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Phytoplankton balance in the oceanic subarctic Pacific: grazing impact of *Metridia pacifica*

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ABSTRACT: Ingestion and respiration by *Metridia pacifica*, the dominant large copepod during autumn and winter in the subarctic Pacific, were investigated by shipboard and laboratory experiments. Diel variation in the rate of grazing on phytoplankton by *M. pacifica* was determined from measurements of gut pigment content and gastric evacuation rate. Both adult females and C_5 copepodites exhibited marked diel variation in gut contents, and thus feeding intensity. Night gut pigment values were 10 times greater than daytime values. Ingestion rates during May 1984 were 51.7 and 9.8 ng chl *a* copepod^{-1} d^{-1} for adult females and C_5 copepodites, respectively. Estimated filtering rates were 76 ml female^{-1} d^{-1} and 15 ml C_5^{-1} d^{-1}. Feeding rates at low food concentrations in incubation bottles were similar to estimates obtained from *in situ* studies. Adult females consumed approximately 7.5 % of body carbon d^{-1}, and C_5 copepodites only 2.5 % d^{-1}. Respiration was 4 to 10 % of body carbon d^{-1} for both C_5 and adults, indicating approximate energy balance for females but higher daily energy expenditure than gain for C_5. Based on the respiration measurements, a model was developed to evaluate the seasonal grazing impact of *M. pacifica* on the phytoplankton standing crop in the subarctic Pacific. During peak phytoplankton production in summer, the low densities of *M. pacifica* require less than 10 % of daily primary production to satisfy metabolic, growth and reproduction requirements. In contrast, during autumn and winter, the *M. pacifica* population requires 36 to 57 % and exceptionally 175 % of daily primary production to satisfy its energy requirements. *M. pacifica* contributes significantly to the total grazing potential responsible for maintaining low stocks of phytoplankton during the unproductive, fall-winter season in the eastern subarctic Pacific.

INTRODUCTION

The oceanic region of the subarctic Pacific has a close temporal and spatial coupling between primary production and herbivore consumption (Heinrich 1962). As a result, the summer increase in primary production does not increase phytoplankton stocks; it increases zooplankton stocks, and the strong seasonal peak of plant biomass, typical of most temperate and boreal ocean regions, does not occur in the subarctic Pacific.

A previous numerical model of the phytoplankton and zooplankton dynamics of the subarctic Pacific (Parslow 1981) represented *Neocalanus plumchrus* and *N. cristatus* as the herbivores primarily responsible for cropping plant production. This principal role of *Neocalanus* was suggested by Heinrich (1957, 1962) because the overwintering strategy and reproduction of these 2 copepods prior to the spring bloom appeared appropriate for immediate grazing control of the spring phytoplankton bloom. Miller et al. (1984) documented the life cycles of the 2 *Neocalanus* spp. at Station P, and concluded that the timing of their life cycles was suitable for grazing control of the spring bloom in the subarctic Pacific. However, models which relied solely upon *Neocalanus* grazing for control of phytoplankton stocks became unbalanced during the autumn after the *Neocalanus* spp. descended to depth and entered diapause. Parslow (1981) concluded that grazing control after the departure of the large grazers from the euphotic zone must be provided by smaller herbivores, but it was difficult to simulate a smooth transition of grazing pressure from the larger *Neocalanus* to smaller unspecified grazers. The copepod *Metridia pacifica* (2.4 to 3.3 mm total length), may be an important grazer during autumn in the subarctic Pacific, since its population size increases soon after the *Neocalanus* spp. depart from the euphotic zone in July (Batchelder 1985). Except for the very small copepods, such as

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Oithona spp., *Metridia* copepodites and adults were the most abundant metazoan herbivores in the surface mixed layer during autumn and winter 1980–1981 (Miller et al. 1984, Batchelder 1985).

In this study a carbon budget for Stage C_5 and female *Metridia pacifica* is presented based upon experimental determination of ingestion and respiration rates. These results are used to model the potential of these smaller herbivores to maintain constant, low phytoplankton stocks in the subarctic Pacific.

METHODS

Collection of copepods. *Metridia pacifica* for experimental studies were collected during summer 1982 and 1983 from coastal Oregon waters (44° 40' N), in summer 1984 from Station P (50° N, 145° W), and in fall 1984 from Dabob Bay, Washington (47° 45' N, 122° 49' W). Zooplankton were sampled using a 0.70 m diameter net of 243 µm mesh equipped with a large volume, slow-filtering cod-end. Vertical or oblique hauls from 50, 70 or 100 m to the surface provided specimens for grazing and respiration incubations. Copepods were either gently poured into a 19 l plastic pail, from which they were sorted, or sorted directly from the cod-end into 0.5 to 1.0 l containers of surface seawater screened at 64 or 200 µm, or Whatman GF/C filtered. Sorting began immediately after collection and was completed within 2 to 3 h.

Diel variation of phytoplankton pigments in gut contents. *In situ* ingestion rate was estimated by measurement of the amount and turnover rate of phytoplankton pigment in the guts of freshly collected copepods. Zooplankton samples collected from the upper 50 to 100 m at Station P every 3 h over a 27 h period on 16 and 17 May 1984 were used to evaluate phytoplankton pigments in the guts of *Metridia pacifica*. After each collection, up to 5 replicates of 8 to 16 individuals of both adult females and C_5 copepodites were sorted into small tubes and kept in the dark. The samples were not frozen prior to sorting; however sorting was completed within 10 to 15 min from the time of collection and at the measured gut evacuation rates this time interval would not affect the *in situ* pigment values much. The method of Mackas & Bohrer (1976), as modified by Dagg & Grill (1980), was used to measure copepod gut fluorescence. For each analysis, the copepods were homogenized in 4 to 6 ml of 90 % acetone, filtered through a Whatman GF/C glass fiber filter, and the fluorescence of the filtrate measured with a Turner Designs Model 10 fluorometer, before and after acidification. The pigment content per copepod was calculated according to the equations:

$$\text{ng chlorophyll ind}^{-1} = \frac{V}{N}(F_o - F_a)\,C \quad (1)$$

$$\text{ng phaeopigment ind}^{-1} = \frac{V}{N}(TF_a - F_o)\,C \quad (2)$$

where F_o and F_a = fluorescence readings before and after acidification, respectively; N = number of copepods; T = maximum acidification ratio; V = volume of acetone used to extract the pigments; and C = a machine-dependent calibration factor. The phaeopigment content of the gut was multiplied by 1.51 as suggested by Shuman & Lorenzen (1975) to correct for the molar conversion of chlorophyll *a* to phaeophorbide to yield the chlorophyll *a* equivalent. Conover et al. (1986) have recently shown that Shuman & Lorenzen (1975) were incorrect in using 1.51 to correct for the molar conversion of chlorophyll *a* to phaeophorbide. In fact, the fluorescence values are already expressed on a molar basis and no correction is necessary. Conover et al. (1986) suggest that the apparent need for a correction arose from destruction (nonconservativeness) of plant pigments during gut passage. It was an unfortunate coincidence that the amount of destruction of pigment in the gut of *Calanus pacificus* (34 %) was the amount corrected by the molar equivalent weight difference of chlorophyll *a* and phaeophorbide. In the current study, destruction of pigment during passage through the gut was not measured. Nevertheless, while it may not be correct to assume that 34 % of the pigments were destroyed during passage through *M. pacifica*, as was found for *C. pacificus*, this assumption was made to allow comparison of the ingestion results reported here with ingestion rates found for other species using this method.

Experiments to determine the gut evacuation rate of *Metridia pacifica*, and thus estimate ingestion from observed *in situ* gut contents, were done both at sea and ashore. Copepods, previously fed on unialgal cultures of either *Thalassiosira weissflogii* (10 to 15 µm diameter) or *Corethron hystrix* (ca 25 µm by 70 µm), were transferred to filtered seawater. Groups of 4 to 10 specimens were removed intermittently over the following 1 to 3 h and analyzed for gut pigment content. Initial gut fullness of *M. pacifica* used in these experiments varied from low values similar to those found in the field, to values (ca 20 ng chl *a* ind^{-1}) much higher than observed in the field.

Incubation grazing experiments. *Metridia pacifica* females collected from off the Oregon coast (Summer 1983), from Dabob Bay, Washington (September 1984), and from Station P (May, August 1984) were used to investigate grazing capabilities. The functional response curve of *M. pacifica* females feeding on *Thalassiosira weissflogii* was determined from 24 h

incubations. Initial and final cell concentrations for experiments during summer 1983 were determined using a model ZBi Coulter Counter equipped with a 70 μm aperture tube. A Particle Data electronic counter, fitted with either a 95 or 190 μm aperture tube, was used to determine cell densities during 1984. In addition, *Corethron hystrix* was used as food in one experiment to investigate the effect of particle size on ingestion. Cell counts and cell volumes for this experiment were determined microscopically.

For each functional response experiment, 2 replicate containers with 10 to 15 copepods, and one control without copepods, were prepared for each of 4 to 5 food levels. Specimens were incubated in 700 ml glass beakers or 500 ml polycarbonate bottles containing 500 ml of the food medium. The differential effect of ammonia excretion by the copepods on phytoplankton growth was minimized by adding 5 to 10 μmol NH_4Cl l^{-1} to each container at the beginning of each experiment. Incubations lasted 20 to 30 h, and were conducted in a constant temperature cold room. All containers were gently stirred several times hourly by a plunger-stirrer, which maintained the phytoplankton in suspension. Incubations during 1983 were conducted at 10 to 12.5 °C under constant cool-light illumination (60 to 80 μE m^{-2} s^{-1}). The September 1984 experiments were performed in constant darkness at 8, 12, and 15 °C. Shipboard experiments were conducted in on-deck incubators at sea surface temperature with the natural daylight cycle. Ingestion and filtration rates were calculated by the equations of Frost (1972). Ingested particle volume was converted to carbon using the equation of Mullin et al. (1966). All food levels and ingestion rates are presented on a carbon basis to facilitate comparison among experiments.

Respiration experiments. Respiratory rate of *Metridia pacifica* was measured in bottle incubations during May and August 1984 at Station P. Copepods were collected by net hauls as described above. Fifteen to 30 C_5 copepodites or adult females were sorted into 300 ml BOD bottles filled with 64 or 200 μm screened surface seawater. Control bottles, filled with identical water but lacking copepods, were run concurrently. The bottles were placed in deck incubators for 12 to 24 h. Oxygen consumption by adult females was measured at 8, 9 and 14.6 °C, but only at 8 to 9 °C for C_5 copepodites. The oxygen concentration in initial, final experimental and final control bottles was measured by Winkler titration. The measured respiration rates in μl O_2 ind^{-1} h^{-1} were converted to μg carbon ind^{-1} h^{-1} using a respiratory quotient of 0.9 (Parsons et al. 1984).

Seasonal length variation and length-weight relations. Seasonal variation of body size of *Metridia pacifica* was described from samples collected at Station P from February 1980 to March 1981 (for collection methods see Miller et al. 1984). Total length, excluding caudal setae, of N_4, N_5, C_3, C_4, C_5 males and females, and adult females was measured using a calibrated ocular micrometer. Usually 25 to 50 individuals of each life stage were measured from each 0 to 100 m sample. On dates when the depth of the mixed layer was shallower than 100 m, 25 to 50 individuals of each stage were measured from both the 100 m to thermocline sample and the thermocline to 0 m sample. An abundance-weighted size distribution was then calculated for the 100 m layer.

A length-weight relation for *Metridia pacifica* was determined from freshly collected individuals of the older life stages (C_4 to adult) and from formalin-preserved C_1 to C_3 copepodites. Specimens were measured for total length, rinsed briefly in distilled water, transferred to precombusted Whatman QM/A quartz fiber filters, and dried at 60 °C. Carbon contents for both live-sorted and formalin-preserved samples were analyzed ashore using a Perkin Elmer Model 240C Elemental Analyzer.

RESULTS

Diel variation of gut content fluorescence

The variation of chlorophyll *a* equivalent per C_5 and female *Metridia pacifica* during a 27 h period in May 1984 is shown in Fig. 1. During daytime, adult females contained little pigment, ranging from 0.4 to 0.6 ng chl *a* $female^{-1}$; whereas females collected at 2200 h and 0100 h averaged 5.7 and 5.9 ng chl *a* $female^{-1}$, respectively. The diel cycle of gut pigment of C_5 copepodites was similar, but of lower amplitude (Fig. 1). Daytime values were always less than 0.24 ng chl *a* C_5^{-1}, compared to 0.8 to 1.2 ng chl *a* C_5^{-1} at night.

Metridia pacifica are dramatic diel vertical migrators (Batchelder 1985), and this alone should result in a diel cycle of gut contents as the copepods descend to depths during the day where chlorophyll values are very low. However, not all individuals left the surface during the day, and to evaluate diel ingestion without the complications of vertical migration, only individuals from the upper mixed layer were analyzed for gut pigment content. Since the percent change in ambient water chlorophyll (Fig. 1) of the upper mixed layer was much less than was observed for gut chlorophyll, the temporal change of chlorophyll equivalent per copepod implies a real difference in feeding intensity between day and night, not an effect of vertical migration or change in food availability. The time course of pigment loss from the guts of adult females after transfer to filtered seawater is shown in Fig. 2 for 5 experi-

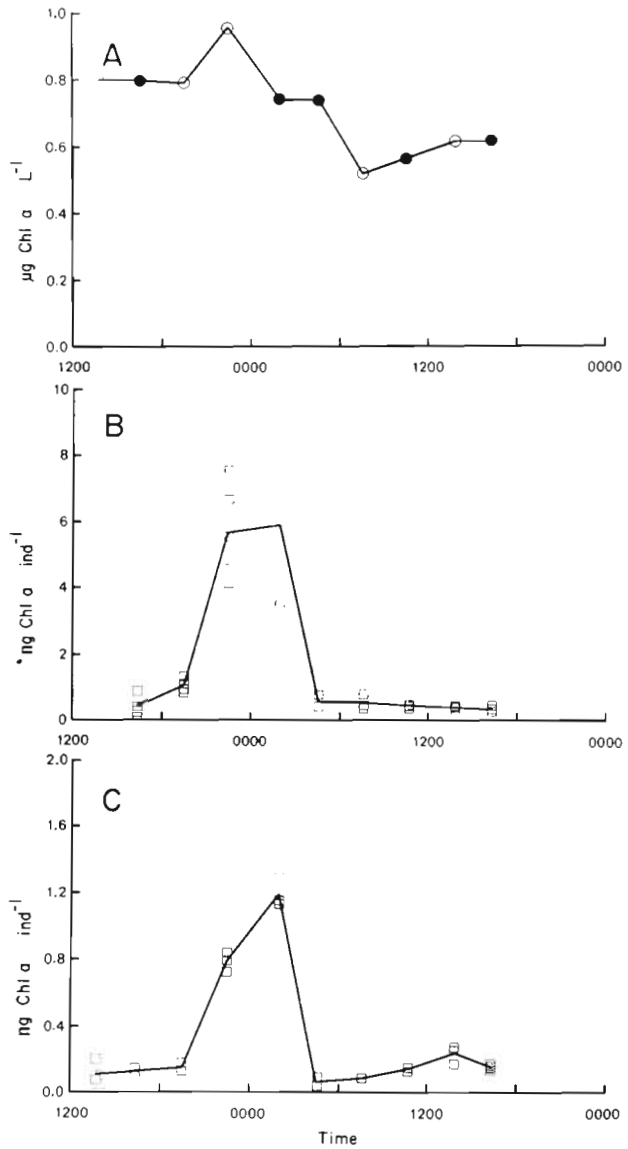

Fig. 1. *Metridia pacifica*. Diel variation of water chlorophyll *a* and pigment content at Station P during 16–17 May 1984. (A) Water chlorophyll (○: measured; ●: interpolated); (B) adult female; (C) C_5 copepodite

ments. Pigment content declined rapidly over the first hour. The gut evacuation rate was described by the exponential relation:

$$S_t = S_o e^{-Et} \quad (3)$$

where S_o = amount of pigment in the gut at time zero; S_t = pigment content at time t; and E = instantaneous gut evacuation rate (min^{-1}) (Dagg & Wyman 1983). Gut evacuation rate ranged from 1.4 to 2.4 % min^{-1} (Table 1), with no consistent relation to temperature, food type or initial gut fullness. Pooling and scaling the data from all 5 experiments yields an overall mean evacuation rate of 1.8 % min^{-1}.

Gut evacuation rate of adult females was independently estimated from the decline in mean gut pigment from 0158 to 0436 h on 17 May 1984, assuming the decline during that interval resulted from cessation of feeding activity. If the copepods stopped feeding at 0158 h, the gut evacuation rate necessary to decrease the gut contents to 0.54 ng pigment ind^{-1} at 0436 h is calculated from Equation (3) to be 1.53 % min^{-1}, in good agreement with the laboratory results.

In situ ingestion rate was determined from the diel cycle of gut pigment (Fig. 1) using an instantaneous gut evacuation rate of 1.8 % min^{-1} (Table 2). Total consumption (C_t) for each time interval (t) was calculated from:

$$C_t = \frac{(S_t - S_o e^{-Et})\, Et}{1 - e^{-Et}} \quad (4)$$

(Elliot & Persson 1978) where S_o and S_t = amount of pigment in the gut at the beginning and end of the time interval, respectively; and E = instantaneous gut evacuation rate. This relation assumes that the evacuation rate is exponential and that consumption rate during the interval remains constant. Ingestion rates of both females and C_5 appear to have been greatest near midnight (Table 2). Total daily consumption was 9.8 and 51.7 ng chl *a* for C_5 and adult females, respectively. Since the specific depth at which the copepods were feeding was not known from vertical collections, the highest chlorophyll *a* concentration of the mixed layer was used to provide conservative estimates of filtration rate for each sampling time (Table 2). Daily volume swept clear was 76 ml ind^{-1} for adult females and 15 ml ind^{-1} for C_5.

Grazing incubations

Table 3 summarizes the experimental conditions and phytoplankton used in the feeding experiments. Functional response curves in most experiments appeared curvilinear and were described by the Ivlev (1955) equation as modified by Parsons et al. (1967):

$$I = I_{max}\,(1 - e^{a(P_o - P)}) \quad (5)$$

where I_{max} = maximum ingestion rate; a = a constant related to the initial slope of the curve; and P_o = threshold food level below which ingestion ceases. In none of the experiments was P_o significantly different from zero. Ingestion rates of *Metridia pacifica* females feeding on *Thalassiosira weissfloggii* were higher in the dark than in the light (Fig. 3A,B).

Metridia pacifica adult females exhibited a hunger response (Runge 1980). Females preconditioned for 36 h at 450 µg carbon l^{-1} of *Thalassiosira weissfloggii* had lower ingestion rates than females which were not

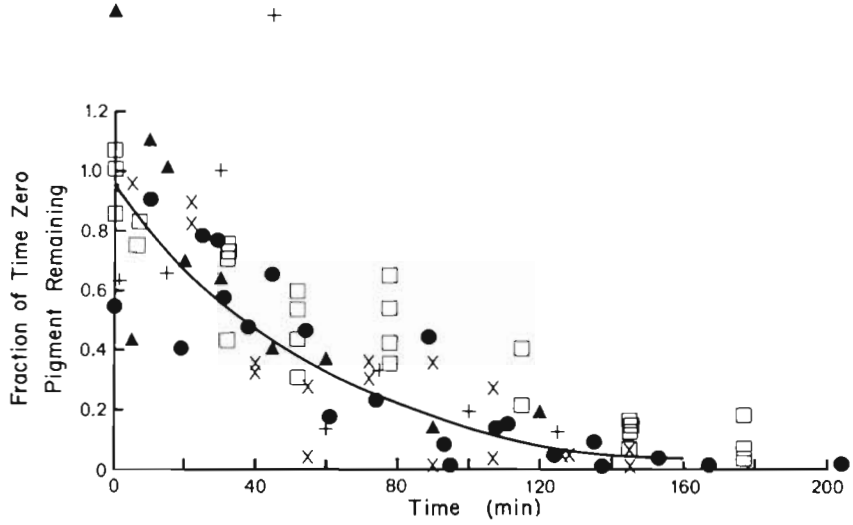

Fig. 2. *Metridia pacifica*. Time course of gut pigment evacuation for adult females. Symbols as in Table 1

Table 1. *Metridia pacifica*. Results of adult female gut evacuation experiments. Tw: *Thalassiosira weissflogii;* Ch: *Corethron hystrix*

Date	Temp. (°C)	Food	Evacuation (min^{-1})	R^2	Symbol in Fig. 2
16 Jun 83	10.2	Tw	0.016	0.538	+
22 Jun 83	10.2	Tw	0.024	0.616	×
23 Jul 83	13.5	Ch	0.014	0.861	□
19 May 84	8.4	Tw	0.022	0.766	●
16 Nov 84	12.0	Tw	0.017	0.762	▲

Table 2. *Metridia pacifica*. Diel dycle of ingestion and filtration rate of C_5 and females at Station P during May 1984. Values in parentheses are the number of replicates

Date	Time (h)	Water chla ($ng\ ml^{-1}$)	Adult female				C_5 copepodite			
			Ingestion ($ng\ ind^{-1}\ h^{-1}$)		Filtration ($ml\ ind^{-1}\ h^{-1}$)		Ingestion ($ng\ ind^{-1}\ h^{-1}$)		Filtration ($ml\ ind^{-1}\ h^{-1}$)	
16 May	1345	0.80	—		—		0.10–0.27	(3)	0.13–0.34	
	1622	0.80*	0.19–1.12	(5)	0.24–1.40		0.16–0.21	(2)	0.20–0.27	
	1930	0.79	1.12–1.80	(4)	1.42–2.28		0.18–0.26	(3)	0.23–0.33	
	2228	0.96	5.54–10.16	(5)	5.77–10.58		0.99–1.70	(3)	1.03–1.32	
17 May	0158	0.74*	4.66–10.23	(3)	6.30–13.82		1.54–1.75	(3)	2.08–2.37	
	0436	0.74*	0.53–1.06	(3)	0.72–1.43		0.07–0.14	(3)	0.09–0.19	
	0737	0.52	0.52–1.08	(4)	1.00–2.08		0.13	(1)	0.25	
	1045	0.57*	0.49–0.66	(3)	0.86–1.16		0.19–0.22	(3)	0.33–0.39	
	1352	0.62	0.45–0.59	(3)	0.73–0.95		0.25–0.38	(3)	0.41–0.62	
	1620	0.62*	0.34–0.61	(3)	0.55–0.98		0.19–0.24	(3)	0.30–0.39	

* Interpolated water chlorophyll values

preconditioned or were preconditioned in filtered seawater for 6 to 18 h (Fig. 3A). I_{max} for specimens preconditioned on high food was 1.92 µg C $ind^{-1}\ d^{-1}$, compared to 4.75 µg C $ind^{-1}\ d^{-1}$ for specimens starved prior to the experiment.

Ingestion rates of *Metridia pacifica* feeding on *Thalassiosira weissfloggii* in the dark were temperature dependent (Fig. 3B). At the 2 lowest food concentrations, 25 and 75 µg C l^{-1}, ingestion rates were similar at 8.0 and 12.0 °C. However at 250 and 570 µg C l^{-1}, ingestion was higher at 12 °C than at 8 °C. I_{max} was 4.9 µg C $ind^{-1}\ d^{-1}$ at 8 °C and 8.2 µg C $ind^{-1}\ d^{-1}$ at 12 °C. Ingestion at 15 °C was linearly, rather than curvilinearly, related to food abundance. Apparently

Table 3. *Metridia pacifica*. Experimental conditions, collection site, and dates of ingestion rate incubations. Tw: *Thalassiosira weissflogii*; Ch: *Corethron hystrix*; FSW: filtered seawater

Date	Collection site	Temp. (°C)	Light ($\mu E\ m^{-2}\ s^{-1}$)	Precondition	Food type	Symbol in Fig. 3A
19 Sep 81	Oregon	8.0	5–20	None	Tw	●
18 May 83	Oregon	12.5	60–80	36 h at 450 $\mu gC\ l^{-1}$	Tw	+
14 Jun 83	Oregon	10.0	60–80	12 h in FSW	Tw	×
21 Jun 83	Oregon	10.2	60–80	6 h in FSW	Tw	□
22 Jul 83	Oregon	13.5	Low light	18 h in FSW	Ch	
11 Sep 84	Dabob Bay	8, 12, 15	Dark	None	Tw	

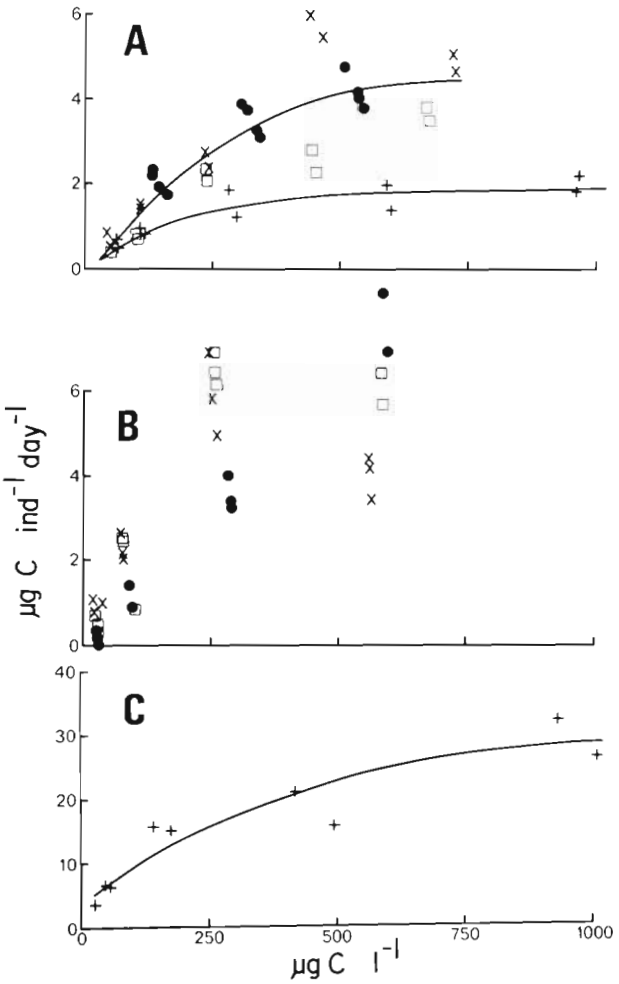

Fig. 3. *Metridia pacifica*. Ingestion rates of adult females. Curves in (A) and (C) are best Ivlev fit to the data. (A) Feeding on *Thalassiosira weissfloggii* in the light (lower curve: high food preconditioned; upper curve: low food preconditioned); (B) feeding on *T. weissfloggii* in the dark (×: 8 °C; □: 12 °C; ● 15 °C); (C) feeding on *Corethron hystrix* (note scale change from (A) and (B))

food levels exceeding 570 $\mu g\ C\ l^{-1}$ are needed to saturate feeding at 15 °C. Although ingestion at the highest food level was greatest at 15 °C, ingestion at intermediate food levels was lower at 15 °C than at 8 or 12 °C.

Metridia pacifica ingested 3 to 4 times more carbon per day and had higher filtration rates when fed *Corethron hystrix* than when fed *Thalassiosira weissfloggii* (Fig. 3C). Daily ingestion was 15 to 20 $\mu g\ C\ ind^{-1}$ at 500 $\mu g\ C\ l^{-1}$ of *C. hystrix*, compared to 2.5 to 6 $\mu g\ C\ ind^{-1}$ when fed *T. weissfloggii*. Maximum ingestion (I_{max}) was 31.3 $\mu g\ C\ ind^{-1}\ d^{-1}$ on the large cell, which is 4 to 6× and 6 to 15× greater than when feeding on *T. weissfloggii* in the dark and light, respectively.

Respiration experiments

Oxygen consumption rates of *Metridia pacifica* females and C_5 copepodites are shown in Table 4. Adult female respiration was not clearly related to temperature. The reason for this is not clear; however, water temperature in the deck incubators during the May and August 1984 cruises was slightly (1 to 3 C°) warmer than that of the surface water. Thus, the copepods experienced higher temperatures in the respiration experiments than they would encounter normally in surface waters at that time; the absence of a relationship between metabolic rate and temperature might be explained by the copepods not being acclimatized to higher than ambient temperatures. Respiration by C_5 copepodites at 8 to 9 °C was approximately half that of adult females at the same temperature. Respiration as fraction of body weight was 4 to 10 % d^{-1} for both C_5 copepodites and adult females.

Seasonal variation in length and length-weight relations

Seasonal variation in total length was most pronounced for adult females (Fig. 4). Mean length of adult females was greatest (3.23 mm) on 21 June and 10 July 1980, and least (2.31 mm) on 1 January 1981. Mean length of C_3 to C_5 copepodites also varied seasonally, although the amplitude of the seasonal pattern was far less than that of adult females (Fig. 4). Length of N_4 and N_5 did not vary seasonally.

Table 4. *Metridia pacifica*. Respiration

Stage	Temp. (°C)	N	Mean (SD) ($\mu l\ O_2\ ind^{-1}\ h^{-1}$)	($\mu g\ C\ ind^{-1}\ h^{-1}$)*
Female	9.0	6	0.397 (0.070)	0.191 (0.034)
Female	8.0	6	0.267 (0.140)	0.129 (0.067)
Female	14.6	2	0.326	0.157
C_5	8–9	6	0.155 (0.028)	0.075 (0.014)

* Respiratory quotient of 0.9 assumed

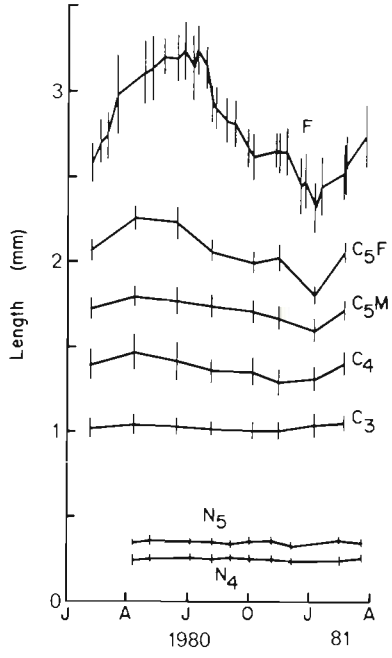

Fig. 4. *Metridia pacifica*. Seasonal total body length during Feb 1980 to Feb 1981

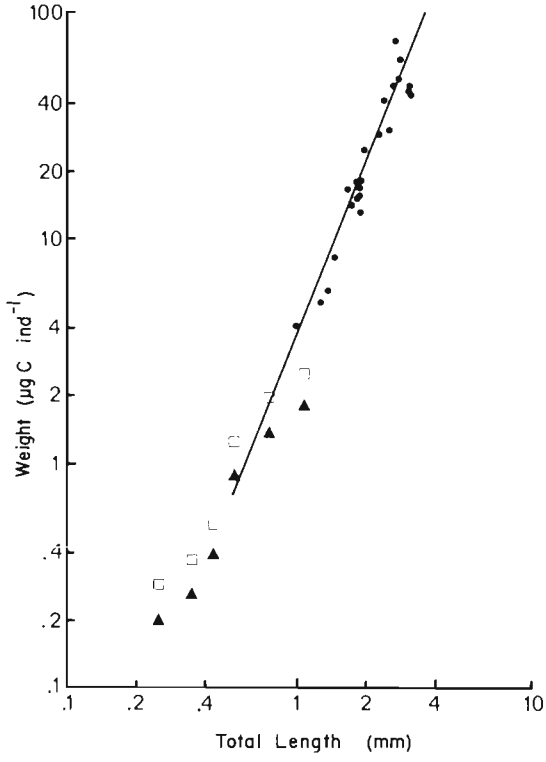

Fig. 5. *Metridia pacifica*. Length-weight relation. (●) Live sorted; (▲) formalin-preserved; (□) corrected formalin-preserved

The length-weight relation for *Metridia pacifica* is shown in Fig. 5. Triangles represent values determined from formalin-preserved samples, which according to Landry (1978) and Omori (1978) underestimate the true carbon values by approximately 30 %. The measured carbon contents of N_4 to C_3 have been multiplied by 1.43 to correct for this weight loss. The corrected values are indicated by squares. For C_1 to adults, the length-weight relation, fit by least-squares regression, was best described by:

$$W = 3.83\ L^{2.46} \quad R^2 = 0.94 \quad N = 27 \qquad (6)$$

where L = total length in mm; and W = body weight as µg carbon.

DISCUSSION

Feeding rates

Metridia pacifica C_5 and females exhibited a marked diel feeding periodicity during May 1984 at Station P; ingestion and filtration rates were an order of magnitude greater at night than during the day. Diel variation in gut pigment content of copepods has been reported previously for *Centropages hamatus* (Nicolajsen et al. 1983, Head et al. 1984), *Centropages typicus* (Mackas & Bohrer 1976, Dagg & Grill 1980), *Metridia lucens* (Mackas & Bohrer 1976), *Pseudocalanus* sp. (Nicolajsen et al. 1983) and *Temora longicornis* (Head

et al. 1984). In several of these earlier gut content studies, however, it was not possible to separate the effects of (1) daytime downward migration away from high food concentration from (2) diel variation in individual feeding behavior. Since chlorophyll *a* values of the upper 70 to 100 m were nearly homogeneous (Lorenzen 1984) in the present study, the diel cycle of gut pigment content reflects a real day-night difference in feeding intensity, similar to that found by Baars & Oosterhuis (1984) for species of *Temora, Pseudocalanus, Centropages* and *Calanus* and by Head et al. (1985) for the non-migratory *Calanus hyperboreus* and *C. glacialis* in the Arctic.

The pigment content of each *Metridia pacifica* female during the daytime represented the filtration of 1 to 2 ml of the surrounding water, whereas the pigment content at night represented filtration of 6 to 8 ml of water. Mackas & Burns (1986) report that recently starved *M. pacifica* females had a first hour filtration rate of 1.9 ml ind^{-1} h^{-1} in low-food (1 µg chl *a* l^{-1}) conditions. The filtration rate estimates reported here following apparent starvation (during the day) are much greater (6 to 13 ml ind^{-1} h^{-1}). Mackas & Burns (1986) also report a turnover time of 0.6 h for *M. pacifica* females. This corresponds to a gut evacuation rate of 1.3 % min^{-1}, similar to my estimate of 1.8 % min^{-1}. Ingestion of chlorophyll by adult females in May 1984 was 51.7 ng chl *a* ind^{-1} when summed over 24 h. Assuming a carbon to chlorophyll *a* ratio of 60 for Station P in May 1984 (Welschmeyer pers. comm.), daily ingestion was 3.1 µg C $female^{-1}$. For adult females of 43 µg C, this ration is equal to 7.2 % of body carbon per day. A similar calculation for C_5 reveals that daily ingestion was 0.59 µg C, which amounts to only 2.4 % of body carbon.

Clearance rates determined for *Metridia pacifica* females in long-term bottle incubation experiments were slightly lower than *in situ* rates estimated from gut pigment content. Maximum clearance rate on small cells (at low concentration (100 µg C l^{-1})) was 30 ml d^{-1} compared to the integrated *in situ* clearance rate of 76 ml d^{-1}. At unnaturally high food concentrations clearance rates in the incubations were even lower (<20 ml ind^{-1} d^{-1}). When food concentrations in bottle incubations were significantly higher than ambient food levels at Station P, daily ration of adult females ranged from 3.9 % of body weight when preconditioned on a high concentration of *Thalassiosira weissfloggii*, to 62 % when fed the large diatom *Corethron hystrix*. However, in containers with food concentrations comparable to those observed at Station P, daily consumption was generally less than 1 % of body carbon.

The results of gut fluorescence analyses and laboratory incubation experiments were consistent in that both indicated that *Metridia pacifica* have relatively low ingestion rates. Ingestion as a fraction of body weight was usually less than 7 % d^{-1}, except when the copepods were offered unnaturally high food concentrations.

There are relatively few other studies of feeding in *Metridia* with which the present results may be compared. Haq (1967) measured the feeding rate of *Metridia lucens* upon several foods, including both phytoplankton cells and *Artemia* nauplii. Ingestion rates depended upon the quantity and type of food offered. Maximum ingestion of phytoplankton food was less on small cells than on large cells. The results from the present experiments agree with those results, as maximum ingestion rates were much higher when *M. pacifica* were offered *Corethron hystrix*, rather than *Thalassiosira weissfloggii*. Moreover, daily consumption of phytoplankton by *M. lucens* was low; ingestion ranged from 0.44 µg C ind^{-1} d^{-1} when fed *Dunaliella* to 2.10 µg C ind^{-1} d^{-1} when fed *Thalassiosira nordenskioldii* (Haq 1967). As mentioned earlier, the gut evacuation rate measured here is quite similar to that reported by Mackas & Burns (1986), although the individual filtration rate, following a starvation period, is roughly 3 to 5× greater in the present study than was found by Mackas & Burns. Daily ration of *M. pacifica* females can be estimated from their data (Table 1 of Mackas & Burns 1986) by applying their gut turnover time (1.3 % min^{-1}) to the average pigment in the gut, assuming that the carbon content of *Metridia* is 43 % of the dry weight, and that the C:Chl ratio of the phytoplankton *(Coscinodiscus)* is 30. These calculations indicate rations of 2.6 % d^{-1} and 22 % d^{-1} for recently starved copepods feeding at low and high food concentrations, respectively. Non-starved specimens had slightly lower rations of 1.9 % d^{-1} and 12.6 % d^{-1} in low and high food concentrations. The low food results are similar to the daily rations obtained for *M. pacifica* in the present study.

Other pelagic crustaceans similar in size to *Metridia pacifica* and *M. lucens* have much greater daily rations. Paffenhöfer (1971) reported daily ration of *Calanus helgolandicus* (= *pacificus*) of 60 µg carbon body weight to be 55 % d^{-1}. Mackas & Burns (1986) observed daily rations of 8 to 12 % d^{-1} and 14 to 96 % d^{-1} for *C. pacificus* feeding on small and large phytoplankters, respectively. Mullin & Brooks (1970), also working on *C. pacificus* (45 µg C), reported the ration as roughly 40 % d^{-1}. *Euphausia pacifica* furcilia of 25 to 50 µg C ingested 17 to 30 % d^{-1} (Ross 1982). It is not clear why the ingestion rate of *Metridia* is so much lower than that observed for other pelagic crustaceans of similar size, but it may be related to the size of the food particles. Most of the studies of *C. pacificus* and *E. pacifica* ingestion were conducted using relatively

large (19 to 64 µm diameter) phytoplankton cells as food. In the present study, *M. pacifica* offered large cells *(Corethron hystrix)* had ingestion rates as high as 62 % of body carbon per day. Offering large cells as food to *M. pacifica* is not entirely appropriate because, although large phytoplankton cells can at times be abundant in the subarctic Pacific (Clemons & Miller 1984), the more usual case is for nanophytoplankton to dominate the flora (Booth et al. 1982, Taylor & Waters 1982). It should be noted also that Mackas & Burns (1986) also found low daily rations (2 to 22 % d^{-1}) with *M. pacifica* feeding on large (40 to 50 µm) cells.

Metabolic rate

Fig. 6 indicates that the respiration rates of *Metridia pacifica* measured in the present study are comparable to previously published data for this species and *M. lucens*. Dagg et al. (1982) present a relation between

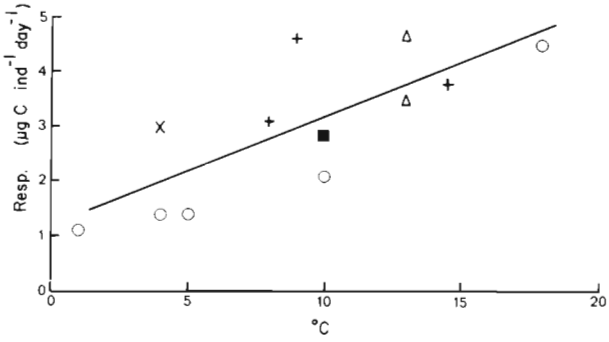

Fig. 6. *Metridia pacifica* and *M. lucens*. Summary of respiration rates of adult females. Data from (■) Marshall & Orr (1962); (○) Haq (1967); (△) Ikeda (1976); (×) Dagg et al. (1982); (+) present study

metabolism and body size determined for zooplankton, including *M. pacifica*, from the Bering Sea. The slope of their relation (b = 0.884) is similar to the slope of boreal (b = 0.834) and subtropical (b = 0.867) species reported by Vidal & Whitledge (1982). Vidal & Whitledge (1982) concluded that the slopes of the allometric equation describing metabolism as a function of body weight did not differ for pelagic crustaceans of boreal and subtropical habitats. In contrast, the intercept of the relation between weight and metabolism increased with increased habitat temperature.

In the present study, respiration of *Metridia pacifica* was measured at a few temperatures only, and only for adult females and C_5 copepodites (Table 4). Respiration rates of younger copepodite stages were assessed indirectly by a relation developed to express respiration as a function of habitat temperature and body size. Adult female respiration increased linearly with temperature over the temperature range from 2 to 18 °C (Fig. 6). *M. pacifica* females in the Bering Sea were larger (~100 µg C) (Dagg et al. 1982) than those from coastal Oregon or Station P; thus, respiration for females from the Bering Sea was calculated for 45 µg individuals using the equations provided by Dagg et al. (1982). Assuming the allometric equation appropriately describes the relation between metabolism and body size, and assuming also that the respiration data shown in Fig. 6 were obtained from adult females of constant body size, an empirical relation was derived to describe the temperature (T) dependence of the respiration constant (a) of the allometric equation. The equation best describing this relation is:

$$a = 0.037 + 0.006\ T \quad R^2 = 0.60 \quad p < 0.005 \qquad (7)$$

Using 0.884 (Dagg et al. 1982) as the slope of the allometric equation then:

$$R = (0.037 + 0.006\ T)W_c^{0.884} \qquad (8)$$

where R = respiration rate in µg C ind^{-1} d^{-1}; T = temperature in °C; and W_c = body weight in µg carbon. Finally, by substituting Equation (6) into (8) we obtain:

$$R = (0.037 + 0.006\ T) \cdot (3.83\ L^{2.46})^{0.884} \qquad (9)$$

which allows a prediction of metabolic rate from habitat temperature and total body length.

An empirical relation such as (8) or (9) must be applied with caution, particularly when it is derived from a small set of data, as is the case here. It is desirable to compare predictions of the equation with experimentally measured values. Since the dependence of the respiration constant (a) on temperature was derived from data on adult females only, a test is to compare the predicted respiration of C_5 copepodites (approximately 25 µg C) at 8.5 °C to that reported in Table 4. The respiration rate of 1.54 µg carbon ind^{-1} d^{-1} predicted by the equation falls within the 95 % confidence interval of the experimentally determined rate for C_5 copepodites (X = 1.80; S = 0.33; N = 6).

Carbon budget of C_5 copepodites and adult females

From the data on respiration and *in situ* feeding rates in May 1984, a carbon budget was constructed to evaluate the ability of *Metridia pacifica* to survive at rations available in the field. Daily carbon ingestion of adult females and C_5 copepodites at Station P during May was estimated from the *in situ* gut content results, and compared to calculated metabolic demands. Assuming that feeding occurs at night at the surface (6.0 °C) and that days are spent at 250 m (3.8 °C), metabolic demands are calculated to be 1.90 and

1.13 µg C copepod^{-1} d^{-1} for females and C_5, respectively. If assimilation efficiency is 70 %, ingestion of 2.71 and 1.61 µg C copepod^{-1} d^{-1} is required for metabolism. Given the carbon to chlorophyll ratio of 60, the daily ingestion per female and C_5, estimated from *in situ* gut pigment determinations and a gut evacuation rate of 1.8 % min^{-1}, are 3.10 and 0.59 µg C copepod^{-1}, respectively. Thus, adult females ingested sufficient food to support their metabolism and have a little left for growth or reproduction, while C_5 obtained food for only 37 % of their daily metabolic needs with no provision for growth.

Several assumptions were made to enable these comparisons, and errors in them, alone or in concert, may cause the poor agreement between metabolic requirements and daily ingestion of the fifth copepodites. The possibilities include the following: the carbon to chlorophyll ratio is in error; respiration rate is overestimated; gut evacuation rate is underestimated; ingestion rate is too low because of pigment destruction; the copepods supplement their diet by feeding on animals or seston; assimilation efficiency is greater than 70 %; or during this particular day *Metridia pacifica* C_5 did not get enough to eat. The last possibility is difficult to test, can only work on the short term, and is not discussed further. The other hypotheses are testable and can be evaluated for C_5. The carbon to chlorophyll value may be in error, but other realistic values for this parameter (20 to 100) fail also to balance the energy budget. Assimilation efficiency, even if assumed to be 100 %, an unlikely value, could not by itself balance the energy budget.

Respiration estimates from several sources (Fig. 6) were used to derive the respiration equation. The container size, acclimation and incubation times, and methods used to measure respiration varied widely, yet the results agree reasonably well. This reduces, but does not eliminate, the possibility of error; the respiration rates from all sources may be elevated above those found *in situ*. Considering the possibility that *Metridia* supplement their diet with animal prey, the guts of a few C_5 and several dozen females were examined microscopically for evidence of animal remains, and none, except a very few nasselarian radiolaria, were found (Batchelder pers. obs.), although both Mullin (1966) and Haq (1967) found that *Metridia* readily ingest and grow on *Artemia* nauplii. However, consumption of colorless flagellates by *Metridia* would likely go undetected in these microscopic examinations. Thus, the role of heterotrophic flagellates in the diet of *M. pacifica* remains unknown.

As was stated earlier, the extent of pigment degradation within the gut of *Metridia* was not evaluated. The present budget calculations assume that pigment destruction was on the order of 34 %, similar to that found in *Calanus pacificus* by Shuman & Lorenzen (1975). If greater than 34 % pigment destruction occurred then the total daily ingestion rate, as estimated from *in situ* gut fluorescence, would be underestimated. Attempting to balance the carbon budget of C_5 by adjusting the pigment destruction rate alone requires that 75 % of the pigment ingested by the copepod be degraded within the gut prior to measurement of the gut fluorescence. Degradation rates greater than 90 % have been reported for *C. glacialis* and *C. hyperboreus* (Conover et al. 1986).

The carbon budget balance turns out to be sensitive to the choice of gut evacuation rate. The gut evacuation rate of 1.8 % min^{-1} that was used in this analysis was determined using adult females only. It may not be appropriate to apply that rate to younger life stages. Furthermore, in the evacuation rate experiments described above the copepods were transferred to filtered seawater to follow the time course of pigment loss from the gut, and perhaps individuals so treated retain the food already in the gut longer than when other food is available (Murtaugh 1984). If so, evacuation rates would be underestimated. All other parameters being unchanged, the carbon budget of C_5 can be balanced so that assimilated carbon equals respired carbon if evacuation rate is increased from 1.8 % min^{-1} to 5.0 % min^{-1}. Although this gut evacuation rate is twice the highest rate (2.4 % min^{-1}) measured for adult females, gut evacuation rates as high as 4 % min^{-1} have been reported for *Neocalanus plumchrus* (Dagg & Wyman 1983) and *Temora, Pseudocalanus, Centropages,* and *Calanus* spp. (Baars & Oosterhuis 1984).

Potential contribution of *Metridia pacifica* herbivory in controlling phytoplankton stocks

The agreement between the measured and predicted respiration of C_5 copepodites encouraged me to use Equation (9) to estimate the metabolism of the C_3 to C_5 copepodite and adult female populations of *Metridia pacifica* at Station P from seasonal abundance estimates (Batchelder 1985) and size distribution. All of these life stages migrate vertically, spending the night near the surface and the day at depth. During this migration, the copepod passes through a marked temperature gradient, the intensity of which varies with season. A simple model was developed using temperature of the surface mixed layer and temperature at 250 m, for night and day periods, respectively. Migration from the surface to 250 m and back were considered to occur instantaneously at sunrise and sunset (U. S. Naval Observatory 1979), respectively.

Respiration by the C_3 to adult populations of *Me-*

Table 5. *Metridia pacifica*. Daily population respiration (mg C m^{-2}) of C_3 to adult female, total daily consumption, and estimated daily primary production (mg C m^{-2}) from Stephens (1968)

Date	C_3	C_4	C_5M	C_5F	Fem.	Sum	(A) Cons.*	(B) Cons.**	(C) Primary prod.	Fraction of production consumed (A/C) ×100	(B/C) ×100
6 Feb 80	0.50	0.79	1.40	1.58	2.48	6.75	9.6	13.8	27.2	35.3	50.7
10 Apr 80	0.40	0.59	0.71	0.43	1.49	3.62	5.2	7.4	94.3	5.5	7.8
11 Jun 80	0.08	0.30	0.39	1.16	5.23	7.16	10.2	14.6	163.2	6.3	8.9
1 Aug 80	0.11	0.98	0.93	0.61	2.85	5.48	7.8	11.2	136.6	5.7	8.2
1 Oct 80	1.12	1.45	1.29	1.37	4.59	9.82	14.0	20.0	58.1	24.1	34.4
9 Nov 80	0.86	1.30	0.33	0.64	2.91	6.04	8.6	12.3	23.0	37.4	53.5
1 Jan 81	2.39	2.70	1.84	1.20	1.95	10.08	14.4	20.6	8.2	175.6	251.2
15 Feb 81	0.08	0.88	0.89	2.25	2.09	6.19	8.8	12.6	35.4	24.9	35.6

* Daily consumption calculated using 70 % assimilation efficiency, and assuming no growth or reproduction
** Daily consumption calculated assuming 70 % assimilation efficiency and 70 % of assimilated carbon respired, leaving 30 % for growth and reproduction

tridia pacifica was calculated for 8 dates from 6 February 1980 to 15 February 1981 (Table 5). Predicted respiration varied from 0.08 mg C m^{-2} d^{-1} for C_3 in June 1980 and February 1981, to 5.2 mg C m^{-2} d^{-1} for the adult female population in June 1980. Adult female respiration generally accounted for 30 to 50 % of the sum of the respiration of all stages. Exceptions were June 1980, when copepodite density was low and 73 % of the total respiration was by females, and January 1981, when copepodite stages were numerous and adult female respiration was only 19 % of total respiration. Total daily consumption by C_3 to adult *M. pacifica* was estimated assuming no growth or reproduction and an assimilation efficiency of 70 % and compared to seasonal average daily primary production (Stephens 1968) (Table 5). Assuming herbivorous feeding only, the percentage of total daily primary production ingested by the older copepodite stages of *M. pacifica* ranged from 5 % during the spring peak of primary production to 175 % during midwinter.

It is important to remember that the consumption estimates discussed to this point provide for neither growth nor reproduction. Yet, development progressed, and growth occurred throughout the year except possibly during late December 1980 to early February 1981 (Batchelder 1985). By making the additional assumption that 70 % of the food assimilated is respired (Sushchenya 1970), with the remaining 30 % channeled to growth and reproduction, an estimate of consumption which provides for growth and reproduction as well as metabolism was obtained (Table 5). Only 8 to 9 % of daily primary production is necessary to satisfy the growth, reproductive and metabolic needs of C_3 to adults during summer. On 1 January 1981, however, consumption to meet metabolic demands alone was 1.7 times production. Batchelder (1986) found that adult female *Metridia pacifica* failed to produce eggs during late December to early February. The results of the model presented here suggest that there was insufficient food at that time to satisfy the metabolic requirements of the copepods, much less provide for growth or reproduction.

The respiration rate of the adult female population was calculated for all dates for which the length distribution was known, and compared to daily primary production (Fig. 7). The results confirm the conclusions derived from the fewer data on the younger stages; less than 5 % of spring and summer daily primary production and roughly 20 to 40 % of autumn and winter production was consumed by adult females. The increased fraction of production which was consumed

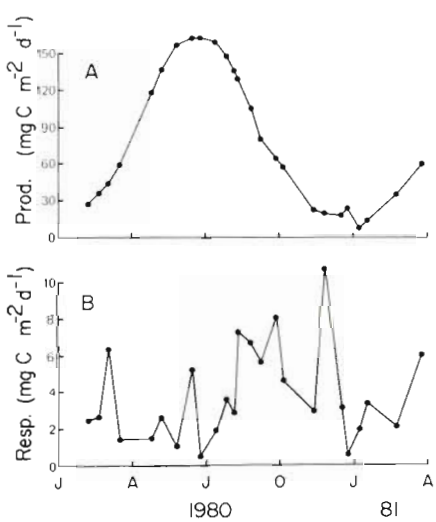

Fig. 7. (A) Seasonal cycle of primary production at Station P. (Approximate mean compiled from Stephens 1968); (B) *Metridia pacifica*. Seasonal cycle of water column respiration by the population of adult females

by females in autumn and winter was due in part to lower primary production, and in part, to the increased number of females. The large fluctuations, as low as 3 % and as high as 80 %, in the percent of primary production consumed by *Metridia pacifica* females during autumn and early winter are caused by the highly variable copepod population density estimates. These calculations suggest that the *M. pacifica* population has the grazing potential to maintain phytoplankton stocks at a low level during autumn and early winter but has relatively little impact on plant populations during the spring and summer peak of primary production.

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