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Impacts of diel vertical migration of the copepod *Metridia pacifica* on primary production and respiratory carbon flux in the subarctic Pacific Ocean

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Abstract

Respiratory oxygen consumption rates (at the two temperatures of 0-50 m and 50-200 m depth strata) and day/night biomass in the top 50 m water column were determined on adult female *Metridia pacifica* at twelve stations in the western/eastern subarctic Pacific and one station in the oceanic Bering Sea during summer. At each station, the respiration rates at 0-50 m depth temperatures were used to estimate ingestion rates during nighttime by assuming empirical carbon budget efficiencies, and rates at 50-200 m to estimate respiratory carbon flux during daytime. The abundance of the females in the upper 50 m at night varied between 27 and 5,422 inds. m^{-2} and no specimen was collected from the same layer at daytime throughout the stations. The size of the females varied regionally from 25 to 77 µg C $ind.^{-1}$. As a result, diel vertical migrant biomass of the females varied greatly from one station to the next (1 and 309 mg C m^{-2}). Weight-specific respiration rates of the females were 2.2-6.3 µl O_2 mg C^{-1} h^{-1}, which was a function of experiment temperatures and body mass (C) of the females. Taking into account of residence time at 0-50 m and 50-200 m in the day, daily population ingestion was estimated as 0.04-11.04 mg C m^{-2} day^{-1}, which accounted for 0-2.4% of primary production at each station. Daily population respiration in the 50-200 m was calculated as 0.02-9.39 mg C m^{-2} day^{-1}, which corresponds to 0-10% of the POC flux down from the euphotic zone.

Key words : Respiratory flux, Active carbon flux, Copepoda, *Metridia pacifica*

Introduction

Diel vertical migration of zooplankton is a phenomenon well documented since 200 years ago, but its ecological implications are not fully understood as yet (cf. Hays, 2003). From a viewpoint of material transport, a possible acceleration of vertical flux by the prey-predator relationship of vertically migrating zooplankton and micronekton has been proposed as the “ladder of migration” hypothesis (Vinogradov, 1968). Active flux (ingestion in the upper layer at night and mineralization in the lower layer during daytime) by diel vertical migration of zooplankton was estimated first by Longhurst and Harrison (1988). As active material flux mediated by diel vertical migration behavior of zooplankton, gut flux (Schnetzer and Steinberg, 2002), respiratory flux (Longhurst and Harrison, 1988), and mortality flux (Zhang and Dam, 1997) are now considered. Among them, respiratory flux has been reported as an important vertical flux process (Morales, 1999). From a methodological viewpoint, the most previous studies on flux are those based on indirect methods, such as ETS assays (Hernández-León et al., 2001 ; Yebra et al., 2005) or application of empirical respiration data (Al-Mutairi and Landry, 2001 ; Roman et al., 2002). The respiratory flux is known to be greater in the subtropical and tropical oceans (Longhurst et al., 1990 ; Dam et al., 1995), but little has been studied in subarctic regions.

Metridia pacifica is a medium-sized oceanic calanoid copepods dominated (the second in abundance and the fifth in biomass) in copepod communities in the subarctic Pacific (Yamaguchi et al., 2002). *M. pacifica* has been known to perform a marked diel vertical migration (Marlowe and Miller, 1975 ; Hirakawa et al., 1990 ; Bollens et al., 1993), although the magnitude of vertical migration varies with location and season (Hattori, 1989 ; Hirakawa, 1991). *M. pacifica* feed mainly on phytoplankton (Dagg et al., 1989) and are preyed upon micronektonic fishes (Moku et al., 2000). Thus, *M. pacifica* is a vital link between primary producer and animals at higher trophic levels. For *Metridia* spp. in the Oyashio region, Takahashi et al. (2009) conducted their active carbon flux, and reported that the annual carbon transport by diel vertical migration as 3.0 g C m^{-2} $year^{-1}$, corresponding to 15% of the annual total particulate organic carbon flux at 150 m depths. While this information provide the importance of *Metridia* spp. in carbon flux, their contributions in the oceanic areas of the subarctic Pacific remains unknown.

In this study, we determined respiration rates and migratory

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abundance of *Metridia pacifica* adult females at stations in the western/eastern subarctic Pacific and the Bering Sea during summer of 2004 as a basis to compute their feeding impact on primary production while they reside in shallow layer, and their respiratory fluxes while they are in deep layer during daytime in the broad subarctic Pacific. The present results are compared with those from the subtropical and tropical oceanic regions reported previously and discussed in the light of pivotal roles of zooplankton in material cycles in the sea.

Materials and methods

Day/night abundance

During the cruise of T/S *Oshoro-Maru*, zooplankton samples were collected by towing a NORPAC net (flowmeter-mounted, 0.10-mm mesh) from 50-m depth to the sea surface, both day and night, at four stations between 41°N and 47°N along 165°E (NW Pacific) during 30 June-4 July, and at eight stations between 41°N and 50°N along 165°W (NE Pacific) during 13-20 July, and at one station in the Bering Sea basin (53°30'N, 177°00'W) on 12 August 2004 (Fig. 1). Sunrise and sunset was 4 : 06-4 : 45 and 19 : 22-20 : 05 (local time), respectively, across the stations (Table 1). Day and night samplings of zooplankton were carried out avoiding two hours just before/after sunrise and sunset (Table 1). Zooplankton samples were preserved in 5% borax-buffered formalin immediately on board. In the land laboratory, adult females of *Metridia pacifica* occurred in these samples were counted on 1/10 sub-samples. From these data, nocturnal migrant abundance (inds. m^{-2}) of this copepod was calculated from their nighttime abundance subtracted the daytime abundance. The prosome length (PL) of twenty adult female *M. pacifica* was measured to the nearest 0.05 mm under a dissecting microscope using an eye-piece micrometer.

Respiration

At each nighttime sampling, an additional sampling from 200-m to the surface was made with an 80-cm ring net (0.33-mm mesh) equipped with a large cod-end. Live adult females of *Metridia pacifica* were sorted under a stereomicroscope and transferred into a beaker filled with chilled surface seawater, which was collected prior to each experiment, filtered through GF/F filters and oxygenated by shaking. Then a batch of 5-10 specimens of *M. pacifica* were transferred into each 75-ml oxygen bottles filled with the oxygen-saturated filtered seawater. Three experiment bottles and two control bottles (no copepod) were prepared concurrently and were incubated in the dark and at two temperatures ; one was that integrated mean over the upper layer (0-50 m), and the other was that integrated mean over the lower layer (50-200 m). Both temperatures were calculated based on the CTD profile at each station. After the incubation for 24 h, dissolved oxygen concentration of seawater sampled from control and experimental bottles were measured by a Winkler titration method. The difference in oxygen concentrations between experimental and control bottles is assumed to be due to respiration by the specimens (sealed-chamber method, cf. Omori and Ikeda, 1984). Respiration was converted to carbon units assuming a respiratory quotient ($[CO_2]/[O_2]$) of 0.97 (protein metabolism, cf. Gnaiger, 1983). After the experiments, the females were collected on a piece of nettings, rinsed briefly with distilled water, placed on pre-weighted aluminum pan and stored in a deep-freezer (–80°C). In the land laboratory, frozen samples were freeze-dried and used for the analyses of carbon with an elemental analyzer (Yanaco CHN Corder).

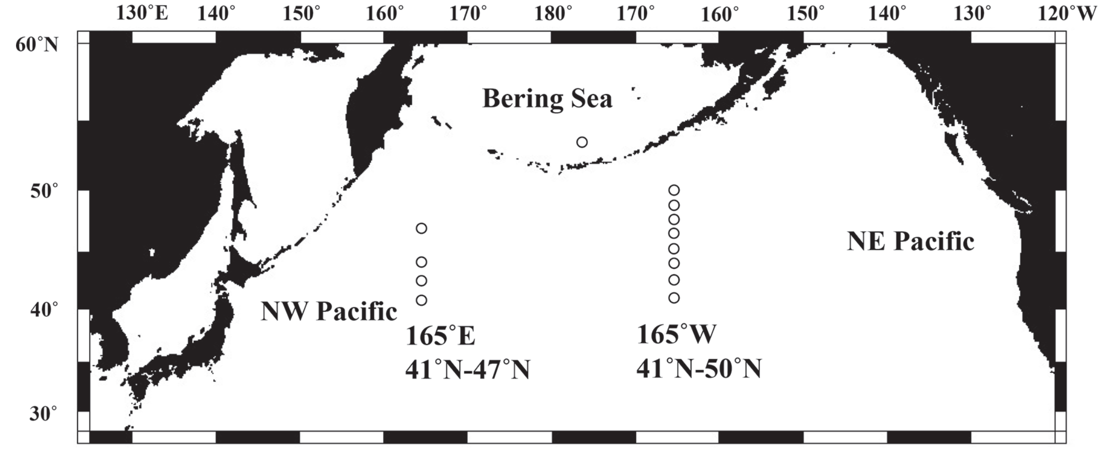

Fig. 1. Location of sampling stations. Four in the northwestern Pacific (41°-47°N along 165°E), eight in the northeastern Pacific (41-50°N along 165°W) and one in the oceanic Bering Sea during June-August 2004.

Table 1. Location and position of sampling station, date (in 2004), sunrise and sunset in local time, total length of night and day, and sampling (0–50 m vertical hauls of 0.1-mm mesh NORPAC net) conducted time during night and day. All of the sampling finished within five minutes.

Location		Local time		Total length		Sampling time	
Position	Date	Sunrise	Sunset	Night	Day	Night	Day
Bering Sea (177°00'W)							
53°30'N	12 Aug.	4 : 23	19 : 22	9 : 01	14 : 59	22 : 20	16 : 50
NW Pacific (165°00'E)							
47°00'N	4 July	4 : 10	19 : 58	8 : 12	15 : 48	2 : 03	6 : 54
44°00'N	2 July	4 : 21	19 : 47	8 : 34	15 : 26	23 : 05	10 : 56
42°30'N	1 July	4 : 26	19 : 42	8 : 44	15 : 16	21 : 33	16 : 14
41°00'N	30 June	4 : 31	19 : 36	8 : 55	15 : 05	23 : 05	11 : 40
NE Pacific (165°00'W)							
50°00'N	13 July	4 : 06	20 : 05	8 : 01	15 : 59	23 : 52	16 : 57
49°00'N	14–15 July	4 : 11	20 : 00	8 : 11	15 : 49	0 : 51	16 : 37
48°00'N	15 July	4 : 16	19 : 55	8 : 21	15 : 39	23 : 33	11 : 16
47°00'N	16 July	4 : 21	19 : 50	8 : 31	15 : 29	23 : 50	11 : 45
45°30'N	17 July	4 : 28	19 : 44	8 : 44	15 : 16	21 : 35	9 : 18
44°00'N	18 July	4 : 34	19 : 38	8 : 56	15 : 04	21 : 53	12 : 58
42°30'N	19 July	4 : 40	19 : 32	9 : 08	14 : 52	23 : 22	12 : 35
41°00'N	20 July	4 : 45	19 : 27	9 : 18	14 : 42	23 : 35	15 : 05

Carbon budget

Carbon budgets of a live copepod is expressed as : Ingestion (I) = Growth (G) + Metabolism (M) + Egestion (E) + Excretion (U). Assuming assimilation efficiency ($[G+M]/I$) and gross growth efficiency (G/I) for general zooplankton to be 70% and 30%, respectively (Ikeda and Motoda, 1978), ingestion rates (I : µg C individual^{-1} h^{-1}) can be calculated by knowing M as $I = M/(0.7-0.3)$.

The distance of diel vertical migration of *Metridia pacifica* in the subarctic Pacific is estimated as 125 m (Yamaguchi et al., 2004). *M. pacifica* has been reported to swim at the velocity of 30–90 m h^{-1} (median : 60 m h^{-1}) for more than an hour (Enright, 1977). Then, the time needed for one-way vertical travel of *M. pacifica* is computed as 2.1 h (= 125/ 60). Subtracting the up-and-down traveling time (2.1 h × 2) from one day (24 h), the residence time at above 50 m (upper layer), and below 50 m (lower layer) everyday was calculated taking into account the time of sunrise and sunset. The ingestion of *M. pacifica* during residence in the upper layer, and their respiration during residence in the lower layer were calculated, and summed on daily bases (mg C m^{-2} day^{-1}).

Based on the data on sea surface temperature, chlorophyll *a* and light intensity (Taekeun Rho, unpublished data), primary production (mg C m^{-2} day^{-1}) at each sampling station was estimated using an algorithm (Kameda and Ishizaka, 2005). Assuming f-ratio (new production/ primary production) as 0.21 (Varela and Harrison, 1999), particulate organic carbon (POC) flux from the euphotic zone is calculated as primary production × 0.21. Thus calculated POC flux from the euphotic zone was compared with the respiratory flux of *Metridia pacifica* at each station, and the respiratory flux was expressed as a fraction of POC flux (= 100 × respiratory flux/ sediment POC flux, %).

Results

Migrant biomass

Adult females of *Metridia pacifica* occurred in all night samples but none in all daytime samples, indicating that they migrated down below 50-m depths during daytime. Geographically, the nighttime abundance of the adult females ranged between 27 and 5,422 inds. m^{-2}, showing a pattern of higher abundance with increasing latitudes of stations (Table 2). Since the daytime abundance was zero throughout the stations, the nocturnal migrant abundance equals to that of the nighttime abundance (Table 2). The prosome length (PL) of the adult females increased from 1.68 to 2.27 mm gradually with increasing latitudes of stations (Table 2). Because of this, carbon mass (CM) of the adult females increased from 24.7 to 75.6 µg C ind.$^{-1}$ toward northernmost stations. The relationship between CM (µg C ind.$^{-1}$) and PL (mm) was expressed as $CM = -74.9 + 65.9 \times PL$ ($r^2 = 0.68, p < 0.0001$).

Respiration

Regional variations in the range of integrated mean temperatures in the 0–50 m and 50–200 m layer among stations were 6.4–14.2°C and 2.8–9.5°C, respectively (Table 3).

Table 2. Abundance (inds. m^{-2} : 0–50 m at night), prosome length (PL) and carbon body mass of *Metridia pacifica* adult females at each sampling station. Values are mean±1sd.

Location Position	Abundance (inds. m^{-2})	PL (mm)	Body mass (μg C $ind.^{-1}$)
Bering Sea (177°00'W)			
53°30'N	3,148.6	2.27±0.09	71.5±10.1
NW Pacific (165°00'E)			
47°00'N	224.7	2.06±0.08	75.6±5.7
44°00'N	200.0	1.94±0.02	62.6±9.7
42°30'N	1,818.2	2.06±0.09	59.5±4.1
41°00'N	384.6	1.67±0.08	43.3±2.3
NE Pacific (165°00'W)			
50°00'N	1,656.0	2.15±0.20	75.1±4.1
49°00'N	5,421.7	2.11±0.06	56.9±4.7
48°00'N	200.0	2.24±0.10	75.1±4.0
47°00'N	294.1	2.15±0.07	63.8±9.3
45°30'N	460.5	2.10±0.05	49.2±5.9
44°00'N	985.9	1.89±0.07	52.1±3.2
42°30'N	87.0	1.87±0.04	41.7±7.5
41°00'N	26.9	1.68±0.07	24.7±1.6

Table 3. Integrated mean temperature at upper (0–50 m) and lower layer (50–200 m) at each sampling station, and oxygen consumption rate of *Metridia pacifica* adult females at temperatures of the upper and lower layers, respectively. Values are mean±1sd.

Location	Temperature (°C)		Oxygen consumption rate (nl O_2 $ind.^{-1}$ h^{-1})	
Position	Upper L.	Lower L.	Upper L.	Lower L.
Bering Sea (177°00'W)				
53°30'N	8.1	3.8	355±39	247±16
NW Pacific (165°00'E)				
47°00'N	6.4	2.8	314±19	202±21
44°00'N	7.3	5.0	275±8	169±8
42°30'N	7.4	4.9	271±7	223±10
41°00'N	14.2	9.1	394±33	251±28
NE Pacific (165°00'W)				
50°00'N	7.9	4.1	303±40	222±16
49°00'N	8.2	4.3	250±22	236±7
48°00'N	8.0	4.5	286±9	278±14
47°00'N	9.2	5.1	244±36	218±42
45°30'N	10.4	5.9	246±15	184±23
44°00'N	10.8	7.3	259±12	189±12
42°30'N	11.0	8.0	224±24	218±21
41°00'N	13.8	9.5	155±14	122±10

Respiration rates ranged from 155 to 355 nl O_2 $ind.^{-1}$ h^{-1} in the 0–50 m layer, and from 122 to 278 nl O_2 $ind.^{-1}$ h^{-1} in the 50–200 m layer. Throughout the stations, respiration rates in the 0–50 m layer was higher than that in the 50–200 m layer by a factor of 1.3 ± 0.2 (mean ± 1sd) (Table 3). All respiration data from the two layers were expressed in terms of the specific rates and plotted against habitat temperatures and body mass of *Metridia pacifica* (Fig. 2), showing that specific respiration rates are a function of temperature (r^2= 0.72) or body mass of individuals (r^2= 0.51) (Fig. 2).

Carbon budget by diel migrant Metridia pacifica

Across the stations, the calculated daily ingestion from the daily respiration in the 0–50 m layer ranged from 0.04 to

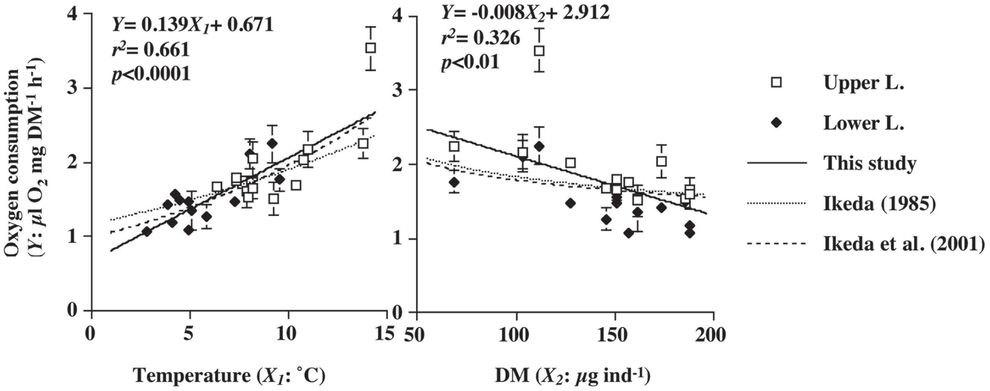

Fig. 2. *Metridia pacifica* adult females. Relationship between weight-specific oxygen consumption and experimental temperature (left), and weight-specific oxygen consumption and dry mass (right). Significant interactions were observed for both relationships. For comparison, regression lines from Ikeda (1985) and Ikeda et al. (2001) are also shown in the panels.

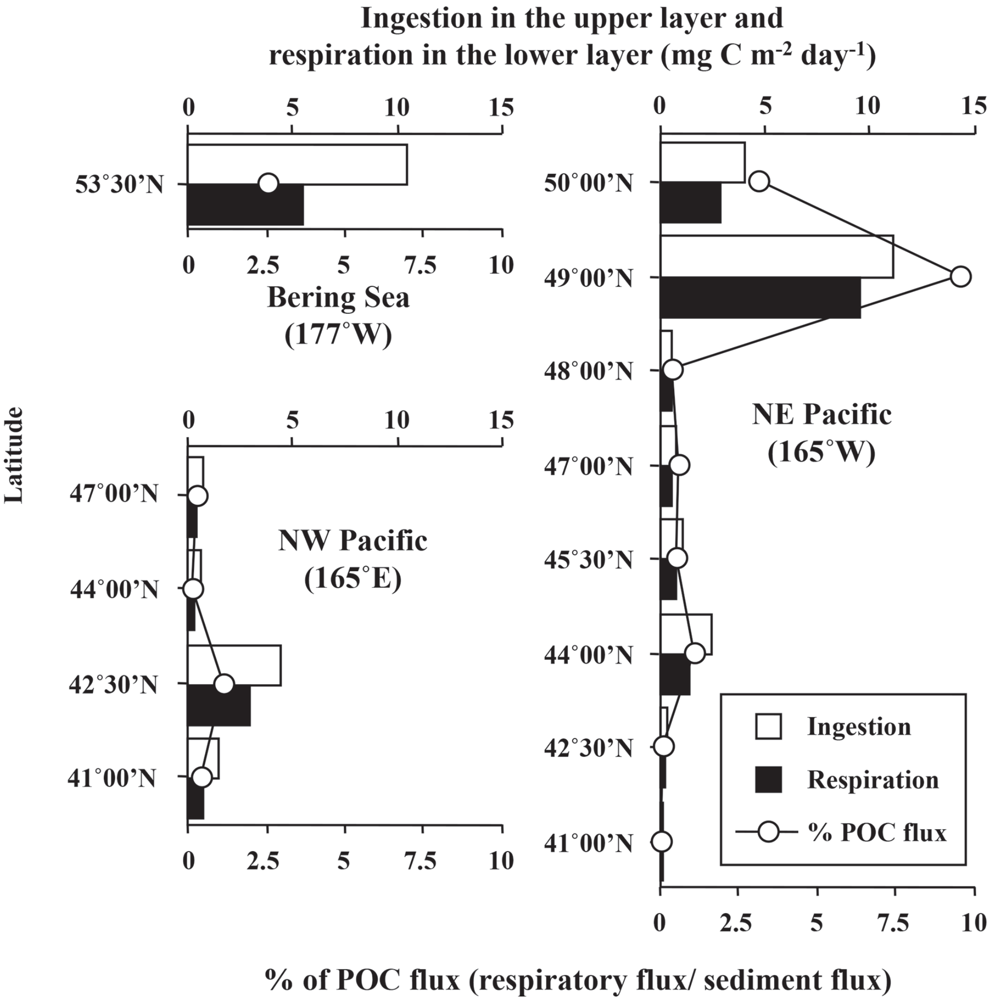

Fig. 3. Ingestion in the upper layer and respiration in the lower layer by *Metridia pacifica* adult females in each sampling station. For comparison, the amount of respiratory flux is expressed as percentage to sedimentation flux from euphotic zone (% POC flux), details of estimated methods see text.

11.04 mg C m^{-2} day^{-1} (mean : 2.83 mg C m^{-2} day^{-1}), and the observed daily respiration in the 50–200 m layer ranged from 0.02 to 9.39 mg C m^{-2} day^{-1} (mean : 1.88 mg C m^{-2} day^{-1}) (Fig. 3). Throughout the station, the daily respiration in the 50–200 m layer were less than the daily ingestion in the 0–50 m layer (63.6 ± 12.3% [mean ± 1sd] of the latter). Primary production and POC flux from the euphotic zone at each station were estimated as 361–1,186 and 76–249 mg C m^{-2} day^{-1}, respectively. Thus, respiratory flux by *Metridia pacifica* adult females varied regionally, from 0% to 10% of the POC flux from the euphotic zone (mean : 2%, Fig. 3).

Discussion

Abundance and biomass

Within broad habitats (subarctic Pacific and its marginal seas), life cycles of *M. pacifica* are known to vary geographically ; generation numbers per year is one (northern Bering Sea and Japan Sea, Heinrich, 1962 ; Hirakawa and Imamura, 1993), two (Oyashio region, Padmavati et al., 2004), three (Gulf of Alaska, Batchelder, 1985) and four (western Bering Sea, Heinrich, 1962). Developmental time from eggs to adults of *M. pacifica* under saturated food concentration were reported as 112 days at 8°C and 182 days at 3°C (Padmavati and Ikeda, 2002).

Across the differences in latitude between 40°N and 55°N, developmental timing of *Neocalanus plumchrus* was evaluated as 5 weeks faster in the southernmost latitudes than those in the northernmost latitudes, and the temperature is probably the most important factor governing the shorter development duration of *N. plumchrus* in southern latitudes (Batten et al., 2003). These latitudinal changes in temperature were also the case of this study (cf. Table 3). Combined effect of differences in life cycle and developmental rate induced by temperature, is a possible cause of geographical changes in *M. pacifica* abundance. Throughout the station, *M. pacifica* adult females absent during daytime and abundant at night from upper 50 m indicate that they are not in resting phase in the study period. Resting phase of *M. pacifica* is reported from Japan Sea (Hirakawa, 1991 ; Hirakawa and Imamura, 1993). Dormancy of *M. pacifica* due to the warming of euphotic layer (>18°C) in the Japan Sea beyond the limit of thermal tolerance for this species (Hirakawa, 1991). Since the temperature at upper 50 m was lower than 15°C throughout the station (Table 3), warming of euphotic layer is not considered as a barrier of migration behavior of *M. pacifica* in the present study.

Based on the large spatial and temporal coverage samples (Continuous Plankton Recorder survey) in the North Atlantic and the North Sea, Hays (1995) revealed that the mean daily length of time that *Metridia* spp. spent near the surface in each month of the year varied seasonally with day length. From this point of view, the surface residence time of *M. pacifica* in the study period (summer) corresponds seems to be minimum of the year. Nighttime length in each station varied from 8 : 01–9 : 18 hours (mean ± 1 sd : 8 : 39 ± 0 : 23, Table 1). *M. pacifica* in Dabob Bay arrived to the surface 0.5 h after sunset, fed at high rates throughout the night until 1.0 h before sunrise, and then returned to depth (Dagg et al., 1989).

Body carbon mass of *Metridia pacifica* adult females varied with station by a factor of 3.1 (= 75.6 / 24.7) (Table 2). Prosome length is also varied with station by a factor of 1.4 (= 2.27/1.67), and larger in the northern stations. Geletin (1976) noted that the two forms of *M. pacifica*, differing in body length and structure of the cephalothorax, can be distinguished in the subarctic Pacific. According to Geletin (1976), the large form (2.70–3.65 mm in total length) is found mainly in water at 2–9°C, and the small form (2.00–2.55 mm in total length) in water at 9–15°C. Some of the copepods ascend at night into warmer water : the large form to water at 15°C and the small form to water at 18°C. The large form is associated with the boreal copepods (*Calanus cristatus*, *C. plumchrus* (= *Neocalanus cristatus*, *N. plumchrus*) and *Eucalanus bungii*), and the small form with species of intermediate zone of the Oyashio–Kuroshio system (*Calanus pacificus* and *E. californicus*). Such the geographical heterogeneous in genetic structure of *M. pacifica* are reported for the populations at a coastal eddy and offshore groups in the California current (Bucklin, 1991).

Respiration and ingestion

Specific respiration rates of *Metridia pacifica* adult females ranged between 1.07 and 3.54 µl O_2 mg DM^{-1} h^{-1} (Fig. 2). According to Ikeda (1974), the specific respiration rates at 4.5–10.5°C of this copepod are 1.69–3.94 µl O_2 mg DM^{-1} h^{-1} which overlap partially the present results. The empirical zooplankton respiration model (Ikeda, 1985) has been employed by previous estimates of carbon flux by migrant zooplankton (cf. Al–Mutairi and Landry 2001, Roman et al., 2002). Later, the empirical respiration rates were updated every nearly decades (Ikeda et al., 2001 ; Ikeda, 2014). The comparison of the present respiration data and with those derived from the empirical model showed that the former differed from the latter by a factor of only 0.8–1.5 (Fig. 2), suggesting a good agreement between the two.

Daily ingestion of *Metridia pacifica* adult females calculated from respiration data by using the carbon budget model (Ikeda and Motoda, 1978) in the present study (1.49–3.60 µg C ind.$^{-1}$ day^{-1}) is consistent to the previous results determined experimentally (2.23 µg C ind.$^{-1}$ day^{-1} by Tsuda and Sugisaki, 1994 ; 3.62 µg C ind.$^{-1}$ day^{-1} by Dagg, 1993). In terms of daily ration, the present results (3.2–8.3%) fall within the extreme range of previous reports e.g. 24% (Ambler and Frost, 1974), 7.5% (Batchelder, 1986) or 2–22% (Mackas and Burns, 1986).

Active flux

The abundance of *Metridia pacifica* adult females varied greatly with location, and ranged from 27 to 5,422 inds m^{-2}, thus by a factor of 200 (= 5,422/ 27) (Table 2). Compared with this large location–to–location variations in the abundance, the respiration rate fell within a small range (122–394 nl O_2 ind.$^{-1}$ h^{-1}, Table 3) or by a factor of 3.2 (= 394/122).

Table 4. Zooplankton active flux estimated by different authors in oceanic regions. Migrating biomass is the integrated night minus day zooplankton biomass in the surface layer. Migratory flux is the amount of dissolved carbon respired or excreted by migrating zooplankton below the euphotic zone. % of mean POC flux = (migratory flux/ sediment trap flux at the depth of euphotic zone)x 100%. Mean and range (given in parentheses). Flux due to mortality at depth is not included here, although it is estimated in some studies.

Location	Migrating biomass (mg C m^{-2})	Migratory flux (mg C m^{-2} day^{-1})	% of POC flux	References
Sub- and tropical Atlantic (September)	-	5.5 (2.8-8.8)	6 (4-14)	Longhurst et al. (1990)
Bermuda (March/April)	191 (82-536)	14.5 (6.2-40.6)	34 (18-70)	Dam et al. (1995)
Eq. Pacific (March/April)	96	4.2	18	Zhang and Dam (1997)
Eq. Pacific (October)	155	7.3	25	Zhang and Dam (1997)
Eq. Pacific oligotrophic	47	3.8	8	Le Borgne and Rodier (1997)
Eq. Pacific HNLC area (September)	53	7.9	4	Rodier and Le Borgne (1997)
North Atlantic (NABE)	(5-480)	-	(19-40)	Morales (1999)
Bermuda (year-round)	50 (0-123)	2.0 (0-9.9)	8 (0-39)	Steinberg et al. (2000)
Hawaii (year-round)	142	3.6 (1.0-9.2)	15 (6-25)	Al-Mutairi and Landry (2001)
Canary Islands (August)	192 (156-300)	2.6 (0.3-4.3)	25 (16-45)	Hernández-León et al. (2001)
Eq. North Pacific (winter)	297 (145-448)	13.2 (7.3-19.1)	24 (13-35)	Hidaka et al. (2001)
Eq. Pacific HNLC area (year-round)	(2.8-3.4)	(0.1-2.5)	(2-4)	Roman et al. (2002)
Canary Islands (July)	(576-1284)	(1.9-8.3)	(12-53)	Yebra et al. (2005)
W. subarctic Pacific (Aug.)	144	3.5	10	Kobari et al. (2008)
Oyashio region (year-round)	558 (63-1676)	5.7 (1.0-15.8)	15	Takahashi et al. (2009)
W. North Pacific (June)	(276-1096)	(3.2-14.1)	(2-11)	Hanamiya et al. (2020)
Subarctic Pacific (summer)	71 (1-309)	1.9 (0-9.4)	2 (0-10)	This study (note that *Metridia pacifica* adult females only)

In fact, daily ingestion in the upper layer and daily respiration in the lower layer showed a strong correlation with the abundance (r^2= 0.93-0.99), while low correlation with respiration rate (r^2= 0.08-0.12) at each station, indicating the abundance to be the most important factor affecting the active carbon flux by *M. pacifica* in the subarctic Pacific.

Daily ingestion of *Metridia pacifica* adult females in the upper layer (0.04-11.04 mg C m^{-2} day^{-1}, cf. Fig. 3) corresponds to 0.01-2.35% of the primary production. Daily respiration of *M. pacifica* adult females in the lower layer (0.02-9.39 mg C m^{-2} day^{-1}) corresponds to 0-10% of the POC flux down from the euphotic zone (Fig. 3). The present results of respiratory flux relative POC flux (0-10% with a mean of 2%) are less than those reported from other regions (mean 4-34%, cf. Table 4). Part of reasons may be that our estimation is on only *M. pacifica* adult females, as compared with entire zooplankton communities in other studies. The estimation of respiration in most previous studies are based on ETS assay (cf. Hernández-León et al., 2001 ; Yebra et al., 2005) or empirical community respiration data of zooplankton (Al-Mutairi and Landry, 2001 ; Roman et al., 2002). Compared with these indirect methods, ours are direct method on *M. pacifica* collected at each study location. The present estimate is limited for one species/stage therefore represents a minimum respiratory flux by migrant zooplankton. Other than *M. pacifica*, euphausiids (such as *Euphausia pacifica*, Bollens et al., 1992), amphipods (*Themisto* spp., Yamada et al., 2004) and micronektonic fishes (Watanabe et al., 1999 ; Moku et al., 2000) are considered to be active components of vertical carbon flux in the subarctic Pacific. To evaluate accurate carbon flux schema in the subarctic Pacific, future study needed to extend to these animals.

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