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Natural diets of zooplankton off southern California

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ABSTRACT: Plant and animal carotenoid pigments were isolated from the guts of the copepods *Calanus pacificus* and *Clausocalanus* sp. and the cladocerans *Evadne* spp. by high performance liquid chromatography. Measured carotenoid concentrations were converted to estimates of class-specific phytoplankton biomass and total microzooplankton biomass in the zooplankton diets. Different pigments were present in the guts at different times of day and night and the timing of peak gut fullness varied between species. In *C. pacificus*, pigment concentrations were highest during the period from evening twilight to midnight. *Evadne* spp. exhibited a midnight peak in gut pigmentation. *Clausocalanus* sp. contained elevated levels of pigments between midnight and noon. The gut contents of *C. pacificus* and *Evadne* spp. were dominated by animal carbon when phytoplankton biomass and productivity were relatively low, and by algal carbon when phytoplankton biomass and productivity were high. *Clausocalanus* sp. did not follow this pattern. Our observations are consistent with the hypothesis that carnivory may represent an important mode of feeding among small zooplankton and, further, that the diets of some species of zooplankton vary in response to quantitative and qualitative attributes of the food environment.

INTRODUCTION

Many small, planktonic crustaceans are thought to be omnivorous (Marshall 1924, Anraku & Omori 1963, Mullin 1966). In addition to phytoplankton, these animals can ingest detritus (Heinle et al. 1977, Roman 1977, Boak & Goulder 1983, Roman et al. 1983, Downs & Lorenzen 1985) and microzooplankton (Lonsdale et al. 1979, Turner & Anderson 1984, Stoecker & Sanders 1985, Dagg & Walser 1986, Sheldon et al. 1986, Sherr et al. 1986, Conley & Turner 1987, Stoecker & Egloff 1987).

Diversity in zooplankton diets may introduce nutritional variability. This, in turn, may affect such processes as growth and egg production (Checkley 1980, Durbin et al. 1983, Ambler 1985). For example, differences in the egg production rate of the copepod *Acartia tonsa* have been attributed to the classes of cultured phytoplankton (diatoms, dinoflagellates) that were used as food (Morey-Gaines 1980), to the use of cultured phytoplankton versus cultured microzooplankton as food (Stoecker & Egloff 1987) and to seasonal variations in the natural diet (Kleppel 1987). Roman (1984) observed better survival and more rapid development of *A. tonsa* when its diet consisted of a mixture of diatoms and detritus than when either food was provided alone.

Little is known, however, about the natural diets of most planktonic crustaceans. Attempts to describe zooplankton diets in situ have frequently involved the determination of plant pigment concentrations in the gut (Mackas & Bohrer 1976, Hallegraeff 1981, Kleppel & Manzanilla 1983, Kleppel & Pieper 1984). Such measurements, however, emphasize the herbivorous aspects of feeding and provide little or no indication of the importance of other dietary components.

In the study described here, plant and animal carotenoid pigments were extracted from the guts of zooplankton and used to infer the quantities and kinds of particles that had been ingested. Carotenoids occur extensively among marine plants and animals (Davies 1965, Herring 1972) and are commonly used as taxonomically-specific biomass analogs for planktonic organisms (Strain et al. 1944, Jeffrey 1974, Liaaen-Jensen 1979, Gieskes & Kraay 1986, Smith et al. 1987).

Carotenoids and their principal metabolic transformation products seem to be reliable tracers of certain trophodynamic processes in the sea (Kleppel 1988).

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They can be chromatographically detected and quantified in zooplankton gut contents and fecal pellets on a semi-routine basis (Hallegraeff 1981, Repeta & Gagosian 1982, Kleppel & Pieper 1984, Nelson 1986). Although carotenoid digestion and metabolism are not yet completely understood, it appears that carotenoids do not degrade in the copepod gut (Nelson 1986). However, different kinds of zooplankton may metabolize ingested carotenoids in different ways (Repeta & Gagosian 1983, Klein et al. 1986, Nelson 1986).

Most carotenoids, whether metabolically transformed or not, appear to remain in the measurable pigment pool while in the guts of crustaceans. The ubiquitous algal pigment beta-carotene is thought to be the only carotenoid that is assimilated by copepods (Paanakker & Hallegraeff 1978, Ringelberg 1980). Beta-carotene is utilized by copepods in the biosynthesis of tissue carotenoids (Castillo et al. 1982).

Tissue carotenoids, such as astaxanthin, occur in crustaceans (Castillo et al. 1982), protistans (Tuttle et al. 1973, Balch & Haxo 1984) and other macro- and microzooplankton. They quench singlet excited oxygen which is responsible for photo-peroxidation of proteins (Krinsky 1971). Such reactions can be induced by 10 % or more of the incident solar radiation (Hairston 1979). Thus, animals in the upper water column (especially those that do not migrate) should be rich in carotenoids.

The tissue carotenoid concentration of an animal is not always apparent from the extent to which it is 'colored' or pigmented. Color seems to be largely the result of carotenoid chemistry (i.e. binding, oxidative state, interactions with other carotenoids), while carotenoid concentration is thought to be, in part, a functional metabolic response to light and possibly other variables (Cheeseman et al. 1967, Hairston 1979, Ringelberg 1980, Byron 1982).

In this study we measured carotenoids extracted from small particles (nano- and microplankton) present in the waters off southern California, USA, and from material in the guts of copepods and cladocerans collected in these waters. We have converted the carotenoid data to estimates of phytoplankton and microzooplankton biomass and have evaluated the importance of carnivory in the diets of macrozooplankton from different food environments.

METHODS

Sampling. Plankton was sampled in the San Pedro Basin, California (Fig. 1) on 6, 11 and 12 March 1987 from RV 'New Horizon' (Scripps Institution of

Fig. 1. Sampling locations in the San Pedro Basin, California, USA, 6 and 11–12 Mar 1987. Dashed line shows the track of a drogue centered at 20 m between 11 and 12 Mar

Oceanography), while the ship followed a drogue centered at 20 m. Zooplankton was collected from the upper mixed layer by hauling a net (0.5 m mouth diameter, 202 μm Nitex mesh) vertically from 30 m to the surface at 01:30 h on 6 March, at 17:00 h (nautical twilight) on 11 March, and at 00:01 h, 07:00 h (twilight) and 12:00 h on 12 March.

Samples were immediately split into halves and the animals in one fraction were narcotized with carbonated water (Kleppel et al. 1988). The zooplankton in the other fraction was transferred, on 202 μm mesh screen, to GF/F filtered seawater for 3.5 h to permit gut evacuation to occur. Microscopic examination of the guts of some of these animals following the evacuation period revealed that most guts were either completely empty or contained small amounts of material in the hindgut. The narcotized animals (which did not evacuate their guts) were transferred to 100 μm mesh screens and frozen in liquid nitrogen. After the gut evacuation period, the animals in filtered seawater were also transferred to screens and frozen.

Water samples (2 l) pumped from discrete depths were passed through GF/C filters and the particles retained on the filters were stored in liquid nitrogen. Periodically, seawater subsamples were preserved with Lugol's iodine for microscopic enumeration of nano- and microplankton (i.e. phytoplankton and microzooplankton).

^{14}C-primary productivity was measured on each sampling date. Replicate light and dark bottles (250 ml) were filled with water from 6 isolume depths, inoculated with 5 μCi of $NaH^{14}CO_3$ and placed into bags made from layers of fiberglass screen to simulate the light intensities of the collection depths (Hitchcock 1986). The samples were incubated on deck for 4 to 6 h in clear plexiglass cylinders through which near-surface water circulated continuously. After incubation, the samples were filtered under low vacuum (< 50 mm Hg) and rinsed with filtered seawater without exposure to air. The filters were acidified with 0.5 *N* HCl for 1 h, then immersed in 3 ml of Aquasol 2 scintillation cocktail (New England Nuclear Corp.) for counting.

Pigment analysis. Plankton samples collected during the cruise were analyzed for pigment content by reverse-phase high performance liquid chromatography (HPLC). HPLC-grade solvents were degassed and filtered prior to use. Pigments were extracted in a cool, dimly lit room.

Similar sized individuals of the dominant zooplankton species were sorted from the frozen screens for analysis. The species studied were the copepod *Calanus pacificus* (late copepodites, length 2.5 to 2.7 mm), cladocerans *Evadne nordmanii* and *E. spinifera*, which were combined as *Evadne* spp., and several small (length 0.9 to 1.0 mm) copepods that were dominated by *Clausocalanus* sp., but which may have included individuals of the genera *Ctenocalanus* and *Paracalanus*. These could not be differentiated on frozen Nitex screens.

The zooplankton were transferred by species (or species group) to 2.5 cm GF/C filters and immersed in 1 to 2 ml of 90 % aqueous acetone. The filters containing phytoplankton and microzooplankton samples were also immersed in 90 % aqueous acetone. The samples were macerated with hand-operated tissue grinders, while being held on ice. After thorough grinding, the samples were refrigerated in the dark for 60 min, then centrifuged for 5 min to remove particulates. Each extract was decanted into a clean, graduated cen-

Table 1. Carotenoids measured in phytoplankton and zooplankton

Pigment	Golden brown algae	Dinoflagellates	Green algae	Prymnesiophytes	Animals	Detritus
Peridinin		+				
Fucoxanthin	+			+		
19'-hexanoyl-fucoxanthin[a]		+		+		
Lutein[b]			+			
Astaxanthin[c]					+	
Canthaxanthin[c]					+	
Echinenone[c]					+	
Peridininol[d]						+
Fucoxanthinol[e]						+

[a] Limited occurrence in the dinoflagellates
[b] Green algal pigments (including chlorophyll *b*) were not detected in any samples, though they were observed, at low concentrations, at other times during the cruise
[c] Animal carotenoids were detected, and their concentrations calculated, individually. Concentrations were then summed and are reported as total animal carotenoids. Heterotrophic dinoflagellates, considered animals in this study, may contain one or more of these pigments
[d] A transformation product of peridinin thought to be produced through digestion by certain heterotrophs
[e] A transformation product of fucoxanthin thought to be produced through digestion by some heterotrophs

trifuge tube and an ion pairing agent, consisting of 1.5 g of tetra-*n*-butyl ammomium acetate + 7.7 g of ammonium acetate per 100 ml of water (Solution P of Mantoura & Llewellyn 1983), was added in a ratio of 0.3 ml Solution P ml^{-1} extract. The extracts were agitated and set aside in darkness for at least 5 min to permit the ion pairing agent to bind appropriately.

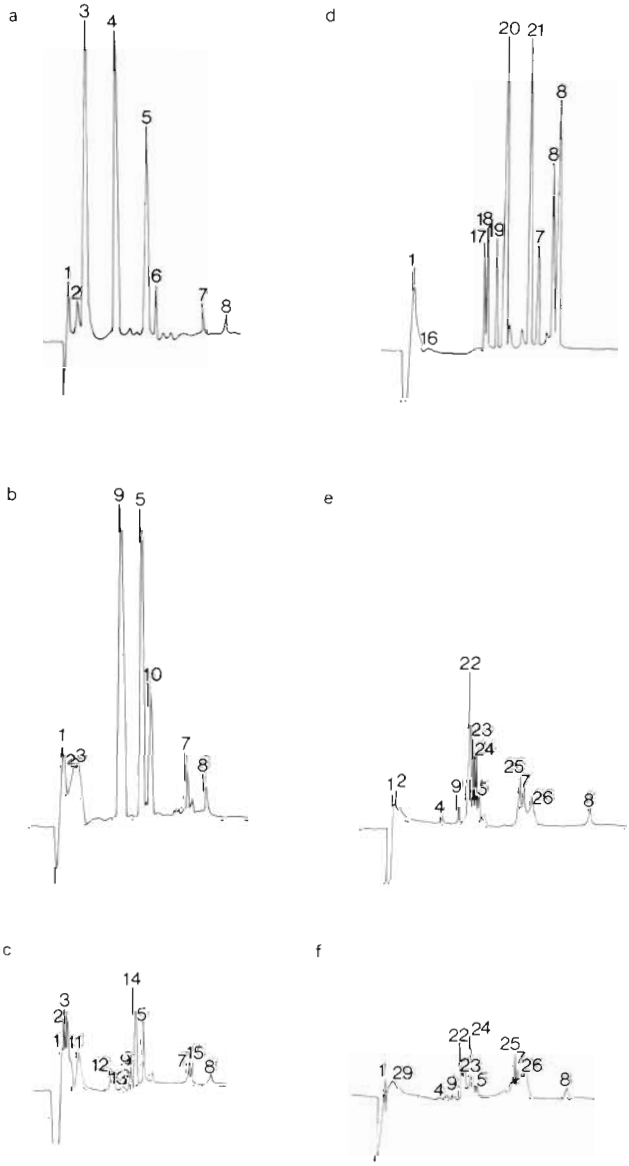

Fig. 2. Chromatograms of the pigments of algae and animals. (a) *Amphidinium* sp.; (b) *Thalassiosira weissflogii*; (c) *Emiliani huxleyi*; (d) *Dunaliella tertiolecta*; (e) *Calanus pacificus* (with food in gut); (f) *Calanus padificus* (after starvation). Pigments: 1, unretained; 2, chlorophyllide *a* (?); 3, chlorophyll c_1 and c_2; 4, peridinin; 5, diadinoxanthin; 6, dinoxanthin; 7, chlorophyll *a*; 8, carotene; 9, fucoxanthin; 10, diatoxanthin; 11, unidentified; 12, 19′-butanoyl-fucoxanthin (?); 13, unidentified; 14, 19′-hexanoyl-fucoxanthin; 15, pheophytin *a*; 16, unidentified; 17, *cis*-neoxanthin; 18, neoxanthin; 19, violoxanthin; 20, lutein; 21, chlorophyll *b*; 22, astaxanthin isomer; 23, astaxanthin isomer; 24, astaxanthin-like carotenoid; 25, canthaxanthin; 26, echinenone. (?) denotes probable but not positive identification

A Waters gradient elution HPLC system, consisting of a model 680 gradient controller, paired model 501 pumps, and a U6K injector, was used to elute pigments from a Beckman, C8 octyl-ultrasphere column (15 cm × 1.5 mm, stainless steel; with octyl-ultrasphere guard column; > 40 000 theoretical plates) with a continuous, 2-solvent gradient. Pigments were detected with a Waters model 481 variable wavelength, UV/vis detector and the signal was plotted and integrated on a Waters model 730 data module.

Solvent 1, a solution of water, methanol and Solution P (8:1:1), was mixed with Solvent 2, a solution of methanol and acetone (8:2), in decreasing proportion from 20 % Solvent 1:80 % Solvent 2, to 100 % Solvent 2 over 10 min, while the flow rate was increased from 1.0 ml min^{-1} to 1.9 ml min^{-1}. Solvent 2 was delivered at a flow rate of 1.9 ml min^{-1} for an additional 10 min.

Numerous chlorophyll and carotenoid pigments can be detected by HPLC. Our interest, however, was in those carotenoids that can be utilized as taxonomic markers of classes or groups of classes of phytoplankton and microzooplankton. Carotenoids used as taxonomic markers in this study are shown in Table 1. Chromatographically isolated pigments were identified by their characteristic retention times (RT) and capacity factors (k′). RT and k′ values were determined from chromatograms of pigment standards prepared from algal cultures and copepod tissues (Fig. 2). Chlorophyll c_1 and c_2, and 19′-butanoyl-fucoxanthin were identified by Dr R. R. Bidigare from chromatograms of pigment standards that we prepared. These identifications are tentative and the pigments were not used as markers in the present study.

To determine the concentration of each pigment in the chromatograms, the area under the peak created by each pigment was multiplied by a pigment-specific concentration:peak-area ratio, then scaled to sample size. The area under each peak is proportional to pigment concentration (Snyder & Kirkland 1979) and peak area varies linearly with concentration in all pigment standards that we have measured. Concentration:peak-area ratios were generated by chromatographing serial dilutions of each pigment standard, collecting the pigment as it eluted and measuring its absorbance at 440 nm with an IBM Instruments, Inc., model 9410 scanning spectrophotometer equipped with small-volume cuvettes (volume = 0.9 ml; pathlength = 1 cm). The measured absorbances of plant pigments were converted to concentration estimates with extinction coefficients from Mantoura & Llewellyn (1983). The extinction coefficient for astaxanthin, given by Hairston (1979), was used to estimate the concentrations of all 3 animal carotenoids because we

have found no extinction coefficients for canthaxanthin or echinenone in the literature. This procedure introduces an error into the calculation of animal carotenoid concentration. However, in the present study the error was probably small because astaxanthin was overwhelmingly the dominant animal pigment in our samples.

Microplankton biomass estimates from pigments. Carotenoid concentrations tend to be proportional to the biomass of the taxonomic groups in which they occur (Liaaen-Jensen 1979, Smith et al. 1987). However, the specific relationship between one carotenoid and carbon biomass is likely to be different from the relationship between another carotenoid and carbon biomass. In addition, physiological and environmental variables can affect the C:carotenoid ratio both within and between taxonomic groups. Therefore, to use pigments as biomass analogs, a specific carotenoid-to-carbon conversion must be determined for each pigment.

To determine the C:carotenoid ratios of the major taxonomic groups of phytoplankton in the water and in the gut contents of the macrozooplankton, the seawater subsamples that had been preserved for microscopic analysis were counted (at 400× magnification) and phytoplankton cell dimensions were measured with an ocular micrometer. The cell plasma volume of each species was calculated from these measurements and converted to estimates of cellular carbon concentration (Strathmann 1967). Estimates of diatom and chrysophycean C, dinoflagellate C, and prymnesiophycean C were made by summing the carbon estimates for the species within each phytoplankton class. The ratio of class-specific C to the measured concentration of the carotenoid used as a biomass analog was then generated (Table 2).

The relationship between the concentrations of carbon and animal pigments in the microzooplankton was evaluated in 2 ways. First, microzooplankton samples were collected by pumping water through a 200 μm mesh screen and then a 64 μm mesh net. The material retained by the smaller mesh was composed of larger microzooplankton, including crustacean larvae, large ciliates, mollusc veligers and polychaete trochophores. Phytoplankton cells were not abundant.

Each sample was split, and one fraction was dried (60 °C for 24 h) and weighed. The animal carotenoids in the other fraction were separated from plant xanthophylls (Kleppel et al. 1985) and measured spectrophotometrically. Dry weights (DW) were converted to estimates of zooplankton carbon using the equation of Weibe et al. (1975):

$$\log DW = 0.977 \log C + 0.508. \quad (1a)$$

Therefore,

$$\log C = 1.02 \log DW - 0.520. \quad (1b)$$

The second prodecure involved collecting microzooplankton by pumping water through a 100 μm mesh screen and a 20 μm mesh screen. The material retained by the 20 μm mesh, which contained small ciliates, dinoflagellates, some copepod nauplii and phytoplankton, was subsampled for HPLC pigment analysis and microscopic enumeration. Heterotrophs were counted and measured, and carbon concentrations were calculated from cell volumes (Beers & Stewart 1970).

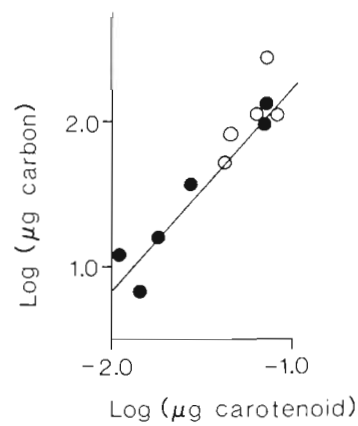

Fig. 3. Regression of estimated microzooplankton carbon biomass on animal carotenoid content. (●) Samples collected in a 64 μm mesh net in which carbon content was estimated from dry weight. (○) Samples collected on a 20 μm mesh screen in which carbon content was estimated from microscopic analysis

Table 2. Carbon:carotenoid ratios for marker pigments of 3 phytoplankton classes from the upper 40 m of the water column in San Pedro Basin, California, March 1987. Samples were collected at 2, 20 and 40 m

Taxonomic group	Marker pigment	C:carotenoid ratio (w:w)	Confidence interval	*N*
Bacillariophyceae[a]	Fucoxanthin	42.6	39.2–46.0	3
Dinophyceae	Peridinin	323.2	281.8–364.6	3
Prymnesiophyceae	19'-hexanoyl-fucoxanthin	15.4	12.9–17.9	3

[a] Includes Chrysophyceae, which were scarce

The data that resulted from the 2 sets of measurements were pooled and the relation between carbon biomass, C, and carotenoid content, P, was determined by regression analysis (Fig. 3). The equation for the relation was,

$$\log C = 1.54 \log P + 3.88, \quad (2)$$

where C and P are expressed in mg. This equation explains 85 % of the variance in the data ($p < 0.001$) with a standard error of 0.12.

To distinguish zooplankton tissue carotenoids from the carotenoids of microzooplankton in their guts, the pigment levels of the zooplankton that were starved in filtered seawater were subtracted from the pigment levels of the zooplankton that were not starved. The tissues should have been the principal source of animal carotenoids in the starved zooplankton. In the zooplankton that were frozen immediately, both tissues and gut contents should have contributed pigments. Thus, the difference was taken as the gut pigment level.

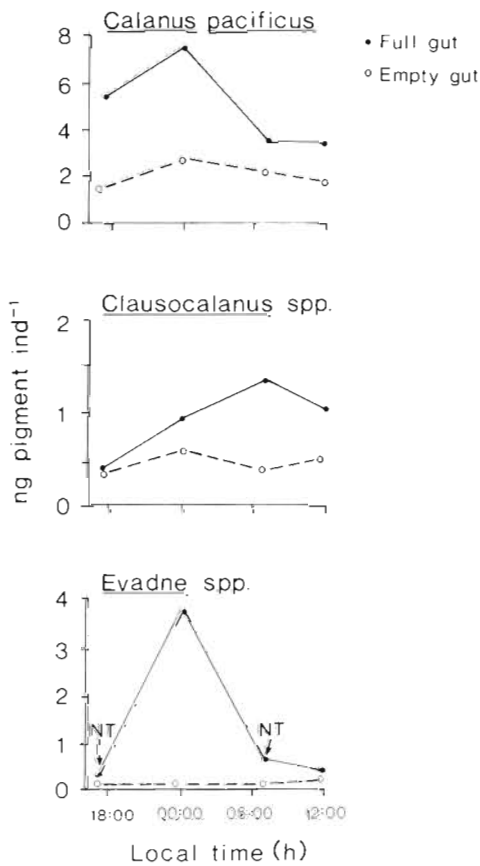

Fig. 4. Concentrations of animal pigments in zooplankton that were frozen immediately upon collection (●), and in starved zooplankton (○). Samples collected 11–12 Mar 1987 NT: Nautical twilight

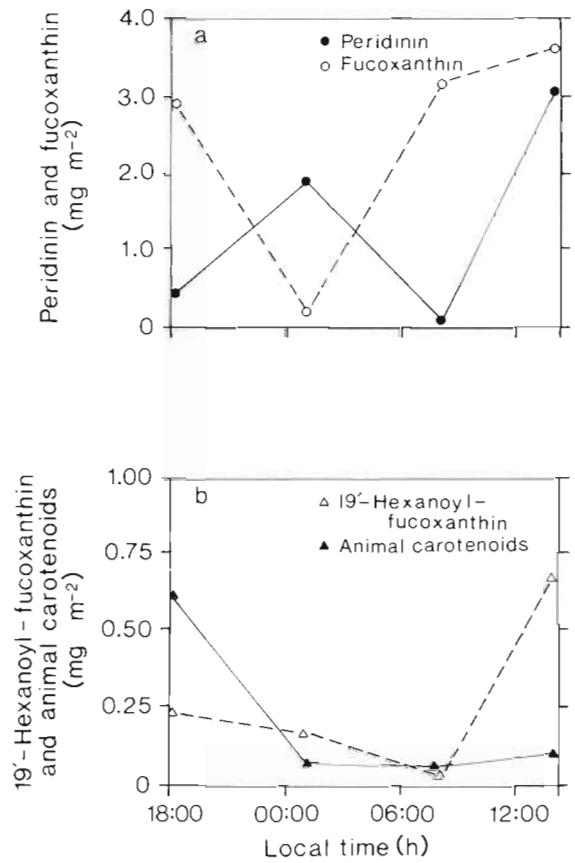

Fig. 5. Depth-integrated carotenoid concentrations from phytoplankton and microzooplankton samples collected through the upper 40 m of the water column during a time series in San Pedro Basin, 11–12 Mar 1987. (a) Fucoxanthin and peridinin; (b) 19′-hexanoyl-fucoxanthin and animal carotenoids. Choice of pigments to plot together was based simply upon typical concentrations encountered

RESULTS

Gut versus tissue pigments

Diel cycling of carotenoids in zooplankton body tissues has been reported in a few studies (Hallegraeff et al. 1978, Ringelberg 1980, Kleppel et al. 1985, but see Hairston 1980) and we evaluated the possibility that such changes occurred during the present investigation. Animal carotenoid levels in the zooplankton that had not evacuated their guts varied 2- to 8-fold in the series of samples collected on 11–12 March. Carotenoid levels were less variable in the zooplankton that were starved in filtered seawater (Fig. 4). Thus, the major diel variations in animal carotenoid content appear to have been due to changes in animal carotenoid levels in the gut rather than to the cycling of carotenoids in the body tissues.

Time series measurements

Although plankton samples for pigment analysis were collected at discrete depths in the water column, integrated values are presented (Fig. 5) to maintain consistency with net-integrated zooplankton gut contents data. In vivo fluorescence profiles performed during the cruise frequently indicated that a chlorophyll maximum was present at 30 to 50 m. The distribution of carotenoids in our discrete samples in the upper 40 m also increased with depth.

Between 11 and 12 March, water column pigment concentrations were notably low in the upper 40 m. Levels of fucoxanthin (mostly from Bacillariophyceae), 19'-hexanoyl-fucoxanthin (Prymnesiophyceae) and animal carotenoids all declined during the night. Conversely, peridinin (Dinophyceae) concentrations, which were low at dusk, rose to a peak in the middle of the night, then fell at dawn (07:00 h). Concentrations of all plant carotenoids increased during the day. Animal carotenoid levels, however, remained low.

Zooplankton gut contents contained both plant and animal pigments (Fig. 6). Gut pigment composition varied temporally within each species and the timing of peak gut fullness varied between species.

Calanus pacificus contained elevated levels of fucoxanthin (Bacillariophyceae) and animal pigments at evening twilight and midnight. Peridinin (Dinophyceae) concentrations were high only at midnight and 19'-hexanoyl-fucoxanthin (Prymnesiophyceae) was present only at morning twilight.

In *Evadne* spp., the concentrations of all microplankton pigments increased to a single peak at midnight, after which the gut was nearly empty. Conversely, the guts of *Clausocalanus* sp. contained pigments during an extended period between midnight and noon, with

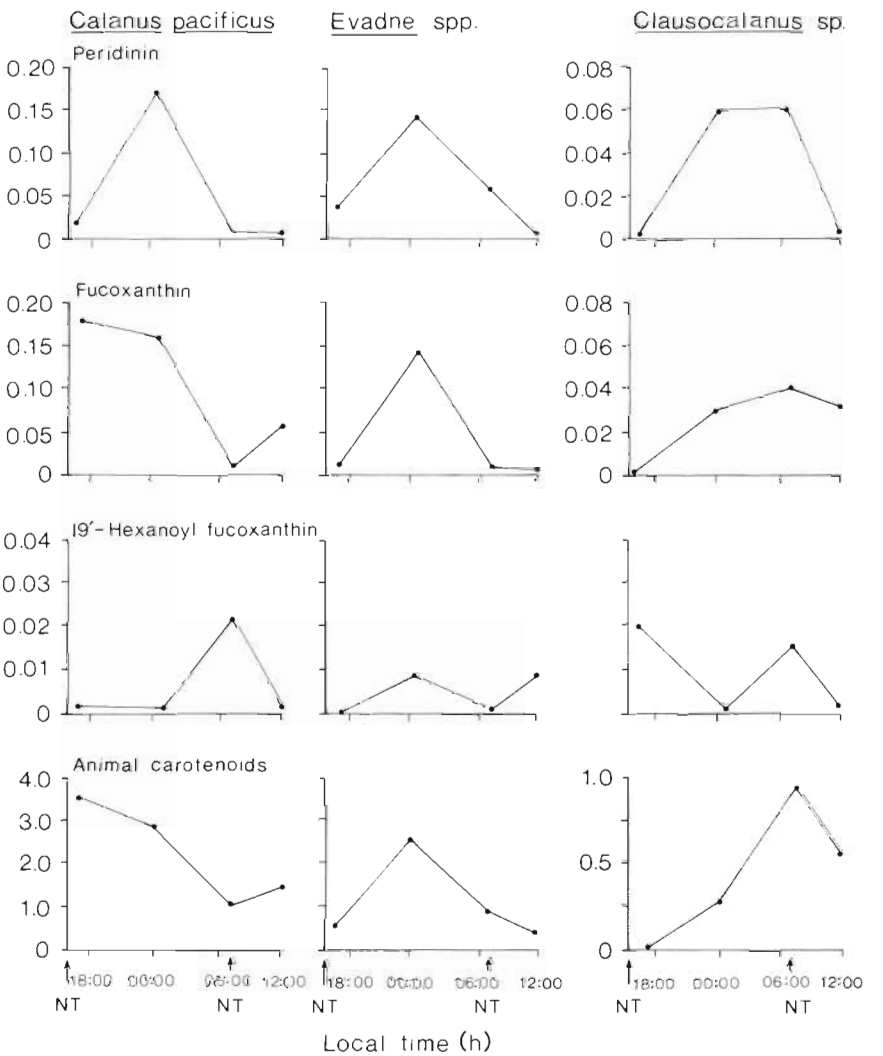

Fig. 6. Carotenoid concentrations (ng ind.$^{-1}$) in the guts of zooplankton collected from the upper 30 m on 11–12 Mar 1987

a peak at 07:00 h. Peridinin levels were elevated at midnight and morning twilight; diatom and animal pigments were present in the midnight, morning and noon samples. The prymnesiophycean pigment was present at both evening and morning twilights. This diel persistence of food in the gut of *Clausocalanus* was observed in an earlier study of gut fluorescence performed in the same region of the San Pedro Basin (unpubl.).

Zooplankton gut carbon contents estimated from carotenoid concentrations are presented in Table 3. Although the confidence limits on these estimates are wide, it is evident that microzooplankton biomass dominated the diets of the macrozooplankton sampled between 11 and 12 March. In all but one case (*Clausocalanus* sp., 17:00 h), microzooplankton is estimated to have contributed >50 % of the total planktonic carbon to the gut contents. In 58 % of the samples (7 out of 12 cases), microzooplankton carbon exceeded 90 % of the total estimated planktonic carbon in the gut.

Comparison of night-time profiles

On 6 March, primary productivity was 4 times higher than on 11 March, and 2 times higher than on 12 March. Depth-integrated phytoplankton biomass was 1.8 times higher on the night of 6 March (01:30 h) than on the night of 11–12 March (midnight samples) (Table 4A).

The gut pigment compositions of all 3 species were markedly different on the 2 nights (Table 4B). *Calanus pacificus* and *Evadne* spp. guts contained greater proportions of algal (particularly dinoflagellate) carbon than animal carbon on 6 March, though the paucity of pigment in the guts of *Evadne* suggests that the cladoceran was not feeding intensely at the time of sampling. Conversely, carotenoid analysis indicates that *Clausocalanus* sp. contained principally animal material in its gut on 6 March.

DISCUSSION

The salient feature of this study is the apparent importance of microzooplankton in the diets of small copepods and cladocerans. Although little is known about the occurrence of carnivory among most planktonic crustaceans, evidence is accumulating to suggest that certain species, long thought to be herbivores, or predominantly herbivorous omnivores, may, in fact, feed intensely on microzooplankton (Gifford & Dagg 1987). Stoecker & Egloff (1987) reported that, in the presence of certain kinds of ciliates, the filtration rate of *Acartia tonsa* was an order of magnitude higher than typically observed in the presence of algae.

Initially, it was surprising that *Evadne* spp. contained animal material in its gut. Cladocerans are considered to be important grazers of nanoplanktonic algae (Falkowski et al. 1983) but are less often thought of as predators. However, heterotrophs may compose on the order of 20 to 50 % of the nanoplankton in certain regions (Rassoulzadegan & Sheldon 1986). Heterotrophic nanoplankton would likely be ingested by the same zooplankton that consume small autotrophs.

The tendency for carnivory by *Calanus pacificus* and possibly *Evadne* spp. was substantially lower on 6 March, when phytoplankton biomass and production were high, than on 11–12 March, when biomass and production were low (Table 4). The ability of zooplankton to alter their diets in response to the food environment has been documented in a number of studies. The presence or relative proportions of phytoplankton and

Table 3. Estimated minimum and maximum plankton carbon concentrations in the gut contents of *Calanus pacificus*, *Evadne* spp. and *Clausocalanus* sp., based on confidence intervals for C:carotenoid ratios for phytoplankton (Table 2) and regression (Eq. 2) for microzooplankton. Also shown are percentages of microzooplankton C relative to total microplankton C in the guts during each sampling interval

Species	Time (h)			
	17:00	00:01	07:00	12:00
Calanus pacificus				
Dietary C: min.–max. (μg ind.$^{-1}$)	0.78–2.32	0.54–1.62	0.12–0.37	0.19–0.57
% Microzooplankton	99.2	93.8	99.9	99.4
Evadne spp.				
Dietary C: min.–max. (μg ind.$^{-1}$)	0.05–0.09	0.48–1.37	0.09–0.25	0.01–0.39
% Microzooplankton	69.8	93.6	74.3	93.7
Clausocalanus sp.				
Dietary C: min.–max. (μg ind.$^{-1}$)	0.011–0.013	0.03–0.07	0.11–0.30	0.04–0.13
% Microzooplankton	0	55.3	88.2	98.3

Table 4. Comparison of food environments and zooplankton diets on 6 and 11–12 March 1987. (A) Characteristics of the food environment in the upper 30 m, with confidence intervals in parentheses; (B) Zooplankton diets

(A) Food environment

	6 Mar	11–12 Mar
Nano- and microplankton carbon (mg m^{-2})		
Dinoflagellates	1068.0 (929.9–1203.1)	615.0 (507.2–656.3)
Diatoms	204.0 (189.0–220.8)	75.0 (72.0–84.0)
Prymnesiophytes	6.0 (5.0–7.0)	2.4 (2.0–2.8)
Animal	699.0 (392.8–1186.3)	552.0 (316.7–956.5)
Primary productivity (mg C m^{-3} h^{-1})	29.8	7.2[a] 11.5[b]

(B) Gut contents

Species	Pigment	6 Mar		11–12 Mar	
		ng pig. copepod^{-1}	% diet C	ng pig. copepod^{-1}	% diet C
Calanus pacificus					
	Peridinin	0.51	74.5	0.17	5.5
	Fucoxanthin	0.15	2.9	0.15	0.7
	19'-hexanoyl-fucoxanthin	0	0	0	0
	Animal	0.41	22.6	2.89	93.8
Evadne spp.					
	Peridinin	0.03	85.1	0.14	5.6
	Fucoxanthin	0.04	14.9	0.14	0.7
	19'-hexanoyl-fucoxanthin	0	0	0.01	< 0.1
	Animal	0	0	2.52	93.6
Clausocalanus sp.					
	Peridinin	< 0.01	0.8	0.06	41.9
	Fucoxanthin	0.02	1.8	0.03	2.8
	19'-hexanoyl-fucoxanthin	0	0	0	0
	Animal	0.40	97.4	0.28	55.3

[a] Productivity 11 Mar
[b] Productivity 12 Mar

microzooplankton in the environment seems to influence the tendency for carnivorous feeding in the copepods *Calanus pacificus* (Landry 1981), *Acartia tonsa* (Stoecker & Sanders 1985) and *Centropages hamatus* (Conley & Turner 1987). Dagg & Walser (1986) reported from field and laboratory investigations that while *Neocalanus plumchrus* is predominantly herbivorous in the Bering Sea, it may obtain substantial nutrition by predation on microzooplankton in the subarctic Pacific Ocean. Periodically, the predatory copepod *Corycaeus anglicus* has been observed to feed on photosynthetic dinoflagellates (Kleppel & Pieper 1984).

Attempts to apply our observations to animals in deeper waters should be undertaken with caution because zooplankton gut composition was measured only in specimens collected only from the upper 30 m. Microzooplankton concentrations off southern California frequently peak near the sea surface and decline sharply with depth (Beers 1986). Thus, there may be a greater tendency for carnivorous feeding near the surface than at depth. Among zooplankton species that feed in the surface waters, periods of intense carnivory may be quite typical.

Carotenoid levels in the phytoplankton and microzooplankton varied 10- to 32-fold during the 11–12 March time series (Fig. 5). Similar changes in pigment content were evident in the guts of the zooplankton (Fig. 6). Such variation is likely the result of both physical and biological forcing. Although we sampled

along a drogue track, advection and mixing most likely influenced the observed pigment distributions.

Biological variability, including diel changes in phytoplankton growth and pigment production rates, and diel changes in zooplankton feeding activities may also have influenced pigment distributions in the water column. The nocturnal decline in all pigments except peridinin, and the recovery of phytoplankton pigment levels during the day, seem consistent with expectations about diel cycles in grazing, predation and phytoplankton growth.

The present study helps to demonstrate the value of pigment markers for assessing the distributions and activities of planktonic organisms. However, many questions are as yet unresolved. Although animal pigments appear useful as microzooplankton biomass analogs, the proportionality between pigmented and unpigmented microzooplankton is unknown. Nor have microzooplankton taxonomic categories been distinguished by their pigments. Despite these limitations, microplankton carotenoids can now be measured precisely, on a semi-routine basis. As such, these pigments can provide useful information about planktonic food webs and trophic structures.

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