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Body Composition and Metabolism of the Larvae of the Pink Shrimp (*Pandalus borealis* Krøyer) Raised in the Laboratory

Kouichi SAOTOME[1),2)] and Tsutomu IKEDA[3)]

Abstract

Body size (body length, carapace length, wet weight, dry weight), body composition (carbon, nitrogen, ash), oxygen consumption rate and buoyancy were measured on each larval stage of the pink shrimp (*Pandalus borealis*) raised in the laboratory. Throughout all larval stages, carbon ranged from 41.1 to 45.1%, nitrogen from 10.6 to 11.2%, and ash from 12.4 to 18.6% of dry weight. The range of water content was from 77.5 to 83.6% of wet weight. The increases of carbon and nitrogen were the greatest at stages II to V. The highest oxygen consmption rate per unit body carbon was seen at stage II, the stage is considered to be most vulnerable to starvation. All stages are negatively buoyant and anethetized specimens sank at a speed of 0.43 to 1.17 $cm \cdot sec^{-1}$. Carbon budget was estimated for the larvae growing from stage I to postlarvae.

Key words *Pandalus borealis*, larval development, oxygen consumption, body composition, carbon budget

Introduction

The pink shrimp *Pandalus borealis* is a discontinuous circumboreal species, growing to 150*mm* in body length, and an important commercial species for many northern countries. In the Japan Sea, this shrimp has been fished with bottom trawls and shrimp traps since the 1950's, and its annual catch has been recorded as 800 to $900 \times 10^3 kg$. According to the recent fishery statistics, landings of this species has declined dramatically from 1982 onward (ISHIKAWA FISHERIES EXPERIMENTAL STATION 1988).

P. borealis exhibits hermaphroditism, smaller specimens are all males and large ones, all females. Females carry fertilized eggs until the hatching of the larvae. Released larvae are planktonic and shift to largely benthic life after metamorphosis.

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1) Notojima Station, Japan Sea-Farming Association, 15-1-1 Magari, Notojima-cho, Kashima-gun, Ishikawa 962-02, Japan.
(〒926-02 石川県鹿島郡能登島町字曲　日本栽培漁業協会能登島事業場)
2) Present address: Marino-Forum 21, Shibata Building 3rd Floor, 2-6-4 Uchikanda, Chiyoda-ku, Tokyo 101, Japan.
(現在：〒101 東京都千代田区内神田2-6-4　柴田ビル3階　マリノフオーラム21)
3) Japan Sea National Fisheries Research Institute, Suido-cho, Niigata 951, Japan.
(〒951 新潟市水道町1丁目5939-22　日本海区水産研究所)

Detailed accounts of the larval developmet of *Pandalus* shrimps including *P. borealis* were given by ROTHLISBERG (1980). The longevity of this shrimp estimated by size-distribution analysis varies geographically from 3 to 8 years. For a review of general biology, ecology and fishery of *P. borealis*, see SHUMWAY *et al.* (1985). KURATA (1957) and ITO (1976) discussed growth, fecundity and life cycle of local populations of this species in the Japan Sea.

Since 1983, the Japan Sea-Farming Association at Notojima has been raising *P. borealis* larvae for release, as an attempt to improve the natural stock size of this shrimp in the Japan Sea. To establish an economical and reliable method of raising the larvae in the laboratory, we investigated body composition and metabolism of the larvae hatched out in the laboratory.

Materials and methods

Larvae: Ovigerous females caught with shrimp traps were maintained in the laboratory to obtain larvae. Newly hatched larvae were subsequently grown in various sized tanks (0.5 to 20m^3 capacity. The diatom *Phaeodactylum tricornutum* was provided as food for early stage larvae (I-V). *Artemia* nauplii and fish meat were given for older stage larvae (III-VII) (Fig. 1). The concentration of *P. tricornutum* used in this experiment was 2 to 4×10^5 cells ml^{-1} and *Artemia* nauplii, 2 to 8 nauplii ml^{-1}. In the course of experiment, water temperature varied from 7.2 to 10.6°C with a mean of 8.3°C. Subsamples of the larvae were taken at regular intervals and developmental stages of the larvae were identified based on the morphological characters of each stage, which are the same to those in HAYNES (1979) until stage V. Beyond StageV there are two stages (VI and VII) before the postlarvae which is

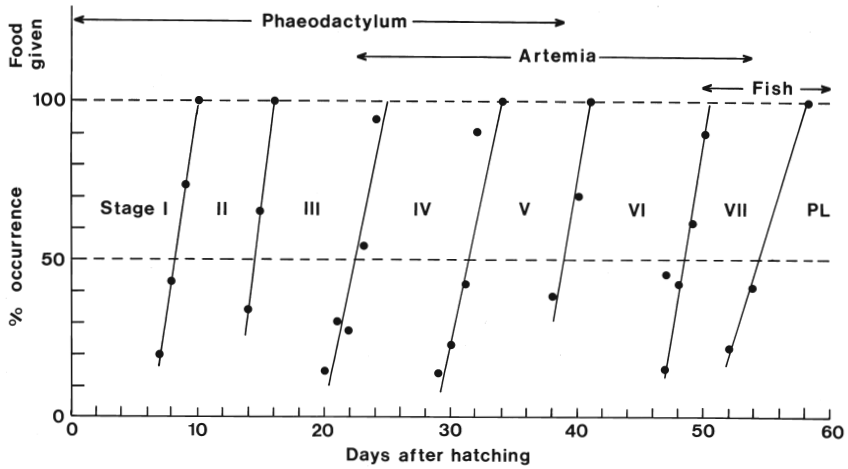

Fig. 1. Occurrence of successive larval stages of the pink shrimp *P. borealis* from the hatching of early February 1986. Day 0 indicates the date of hatching of the larvae. As food the diatom *Phaeodactylum tricornutum* (Phaeodactylum), *Artemia* nauplii (Artemia) and fish meat (Fish) were provided as shown on the top of this figure. Stage PL=postlarva.

characterized by front projected eye (side-projected eye in all larval stages) and an almost adult complement of the rostral spination. The number of caudal spine of the telson reduces from 10 to 5 when stage VII moults to postlarva (ARITAKI unpublished). Detailed accounts of larval morphology of *Pandalus* shrimps were given by ROTHLISBERG (1980). The date of development from one stage to the next was determined when the new stage larvae exceeded 50% of the total number. The larvae used for the following experiments were 3 to 6 day-old specimens of each stage, excepting for the use of 0 day-old specimens of stage I and 9 day-old specimens of postlarvae. Body composition was studied on the larvae raised in 1986 and metabolism and buoyancy on those raised in 1988.

Metabolism: Oxygen consumption rate was measured by a water bottle method (OMORI and IKEDA 1984). Five to 34 individuals, depending on the size of the larvae, were placed in 100*ml* glass bottles filled with filtered and well aerated seawater. Control bottles without animals were prepared concurrently. Experiments were run for 6 *h* in the dark at 5 to 11°C. At the end of experiment oxygen concentrations of both experimental and control bottles were determined with an oxygen monitor system (YSI DO meter model 58 fitted with YSI oxygen electrode 5739).

Buoyancy: Buoyancy of larvae anesthetized with MS-222 were measured using a 2 litre measuring cylinder (84*mm* diameter) filled with seawater (salinity 34.2psu) collected from 500*m* depth of slope water of the Japan Sea. The cylinder was placed in a temperature controlled cabinet and the measurement was made at 1°C. This combination of salinity and temperature is the maximum density of seawater, to which the newly hatched larvae may encounter in the Japan sea. The larvae of all stages exhibited negative buoyancy. Time required to sink the single larva between 10 *cm* mark and 25 *cm* mark from the top of the water was read by a stop-watch, which was accurate to 0.01 *sec*. The measurement was replicated on 10–16 individuals of each larval stage. No correction for "wall-effect" was made to the result, but readings for the larvae which contacted the wall in the course of measurements were discarded.

Chemical composition: Eighty to 1000 larvae at each stage were taken from tanks and they were maintained in small containers filled with filtered seawater for 12 *h* to facilitate their defaecation. They were then rinsed with a small amount of distilled water on a filtering disc to which a constant gentle suction pressure was applied. Rinsed larvae were weighed (wet weight) and stored frozen (−45°C) until analysed. Frozen larvae were freeze-dried to obtain dry weight. Then dried larvae were ground with a ceramic mortar and pestle. Powdered samples were used for the analyses of carbon and nitrogen with a Yanaco CHN Corder (MT-3) using antipyrine as a standard. Ash was determined on powdered samples incinerated at 450°C for 6 *h*. Elemental analyses and ash determinations were made in duplicate. Coefficients of variation of these measurements were 2% for carbon, 10% for nitrogen, and 15% for ash.

Results

Development: At 7.2–10.6°C (mean: 8.3°C) fifty percent of newly hatched larvae (stage I) reached stage II in 8 days, stage III in 15 days, stage IV in 22 days, stage V in 31 days, stageVI in 39 days, stage VII in 49 days and postlarvae in 54 days (Fig. 1). Residence time in each stage varied from 5 days to 10 days. Survival of the larvae in the course of development from stage I to postlarvae was around 30%.

Oxygen consumption: As the the development of the larvae oxygen consumption rate increased progressively from 0.23 μl O_2 individual^{-1} h^{-1} for stage I to 2.18 μl O_2 individual^{-1} h^{-1} for stage VI. An exception to this pattern was the oxygen consumption rate of stage VII which was lower than the rate of stage VI (Table 1a). Since the experimental temperatures ranged from 5 to 11°C, all data were standardized to the rate at 8°C, using a Q_{10} value of 3.74, which has been established for stage I larvae of this species by PAUL and NUNES (1983) (Table 1a). However, the changing pattern with development of standardized oxygen consumption rates remained the same to that of non-standardized rates.

Buoyancy: Stage I larvae sank 0.43 $cm \cdot sec^{-1}$ (Table 1b). The sinking rate increased with the development of the larvae, reaching the maximum rate of 1.17 $cm \cdot sec^{-1}$ at the stage of postlarvae.

Body composition: Water content and ash increased from stage I to II, followed by a decrease to stage V, and then recovered to postlarvae. Another pattern was seen for carbon; it decreased from stage I to II, and remained at the same level until stage III. From stage III to V carbon increased and decreased to postlarvae. Changes in the ratio of body carbon to nitrogen (C/N ratio) were paralleled with those of carbon, reflecting a rather stable level of nitrogen throughout all stages (10.6 to 11.2% of dry weight) (Table 2). All these changing patterns observed in each component were significant ($p<0.05$), as judged by run test (TATE and CLELLAND 1957).

Body components (water, ash, carbon, nitrogen), expressed as percent of wet weight or dry weight in Table 2, were converted per individual basis to examine between-stage increase in each component. Between-stage increase (percent change from one stageto the next) thus calculated showed near 100% (89 to 110%) increase in carbon and nitrogen between stages II and III, III and IV, and IV and V (Fig. 2). The increase of these components between stages I and II, V and VI, and VI and VII were lower (15 to 40%) and the between stages VII and postlarvae, the lowest (12 to 17%) (Fig. 2). Changing pattern of ash was similar to those of carbon and nitrogen in that its higher increase (66 to 87%) was seen in stages II and III, III and IV, and IV and V. Between-stage increase in ash dropped in stages V and VI, and VI and VII, then increased from VII to postlarvae, the latter recovery was different from the pattern seen in carbon and nitrogen. Between-stage increase in water was simpler; it increased until stage IV to V (107%) then declined in

Table 1. Oxygen consumption and sinking rates of the larvae of the pink shrimp *Pandalus borealis*. Means±1 SD, N=number of replicates. - =not determined

Stage	I	II	III	IV	V	VI	VII	Post-larvae
(a) Oxygen consumption rate ($\mu l\ O_2$ individual$^{-1}h^{-1}$)								
Observed	0.23±0.06	0.31±0.07	0.69±0.05	0.67±0.05	1.20±0.05	2.18±0.02	1.40±0.12	-
N	8	9	9	8	4	9	9	
Expt T (°C)	7	5	8	5	9	9	10	
Standardized at 8°C	0.27±0.06	0.46±0.10	0.69±0.05	0.99±0.08	1.05±0.04	1.91±0.02	1.08±0.09	-
(b) Sinking rate ($cm \cdot sec^{-1}$)	0.43±0.3	0.55±0.03	0.66±0.08	0.71±0.05	0.91±0.10	0.97±0.07	1.10±0.14	1.17±0.28
N	10	10	10	10	16	14	13	10

Table 2. Body length (BL), carapace length (CL), wet weight (WW), dry weight (DW), water content (H_2O), ash content (Ash), carbon content (C), nitrogen content (N) and the ratio of carbon to nitrogen (C/N) of the larvae of the pink shrimp *Pandalus borealis*. Means±1 SD on N individuals (in parentheses) for BL, CL, WW and DW, single measurement on a batch of 80-1000 individuals for H_2O, and duplicate measurements on powdered samples for Ash, C and N

Stage	I	II	III	IV	V	VI	VII	Post-larva
BL (*mm*)*	5.92±0.19 (25)	6.79±0.20 (25)	8.10±0.25 (25)	9.39±0.32 (25)	11.30±0.31 (25)	13.01±0.41 (25)	15.71±0.40 (25)	16.05±0.86 (25)
CL (*mm*)	0.97±0.03 (20)	1.27±0.07 (20)	1.49±0.08 (20)	1.86±0.08 (20)	2.44±0.18 (11)	2.64±0.14 (20)	3.11±0.13 (17)	3.22±0.24 (20)
WW (*mg*)	1.11±0.07 (20)	1.55±0.21 (20)	2.67±0.38 (20)	4.93±0.98 (20)	10.35±1.61 (11)	17.10±1.80 (20)	21.25±2.80 (18)	21.85±3.72 (20)
DW (*mg*)	0.23±0.03 (20)	0.28±0.03 (20)	0.58±0.08 (20)	1.14±0.16 (20)	2.26±0.23 (20)	3.17±0.60 (20)	3.95±0.63 (20)	4.72±0.98 (20)
H_2O (%WW)	82.9	83.6	79.9	78.7	77.5	78.4	79.0	79.8
Ash (%DW)	15.1	18.4	16.7	14.1	12.4	13.0	14.6	18.6
C (%DW)	43.4	41.1	41.1	43.9	45.1	44.6	43.3	40.7
N (%DW)	11.2	11.0	11.1	10.6	10.6	10.6	11.1	10.9
C/N	3.89	3.75	3.70	4.14	4.26	4.23	3.91	3.75

*Distance between the tip of the rostrum and the end of the telson

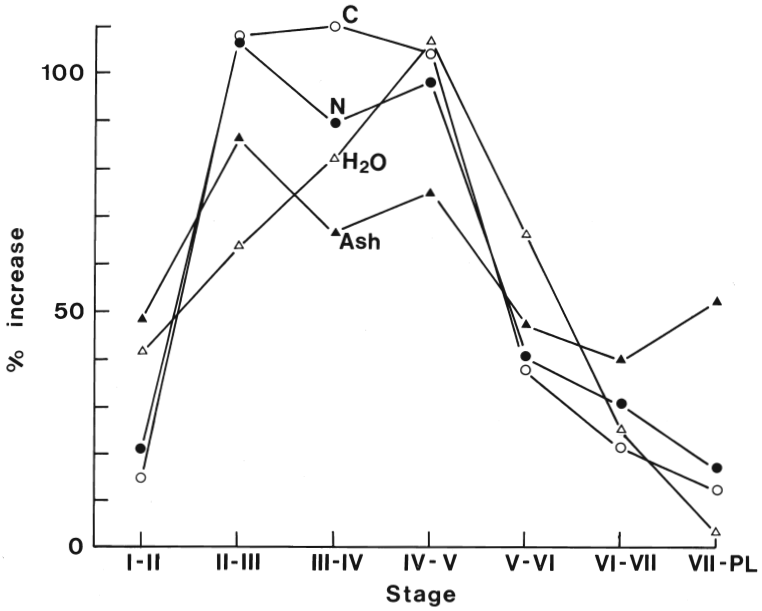

Fig. 2. Between-stage increment in body carbon (C), nitrogen (N), water (H_2O), and ash in the larvae of the pink shrimp *Pandalus borealis*. Stage PL=postlarva.

stage VII to postlarvae (4%).

Discussion

The duration of all larval stages from I to postlarvae was 54 days in the present experiment. Larval duration of *P. borealis* has been known to be a function of temperature (SHUMWAY *et al.* 1985), and the 54 days at the mean temperature of 8. 3°C observed here is consistent with the duration predicted from the relationship between larval duration and temperature for the pink shrimp of SHUMWAY *et al.* (1985). While the intermoult period of *P. borealis* larvae calculated from the 50% occurrence of new stages varied from 5 to 10 days, a near equal intermoult between larval stages has been reported on the larvae of other *Pandalus* shrimp (*P. jordani*) by ROTHLISBERG (1979). Unequal intermoult periods found in the present study may be caused by the fluctuation of experimental temperature.

Except for isolated data on eggs by HOPKINS (179), no data are presently available on the body composition of *P. borealis* larvae. However, carbon (41 to 45% of dry weight) and the body C/N ratio (3.7 to 4.3) observed in this study are similar to the results repoted on various brachyuran larvae; *Hyas araneus* (C=39% of dry weight, C/N=4.4, ANGER 1986), *Inachus dorsettensis* (C=35–44% of dry weight, C/N=3.8–4.5, ANGER 1988), and *Carcinus maenas* (C=32–36% of dry weight, C/N=3.8–4.3, DAWIRS 1987). These body composition data of *P. borealis* and other decapod larvae suggest low food reserves in their bodies, as compared with some pelagic crustaceans which contain carbon more than 60% of dry weight and exhibit body C/N ratio as high as

10 to 11 (IKEDA 1974). In fact, it has been known that feeding shortly after hatching is necessary for further successful development in many dacapod crustaceans (cf. DAWIRS 1987, and references therein). In *P. borealis* accumulation of various body components during the development from stage I to II was low and the most active growth was seen between stages II and V. During this most active growth phase body C/N ratio increased from 3.8 to 4.3, indicating that relatively more carbon was accumulated in the body than nitrogen. Growth of the larvae slowed down from stage V onward. The stages from VII to postlarvae are transitional phases from pelagic life to benthic life of this shrimp. Ash was the only body component that showed the highest increase during this transitional phase.

Oxygen consumption rates of the larvae was compared with the rate of "general zooplankton" of IKEDA (1985) on body carbon basis (Fig. 3). For interspecific metabolic comparison, carbon is known to be superior to dry weight (IKEDA 1985) thereby carbon specific oxygen consumption rate of each larval stage was calculated from the data in Tables 1a and 2. Stage II larvae are almost at the typical pelagic metabolism. Larvae older than stage II indicate carbon specific oxygen consumption rates much lower than typical pelagic metabolism. This high oxygen consumption

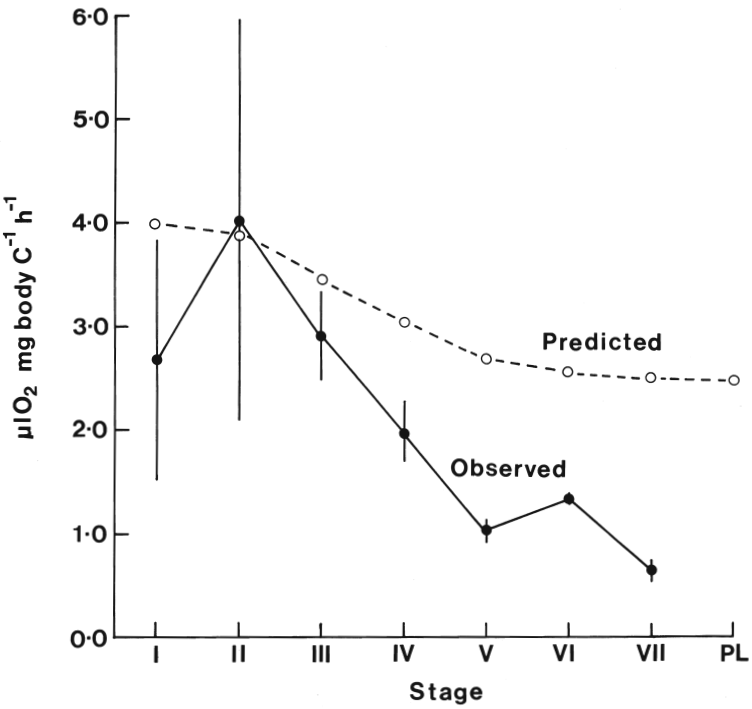

Fig. 3. Changes in oxygen consumption rate of the larvae of the pink shrimp *Pandalus borealis* observed (standardized at 8°C, means ±95% confidence interval) and the rate predicted from the equation for "general zooplankton" of Ikeda (1985); ln Y=0.5254 + 0.8354 ln X_1+0.0601 X_2, where Y is μl O_2 individual$^{-1}h^{-1}$, X_1 is *mg* carbon, and X_2 is temperature (8°C in here). Stage PL= postlarva.

rate of stage II larvae combined with the low body carbon (41.1% of dry weight) strongly suggest that the stage II is the most critical larval stage under food limited conditions.

STICKNEY and PERKINS (1981) examined stomach contents of the larvae from Sheepscot Bay, Maine, and reported that diatoms (including large *Coscinodiscus*) were the main components. In Sheepscot Bay, they also observed the close relationship between diatom abundance and successful development of stage I larvae to the following stages. In the Japan Sea, ecology of *P. borealis* larvae is poorly known, but the hatching season of the larvae is deduced to be January to April as judged from the occurrence of ovigerous females (KURATA 1957; ITO 1976; ISHIKAWA FISHERIES EXPERIMENTAL STATION 1988). According to the recent data of ISHIKAWA FISHERIES EXPERIMENTAL STATION (1988), the stage I larvae have been collected in January to February from a 250*m* depth off Noto Peninsula where water temperatures are 2 to 5°C. Since the phytoplankton bloom in this region generally occurs from February through May (IMAI *et al.* 1988) stage II larvae which develop from stage I in 8 days may encounter food limitation. In the laboratory experiment the stage I larvae die off without feeding in 14 to 22 days at 6 to 8°C (STICKNEY and PERKINS 1981). Clearly, future research on the timing of phytoplankton bloom and the hatching of the larvae is required for the evaluation of population dynamics of *P. borealis* in the Japan Sea.

Critical environmental factors affecting larval mortality have been studied on *P. jordani* off Oregon coast by ROTHLISBERG and MILLER (1983). Accordingt to their results, larval survival of *P. jordani* larvae is enhanced by the temperature <12°C, which is maintained by strong upwelling there. While ROTHLISBERG and MILLER (1983) did not discuss feeding conditions of *P. jordani* larvae, strong upwelling is also known to enhance phytoplankton growth.

The buoyancy test indicated that all larval stages of *P. borealis* were heavier than seawater. Therefore, larvae always require some energy to maintain themselves in the water column unless there are upward current in the order of 0.43 to 1.1 $cm \cdot sec^{-1}$. KILS (1981) established the relationship between sinking rate (Y $cm \cdot sec^{-1}$) and body length (X mm) for euphausiids as $Y=0.0609\ X^{1.07}$ From this equation, Y for X of 5.92 mm (stage I larvae) and 16.05mm (postlarvae) is predicted as 0. 42 and 1.19 $mm \cdot sec^{-1}$ respectively, both of which are in good agreement with the observed sinking rates of respective stages (Table 1b).

Carbon budget of the larvae growing from stage I to postlarvae was established based on the present data (Table 3). Carbon utilized for the growth is given by the difference in body carbon between postlarvae and stage I larvae. While moults were not collected in this study, carbon loss at each moulting has been estimated as 1.3 to 2.3% in euphausiids (IKEDA and DIXON 1982; DALPADADO and IKEDA 1989). In this calculation loss of 2% of body carbon was assumed at each moulting. Metabolic loss measured on the larvae placed in filtered seawter in this study represents routine metabolism and specific dynamic action (SDA) due to feeding is not included.

Table 3. Carbon budget of the larvae of the pink shrimp *Pandalus borealis* growing from stage I to postlarvae at 8°C. See text for details

(1)	Growth: 1920–100	=1820 μgC
(2)	Moult: 5096×0.02	=102 μgC
(3)	Metabolism: 649×2	=1298 μgC
(4)	Assimilation: (1)+(2)+(3)	=3220 μgC
(5)	Ingestion: (4)/0.8	=4025 μgC
(6)	Net growth efficiency: (1)/(4)×100	=56.5%
(7)	Gross growth efficiency: (1)/(5)×100	=45.2%

According to a recent study (KIØRBOE *et al.* 1985, 1987) SDA is the extra cost for growth of animals. SDA of the larvae was assumed to equate routine metabolism from the data of krill *Euphausia superba* (IKEDA and DIXON 1984). Oxygen consumption was converted to carbon unit using a RQ of 0.97 (protein metabolism, see GNAIGER 1983). The amounts of carbon utilized for growth, moults and metabolism for *P. borealis* larvae in this study totaled 3220 μg (Table 3).

In terms of carbon net growth efficiency (growth/assimilation × 100) of the larvae raised in this study is 56.5%, and allocation of assimilated carbon for the metabolism is 40.3%, and that for moults is 3.2%. When assimilation (digestion) efficiency of the larvae is assumed to be 80%, the amount of food carbon ingested by the larvae growing from stage I to postlarvae is 4025 μg. From this, carbon based gross growth efficiency (growth/ingestion × 100) is computed as 45.2%, which is close to 45.9% for the larvae of krill *Euphausia superba* (IKEDA 1984), 39.7% for the larvae of an oceanic shrimp *Sergestes similis* (OMORI 1979), and 33.4 to 46.8% for the larvae of a swimming crab *Portunus trituberculatus* (MORIOKA *et al.* 1988). All these gross growth efficiencies fall between the general range of 35 to 50% being reported for many heterotrophic organisms (cf. CALOW 1977).

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実験室で得られたホッコクアカエビ（*Pandlus borealis* Krøyer）の幼生各期の体成分と代謝活性

早乙女　浩　一・池　田　　勉

実験室で採卵・孵化・飼育されたホッコクアカエビの幼生全期（Ⅰ～Ⅶ），後期幼生の体長，甲殻長，湿重量，乾重量，炭素量，窒素量，灰分量とともに酸素消費量，沈降速度を測定した。全幼生期を通じて，水分含量は湿重量の77.5～83.6%，炭素・窒素含量は乾重量のそれぞれ41.1～45.1%，12.4～18.6%であった。炭素・窒素は幼生の発育に伴い増加するが，Ⅱ～Ⅴ期間での増加が著るしかった。幼生の単位炭素量当りの酸素消費量はⅡ期で最高を示し，全幼生期のうちでⅡ期が餌不足に最も弱いことが示唆された。全幼生期を通じて，幼生は海水よりも比重が大きく，沈降速度は0.43～1.17$cm \cdot s^{-1}$であった。本実験結果よりⅠ期が後期幼生に成長するまでの炭素収支を計算した。