, M. Sears, ed., Am. Assoc. Advmt. Sci. Washington, DC., 421 pp.

Tande, K. S. and U. Båmstedt. 1985. Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea. Mar. Biol., *87*, 251–258.

Taniguchi, A. and R. Kawakami. 1985. Feeding activity of a tintinnid ciliate *Favella taraikensis* and its variability observed in laboratory cultures. Mar. Micro. Food Webs, *1*, 17–34.

Wang, R. and R. J. Conover. 1986. Dynamics of gut pigment in the copepod *Temora longicornis* and the determination of *in situ* grazing rates. Limnol. Oceanogr., *31*, 867–877.

Weiler, C. S. and R. W. Eppley. 1979. Temporal pattern of division in the dinoflagellate genus *Ceratium* and its application to the determination of growth rate. J. Exp. Mar. Biol. Ecol., *39*, 1–24.

Wroblewski, J. S. 1977. Vertically migrating herbivorous plankton—their possible role in the creation of small scale phytoplankton patchiness in the ocean, *in*, Oceanic Sound Scattering Prediction, N. R. Andersen and B. J. Zahuranec, eds., Plenum Press, 817–847.

Zagorodnyaya, Y.-A. 1975. Feeding habits and migration of the Black Sea copepod *Pseudocalanus elongatus* (Boeck) in winter. Hydrobiol. J., *10*, 35–41.

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