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RESEARCH ARTICLE

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Metabolism and body composition of a copepod (*Neocalanus cristatus*: Crustacea) from the bathypelagic zone of the Oyashio region, western subarctic Pacific

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Abstract Metabolism [respiratory oxygen consumption, electron-transfer-system (ETS) activity] and body composition [water, ash, carbon (C), nitrogen (N), carbon/nitrogen (C/N) ratio] of stage C5/C6 *Neocalanus cristatus* from 1000 to 2000 m depth of the Oyashio region, western subarctic Pacific, were determined during the period of July 2000 through June 2003. Compared with the C5 specimens from shallow depths (< 250 m), those from 1000 to 2000 m were characterized by quiescent behavior, reduced respiration rates (30% of the rates at active feeding), very low water content (61–70% of wet weight), but high C content (56–64% of dry weight) and C/N ratios (7.2–10.6, by weight). Artifacts due to the recovery of live specimens from the bathypelagic zone appeared to be unlikely in this study, as judged by the consistent results between re-compression (100 atm) and non-compression (1 atm) respiration experiments, and between ETS activities and respiration rates directly measured. In addition, the respiration rates of C6 males and females of *N. cristatus* from the same 1000–2000 m depth were two to three times higher than the rates of C5 individuals, but were similar to the rates of a bathypelagic copepod, *Paraeuchaeta rubra*. Combining these results with literature data, C budgets of: (1) diapausing C5 specimens, weighing 6–10 mg dry weight; (2) molt to C6 females; and (3) the complete the life span were established, taking into account assorted losses in respiration during diapause at stages C5 and C6, molt production and egg production. Respiratory C losses by C5 and C6 specimens were estimated on the basis of body N as adjusted metabolic rates [AMR; μl O_2 (mg body N)$^{-0.843}$ h^{-1}], then N budgets were also computed subtracting N lost in the form of cast molts and eggs from the initial stock. Calculations revealed that allocation of the C stock was greatest to egg production (34–57%), followed by respiration (27%) and cast molts (3%), leaving residual C of 13–36% in spent C6 females. The present results for *N. cristatus* from the North Pacific are compared with those of *Calanus* spp. in the North Atlantic.

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Introduction

Neocalanus cristatus, *N. plumchrus* and *N. flemingeri* are large grazing copepods, occurring abundantly from surface layers to > 1000 m depth in the subarctic Pacific and the adjacent Bering, Okhotsk and Japan Seas (Zenkevitch 1963; Vinogradov and Arashkevich 1969; Motoda and Minoda 1974; Mackas and Tsuda 1999), and they are reported to be important prey components for pelagic fishes, whales and seabirds (Nemoto 1963; Odate 1994; Hunt et al. 1998). These *Neocalanus* spp., together with another grazing copepod, *Eucalanus bungii*, often account for 80–95% of zooplankton biomass in the surface zone (Vinogradov 1970). In the Oyashio region, western subarctic Pacific, the most dominant copepod in terms of annual mean biomass integrated over 0–2000 m depth is *N. cristatus*, followed by *N. plumchrus*, *E. bungii* and *N. flemingeri* (Kobari and Ikeda 2000; Ikeda unpublished).

The life cycle and associated ontogenetic vertical migration of *N. cristatus* have been evaluated to be similar across the subarctic Pacific (Miller et al. 1984; Kobari and Ikeda 1999). The reproduction of *N. cristatus* continues throughout the year at depth, with its peak in autumn–early winter. Eggs hatch at depth, and resultant nauplii develop to early copepodites during their journey to the surface layer. The early copepodites grow rapidly to copepodite stage 5 (C5) during the spring phytoplankton bloom. C5 specimens descend

to 1000–2000 m depth in mid-summer and enter diapause for several months. Then, C5 individuals molt to C6 males or females, reproduce and die off at depth, completing the life cycle in 1 year. Since C6 adults cease feeding, the energy needed for metabolism, molting and gonad production is considered to be supplied from lipids deposited in the body of C5s prior to sinking to depth. Nevertheless, almost nothing is known about the metabolism and biochemical composition of *N. cristatus* that would define their life-history segments in the deep sea, except an isolated observation on embryonic and post-embryonic development of released eggs in the laboratory (Saito and Tsuda 2000) and a study of the elemental composition (C, N and H) of C5 and C6 males and females from submerged Oyashio water, off Central Honshu, Japan (Omori 1970).

Similar to *Neocalanus* spp. in the North Pacific, *Calanus* spp. in the North Atlantic undergo extensive ontogenetic vertical migrations before overwintering (Conover 1988). Overwintering populations at depth are in diapause, characterized by reduced metabolism, little or no movement, and/or a large accumulation of lipids in the body, as has been demonstrated on *Calanus finmarchicus* (Hirche 1983; Ingvarsdottir et al. 1999), *C. glacialis* (Hirche 1998) and *C. hyperboreus* (Conover 1962; Hirche 1998; Auel et al. 2003). In contrast to diapausing C5 *Calanus* spp., which return to the surface layer at C6 and feed again for reproduction, diapausing C5 *Neocalanus* spp. molt to C6 and reproduce at depth without feeding (cf. Conover 1988). Because of this fundamental difference between *Calanus* and *Neocalanus*, direct application of the results of the former to the latter may not be valid.

The aims of this study were: (1) to gain information about metabolism and biochemical condition of C5 and C6 *N. cristatus* occurring at 1000–2000 m depth and (2) to calculate the balance between initially deposited energy (lipids) in the body of C5 specimens and its subsequent allocation to metabolism during stages C5 and C6, and during molting events and egg production of C6 females.

Materials and methods

Copepods

Samples were collected at site H (41°30′N; 145°50′E), station Knot (44°00′N; 155°00′E) and some other stations during a total of six cruises of T.S. ''Hokusei Maru'' and T.S. ''Oshoro Maru'' to the western subarctic Pacific, July 2000 through June 2003 (Table 1). A vertical closing net (Kawamura 1968) equipped with a large cod-end (1–2 l capacity) was used to retrieve live zooplankton from 1000 to 2000 m depth. The closing net was designed to sink at a speed of 1 m s^{-1} down to 2000 m depth, towed upward at the same speed (1 m s^{-1}) to 1000 m depth then retrieved to the surface at 2 m s^{-1} after closing the net mechanically with a messenger weight. After closing at 1000 m depth, the time required to retrieve the net to the surface was 8–9 min. During this study, a closing cod-end was developed (Ikeda, unpublished data) and used to maintain bathy-

Table 1 *Neocalanus cristatus*. Sampling data for C5 and C6 male and female specimens with nets equipped with the closing cod-end or with the non-closing cod-end. *Asterisk* indicates nets tinted brown by high phytoplankton concentration

Stage	Expt no.	Date	Collection site	Depth of sampling	Use of closing cod-end
Respiration					
C5	D-1	29 Jul 2000	41°30′N; 145°50′E (site H)	1000–2000	No
	D-2	1 Aug 2000	44°00′N; 155°00′E (Knot)	1000–2000	No
	D-3	3 Aug 2000	39°30′N; 155°00′E	1000–2000	No
	D-4	9 Aug 2000	41°30′N; 145°50′E (site H)	1000–2000	No
	D-5	1 Mar 2001	41°30′N; 145°50′E (site H)	1000–2000	No
	D-6	10 Jul 2001	41°30′N; 145°50′E (site H)	1000–2000	Yes
	D-7	15 Jul 2001	42°30′N; 155°00′E	1000–2000	Yes
	D-8	18 Dec 2002	41°30′N; 145°50′E (site H)	1000–2000	Yes
	D-9	7 Jun 2003	44°00′N; 155°00′E (Knot)	1000–2000	Yes
	D-10	15 Jun 2003	41°30′N; 145°50′E (site H)	1000–2000	Yes
	S-1	9 Aug 2000	41°30′N; 145°50′E (site H)	25–250	No
	S-2	1 Mar 2001	41°30′N; 145°50′E (site H)	0–100*	No
	S-3	14 Jul 2001	43°46′N; 154°17′E	0–50*	No
	S-4	11 Mar 2002	41°30′N; 145°50′E (site H)	0–250	No
C6♀	D-11	21 Jul 2001	41°30′N; 145°50′E (site H)	1000–2000	Yes
	D-12	11 Mar 2002	41°30′N; 145°50′E (site H)	1000–2000	Yes
C6♂	D-13	16 Jul 2001	42°30′N; 155°00′E	1000–2000	Yes
	D-14	9 Jun 2003	41°00′N; 155°00′E	1000–2000	yes
ETS					
C5	D-15	11 Jun 2002	44°00′N; 155°00′E (Knot)	1000–2000	Yes
	D-8	18 Dec 2002	41°30′N; 145°50′E (site H)	1000–2000	Yes
C6♀	D-15	11 Jun 2002	44°00′N; 155°00′E (Knot)	1000–2000	Yes
C6♂	D-15	11 Jun 2002	44°00′N; 155°00′E (Knot)	1000–2000	Yes

pelagic temperature of the zooplankton samples during the course of net retrieval (Table 1).

Upon retrieval of the net from 1000 to 2000 m depth, undamaged specimens of C5/C6 *Neocalanus cristatus* were sorted immediately. For stage C6, "spawning" females (cf. Miller et al. 1984) were selected, but such selections based on maturity could not be made for the males. In addition, the copepod *Paraeuchaeta rubra* from 1000 to 2000 m depth and C5 *N. cristatus* from shallow layers (< 250 m) were sorted for comparative experiments. Sorted specimens were placed in 1-l glass containers filled with seawater from the mid-depth range of their collection (e.g. 1500 m for the specimens collected from 1000 to 2000 m). The seawater was collected with 20-l Niskin bottles just prior to zooplankton collection for each experiment. Temperature and salinity profiles were determined by using a CTD rosette system fitted with 10- or 20-l Niskin bottles. Dissolved oxygen concentrations in seawater were determined by a Winkler titration method.

Respiration

A sealed-chamber method (cf. Ikeda et al. 2000) with glass bottles (70 ml capacity) was used to determine respiration rates of *N. cristatus* and *P. rubra*. It is noted that the 1000–2000 m depth in the Oyashio region is characterized by low oxygen (1.0–2.0 ml O_2 l^{-1}, or 13–27% saturation, cf. Fig. 1), a parameter affecting respiration rates of zooplankton (cf. Ikeda et al. 2000). In order to obtain respiration rates under nearly natural oxygen concentrations, seawater was collected from 1500 m, filtered gently through 10-μm mesh netting to remove large particles and used (oxygen concentration of seawater thus prepared was 1.6–2.0 ml O_2 l^{-1}). Experiments started within 1–3 h of the collection of the specimens. Experimental bottles containing specimens (one or two individuals) and control bottles without specimens were prepared simultaneously and were incubated at 2°C in the dark for 24 h. A temperature of 2°C was chosen as the representative temperature between 1000 m (ca. 2.8°C) and 2000 m depth (1.9°C) in the Oyashio region. At the end of each experiment, dissolved oxygen concentration was determined by a Winkler titration method on subsamples siphoned out of the bottles and into two small oxygen vials (7 or 14 ml capacity).

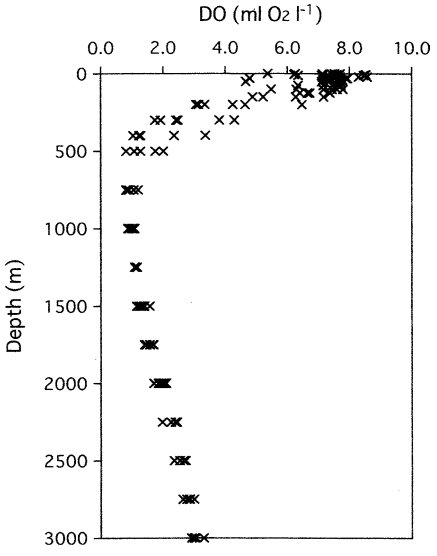

Fig. 1 Vertical profile of dissolved oxygen (*DO*) recorded at sampling sites during the present study. Note that the oxygen is lowest between 500 and 1000 m depth and increases gradually down to 3000 m depth. This pattern is consistent throughout the year

For a total of ten experiments on C5 *N. cristatus* from 1000 to 2000 m (D-1 to D-10, Table 2), both experimental and control bottles were separated into two groups in two experiments (D-9 and D-10). For one group, oxygen consumption rates of C5 specimens were determined under normal pressure (1 atm), following the procedure mentioned above, and, for the other group, the rates were determined applying a pressure of 100 atm (equivalent to the hydrostatic pressure at 1000 m depth). For the experiment at 100 atm, a newly designed recompression chamber (Tsurumi Seiki) connected with a hand-operated hydraulic pump (model PH-10, Yamasui) was used. At the start and end of the experiments, the pressure was applied to and released from the chamber, respectively, almost immediately.

Respiration rates of shallow-living (< 250 m) C5 specimens of *N. cristatus* were also determined under the temperature and oxygen concentrations close to those at the depths of the specimens origin (S1–S4, Table 1).

All specimens used for experiments were frozen at −60°C on board the ship for later determination of body mass and body composition at a land laboratory.

Electron-transfer-system (ETS) activity

All specimens for ETS assay were preserved in liquid nitrogen on board the ship and brought back to the land laboratory. Within 1 month after collection, the frozen specimens were weighed quickly (wet weight, WW) and homogenized for the ETS assay. The method described by Owens and King (1975) was used for this assay, but the final reaction volume was reduced from 6 to 1.5 ml. Preliminary tests indicated that the ETS activity of single C5 specimens was too low to measure at the in situ temperature (2°C). To overcome this problem, the assay was made at 2°C using a batch of two to three specimens or at 10°C on single specimens. In order to extrapolate the activity at 10°C to that at 2°C, the relationship between ETS activity and temperature was established. To convert ETS activity to respiration rate (R), ETS activities were determined on the C5 specimens for which the respiration rates were determined by the sealed-chamber method, to obtain R/ETS ratios. The effect of hydrostatic pressure on ETS activities of crustacean plankton

Table 2 *Neocalanus cristatus*, *Paraeuchaeta rubra*. Respiration (*R*), body composition (water, ash, C, N and C/N ratio), and adjusted metabolic rate (*AMR*) data of C5 and C6 males and females in the Oyashio region, western subarctic Pacific. As part of the experiment number, "D" denotes samplings from 1000 to 2000 m depth and "S" those from < 250 m depth. See Table 1for details on each experiment (*$P > 0.05$)) (*WW* wet weight;*DW* dry weight)

Stage	Expt no.	Temp. (°C)	*N*	*R*		WW (mg ind.$^{-1}$)	DW (mg ind.$^{-1}$)	Water (% of WW)	Ash (% of DW)	C (% of DW)	N (% of DW)	C/N (by wt)	AMR at 2°C [µl O_2 (mg body N)$^{-0.843}$ h^{-1}]
				(µl O_2 ind.$^{-1}$ h^{-1})	(µl O_2 mg^{-1} WW h^{-1})								
N.cristatus													
C5	D-1	2	5	0.54 ± 0.13	0.025 ± 0.004	21.0 ± 2.8	6.80 ± 1.54	67.6 ± 6.4	4.96 ± 0.58	60.1 ± 1.1	7.54 ± 0.48	7.99 ± 0.64	0.95 ± 0.13
	D-2	2	6	0.47 ± 0.08	0.020 ± 0.003	23.0 ± 2.7	8.32 ± 1.27	63.9 ± 2.7	4.42 ± 0.59	61.5 ± 2.4	6.75 ± 0.91	9.27 ± 1.54	0.77 ± 0.12
	D-3	2	4	0.61 ± 0.23	0.031 ± 0.006	19.5 ± 4.6	5.79 ± 1.43	70.3 ± 3.0	5.84 ± 0.85	57.2 ± 3.5	8.10 ± 1.72	7.23 ± 1.15	1.24 ± 0.26
	D-4	2	6	0.66 ± 0.15	0.031 ± 0.007	22.1 ± 5.0	7.27 ± 2.42	67.8 ± 3.9	4.25 ± 0.69	60.3 ± 1.0	6.97 ± 0.87	8.75 ± 1.26	1.23 ± 0.30
	D-5	2	6	0.36 ± 0.06	0.021 ± 0.003	17.2 ± 3.1	6.11 ± 0.86	63.7 ± 7.3	4.66 ± 0.58	55.9 ± 1.4	8.33 ± 0.39	6.73 ± 0.48	0.65 ± 0.17
	D-6	2	4	0.63 ± 0.12	0.027 ± 0.002	23.6 ± 4.2	8.65 ± 1.95	63.5 ± 3.7	4.14 ± 0.30	58.8 ± 2.2	6.89 ± 0.57	8.60 ± 1.02	0.98 ± 0.07
	D-7	2	4	0.75 ± 0.07	0.029 ± 0.003	26.0 ± 2.1	10.0 ± 0.4	61.3 ± 1.8	4.54 ± 0.28	58.5 ± 1.8	6.87 ± 0.58	8.57 ± 1.01	1.04 ± 0.09
	D-8	2	6	0.59 ± 0.07	0.022 ± 0.003	26.4 ± 0.9	9.33 ± 1.08	64.5 ± 2.3	4.88 ± 0.73	63.0 + 2.0	7.41 + 0.80	8.59 + 1.27	0.81 + 0.10
	D-9	2	8	0.57 ± 0.15	0.024 ± 0.006	24.2 ± 2.0	7.97 ± 1.00	67.2 ± 3.2	4.46 ± 0.61	64.1 ± 0.6	5.86 ± 0.16	10.94 ± 0.20	1.03 ± 0.31
	(at 100 atm		6	0.52 ± 0.17	0.020 ± 0.007*	24.6 ± 1.2)							
	D-10	2	6	0.64 ± 0.05	0.024 ± 0.003	26.9 ± 1.6	9.08 ± 0.89	65.6 ± 2.3	4.20 ± 0.38	64.3 ± 0.4	6.09 ± 0.10	10.63 ± 0.31	0.96 ± 0.26
	(at 100 atm		5	0.51 ± 0.19	0.020 ± 0.010*	25.8 ± 1.9)							
	S-1	8	5	1.00 ± 0.19	0.051 ± 0.009	19.2 ± 1.4	2.09 ± 0.60	89.4 ± 3.0	9.79 ± 1.01	44.0 ± 0.1	10.4 ± 0.41	4.27 ± 0.17	2.52 ± 0.63
	S-2	2	8	0.63 ± 0.09	0.082 ± 0.028	9.0 ± 2.2	1.70 ± 0.63	81.5 ± 5.3	9.25 ± 0.25	39.0 ± 1.9	10.8 ± 1.0	3.66 ± 0.54	2.82 ± 0.65
	S-3	6	5	1.00 ± 0.33	0.059 ± 0.014	16.6 + 1.9	1.72 ± 0.80	89.8 ± 4.2	15.4 ± 1.6	39.3 ± 0.8	9.60 ± 0.34	4.10 ± 0.20	3.65 ± 0.65
	S-4	2	8	0.67 ± 0.13	0.033 ± 0.006	20.6 ± 0.9	3.55 ± 0.82	82.9 ± 3.4	11.7 ± 0.5	53.9 ± 0.7	9.01 ± 0.34	5.99 ± 0.24	1.81 ± 0.41
C6♀	D-11	2	5	1.04 ± 0.14	0.046 ± 0.004	22.6 ± 3.4	6.18 ± 1.34	72.2 ± 7.4	8.38 ± 0.52	56.2 ± 0.3	6.85 ± 0.01	8.21 ± 0.12	2.22 ± 0.56
	D-12	2	4	1.03 ± 0.21	0.035 ± 0.008	29.9 ± 1.1	6.63 ± 1.36	77.7 ± 5.1	14.1 ± 4.1	57.6 ± 1.1	8.50 + 0.16	7.85 + 0.06	1.89 + 0.17
C6♂	D-13	2	10	1.55 ± 0.56	0.081 ± 0.036	20.2 ± 4.4	5.24 ± 1.59	74.1 ± 5.4	4.53 ± 2.07	54.2 ± 0.8	7.75 ± 0.55	7.03 ± 0.58	3.59 ± 1.86
	D-14	2	5	0.67 ± 0.29	0.044 ± 0.016	15.3 ± 3.0	2.65 ± 0.94	83.1 ± 4.2	7.54 ± 0.23	52.5 ± 0.1	8.63 ± 0.04	6.07 ± 0.03	2.61 ± 1.62
P.rubra													
C6♀	D-6, D-7	2	6	0.74 ± 0.10	0.059 ± 0.011	13.1 ± 3.5	3.83 ± 0.27	69.1 ± 8.0	6.53 ± 0.61	55.6 ± 1.0	7.29 ± 0.15	7.64 ± 0.30	2.17 ± 0.21

has been demonstrated to be non-significant, at least to 265 atm (King and Packard 1975).

Body mass and body composition

Frozen specimens were weighed (WW) then freeze-dried to obtain dry weight (DW). Specimens were pooled according to experiments and ground into a fine powder with a ceramic mortar and pestle. Powdered samples were used for carbon and nitrogen composition analysis with a CHN elemental analyzer (Elementar Vario EL), using acetanilide as a standard. Weighed fractions of powdered samples were incinerated at 480°C for 5 h and reweighed for ash (ASH) determination. Most measurements were made in triplicate. Precision (coefficient of variation, CV) for these measurements was 3% for C, 7% for N and 10% for ash.

Water content (WATER) was computed as: WATER = 100(WW−DW)/WW, and was expressed as a percentage of WW. Ash-free dry weight (AFDW) was computed as: AFDW = DW−ASH.

Results

Hydrography

As annual hydrographic features, the annual ranges of sea-surface temperature and salinity have been reported as 2–18°C and 32.2–34.1 at site H (Kobari and Ikeda 1999) and 2–15°C and 32.8–33.5 at station Knot (Tsurushima et al. 2002). Seasonal and regional differences in temperature and salinity between site H and station Knot are not seen below 200 m depth (2–3°C and 33.5–34.5 for 200–1500 m depth). Throughout the year, the minimum layer of dissolved oxygen is at 500–1000 m in the western subarctic Pacific (cf. Favorite et al. 1976). In the minimum layer, our seasonal observation showed that the oxygen concentration reaches 0.8 ml O_2 l^{-1} (or 10% saturation) at site H and 0.6 ml O_2 l^{-1} (or 6% saturation) at station Knot (Fig. 1).

C5 and C6 *Neoclanus cristatus*

Regardless of the season of collection, live C5 specimens from 1000 to 2000 m were characterized by a reddish body color, a lack of motion and floating near the surface of the container, a weak escape response against a light touch with a glass pipette, and invisible gut content. In contrast, the C5 specimens from < 250 m were transparent, with a reddish tint, remained suspending in the water column of the container, had an active escape reaction against a light touch with the glass pipette, and often had brown/greenish gut contents. De-compression effects are unlikely to cause the inactive behavior of C5s from 1000 to 2000 m depth, since C6 male/female specimens from the same depth exhibited a similar active response to that seen in C5 individuals from < 250 m depth. The body color and swimming behavior of C6 males were different from those of C6 females, in that the former were characterized by white-opaque coloration (no reddish tint) and continuous swimming in contrast to a reddish tint and only an occasional hopping movement of the latter. C6 females of *Paraeuchaeta rubra* from 1000 to 2000 m depth were also as active as C6 individuals of *N. cristatus*.

Respiration

Respiration rates (R; µl O_2 ind.$^{-1}$ h^{-1}) of C5s from 1000 to 2000 m and < 250 m ranged from 0.36 to 0.75 at 2°C and from 0.63 to 1.00 at 2–8°C, respectively (Table 2). The rates were 1.03–1.04 for C6 females and 0.67–1.55 for C6 males. The effect of re-compression (100 atm, expts D-9, D-10, cf. Table 2) on the respiration rates of C5 individuals in diapause was not significant (t-test, $P > 0.25$), allowing the data from re-compressed and non-compressed (1 atm, as control) specimens to be pooled for subsequent analyses. As body mass units, both WW and DW of the C5 specimens varied greatly between experiments (9.0–26.9 mg for WW, 1.72–10.0 mg for DW, cf. Table 2). Because of large differences in body masses of specimens between experiments (and in experimental temperatures for experiments on C5 specimens from shallow layers), direct comparison of R-values among experiments may be meaningless. To overcome this problem, R was converted to adjusted metabolic rate (AMR) by using the global model for the metabolism of marine epipelagic copepods (Ikeda et al. 2001): $\ln Y = 1.640 + 0.843 \ln X_1 + 0.068 X_2$ or $Y = e^{1.64 + 0.068 X_2} \times X_1^{0.843}$, where Y is R, X_1 is body N (mg) and X_2 is temperature (°C). AMR is defined as R interpolated/extrapolated to the rate at 2°C (Q_{10} is calculated from the coefficient of X_2 above as $e^{10 \times 0.068} = 1.97$, cf. Ikeda et al. 2001) and then 1 mg body N ($R \times X_1^{-0.843}$). Resultant AMRs [µl O_2 (mg body N)$^{-0.843}$ h^{-1}] at 2°C of *N. cristatus* were 0.65–1.23 (mean: 0.97) for C5s from 1000 to 2000 m depth, 1.81–3.65 (mean: 2.70) for C5s from < 250 m depth, 1.89–2.22 (mean: 2.06) for C6 females and 2.61–3.59 (mean: 3.10) for C6 males (Table 2). Mean AMR at 2°C of *P. rubra* was 2.17 (mean) (Table 2).

The differences in the AMR values among experiments in which the C5 specimens were collected with nets equipped with the closing cod-end (expts D-6 to D-10, Table 2) and the non-closing cod-end (D-1 to D-4) were insignificant (t-test, $P > 0.25$). D-5 data were omitted in this comparison, since the temperature of the water column in this season (March) was homogenous vertically. Since no clear seasonal trends were observed in the AMR data of C5 specimens from 1000 to 2000 m, the respiration data of D-1 through D-10 were pooled in the following analyses.

ETS assay

The ETS assay was made on a batch of four C5 specimens at 2°C and on single C5 or C6 specimens at 10°C,

both from 1000 to 2000 m depth. The relationship between ETS activity (Y; µl O_2 ind.$^{-1}$ h^{-1}) and temperature (X; °C) was established as: ln $Y = 0.0955X + 0.364$ ($r^2 = 0.993$). From the slope (0.0955) of the regression line, Q_{10} is computed as: $Q_{10} = e^{10\times0.0955} = 2.60$. From the Q_{10} value, ETS activity determined at 10°C was converted to the activity at the in situ temperature (2°C), and resultant ETS activities ranged from 0.030 (C5) to 0.441 (C6 males). R/ETS ratios were determined as 0.76 ± 0.10 ($N = 4$) for C5 specimens from 1000 to 2000 m (Table 2). Using the R/ETS ratio, the ETS activity of the C5s assayed at 10°C was then converted to R at the in situ temperature (2°C) as 0.28 µl O_2 mg^{-1} WW h^{-1}. Assuming the R/ETS ratio is the same between stages C5 and C6 of *N. cristatus*, the ETS activity data for C6 males and females can also be converted to R as 0.69 and 0.156 µl O_2 mg^{-1} WW h^{-1}, respectively.

Water, ash and C and N composition

C5 specimens from 1000 to 2000 m depth were characterized by lower water content (61.2–70.3% of WW) and lower ash content (4.1–5.8% of DW), compared with those from < 250 m depth (81.5–89.8% of WW and 9.3–15.4% of DW, respectively, cf. Table 2). C and N contents of the former were 55.9–58.8% of DW and 6.8–9.3% of DW, respectively, which are much higher in C (39.0–53.9% of DW) but lower in N (9.0–10.8% of DW) than the latter. As a consequence, C/N ratios of C5s from 1000 to 2000 m depth became markedly greater (6.7–9.3, by weight) than those (3.7–6.0) of C5s from < 250 m depth. WATER, ASH, C, N and C/N ratios of C6 males and females fell within the ranges of those seen in the C5 specimens. Correlation analyses between parameters, including body components and AMR at 2°C, revealed that WATER is the best parameter (correlation coefficients > 0.8, $P < 0.0001$) to predict the other parameters (Fig. 2).

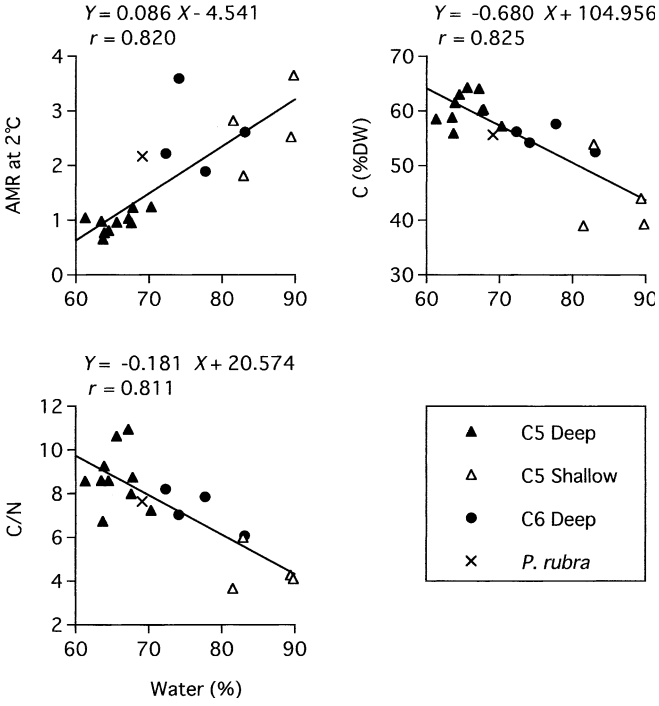

Fig. 2 *Neocalanus cristatus*. Relationships between water content (% of wet weight) and adjusted metabolic rate (AMR) at 2°C [µl O_2 (mg body N)$^{-0.843}$ h^{-1}], C composition (% of dry weight) and C/N ratio (by weight) of C5 specimens from 1000 to 2000 m depth (*C5 Deep*) and < 250 m depth (*C5 Shallow*), and C6 males and females from 1000 to 2000 m depth (*C6 Deep*). Correlation coefficients are highly significant in all cases ($P < 0.01$). Data for the copepod *Paraeuchaeta rubra* (C6 females) are superimposed for comparison (*P. rubra*)

Discussion

Live specimens of *Neocalanus cristatus* retrieved with nets from great depth (1000–2000 m) and used for respiration experiments might suffer severe physiological (de-compression, thermal shock) and physical stresses (entanglement in the net) in the course of sampling, despite the fact that the time needed for collection was relatively short in the present study (< 10 min after closing nets at 1000 m depth). Capture stress of this sort, if it existed, may have contributed to the slow escape response of the C5 specimens observed and their lowered respiration rates. To prove the presence or absence of this capture stress in the respiration data of this study, we compared: (1) respiration rates determined at 1 atm and the rates of specimens re-compressed to 100 atm in the laboratory, (2) ETS activity and respiration rates, (3) respiration rates of C5 individuals and versus those of the C6 specimens taken from the same depth (1000–2000 m), and (4) respiration rates of C5 *N. cristatus* and C6 female *Paraeuchaeta rubra* from the same 1000–2000 m.

For point 1, the lack of appreciable effects of hydrostatic pressure on respiration rates of C5 *N. cristatus* in the present study (Table 2) may not be surprising, since the same results have been well documented for deeper living pelagic copepods and other crustaceans (Quetin and Childress 1976; Childress 1977; Thuesen et al. 1998). With regard to point 2, Owens and King's (1975) method for measuring ETS activities is, in fact, a measure of the amount of enzyme, since the activity is obtained at saturating substrate, i.e. at V_{max} (Ikeda et al. 2000). Furthermore, ETS activities of marine zooplankton have been demonstrated to be unaffected by hydrostatic pressure at least up to 265 atm (King and Packerd 1975). Therefore, ETS activity is thought to be a stable measure of metabolism, free from capture stress on short time scales. As was seen in directly measured respiration rates with the sealed-chamber method, diapausing C5s exhibited a reduced ETS activity as compared with those of C6 males and females at the in situ temperature (2°C, cf. Table 3). R/ETS ratios (0.76) obtained from diapausing C5 specimens in this study fall well within the range reported for marine

zooplankton (cf. Ikeda et al. 2000). This, combined with the Q_{10} value of 2.6 established in this study for ETS activities, indicated that respiration rates (R) of C5s at 2°C (Table 3) derived from the ETS assay were consistent with rates determined by the sealed-chamber method. R-values at 2°C for C6 males and females derived from ETS appear to be higher than those directly measured, suggesting possible differences in Q_{10} or R/ETS or both between C5 and C6 specimens (note that the calculations in Table 3 are based on the data derived from the C5 stage). For point 3, while the C5 and C6 males and females were collected from the same depth (1000–2000 m), the C6 specimens, especially males, were very active, gliding through the entire water column of the containers continuously. While the age of adult males was unknown, lower respiration rates measured in one experiment (D-14) might be indicative of older specimens than those used in the other experiment (D-13). These behavioral differences among C5 specimens, C6 males and C6 females were reflected in the respiration rates of the three (Table 2). For point 4, *P. rubra* is one of most dominant paraeuchaetid copepods in the western subarctic Pacific. It is distributed mainly in the bathypelagic zone (Yamaguchi and Ikeda 2002). This copepod, collected together with C5 and C6 *N. cristatus* from 100 to 2000 m, exhibited a rapid escape reaction against a light touch with a glass pipette. Oxygen consumption rates expressed as AMR at 2°C of C6 female *P. rubra* (2.17) were nearly two times greater than those of C5 *N. cristatus* (mean: 0.97), but similar to those of C6 female *N. cristatus* (2.05). All these results from point 1 through point 4 suggest that the inactive response and low oxygen consumption rates observed in C5 specimens from 1000 to 2000 m are real and not due to capture stress.

Thus, the diapause metabolism of C5 *N. cristatus* was established as 0.97 ± 0.19 µl O_2 (mg body N)$^{-0.843}$ h^{-1} (Table 2) at the in situ temperature (2°C) (which is equivalent to 0.026 ± 0.004 µl O_2 mg^{-1} WW h^{-1} or 0.075 ± 0.016 µl O_2 mg^{-1} DW h^{-1}). In terms of AMR at 2°C, the metabolism of diapausing C5 *N. cristatus* is 36% of that of non-diapausing C5 from shallow layers [mean: 2.70 µl O_2 (mg body N)$^{-0.843}$ h^{-1}], 47% of that of C6 females [2.70 µl O_2 (mg body N)$^{-0.843}$ h^{-1}] and 31% of that of C6 males [3.10 µl O_2 (mg body N)$^{-0.843}$ h^{-1}] of the same species, and 45% of that of C6 female *P. rubra* [2.17 µl O_2 (mg body N)$^{-0.843}$ h^{-1}]. Since AMR is based on body N, a conspicuous accumulation of lipid in the body of diapausing C5 *N. cristatus* (discussed below) does not affect these comparisons, e.g. the observed reduction in respiration is not due to the deposition of metabolically inactive C-rich substance (lipids). Among four experiments on non-diapausing C5 (S-1 through S-4, cf. Table 2) from shallow layers, two experiments (S-2, S-3) were on specimens from a phytoplankton bloom season. AMR at 2°C for these specimens was the highest [mean: 3.24 ± 0.59 µl O_2 (mg body N)$^{-0.843}$ h^{-1}], against which the AMR at 2°C of diapausing C5s was only 30%. Increased respiration rates of grazing copepods (*Calanus finmarchicus*, *C. hyperboreus*, *Metridia longa*, etc.) during a phytoplankton bloom have been observed in the North Atlantic (cf. review of Marshall 1973). The reduced respiration by diapause has been reported as 0.11 µl O_2 mg^{-1} DW h^{-1} (or 20% of that of non-diapausing specimens) at 6°C for C5 *C. finmarchicus* in a Norwegian fjord (Hirche 1983) and 0.24–0.26 µl O_2 mg^{-1} DW h^{-1} (or 50% of that of non-diapausing specimens) at 0°C for C5/C6 female *C. hyperboreus* from 2290 m in the Arctic Fram Strait (Auel et al. 2003). According to Alekseev and Starobogatov (1996), the reduction in metabolism of diapausing crustaceans is a function of the duration of diapause. Such a decline in respiration rates with time has been observed for *C. hyperboreus* (Conover 1964) and *N. cristatus* (Omori 1970) starved in laboratory experiments. In contrast to laboratory experiments, evaluation of the declines in field populations is difficult, mainly due to the difficulty of knowing the history of specimens collected. This is particularly true for *N. cristatus* in the present study, since diapausing C5s are recruited during all seasons of the year (i.e. year-round spawning of this species).

Like *Calanus* spp. in the North Atlantic, deposition of a significant amount of lipids in the body has been reported for *N. cristatus* (Ikeda 1974). These lipids are largely in the form of wax esters (Saito and Kotani 2000), a typical lipid class deposited as and energy store for long-term usage. A progressive decrease in lipid contents has been reported in starved *C. hyperboreus* (Conover 1964; Lee 1974) and *C. glacialis* (Arashkevich and Kosobokova 1988) in the laboratory. Evanson et al. (2000) observed a rapid decrease in lipid contents of *N.*

Table 3 *Neocalanus cristatus*. Electron-transfer-system (*ETS*) activities and estimated respiration (R) rates of C5 and C6 males and females from 1000 to 2000 m depth in the Oyashio region, western subarctic Pacific. *Asterisk* denotes R/ETS = 0.76 ± 0.10 ($N = 4$) and $Q_{10} = 2.6$ were used, both of which were derived from C5 specimens (D-8 subsample) (*WW* wet weight)

Stage	Expt no.	Assay temp. (°C)	N	WW (mg ind.$^{-1}$)	ETS (µl O_2 mg WW^{-1} h^{-1})	ETS at 2°C*	R equivalent at 2°C* (µl O_2 mg^{-1} WW h^{-1})
C5	D-12	10	7	28.1 ± 3.2	0.079 ± 0.038	0.037 ± 0.018	0.028 ± 0.014
	D-8	2	4	26.5 ± 0.9	0.030 ± 0.006	0.030 ± 0.006	0.023 ± 0.005
C6♀	D-12	10	2	24.7 ± 0.7	0.195 ± 0.001	0.091 ± 0.001	0.069 ± 0.001
C6♂	D-12	10	7	19.2 ± 0.5	0.441 ± 0.253	0.205 ± 0.118	0.156 ± 0.062

Table 4 *Neocalanus cristatus*. C and N budgets for hypothetical C5 specimens with 6.0 mg DW (*A*), 8.0 mg DW (*B*) and 10.0 mg DW (*C*) which enter diapause, molt to C6 females and spawn in the bathypelagic zone (temperature = 2°C) of the Oyashio region, western subarctic Pacific. For comparison, C budgets of C5 specimens which do not enter diapause were calculated. See "Discussion" for details (*DW* dry weight)

Specimen	State	Carbon				Nitrogen			
		A	B	C	Comments	A	B	C	Comments
Initial body size (mg)		3.624	4.832	6.040	DW×0.604	0.426	0.568	0.710	DW×0.071
Expenditure (mg)									
C5 respiration	Diapausing	0.383	0.488	0.589	0.97 µl O_2 (mg body N)$^{-0.843}$ h^{-1} for 3 months	0	0	0	Assumed lipid metabolism
	Not diapausing	1.065	1.358	1.639	2.70 µl O_2 (mg body N)$^{-0.843}$ h^{-1} for 3 months	0	0	0	As above
Molt	Diapausing	0.123	0.165	0.207	3.8% of body C, Vidal (1980)	0.025	0.033	0.041	Molt C/N = 5, Iguchi and Ikeda (1998)
	Not diapausing	0.097	0.132	0.167	As above	0.019	0.026	0.033	As above
Egg		2.057	2.057	2.057	386 eggs×5.33 µg C, Saito and Tsuda (2000)	0.197	0.197	0.197	386 eggs×0.51 µg N, Saito and Tsuda (2000)
C6 respiration	Diapausing	0.605	0.827	1.038	2.06 µl O_2 (mg body N)$^{-0.843}$ h^{-1} for 3 months	0	0	0	Assumed lipid metabolism
	Not diapausing	0.619	0.841	1.051	As above	0	0	0	As above
Initial–Expenditure									
	Diapausing	0.456	1.291	2.147		0.204	0.338	0.472	
	Not diapausing	−0.215	0.444	1.125		0.210	0.345	0.480	

plumchrus during overwintering in the Strait of Georgia, British Columbia. In the present study, the amount of lipids in *N. cristatus* was represented indirectly by C composition and C/N ratios. As an extreme case, copepods with bodies filled almost entirely with lipids exhibit a C content of as high as 60–65% of DW and a C/N ratio of nearly 10 (Ikeda 1974; present study). In this study, C composition of non-diapausing C5 specimens of *N. cristatus* from < 250 m depth and those in diapause from 1000 to 2000 m depth were markedly different (Table 2). Compared with non-diapausing C5s, diapausing C5s were much greater in DW (5.8–10.0 mg vs. 1.7–3.6 mg), C composition (55.9–64.3% vs. 39.0–53.9% of DW) and C/N ratio (6.7–10.9 vs. 3.7–6.0), but lower in water content (61.3–70.3% vs. 81.5–89.8% of WW) and ash content (4.1–5.8% vs. 9.3–15.4% of DW). As the major body component, a significant portion of water in C5 specimens was replaced by C-rich substances (lipids) in the course of entering diapause. A calculation indicates that non-diapausing C5s containing a water content of 90% (of its WW) could increase in dry weight fourfold without a change in body volume, simply by replacing water to the level of 60% of WW with lipid. Since C6 individuals cease feeding and their energy demands for metabolism and reproduction are fueled by lipids deposited in diapausing C5s, the body composition in the C6 stage is anticipated to be somewhere between those of diapausing and non-diapausing C5 specimens. This mobilization of water and elemental compounds within the nearly fixed body volume of C5s is well represented by coupled variations in the relative proportions of WATER, ASH and C and N components (an increase in one element causes a decrease in the other elements, cf. Fig. 2). In this study, we investigated the inter-relationships between elements and found that water content can be used as an index to diagnose the major body components and metabolic activity of *N. cristatus* (Fig. 2). Except the much smaller C5 stage (with DWTable 2), overall results of the C and N composition and their ratios in C5 specimens and C6 males and females from submerged Oyashio water (Omori 1970) are similar to those obtained for the respective stages in this study.

Presently available information about metabolism and body composition of diapausing oceanic copepods is from *C. finmarchicus*/*helgolandicus* (Hirche 1983; Ingvarsdottir et al. 1999) and *C. hyperboreus* (Conover 1962; Auel et al. 2003) in the North Atlantic. Compared with these *Calanus* spp. which diapause at stage C5 and start feeding again at stage C6 for spawning, *N. cristatus* (and *N. plumchrus* and *N. flemingeri* as well, cf. Bradford and Jillett 1974) reduce mouth parts at stage C6 and spawn without feeding. A question may arise immediately: how does a C5 specimen in diapause allocate energy to storage to meet the anticipated costs of metabolic expenditures during C5 and C6, cast molts and egg production? In order to answer the question, let us consider typical C5 specimens weighing 6, 8 or 10 mg DW (Table 2), and all molt to C6 females. The choice of

females is simply due to the lack of appropriate data for sperm production in C6 males. By using mean C and N composition data of the diapausing C5s observed in this study (60.4% and 7.1%, respectively, of DW), these three specimens are equivalent to 3.624, 4.832 and 6.040 mg C, respectively, or 0.426, 0.488 and 0.710 mg N, respectively (Table 4). Following the life cycle of the major *N. cristatus* population in the Oyashio region (Kobari and Ikeda 1999), the period of diapause was designated as 3 months, followed by molting to stage C6. At the in situ temperature (2°C) of the bathypelagic zone (1000–2000 m) in the Oyashio region, C6 females release more than five clutches of eggs successively in a 3-month period, each separated by ca. 2 weeks, with a mean lifetime fecundity of 386 eggs (Saito and Tsuda 2000).

Following this life-history trajectory, C and N budgets of the C5 specimens were calculated (Table 4). C losses in metabolism of diapausing C5 and C6 females were calculated from the mean AMR values at 2°C [0.97 and 2.06 μl O_2 (mg body N)$^{-0.843}$ h^{-1}, respectively, Table 2] by substituting the N contents of each stage. In order to assess the effect of diapause metabolism of the C5 stage on overall C budgets, C loss through the metabolism of non-diapausing C5s was also computed from the mean AMR at 2°C [2.70 μl O_2 (mg body N)$^{-0.843}$ h^{-1}, Table 2]. Since we assumed lipid metabolism (see below), there will be no N loss through the metabolism of either C5 or C6 females. Then, the initial size values were taken for C5 individuals, and the means before (= initial size−molt) and after spawning (= initial size−molt−eggs) were taken for C6 specimens. Oxygen respired was converted to C units (C-CO_2) assuming lipid metabolism (RQ = 0.7, Gnaiger 1983). C loss in the molt was estimated to be 3.8% of body C, as was evaluated for the copepod *Calanus pacificus* (Vidal 1980), for the former; a rounded C/N ratio of 5 for pelagic crustacean molts was summarized by Iguchi and Ikeda 1998) to indicate N loss. From laboratory experiments, a single egg of *N. cristauts* is known to weigh 5.33 μg C or 0.51 μg N (cf. Saito and Tsuda 2000). Resultant C budgets for the three diapausing C5s with 6.0–10.0 mg DW show that the major cost is egg production (34–57% of the initially stored C), followed by respiration (27%) and cast molts (3%), leaving residual C of 13–36% in spent C6 females. The calculation in which all C expenditures were subtracted from the initial body size shows that the residual C is 0.456–2.147 mg C or 12.6–35.5% of the initial C for diapausing C5s, but is −0.215 to 1.125 mg C or < 18.6% of the initial C for non-diapausing C5s. Since the spent C6 females of *N. cristatus* are almost transparent, and its ash-free dry weights are only one-tenth that of diapausing C5 specimens (Ikeda, unpublished data), the amount of body C in the three typical C5 specimens weighing > 6 mg DW (Table 4) is sufficient to complete the hypothesized life-history trajectory and reproduce successfully only when their metabolic expenditure is reduced by diapausing at stage C5. The failure to diapause at stage C5 could result in a severe reduction of the number of spawning eggs for specimens less than ca. 8 mg DW. Since C5 specimens < 8 mg DW occurred frequently during this study (cf. Table 2), diapause is an integral life-history trait of *N. cristatus* to maintain their population in the field.

Thus, our C and N budget calculations indicate clearly the amount of C storage observed and the degree of metabolic reduction determined on diapausing C5 *N. cristatus* are sufficient for them to molt to stage C6 and to produce eggs, i.e. to repeat generations in the Oyashio region. In the future comparative study is needed on congeners (*N. plumchrus*, *N. flemingeri*) in the Oyashio region.

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