NUTRITIONAL ECOLOGY OF MARINE ZOOPLANKTON*

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Contents

I. Introduction

Zooplankton are distributed more or less overall the worlds oceans inhabiting depths from the surface to the deep waters, so that their nutritional function is difinitely of great importance in marine ecology. Existence of zooplankton primarily depends on the primary production, directly or indirectly, which

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differs geographically. The temperature of their habitats is also one of the most dominant factors which reflect on the geographical distribution of marine zooplankton. A great variation of the sea temperature, from near 30°C in the tropical seas to less than 0°C in the polar seas, would be a major factor regulating the nutritional function of zooplankton. In early stage of the studies on the metabolism of poikilothermal animals it was observed that the animals in the cold waters were as active as those in warm waters in the natural conditions, in spite of the large difference of temperature, but warm water animals often died with cold rigor when they were transferred into cold water. This fact suggested the existence of adaptation in cold water animals that makes it possible to maintain a high metabolic rate even at low temperature. Fox (1936) has reported for the first time that the metabolic rate of warm water marine forms (echinoderms, sipunculids and crustaceans) is higher than that of cold water forms at normal temperature in their habitats. Later extensive work of Scholander *et al.* (1953) dealing with aquatic as well as terrestrial animals in the tropical and arctic areas has shown that there occurred a distinct metabolic adaptation in arctic aquatic animals (crustaceans and fishes). Further, Wohlschlag (1964) and Edwards *et al.* (1970, 1971) ascertained that metabolic adaptation takes place in the antarctic and tropical fishes. Important findings by these workers are that the metabolic levels of animals in extreme circumstances such as tropical warmth or polar coldness are far different from those obtained in the laboratory experiments by graded temperatures.

The experiments on the metabolism of zooplankton by the previous workers have been made on the boreal and temperate species and mostly on copepods and euphausiids. This author experimented on zooplankton species from tropical, temperate and boreal seas (Ikeda, 1970). Zooplankton are a link in food chain between the primary producers and nektonic and benthic animals in higher trophic levels. Their functions decrease phytoplankton populations through grazing (cf. Raymont, 1963, 1966), accelerate phytoplankton growth by excreting nutrient substances which are finally metabolized (Ketchum, 1962; Corner and Davies, 1971), and supply themselves as food of predators.

In the present studies rates of respiration and ammonia excretion in many species of marine zooplankton were determined with chemical analyses of their bodies in an attempt to test the assumption that body size and habitat temperature are major factors deciding physiological conditions of these animals. Attention was also paid to the physiology of zooplankton under starvation. The results of the experiments lead the author to conclude that the mode of nutritional function in marine zooplankton is beautifully associated with the temperature in their habitats, and, in turn, their geographical locations.

II. Previous work

The first work on the respiration of marine zooplankton was made by Ostenfeld (1913) on *Calanus hyperboreus*, and then, Pütter (1922, 1923, 1924–25) conducted a long series of measurements on mixed copepod populations (see the criticism of Krough, 1931). In 1935 Marshall *et al.* measured respiration of *Calanus finmarchicus* in relation to environmental conditions such as temperature, hydrogen-ion concentration, oxygen content, salinity of medium water, and light. Clark and Bonnet (1939) observed the effect of temperature on the respiration rate of the same species. Effects of light, temperature, seasonal adaptation, reproduction, sexual difference, feeding and maintenance period in laboratory conditions of test animals on the respiration were studied on *Acartia clausi* and *A. tonsa* by Conover (1956). The works of Raymont and Gauld (1951), Gauld and Raymont (1953) and Raymont (1959) indicated that the oxygen consumption of some species of neritic copepods was related to their body length. Raymont and Conover (1961) estimated the respiration rate of *Calanus hyperboreus*, *Nematoscelis megalops* and *Neomysis americana* in relation to the role of body carbohydrate as metabolic substrate. Marshall and Orr (1962) summarized the data published until 1962 together with their unpublished data on the respiration of copepods. Seasonal change in the rate of respiration was reported by Marshall and Orr (1958) on *Calanus finmarchicus*, by Conover (1959) on some neritic copepods, by Conover (1962) on *Calanus hyperboreus*, by Cowey and Corner (1963) on *Calanus helgolandicus*, by Raymont *et al.* (1966) on *Neomysis integer*, by Marshall and Orr (1966) on small sized copepods, by Haq (1967) on *Metridia lucens* and *M. longa*, and by Conover and Corner (1968) on some boreal copepods. Berner (1962) and Lasker (1966) examined the rate of respiration of *Temora longicornis* and *Euphausia pacifica* respectively. Halcrow (1963) tested acclimation of the respiration to various temperature in *Calanus finmarchicus*. Effect of crowding of individuals on the respiration was investigated by Zeiss (1963). Anraku (1964) found that the respiration-temperature curve of *Calanus finmarchicus*, *Pseudocalanus minutus*, *Labidocera aestiva*, *Acartia tonsa* and *A. clausi* was closely correlated with the hydrographical conditions in nature in which these species occur. Respiration of *Acartia clausi* was reported by Lance (1965) in relation to the osmotic behaviour of this species. Conover (1960) studied on the relationship between body size (weight) and respiration rate of various boreal zooplankton (copepods, amphipods and euphausiids), finding that there is a high correlation between these two factors. This relationship was further investigated together with the influence of temperature on *Euphausia pacifica* and *Thysanoessa spinifera* by Small *et al.* (1966), and on *E. pacifica* by Small and Hebard (1967) and Paranjape (1967). Pearcy *et al.* (1969) failed to observe a diurnal change of respiration in *E.*

pacifica, but observed the effect of body size on respiration rate in this species. Teal and Carey (1967a) demonstrated high capability of oxygen uptake on *Euphausia mucronata* inhabiting the oxygen minimum layer where the oxygen pressure is below 0.5% atm, in the eastern Pacific Ocean. Mullin and Brooks (1970) compared the respiration rate of *Rhincalanus nasutus* and *Calanus helgolandicus* raised from eggs to adults in the laboratory with those collected from natural sea. Recently Lillelund and Lasker (1971) and Sushkina *et al.* (1971) reported the respiration rate of *Labidocera* spp. and *Neomysis mirabilis* respectively. Except the works of Conover (1960) and Conover and Corner (1968), zooplankters used for experiments above mentioned were those inhabiting boreal or temperate seas and most zooplankton species treated were limited to a few neritic copepods, euphausiids and mysids. Studies of McWhinnie and Marciniak (1964) on the temperature response in oxygen consumption of antarctic krill, *Euphausia superba*, which is an inhabitant of oceanic waters is of great interest in this point.

Rajagopal (1962) found that the respiration rate of a hydromedusa, ctenophores, copepods and a tunicate in the tropical sea was correlated with dry body weight. Respiration of a tropical chaetognath, *Sagitta hispida*, was reported by Reeve (1966) and Reeve *et al.* (1970). Respiration-temperature curve for tropical copepods from different bathymetric levels was reported by Champalbert and Gaudy (1972). In the previous studies of the author (Ikeda, 1970) on a total of 77 species of zooplankton covering almost all important groups of marine zooplankton from boreal, temperate and tropical sea areas it was concluded that respiration rate-body weight relation was a function of habitat temperature.

The effect of hydrostatic pressure on the metabolic rate of deep-sea zooplankton is little known (see general review of Cattell, 1936; Morita, 1967; Schlieper, 1968). Napora (1964) measured the respiration rate and phosphorus excretion of a prawn, *Systellaspis debilis*, under the conditions of various degrees of hydrostatic pressure and temperature. The experiments of Teal and Carey (1967b) on euphausiids demonstrated that the oxygen consumption of animals was not affected by pressure in the normal range of depths of their natural habitats, but affected by varying temperature alone. Similar results were obtained by Pearcy and Small (1968) on *Euphausia pacifica* and *Thysanoessa spinifera*. Recently, Teal (1971) experimented on the respiration of five decapod species and Macdonald *et al.* (1972) on *Gigantocypris mulleri* and *Systellaspis debilis* under the condition of high pressure.

Data on excretion of nitrogenous substances by zooplankton are fewer than those on respiration. It is well documented in the field of comparative biochemistry of animals that end-products of nitrogenous substances in aquatic invertebrates

are largely in the form of ammonia* (Prosser, 1961; Baldwin, 1963). The experiments on *Calanus finmarchicus* and *C. helgolandicus* by Corner *et al.* (1965), Corner and Newell (1967) and Butler *et al.* (1970), and on *Neomysis rayii* and *Euphausia pacifica* by Jawed (1969) verified this point in zooplankton, i.e., more than 70% of total nitrogen excreted by these zooplankters was in the form of ammonia. The first estimation of ammonia excretion of zooplankton was carried out by Harris (1959) on mixed zooplankton specimens (mainly *Acartia clausi*). Change of excretion rate with developmental stages and with seasons was shown for *Calanus finmarchicus* and *C. helgolandicus* by Corner *et al.* (1965), Corner and Newell (1967), Corner *et al.* (1967) and Butler *et al.* (1969, 1970). Conover and Corner (1968) reported seasonal change of nitrogen excretion of several boreal copepods (*Calanus hyperboreus*, *C. finmarchicus*, *Metridia longa*, *Pareuchaeta norvegica* and others). Nitrogen excretion of *Neomysis rayii* and *Euphausia pacifica* was investigated by Jawed (1969). Ammonia excretion of *Neomysis integer* at different salinities of medium water was studied by Raymont *et al.* (1968). For tropical zooplankton species Beers (1964) and Reeve *et al.* (1970) measured nitrogen excretion of a chaetognath, *Sagitta hispida*. Thus, experiments on the nitrogen excretion of zooplankton has been made on quite a limited number of species (Corner and Cowey, 1968; Corner and Davies, 1971).

Studies on chemical composition of zooplankton have been diversified with workers due to different purposes of studies. One analyzed one or several gross organic matter such as protein, lipid and carbohydrate (cf. Ikeda, 1972), while the others analyzed particular components such as amino acids (Corner and Cowey, 1968), fatty acids (Yamada, 1972) and so forth. Analyses were made on mixed specimens of several species in some experiments but on a single species in other experiments. Here, the history of analyses of chemical composition of zooplankton is concerned with only elemental compositions. Earlier works on the elementary composition of zooplankton together with other marine organisms were compiled by Vinogradov (1953). Thereafter, Harris and Riley (1956) reported nitrogen and phosphorus on mixed zooplankton collected from Long Island Sound at different seasons of the year. Curl (1962a, b) investigated carbon, nitrogen and phosphorus in a single species of various zooplankton (Cnidaria, Ctenophora, Mollusca, Arthropoda, Chaetognatha and Tunicata). For tropical zooplankton Beers (1966) made one year measurements on the nitrogen, carbon and phosphorus contents of major zooplankton groups from the Sargasso Sea off Bermuda (copepods, euphausiids-mysids, other Crustacea, chaetognaths, fish and fish larvae,

* Johannes and Webb (1965) and Webb and Johannes (1967) have reported that zooplankton release large amount of dissolved amino acids but their results were not confirmed in the experiments of Corner and Newell (1967) and Jawed (1969). Webb and Johannes (1969) discussed these conflicting results.

polychaetes, siphonophores, hydromedusae, pteropods and salps). Omori (1969) analyzed carbon, nitrogen and hydrogen of 33 zooplankton species collected mainly from boreal sea of the Pacific. The zooplankton species examined by Omori covered a dinoflagellate, pteropods, copepods, amphipods, a mysid, euphausiids, a decapod, a marine insect, chaetognaths and fishes and their larvae. Vinogradov *et al.* (1970) determined carbon and nitrogen on mixed specimens of several species and on single species such as *Calanus cristatus*, *Gennadas borealis*, *Hymenodora frontalis*, *H. glacialis* and *Gnathophausia gigas* sampled from different depths of the northwestern Pacific Ocean.

III. Methods and materials

Sampling: In one series of experiments, sampling was carried out in Oshoro Bay, west coast of Hokkaido (June-July 1970) and on the coast of Usujiri, outside of Volcano Bay, the northeast coast of Kameda Peninsula, southern Hokkaido (May-June 1971). Sampling of other series of experiments was made on board the Kaiyo-Maru of the Fisheries Agency on her cruise to the South Africa (October 1971-March 1972). In addition, sampling of material was also made only for the determination of chemical composition of zooplankton on the Nanae-hama coast, southern Hokkaido (March-April 1971) and off Kitami, northern coast of Hokkaido (September 1970). Locations of sampling the material are illustrated in Fig. 1.

On the seashore stations at Oshoro and Usujiri a specially designed net, 0.35 mm in mesh aperture, 50 cm in mouth diameter, 150 cm in length, conical, with 2 liter polyethylene wide tail bucket at the cod end which enabled us to obtain materials in good condition, was towed from a boat at about 2–4 hours after the sunset. The net was towed gently for 5–10 minutes through 0–10 meter depth. On board the Kaiyo-Maru a similar type of the net was towed for 15 minutes during the slow wind drift of the ship. Sometimes the materials were obtained from the samples taken by towing a fish larva net. Large agile zooplankton such as amphipods, stomatopod larvae etc. were collected by this method. The larva net, 130 cm in diameter, made of stramin in major portions and 0.33 mm mesh cloth near the cod end, was towed at 1–1.5 hours after the sunset. For collecting deep-sea zooplankton MTD vertical closing net and sometimes MTD horizontal closing net (Motoda, 1969) were used.

Respiration and ammonia excretion: In the land experiments, zooplankton collected was diluted in large polyethylene buckets filled with raw sea water on the boat, transported to the land laboratory and then sorted according to species in one liter glass bottles filled with raw sea water dipped up from the sea at the same time of the net towing. The sorting of animals to a single species was made with various pore size pipettes. Sometimes, a binocular microscope was used for the sorting of small animals. The time required from the sampling to the comple-

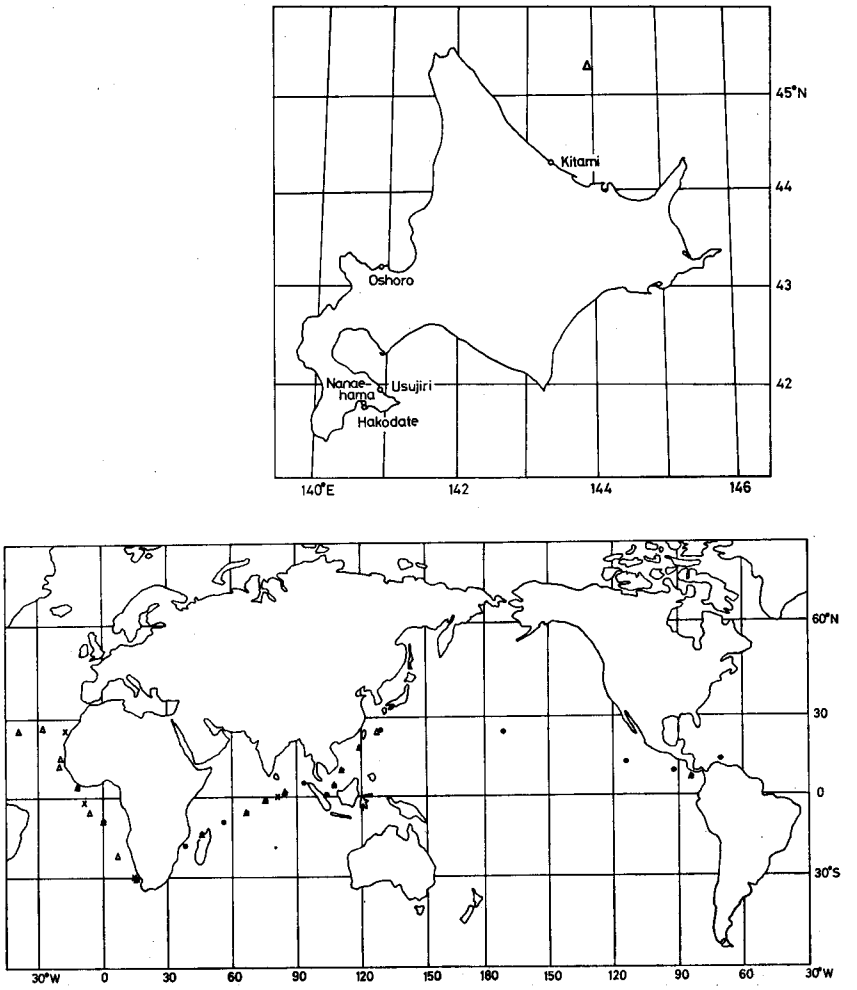

Fig. 1. Map showing locations where zooplankton were collected.
Upper map: locations of Oshoro Bay, Usujiri, Nanae-hama coast and a station at off Kitami (open triangle).
Lower map: stations covering during the cruise of the Kaiyo-Maru. Stations of zooplankton sampling for the measurements of respiration and ammonia excretion are shown in solid circle, and for chemical composition in open triangle. Stations of deep-sea zooplankton sampling with MTD vertical closing net is shown as a cross.

tion of sorting was not longer than 1.5 hour. In experiments on board, collected samples were sorted immediately in the laboratory of the ship within one hour after the sampling. Then, one liter glass bottles with sorted animals were dipped in a water bath for about one day. The temperature of the water bath was kept close to natural temperature for animals by pumping sea water in the land laboratory and by using a thermoregulator on board.

Concurrent with the above procedure, the surface sea water dipped up from the same place as the net sampling was filtered through glass fiber filter (Whatman) and aerated thoroughly at the natural temperature. The water was used as "conditioning water" described below.

After the maintenance of animals for about one day in a raw sea water after sampling, one to several animals of the same size and the same species were transferred into 250 or 300 ml BOD bottles or into one liter well stoppered glass bottle filled with conditioning water. Bottle size was determined for convenience by the animal size and water temperature during the incubation of animals. As a special case, at Oshoro Bay, a 100 ml oxygen bottle was used for the determination of the respiration of extremely small forms only. Then, a rubber stopper with an outlet tube and an inlet tube, the former covered with fine mesh net to prevent escape of animals and the latter connected to a large reservoir of conditioning water, was fitted firmly at the mouth of the bottle. Conditioning water was flowed gently through the bottle containing animals 6–7 times of the bottle volume to replace its content with conditioning water. Typical series experiments with 250 ml BOD bottles, usually 8–9 bottles were successively prepared in this way, making the first and the last bottles as control without animals. Each bottle was wrapped with an alminium foil as soon as the replacement of conditioning water had been completed and immersed into the water bath again. The time for preparation of one series of bottles was about one hour. The time of incubation varied with animal size and water temperature, but roughly 12–24 hours in the land experiments and 4–10 hours for the on board experiments. Thus, the water temperature experienced by animals was the same throughout the sampling to the end of the experiments.

At the end of incubation, the conditioning water in each bottle was siphoned to a 100 ml oxygen bottle for the determination of dissolved oxygen, and then, 50 ml aliquot of sample water was pipetted out in two Erlenmyer flasks for the determination of ammonia. When dead animals were observed at the end of the incubation period, the results were abandoned. Some faecal pellets produced during the incubation were removed by means of a pipette. But, in most of all experiments no production of faecal pellet was observed. The animals remaining with a small volume of conditioning water were picked up with a dessecting needle on blotting paper and the excess of sea water adhering on the animal's body was removed. The animals were transferred into an air-tight plastic pot, the bottom being covered with a glass fiber filter or lining with an aluminium foil for jelly forms. The pots were preserved in a desiccator in a deep freezer for a later measurement of body weight of the animals on land.

Dissolved oxygen was analyzed following the Winkler method described by Strickland and Parsons (1965) with a slight modification for the small water sample

volume. The standard deviation of 11 replicates was 0.030 ml/l on the air-saturated sea water at 20°C (4.917 ml/l). Analysis of ammonia was completed within 3 hours after the end of incubation on board and at the land laboratory by the phenolhypochlorite method of Solórzano (1969) with a standard deviation of 0.43 μg-at N/l on 8 replicates at a concentration of 6.00 μg-at NH_3-N/l.

The rates of respiration and ammonia excretion were calculated from the difference of the concentration between the experimental and the control bottles. Since the respiration rate may be affected with a partial pressure of oxygen in the medium water as it is known in other marine animals (Zeuthen, 1955; Nicol, 1960; Wolvekamp and Waterman, 1960; Prosser, 1961; Kinne, 1970), the oxygen concentration of the experimental bottles at the end of incubation was kept at not less than 80% saturation.

Metabolic rate was classfied according to the activity of the animals during the measurements, as a basal, standard and activity metabolism (Prosser, 1961). According to Prosser's difinition, the rates measured in the present studies fall between standard and activity metabolism.

Respiration of deep-sea zooplankton under high pressure condition: On board the Kaiyo-Maru deep-sea zooplankton was collected from 2000 m to 1500 m by vertical tow of MTD vertical closing double net (Motoda, 1969) with a modified cod-end to prevent water passing through it while towing at undesired depths. Samplings were carried out at 30°37.1'S 15°08.5'E (Nov. 23, 1971) and 26°30.0'N 17°00.4' W (Jan. 8, 1972). Time required for one haul was about 1 hour. As soon as the net came up on deck, the animals in the cod-end were transferred to a glass container filled with sea water of similar temperature to that of their habitats (ca. 3–4°C). The collection of sea water from 2000–1500 m depths being unable to be carried out in the present case, surface sea water was used for the measurements of respiration, though the surface sea water was slightly higher in salinity than at 2000–1500 m depths. Animals were kept at 3–4°C in a water bath. During the period of rearing, *Artemia* nauplii were tried as food, however these nauplii were found to be unsuitable food for zooplankton. For the experiment under the condition of high pressure, a TSK pressurized deep-sea bacteria cultivator was employed. Two 100 ml oxygen bottles, one with animals and the other as control without animals, were placed into a cultivating tank made of stainless steel and filled with conditioning water. Adjustment of concentration of dissolved oxygen to that *in situ* for deep-sea zooplankton was difficult so that air-saturated sea water described above was used as conditioning water. The preparation of experimental and control bottles for the experiment was quite the same as the above mentioned. Two 100 ml of oxygen bottles were fitted with a rubber stopper through which pressure relief during the stoppering procedure was provided by means of an injection syringe. After being pressurized to 200 atm (atmosphere)

the incubator was replaced into the water bath at 3–4°C and was kept in that condition for 1 or 3 days for small animals. To increase the pressure to 200 atm, a few minutes were needed and the pressure was released rapidly to one atm at the end of incubation. Then, the water in each bottle was siphoned into 50 ml oxygen bottle for the determination of dissolved oxygen. Animals remaining in the bottle with a small volume of water was subjected to experiment under normal pressure (1 atm) again. Thus, the experiment under high and normal pressure was repeated in turn for the same individuals till the animals became lifeless. Accordingly, experimental animals were compelled to a starving condition throughout the successive experiment.

Chemical composition: Zooplankton collected were sorted into a single species as early as possible by means of a dessecting needle or pipette and was transferred into a blotting paper to remove water adhering on the body surface of the animals. The microscopic observation confirmed that almost all water adhering on the body surface was removed by this procedure. Then, the animals were replaced in the air-tight plastic pots covered at the bottom with a glass fiber filter or lining with an aluminium foil for jelly-forms. The pots were preserved in a desiccator (desiccant: silica gel) placed in a deep freezer. Prior to the analysis samples were desiccated at the room temperature till the constant weight was obtained. The total amounts of nitrogen, carbon and hydrogen were determined with the Hitachi 026 CHN analyzer at the land laboratory. The capacity of the analyzer was 500–1500 μg of dry material so that for animals weighing less than 500 μg several individuals were combusted together and for those weighing more than 1500 μg an aliquot of ground animal combusted for a single determination. Seven replications of determination of each element for a pteropod, *Hydromyles globulosa*, gave 0.1, 0.2 and 0.1 for a standard deviation of per cent nitrogen, per cent carbon and per cent hydrogen of dry weight, respectively. For fatty animals, the standard deviation of each element was slightly larger than this.

IV. Respiration and ammonia excretion

The rates of respiration and ammonia excretion are very variable with some factors. For example, Fig. 2 shows the variation of both rates in *Neocalanus gracilis*, *Euphausia krohnii* and *Phronima sedentaria* held under laboratory conditions. Both respiration and ammonia excretion rates decreased with the progress of maintenance periods. At the end of four days maintenance, the rates were about one half for *N. gracilis* and *E. krohnii* to one fourth for *P. sedentaria* of the first day's figures, though the patterns of decrease differed with species. High respiration rate measured just after the sampling of animals has been reported by some workers for zooplankton (Marshall *et al.*, 1935; Conover, 1956; Berner, 1962;

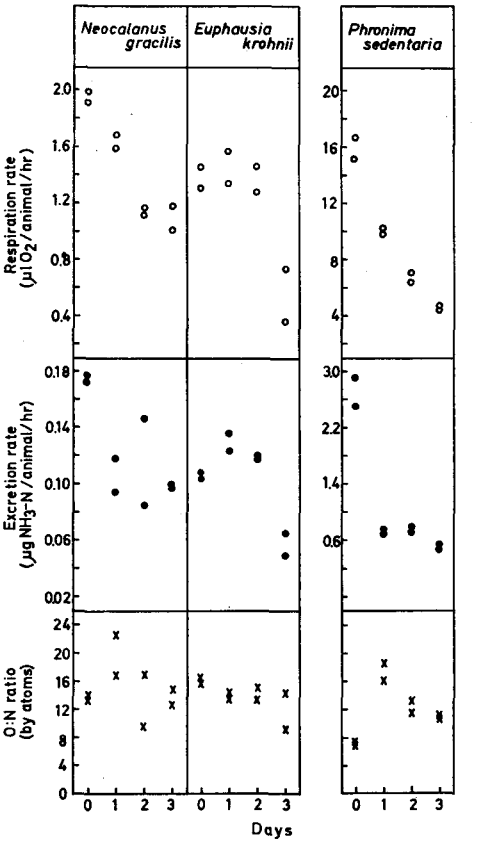

Fig. 2. Changes in the rates of respiration and ammonia excretion and the O:N ratio of zooplankton during the maintenance in the laboratory after sampling. Animals were collected at 13°48.7′S 00°55.9′E on Nov. 27, 1971. Experiments were conducted at 19.7°C. Experimental animals were different individuals of the same catch for *Neocalanus gracilis* and *Euphausia krohnii*, and were the same two individuals for *Phronima sedentaria*.

Ikeda, 1970). The O:N ratio varied irregularly owing to the difference in the changing patterns of respiration and ammonia excretion (Fig. 2). At present status, it is difficult to conclude whether the initial higher figures represented more realistic rates of zooplankton in the natural sea or whether the later lower figures were normal rates. In a comparative sense, one way to overcome this difficulty is to conduct experiments under standard conditions. In the present experiments, as a standard condition, zooplankton species spending one day after their capture, at a water temperature close to their natural conditions, was taken for measurement.

Data obtained in the present studies are summarized in the Appendix, and are arbitrary devided into four classes according to the habitat temperature of zooplankton.

Tropical species (25.7–28.5°C); data obtained in the Kaiyo-Maru cruise
Subtropical species (17.3–22.5°C); data obtained in the Kaiyo-Maru cruise
Temperate water species (11.7–17.5°C); data obtained at Oshoro Bay
Boreal species (4.5–14.3°C); data obtained at Usujiri

A total of 112 species including 50 species for tropical, 13 species for subtropical, 26 species for temperate and 27 species for boreal species were subjected to respiration measurement (Table 1), and 81 species including 46 species for tropical, 13 species for subtropical, 7 species for temperate and 19 species for boreal species for ammonia excretion measurement (Table 2). These animals used for the present

Table 1. *Groups and number of species of boreal, temperate, subtropical and tropical zooplankton for which respiration rate was measured.*

Groups	Boreal	Temperate	Subtropical	Tropical
Coelenterata	1	3	0	5
Ctenophora	2	0	0	0
Heteropoda	0	0	1	1
Pteropoda	2	1	3	2
Gastropoda	0	1*	0	0
Polychaeta	0	1*	1	1
Ostracoda	1	0	0	0
Copepoda	7	10	2	12
Mysidacea	2	1	0	1
Cumacea	2	1	0	0
Amphipoda	3	1	2	5
Euphausiacea	3*	0	1	4*
Decapoda	2*	2*	0	6*
Stomatopoda	0	0	0	2*
Chaetognatha	1	1	0	4
Tunicata	0	1	2	4
Pisces	1	3	1	3
Total	27	26	13	50

* Including larvae unidentified

Table 2. *Groups and number of species of boreal, temperate, subtropical and tropical zooplankton for which ammonia excretion rate was measured.*

Groups	Boreal	Temperate	Subtropical	Tropical
Coelenterata	1	1	0	3
Heteropoda	0	0	1	1
Pteropoda	2	0	3	2
Polychaeta	0	0	1	1
Copepoda	7	2	2	12
Mysidacea	1	1	0	1
Cumacea	1	1	0	0
Amphipoda	1	0	2	5
Euphausiacea	3*	0	1	4*
Decapoda	2*	0	0	4*
Stomatopoda	0	0	0	2*
Chaetognatha	1	1	0	4
Tunicata	0	0	2	4
Pisces	0	1	1	3
Total	19	7	13	46

* Including larvae unidentified

experiments cover most of the major groups of zooplankton in the seas.

1. *Respiration*

It is well documented that the metabolic rate (respiration rate) of organisms is the power function of body weight (cf. Prosser, 1961). Mathematically this relationship is expressed as follows;

$$R = aW^b \quad (1),$$

where R is total respiration rate (μl O_2/animal/hr), W is body dry weight (mg/animal), b is an exponential constant and a is a constant of proportionality. In terms of logarithmic form, equation (1) is rewritten as;

$$\log R = b \cdot \log W + \log a \quad (2).$$

Similarly, the weight specific respiration rate (R/W: μl O_2/mg dry weight/hr) is derived from equation (1) by deviding through W as follows;

$$\log (R/W) = (b-1) \log W + \log a \quad (3).$$

The regression equation and the correlation coefficient between total respiration rate and body weight of zooplankton from tropical, subtropical, temperate and boreal waters were calculated and the results are given in Table 3. Prior to the calculation data of three tropical fish larvae collected with fish larva net were excluded, for they were very agile and unusual plankton for the present experiment. The correlation coefficients varied from 0.959 for boreal species to 0.886 for tropical species, but were highly significant in all four groups ($P<0.001$). Fig. 3 shows a scatter diagram of weight specific respiration rate and body weight for each group with regression lines, which were calculated from Table 3 in equation (3). The fact that weight specific respiration rate decreases with increase in body weight and with decrease in habitat temperature is well illustrated in Fig. 3.

In the Table 3 remainder terms (log a in equation (2)) increased with habitat

Table 3. *Regression statistics of log total respiration rate (R: μl O_2/animal/hr) on log body dry weight (W: mg/animal) in zooplankton.*

Zoo-plankton	Temperature	n	Equation of regression line $\log R = b \log W + \log a$	r	$S_{y \cdot x}$	S_b
Boreal species	8.6°C(4.5−14.3)	78	$\log R = 0.783 \log W + 0.057$	0.959**	0.233	0.026
Temperate species	15.0°C(11.7−17.5)	64	$\log R = 0.756 \log W + 0.127$	0.955**	0.259	0.029
Subtropical species	20.2°C(17.3−22.5)	21	$\log R = 0.664 \log W + 0.321$	0.915**	0.268	0.066
Tropical species	26.8°C(25.7−28.5)	98	$\log R = 0.595 \log W + 0.481$	0.886**	0.265	0.031

** Significant at 0.1% level.

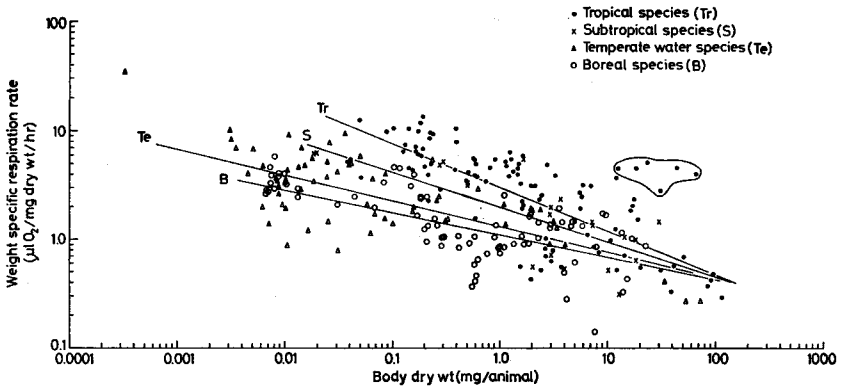

Fig. 3. Relationship between weight specific respiration rate and body dry weight for tropical, subtropical, temperate and boreal zooplankton. Points encircled are data from tropical fish larvae collected with fish larva net.

temperature and was accompanied by a decrease in the inclination of the regression line (b in equation (2)). Statistical test showed that the difference of the inclination of each regression line was highly significant (Variance ratio $F=7.89>F_{0.01}$ [3, 253]=2.64). The same results were also obtained in the previous studies (Ikeda, 1970). To examine these relationships between log a and b and habitat temperature (T) the former two were plotted against the latter, and then by fitting the data to a straight line by the method of least squares the regression equations and the correlation coefficients were calculated as seen in Fig. 4. From the fact that high correlation was resulted, the respiration rate of zooplankton (R: μl O_2/animal/hr) will be predictable if its habitat temperature (T: °C) and its body weight (W: mg dry weight/animal) are known, from the log a-T and b-T relations, and equation (2) as;

$$\log R = (-0.01089T+0.8918)\log W+(0.02438T-0.1838)^{*} \qquad (4).$$

The possible cause of the difference in the inclination (b) of regression lines among tropical, subtropical, temperate and boreal species cannot be attributed to the difference in habitat temperature of animals only, because the species and their size distributions of a particular animal group are not the same in the four zooplankton groups. For instance, experiments were conducted on copepods

* Errors in the estimation of b and log a from T are calculated from following equation;

$$4.303S_{y.x}\sqrt{1.25+(17.65-T)^2/179.15}\ (95\%\ \text{confidence limits})$$

where, $S_{y.x}=0.02317$ in b-T relation and
$S_{y.x}=0.04618$ in log a-T relation.
To estimate total errors for the calculation of R from equation (4) errors in R-W relations in Table 3 must be combined with the above. But the combined total errors are difficult to calculate for the present author, so that the latter source of error was neglected in the calculation of R from equation (4) in the following chapter (V and IX).

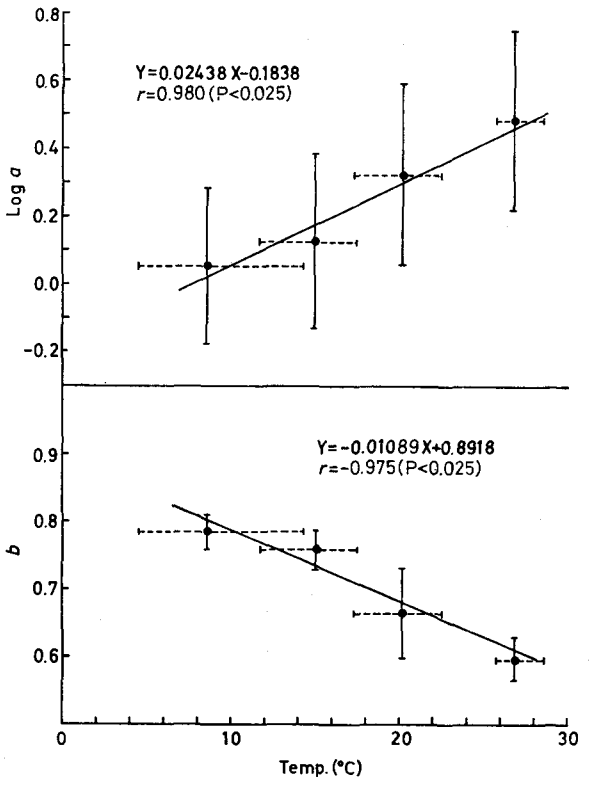

Fig. 4. Relationships between log a and habitat temperature (upper) and between b and habitat temperature (lower) in respiration-body weight relationship. Vertical lines (solid) represent standard deviations and horizontal lines (dotted) ranges of temperature.

weighing from 2.27 mg to 0.0068 mg in boreal waters but the range of weight for tropical copepods used in these experiments was 0.818 mg to 0.0381 mg with no species common to in both habitats. According to Bertalanffy (1951) the relation between metabolism and body weight of various animal groups is classfied into three types, i.e., surface proportional (b=2/3), weight proportional (b=1) and intermediate between the two (b=2/3–1). He also found that the relation is, however, variable with physiological and experimental conditions of animals within a single species (Bertalanffy, 1964). Therefore, the present results of the systematic change in figure b with habitat temperature should be regarded as a general characteristic of zooplankton community from each habitat.

The Q_{10} of respiration was calculated from the relationship between respiration rate and body weight of zooplankton with different habitat temperatures shown in Table 3 and average Q_{10} from equation (4), on the animals weighing 0.1 mg, 1.0 mg and 10 mg as a representative of animal weight (Table 4). The result indicated

Table 4. *The Q_{10} for respiration rate calculated from the differences in the relationship between respiration rate and body weight in zooplankton taken from different habitats (Tabel 3), and average Q_{10} from equation (4) in parenthesis.*

	Body dry weight (mg/animal)		
	0.1	1.0	10
Boreal species (8.6°C)–Temperate species (15.0°C)	1.4(2.3)	1.3(1.8)	1.2(1.4)
Temperate species (15.0°C)–Subtropical species (20.2°C)	3.5(2.3)	2.4(1.8)	1.6(1.4)
Subtropical species (20.2°C)–Tropical species (26.8°C)	2.2(2.3)	1.7(1.8)	1.4(1.4)

that the effect of temperature on the zooplankton respiration was larger for the smaller forms than for the larger. Rao and Bullock (1954) discussed the possible effect of animal's body size and its habitat temperature on the Q_{10} value of metabolic rate or other rate functions of animals. Their discussion concerned the Q_{10} value with not adapted but with acclimated animals. So that situation was too different from the present results to make any comparison. Scholander *et al.* (1953) studied metabolic response of aquatic and terrestrial animals, from tropical (30°C) and arctic (0°C), to graded temperature. According to them the respiration rates of tropical aquatic crustaceans and fishes at their natural habitat temperatures were as high as 4 to 6 times for their arctic aquatic counterparts. The Q_{10} value of respiration was thus calculated as 1.6–1.8, and the value did not change with body size of animals, differing from the present studies on zooplankton. Wohlschlag (1964) summarizing data on metabolism and habitat temperature on fishes living from tropical to antarctic and arctic seas, proposed an empirical equation for the fish of the order of 5 g as $\log R=1.75+0.02T$, where R was mg O_2/Kg/hr and T was habitat temperature in °C. From this the Q_{10} for respiration was easily counted as 1.6. In the present studies the range of habitat temperature was narrower than those of Scholander *et al.* (1953) (average; 8.6–26.8°C). The average of Q_{10} value calculated for animals weighing 0.1 mg–10 mg based on the data of two extreme habitat temperatures of boreal and tropical was 1.4–2.3, which covered the range mentioned by Scholander *et al.* (1953) and of Wohlschlag (1964).

Here, the difference in the level of respiration originating from specific differences is briefly discussed. More active animal groups such as Euphausiacea, Amphipoda and fish larvae respire at a slightly higher rate than the other zooplankton groups with the same size, while jelly-forms such as Coelenterata, Ctenophora and Tunicata and some benthos larvae are a group with a lower respiration rate. Conover (1960) and Conover and Corner (1968) reported that the respiration rate of carnivorous zooplankton species was higher than that of herbivorous species.

Such a difference in the rate between herbivores and carnivores was not observed in the present and in the previous studies (Ikeda, 1970). For instance, the respiration rate of typical carnivorous animals of Ctenophora and Coelenterata was lower than that of other plankton animals with the same size as mentioned above. The reversed fact was also found in largely herbivorous forms of *Euphausia pacifica*. This different result observed by Conover (1960) and Conover and Corner (1968) might be caused from the experiments in which they were concerned with only crustaceans in contrast with taxonomically wide variety of animals as in the present case. It is noted that animals with higher respiratory rate had a highly developed respiratory gill organ.

Among the few studies on the relationship between respiration rate and body weight in zooplankton, the results of Conover (1960) and Rajagopal (1962) are comparable to a great extent with the present results on boreal and tropical species respectively. Their experiments dealt with a variety of animal groups as well as body size range. Conover's results (1960) were almost the same as those of boreal species in the present studies. The results of Rajagopal (1962) showed a slightly higher value than those of tropical species in the present studies, even when the difference in experimental temperature and in body size were taken into consideration. This was especially true for smaller sized animals. In comparison with the previous studies by the present author (Ikeda, 1970), b-T relation shown in Fig. 4 were almost the same. However, log a-T relation obtained in the previous studies was slightly different compared with the relation in the present studies, i.e., increase in log a with a raise in T was larger in the former study than in the present study. In the previous experiments, the dry body weight of animals was determined on specimens preserved in 10% formalin-sea water. This different condition might cause the different results as mentioned above, because most substances of body which are lost during the preservation of animals in formalin solution are nitrogen rich ones, i.e., protein (Fudge, 1968; Hopkins, 1968) and the proportion of protein in the total body substances increased with habitat temperature. Hence, the effect of formalin preservation is larger in tropical species than in boreal species which stored higher level of fat.

2. *Ammonia excretion*

The relation between the rate of ammonia-nitrogen excretion and body weight of tropical, subtropical, temperate and boreal species was obtained by using the same procedure as for respiration. The results are given in Table 5. Data on three tropical fish larvae were omitted from those of tropical species for the same reason as mentioned in the experiments on respiration. The correlation coefficient was highly significant in all zooplankton groups ($P<0.001$). The remainder terms (log a in equation (2)) increased with habitat temperature. While the inclination

Table 5. *Regression statistics of log total ammonia-nitrogen excretion rate (E: μg NH_3-N/animal/hr) on log body dry weight (W: mg/animal) in zooplankton.*

Zoo-plankton	Temperature	n	Equation of regression line $\log E = b \log W + \log a$	r	$S_{y \cdot x}$	S_b
Boreal species	8.2°C(4.5−14.3)	53	$\log E = 0.790 \log W - 1.198$	0.932**	0.321	0.043
Temperate species	15.0°C(13.8−16.0)	19	$\log E = 0.635 \log W - 0.857$	0.964**	0.225	0.042
Subtropical species	20.2°C(17.3−22.5)	21	$\log E = 0.654 \log W - 0.767$	0.921**	0.255	0.063
Tropical species	27.3°C(25.7−28.5)	94	$\log E = 0.591 \log W - 0.639$	0.843**	0.320	0.039

** Significant at 0.1% level.

(b in equation (2)) tended to decrease with the increase of habitat temperature, the difference of the inclination of each regression line was statistically highly significant (variance ratio $F = 4.47 > F_{0.01}$ [3, 179]$= 3.90$). Accordingly, the effect of habitat temperature on the relationship between the rate of ammonia-nitrogen excretion and body weight was quite the same as in the case of respiration. Regression equations of weight specific rate of ammonia-nitrogen excretion versus body weight was calculated from Table 5 and were given in the scatter diagram of Fig. 5. Weight specific excretion rate of ammonia-nitrogen increased with the decrease in body weight and increase of habitat temperature. In the section of respiration it is described that Euphausiacea, Amphipoda and fish larvae belonged to a higher rate group, and Coelenterata, Ctenophora, Tunicata and some benthos

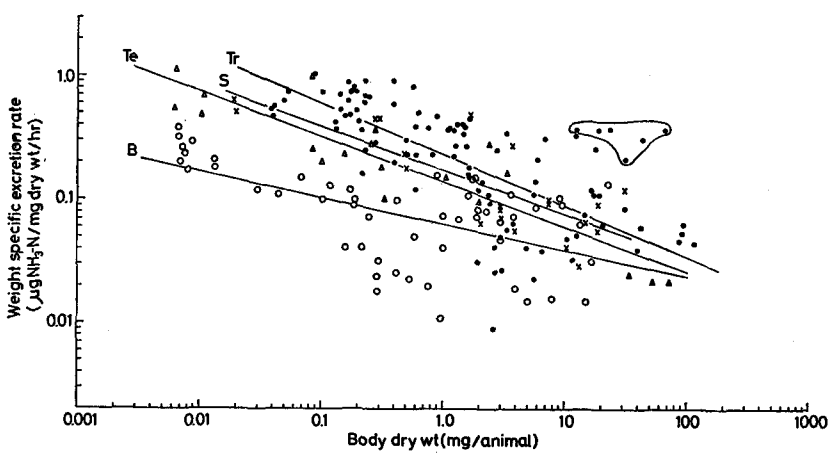

Fig. 5. Relationship between weight specific excretion rate of ammonia-nitrogen and body dry weight for tropical, subtropical, temperate and boreal zooplankton. Points encircled are data for tropical fish larvae collected with fish larva net. Symbols as in Fig. 3.

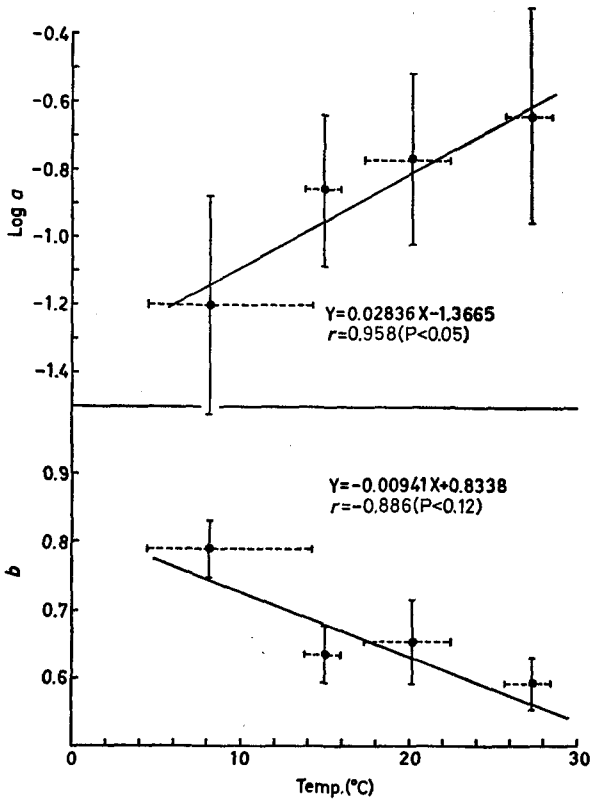

Fig. 6. Relationships between log a and habitat temperature (upper) and between b and habitat temperature (lower) in ammonia excretion-body weight relationship. Vertical lines (solid) represent standard deviations and horizontal lines (dotted) ranges of temperature.

larvae were of a lower rate group compared with those of average zooplankton. The same tendency was also observed in ammonia excretion. Among the lower rate group, those of decapod megalopa larvae of tropical species were conspicuous.

Then, b and log a in the Table 5 were plotted against habitat temperature (T°C), and regression equations and correlation coefficients were calculated by fitting the data to a straight line by the least square method (Fig. 6). In the relation of b-T, b the temperate species deviated rather largely from the regression line, resulting in a correlation coefficient of 0.886 lower than 0.975 for b-T relation in the respiration. The correlation coefficient of log a-T relation for ammonia-nitrogen excretion (0.958) was somewhat lower than that of respiration (0.980). However, these differences are not significant statistically ($P>0.5$), owing to the small amount of data.

Accordingly, the excretion rate of ammonia-nitrogen for average zooplankton (E: μg NH_3-N/animal/hr) was estimated by knowing its individual body weight

Table 6. *The Q_{10} for ammonia-nitrogen excretion rate calculated from the differences in the relationship between ammonia-nitrogen excretion rate and body weight in zooplankton from different habitats (Table 5), and average Q_{10} from equation (5) in parenthesis.*

	Body dry weight (mg/animal)		
	0.1	1.0	10
Boreal species (8.2°C)–Temperate species (15.0°C)	5.4(2.4)	3.2(1.9)	1.9(1.6)
Temperate species (15.0°C)–Subtropical species (20.2°C)	1.4(2.4)	1.5(1.9)	1.6(1.6)
Subtropical species (20.2°C)–Tropical species (27.3°C)	1.9(2.4)	1.5(1.9)	1.2(1.6)

(W: mg dry weight/animal) and its habitat temperature (T: °C) from the following equation;

$$\log E=(-0.00941T+0.8338)\log W+(0.02836T-1.3665)^{*} \qquad (5).$$

Table 6 gives the Q_{10} for ammonia-nitrogen excretion rate of animals weighing 0.1 mg, 1.0 mg and 10 mg dry weight calculated from Table 5, and average Q_{10} of the rate from equation (5). Apparently, the Q_{10} value increased with a decrease in the body weight of animals. In comparison to the average Q_{10} value of respiration from equation (4) the value of ammonia-nitrogen excretion from equation (5) was higher, indicating larger effect of temperature on the excretion rate than the respiration rate.

The results of nitrogen excretion in zooplankton by other authors were compared with the present results, taking into consideration such differences as experimental temperature and body size of experimental animals. Harris's figure (1956) for the average excretion rate of nitrogen of mixed populations of zooplankton (mainly *Acartia clausi*) was 1.5 μg N/mg dry wt/hr at 4.5–18.5°C. The mean of body weight per individual was calculated as 4 μg. In the present experiment, the rate of the same species weighing 6–11 μg/animal at 14–16°C was 0.5–1.1 μg N/mg dry wt/hr, which was roughly comparable to the figure of Harris. Here, one should keep in mind that there are many sources of error in the experiments on smaller forms under a crowded condition. The loss and death of animals by handling and cannibalism during the incubation period are common phenomena and are especially serious in the experiment on mixed species by Harris. Moreover, Harris used unfiltered natural sea water as conditioning water which contained some food materials for animals in his experiment. Feeding of zooplankton

* Errors in the estimation of b and log a from T are calculated from following equation;
$4.303S_{y\cdot x}\sqrt{1.25+(17.675-T)^2/195.9475}$ (95% confidence limits)
where, $S_{y\cdot x}=0.04868$ in b-T relation and
$S_{y\cdot x}=0.08386$ in log a-T relation. See foot note on page 14.

accelerated the rate of excretion (Corner *et al.*, 1965; Butler *et al.*, 1970). Conversely, ammonia thus excreted in the water was utilized simultaneously by plant populations in it. For such a complex balance of positive and negative effects on the nitrogen excretion measurements of animals, some corrections should be made. For *C. finmarchicus* and *C. helgolandicus* rates of ammonia excretion by some investigators (Corner *et al.*, 1965; Corner and Newell, 1967; Corner *et al.*, 1967; Butler *et al.*, 1969) fall in the range of the present result, though Butler *et al.* (1970)'s figures were slightly lower. The results of some boreal zooplankton presented by Conover and Corner (1968) agreed fairly well with the present results. Similar results were also obtained by Jawed (1969) on *Neomysis rayii* and *Euphausia pacifica*, and Beers (1964) and Reeve *et al.* (1970) also on *Sagitta hispida*.

3. *O:N ratio*

When pure protein (16% nitrogen and 1.04 *l* O_2 needed for complete combustion of 1 g) is burned only in the body of animals and nitrogenous end-product is entirely in the form of ammonia, the ratio of oxygen respired and ammonia-nitrogen excreted is approximately 8 by atoms, and the ratio close to 24 when the equivalent amount of protein and lipid (2.02 *l* O_2 is demanded for complete combustion of 1 g) is burned simultaneously. Thus, the O:N ratio is a good index to deduce the metabolite in the animal body under starvation conditions. When the ratio is higher than 24, a major metabolite is fat quantitatively and when it is lower than 24, protein becomes a major metabolite. Carbohydrate is not considered here, because its relative amount in zooplankton body is too small to serve for a major metabolite under starved condition (Raymont and Krishnaswamy, 1960; Raymont and Conover, 1961; Ikeda, 1971a, 1972).

From Tables 3 and 5 the regression coefficients of the rates of respiration and of ammonia excretion and the body weight were nearly the same in tropical, subtropical and boreal species (temperate water species were an exception). This indicates that the O:N ratio is not related to body size.

The relative frequency of the ratio was represented in each zooplankton group (Fig. 7). It is apparent from Fig. 7 that the O:N ratio of tropical, subtropical and temperate species tend to concentrate into low figures. While that of boreal species exist widely at 7 to 93. In some cases, ammonia excretion was not detected in some boreal species so that the O:N ratio was infinitive. These infinitive ratios were neglected in the calculation of relative frequency showed in Fig. 7. In tropical species, the O:N ratio of decapod megalopa larvae was more than 100. This seems to be an exceptional case. For tropical, subtropical and temperate species, the majority of the O:N ratio was lower than 24, suggesting that the major metabolite was protein. For boreal species, nearly half of the ratios obtained were larger than 24, indicating that the major metabolite of these boreal species was

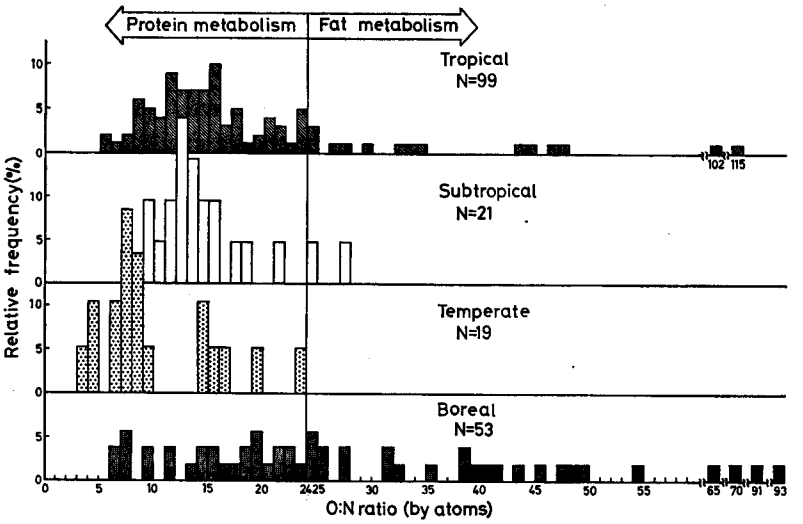

Fig. 7. Relative frequency (%) of the O:N ratio by atoms, calculated from respiration and ammonia-nitrogen excretion, for tropical, subtropical, temperate and boreal zooplankton.

fat. In some animals, the O:N ratio was lower than 8, which was the lowest figure calculated theoretically on pure protein. In addition to experimental errors, the deviation of each elementary composition of body protein from that of pure protein caused these different results. For instance, Raymont *et al.* (1968) estimated 13.3% nitrogen, instead of 16%, for body protein of *Neomysis integer* from amino acid composition in the body.

Harris (1959) reported the ratio of 7.7 for a mixed populations, composed mainly of *Acartia clausi*. The figure was comparable to that of the same species in the present studies. Corner *et al.* (1965) showed that the ratio was 9.8–15.5 on *C. helgolandicus*. Conover and Corner (1968) revealed that the O:N ratio changed with seasons in a given species. For example, the ratio of *C. hyperboreus* was the highest at the period of vernal blooming of phytoplankton, and decreased toward the minimum level in winter and early spring the next year. The O:N ratio obtained in the present studies was concerned only in a certain season, but such a wide variability of the ratio of boreal species seemed to be a charactor for boreal species. In their statistical analysis Conover and Corner (1968) indicated that herbivorous species showed a higher ratio than that of carnivorous species. The same tendency was also seen in boreal species in the present studies, and the ratio of herbivores was more variable from lower value to higher one according to the difference of nutritional conditions as compared with carnivores. This phenomenon was not clearly seen in tropical species. According to Reeve *et al.* (1970), the O:N

ratio for *Sagitta hispida* was 6.8. This value was low compared with those of tropical chaetognaths in the present studies.

It is well known that the average plankton material in the sea has the ratios of C:N:P=106:16:1 (Redfield *et al.*, 1963). Richards (1965) constructed a model of an average organic matter in the sea using these ratios. The empirical formula and its biological oxidation are as follows;

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4+106O_2=106CO_2+16NH_3+H_3PO_4+106H_2O$$
$$16NH_3+32O_2=16HNO_3+16H_2O$$

hence,

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4+138O_2=106CO_2+122H_2O+16HNO_3+H_3PO_4.$$

It was noted that the end-product of nitrogenous substances in zooplankton was not nitrate, but ammonia. Thereupon, the O:N ratio was calculated as $106\times2/16=13$. The present results deversified too much with species and with habitats to justify this value, whereas in the sense of generosity this figure falls in the center of ranges of tropical and subtropical species.

The present author's conclusion are as follows: the O:N ratio changes not with the body size of zooplankton but with the habitat temperature. A ratio lower than 24 observed in the majority of temperate, subtropical and tropical species suggests that protein occupies the major metabolite during the starvation period in these species. While a ratio higher than 24 observed in some boreal herbivorous species means that fat is an important metabolic substrate. In the other boreal species including both herbivores and carnivores a ratio lower than 24 is found. Thus, herbivorous species in the boreal seas have a wide variety of the O:N ratio, possibly on account of their nutritional conditions. The difference of the O:N ratio related to food habits of animals is not distinct in temperate, subtropical and tropical species.

V. Effect of hydrostatic pressure on the respiration of zooplankton

Most of the results of respiration hitherto obtained were those of the epipelagic zooplankton. The effect of pressure on the metabolism of marine animals including zooplankton is little known. Napora (1964) worked on the pelagic decapod, *Systellaspis debilis*, which was characterized by an extensive diurnal vertical migration, and he showed that the increase of pressure accelerate the metabolism of the animal just enough to offset the effect of temperature decrease, so that the level of metabolism of animals remained constant at various depths in the ocean. Recently, Teal (1971) obtained similar result on five species of decapod. Similar types of experiments were followed by Teal and Carey (1967b) and Pearcy and Small (1968) on some euphausiids and decapods. They concluded that the respiration was determined largely not by pressure but by temperature alone in the normal

range of depths in the seas.

There exist some evidences suggesting that temperature has a more important factor than hydrostatic pressure to limit the distribution of zooplankton. The present author has experienced commonly that the maintenance of bathypelagic zooplankton is not so difficult by adjusting only temperature of culture to *in situ* temperature apart from hydrostatic pressure. On board the Kaiyo-Maru, for instance, bathypelagic zooplankton survived from several weeks to more than 3 months, the end of her cruise, by adjusting the temperature only. Such survivors of the zooplankton species were *Metridia princeps, Chirundina streetsi, Pareuchaeta* sp., *Desseta palumboi, Euchirella bitumida, E. pulchra* etc. This fact indicated that bathypelagic zooplankton can tolerate the decrease of a hydrostatic pressure. *Artemia* nauplii were given as food during the period of maintenance, but they did not take that food as already mentioned. Sometimes, faecal pellets of the animals on the bottom of the rearing bottles were observed suggesting an occurrence of cannibalism or necrophagy. For shallow water species, it is well known that there are equatorial submergence of some cold water species of zooplankton and an ontogenetic migration to deep-layers for some species inhabiting the seas at high latitudes (Ekman, 1953; Vinogradov, 1968).

The present author took interest in whether the level of metabolism of bathypelagic zooplankton in their natural habitats was the same to that of epipelagic counterparts or not, differing from that of the previous workers whose interests were largely focussed into the vertical migration of animals. In other words, whether the relations among respiration, body size and habitat temperature of epipelagic species of zooplankton verified above are applicable or not to bathypelagic zooplankton. The results of experiment in which the respiration rate of some bathypelagic zooplankton species measured under successive conditions of high pressure and normal pressure were shown in Fig. 8. From that figure it is evident that the effect of pressure on the respiration of bathypelagic zooplankton apparently differed with species. The respiration rate of three species of copepods and a species of ostracod augmented with an increasing pressure, but the reverse was the case for a nemertean species. The variation of the rate was larger in an ostracod and in a nemertean species than in three copepod species. Macdonald *et al.* (1972) observed an increase of the metabolic rate of a decapod, *Systellaspis debilis*, and a decrease of an ostracod, *Gigantocypris mulleri*, under the condition of high pressure. The respiration rate of some species increased in the present studies as successive incubation progressed (Fig. 8). It is difficult to give an explanation to this. The data on each species under the condition of pressure were averaged and plotted against the body weight in comparison of metabolic level of those zooplankton which was predicted from equation (4) (Fig. 9). Respiration rate of *Gennadas* sp., on which experiment was carried out under pressurized condition

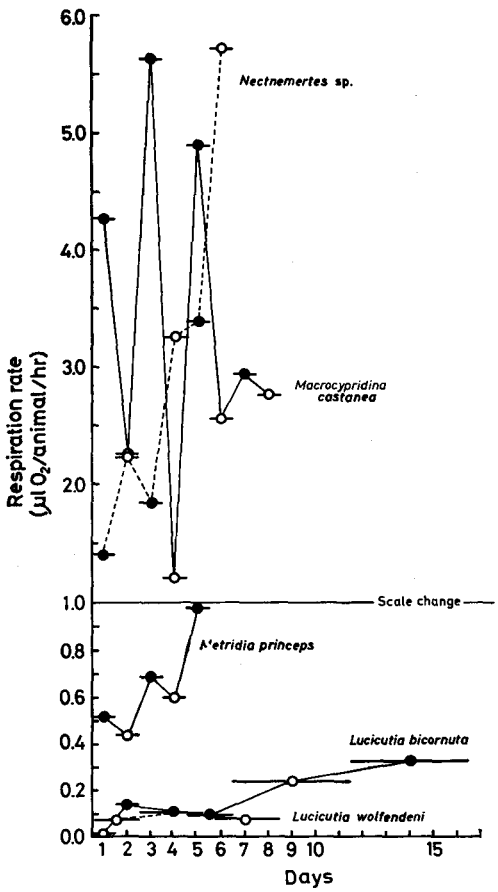

Fig. 8. Change in the respiration rate of bathypelagic zooplankton species during the successive experiments under repeated conditions of pressure (200 atm: solid circle) and of non-pressure (1 atm: open circle).

only, was added in Fig. 9. In spite of small numbers and large scatter of data, the level of respiration rate which was directly measured in some bathypelagic zooplankton did not deviate so largely from that predicted from respiration-body weight in relation to epipelagic zooplankton at 3.5°C. Although further accumulation of data under a simulated *in situ* condition of animals is apparently necessary for conclusion, as far as the present studies are concerned, it supported the hypothesis that the metabolic level of deep-water zooplankton did not so differ from that of shallow water relatives in their normal habitats. In other words, there is a possibility to apply the respiration relations obtained on epipelagic zooplankton to bathypelagic counterparts. Childress (1971) mentioned that deep-living species respired at a lower rate than those of shallow-living species under comparable conditions. In his comparable conditions, both temperature and pressure were far different from those in nature for deep-living species so that his result was not comparable with the present result mentioned above.

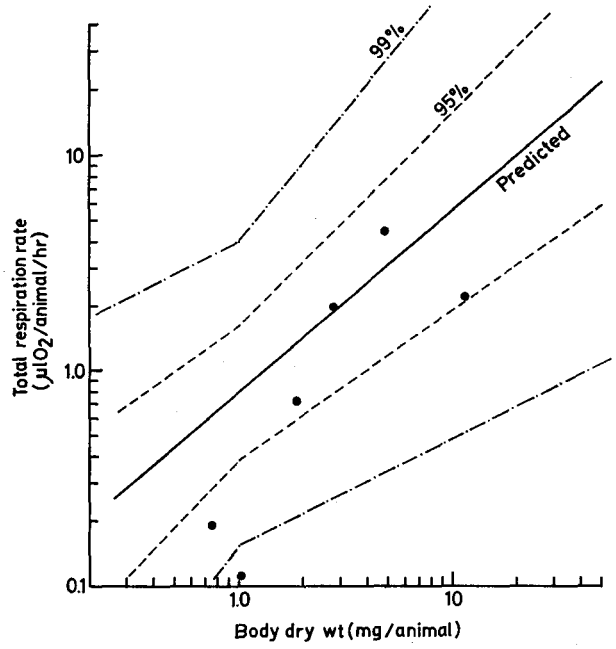

Fig. 9. Relationship between total respiration rate measured near their natural conditions in temperature and hydrostatic pressure and body dry weight for bathypelagic zooplankton. Regression line was predicted from respiration-body weight relation for epipelagic zooplankton at the average experimental temperature of 3.5°C. Dotted and chain lines represent 95% and 99% confidence limits of the predicted line respectively.

VI. Chemical composition

Table 7 shows a list of zooplankton groups and number of species analyzed. All data obtained in the present studies are given in the Appendix. Analyzed zooplankton were grouped according to habitat temperature.

Boreal and deep-water species (ca. 0–13°C); zooplankton collected off Kitami, Usujiri and Nanae-hama coasts, and on the Kaiyo-Maru with MTD vertical closing net from 1500–2000 m depths

Temperate water species (ca. 12–18°C); zooplankton collected at Oshoro Bay

Subtropical species (ca. 17–24°C); zooplankton collected on the Kaiyo-Maru

Tropical species (ca. 26–28°C); zooplankton collected on the Kaiyo-Maru.

One hundred and eleven species in total, including 38 species of tropical, 14 species of subtropical, 17 species of temperate and 48 species of boreal and deep-water species, were analyzed. Among the boreal species animals collected from off Kitami were distinguished from the others because of extremity low habitat temperature.

Table 7. *Groups and number of species of boreal and deep-water, temperate, subtropical, and tropical zooplankton submitted to chemical analysis.*

Groups	Boreal & Deep water (off Kitami)	Temperate	Subtropical	Tropical
Coelenterata	1(1)	0	1	1
Ctenophora	0	1	0	0
Heteropoda	0	0	0	1
Pteropoda	2(1)	1	1	5
Polychaeta	0	0	1	1
Ostracoda	1	0	0	0
Copepoda	14(5)	6	4	8
Isopoda	0	0	1	0
Mysidacea	2(2)	1	1	1
Cumacea	3	1	0	0
Tanaidacea	1	0	0	0
Amphipoda	4(1)	1	1	5
Euphausiacea	4*(1)	0	2	4*
Decapoda	4*(1)	2*	0	5*
Stomatopoda	0	0	0	2*
Insecta	0	0	0	1
Chaetognatha	2(1)	1	1	1
Tunicata	0	0	1	0
Pisces	3	3	0	3
Total	41(13)	17	14	38

* Including larvae unidentified

1. *Nitrogen*

Nitrogen expressed as per cent of dry body weight for tropical, subtropical, temperate, and boreal and deep-water species was plotted against dry weight of animals (Fig. 10). The values scattered widely and no consistent trend was shown.

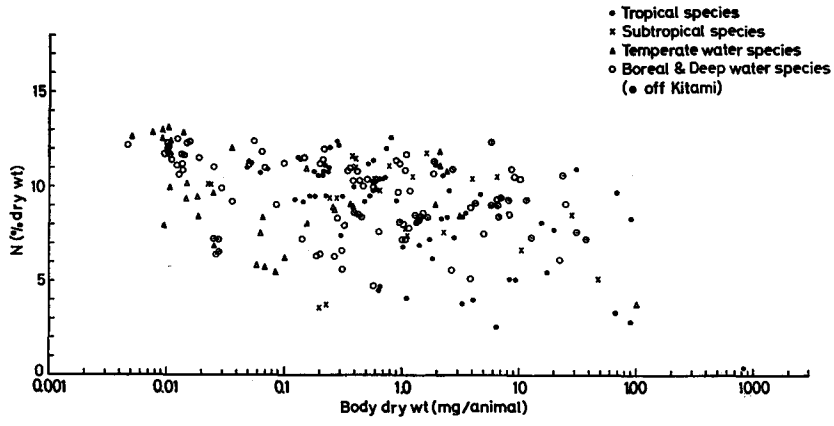

Fig. 10. Relationship between per cent nitrogen of dry weight and the body dry weight for tropical, subtropical, temperate, and boreal and deep-water zooplankton species.

However, the upper limit of nitrogen tended to increase slightly with a decrease of dry body weight. The maximum per cent nitrogen of dry weight was 13% for most of the four zooplankton groups and the minimum value was 0.4% for a salp. The higher value of nitrogen showed no difference among the tropical, subtropical, temperate, boreal and deep-water species. The lower value, however, was held by most of the tropical and subtropical species. With regard to taxonomical groups of animals, copepods, euphausiids, chaetognaths, mysids and fish larvae had higher values, and salps, pteropods, medusae, decapod larvae (megalopa), ostracods and cumaceans had lower values. Some animals other than common plankton such as *Tanais* sp., *Pleustes panopla*, *Pontogeneia* sp., *Corophium uenoi*, *Idotea metalica* and a species of Portunidae belonged to the low nitrogen group.

According to the results of Curl (1962b) the highest and the lowest values were 7.8% for *Sagitta elegans* and 0.2–0.4% for *Mnemiopsis* sp. (Ctenophora) and *Pyrosoma* sp., respectively, collected from continental shelf waters, south of New York; Beers (1966) also reported that the highest and the lowest values were 11.17–11.18% for copepods and polychaetes and 0.98% for siphonophores from the Sargasso Sea, off Bermuda; Omori (1969) showed the highest value of 12.9–13.1% for copepods, *Pleuromamma xiphias* and *Labidocera acutifrons*, and the lowest value of 1.5% for *Limacina inflata* respectively from largely boreal zooplankton. Vinogradov *et al.* (1970) ascertained that a nitrogen content of 10.3% for mixed zooplankton (predominantly copepods) was the highest and 6.7% for *Gennadas borealis* was the lowest. These specimens were collected from different depths in north western Pacific.

Thus, the maximum and the minimum levels of nitrogen content of the animal body differed with workers reflecting the difference in the zooplankton species analyzed. The works of Curl (1962b) and Omori (1969) were more comparable to the present results in respect of the large variety of zooplankton groups employed. At any rate, it is expected that 13% of body dry weight corresponds to the upper limit of nitrogen content in the body of zooplankton. It is concluded from the present results that nitrogen content of zooplankton changes greatly from species to species and that there exists no consistent relation to body size and to habitat temperature.

2. *Carbon*

The carbon percentage of dry weight was plotted against dry body weight of animals in each group of zooplankton (Fig. 11). As in the case of nitrogen, no consistent trend is shown in the diagram. However, there was a remarkable difference between the boreal and tropical species. It was observed that the carbon content of most of tropical species did not exceed 45% of dry weight, and some of boreal species contained more than 65% of dry body weight. The values

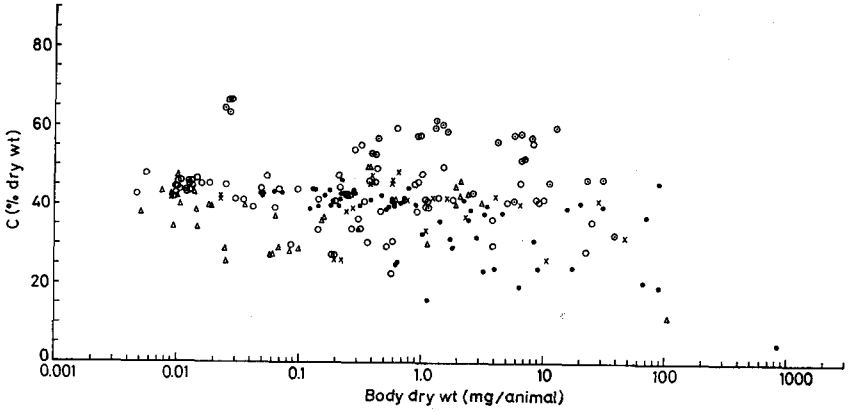

Fig. 11. Relationship between per cent carbon of dry weight and the body dry weight for tropical, subtropical, temperate, and boreal and deep-water zooplankton species. Symbols as in Fig. 10.

for subtropical and temperate species were distributed between the two extreme values of tropical, and boreal and deep-water species. A tropical insect, *Halobates sericeus*, showed 54.6% of dry weight of animal. This value exceeded the 52.6% obtained by Omori (1969) on this species. Although *Halobates* is collected frequently with plankton net at certain sea areas, this insect does not live in the sea but lives on the surface of the sea. This different life form from general zooplankton means different type of nutrition, so that data on chemical composition of *Halobates* was not included in the figures.

Among higher carbon values observed in some boreal species, the highest one was 63.3–66.7% of dry weight of *Pseudocalanus minutus*. Copepods, a decapod and mysids in boreal species also contained a higher amount of carbon. A salp showed the lowest value of 4.6% of dry weight. Medusae, pteropods, amphipods, cumaceans and decapod larvae of tropical and subtropical species belonged to a lower carbon content group. Besides these, animals such as *Tanais* sp., *Pleustes panopla*, *Pontogeneia* sp., *Corophium uenoi*, *Idotea metalica* and a species of Portunidae showed a lower value of carbon percentage of dry body weight as well as nitrogen.

Curl (1962a, b) found the maximum and the minimum value of per cent carbon of dry weight was 46.8% for *Lophogaster* sp. and 3.6% for *Salpa* sp. respectively. Beers (1966) reported 47.6% for copepods and 3.0% for siphonophores. Further, a maximum of 63.6% for *Metridia okhotensis* and a minimum of 17.0% for *Limacina inflata* were observed by Omori (1969) and a maximum of 65.23% for *Gnathophausia gigas* and a minimum of 41.00% for mixed zooplankton (mainly copepods) were obtained by Vinogradov *et al.* (1970). The results obtained in this study covered the range of values of carbon content by these previous workers.

It is concluded that carbon content of the animal body is more variable with species than in nitrogen content. The variation of carbon content depends not on body size, but on habitat temperature. The latter fact is not the case in nitrogen.

3. *Hydrogen*

The distribution pattern of per cent hydrogen against body dry weight was nearly the same that of carbon. A correlation between hydrogen percentage of dry weight and habitat temperature was observed. For tropical and subtropical species the upper limit of values of hydrogen content stayed at 7%, with an exception of 8.2% in *Halobates*. For boreal species the highest value was 10.7% in *Calanus cristatus*. On the other hand, Omori (1969) also obtained the highest value of 10.1% in *C. cristatus* in his studies.

4. *Ratios of elements*

According to Corner and Cowey (1964, 1968) and Raymont *et al.* (1968) protein nitrogen generally amounts to more than 75% of total nitrogen in the body of some zooplankton species. A low value of about 50% has been reported for *Sagitta hispida* (Reeve *et al.*, 1970). Generally, planktonic animals contain less amount of inorganic carbon (carbonate) in their bodies than benthic forms (Vinogradov, 1953). Curl (1962b) found measurable quantities of carbonate carbon (less than 3% CO_3-C/dry weight) in only few zooplankton species (*Limacina* sp. and *Idotea metalica*). From these results it is considered that most of the nitrogen, carbon and hydrogen measured here were derived from organic matter in the animal body.

Ratios of elements largely concern the nature of organic constituents of the animal body. Table 8 shows the average composition of nitrogen, carbon and hydrogen of protein and of fat presented by Rogers (1927). Carbohydrate was neglected here since its quantity in the total dry matter of zooplankton body was about 1–3% dry weight (Raymont and Krishnaswamy, 1960; Raymont and Conover, 1961; Beers, 1966; Ikeda, 1972) and was too small to contribute to the

Table 8. *Average composition of organic matter taken from Rogers (1927).*

Element	Lipid	Protein
C	69.05	51.3
N	0.61	17.8
H	10.00	6.9
H/N	16.4	0.4
C/H	6.9	7.4
C/N	113.2	2.9

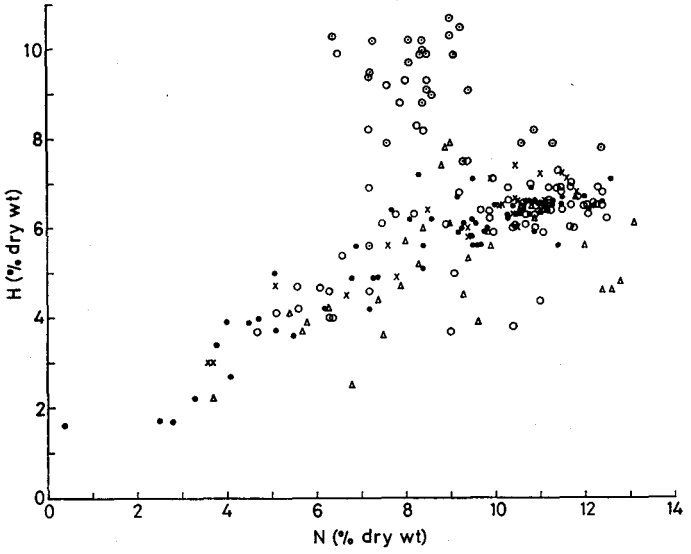

Fig. 12. Relationship between per cent hydrogen and per cent nitrogen of the body dry weight for tropical, subtropical, temperate, and boreal and deep-water zooplankton species. Symbols as in Fig. 10.

total nitrogen, carbon and hydrogen. It is known that protein and fat were major constituents in the body and occupied 70–90% of dry weight of animals (Nakai, 1955; Ikeda, 1972).

H:N ratio: According to the results of Rogers the H:N ratio was about 0.4 for protein and 16.4 for fat. Therefore, this ratio is a good index to the relative proportion of protein and fat in the body of zooplankton. In Fig. 12 the percentage of nitrogen was plotted against hydrogen percentage. For tropical, subtropical, temperate and some boreal and deep-water species the per cent hydrogen was correlated to the per cent nitrogen in a parabolic manner, while in other boreal and deep-water species, which were collected mainly at off Kitami, large deviation from this tendency occurred. This fact suggested deposition of fat in animal bodies.

C:H ratio: Fig. 13 shows a scatter diagram of per cent content of hydrogen and per cent content of carbon of animal body. The percentage of hydrogen was correlated to the carbon percentage in a linear manner for all groups of zooplankton. Such a fact was observed from Rogers's results in Table 8. In short, the C:H ratio is not a suitable index to distinguish protein from fat. In the present studies the C:H ratio was around 6–7 as in Fig. 13 for all groups of zooplankton with exception of 5–6 for some boreal species from off Kitami.

Vinogradov *et al.* (1970) analyzed carbon and hydrogen in the lipids extracted

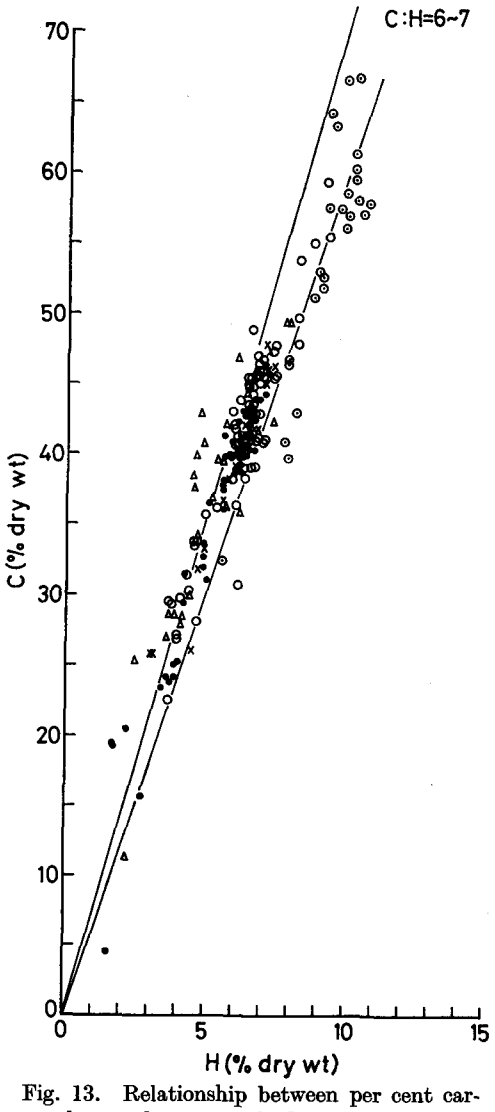

Fig. 13. Relationship between per cent carbon and per cent hydrogen of the body dry weight for tropical, subtropical, temperate, and boreal and deep-water zooplankton species. Symbols as in Fig. 10.

with chloroform from some boreal zooplankton. Their results of 77–79% of carbon and 11.5–12.5% of hydrogen were slightly higher when compared with those of Rogers, but the C:H ratio remained around the same value. In the present studies, the highest value of carbon and nearly the highest value of hydrogen was 64–67% and 9–10% respectively of dry weight of *Pseudocalanus minutus* collected from off Kitami. These figures of carbon and hydrogen were similar to those lipid of Rogers and Vinogradov *et al.* The fact that the body of *P. minutus* from off Kitami comprized a considerable amount of fat was easy to explain from a visual examination in Fig. 19.

C:N ratio: Rogers's results (Table 8) suggested that the C:N ratio was a useful index to distinguish protein from fat, because the ratio differed greatly from each other (about 3 for protein and over 100 for fat). Fig. 14 indicates a relative frequency of the ratio for tropical, subtropical, temperate, and boreal and deep-water species in the present studies. Throughout the groups of zooplankton a high frequency was found in the ratio of 3 and 4. Compared with other three zooplankton groups, a relative frequency of a higher ratio than 4 was found in boreal and deep-water species, which was attributed largely to the materials from off Kitami (Fig. 14).

Redfield (1934) pointed out at first that the C:N ratio in zooplankton was 6.24 (7.28 in atomic ratio) and was identical with that in phytoplankton and in ocean water (Redfield *et al.*, 1963). Curl (1962b) showed that the ratio varied

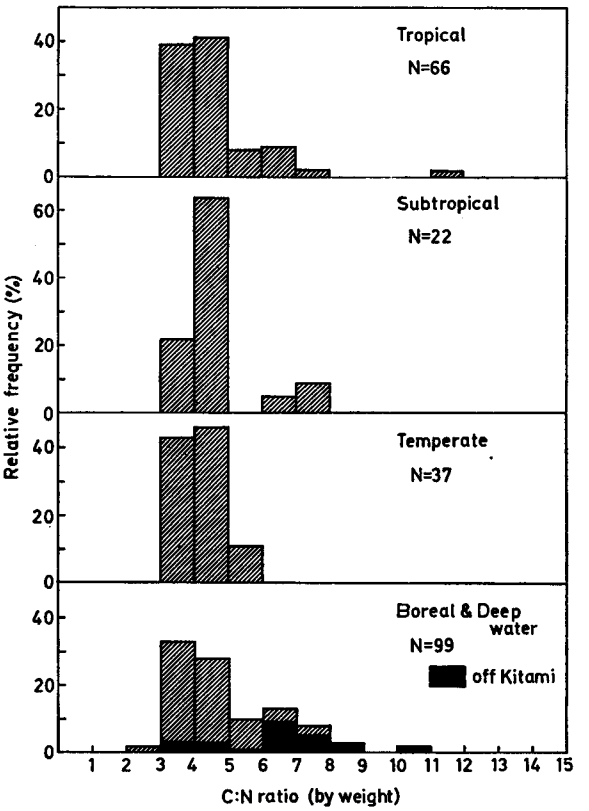

Fig. 14. Relative frequency (%) of the C:N ratio by weight in the body of tropical, subtropical, temperate, and boreal and deep-water zooplankton species.

greatly from 4.5 for *Centropages* spp. to 45 for *Aequorea vitrina* (calculated by the present author). On the other hand, Beers (1966) showed that in subtropical zooplankton the C:N ratio was quite constant (3–4) with the exception of two extremes (2.4 for hydromedusae and 6.9 for pteropods). Omori (1969) also reported that the ratio was 3 and 4 with the maximum value of 11.1 for *Limacina inflata*. Vinogradov *et al.* (1970) observed that the highest ratio was 11.2 for *Gennadas borealis* and the lowest was 5.2 for mixed zooplankton (mainly copepods). Except for the high ratio obtained by Curl (1962b), the ratio reported by previous authors coincided with the results of the present studies. The high value of Curl (1962b) may have resulted from a low value of nitrogen due to an incomplete hydrolysis in nitrogen determination.

The relation between the percentage of nitrogen and the percentage of carbon are illustrated in Fig. 15. The per cent of nitrogen increased with the per cent of carbon in a linear manner up to approximately 45% for carbon, and then, it decreased with the increase of the percentage of carbon. In the linearly propor-

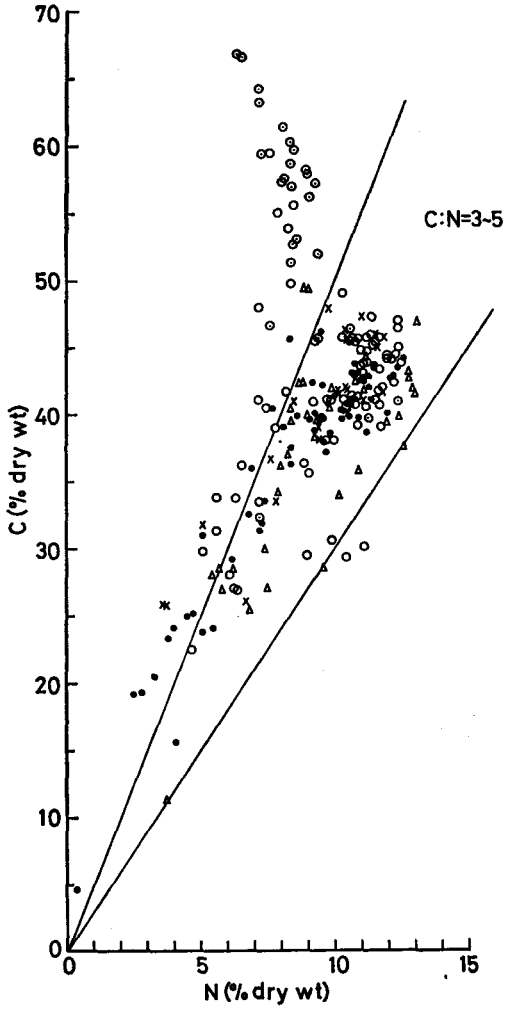

Fig. 15. Relationship between per cent carbon and per cent nitrogen of the body dry weight for tropical, subtropical, temperate, and boreal and deep-water zooplankton species. Symbols as in Fig. 10.

tional phase of the per cent of nitrogen to the per cent of carbon, the slope was between 3–5 as known in Fig. 14. This suggests that the main body constituents are largely protein for the majority of tropical, subtropical, temperate and roughly half of the boreal and deep-water species. The other half of the boreal and deep-water species showing an inverse relationship between the per cent of nitrogen and the per cent of carbon were mostly those collected from off Kitami. The high carbon value means a high proportion of organic matter in the animal body, and the low nitrogen value indicates the low proportion of protein. Therefore, high percentage of carbon and low percentage of nitrogen in some boreal and deep-water species suggested that a larger amount of fat was stored in the body in these

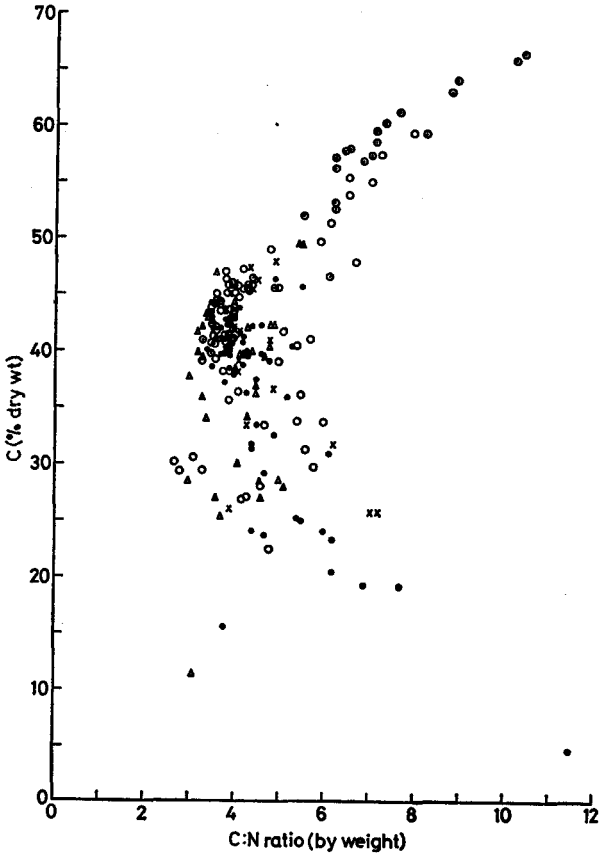

Fig. 16. Relationship between per cent carbon of body dry weight and the C:N ratio for tropical, subtropical, temperate, and boreal and deep-water zooplankton species. Symbols as in Fig. 10.

species. Fig. 15 shows that the large deposition of fat in the body was occupied by the animals with carbon content more than 45% body dry weight.

C:C/N ratio: The percentage of carbon of dry weight as an indicator of the proportion of organic matter in the animal body was plotted against the C:N ratio (Fig. 16). As seen in Fig. 16 a high C:N ratio in boreal and deep-water species means a higher amount of organic matter in the body but a lower amount of organic matter in the tropical and subtropical species. Animal groups belong to the higher case were almost all the species from off Kitami and lower case were in limited taxonomic groups such as shelled pteropods, decapod megalopa larvae and tunicates. High C:N ratio in tropical shelled pteropods is caused from low nitrogen content compared with that of boreal shelled pteropods (cf. Appendix).

5. *Changes in per cent nitrogen and in per cent carbon of dry weight in some taxonomic groups with habitat temperature*

Some taxonomic groups of animal collected from most of sea areas covering tropical to boreal were analyzed for per cent content of nitrogen, per cent content of carbon and the C:N ratio of the animal body. Further, for an index of proportion of organic matter in the animal body the sum total of the per cent nitrogen and the per cent carbon were arranged on the basis of the habitat temperature of animals (Fig. 17).

In copepods, the per cent of nitrogen tended to increase with increase of habitat temperature and in euphausiids, decapods and mysids there was no consistency with the habitat temperature. In amphipods and chaetognaths the percentage of nitrogen in the animal body decreased with an increase in habitat temperature. Thus, as seen in Fig. 10 the per cent nitrogen related to neither body size nor to the habitat temperature of animals is treated as a total in disregard of taxonomi-

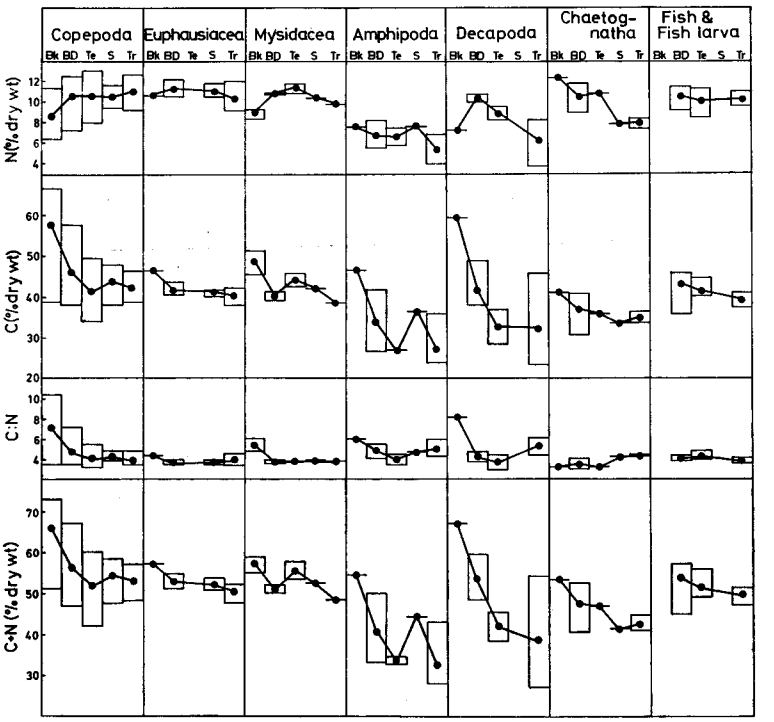

Fig. 17. Changes in per cent nitrogen, per cent carbon and the C:N ratio, and the sum total of per cent nitrogen and per cent carbon with habitat temperature for taxonomic groups of zooplankton. Average value is shown as a dot and its range by length of column (Bk; boreal species collected off Kitami, BD; other boreal species and deep-water species, Te; temperate water species, S; subtropical species, Tr; tropical species).

cal difference of animals. However, there exists an interspecific difference as shown in Fig. 17.

The per cent content of carbon decreased with the increase of habitat temperature in all taxonomic groups and was especially conspicuous in copepods and decapods. These different patterns of change in nitrogen and in carbon with habitat temperature reflected the C:N ratio of animals in each taxonomic group. The decrease in the C:N ratio was observed in copepods and in decapods, especially in the upper limit of carbon per cent. The same tendency, although not so remarkable as in copepods, was seen in mysids and amphipods. The C:N ratio remained almost at a constant level in euphausiids, chaetognaths and fish larvae. The sum total of the per cent nitrogen and the per cent carbon can be taken as an index for the estimation of proportion of organic matter in the animal body, because carbon and nitrogen are major constituents of organic matter. The per cent hydrogen was neglected here because it was proportional to the per cent carbon as seen in Fig. 13. The total of per cent nitrogen and per cent carbon tended to decrease with an increase of habitat temperature in all taxonomic groups. This suggests that the proportion of organic matter in the body decreases with the increase of habitat temperature.

The number of species in each taxonomic group differed and except for copepods only a few species were measured. It is possible however to generalize on the interspecific difference of the effect of habitat temperature on the chemical composition of the body (Fig. 17).

6. *Discussion*

Biochemical composition of zooplankton will change with seasons and with sampling locations even in a given species (Marshall *et al.*, 1934; Orr, 1934a, b; Fisher, 1962; Linford, 1965; Raymont *et al.*, 1966; Conover and Corner, 1968; Raymont *et al.*, 1969a; Reeve *et al.*, 1970; Raymont *et al.*, 1971). There are several explanations for this variation. The most important is the change in the amount of available foods for most animals, which is highly variable from season to season especially at high latitudes. According to the studies by Conover and Corner (1968), the amount of fat deposited in the bodies of some boreal copepods increased through spring blooming with phytoplankton and decreased with the progress of seasons. It reached its minimum just before the next spring bloom. In spite of such a large variation of fat a constant level of per cent nitrogen of dry weight of animals held throughout all seasons of the year.

The collection of boreal zooplankton in the present studies were made in September 1970 off Kitami, in March 1970 at Nanae-hama coast and from May to June 1971 off Usujiri. Concurrent with the sampling of zooplankton for the present studies, the standing crop of phytoplankton, measured in terms of chloro-

phyll *a*, was about 1–3 mg/m³ at 0–50 m depth of off Kitami (Fac. Fish., Hokkaido Univ., 1972). Since there is no simultaneous data on phytoplankton standing crop off Usujiri, a previous result of about 1.2 mg chl. *a*/m³ of water in the same month (July 1968) (Shiga, 1969) is used. At Nanae-hama coast, the net was clogged with phytoplankton during vernal blooming. Thus, the boreal species analyzed in the present studies have not been deficient in food available when they were collected.

Fig. 18 shows a particular case in which the chemical composition of *Calanus cristatus* and *C. plumchrus* of boreal species is affected according to their specific difference in their abilities of temperature tolerance (eurythermal or stenothermal) throughout their life cycles. According to Beklemishev (1954) and Heinrich (1962), the reproduction of *C. cristatus* and *C. plumchrus*, both being dominant species of copepods in northern North Pacific Ocean, occurred in winter with one brood a year. The new brood developed into the I-II copepodite stages by the beginning of the period of phytoplankton growth. In these stages they fed on phytoplankton

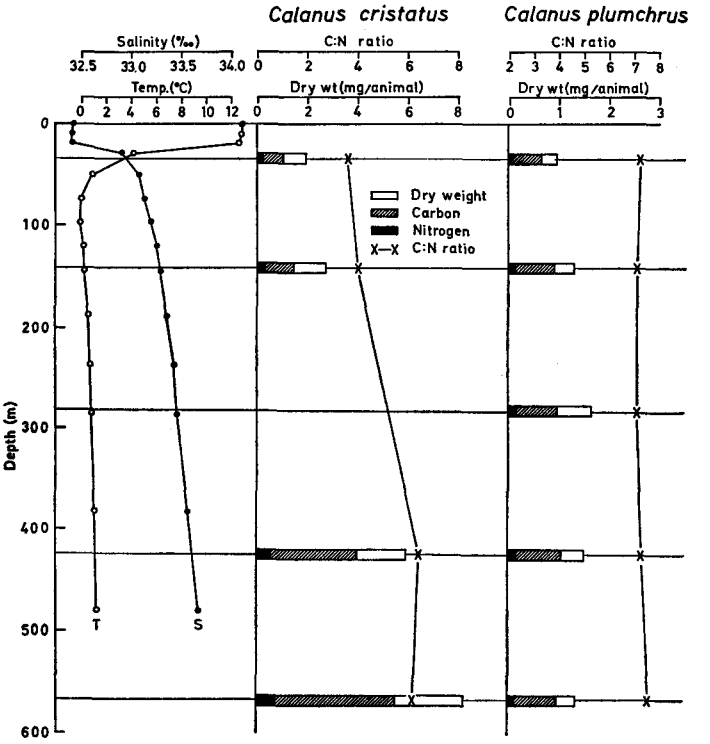

Fig. 18. Changes in body dry weight, and in amount of carbon, nitrogen and the C:N ratio, with depth, in the body of two representative of boreal copepods, *Calanus cristatus* (V stage) and *C. plumchrus* (V stage), collected off Kitami (Sept. 1970).

and rapidly grew to stage V copepodite. They stored large reserves of fat. The stage V copepodite began to sink to the deep-waters in late summer. After they molted to adults in the deep-sea, the masticatory edges of their mandibles degenerated and they no longer took any food. They subsisted, at depths greater than 200 m, on the fat stored in their bodies.

In the present studies sampling was carried out in September corresponding to the sinking season for both species. As shown in Fig. 18, dry weight, carbon content, nitrogen content and the C:N ratio of the animal body for *C. plumchrus* did not change with depths, but these increased with depths for *C. cristatus*. Coloration of *C. cristatus* from deeper depths was bright red, while that from shallower depths was faded red. The body length was 7.3–7.7 mm for *C. cristatus* and 3.7–3.9 mm for *C. plumchrus* throughout the depths. A difference of body length with depths was not observed in the two species.

Such differences between these allied copepods may be explained on the basis of results obtained by Beklemishev (1954) and Heinrich (1962). Therefore, in the present studies *C. cristatus* sampled from deep-layers was in good nutritive condition through the vernal blooming of phytoplankton. While, lean *C. cristatus* obtained from shallow depths was more delayed in development than those in deep-layers and it could not feed on enough phytoplankton in the euphotic layer because of the establishment of a thermocline. It was then forced to sink beneath the thermocline. *C. plumchrus*, differing from *C. cristatus*, is a eurythermal species. Hence, the establishment of the thermocline had no effect on the feeding behavior of this species. In fact, surface tow at night indicated that *C. plumchrus* migrated through the thermocline to the surface.

In respect to the chemical composition of animal body, the deposition of a large amount of fat in the bodies of the majority of boreal and some of deep-water species is a remarkable fact, which is indicated in Figs. 12, 13 and 16 in the present studies. Further, Fig. 17 shows that the deposition of fat was negatively correlated with habitat temperature, though its degree differed with taxonomic groups. Intraspecifically, this relation was well represented in *Acartia clausi* from Nanaehama coast and Oshoro Bay, and in *Calanus plumchrus* from off Kitami, off Usujiri and Oshoro Bay in the present studies (*see* Appendix). Relevant here, Wimpenny (1941) reported that the stored fat of the mixed zooplankton from upper layers of the sea increased from low to high latitudes. Littlepage (1964) reported the negative correlation between the amount of fat and the habitat temperature on *Euchaeta antarctica* and *Euphausia crystallorophias* from the antarctic. Extensive studies on many species of copepods by Lee *et al.* (1971) revealed that more fat was deposited in copepods of higher latitudes and of deeper-waters in the sea.

In some species of boreal copepods with transparent body, fat deposited was easily observed by naked eye, and has been called the "oil-sac" or "oil-droplets"

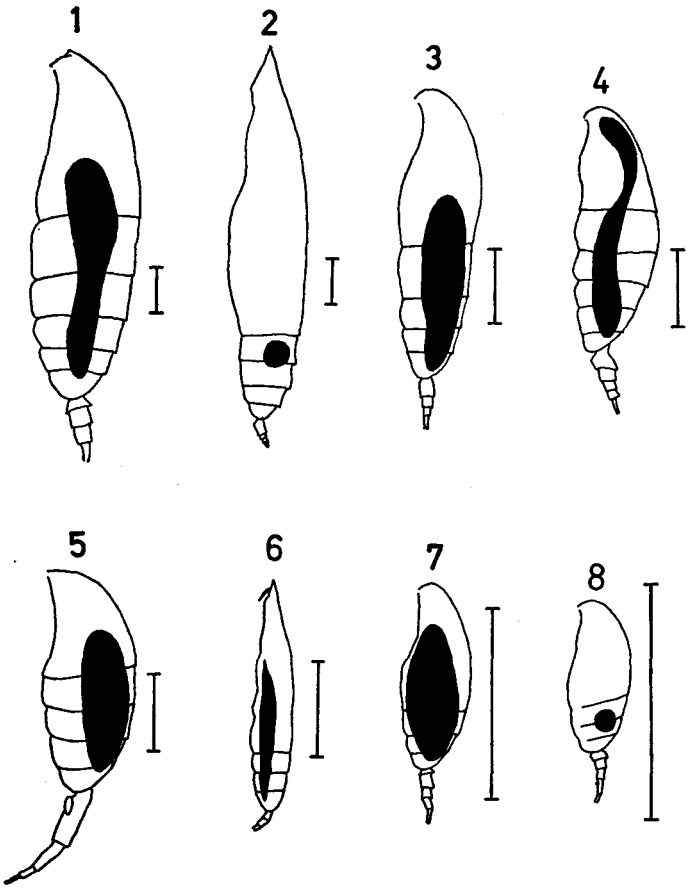

Fig. 19. Various shapes of oil-sac in the bodies of different copepods (lateral view). Vertical bars alongside of animals show a relative length of 1 mm. *Calanus cristatus* V (1), *C. plumchrus* V (3), *C. glacialis* (4) and *Eucalanus bungii bungii* (2) were collected from the Bering Sea (June-Aug. 1968); *Metridia okhotensis* (5) and *Pseudocalanus minutus* V (7) off Kitami (Sept. 1970); *Rhincalanus nasutus* (6) off Cape Garnet, Spanish Sahara, Africa (Jan. 1972) and *Paracalanus parvus* (8) from Oshoro Bay (June-July 1970).

(cf. Marshall and Orr, 1955). As seen in Fig. 19, there was a difference in the shape and in the dimension of oil-sac among certain species though these differed with individuals of the same species. For instance, the shape of the oil-sac of *Eucalanus bungii bungii* was almost spherical, differing distinctly from the one of an allied species *Rhincalanus nasutus*. During the cruise of the Kaiyo-Maru, raw materials of tropical copepods examined under the microscope had no oil-sac in their transparent bodies. The same was true for specimens taken from sea areas where the water temperature higher than 25°C. At stations where water temperature was

about 20°C, *Neocalanus gracilis* with a small oil-sac occurred in small numbers.

In tropical and subtropical seas most of the environmental factors are almost uniform in all seasons and the primary production is low but continuous throughout a year, in contrast with a high but great variability in the seas at high latitudes (Ryther, 1963; Strickland, 1965). Beers (1966) studied the chemical composition of major zooplankton groups in the Sargasso Sea, off Bermuda, monthly throughout the year. Variation of the percentage of carbon of dry weight, which was a more variable element than nitrogen and hydrogen as verified in the present studies, ranged from 35.2% to 47.6% in copepods. That range was similar to the present results for tropical and subtropical copepods. This range of carbon content was far narrower compared with that of 38.3%–66.7% for boreal copepods found in the present studies at certain periods of the year, indicating that seasonal variation of chemical composition in the body was less pronounced in tropical zooplankton.

In conclusion, chemical composition of zooplankton sampled from tropical, subtropical, temperate and boreal seas and from deep-waters in terms of per cent nitrogen, per cent carbon and per cent hydrogen of dry weight is not related to body weight of animals. Among three elements, the amount of carbon is directly proportional to the amount of hydrogen (or vice versa). Both elements, the percentage of carbon and the percentage of hydrogen of dry weight, increase with a decrease in habitat temperature. Such a fact indicates the deposition of fat in the body of boreal and deep-water species. The results suggest a possibility of the difference in the effect of habitat temperature on the chemical composition of animal body in each taxonomic group.

VII. Physiological effects of starvation on zooplankton

From the results above mentioned it is supposed that zooplankton inhabiting higher habitat temperatures need a larger amount of food continuously due to acceleration of the metabolic rate with habitat temperature. Further, the proportion of organic matter, especially fat as a energy reserve, in the animal body tended to decrease with the increase of habitat temperature. These characteristics in zooplankton nutrition due to the habitat temperature suggest that zooplankton living in the warmer waters have little tolerance against starvation compared with those in the colder waters. To ascertain the above fact a knowledges of the ability of metabolic regulation and metabolic substrate of zooplankton under long-term starvation is necessary.

In the present studies the change in the respiration rate and metabolic substrate under the long-term starvation were ascertained. Some factors which determine the survival time under starvation were also investigated.

1. *Respiration*

Three species of boreal copepods, *Calanus cristatus*, *C. plumchrus* and *Eucalanus bungii bungii*, were starved for about 2 months and their respiration rates at the end of starvation period were compared with those at the beginning of the starvation period (Table 9). In *C. cristatus* the rate lowered roughly to a half of those at the beginning of the starvation period, while in *E. bungii bungii* the decrease of the rate was not so large as compared with *C. cristatus*. In *C. plumchrus* the respiration rate remained almost unchanging. In previous works, the respiration rate of *Acartia clausi* and *A. tonsa* decreased to a half and to a third when artificial fasting lasted for 6 days (Conover, 1956). *Calanus hyperboreus* reduced its metabolism under starved condition (Conover, 1962, 1964). *C. cristatus* maintained without food for a month showed a lower metabolic rate (Ikeda, 1971a). The degree of reduction of metabolic rate in both *C. hyperboreus* (Conover, 1962, 1964) and *C. cristatus* (Ikeda, 1971a) was about a half of the initial rate. Reduction of metabolic rate under starvation is general phenomenon throughout all animal kingdom from protozoan to higher animals (Krogh, 1916; Winberg, 1956; Vernberg, 1959; Farmanfarmaian, 1966; Jørgensen, 1966; and references therein), but exceptions are noted by Stikle and Duerr (1970).

Table 9. *Change in the respiration rate of zooplankton during starvation. Animals were collected from off Usujiri (May 1971) and were maintained at near their natural habitat temperature.*

Animals	Culture No.	Starvation period in days	Respiration rate (μl O_2/animal/hr)
Calanus cristatus V	1	1	2.33
	2	1	1.74
	1+2	52	1.20
Calanus plumchrus V	1	1	0.48
	2	1	0.63
	1	60	0.43
	2	67	0.76
Eucalanus bungii bungii	1	1	0.84
	2	1	0.75
	1	64	0.69
	2	64	0.57

2. *Metabolic substrate*

Table 10 shows the results of a boreal copepod, *Calanus cristatus*, for a 13 day's starvation. A decrease of all organic matter of the body, but of chitin, was very rapid in the first 7 day's starvation. Absolute loss was larger in protein than lipid, but in terms of per cent loss of initial (0 day) amount, the lipid was the largest. Change in the amount of carbohydrate was little. In previous studies (Ikeda, 1971a), the rate of decrease for each kind of organic matter of the same

Table 10. *Changes in dry weight, total lipid, total protein, total chitin, and in total carbohydrate in* Calanus cristatus (*V stage*) *during starvation* (*μg/animal: mean of eight determinations±standard deviation*). *Analytical methods used are the same as in Ikeda* (*1971a*). *Animals were collected in the Bering Sea* (*54°17'N 167°58'W, June 18 1969*) *and were maintained at 6–9°C.*

Days of starvation	Dry weight	Ash weight	Lipid	Protein	Chitin	Carbohydrate
0	2203	308	474	1311±143	94±9	14±1
3	1599	355	218	931±125	82±12	12±3
7	1209	348	35	715±103	99±10	12±1
13	1218	308	108	696±129	91±11	14±2

species was slower than that observed in the present experiments and some chitin was lost during the starvation. The reasons causing the different results are uncertain.

In *Calanus plumchrus, Acartia clausi* and *A. longiremis* changes in dry weight, and in carbon, nitrogen and hydrogen in the body were studied under starvation conditions (Table 11). Decrease of body weight was well pronounced, but the change in each element expressed as per cent of body dry weight was not so remarkable in three species, especially in *C. plumchrus*. The slight decrease in the percentage of nitrogen for *A. clausi* and a similar decrease in the percentage of carbon for *A. longiremis* suggested that the relative utilization of nitrogen as metabolite was larger for the former species and reversed fact was the case for the latter species. There is no doubt that in both species of *A. clausi* and *A. longiremis* the major substrate utilized as metabolite during the starvation period was protein. For this reason, the C:N ratio, close to that of protein in Rogers's result (Table 8), remained unchanging during the starvation periods. Identically, the maintenance of the same C:N ratio of *C. plumchrus* through the starvation period suggested that a large amount of protein was metabolized in this species.

Table 12 shows the result of longer starvation period than that in Table 11. Since the number of individuals of animals analyzed were few, the reliability of the result was low. Compared with the initial percentage obtained in the beginning of experiment, the decrease of nitrogen, carbon and of hydrogen was large in all species. Loss in the percentage of carbon of dry weight larger than 50% of initial value was observed in *C. cristatus* and *E. bungii bungii*. The C:N ratio decreased with the progress of starvation period and fell to about 3 in all species at the end of the experiment. This C:N ratio of about 3 closed to that of protein from Rogers's result which has already been described in the chapter of chemical composition, indicating that relatively more carbon than nitrogen was utilized as a metabolic substrate. A certain amount of fat in the body was exhausted and consequently protein occupied a major constituent of the body through starvation

Table 11. *Changes in dry weight, per cent nitrogen, per cent carbon, per cent hydrogen, the starvation. Animals were collected from Oshoro Bay (June 1970) and on the coast of*

Animals	Temp. (°C)	Starvation period (days)	No. of animals analyzed
Calanus plumchrus V (O)	13.8–16.0	0	3
			3
			3
			3
		14	3
			2
			5
Acartia clausi (O)	13.8–14.5	0	30
			35
		5	64
			68
Acartia longiremis (U)	11.8–14.3	0	100
			100
		2	100
			100
		10	100
			100
			100

(O): at Oshoro Bay, (U): at Usujiri Coast

Table 12. *Changes in dry weight, per cent nitrogen, per cent carbon, per cent hydrogen, the starvation. Animals were collected from off Usujiri (May-June 1971) and were main-*

Animals	Days of starvation	No. of animals analyzed	Average dry weight (mg/animal)
Copepoda			
Calanus cristatus V	0	4	1.53
	37	1	1.03865
	39	1	0.38341
	70	1	0.95950
	70	1	0.53915
Calanus plumchrus V	0	23	1.03
	62	1	0.48903
	74	1	0.25330
Eucalanus bungii bungii	0	4	0.942
	47	1	0.53942
	99	1	0.50200
	113	3	0.206
Metridia pacifica	0	6	0.221
	28	3	0.09105
	30	4	0.07551
Amphipoda			
Parathemisto japonica	0	7	5.14
	38	1	4.89
	58	1	3.78

sum total per cent nitrogen plus carbon, and in the C:N ratio in zooplankton during Usujiri (June 1971), and were maintained at near their natural habitat temperature.

Average dry weight (mg/animal)	Percent of body dry weight				Carbon/ Nitrogen
	Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
0.38640	8.9	49.5	7.8	58.4	5.5
0.27054	8.7	42.4	2.0?	51.1	4.9
0.26299	8.8	42.4	7.4	51.2	4.8
0.36535	9.0	49.5	7.9	58.5	5.5
0.26538	8.3	46.5	7.3	54.8	5.6
0.29430	8.3	46.6	7.4	54.9	5.6
0.25877	9.5	44.5	7.7	54.0	4.7
0.00927	12.6	41.7	—	54.7	3.2
0.00922	12.9	42.1	—	55.0	3.3
0.00637	11.0	39.4	5.8	50.4	3.6
0.00640	10.8	42.1	6.5	52.9	3.9
0.01025	11.8	42.1	6.0	53.9	3.6
0.00973	11.7	41.9	6.0	53.6	3.6
0.00668	14.4	40.3	5.9	54.7	2.8
0.00689	11.3	39.8	5.6	51.1	3.5
0.00584	11.0	37.8	5.4	48.8	3.4
0.00576	14.4	37.7	5.3	52.1	2.6
0.00626	11.2	38.1	5.4	49.3	3.4

sum total of per cent nitrogen plus carbon, and in the C:N ratio in zooplankton during tained at near their natural habitat temperature.

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
8.4	49.8	8.2	58.2	5.9
5.5	29.5	5.2	35.0	5.3
7.7	30.9	4.4	38.6	4.0
5.1	19.6	3.2	24.7	3.8
2.8?	23.4	5.1	26.2?	8.3?
8.0	57.6	9.3	65.6	7.2
6.5	42.7	6.8	49.2	6.5
10.8	35.5	5.6	46.3	3.2
9.7	38.3	6.4	48.0	3.9
7.3	20.7	3.7	28.0	2.8
8.9	15.2	2.8	24.0	1.7
6.8	20.4	3.8	27.2	3.0
11.7	40.8	6.9	52.5	3.9
9.9	34.6	5.0	44.5	3.5
10.0	33.1	4.7	43.1	3.3
7.5	40.5	6.1	48.0	5.4
7.3	36.0	5.4	43.3	4.9
8.0	29.4	4.3	37.4	3.7

periods in these boreal zooplankton. Omori (1970) observed that the C:N ratio of a representative herbivorous copepod, *Calanus cristatus*, decreased during the long journey in the submerged Oyashio current.

A decrease of body weight under the starvation occurred in all zooplankton species in the present studies. For animals with a hard exoskeleton such as crustaceans, the decrease of body weight was not accompanied by a decrease of body length. The fading of body color occurred in some species. For animals without a exoskeleton, a shrinkage of body length followed the decrease of body weight. Fig. 20 shows the decrease of body length of a boreal chaetognath, *Sagitta elegans*. Lalli (1970) and Reeve *et al.* (1970) reported the same phenomenon in a pteropod, *Clione limacina*, and also in a chaetognath, *Sagitta hispida*.

Cowey and Corner (1963) and Linford (1965) stated that protein was mainly utilized in *Calanus helgolandicus*, *Praunas neglectus* and *Neomysis integer* under starvation conditions. Conover (1964) and Lee *et al.* (1970) showed that fat decreased in *Calanus hyperboreus* and *C. helgolandicus* respectively under starvation. The difference of metabolite utilized under starvation is apparently the result of the initial condition of animals, that is, whether the experimental animals was fatty or lean. Conover and Corner (1968) studied the seasonal change of chemical composition of boreal copepods. Their results agreed with the conclusion of the present author. That is, dry weight of animal and the percentage of fat in dry weight decreased toward the end of winter, while the percentage of nitrogen in dry weight of animal remained at a constant level. The fact suggests that fat was utilized in a larger amount than protein as metabolic substrate. The

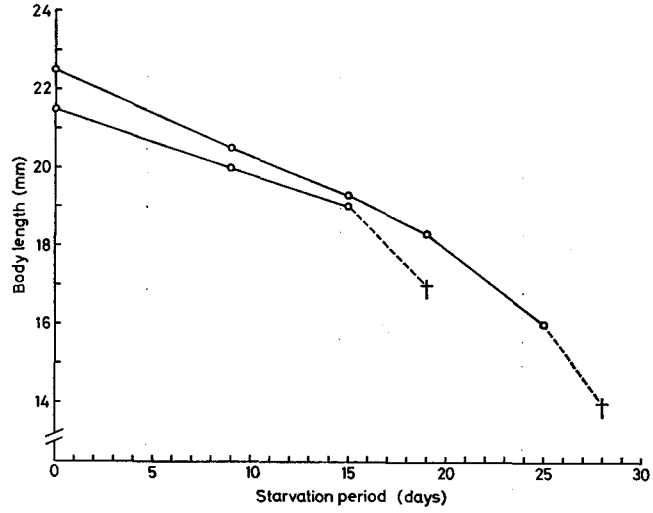

Fig. 20. Shrinkage in body length of 2 specimens of *Sagitta elegans* with the progress of starvation period. The cross denotes the death of animal.

extensive review of Giese (1966) on lipids in marine invertebrates stated that some animals utilized lipids as energy source under the starvation, but other animals metabolized protein or carbohydrate under the condition. In zooplankton, however, carbohydrate cannot be a major metabolite under starvation, because of the small quantity of body content as mentioned above.

In conclusion, although the utilization of metabolic substrates under starvation will vary with the difference of species in zooplankton, a major substrate is two substances, protein and fat. In a prolonged starvation, when fat stored has been exhausted, a major substrate was occupied by protein. In animals such as *Acartia* with little amount of stored fat, protein will be metabolized at the beginning of starvation. From the results of O:N ratio and chemical analysis of the animal body mentioned above, the situation will be analogous in most of temperate, subtropical and tropical zooplankton.

3. *Survival length of zooplankton under starvation*

Ivlev (1955) has first stressed the significance of a phenomenon of starvation in the feeding ecology of fishes. In his starvation experiments on fishes the decrease of body weight during a certain period of starvation was larger in small fishes. Recently, Edwards *et al.* (1971) reported the same fact on tropical fishes. In the present studies showed in Table 11 the temperature and the duration of starvation were not standardized and the calculated daily loss in body weight was 1% for *C. plumchrus*, 6% for *A. clausi* and 1.5% (2–10 days starvation)–16% (0–2 days starvation) for *A. longiremis*. Such a large decrease of body weight in smaller size animals will be caused by a higher metabolic rate per unit weight in smaller animals and the metabolic rate did not decrease so largely under a starving condition. Thus, it is reasonable that the level of weight specific metabolic rate is a major factor which decides the survival length of time of starved animals.

When 1.2 l O_2 is oxidizable 1 g organic matter, the product of (1/1.2) and weight specific respiration rate (μl O_2/mg dry wt/hr) of zooplankton shows the speed of loss in bodily organic matter per 1 hour. Further, the reciprocal of the product becomes the length of time when all bodily organic matter are utilized for the respiration of animals. Hence, the survival time (days) of animals under starvation (SL) will be

$$\mathrm{SL} = 1.2 \cdot 1000 \cdot C/(24 \cdot \mathrm{WRR}) = 50 \cdot C/\mathrm{WRR} \qquad (6),$$

where, WRR is weight specific respiration rate and C is a constant indicating the degree of loss in body organic matter that causes death of animals under starvation. When C is 1, equation (6), means that animals can survive under starved condition by metabolizing the total amount of organic matter in the body. In fact, $C=1$ is unlikely and usually C falls between 0 and 1 ($0<C<1$). To make

sure of the relation between SL and WRR species of boreal, temperate and tropical zooplankton were maintained without food. The relation between the length of time when just a half of initial (0 day's) number of individuals died ($T_{1/2}D$) as a representative value of SL and the weight specific respiration rate at the beginning of starvation was examined. Initial number of individuals varied from 20 to 60 depending on species. Fig. 21 illustrates the result. By using the least square method regression equation between $T_{1/2}D$ and WRR becomes;

$$SL \approx T_{1/2}D = 38.8/WRR + 1.9 \quad (7).$$

From equations (6) and (7),

$$C = 0.78 + 0.038WRR \quad (8).$$

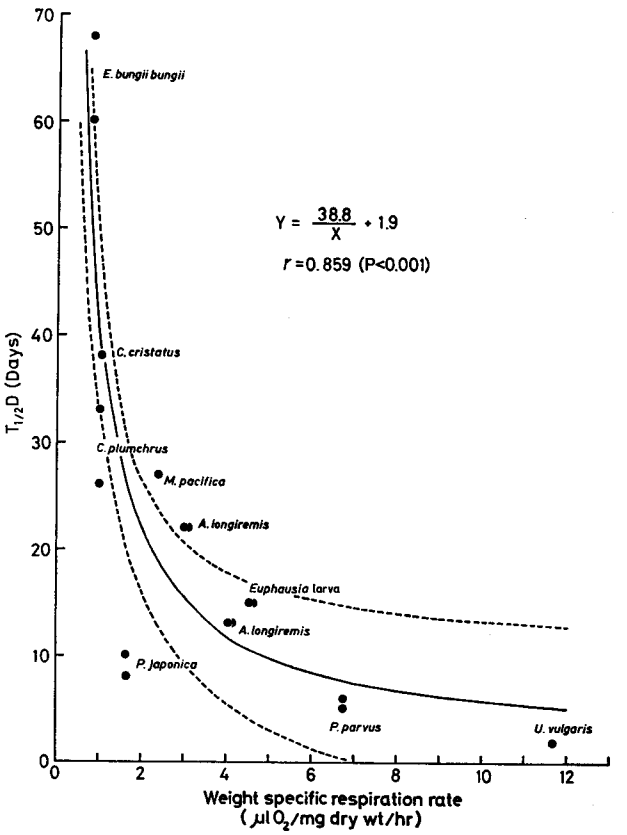

Fig. 21. Scatter diagram showing the relationship between weight specific respiration rate and $T_{1/2}D$ for tropical (*Undinula vulgaris*), temperate (*Paracalanus parvus*) and boreal zooplankton species (*Calanus cristatus* V, *C. plumchrus* V, *Eucalanus bungii bungii*, *Metridia pacifica*, *Acartia longiremis*, *Parathemisto japonica* and euphausiid Cyrtopia larva). Dotted line represents 95% confidence limits of the regression curve. See text.

Equation (8) suggests that the value of C increases with WRR and exceeds 1 when WRR becomes 5.9 (μl O_2/mg dry wt/hr). This is however unreasonable theoretically. Alternative explanation to this is that the degree of reduction of metabolic rate under the starvation, which is not considered in the above calculation, is larger for animals with high metabolic rate than those with low metabolic rate. At any rate, zooplankton seem to be able to survive without food till their body organic matter loss is nearly 80% of the initial amount. Although the differences of chemical composition of the animal body (especially fatty or lean) and the degree of reduction of metabolic rate in experimental animals were not taken into account, a fairly high correlation coefficient (0.859, $P<0.001$) was obtained. The result leads to the conclusion that a main factor which decides the survival time of zooplankton under starvation is the weight specific respiration rate, or body size and habitat temperature of animals. It is reasons that the respiration rate of zooplankton is the functions of the latter two.

The hyperbolic curve in Fig. 21 indicates that for animals with a low weight specific respiration rate, a slight change in the rate results in large effect on the survival time, whereas this effect is not so large for the animals with high weight specific respiration rate. This is very important to the nutritional ecology of zooplankton. For tropical zooplankton with high metabolic rate the reduction of the rate under the condition of food shortage is not an effective survival mechanism. But, the reduction of the metabolic rate has high survival value under the condition of starvation for boreal zooplankton with low metabolic rate, even though the degree of the reduction is small.

In the present starvation experiments, the chemical composition and respiration of animals are probably overestimated, because the animals tested were only those which survived to the end of experiment and animals dying during the course of starvation were not taken into account.

VIII. General discussion on the nutritional ecology of marine zooplankton

It is known that there exists geographical variation in primary production; at high latitudes it is generally high but very variable due to the seasonal variations of solar radiation, water temperature, and of water stratification. Therefore, for animals depending directly on phytoplankton any shortage of foods would be seasonal in these sea areas. In contrast, such seasonal variations are negligible at low latitudes so that the primary production is low but continuous throughout a year (Ryther, 1963; Strickland, 1965). From the present studies the mode of nutrition of zooplankton inhabiting various sea areas seems well fit to the manner of primary production in their habitats.

Tropical species, which are less tolerable to food shortage due to higher metabolic rate and to a lean body, are well adapted to the continuous food production in tropical seas. A higher metabolic rate indicates faster turnover times of some elements in the body of the animal and such a phenomenon would support a continuous but low production of phytoplankton in tropical seas and vice versa. The turnover time of almost all tropical copepods studied here was about 5–10 days in nitrogen and 2–6 days in carbon. While, boreal species with a large amount of fat and with lower metabolic rate due to lower habitat temperature would be well suited to survive through the food shortage periods at high latitudes as was indicated well in Fig. 21. Fat is superior than protein and carbohydrate as energy reserve, for its heat production of unit weight is more than two times that of the latter two. This large deposition of fat in the body has long been known for both invertebrates and vertebrates with no-feeding periods such as migration and hibernation in their life spans (cf. Giese, 1966). Among the boreal species, certain species do not deposit a large amount of fat in the bodies, such typical carnivorous forms as chaetognaths, amphipods and fish larvae. These animals take animal foods which are more stable than plant foods in boreal regions. The difference in chemical composition of the body of zooplankton species also reflected the difference of their metabolites under starvation, i.e., the major metabolite of tropical and boreal species without a large amount of fat is protein and that of boreal species with plenty of fat is fat as supported in the O:N ratio and in the starvation experiments previously discussed.

The habitat temperature and body size are two major factors in the nutrition of zooplankton. There are some reasons to assume that the body size of animals is related to the habitat temperature of animals. This is known as Bergmann's rule (Bergmann, 1847, cited from Mayr, 1971) intraspecifically for warm-blooded vertebrates. In the recent reviews by Kinne (1970) and Garside (1970) the rule of the larger size in the colder habitat held in many marine organisms. In zooplankton, body size-habitat temperature relationship has been also observed (Sverdrup *et al.*, 1942; Wimpenny, 1966). From detailed examination of common taxonomic groups of zooplankton inhabiting surface waters, it is clear that the rule of the larger size in colder habitats was applicable not intraspecifically as Bergmann's rule but interspecifically to copepods of Family Calanidae and to euphausiids of Genus Euphausia in which a large number of herbivorous species is contained (Anraku, 1963; Anraku and Omori, 1963; Mullin, 1966; Nemoto, 1967). The rule is not true for such carnivores as chaetognaths and amphipods.

Larger body size in boreal herbivorous species has a great advantage; it helps the animal to survive food shortage periods because body size is a main factor to determine the survival length of time of animals under the starvation as already mentioned. Thus, the mode of nutrition of zooplankton seems to be well fit to

the condition of food production in their habitats but of their trophic levels also not only.

In the present studies most zooplankton species employed were limited in body size large enough to be sorted by naked eye. However, in natural seas from tropical to boreal areas there exist many zooplankton species too small in size to be sorted by naked eye. A small body size means higher metabolic rate and such an animal requires a continuous supply of food materials. This mode of nutrition is commonly observed in tropical seas as mentioned above. In boreal seas, animals with such a mode of nutrition cannot survive depending on phytoplankton, unless they have resting stages such as resting egg or diapause at unfavorable periods. In marine zooplankton such resting stages are not verified to date (Conover, 1964). Possibly, they may subsist on more stable food sources like omnivorous or carnivorous feeding, or feeding on detritus in boreal seas.

In the seas at higher latitudes, the fauna in neritic areas is different from that in oceanic areas. In neritic areas small size animals such as *Acartia*, *Paracalanus*, cladocerans, etc. are abundant. Generally, standing stocks of phytoplankton and particulate organic matter are richer in neritic areas than in open oceans, though the seasonal change of standing crop is large (Jørgensen, 1966). Considering the food requirement of zooplankton populations, high standing stock of food materials in neritic waters means the superabundance of foods for zooplankton. Such regions are suitable for the inhabitation by small size zooplankton. A large accumulation of fat in the body of neritic zooplankton collected from Oshoro Bay and Nanaehama coast was not observed and this result supports the above assumption.

Conover (1968) maintained, from respiration-body weight relation in zooplankton, that small, tropical or neritic zooplankton was limited in the storage of energy substances. For the justification of his hypothesis the following two assumptions must be allowed in a rigid sense 1) metabolic rate does not decrease significantly under starving, and 2) deposition of large amount of fat as energy reserve is not the case in small neritic species compared to large size oceanic zooplankton. These two assumptions were well proved in the results of the present studies.

Only a few experiments were conducted to determine the metabolic rate of deep-sea zooplankton. The small amount of data obtained suggested that metabolic rate-body weight-habitat temperature relationships of shallow water zooplankton were possibly applicable to deep-water species. The chemical composition of deep-water species collected by means of the MTD net resembled that of boreal species. Raymont *et al.* (1969b) observed large deposition of fat in the body of bathypelagic mysids. Recently, Lee *et al.* (1971) analyzed lipids from various species of copepods collected from wide areas of different waters, and also reported large amounts of lipid in the body of copepods from deep-water and cold water habitats, and the similarity of some chemical nature of lipids of copepods

from both habitats. Thus, some similarities in the mode of nutrition are expected between zooplankton inhabiting deep-waters and those seas at high latitudes. One of the marked difference, however, is the lack of representative herbivorous species in deep-waters. Vinogradov (1962, 1968) discussed food sources of deep-sea zooplankton and proposed a scheme of "ladder migrations" through which organic matter produced in the euphotic layer by photosynthesis of phytoplankton was actively transferred to deep-layers. Usually, food sources for the animals at higher trophic levels are more stable, for they can make good use of adaptations of the prey animals in turn. Therefore, it is reasonable to suppose that the food supply for deep-sea zooplankton is stable. Then, a question arises: why do deep-sea species have fat in their bodies even in the tropical sea areas where food production for zooplankton is largely continuous? The author thinks that the fat deposited in the bathypelagic species is an energy reserve for the youger stages of the next generation, i.e., in deep-layers there would be a shortage in food materials for young animals. The concentration of particulate organic matter is too low to support younger stages (Vinogradov, 1962, 1968) as their locomotive activity is too poor to help them catch and eat prey animals for carnivorous feeding. The production of small numbers of large eggs which is observed in some deep-sea zooplankton (Vinogradov, 1968) assures the hatch out of large larvae and is an adaptation of the same direction. This possible food shortage in the younger stages in deep-sea zooplankton contrasts markedly with the food shortage in older stages for zooplankton inhabiting the seas at high latitudes where rapid development of younger stages concur with the spring blooming of phytoplankton.

IX. Tentative estimation of carbon requirement for respiration and ammonia-nitrogen excretion by zooplankton in natural seas

Although there are many factors which control the size of phytoplankton crop, grazing by zooplankton is the most important factor, especially at high latitudes (cf. Raymont, 1963, 1966). The ecological significance of respiration of animals is largely centered around the estimation of minimum food requirement of animals. Marshall *et al.* (1935) estimated that the daily food requirement for *Calanus finmarchicus* was 1.3–7.6% of its body weight. Menzel and Ryther (1961) reported a daily requirement of 12% of body weight for mixed zooplankton at the Sargasso Sea. Pomeroy and Johannes (1966, 1968) measured directly the respiration rate of ultraplankton (size$<$10 μ) by gentle concentration. From the activity of the respiratory electron transport system Packard *et al.* (1971) estimated indirectly the respiration rate of "plankton", i.e., substances remained on the Gelman type A glass filter, through which the natural sea water filtered. In both cases i.e., Pomeroy and Johannes (1966, 1968) and Packard *et al.* (1971) measurement or estimation concerned organisms which escaped in the usual sampling procedure

with a plankton net.

Harris (1959) studied the nitrogen cycle in Long Island Sound and found that 77% of the nitrogen required daily for phytoplankton growth was supplied by ammonia excreted by zooplankton. Ketchem (1962) emphasized that in many parts of the ocean primary production by phytoplankton would exhaust the available nutrients in the water in a few days, but the production depending upon the direct excretion by zooplankton continues for much longer periods. This process is unquestionably of great importance but it has so far been inadequately evaluated. Recent studies revealed that ammonia was used preferentially by phytoplankton as nitrogen source when both ammonia and nitrate were present in their media (Grant *et al.*, 1967; Strickland *et al.*, 1969). A similar phenomenon was ascertained in the natural sea with the use of ^{15}N-labeled compound (Dugdale and Goering, 1967; MacIsaac and Dugdale, 1972) and it was remarkable in oligotrophic seas (MacIsaac and Dugdale, 1972). Thomas (1967), and Thomas and Owen (1971) also emphasized the significance of ammonia as nitrogen source for phytoplankton in the eastern tropical Pacific Ocean.

The present studies gave a reasonable result for the estimation of carbon requirement by the respiration of "net" zooplankton which was composed of species of various size and for ammonia-nitrogen regeneration by "net" zooplankton in the sea, in consideration of differences in body size and habitat temperature of animals. At first, total respiration of zooplankton (SR) in a certain sea area is given from equation (1) as;

$$SR = a(W_1^b \cdot B_1 + W_2^b \cdot B_2 + W_3^b \cdot B_3 + \cdots + W_n^b \cdot B_n) = a\sum W_i^b \cdot B_i \qquad (9),$$

where, W_1, W_2, W_3,.....W_n are body weight of each zooplankton species and B_1, B_2, B_3,.....B_n are the number of individuals in each body weight category. Little is known of the size distribution of zooplankton. Hence, as a first approximation,

$$W_1 = W_2 = W_3 = \cdots = W_n = \sum W_i / \sum B_i \qquad (10),$$

where, $\sum W_i$ is total biomass in terms of mg dry weight converted from wet weight multipling by 0.1, and $\sum B_i$ is a total of individual numbers in the biomass. Accordingly, equation (9) is rewritten as;

$$SR = a(\sum W_i / \sum B_i)^b \cdot \sum B_i \qquad (11)$$

or

$$\log SR = b \cdot \log (\sum W_i / \sum B_i) + \log a + \log \sum B_i \qquad (12).$$

Here, log a and b are determined by habitat temperature only from equation (4). Then, to convert total respiration to total carbon requirement, it is assumed that assimilation efficiency is 100% and respiratory quotent is 0.7 (fat metabolism) for boreal species and 0.8 (protein metabolism) for tropical species. It is expressed in the following equation,

$$\text{Total carbon requirement} = SR \cdot (0.8 \text{ or } 0.7) \cdot 12/22.4 \quad (13).$$

Similarly, as in equations (10), (11) and (12), ammonia-nitrogen regeneration by total "net" zooplankton biomass is calculated as,

$$\text{Total nitrogen regeneration} = a(\Sigma W_i/\Sigma B_i)^b \cdot \Sigma B_i \quad (14),$$

where, $\log a$ and b are determined from equation (5) by knowing the habitat temperature.

Table 13. *Tentative estimation of carbon requirement for respiration and ammonia-nitrogen excretion by net zooplankton in the euphotic layer of natural seas (95% confidence limits in parenthesis).*

Sea area	Depth of the euphotic layer (m)	Average temp. in the euphotic layer (°C)	Zooplankton standing stock in the euphotic layer (mg dry wt/m²)	*In situ* primary production (mgC/m²/day)	Standing stock of ammonia-nitrogen in the euphotic layer (mgN/m²)	Average body weight of zooplankton (mg dry wt/animal)	Calculated carbon requirement for respiration by zooplankton in the euphotic layer (mgC/m²/day)	Calculated ammonia-nitrogen excretion by zooplankton in the euphotic layer (mgN/m²/day)
Bering Sea[1]	50	5	3112[3]	500[4]	650	0.36	28.6 (12.6-65.0)	5.5 (1.2-24.8)
Northwestern subtropical Pacific[2]	100	25	323[3]	28-53[5]	130	0.051	27.4 (10.7-70.2)	5.6 (0.9-33.8)

1) Average of four stations (52°30', 56°30', 57°30' and 59°30'N on 178°30'W, June 1968)
2) 22°00'N 141°50'E, Jan. 1967
3) Wet weight × 0.10
4) Not simultaneous measurement, but measured in the same month of the previous year
5) Not simultaneous measurement, but obtained near the station

Table 13 shows results calculated from data obtained by the T.S. Oshoro-Maru cruise to the Bering Sea (ocean part) and northwestern subtropical Pacific Ocean. In the Bering Sea, the daily carbon requirement by "net" zooplankton was only about one twentieth of the primary production and the supply of ammonia-nitrogen in the euphotic zone by the excretion of zooplankton was small compared with the large standing stock of ammonia. In the northwestern Pacific, the daily carbon requirement by zooplankton was significant, attaining nearly the same level as primary production. Approximately, one twentieth of the standing stock of ammonia-nitrogen in the euphotic zone is contributed by zooplankton excretion in this area. It must be borne in mind, however, that upper and lower values of 95% confidence limits are fairly large in the estimations of carbon requirement and ammonia-nitrogen excretion through present calculations. Apart from this diffi-

culty, it is noted that zooplankton biomass in the northwestern Pacific is about one tenth of that in the Bering Sea but the daily carbon requirement of zooplankton and nitrogen excretion by zooplankton is almost at the same level as those in the Bering Sea, due to smaller body size and higher habitat temperature. This rapid metabolic rate of tropical zooplankton would be suggestive of the rapid growth rate (or higher production rate) of the tropical zooplankton, as indicated by Engelmann (1969), Hughes (1970) and McNeill and Lawton (1970) on terrestrial and aquatic (benthic) animals.

In the comparison with primary production, the carbon requirement of zooplankton in the northwestern Pacific cannot be compared directly with that of in the Bering Sea, for relative proportion of carnivorous species in the total zooplankton species increase with the rising of habitat temperature (Vinogradov, 1968). Carnivorous species depend on other zooplankton species, which depend primarily on phytoplankton. Thus, more phytoplankton is necessary to support the life of unit biomass of carnivorous forms than that of herbivorous forms, even if both of them have the same metabolic rate because ecological efficiency is always less than 100%.

Of course, this is a tentative calculation and our attention is not focussed on the accuracy of all parameters which affect to the result (error considered in Table 13 is only for the estimation of constants a and b in equations (4) and (5)). This author cannot say how close the result is to natural conditions. A knowledge of the size distribution of zooplankton species is very important for the accurate calculation. In addition, it is not possible to tell how close the rates of respiration and excretion measured on a single species confined to a bottle without food, as in the present studies, are to those in nature. Ikeda (1971a) attempted to measure respiration rate of *Calanus cristatus* under the closed condition of natural habitat of this species in the Bering Sea by means of continuous flow system of natural sea water. The maximum rate obtained was about two times as high as that measured using closed bottle technique adopted here. However, this result is not conclusive because of small amount of data. Petipa (1966) reported from field observation of accumulation and consumption of fat droplets in *Calanus helgolandicus*, that the metabolic rate of this species was 35 times higher than that measured in the laboratory. This finding was denied by Vlymen (1970).* Besides

* In connection with this subject, a recent study by Schmidt-Nielsen (1972) concerning the energy cost of swimming, flying and running of animals is of great interest. He showed that the energy cost increased with the decrease of the body size of the animals in the three types of locomotion. According to his Fig. 1b, the linear relation between the body weight of animals and its energy cost of swimming (cal./g wet wt/km) on log-log graph, energy cost of swimming of *Calanus helgolandicus* weighing 1 mg wet weight (=0.2 mg dry weight) is calculated roughly as 20 cal./g wet wt/km. If it is assumed

plankton animals, there is little information on the respiration rate of aquatic animals under the natural environment. Mishima and Odum (1963) and Edwards (1967) studied the respiration of a mollusc and a fish using Zinc-65 under natural conditions. They found that the rate under such conditions was twice as high as that measured under laboratory conditions. For nitrogen excretion, Corner *et al.* (1965), Conover and Corner (1968) and Butler *et al.* (1970) observed a slowdown of the rates in *Calanus helgolandicus* and *C. hyperboreus* during prolonged starvation periods.

The estimation of the physiological activities of zooplankton in the natural seas has been worked upon by many scientists by means of laboratory studies and field observations (on this account, see the recent review of Mullin, 1969).

In the present studies, an important approach to the nutrition of zooplankton was presented taking into consideration body size and the habitat temperature of zooplankton species.

X. Summary

1) Rates of respiration and ammonia-nitrogen excretion, and the chemical composition (nitrogen, carbon and hydrogen) of zooplankton collected from tropical, subtropical, temperate and boreal waters were studied in relation to their body size and habitat temperature. The zooplankton used for the present studies were 112 species for respiration, 81 species for ammonia-nitrogen excretion and 111 species for chemical composition. In addition, the studies on the chemical composition and the respiration rate of animals under the condition of pressure were carried on deep-sea zooplankton.

2) Both rates of respiration and ammonia-nitrogen excretion of zooplankton are well correlated to the body weight and the habitat temperature of zooplankton. For the animals with W mg dry weight and in the habitat temperature of T°C, the respiration rate R (μl O_2/animal/hr) and rate of ammonia-nitrogen excretion E (μg NH_3-N/animal/hr) is given as;

$\log R=(-0.01089T+0.8918) \log W+(0.02438T-0.1838)$

$\log E=(-0.00941T+0.8338) \log W+(0.02836T-1.3665)$.

3) The ratio of oxygen respired and nitrogen excreted in the form of ammo-

that animals were engaging in a diurnal vertical migration in the order of 100 m, the total energy cost for migration would be 4 cal./g wet wt/day (=3.2 μl O_2/mg dry wt/day). The respiration rate of animals was estimated from equation (4) as 82 μl O_2/mg dry wt/day in the present studies assuming water temperature of 20°C. The result of this calculation suggests that the energy expenditure for swimming by zooplankton is negligible compared with the energy expenditure for maintenance, which were measured in the closed bottles in the laboratory conditions (metabolic rate thus measured fell between standard and activity metabolism). Accordingly, we reached to the same conclusion of Vlymen (1970), but through a different method of calculation.

nia (O:N ratio) was not related to the body weight but to the habitat temperature. This suggests that the major metabolite of zooplankton under starvation was occupied by protein for tropical species, and by fat for some boreal species.

4) The respiration rate of certain bathypelagic zooplankton did not differ so much from the rate predicted by the above equation in the measurement under near *in situ* hydrostatic pressure and habitat temperature.

5) No consistency was observed between the chemical composition, in terms of per cent nitrogen, per cent carbon and per cent hydrogen of dry weight and the body dry weight of zooplankton. Only the percentage of carbon and of hydrogen of dry weight, not the percentage of nitrogen, increased with the decrease of their habitat temperatures. The proportion of organic matter in the body, estimated from the sum total of per cent nitrogen and per cent carbon, decreased with the increase of habitat temperature in all taxonomic groups of zooplankton.

6) The chemical composition of zooplankton is highly variable specifically. But, the ratios of C:N and C:H remaind constant (C:N=3–5, C:H=6–7) without the specific difference. A slight deviation in these ratios was observed in boreal and deep-water species due to the deposition of a large amount of fat in their bodies.

7) From the starvation experiment it becomes clear that the reduction of the respiration rate was not so large, about a half of the initial rate at the most, and the major metabolite in such condition was protein and fat. Further, the factor which decided the survival length of time under the starvation was proved to be body weight and habitat temperature of zooplankton.

8) Tropical zooplankton, which could not survive long under starvation conditions due to a lean body and higher metabolic rate, was well suited to low but continuous primary production in their habitats. In higher latitudes where the variation of primary production was high due to the seasons, zooplankton was characterized by lower metabolic rate, deposition of a larger amount of fat and a larger body size. Such a kind of adaptation was more conspicuous in herbivorous forms than in carnivorous forms in boreal species, while it is not definite in tropical species. The situation between deep-sea zooplankton and boreal zooplankton may be analogous. A possible food shortage for younger stage animals of deep-sea zooplankton in their habitats was suggested.

9) From the difference in body size and habitat temperature of zooplankton, an important approach to estimate the carbon requirement for respiration and ammonia-nitrogen excretion by the total "net" zooplankton populations, in the natural sea, was proposed. Tentative calculations led to the conclusion that the biomass of zooplankton in the Bering Sea corresponded to ten times that in the northwestern subtropical Pacific, whereas the daily carbon requirement and ammonia-nitrogen excretion calculated were almost at the same levels as those in

the northwestern subtropical Pacific.

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Appendix

1. Zooplankters with asterisks were typical herbivores or filter-feeders and those without asterisk were carnivores which were classified by the direct observation by the present author and by referring the previous literatures.

2. In the tables of elemental composition of zooplankton, the figure in parenthesis denotes the number of replication of determinations.

(Usujiri, May-June 1971)

Animals	Sampling date	Experimental temp. (°C)	No. of animals/250 ml bottle
Coelenterata			
Aglantha digitale	May 12	6.5-7.0	1
	May 23	9.6-10.7	3
Ctenophora			
Pleurobrachia pileus	May 17	7.0-7.5	2
	May 17	7.0-7.5	2
Beroe cucumis	June 15	12.6-12.8	1
Pteropoda			
**Limacina helicina helicina*	May 11	4.5-5.5	7
	May 23	9.6-10.7	13
Clione limacina limacina	June 15	12.6-12.8	1
Ostracoda			
Philomedes interpuncta ♂	May 21	8.2-10.5	19
	May 21	8.2-10.5	13
	May 21	8.2-10.5	12
	June 1	7.8-11.8	14
	June 1	7.8-11.8	9
Copepoda			
**Calanus cristatus* V	May 9	5.5-6.5	7
	May 9	5.5-6.5	5
	May 15	6.8-7.0	5
**Calanus plumchrus* IV	May 11	4.5-5.5	19
	May 11	4.5-5.5	10
	May 15	6.8-7.0	38
V	May 11	4.5-5.5	14
	May 11	4.5-5.5	8
	May 14	7.0	19
	May 21	8.2-10.5	13
	May 23	9.6-10.7	15
**Eucalanus bungii bungii* ♀	May 9	5.5-6.5	9
	May 9	5.5-6.5	5
**Pseudocalanus elongatus*	May 12	6.5-7.0	47
	May 12	6.5-7.0	42
	June 13	12.0-12.4	76
**Metridia pacifica* V	May 15	6.8-7.0	34
♀	May 11	4.5-5.5	16
	May 21	8.2-10.5	32
	May 21	8.2-10.5	15
	May 28	8.5-9.7	33
	May 28	8.5-9.7	21
**Acartia longiremis*	May 17	7.0-7.5	75
	May 17	7.0-7.5	98
	May 17	7.0-7.5	97
	May 19	9.0	113
	May 19	9.0	145
	May 30	8.9-11.0	95
	June 3	8.4-11.0	454
	June 3	8.4-11.0	482

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/animal/hr	μl O_2/mg dry wt/hr	μg NH_3-N/animal/hr	μg NH_3-N/mg dry wt/hr	
2.98	4.09	1.37	0.20	0.070	24
3.80	5.38	1.41	0.28	0.074	23
7.50	1.08	0.14	—	—	—
4.10	1.17	0.28	—	—	—
13.94	4.62	0.33	—	—	—
0.421	0.35	0.83	0.043	0.10	10
0.250	0.39	1.58	0.018	0.074	26
22.53	20.0	0.88	3.02	0.134	8
0.608	0.29	0.47	—	—	—
0.630	0.41	0.65	—	—	—
0.588	0.35	0.59	—	—	—
0.596	0.24	0.41	—	—	—
0.556	0.21	0.37	—	—	—
2.27	2.33	1.02	0.184	0.0814	15
1.60	1.74	1.08	0.172	0.107	12
0.892	0.94	1.05	0.137	0.154	8
0.284	0.25	0.87	0.0070	0.024	44
0.289	0.30	1.03	0.0053	0.018	70
0.217	0.29	1.35	0.0092	0.042	39
0.523	0.48	0.93	0.012	0.023	48
0.589	0.63	1.07	0.030	0.051	25
0.759	0.56	0.74	0.015	0.020	46
1.08	0.92	0.85	—	—	—
0.975	0.81	0.83	0.011	0.011	91
1.01	0.84	0.83	0.041	0.041	25
1.01	0.75	0.74	0.074	0.073	12
0.0135	0.039	2.91	0.0025	0.18	19
0.0133	0.033	2.47	0.0029	0.21	14
0.0081	0.047	5.82	0.0014	0.17	42
0.0304	0.063	2.07	0.0039	0.12	20
0.171	0.28	1.69	0.021	0.12	16
0.149	0.63	3.08	—	—	—
0.160	0.45	3.94	0.0061	0.041	93
0.188	0.43	2.33	0.017	0.090	32
0.187	0.44	2.40	0.019	0.10	28
0.0086	0.032	3.72	—	—	—
0.0082	0.024	2.91	—	—	—
0.0076	0.025	3.28	—	—	—
0.0101	0.040	4.03	—	—	—
0.0104	0.034	3.26	—	—	—
0.0088	0.036	4.08	0.0025	0.29	18
0.0068	0.019	2.80	0.0022	0.32	10
0.0068	0.017	2.59	0.0026	0.38	8

Animals	Sampling date	Experimental temp. (°C)	No. of animals/250 ml bottle
**Acartia longiremis*	June 3	8.4-11.0	211
	June 8	11.8-14-3	279
	June 8	11.8-14.3	209
Tortanus discaudatus ♂	May 14	7.0	49
♀	May 14	7.0	22
Mysidacea			
**Siriella* sp.	May 19	9.0	1
**Acanthomysis* sp.	May 30	8.9-11.0	3
Cumacea			
Leptocuma sp.	June 16	12.8-13.3	11
Diastylis sp. ♂	May 15	6.8-7.0	2
	May 15	6.8-7.0	1
Amphipoda			
Parathemisto japonica ♂			
	May 12	6.5-7.0	9
	May 12	6.5-7.0	5
	May 19	9.0	2
	May 19	9.0	2
	May 27	8.9-9.1	7
	May 27	8.9-9.1	5
Pleustes panopla	May 19	9.0	1
Pontogeneia sp. ♀	June 1	7.8-11.8	15
	June 1	7.8-11.8	10
Euphausiacea			
*Cyrtopia larva	May 15	6.8- 7.0	14
	June 8	11.8-14.3	16
	June 8	11.8-14.3	13
**Euphausia pacifica* ♀	May 14	7.0	1
	May 23	9.6-10.7	1
	May 23	9.6-10.7	1
	May 23	9.6-10.7	2
**Thysanoessa longipes* ♂	June 13	12.0-12.4	1
Decapoda			
Macruran decapodid larva	May 14	7.0	8
Eualus gracilirostris	May 12	6.5-7.0	1
Chaetognatha			
Sagitta elegans	May 9	5.5-6.5	6
	May 9	5.5-6.5	4
	May 14	7.0	3
	June 9	12.0-12.5	6
	June 9	12.0-12.5	7
Pisces			
Ammodytes sp. juv.	May 17	7.0-7.5	2

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/animal/hr	μl O_2/mg dry wt/hr	μg NH_3-N/animal/hr	μg NH_3-N/mg dry wt/hr	
0.0070	0.019	2.77	0.0014	0.20	17
0.0076	0.029	3.89	0.0018	0.23	20
0.0073	0.033	4.63	0.0019	0.26	21
0.0449	0.11	2.47	0.0053	0.11	26
0.0689	0.13	1.96	0.010	0.15	16
1.10	2.82	2.55	—	—	—
1.89	3.10	1.64	0.13	0.072	28
0.265	0.35	1.35	—	—	—
3.92	2.01	0.51	0.074	0.019	33
4.93	3.02	0.61	0.076	0.015	49
2.94	3.75	1.27	0.144	0.048	32
1.94	3.37	1.73	0.163	0.084	25
4.69	6.95	1.48	—	—	—
4.57	6.49	1.41	—	—	—
5.76	7.57	1.31	0.497	0.086	19
3.51	6.95	1.97	0.389	0.110	22
2.24	3.21	1.43	—	—	—
0.210	0.20	0.96	—	—	—
0.202	0.25	1.26	—	—	—
0.299	0.30	1.03	0.0095	0.032	40
0.118	0.53	4.51	0.016	0.13	41
0.102	0.46	4.62	0.010	0.10	55
7.78	6.71	0.86	0.12	0.016	65
16.60	17.24	1.03	0.540	0.032	39
13.30	15.77	1.18	0.865	0.064	22
8.94	15.30	1.71	0.939	0.105	20
9.45	15.92	1.68	0.861	0.091	23
0.419	0.45	1.07	0.011	0.026	50
14.95	6.69	0.44	0.23	0.015	36
1.67	1.50	0.90	0.268	0.15	7
1.85	1.69	0.91	0.291	0.15	7
1.35	1.21	0.89	0.096	0.070	15
0.211	0.52	2.46	—	—	—
0.084	0.28	3.34	—	—	—
0.943	1.30	1.38	—	—	—

(Oshoro Bay, June-July 1970)

Animals	Sampling date	Experimental temp. (°C)
Coelenterata		
Rathkea octopunctata	June 10	14.5-17.5
Aglantha digitale	June 10	14.5-17.5
Beroe cucumis	June 11	14.5-16.2
	June 11	14.5-16.2
Pteropoda		
**Limacina helicina helicina*	June 16	14.2-16.8
	June 16	14.2-16.8
Gastropoda		
*Veliger larva	June 14	11.7-16.5
	June 20	15.2-16.4
Polychaeta		
Polynoë larva	June 16	14.2-16.8
Copepoda		
**Calanus tenuicornis* ♀	June 16	14.2-16.8
	June 18	15.0-16.7
	June 18	15.0-16.7
**Calanus plumchrus* III	June 10	14.5-17.5
IV	June 13	11.7-14.5
**Paracalanus parvus*	June 9	14.5-16.3
	June 13	11.7-14.5
	June 13	11.7-14.5
Centropages abdominalis ♀	June 18	15.0-16.7
♂	June 18	15.0-16.7
**Pseudodiaptomus marinus* ♀	June 11	14.5-16.2
♂	June 11	14.5-16.2
♀	June 13	11.7-14.5
♂	June 13	11.7-14.5
**Acartia clausi*	June 9	14.5-16.3
	June 26	13.0-14.0
	June 26	13.0-14.0
Tortanus discaudatus ♀	June 9	14.5-16.3
Cyclopina longicornis ♀	June 11	14.5-16.2
	June 13	11.7-14.5
	June 20	15.2-16.4
Macrosetella sp.	June 20	15.2-16.4
	June 20	15.2-16.4
Oithona fallax ♀	June 26	13.0-14.0
Cumacea		
Lamprops sp.	June 9	14.5-16.3
	June 10	14.5-17.5
Amphipoda		
Corophium uenoi	June 14	11.7-16.5
	June 14	11.7-16.5

No. of animals/ 100 (*) or 250 ml bottle (**)	Average dry weight (mg/animal)	Respiration	
		μl O_2/ animal/hr	μl O_2/mg dry wt/hr
10*	0.0089	0.027	3.02
2*	0.236	1.25	5.29
1**	4.00	3.51	0.87
1**	2.85	2.52	0.88
11*	0.0255	0.037	1.47
4*	0.0313	0.024	0.78
14*	0.0089	0.023	2.58
10*	0.0106	0.0095	0.88
7*	0.0135	0.062	4.62
7**	0.0368	0.34	9.28
2*	0.0307	0.12	4.18
2*	0.0263	0.20	7.73
2*	0.0503	0.29	5.79
4**	0.160	0.31	1.95
13*	0.0032	0.027	8.29
13*	0.0031	0.031	9.92
23*	0.0051	0.035	6.74
4*	0.0180	0.098	5.41
5*	0.0153	0.073	4.75
14*	0.0145	0.101	6.92
31*	0.0096	0.020	2.07
16*	0.0187	0.063	3.39
7*	0.0140	0.041	2.89
8*	0.0101	0.034	3.33
22**	0.0085	0.031	3.67
19**	0.0083	0.028	3.41
5*	0.0251	0.12	5.10
15*	0.0072	0.010	1.39
18*	0.0046	0.019	4.07
13*	0.0036	0.026	6.99
9*	0.0104	0.020	1.93
6*	0.0168	0.020	1.20
18*	0.00033	0.011	34.9
8**	0.0691	0.12	1.73
1*	1.12	1.50	1.34
4*	0.0637	0.071	1.11
11**	0.0598	0.12	2.08

Animals	Sampling date	Experimental temp. (°C)
Decapoda		
Macruran mysis larva	June 9	14.5-16.3
Brachyuran zoea larva	June 9	14.5-16.3
Chaetognatha		
Sagitta minima	June 16	14.2-16.8
Copelata		
**Oikopleura dioica*	June 16	14.2-16.8
	June 20	15.2-16.4
Pisces		
Callionymus sp. juv.	June 10	14.5-17.5
Hexagrammos otakii juv.	June 14	11.7-16.5
	June 14	11.7-16.5

(Oshoro Bay, June-July 1970)

Animals	Sampling date	Experimental temp. (°C)	No. of animals/250 ml bottle
Coelenterata			
Beroe cucumis	July 3	15.0-15.3	1
	July 3	15.0-15.3	1
	July 3	15.0-15.3	1
Copepoda			
**Calanus plumchrus* V	June 28	13.8-14.5	15
	June 28	13.8-14.5	19
	July 9	15.8-16.0	8
	July 9	15.8-16.0	8
**Acartia clausi*	June 28	13.8-14.5	64
	June 28	13.8-14.5	68
	July 5	15.0-15.7	40
	July 5	15.0-15.7	17
Mysidacea			
**Acanthomysis pseudomacropsis* ♀	July 1	14.5-15.3	2
	July 1	14.5-15.3	1
Cumacea			
Lamprops sp.	July 5	15.0-15.7	26
	July 5	15.0-15.7	22
Chaetognatha			
Sagitta minima	July 1	14.5-15.3	5
	July 1	14.5-15.3	5
Pisces			
Scombresocidae sp. juv.	July 9	15.8-16.0	2
	July 9	15.8-16.0	1

No. of animals/ 100(*) or 250 ml bottle (**)	Average dry weight (mg/animal)	Respiratian	
		μl O_2/ animal/hr	μl O_2/mg dry wt/hr
9**	0.0663	0.23	3.57
5*	0.0250	0.092	3.67
5**	0.0404	0.19	4.80
4*	0.0109	0.098	9.01
3*	0.0418	0.20	4.97
1**	1.98	3.76	1.89
1**	0.604	1.73	2.87
1**	3.12	4.58	1.47

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/ animal/hr	μl O_2/mg dry wt/hr	μg NH_3-N/ animal/hr	μg NH_3-N/mg dry wt/hr	
33.24	13.8	0.41	0.841	0.025	20
52.06	14.5	0.27	1.14	0.022	15
71.10	19.2	0.27	1.59	0.022	15
0.314	0.46	1.47	0.057	0.18	10
0.328	0.50	1.53	0.035	0.10	17
0.258	0.58	2.26	0.074	0.28	9
0.276	0.68	2.45	0.099	0.36	8
0.0063	0.013	2.00	0.0035	0.54	4
0.0064	0.030	4.75	0.0071	1.10	5
0.0104	0.035	3.54	0.0050	0.48	8
0.0108	0.044	4.27	0.0074	0.68	7
2.40	4.45	1.85	0.697	0.28	8
3.35	4.26	1.27	0.562	0.16	9
0.085	0.13	1.54	0.022	0.25	7
0.101	0.14	1.39	0.021	0.20	8
0.086	0.34	3.95	0.085	0.98	5
0.156	0.27	1.78	0.036	0.23	9
1.07	2.23	2.07	0.165	0.15	16
1.99	3.71	1.87	0.193	0.096	24

(Kaiyo-Maru, Oct. 1971-Mar. 1972)

Animals	Sampling data	Experimental temp. (°C)	No. of animals/ 250 (*), 300 (**) or 1000 ml (***) bottle
Coelenterata			
Liriope tetraphylla	R12	27.0	1*
	R15	26.6-27.1	2*
Diphyes dispar	R 1	26.3-27.0	2*
Diphyes sp.	R12	27.0	4**
Abyla leuckarti ?	R10	27.4-27.5	2*
Crystallomia sp.	R15	26.6-27.1	1**
Heteropoda			
**Oxygyrus keraudreni*	R20	22.2-22.5	1**
Cardiapoda sublaevis	R17	28.4	1**
	R17	28.4	1**
	R17	28.4	1**
Pteropoda			
**Euclio cuspidata*	R20	22.2-22.5	1***
**Diacrea trispinosa*	R 2	27.3-27.5	1*
**Cavolinia globulosa*	R 2	27.3-27.5	2*
	R20	22.2-22.5	1**
**Cavolinia uncinata*	R14	19.7	1*
Hydromyles globulosa	R 2	27.3-27.5	7*
	R 2	27.3-27.5	6*
	R 2	27.3-27.5	4*
Polychaeta			
Naiades cantrainii	R14	19.7	1**
Tomopteris sp.	R17	28.4	1*
Copepoda			
**Calanus minor* V ♀	R15	26.6-27.1	22*
	R15	26.6-27.1	28*
	R15	26.6-27.1	41*
**Neocalanus gracilis* ♀	R 3	27.8	6*
	R14	19.7	4*
	R14	19.7	4*
**Neocalanus robustior*	R 1	26.3-27.0	6*
**Undinula darwinii*	R 3	27.8	29*
**Undinula vulgaris* ♀	R 4	27.8	16*
	R 4	27.8	11*
	R 5	28.5	13*
	R 5	28.5	10*
	R 5	28.5	5*
	R 6	27.3-27.4	7*
	R12	27.0	9*
	R16	26.4	14*
	R16	26.4	12*
**Eucalanus attenuatus* ♀	R 1	26.3-27.0	9*
	R 3	27.8	8*
	R 3	27.8	9*
	R 6	27.3-27.4	6*
Euchaeta flava ♀	R 6	27.3-27.4	3*

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/ animal/hr	μl O_2/mg dry wt/hr	μgNH_3-N/ animal/hr	μg NH_3-N/mg dry wt/hr	
1.91	0.81	0.42	0.060	0.031	16
2.63	1.81	0.69	0.11	0.042	20
2.40	1.22	0.51	—	—	—
3.05	2.42	0.79	0.084	0.027	35
1.52	0.85	0.56	—	—	—
20.05	11.16	0.55	1.28	0.063	10
14.60	15.11	1.03	0.97	0.066	19
1.24	7.70	6.21	0.45	0.36	21
11.71	14.33	1.22	0.39	0.033	45
10.31	9.90	0.96	0.51	0.049	24
30.00	44.01	1.46	3.8	0.12	14
12.26	6.44	0.52	0.63	0.051	12
14.34	10.20	0.71	1.08	0.075	11
18.65	18.45	0.99	1.73	0.092	13
18.50	11.71	0.63	1.04	0.056	14
2.97	1.89	0.63	0.14	0.049	16
3.75	2.05	0.54	0.24	0.064	10
3.38	—	—	0.19	0.057	—
3.66	8.50	2.32	0.99	0.27	10
2.44	6.16	2.52	0.23	0.094	33
0.0381	0.20	5.26	0.020	0.53	12
0.0412	0.22	5.47	0.023	0.56	12
0.0409	0.21	5.32	0.019	0.47	14
0.195	1.36	6.96	0.10	0.52	16
0.500	1.69	3.38	0.094	0.18	22
0.500	1.59	3.18	0.11	0.23	16
0.217	0.49	2.25	0.037	0.16	16
0.0517	0.19	3.78	0.038	0.74	6
0.166	1.17	7.09	0.104	0.62	14
0.188	1.10	5.89	0.143	0.76	9
0.183	2.16	11.80	0.150	0.81	18
0.176	1.74	9.90	0.131	0.74	16
0.192	2.58	13.42	0.145	0.75	22
0.164	1.06	6.46	0.14	0.88	9
0.142	1.48	10.41	0.10	0.70	18
0.143	0.64	4.52	0.076	0.53	10
0.152	0.66	4.36	0.072	0.47	11
0.0885	0.88	9.94	0.091	1.03	12
0.129	0.84	6.52	0.054	0.42	19
0.131	0.97	7.43	0.049	0.37	24
0.201	0.93	4.64	0.086	0.43	13
0.174	1.05	6.01	0.084	0.48	15

Animals	Sampling data	Experimental temp. (°C)	No. of animals/ 250 (*), 300 (**) or 1000 ml (***) bottle
Centropages brachiatus	R13	17.3	49*
	R13	17.3	38*
Pleuromamma robusta ♀	R 3	27.8	9*
Candacia aethiopica	R12	27.0	8*
Labidocera acuta	R 5	28.5	6*
	R 5	28.5	7*
	R 5	28.5	7*
Labidocera nerii	R16	26.4	5**
	R16	26.4	2**
Pontella danae	R18	26.4	1**
	R18	26.4	2**
Mysidacea			
**Siriella thompsoni*	R 9	27.7-27.8	2*
	R 9	27.7-27.8	2*
Amphipoda			
Scina cornigera	R20	22.2-22.5	1**
	R20	22.2-22.5	1**
Vibilia sp.	R 9	27.7-27.8	3**
	R 9	27.7-27.8	2**
Phronima sedentaria ♀	R 7	27.3-27.4	1**
	R 7	27.3-27.4	1**
	R14	19.7	1**
	R14	19.7	1**
Hemityphis tenuimanus	R16	26.4	3**
	R16	26.4	2**
Thamneus platyrrhynchus	R 7	27.3-27.4	3*
	R 7	27.3-27.4	2*
Oxycephalus porcellus	R 7	27.3-27.4	1***
Euphausiacea			
*Cyrtopia larva	R 3	27.8	4*
	R 3	27.8	7*
**Euphausia diomedeae*	R11	27.2	1**
	R11	27.2	1**
**Euphausia tenera*	R 6	27.3-27.4	1*
	R 6	27.3-27.4	2*
	R10	27.4-27.5	3*
	R10	27.4-27.5	5*
	R10	27.4-27.5	2*
	R12	27.0	2**
	R12	27.0	2**
	R15	26.6-27.1	4**
	R15	26.6-27.1	4**
**Euphausia distinguenda*	R19	25.7	3**
	R19	25.7	2**
**Euphausia krohnii* juv.	R14	19.7	10**
	R14	19.7	7**
Decapoda			
Phyllosoma larva	R 9	27.7-27.8	1***

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/animal/hr	μl O_2/mg dry wt/hr	μg NH_3-N/animal/hr	μg NH_3-N/mg dry wt/hr	
0.0203	0.12	6.20	0.010	0.50	15
0.0192	0.11	6.06	0.012	0.63	12
0.0494	0.61	12.43	0.030	0.62	25
0.103	1.07	10.43	0.075	0.73	17
0.222	—	—	0.15	0.68	—
0.223	1.91	8.53	0.13	0.60	17
0.240	2.23	9.31	0.16	0.67	17
0.214	0.85	3.97	0.078	0.36	13
0.228	2.18	9.57	0.20	0.90	13
0.582	3.14	5.39	—	—	—
0.818	3.72	4.55	0.19	0.23	23
1.62	9.44	5.83	0.74	0.45	15
1.31	5.48	4.18	0.53	0.40	12
2.98	5.04	1.69	0.24	0.083	25
3.00	5.96	1.98	0.26	0.086	28
1.26	6.75	5.35	0.35	0.27	24
1.22	4.60	3.77	0.27	0.22	20
6.86	20.95	3.05	2.16	0.31	12
12.09	43.83	3.62	4.05	0.33	13
7.30	9.83	1.34	0.76	0.10	16
7.28	10.27	1.41	0.69	0.094	18
1.63	3.41	2.08	0.25	0.15	16
1.60	3.05	1.91	0.26	0.16	14
2.78	13.71	4.93	0.70	0.25	24
2.10	6.51	3.10	0.29	0.14	27
17.67	40.97	2.31	4.76	0.26	10
0.588	2.90	4.94	0.14	0.23	25
0.493	1.68	3.42	0.15	0.30	14
5.90	18.81	3.18	1.26	0.21	18
3.27	12.46	3.81	1.11	0.34	13
1.46	6.56	4.48	0.50	0.34	16
0.607	2.29	3.78	0.30	0.50	9
0.382	1.67	4.36	0.34	0.90	6
0.230	1.13	4.92	0.058	0.25	24
0.278	0.80	2.88	0.081	0.29	12
1.13	5.79	5.10	0.44	0.38	16
1.50	7.47	4.98	0.58	0.39	15
0.595	2.29	3.85	0.23	0.39	12
0.748	2.57	3.44	0.28	0.38	11
2.32	5.40	2.32	0.26	0.11	25
1.45	5.69	3.92	0.58	0.40	12
0.274	1.34	4.90	0.12	0.45	13
0.300	1.57	5.23	0.13	0.45	14
91.47	39.15	0.42	5.02	0.054	9

Animals	Sampling data	Experimental temp. (°C)	No. of animals/ 250 (*), 300 (**) or 1000 ml (***) bottle
Puerulus larva	R11	27.2	1***
Megalopa larva A	R 9	27.7-27.8	4*
	R 9	27.7-27.8	4*
Megalopa larva B	R18	26.4	2**
Megalopa larva C	R18	26.4	2**
	R18	26.4	2**
Portunidae sp.	R 4	27.8	6*
	R 4	27.8	5*
Stomatopoda			
Coronideriehthus larva	R11	27.2	1**
	R11	27.2	1**
	R11	27.2	1**
Alima larva	R 2	27.3-27.5	2***
Chaetognatha			
Sagitta enflata	R 6	27.3-27.4	1*
Sagitta bipunctata	R10	27.4-27.5	1*
	R10	27.4-27.5	1*
Sagitta robusta	R 6	27.3-27.4	1*
	R 8	27.4	3*
Sagitta serratodentata	R 8	27.4	2*
	R 8	27.4	3*
Tunicata			
**Iasis zonaria* chain	R12	27.0	1**
**Thalia democratica* sol.	R13	17.3	3**
	R13	17.3	4**
	R13	17.3	4**
**Pegea confoederata* sol.	R19	25.7	1**
	R19	25.7	1**
	R19	25.7	1***
**Salpa fusiformis* chain	R 8	27.4	1**
	R 8	27.4	1**
	R 8	27.4	2**
	R 8	27.4	1**
**Salpa fusiformis* sol.	R13	17.3	1**
	R13	17.3	1**
**Pyrosoma verticillatum*	R19	25.7	1**
	R19	25.7	1***
Pisces			
Cypselurus sp. juv.	R16	26.4	1***
Galeoides sp. juv.	R18	26.4	1***
Longirostrum delicatissimus juv.	R18	26.4	1***
	R17	28.4	1**
	R17	28.4	1**
	R17	28.4	1***
Ranzania laevis Ostracion boops stage	R20	22.2-22.5	3**

Average dry weight (mg/animal)	Respiration		Excretion		O:N ratio by atoms
	μl O_2/animal/hr	μl O_2/mg dry wt/hr	μg NH_3-N/animal/hr	μg NH_3-N/mg dry wt/hr	
50.68	35.14	0.69	—	—	—
2.60	2.11	0.81	0.022	0.009	115
2.66	2.68	1.00	0.070	0.026	47
5.50	10.47	1.90	0.12	0.023	102
8.16	6.11	0.74	—	—	—
7.32	6.18	0.84	—	—	—
1.53	5.03	3.28	0.42	0.27	14
1.61	3.58	2.22	0.30	0.18	14
18.95	28.54	1.50	2.12	0.11	16
16.88	34.02	2.01	1.99	0.11	21
16.09	29.85	1.85	2.03	0.12	18
30.14	15.90	0.52	2.59	0.086	7
0.592	0.92	1.56	0.072	0.12	15
0.400	3.17	7.93	0.081	0.20	48
0.502	2.06	4.12	0.11	0.23	22
1.11	5.27	4.72	0.41	0.37	15
0.391	4.09	10.46	0.23	0.59	22
0.901	4.85	5.39	0.43	0.47	14
0.566	3.09	5.45	0.46	0.82	8
4.94	7.27	1.47	0.20	0.041	44
3.01	2.12	0.70	0.21	0.070	12
3.86	2.05	0.53	0.21	0.056	11
2.04	1.13	0.55	0.13	0.065	10
86.60	32.24	0.37	4.08	0.047	9
42.09	24.28	0.57	2.58	0.061	11
117.20	34.85	0.29	5.32	0.045	8
5.69	13.88	2.44	0.80	0.14	21
6.45	7.11	1.10	0.25	0.039	34
1.91	5.78	3.03	0.23	0.12	30
5.45	14.73	2.70	0.64	0.11	28
13.00	4.04	0.31	0.38	0.029	13
10.27	5.37	0.52	0.43	0.042	15
39.44	13.11	0.33	1.57	0.040	10
90.60	43.87	0.48	5.93	0.065	9
30.52	115.6	3.78	6.58	0.215	21
43.94	197.2	4.48	13.64	0.310	18
23.05	117.6	5.10	8.69	0.377	16
12.20	54.9	4.50	4.47	0.366	15
18.70	85.0	4.54	6.82	0.364	15
64.30	259.0	4.02	23.45	0.364	13
1.67	9.11	5.44	0.81	0.48	13

	Date	Locality	Net used
R 1	Oct. 15, 1971	26°36.4′N 128°26.8′E	Ikeda net
R 2	Oct. 17, 1971	18°11.0′N 119°36.7′E	Fish-larva net
R 3	Oct. 19, 1971	11°38.8′N 112°36.2′E	Ikeda net
R 4	Oct. 21, 1971	05°24.0′N 107°14.7′E	Fish-larva net
R 5	Oct. 22, 1971	02°36.9′N 104°40.6′E	Ikeda net
R 6	Oct. 29, 1971	05°27.0′N 93°30.2′E	Ikeda net
R 7	Oct. 31, 1971	01°54.0′N 84°26.3′E	Fish-larva net
R 8	Nov. 2, 1971	01°46.0′S 76°05.1′E	Ikeda net
R 9	Nov. 4, 1971	05°45.7′S 67°03.0′E	Fish-larva net
R10	Nov. 6, 1971	08°55.2′S 56°18.8′E	Ikeda net
R11	Nov. 8, 1971	13°47.8′S 46°19.8′E	Fish-larva net
R12	Nov. 10, 1971	18°04.9′S 37°55.6′E	Ikeda net
R13	Nov. 23, 1971	30°37.1′S 15°08.5′E	Ikeda net
R14	Nov. 27, 1971	13°48.7′S 00°55.9′E	Ikeda net
R15	Dec. 1, 1971	03°27.5′N 12°23.7′W	Ikeda net
R16	Jan. 27, 1972	14°39.9′N 70°38.5′W	Fish-larva net
R17	Feb. 5, 1972	07°18.2′N 83°16.5′W	Ikeda net
R18	Feb. 7, 1972	09°08.5′N 92°39.9′W	Fish-larva net
R19	Feb. 11, 1972	13°13.4′N 114°34.3′W	Ikeda net
R20	Mar. 1, 1972	24°10.8′N 171°28.0′E	Fish-larva net

(Off Kitami, Sept. 1970) MTD-Horizontal closing net

Animals	Sampling depth (m)	Temp. (°C)	Average dry weight (mg/animal)
Coelenterata			
Halicreas papillosum	566	1.40	38.35
Pterpoda			
Clione limacina limacina	141	0.34	7.10
Copepoda			
**Calanus cristatus* V	35	4.0	1.98
	141	0.34	2.73
	424	1.40	5.95
	566	1.40	8.28
♂	566	1.40	4.31
**Calanus plumchrus* V	35	4.0	0.99
	141	0.34	1.32
	283	0.95	1.69
	424	1.40	1.51
	566	1.40	1.35
**Pseudocalanus elongatus* V	350	1.20	0.02550
			0.02719
			0.02790
			0.02770
Pareuchaeta japonica ♀	424	1.40	6.68
**Metridia okhotensis* ♀	283	0.95	0.43025
			0.45533
			0.40454

Condition of animals analyzed (G: grind) (W: whole)	Percent of body dry weight				Carbon/ Nitrogen
	Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
G(2)	7.2	32.4	5.6	39.6	4.5
G(2)	9.4	52.0	9.1	61.4	5.5
G(3)	11.3	39.8	7.9	51.1	3.5
G(3)	10.9	43.0	8.2	53.9	3.9
G(3)	9.0	57.9	10.7	66.9	6.4
G(4)	9.3	57.2	10.5	66.5	6.2
G(2)	9.1	56.2	9.9	65.3	6.2
G(6)	8.1	57.5	9.7	65.6	7.0
G(5)	8.5	59.7	9.9	68.2	7.1
G(5)	8.4	58.7	9.9	67.1	7.1
G(4)	8.4	60.3	10.2	68.7	7.3
G(6)	8.1	61.4	10.2	69.4	7.6
W	7.2	64.2	9.4	71.4	8.9
W	6.4	66.7	10.3	73.1	10.4
W	6.5	66.6	9.9	73.1	10.2
W	7.2	63.3	9.5	70.5	8.8
G(2)	9.0	58.1	10.3	67.1	6.5
W	8.5	52.8	9.1	61.3	6.2
W	8.4	57.0	10.0	65.4	6.8
W	8.6	53.1	9.0	61.7	6.2

Animals	Sampling depth (m)	Temp. (°C)	Average dry weight (mg/animal)
Mysidacea			
Eucopia sp.	566	1.40	6.82
Meterythrops microphthalma ♂	566	1.40	11.54
Amphipoda			
Primno menevillei	566	1.40	30.83
Euphausiacea			
**Euphausia pacifica*	283	0.95	23.59
Decapoda			
Hymenodora frontalis	566	1.40	12.94
Chaetognatha			
Sagitta elegans	141	0.34	5.97

(Nanae-hama coast, March-April 1971) Water temp.=4.3–6.0°C

Animals	Sampling date	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Coelenterata			
Aglantha digitale	April 4	0.37045	W
Copepoda			
**Eucalanus bungii bungii* copepodid	April 4	0.03595	W
Eurytemora pacifica ♂	April 4	0.01916	W
♂	April 4	0.02531	W
♀	April 4	0.05575	W
**Acartia clausi*	March 28	0.01237	W
	March 28	0.01332	W
	March 28	0.01379	W
	April 4	0.01291	W
	April 4	0.01355	W
	April 4	0.01337	W
Oithona fallax	April 4	0.00565	W
Zaus sp.	April 4	0.01220	W
Cumacea			
Hemilamprops sp.	March 28	0.08725	W
Tanaidacea			
Tanais sp.	March 28	0.14564	W
Amphipoda			
Pleustes panopla	March 28	0.31227	W

Condition of animals analyzed (G: grind) (w: whole)	Percent of body dry weight				Carbon/ Nitrogen
	Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
G(2)	8.4	51.4	8.8	59.8	6.1
G(2)	9.3	45.7	7.5	55.0	4.9
G(3)	7.6	46.7	7.9	54.3	6.1
G(2)	10.6	46.5	7.9	57.1	4.4
G(2)	7.3	59.6	10.2	66.9	8.2
G(2)	12.4	41.0	7.8	53.4	3.3

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Nitrogen +Carbon	
11.0	30.2	4.4	41.2	2.7
9.2	41.0	6.8	50.2	4.4
11.5	45.2	6.4	56.7	3.9
11.0	44.8	6.5	55.8	4.1
12.4	47.1	6.8	59.5	3.8
12.5	43.9	6.2	56.4	3.5
11.7	43.5	6.5	55.2	3.7
11.2	44.7	6.6	55.9	4.0
10.6	45.6	6.5	56.2	4.3
10.8	45.5	6.6	56.3	4.2
10.7	45.6	6.6	56.3	4.3
—	47.8	7.4	—	—
11.1	43.1	5.9	54.2	3.9
9.0	29.5	3.7	38.5	3.3
7.2	33.5	4.6	40.7	4.7
6.6	36.2	5.4	42.8	5.5

Animals	Sampling date	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Decapoda			
Macruran mysis larva	April 4	0.04336	W
Crangon sp.	March 28	0.44661	W
Chaetognatha			
Sagitta elegans	March 28	0.5920	W
	April 4	0.0646	W
Pisces			
Theragra chalcogramma juv.	April 4	0.42615	W
	April 4	0.39409	W
(Usujiri, May-June 1971) Water temp.=4.5–13.0°C			
Pteropoda			
**Limacina helicina helicina*	May 12	0.52792	W
Clione limacina limacina	June 16	22.53	G(2)
Ostracoda			
Philomedes interpuncta	May 20	0.580	G(2)
Copepoda			
**Calanus cristatus* V	June 7	1.53	G(2)
**Calanus plumchrus* IV	May 12	0.65685	W
	May 12	0.28894	W
	May 12	0.32838	W
V	May 12	1.03	G(2)
**Eucalanus bungii bungii*	May 12	0.942	G(2)
	June 7	1.20	G(2)
**Pseudocalanus elongatus*	May 12	0.01636	W
	May 12	0.01500	W
	June 13	0.01117	W
	June 13	0.01073	W
**Metridia pacifica* V	May 16	0.03041	W
♀	June 7	0.21977	W
	June 7	0.22313	W
**Acartia longiremis*	May 16	0.01048	W
	May 16	0.01058	W
	May 16	0.01015	W
	June 9	0.01025	W
	June 9	0.00973	W
Tortanus discaudatus	May 13	0.05027	W
	May 13	0.10035	W
Mysidacea			
**Siriella* sp.	May 20	1.10790	W
**Acanthomysis* sp.	May 31	1.89	G(2)
Cumacea			
Leptocuma sp.	June 17	0.31775	W

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Nitrogen +Carbon	
—	39.2	5.6	—	—
10.3	49.1	6.6	59.4	4.8
9.9	30.6	6.2	40.5	3.1
11.8	39.2	6.7	51.0	3.3
10.8	45.8	7.0	56.6	4.3
10.3	45.8	6.9	56.1	4.4
10.4	29.4	3.8	39.8	2.8
6.1	28.1	4.7	34.2	4.6
4.7	22.5	3.7	27.2	4.8
8.4	49.8	8.2	58.2	5.9
7.6	59.5	9.2	67.1	7.9
8.3	53.9	8.3	62.2	6.5
7.9	55.1	8.8	63.0	7.0
8.0	57.6	9.3	65.6	7.2
9.7	38.3	6.4	48.0	3.9
9.8	41.2	7.1	51.0	4.2
12.4	45.1	6.5	57.5	3.6
12.3	46.5	6.9	58.8	3.8
11.4	46.0	6.9	57.4	4.0
11.7	45.8	6.9	57.5	3.9
9.9	41.2	6.4	51.1	4.2
11.4	47.4	7.3	58.8	4.2
12.0	44.2	6.5	56.2	3.7
12.0	44.4	6.5	56.4	3.7
12.1	44.2	6.3	56.3	3.6
12.3	44.5	6.5	56.8	3.6
11.8	42.1	6.0	53.9	3.6
11.7	41.9	6.0	53.6	3.6
11.1	43.9	6.6	55.0	4.0
11.2	43.9	6.6	55.1	3.9
10.9	39.3	6.0	50.2	3.6
10.7	41.4	6.1	52.1	3.9
5.6	33.8	4.7	39.4	6.0

Animals	Sampling date	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Leptocuma sp.	June 17	0.27416	W
Diastylis sp.	May 16	3.92	G(3)
Amphipoda			
Parathemisto japonica	May 12	1.40	G(2)
	May 26	5.14	G(3)
Pontogeneia sp.	June 13	0.20847	W
	June 13	0.19067	W
Euphausiacea			
*Calyptopis larva	May 16	0.00470	W
*Cyrtopia larva	May 12	0.07056	W
	June 7	0.14902	W
	June 7	0.20857	W
**Euphausia pacifica*	May 24	8.94	G(2)
**Thysanoessa longipes* ♂	June 14	9.45	G(2)
Decapoda			
Macruran decapodid larva	May 15	0.35070	W
Eualus gracilirostris	May 15	0.47977	W
Chaetognatha			
Sagitta elegans	May 12	1.105	G(2)
Pisces			
Ammodytes sp. juv.	May 18	0.97199	W
	May 18	0.91450	W
Theragra chalcogramma juv.	May 23	10.20	G(2)

(Kaiyo-Maru, Oct. 1971-Mar. 1972) MTD-Vertical closing net, Water temp. 3–4°C

Copepoda			
Chirundina streetsi ♀	P1	8.32	G(2)
Metridia princeps ♀	P1	1.05093	W
		1.18945	W
		1.11740	W
Pareuchaeta norvegica V ?	P1	6.66	G(2)
Amphipoda			
Lanceola sp.	P1	2.71	G(2)
Chaetognatha			
Eukrohnia fowleri	P3	3.90384	G(3)
Pisces			
Sternoptyx diaphana	P2	25.28	G(2)

	Date	Locality	Sampling depth
P1	Nov. 1, 1971	01°02.7′N 81°57.0′E	2000–1500 m
P2	Nov. 30, 1971	02°07.0′S 08°11.2′W	2000–1500 m
P3	Jan. 8, 1972	26°30.0′N 17°00.4′W	2000–1500 m

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
6.3	33.8	4.6	40.1	5.4
5.1	29.8	4.1	34.9	5.8
8.2	41.8	6.3	50.0	5.1
7.5	40.5	6.1	48.0	5.4
6.4	26.9	4.0	33.3	4.2
6.3	27.1	4.0	33.4	4.3
12.2	42.5	6.5	54.7	3.5
11.0	43.7	6.5	54.7	4.0
11.5	41.2	6.8	52.7	3.6
11.2	40.6	6.4	51.8	3.6
10.9	41.4	6.3	52.3	3.8
10.5	40.7	6.0	51.2	3.9
10.8	40.8	6.3	51.6	3.8
10.0	38.2	5.9	48.2	3.8
11.7	40.8	7.0	52.5	3.5
11.2	45.8	6.9	57.0	4.1
11.4	45.2	6.9	56.6	4.0
10.4	41.2	6.0	51.6	4.0
8.5	55.6	9.3	64.1	6.5
7.2	48.0	8.2	55.2	6.7
7.8	39.1	6.3	46.9	5.0
7.2	41.1	6.9	48.3	5.7
9.3	45.6	7.5	54.9	4.9
5.6	31.4	4.2	37.0	5.6
8.9	36.4	6.1	45.3	4.1
9.1	35.7	5.0	44.8	3.9

(Oshoro Bay, June-July 1970) Water temp.=11.7–17.5°C

Animals	Sampling date	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Ctenophora			
Beroe cucumis	June 11	100. 24	G(4)
Pteropoda			
**Limacina helicina helicina*	June 16	0. 02552	W
Copepoda			
**Calanus tenuicornis* ♀	June 16	0. 03687	W
**Calanus plumchrus* III	June 13	0. 16079	W
IV	June 28	0. 38640	W
V	June 28	0. 27054	W
	June 28	0. 26299	W
	June 28	0. 36535	W
**Paracalanus parvus*	June 13	0. 00516	W
	June 16	0. 00774	W
**Pseudodiaptomus marinus* ♀	June 10	0. 01845	W
♂	June 10	0. 01491	W
♀	June 11	0. 01454	W
♂	June 11	0. 00961	W
♀	June 13	0. 01874	W
♂	June 13	0. 01403	W
**Acartia clausi*	June 24	0. 00927	W
	June 24	0. 00922	W
	July 5	0. 01089	W
	July 5	0. 01041	W
Macrosetella sp.	June 20	0. 01040	W
Mysidacea			
**Acanthomysis pseudomacropsis* ♀	July 1	2. 46	G(2)
	July 1	2. 14	G(2)
Cumacea			
Lamprops sp. ♂	June 9	0. 06914	W
♀	June 10	1. 12230	W
	July 5	0. 10151	W
	July 5	0. 08544	W
Amphipoda			
Corophium uenoi	June 14	0. 06379	W
	June 14	0. 05980	W
Decapoda			
Macruran mysis larva	June 9	0. 06634	W
Brachyuran zoea larva	June 9	0. 02505	W
Chaetognatna			
Sagitta minima	July 1	0. 15690	W
Pisces			
Scombresocidae sp. juv.	July 9	1. 99063	G(1)
	July 9	2. 15	G(2)

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
3.7	11.3	2.2	15.0	3.1
6.8	25.4	2.5	32.2	3.7
12.0	39.5	5.6	51.5	3.3
8.0	36.2	5.7	44.2	4.5
8.9	49.5	7.8	58.4	5.5
8.7	42.4	—	51.1	4.9
8.8	42.4	7.4	51.2	4.8
9.0	49.5	7.9	58.5	5.5
12.6	37.7	4.6	50.3	3.0
12.8	43.3	—	56.1	3.4
8.4	39.6	—	48.0	4.7
10.1	34.0	—	44.1	3.4
9.3	38.3	4.5	47.6	4.1
7.9	34.2	4.7	42.1	4.3
9.4	39.7	5.3	49.1	4.2
12.8	42.9	4.8	55.7	3.4
13.0	41.7	—	54.7	3.2
12.9	42.1	—	55.0	3.3
12.4	39.9	4.6	52.3	3.2
9.9	42.1	5.6	52.0	4.3
13.1	47.0	6.1	60.1	3.6
10.8	42.6	6.5	53.4	3.9
11.8	45.9	6.7	57.7	3.9
5.7	28.6	3.7	34.3	5.0
7.4	30.0	4.4	37.4	4.1
6.2	28.5	4.2	34.7	4.6
5.4	28.0	4.1	33.4	5.1
7.5	27.0	3.6	34.5	3.6
5.8	27.0	3.9	32.8	4.6
8.3	37.0	5.2	45.3	4.5
9.6	28.6	3.9	38.2	3.0
10.9	35.9	6.2	46.8	3.3
11.2	44.4	6.4	55.6	4.0
11.1	42.0	6.4	53.1	4.0

Animals	Sampling date	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: Whole)
Callionymus sp. juv.	June 10	1.98905	G(2)
Hexagrammos otakii juv.	June 14	0.60469	W
	June 14	3.12	G(1)

(Kaiyo-Maru, Oct. 1971-Mar. 1972)

Coelenterata			
Diphyes dispar	C 3	1.12341	W
Abyla sp.	C10	10.70	G(2)
Heteropoda			
Cardiapoda sublaevis	C18	1.77	G(1)
Pteropoda			
**Cuvierina columnella* f. *columnella*	C 7	6.52	G(2)
**Euclio balantium*	C14	66.30	G(2)
**Cavolinia globulosa*	C 5	90.00	G(2)
**Limacina bulimoides*	C10	0.22902	W
		0.20003	W
Clionina sp.	C14	15.84	G(2)
Hydromyles globulosa	C 2	3.35	G(7)
Polychaeta			
Naiades cantrainii	C12	28.39	G(2)
Tomopteris sp.	C18	0.92246	W
Copepoda			
**Calanus minor* V ♀	C13	0.05106	W
		0.05243	W
		0.04903	W
**Neocalanus gracilis* ♀	C 3	0.22503	W
		0.16677	W
	C11	0.58619	W
		0.65399	W
		0.58386	W
	C17	0.18353	W
**Undinula darwinii* V ♀	C 6	0.06384	W
		0.07357	W
**Undinula vulgaris* ♀	C 4	0.24014	W
		0.22572	W
		0.24718	W
	C 8	0.19710	W
		0.21983	W
		0.21420	W
**Eucalanus attenuatus* ♀	C 3	0.14684	W
		0.12533	W
		0.18438	W
	C16	0.24123	W
		0.27792	W

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
9.0	40.0	6.1	49.0	4.4
9.8	40.8	5.9	50.6	4.2
8.4	40.5	6.0	48.9	4.8
4.1	15.6	2.7	19.7	3.8
6.7	26.0	4.5	32.7	3.9
7.2	31.4	4.2	38.6	4.4
2.5	19.2	1.7	21.7	7.7
3.3	20.5	2.2	23.8	6.2
2.8	19.3	1.7	22.1	6.9
3.7	25.8	3.0	29.5	7.0
3.6	25.8	3.0	29.4	7.2
8.1	39.2	6.2	47.3	4.8
8.4	37.7	5.6	46.1	4.5
8.5	41.0	6.4	49.5	4.8
9.3	40.1	6.1	49.4	4.3
11.3	42.1	6.5	53.4	3.7
11.3	42.9	6.6	54.2	3.8
11.0	42.7	6.5	53.7	3.9
9.5	46.4	7.1	55.9	4.9
9.6	42.3	6.1	51.9	4.4
10.4	45.6	6.7	56.0	4.4
9.8	48.0	7.1	57.8	4.9
10.4	46.4	7.4	56.8	4.5
10.8	43.9	6.9	54.7	4.1
10.7	43.2	6.6	53.9	4.0
10.9	43.2	6.6	54.1	4.0
10.8	43.0	6.3	53.8	4.0
11.1	42.9	6.5	54.0	3.9
11.0	42.6	6.5	53.6	3.9
10.6	40.7	6.3	51.3	3.9
10.8	41.2	6.6	52.0	3.8
10.6	39.9	6.4	50.5	3.8
9.2	39.7	5.9	48.9	4.3
9.3	38.9	6.0	48.2	4.2
9.5	39.7	6.2	49.2	4.2
9.4	38.2	5.8	47.6	4.1
9.4	39.1	6.0	48.5	4.1

Animals	Sampling data	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Undeuchaeta pulmosa ♀	C16	0.40813	W
		0.40741	W
		0.38544	W
Centropages brachiatus	C 9	0.02324	W
		0.02337	W
Labidocera acuta	C 4	0.28367	W
		0.29830	W
		0.25001	W
Labidocera detruncata ♂	C 7	0.14081	W
		0.13651	W
Pontella danae	C19	0.58280	W
		0.81787	W
Isopoda			
Idotea metalica	C10	47.06	G(2)
Mysidacea			
**Siriella thompsoni*	C 8	2.60	G(2)
	C10	4.03	G(2)
Amphipoda			
Vibilia propinqua	C 7	1.02000	W
		1.42661	W
	C 9	2.32	G(2)
Phronima sedentaria	C 5	9.48	G(2)
Hemityphis tenuimanus	C 7	0.66427	W
		0.64875	W
Thamneus platyrrhynchus	C 5	4.15	G(2)
Oxycephalus porcellus	C 5	17.67	G(2)
Euphausiacea			
*Cyrtopia larva	C 3	0.48094	W
		0.39558	W
**Euphausia recurva*	C10	6.52	G(2)
**Euphausia diomedeae*	C 8	0.53087	W
		0.75365	W
		4.71	G(2)
**Euphausia tenera*	C 1	0.60745	W
		0.32175	W
	C13	0.58580	W
		0.70558	W
		0.60048	W
**Euphausia distinguenda*	C18	2.24	G(2)
**Euphausia lucens*	C 9	1.25754	W
		1.65678	W
		0.78295	W
Decapoda			
Phyllosoma larva	C 7	91.47	G(2)
Leptochela sp.	C 4	2.87	G(2)
Megalopa larva	C 5	3.32	G(3)

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
11.0	47.4	7.2	58.4	4.3
11.5	46.0	7.2	57.5	4.0
11.6	45.1	7.1	56.7	3.9
10.1	41.6	6.5	51.7	4.1
10.1	41.8	6.5	51.9	4.1
12.4	43.6	6.6	56.0	3.5
12.2	43.0	6.5	55.2	3.5
12.1	42.8	6.4	54.9	3.5
11.5	43.9	6.7	55.4	3.8
11.5	43.8	6.5	55.3	3.8
11.4	41.2	5.6	52.6	3.6
12.6	44.3	7.1	56.9	3.5
5.1	31.8	4.7	36.9	6.2
9.8	38.6	6.0	48.4	3.9
10.4	42.1	6.3	52.5	4.0
6.8	32.6	4.9	39.4	4.8
6.9	36.0	5.6	42.9	5.2
7.6	36.7	5.6	44.3	4.8
5.1	23.8	3.7	28.9	4.7
4.7	25.2	4.0	29.9	5.4
4.5	25.0	3.9	29.5	5.5
4.0	24.1	3.9	28.1	6.0
5.5	24.1	3.6	29.6	4.4
9.2	42.4	6.7	51.6	4.6
10.0	41.4	6.5	51.4	4.2
10.5	40.2	6.0	50.7	3.8
11.2	38.7	6.4	49.9	3.5
12.0	40.2	6.7	52.2	3.4
9.6	38.0	5.6	47.6	4.0
10.3	39.7	6.2	50.0	3.9
9.5	39.9	5.8	49.4	4.2
9.8	40.9	5.9	50.7	4.2
10.4	40.3	6.5	50.7	3.9
10.3	40.4	6.3	50.7	3.9
10.6	41.3	6.4	51.9	3.9
10.5	41.9	6.6	52.4	4.0
11.8	41.8	6.8	53.6	3.5
11.1	41.1	6.6	52.2	3.7
8.3	45.8	7.2	54.1	5.5
7.3	31.9	4.9	39.2	4.4
3.8	23.4	3.4	27.2	6.2

Animals	Sampling data	Average dry weight (mg/animal)	Condition of animals analyzed (G: grind) (W: whole)
Megalopa larva	C 8	8.60	G(2)
Portunidae sp.	C 4	1.85	G(2)
Stomatopoda			
Coronideriehthus larva	C 8	20.24	G(2)
Alima larva	C 4	3.50	G(2)
Insecta			
Halobates sericeus	C19	2.21	G(2)
Chaetognatha			
Sagitta hexaptera	C16	1.10	G(2)
Sagitta enflata	C18	2.45	W
		0.304	G(2)
Tunicata			
**Thetys vagina* sol.	C12	847.70	G(3)
Pisces			
Sardinops sp. juv.	C15	0.54432	W
		0.73256	W
Myctophum spinosum	C 5	70.81	G(2)
Longirostrum delicatissimus	C18	31.73	G(2)

	Date	Locality		Surface temp. (°C)
C 1	Oct. 15, 1971	25°13.0′N	127°03.0′E	26.4
C 2	Oct. 17, 1971	18°11.0′N	119°36.7′E	27.8
C 3	Oct. 19, 1971	11°38.8′N	112°56.2′E	28.1
C 4	Oct. 21, 1971	05°24.0′N	107°14.7′E	28.0
C 5	Oct. 31, 1971	01°54.0′N	84°26.3′E	27.4
C 6	Nov. 2, 1971	01°46.0′S	76°05.1′E	27.7
C 7	Nov. 4, 1971	05°45.7′S	67°03.0′E	28.0
C 8	Nov. 8, 1971	13°47.8′S	46°19.8′E	26.9
C 9	Nov. 23, 1971	30°37.1′S	15°08.5′E	17.3
C10	Nov. 25, 1971	22°05.8′S	07°46.4′E	19.0
C11	Nov. 27, 1971	13°48.7′S	00°55.9′E	19.5
C12	Nov. 29, 1971	05°13.9′S	05°43.0′W	23.9
C13	Dec. 1, 1971	03°27.5′N	12°23.7′W	26.9
C14	Dec. 3, 1971	12°33.5′N	18°14.8′W	26.9
C15	Dec. 4, 1971	15°10.8′N	17°14.5′W	25.4
C16	Jan. 19, 1972	26°54.9′N	27°40.5′W	20.0
C17	Jan. 21, 1972	25°24.9′N	38°28.7′W	21.8
C18	Feb. 5, 1972	07°18.2′N	83°16.5′W	28.4
C19	Feb. 7, 1972	09°08.5′N	92°39.9′W	26.4

Percent of body dry weight				Carbon/ Nitrogen
Nitrogen	Carbon	Hydrogen	Carbon+ Nitrogen	
5.1	31.0	5.0	36.1	6.1
6.2	29.3	4.2	35.5	4.7
7.7	40.5	6.4	48.2	5.3
8.6	39.9	6.2	48.5	4.6
8.3	54.6	8.2	62.9	6.6
7.8	33.5	4.9	41.3	4.3
8.4	36.4	5.1	44.8	4.3
7.4	33.6	4.9	41.0	4.5
0.4	4.6	1.6	5.0	11.5
9.5	39.7	5.6	49.2	4.2
10.5	40.8	6.3	51.3	3.9
9.7	37.3	5.6	47.0	3.8
10.9	39.8	5.9	50.7	3.7