ECOLOGICAL STUDIES ON *NEOMYSIS INTERMEDIA* CZERNIAWSKY POPULATION IN A HYPEREUTROPHIC LAKE

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ABSTRACT

The environmental control on an animal population in the field was investigated using a zooplankton species, Neomysis intermedia. The growth of individual animals was particularly emphasized. The study was conducted using the approach of experimental ecology in the hypereutrophic lake, Lake Kasumigaura, and in the laboratory.

The observations made in the lake revealed the following three new ecological characteristics of the species. (1) N. intermedia showed conspicuous diel vertical movements at all growth stages throughout the year. The mysids concentrated near the lake bottom during the daytime and dispersed throughout the whole water column at night, and the movement timing closely correlated with sunset and sunrise. (2) The distribution of the mysids was uniform over the whole lake area from offshore to the nearshore region throughout the year. (3) Frequent weekly samplings revealed that there were two bursts of N. intermedia population in spring and in fall, reaching more than 10,000 individuals per m^2 or 5 g dry weight per m^2. Mysid density extremely decreased in summer and in winter to less than 100 individuals per m^2 or 0.05 g dry weight per m^2.

The individual growth of the post-embryonic mysid can be visualized from three aspects of the growth pattern; the initial and the maturation body weights, and the growth

rate. The cohort analysis of the two overwintering populations and 5 spring cohorts, recognized over a 2-yr period, gave the *in situ* growth of *N. intermedia* at the post embryonic stage. Increase in body weight was almost exponential with time, and the specific growth rate determined varied between 0.001 and 0.16 (day^{-1}), which showed a strong correlation with temperature. The average size of newborn individuals was consistent regardless of seasons, but the average maturation size was highly temperature dependent.

The temperature effect on the growth of post-embryonic stage *N. intermedia* was evaluated under no food limitation in the laboratory. A negligibly small effect of temperature on the body size of newly released animals was confirmed, and an inverse relationship between body size and temperature was also confirmed. Individual *N. intermedia* showed a rectilinear growth pattern against time at every temperature, both in body length and in log-transformed body weight. The growth rate at the post-embryonic stage increased exponentially with Q_{10} of 4.6 from 0.018 day^{-1} at 3°C to 0.21 day^{-1} at 20°C in juveniles, and with Q_{10} of 2.7 from 0.006 day^{-1} at 3°C to 0.05 day^{-1} at 25°C in adults including males and females. The daily reproduction rate increased exponentially with Q_{10} of 3.2 from 0.009 day^{-1} at 10°C to 0.05 day^{-1} at 25°C. The growth rates determined at different temperatures in the laboratory were identical to those in the field, which

confirmed that the growth rate of N. intermedia was primarily controlled by temperature in the field.

The large temperature dependency of the growth of N. intermedia was further investigated in terms of metabolic activities; ingestion, egestion, molting, respiration, and leakage/excretion. The rates of growth, ingestion, egestion, and molting all showed a large temperature dependency. However, the rates of respiration and leakage/excretion were lesser affected by temperature. Due to the small allocation percentages of the assimilated materials for the molting and leakage/excretion, their effects on the growth process can be ignored. The strong temperature dependency of the growth rate of N. intermedia then mainly resulted from the large temperature dependency of the ingestion and assimilation rates, and furthermore, from the amplified effects created by the difference in temperature dependency between respective metabolic activities.

The temperature effects on the individual growth of N. intermedia can be summarized as follows; the initial body weight had no temperature dependency, and the maturation body weight and the specific growth rate both had temperature dependencies of $Q_{10} = 1.7 - 1.8$ and $Q_{10} = 4.6$, respectively. The maturation time, which reflected the combined effects of the three growth aspects mentioned above, had then the greatest temperature dependency of $Q_{10} = 5.4$.

ACKOWLEDGEMENTS

I would like to express my great appreciation and thanks to Professor Shun-ei Ichimura and Dr. Masayuki Takahashi for guidance and support during the course of this study.

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CHAPTER I

General Introduction

There is a tremendous number of populations on the earth. These populations are believed to be under the control of various environmental factors which include both biological and non-biological parameters. In order to continue to exist, the population must have a zero or positive increasing rate. Otherwise if the population has a negative increasing rate, it will become extinct with time. All populations should have their own survival strategy for existence against environmental pressures.

The increase of an animal population is supported by the growth of individual organisms which constitute the population. It is therefore essential to analyze individual growth under natural conditions, and study the environmental controlling mechanisms on growth in order to understand the maintaining mechanisms of an animal population. The individual growth of a given animal species is controlled by various environmental parameters. Among those parameters, temperature and food availability are considered to be of great importance for growth.

Laboratory growth experiments on marine copepods indicate that the growth rate is proportional to food concentration to some extent (Paffenhöfer, 1976; Paffenhöfer and Harris, 1976; Harris and Paffenhöfer,

1976), and is strongly influenced by the quality of food (Mullin and Brooks, 1970; Paffenhöfer, 1976). Under a condition of no food limitation, the growth rate of copepods increased with an increase in temperature (Mullin and Brooks, 1970; Landry, 1975). Recently, Vidal (1980a, b) found the combined effects of both food concentration and temperature on the growth of two species of marine planktonic copepods in a laboratory.

Under natural conditions, the respective effects of temperature and food on the growth of zooplankton vary spacially and temporally. For example, in tropical and sub-tropical waters, where temperature varies within a small range, the growth of zooplankton is intensively affected by food concentration (e.g. Elmore, 1983). On the other hand, temperature is more effective than food at the higher latitudes, where seasonal variation of temperature is large (e.g. Deevey, 1960) and food is generally sufficient (McLaren, 1978). Food quantity and quality, however, often varies with temperature in temperate waters, where both temperature and food possibly affect the growth of zooplankton (Landry, 1978).

A question is how these environmental parameters control the individual growth of zooplankton under natural conditions. Such a question can be answered from a study visualizing the actual growth pattern of zooplankton under natural conditions, and experimentally analyzing the environmental controlling mechanisms on the growth process

under defined conditions.

In the present study the environmental controlling mechanism on the individual growth of a zooplankton population in the field has been evaluated by a procedure of experimental ecology. A mysid shrimp, Neomysis intermedia Czerniawsky, was chosen for the species to be studied, which is the most abundant zooplankton in the hypereutrophic lake, Lake Kasumigaura (Toda et al., 1982). Field observations and laboratory culture experiments were both intensively conducted for the determination of the environmental parameters which primarily affect the individual growth. A particular emphasis has further been made on the evaluation of environmental control on various growth processes, which are studied physiologically under defined culture conditions. The content of this study has been partially published elsewhere (Toda et al., 1981; Toda et al., 1982; Toda and Takahashi, 1982; Toda et al., 1983a, 1983b, 1983c).

CHAPTER II

Ecological Characteristics of *Neomysis intermedia* Population in a Lake

II-1. Introduction

The first description of the opposum shrimp, *Neomysis intermedia* Czerniawsky, in Japan was made by Ii (1954), who described the morphological characteristics of adults of the species, and reported that the species was distributed in brackish waters in the northern part of the Japanese Islands. It is now believed that Lake Kasumigaura is the southern limit of the geographical distribution of *N. intermedia* (Murano, 1963). In the 1960s, Murano made extensive studies on the life history of *N. intermedia*, and described the morphological changes at the embryonic stage, growth rate, and the generation time under a given laboratory condition (Murano, 1964a, b). However, there has been no information available for the behavior of individual animals, their areal distribution, and the temporal changes in abundance of *N. intermedia* under natural conditions.

Some mysid species have been known to show the diel vertical movements associated with the change in solar radiation even in shallow estuaries; *Neomysis americana* (Hulburt, 1957; Herman, 1963) and *Neomysis mercedis* (Heubach, 1969). In addition to the vertical movements,

the heterogenous horizontal distribution was also reported for those mysids (Hulburt, 1957; Heubach, 1969; Siegfried et al., 1979). Furthermore, the active aggregation behavior was often noticed for many mysid species. A shoaling behavior was observed for Mysidium columbiae (Steven, 1961), for Mysis gaspensis (Dadswell, 1975), and for Neomysis japonica and Acanthomysis sp. (Omori and Hamner, 1982). Some nearshore mysids such as Metamysidopsis elongata formed a zonation parallel with the shoreline (Clutter, 1967). Zelickman (1974) observed the swarming behavior of Neomysis mirabilis in a laboratory as well as in the field. Morgan and Threlkeld (1982) recorded the seasonal horizontal migration of a Mysis relicta in a freshwater lake.

In this chapter, the behavioral vertical movements and areal distribution of Neomysis intermedia in Lake Kasumigaura are described. The seasonal change in abundance and composition of the mysid population in the lake are then described based on the data collected frequently with special care concerning the specific characteristics of behavior and distribution of the mysid.

II-2. Materials and Methods

Study Area

Lake Kasumigaura is a shallow lake with a mean depth of 4 m, maximum depth of 7 m, and a surface area of 168 km^2 (Fig. 1). The lake bottom is mostly mud, while some

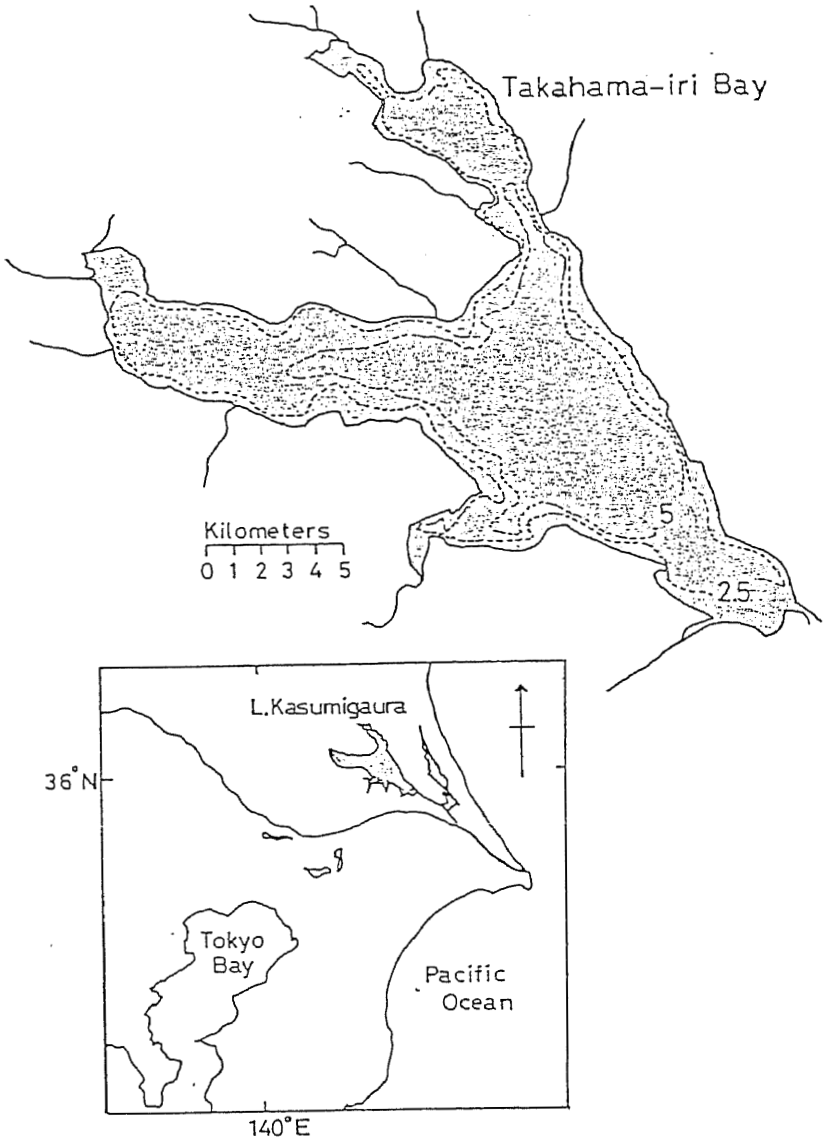

Fig. 1. Geographical location and morphometry of Lake Kasumigaura. Dotted line indicates depth contour at 2.5 m intervals.

nearshore areas are sandy. Drainage into the lake is supplied from more than ten small rivers around the lake, and in turn, the lake water discharges through one river at the southern end to the Pacific Ocean which is less than 40 km away. The lake is approximately 1 m above mean sea level. The simple turnover rate of lake water is estimated to be 7 months. A sluice gate constructed at the outlet in 1963 stopped the intrusion of seawater into the lake. Presently the chlorinity, assumed to be of marine origin, is 20 - 60 mg $Cl \cdot l^{-1}$. Prevailing seasonal winds keep the lake water well mixed vertically. The lake became eutrophied in the early 1900s, and its eutrophication process has been accelerated markedly since 1965 (Toda et al., 1981).

Collection of mysids

Mysids in a water column were collected by horizontal tows at a speed of about 0.5 $m \cdot sec^{-1}$ over a distance of 20 - 40 m with an ordinary plankton net (mouth area 0.102 m^2, mesh size 297 μm) or a quadrangular net (mouth area 0.3 m^2, mesh size 630 μm). Mysids near the lake bottom were collected with the quadrangular net attached to a sled. Mysids in a whole water column were sampled at night by vertical tows from the bottom to the surface with the quadrangular net or a conical net (mouth area 0.2 m^2, mesh size 493 μm) in the offshore region (depth > 2 m), or in the daytime by vertical push from the surface to the bottom with a macroplankton net (mouth area 0.25 m^2 or 0.5

m^2, mesh size 493 μm) in the nearshore region. The macroplankton net is designed to close at the lake bottom when a string attached to the frame is pulled, and can collect the mysids near the lake bottom (Yamamoto and Seki, 1979).

Treatment of samples

The samples of mysids were immediately preserved in 5 - 10% formalin. After September 1980, sucrose was added to the sample at the final concentration of 50 $g \cdot l^{-1}$ in order to reduce the loss of eggs from the marsupium (Toda and Takahashi, 1982). All individual mysids in whole samples or subsamples were counted, and their wet weights were determined with an electrobalance after the removal of excess water by absorption paper. The wet weight was converted to dry weight using a conversion factor of 0.176. Mysid individuals examined were classified into 3 major groups according to the growth stage and sex; juvenile, male, and female. It was further distinguished whether males and females were in the mature or immature stages whenever required. Males and females were identified by the presence of a penis or of a marsupium, respectively. Males with the 4th pleopod longer than the base of telson and females bearing embryos were treated as adult mysids. All others which did not show sex characteristics mentioned above were classified as juveniles.

Determinations of environmental parameters

Water temperature was measured with a mercury thermometer or a thermistor thermometer. Light intensity was measured with a quantum meter (Lambda, LI-185). Chlorinity was determined by the Mohr's silver titration method.

II-3. Results and Discussion

II-3-1. Diel vertical movement of N. intermedia in Lake Kasumigaura

Diel changes in the vertical distributions of the mysid collected from Stns. 2, 3, and 6', representing the different depths (Fig. 2), showed almost the same pattern throughout the year. Representative patterns are shown in Figs. 3 and 4. In both cases, mysids concentrated near the lake bottom during the daytime and they began to disperse upward in the evening just after sunset, distributing throughout the whole water column during the night. Early next morning, mysids moved to the deeper layer and again formed a dense population near the bottom. Although some differences have been reported in the vertical distribution of mysids between different growth stages (Beeton, 1960; Herman, 1963), the diel vertical movement of N. intermedia in the present study was fairly similar at all stages in both sexes, except that large mature mysids tended to accumulate at deeper layers even

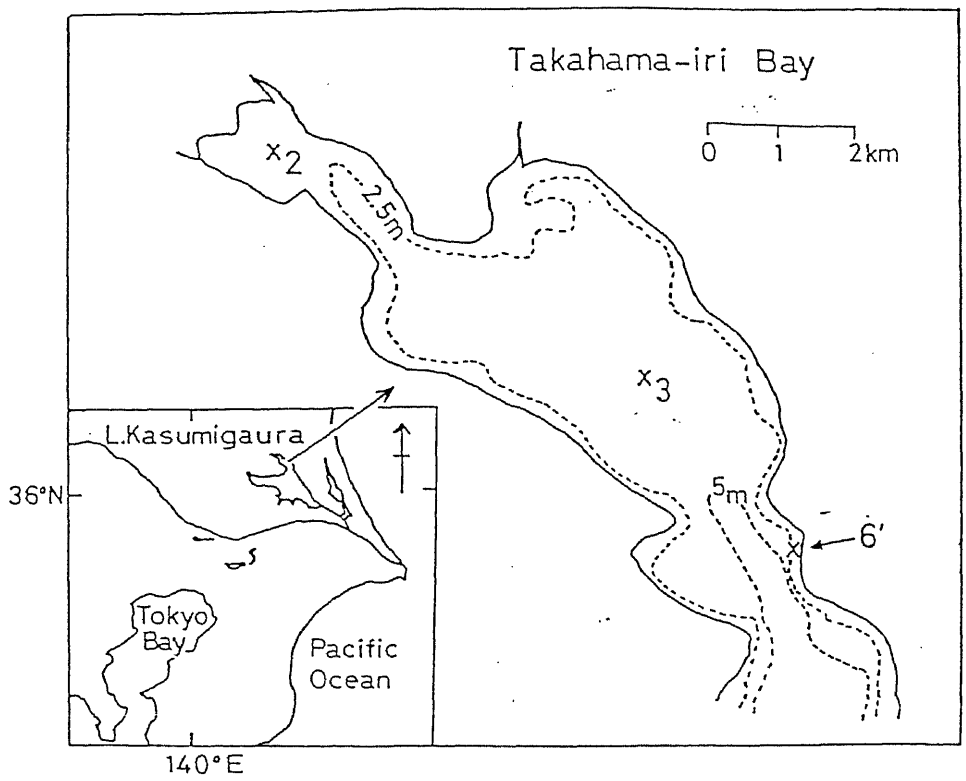

Fig. 2. Takahama-iri Bay of Lake Kasumigaura and sampling stations (x). Depth contour interval is 2.5 m (dotted line).

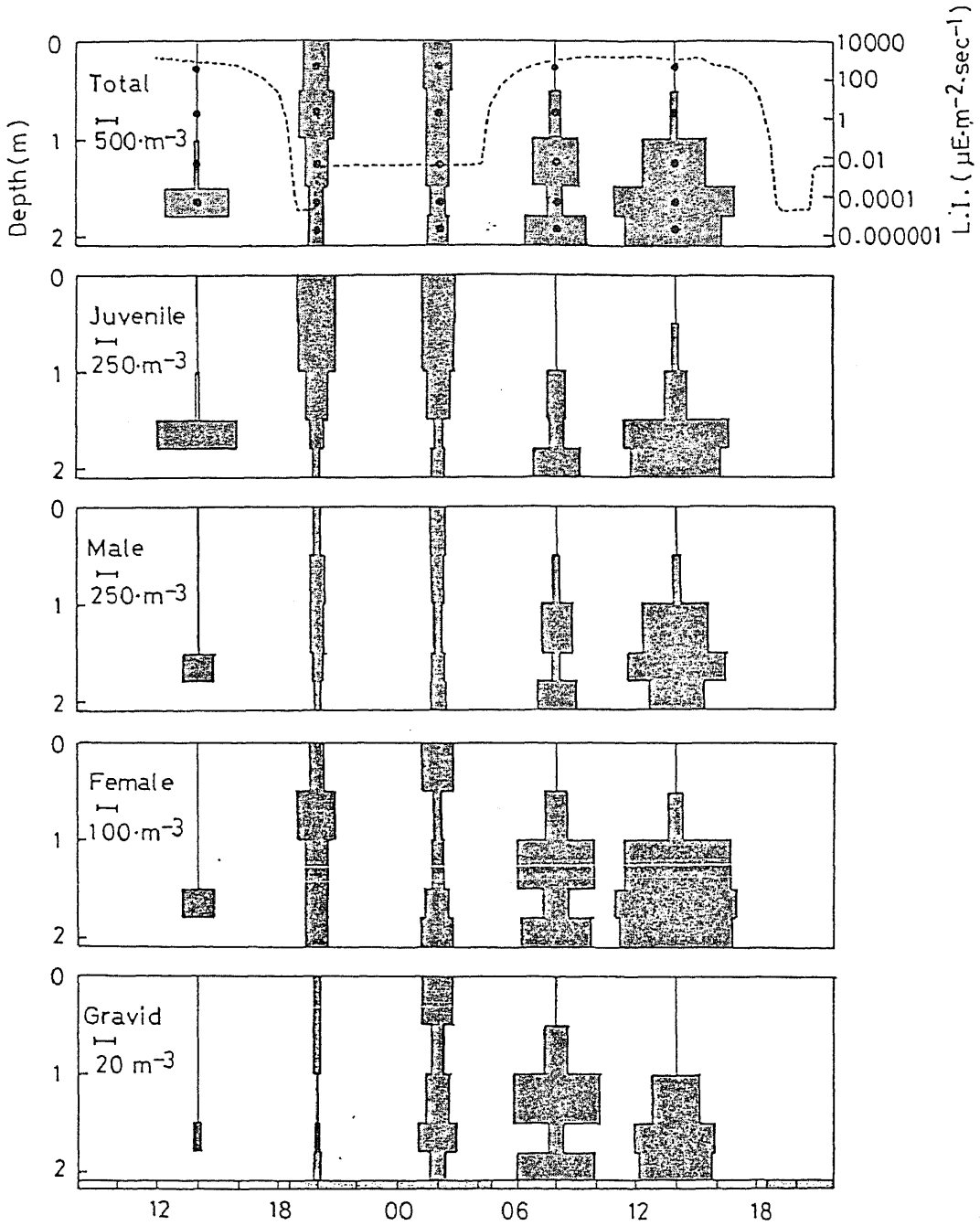

Fig. 3. Diel changes in the vertical distribution of N. intermedia and the surface light intensity (dotted line) on 2 - 3 May 1980 at St. 6'. Black circles indicate the center position of net mouth.

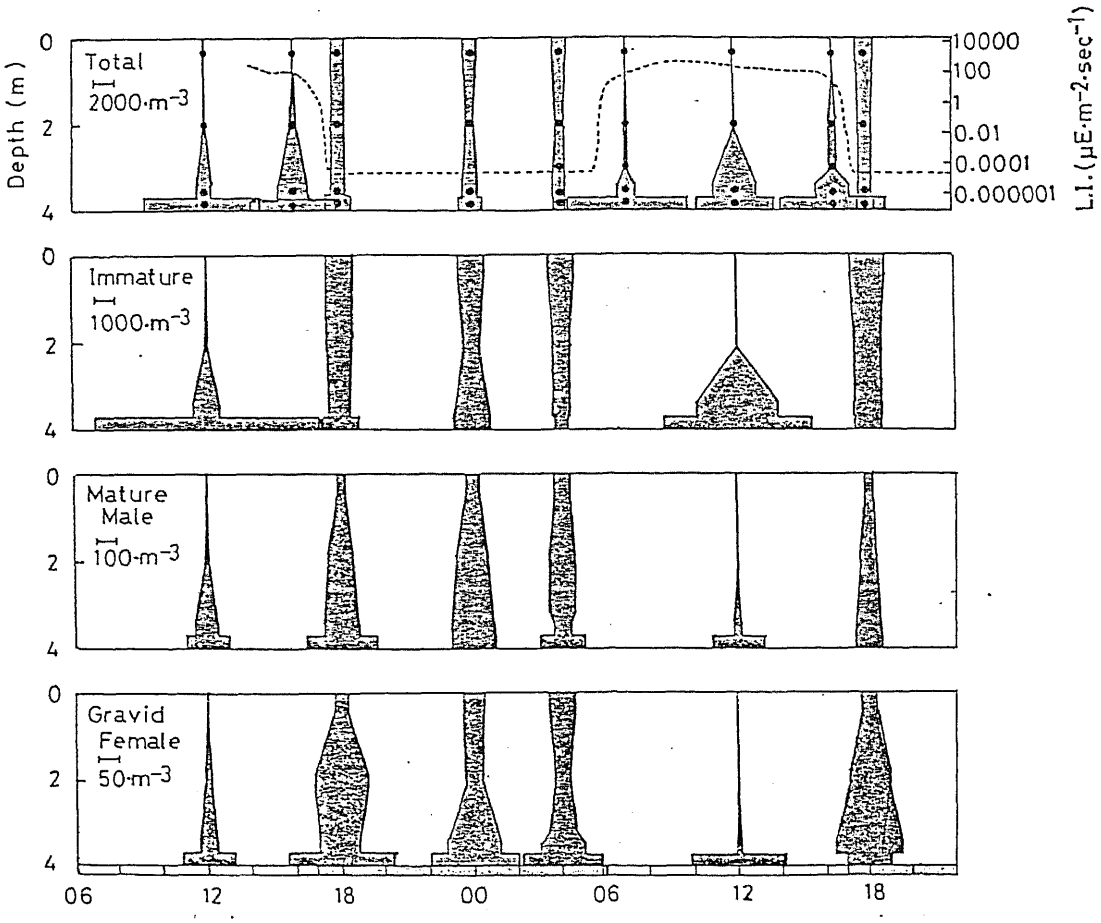

Fig. 4. Diel changes in the vertical distribution of N. intermedia and the surface light intensity (dotted line) on 18 - 19 October 1980 at St. 3. Black circles indicate the center position of net mouth.

during the night (Fig. 4).

Although no actual data are presented here, several following irregular distribution patterns of the mysids were noticed. On a dark rainy day in July, a considerable amount of mysids was collected in the water column about one hour before sunset, and in February many mysids were distributed at the intermediate depth of water in the morning. Another exception in the diel vertical movement of mysid population was observed in a shallow nearshore region, where the mysids formed a dense swarm in winter. They appeared near the surface even during the daytime.

It has been known that light controls the distribution of mysids. Heubach (1969) stated that the distribution of N. mercedis in the daytime was clearly defined in the water column by a certain critical light intensity (10^{-5} lux = 1.9 x10^{-7} $\mu E \cdot m^{-2} \cdot sec^{-1}$). The light intensity at the surface of Lake Kasumigaura was 10^{2} - 10^{3} $\mu E \cdot m^{-2} \cdot sec^{-1}$during the daytime and was expected to be 10^{-5} - 10^{-3} $\mu E \cdot m^{-2} \cdot sec^{-1}$ during the night according to Beeton (1960) (Figs. 3 and 4). Figure 5 shows the vertical profiles of light intensity and temperature in Lake Kasumigaura. Light reduced rapidly with depth, and the calculated extinction coefficients ranged from a minimum of 2.4 (m^{-1}) in February with low algal biomass to a maximum of 4.2 (m^{-1}) in July when blue-green algae grew densely. Consequently the relative light intensity near the lake bottom was estimated to be 0.003 - 0.9% of the

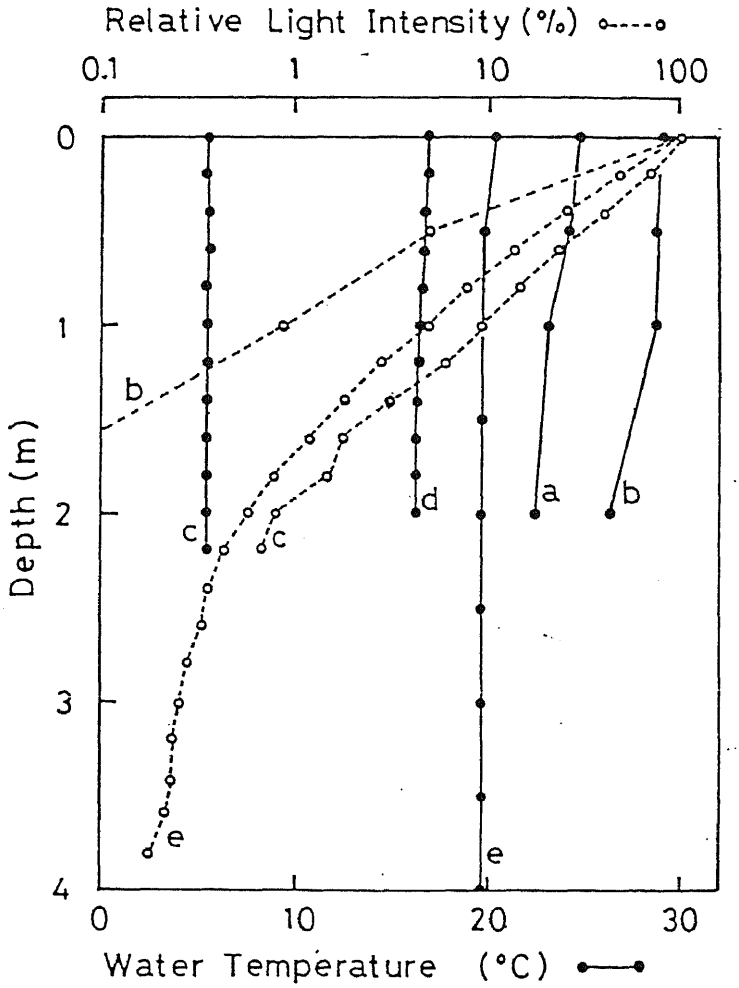

Fig. 5. Vertical profiles of water temperature (solid line) and relative light intensity (dotted line): a, 4 June 1979 (cited from Aizaki et al., 1981); b, 25 July 1979 (cited from Aizaki et al., 1981); c, 9 February 1980; d, 2 May 1980; e, 19 October 1980.

surface light intensity, which corresponded to 3×10^{-3} - 0.9×10^{1} $\mu E \cdot m^{-2} \cdot sec^{-1}$ during the daytime.

For the evaluation of possible relationship between light intensity and mysid movement, the timing of diel movement was further examined by surface sampling made at short time intervals of 30 - 60 minutes. Two examples obtained under short and long day conditions are shown in Fig. 6. Under a short day condition in February (Fig. 6a), the biomass of mysids in the surface layer began to increase rapidly just after sunset when surface light intensity decreased from 10^{0} to 10^{-5} $\mu E \cdot m^{-2} \cdot sec^{-1}$. Three peaks were noticed at 18:30, midnight, and 05:00. They almost completely disappeared from the surface layer before sunrise when surface light intensity sharply increased from 10^{-5} to 10^{0} $\mu E \cdot m^{-2} \cdot sec^{-1}$. Under a long day condition (Fig. 6b), the mysid biomass in the surface layer also began to increase just after sunset when surface light intensity greatly decreased. The biomass reached a peak at 19:30, decreased at midnight, and again increased at 03:00 - 04:00. An abrupt decrease in mysid biomass occurred after 04:00, when surface light intensity sharply increased; a very small amount of mysids remained in the surface layer just before sunrise. Mysids appeared in the surface layer by 18:00 in February and by 19:00 in May, and disappeared by 06:30 in the former and by 04:30 in the latter. Mysids appeared about one hour later and disappeared two hours earlier during a long day as opposed

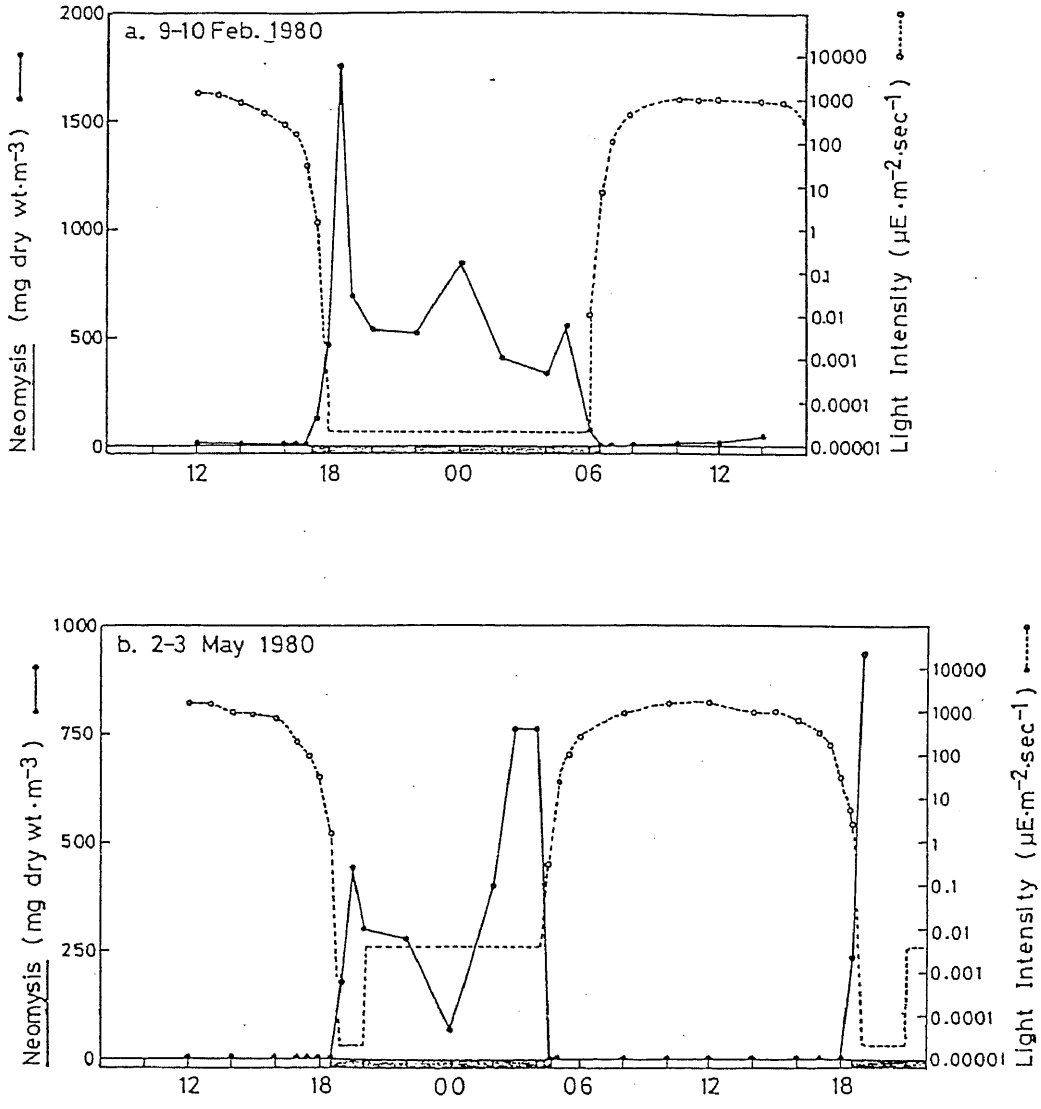

Fig. 6. Diel changes in the biomass of N. intermedia in the surface layer (Ø - Ø.5 m) (solid line) and the surface light intensity (dotted line) at St. 6'. a, 9 - 1Ø February 198Ø; b, 2 - 3 May 198Ø.

to a short day. This suggests that diel vertical movement of N. intermedia is regulated by a certain threshold light intensity encountered at certain times of sunset and sunrise, probably between 10^{0} and 10^{-5} $\mu E \cdot m^{-2} \cdot sec^{-1}$. When the light intensity is less than the threshold, mysids may be released from the light pressure and they disperse into the whole water column. While under the light intensity higher than the threshold, mysids are affected negatively by the light and move toward the deeper layer. Thus, they concentrate near the lake bottom in a shallow water body.

Bright moonlight has been considered to affect the vertical movements of mysids (Beeton, 1960; Herman, 1963). During the present study, bright moonlight ($2 - 6 \times 10^{-3}$ $\mu E \cdot m^{-2} \cdot sec^{-1}$; Beeton, 1960) was observed in May. However, the disturbance in the distribution pattern of N. intermedia was negligibly small (Fig. 3). A sharp temperature gradient or warm water has also been known to prevent the vertical movement of mysids (Beeton, 1960; Herman, 1963). In the shallow Lake Kasumigaura, thermal stratification is naturally slight (Fig. 5), and N. intermedia appeared in the surface layer even in summer. It seems, therefore, unlikely that the temperature gradient or warm water restricts the diel movement of the mysids in Lake Kasumigaura.

II-3-2. Areal distribution of N. intermedia in Lake Kasumigaura

From the samplings conducted three times in 1980 in the offshore region of Lake Kasumigaura, it became clear that N. intermedia was distributed throughout the lake (Fig. 7). The density of mysids was high in spring and fall, while it was low in summer. The geometric mean density in spring, summer, and fall was 6.1, 0.4, and 3.6 g dry weight per m^2, respectively, except for the innermost part of Takahama-iri Bay. The logarithmic coefficient of variation between stations was 50% in spring, 300% in summer, and 55% in fall. It is therefore concluded that N. intermedia was fairly uniformly distributed at least throughout the offshore region in the lake. The large value of the coefficient calculated in summer was attributable to some extremely low densities.

Figure 8 shows the detailed areal distribution of N. intermedia including nearshore region in Takahama-iri Bay. In order to make clear the seasonal change in the pattern of the mysid distribution, the results were presented according to season regardless of year. In spring, the mysid population was abundant and was distributed over the entire bay from nearshore region to the offshore region. The mysid population extremely decreased in density in summer and disappeared from the nearshore region. From fall to winter the mysid population increased again in density and was distributed in both nearshore and offshore

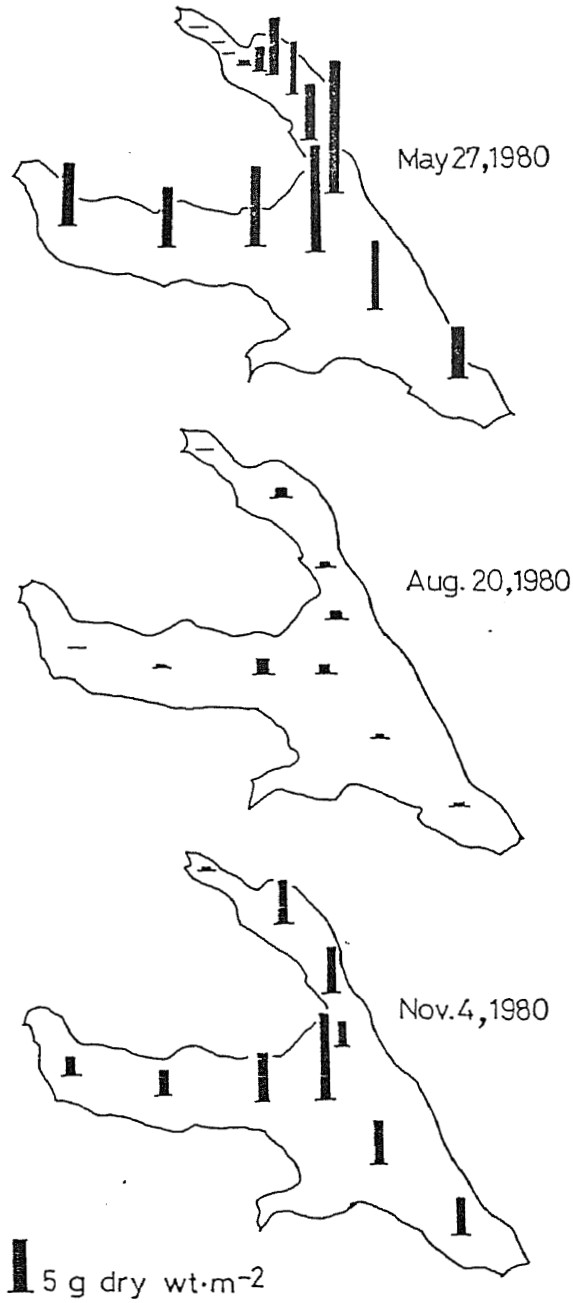

Fig. 7. Areal distribution of N. intermedia population in Lake Kasumigaura.

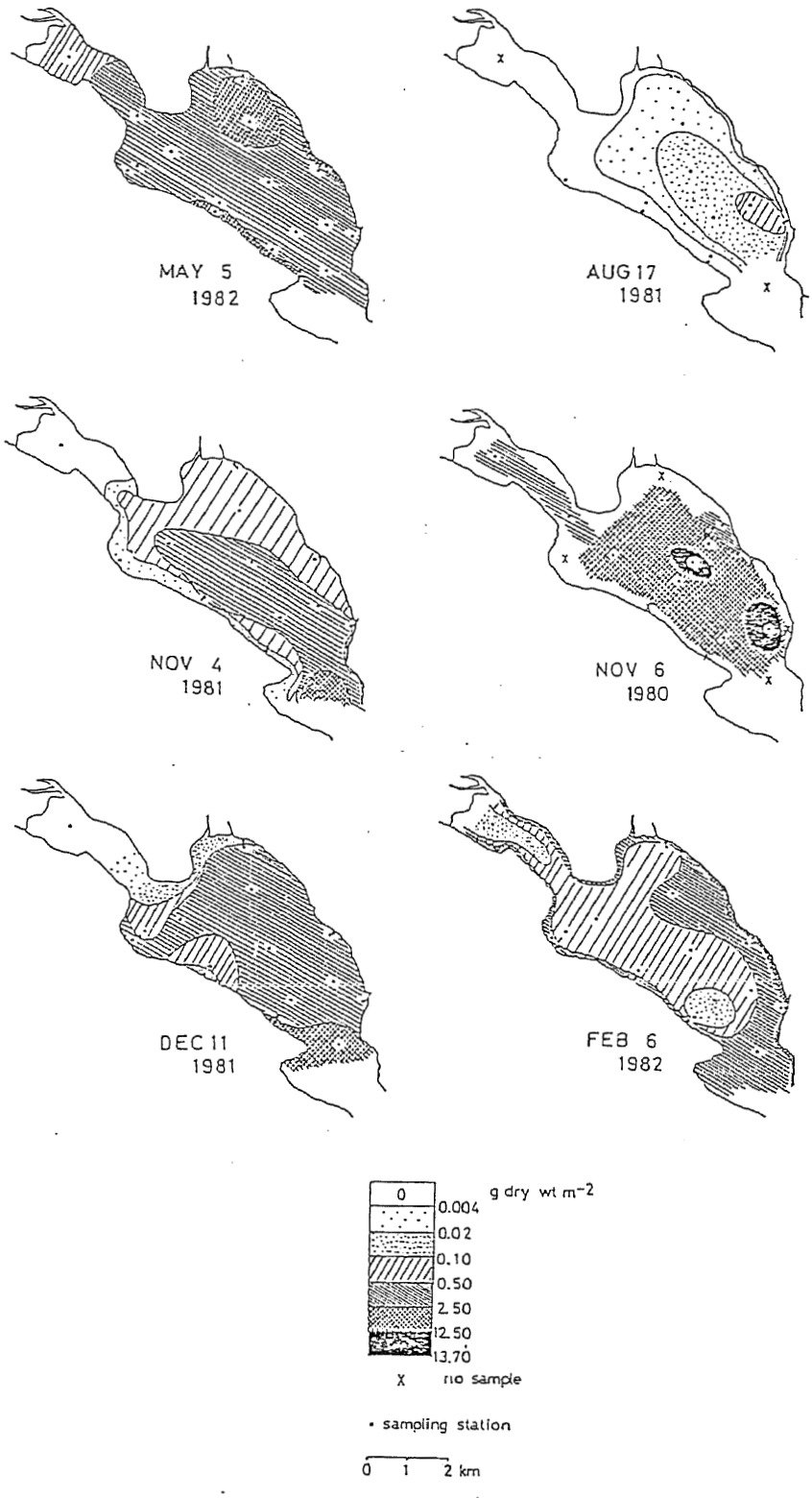

Fig. 8. Detailed areal distribution of N. intermedia population in Takahama-iri Bay.

regions. A particular distribution pattern of the mysid was observed in mid-winter (February). Dense swarms of mysids were found in the nearshore region. Even on that occasion, however, 80% of the mysids was still distributed in the offshore region, due to the overwhelming large area of the offshore region.

Few mysids were collected in the innermost part of Takahama-iri Bay, where chlorinity was less than 20 mg $Cl \cdot l^{-1}$ due to the inflow of river water. The low chlorinity might limit the mysid distribution in the mouth of the river, because high mortality of the mysid was observed at such a low chlorinity by Murano (1966).

In some estuarine environments, mysid species, Neomysis americana (Hulburt, 1957) and Neomysis mercedis (Heubach, 1969; Siegfried et al., 1979) showed a kind of contagious distribution horizontally as well as vertically, which was associated with a sharp gradient of environmental parameters such as salinity, water current, and tide. In Lake Kasumigaura, however, there is almost no or only a slight gradient in environmental parameters, and then N. intermedia was distributed fairly evenly over the whole lake area throughout the year. The nearshore dense swarm observed in mid-winter might be attributable to the active aggregation behavior of the mysids themselves.

II-3-3. Seasonal change in abundance and composition of *N. intermedia* population in Lake Kasumigaura

Seasonal change in surface temperature at St. 3 in 1980, 1981, and 1982 was shown in Fig. 9. The lake water is well mixed vertically and thermal stratification seldom develops throughout the year in Lake Kasumigaura (cf. Fig. 5). Thus the surface water temperature represents the whole water column. The temperature increased rapidly from March to June, July, or August, and decreased from September to January. It ranged over 27°C from a minimum of 3°C in winter to a maximum of 30°C in summer.

Surface chlorinity at St. 3 was nearly constant throughout the year, and averaged 34.0 mg $Cl \cdot l^{-1}$ from April 1980 to May 1981 (not shown in the figure).

Seasonal change in density of *N. intermedia* at St. 3 over the 3 years was shown in numbers and in dry weight (Fig. 10). The mysid population showed two sharp peaks in a year; in spring and fall. The maximum density exceeded 10,000 individuals$\cdot m^{-2}$ or 5 g dry wt$\cdot m^{-2}$, but the period of each peak was maintained during only a short time period; the duration which exceeded 5,000 individuals$\cdot m^{-2}$ or 2.5 g dry weight$\cdot m^{-2}$ was 1.5 - 3 months for each peak. On the other hand in summer and in winter, the density of mysid extremely decreased to less than 100 individuals$\cdot m^{-2}$ or 0.05 g dry wt$\cdot m^{-2}$. As a result, the annual variation in mysid density reached more than two orders of magnitude. The specific rate of increase in biomass (dry

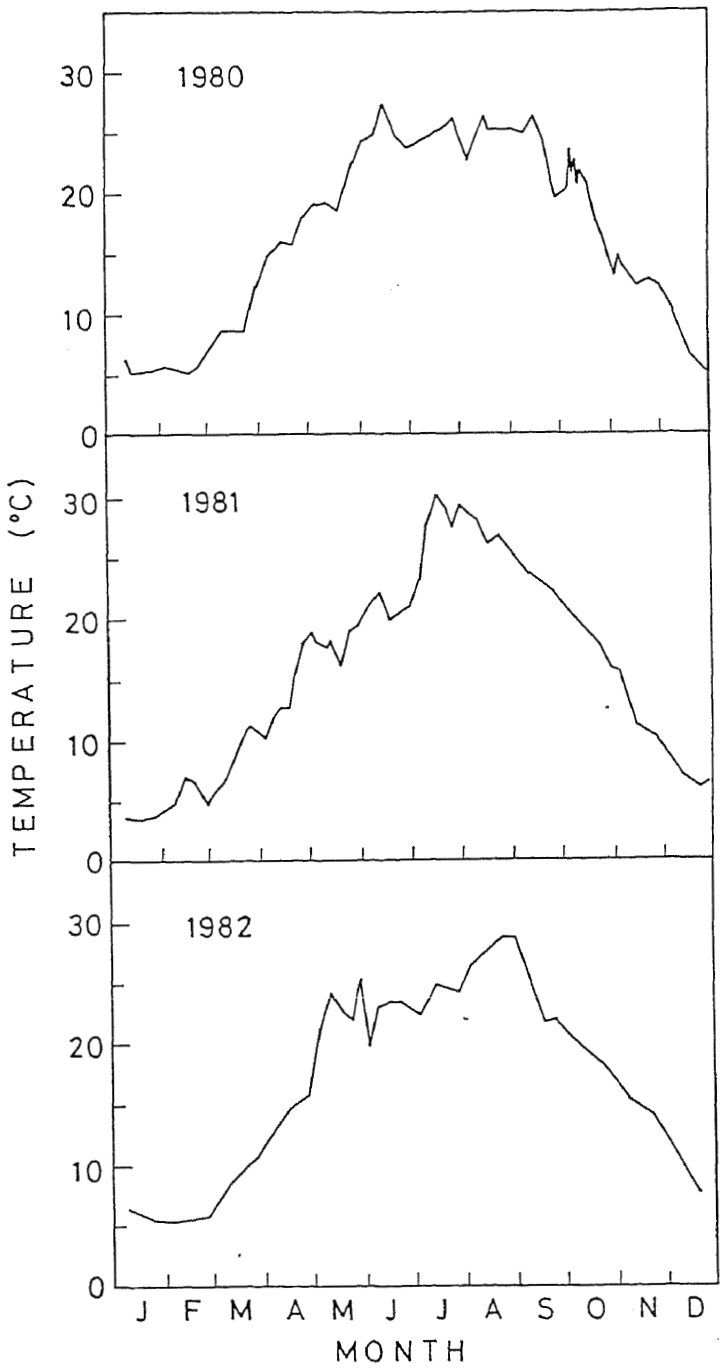

Fig. 9. Seasonal change in surface water temperature at St. 3 in 1980 (top), 1981 (middle), and 1982 (bottom).

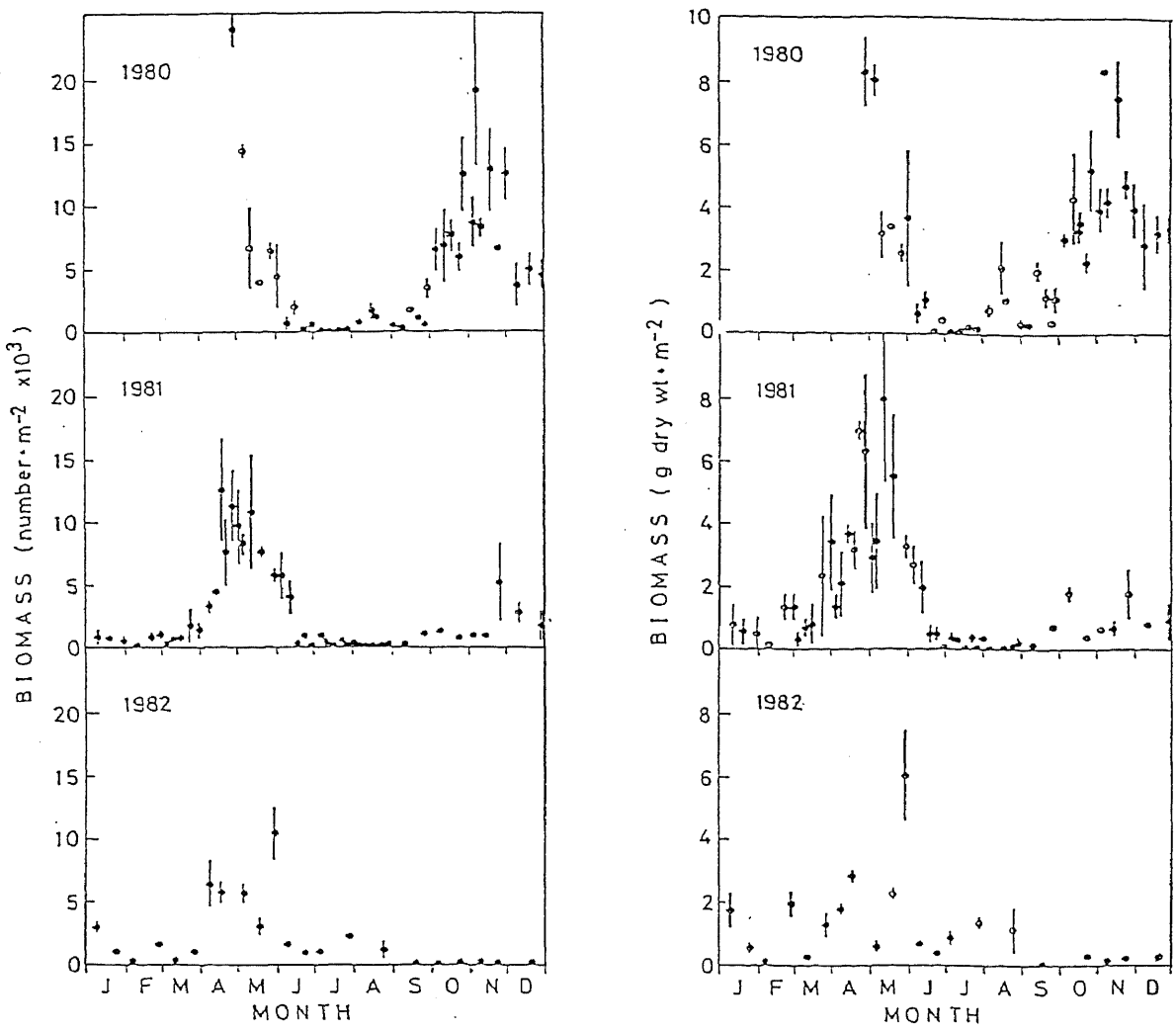

Fig. 1Ø. Seasonal change in biomass of N. intermedia population at St. 3 in 198Ø (top), 1981 (middle), and 1982 (bottom): left, number; right, dry weight. Vertical bars indicate the standard deviation.

weight) of N. intermedia population was Ø.Ø38 - Ø.Ø41 (day^{-1}) in the period of spring and fall increase, while the specific rate of decrease was -Ø.Ø42 - -Ø.Ø89 (day^{-1}) in the period of summer and winter decline.

Fall peak in mysid density was slight in 1981 and disappeared in 1982. The flood water from the watershed caused by typhoons in both years might be responsible for the disappearance of the fall peak. Mysids might be carried away by the flood or died off due to the low chlorinity of the flood water.

The maximum mysid density observed for N. intermedia in this study is comparable with or exceeds that for some estuarine mysids. Heubach (1969) and Siegfried et al. (1979) reported the maximum value of 5,ØØØ - 1Ø,ØØØ individuals$\cdot m^{-2}$ for N. mercedis. Hulburt (1957) obtained the maximum of 1,ØØØ - 2,5ØØ individuals$\cdot m^{-2}$ for N. americana. The maximum density of the freshwater mysid, Mysis relicta, is much lower in oligotrophic and mesotrophic lakes ; 1ØØ - 1,ØØØ individuals$\cdot m^{-2}$ (Carpenter et al., 1974; Hakala, 1978; Morgan et al., 1978, Grossnickle and Morgan, 1979). From these comparisons, it appears that Lake Kasumigaura supports a highest mysid population.

Large annual variation in abundance was reported for other estuarine mysids, N. mercedis (Heubach, 1969; Siegfried et al., 1979), N. americana, and Mysidopsis bigelow (Hopkins, 1965). Hakala (1978) observed a large

annual variation in population size for M. relicta in an arctic oligotrohic lake, but Grossnickle and Morgan (1979) found less seasonal fluctuation in density for the same species in Lake Michigan. At present it seems that the large annual variation in abundance is characteristic at least among estuarine mysid populations.

Figure 11 shows the composition of the mysid population from January 1980 to May 1981. Juveniles predominated in the population most of the year except for winter when the bulk of the population consisted of adults. The proportion of juveniles in the total population was 43% on average in 1980. Gravid females continued to be present over 9 months from late February to the end of November. The proportion of gravid females in the total population was 5 - 30%, being high in mid-March to mid-April and mid-July to September. No gravid females were found from December to mid-February. The male to female ratio fluctuated each sampling and was 42 : 58 on average in 1980.

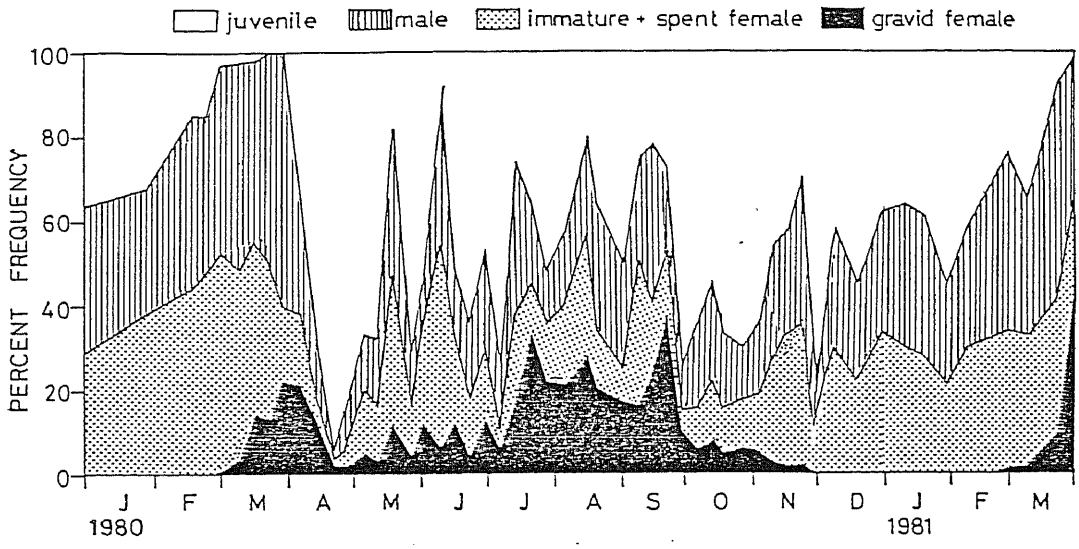

Fig. 11. Seasonal change in composition of N. intermedia population at St. 3 from January 1980 to May 1981.

CHAPTER III

In situ Growth of *Neomysis intermedia* and its Relation to Environmental Factors under Field Conditions

III-1. Introduction

The growth process of zooplankton is subdivided into embryonic and post-embryonic stages. During the embryonic stage, the growth occurs by the utilization of storage materials in the yolk, and is primarily controlled by temperature (McLaren, 1965; Corkett and McLaren, 1970). Whereas during the post-embryonic stage, it can be expected that animals depend more heavily on the surrounding environment than at the embryonic stage because they have to take food from the environment in order to maintain their metabolism and to increase their body weight.

The post-embryonic growth of zooplankton can be generally represented with a growth curve which expresses the weight change of the individual animal with time. A given growth curve can be basically characterized with the following three aspects; the initial body weight, the body weight at maturation, and the increasing rate (growth rate) of the body weight.

The growth of zooplankton under natural aquatic environments is usually analyzed by a cohort analysis. For the analysis, the same cohort has to be followed

throughout the investigation. Sampling frequency is also important for the cohort analysis, and should be conducted at least a few times during one generation time period for the target species.

In the present study, the frequent field observations were undertaken in Lake Kasumigaura in order to determine the actual post-embryonic growth pattern of N. intermedia by the cohort analysis. The growth aspects, the growth rate and the body sizes mentioned above were particularly emphasized. Those results obtained were then evaluated by the correlation analysis with the environmental parameters.

III-2. Materials and Methods

Growth analyses were undertaken on samples collected at St. 3 by the periodical samplings (see Chapter II). Carapace length (from the tip of rostrum to the end of telson) was used as a measure of the size of individuals, because it can be determined more easily and exactly than the body length under a stereoscopic microscope. The size of 200 - 300 individuals was measured for each sample. In addition, the carapace length and brood size of 20 - 100 gravid females were examined. Dry weights of mysids were determined several times during the field survey for fresh materials collected from the lake. One to 15 individuals of the same size were placed on a glass fiber filter paper or an aluminum pan, dried for 2 days at 60^{o}C, and weighed

with an electrobalance.

Growth analyses were restricted within the period between January 1980 and May 1981, when samplings were performed most intensively. They were carried out for males and females separately, assuming the potential sex ratio of 1 : 1 for juveniles. There was no release of young in winter (Chapter II), and the growth of overwintering individuals was determined by the change in average carapace length of all individuals. Young mysids were released almost continuously during the period from April to November when gravid females were present. During the period of continuous release of young, it was possible to extract some cohorts by the probability graphic analysis proposed by Cassie (1954). In this method it is assumed that any given cohort shows a normal size distribution, and then the cumulative percent frequency indicates a straight line on the probability paper over the size range where there is a cohort. If there are a plural number of cohorts overlapping each other, several straight lines can be expected and the overlapping can be visualized by points of inflexion.

III-3. Results

Seasonal change in size distribution of N. intermedia population

The winter population consisted of individuals which were born at different times in the previous fall, and

there was no distinctive cohort visualized in this population (Fig. 12). The carapace length of mysids was in the range of 0.6 and 4.2 mm in January 1980. From early February to early April the size distribution pattern was skewed towards the larger carapace size and the range narrowed by early April. Thereafter the same size distribution was maintained until early May when all the overwintering individuals disappeared. Gravid females first appeared in late February and increased their proportion in females up to >50% by late March. They had 27.8 eggs per brood on average.

Newly released individuals first appeared at the beginning of April 1980. There were four cohorts detected between April and June. The first cohort observed in early April was followed until early May. The second cohort was observed in the middle of April and was followed until the middle of May. The third and fourth cohorts were observed in early May and in late May, respectively. The second, third and fourth cohorts could be followed until maturation within 3 - 4 weeks. Gravid females carried 11.4 eggs per brood on average in these cohorts.

Between late June and late November several newborn cohorts were observed as shown in Fig. 13. However, they soon merged into the existing population and it was unable to follow any cohort over a prolonged time period.

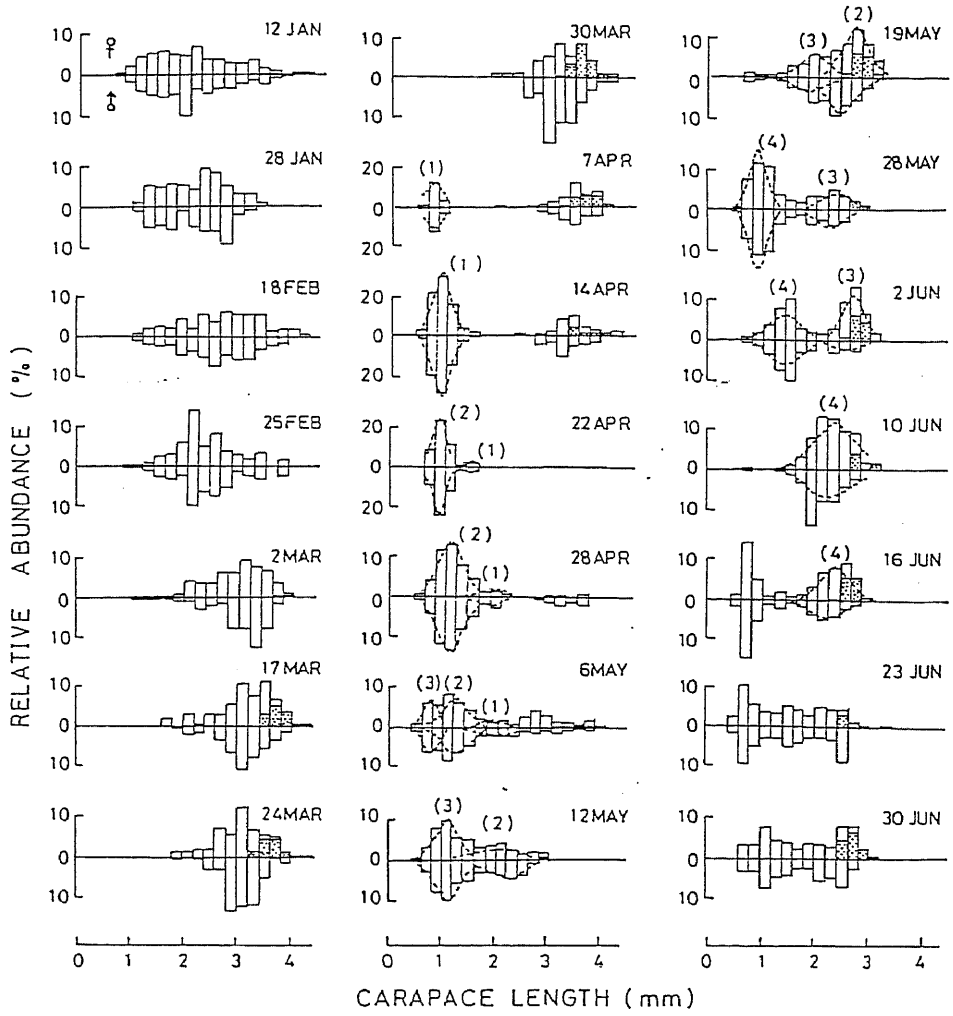

Fig. 12. Size frequency distributions of N. intermedia population from 12 January to 30 June 1980. The juvenile stage of indistinguishable sex were separated into males and females at 1:1 ratio. Dotted bars indicate adult females. Numbers in parentheses show each cohort distinguished by the normal frequency distribution curve analysis, shown by dashed line.

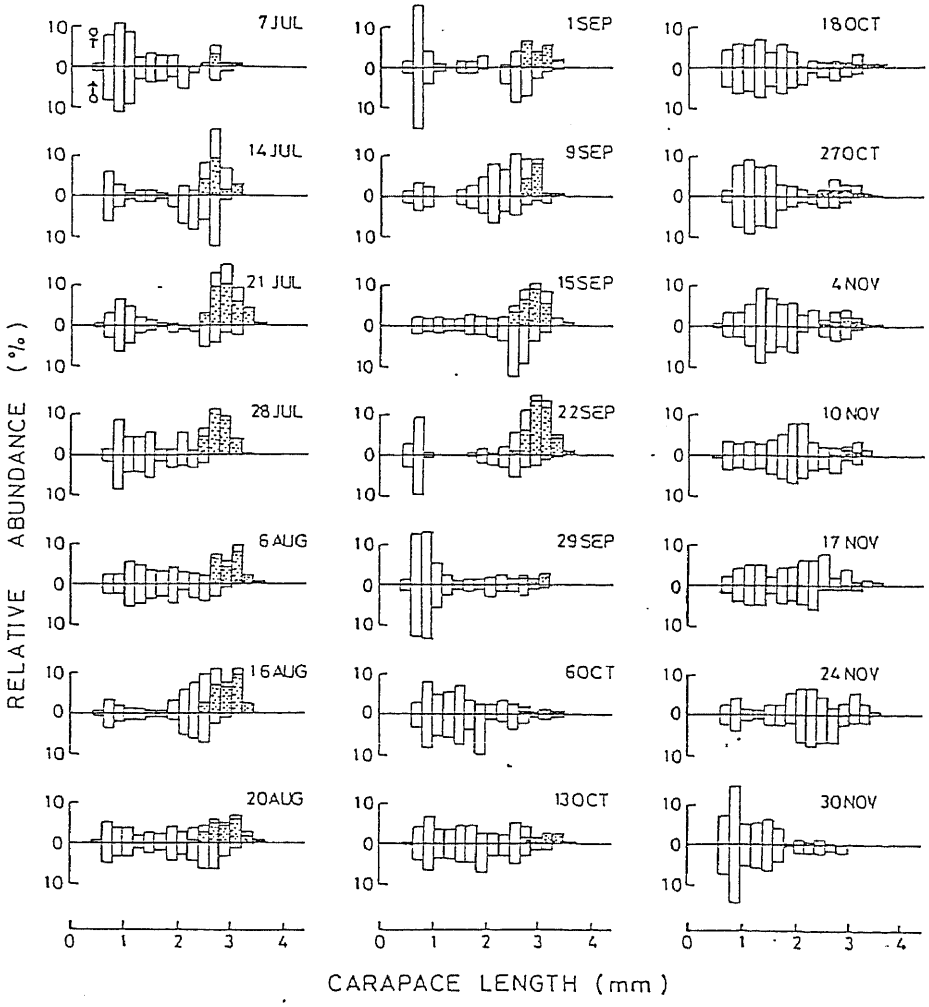

Fig. 13. Size frequency distributions of N. intermedia population from 7 July to 30 November 1980. See Fig. 12 for detail.

Between December 1980 and May 1981, the overwintering population showed a growth in a similar manner as in the previous winter (Fig. 14). The newborn cohort which appeared in mid-April was followed until mid-May. By that time most members had matured. They had an average of 18.6 eggs per brood. There were also several other newborn cohorts observed until 20 May 1981, but the follow up of those cohorts was unsuccessful.

Seasonal change in growth rate of N. intermedia

Growth rates were computed for overwintering populations and cohorts observed. The carapace length was converted into the body length using the following equation (Fig. 15),

$$BL = 3.44 \cdot CL - 0.28 \qquad (n=59,\ r=0.988) \qquad (1)$$

where BL is body length in mm and CL is carapace length in mm.

Body length of individuals in the overwintering populations varied in each sampling with a wide range as shown in Fig. 16, because the overwintering population consisted of individuals at various growth stages. There occurred three steps in the growth patterns; the first was slow or no growth in December and January, the second was a consistent growth between early February and early April, and the third was a cessation of growth thereafter. In the second growth step some difference was noticed between the two years: a comparatively rapid growth

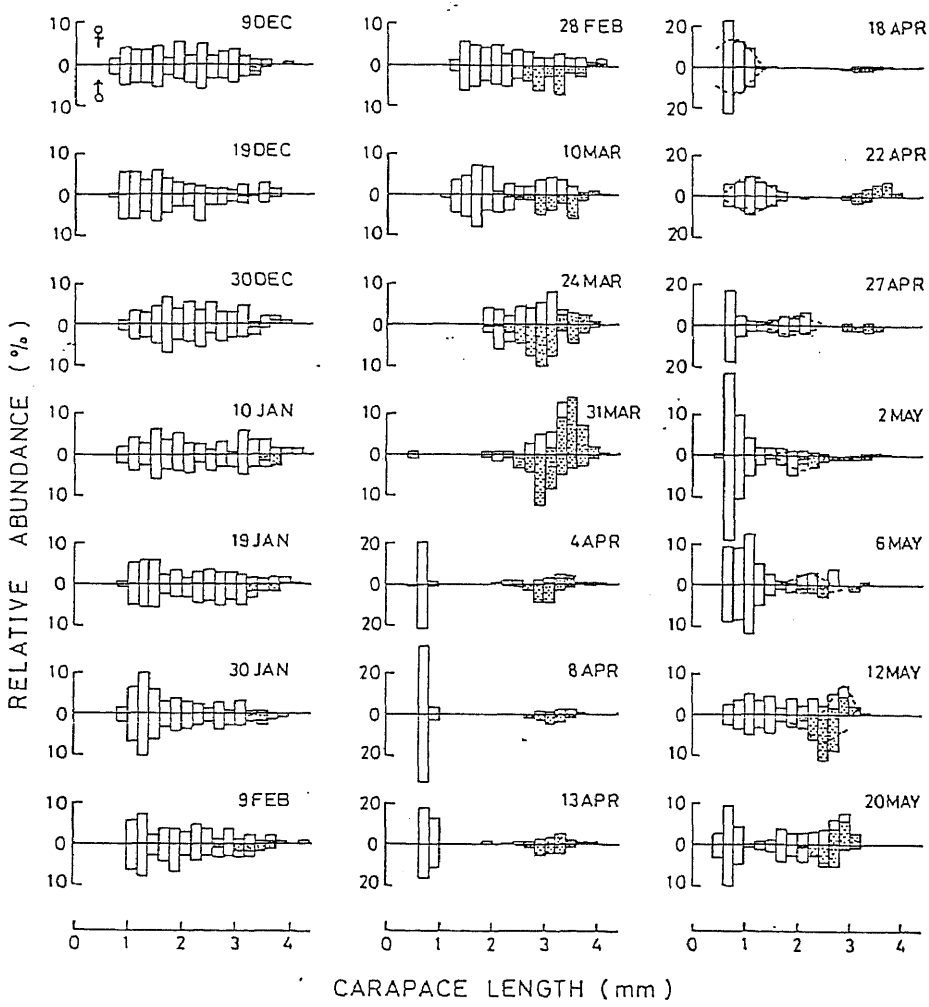

Fig. 14. Size frequency distributions of N. intermedia population from 9 December 1980 to 20 May 1981. Dotted bars represent adult individuals for both sex. See Fig. 12 for detail.

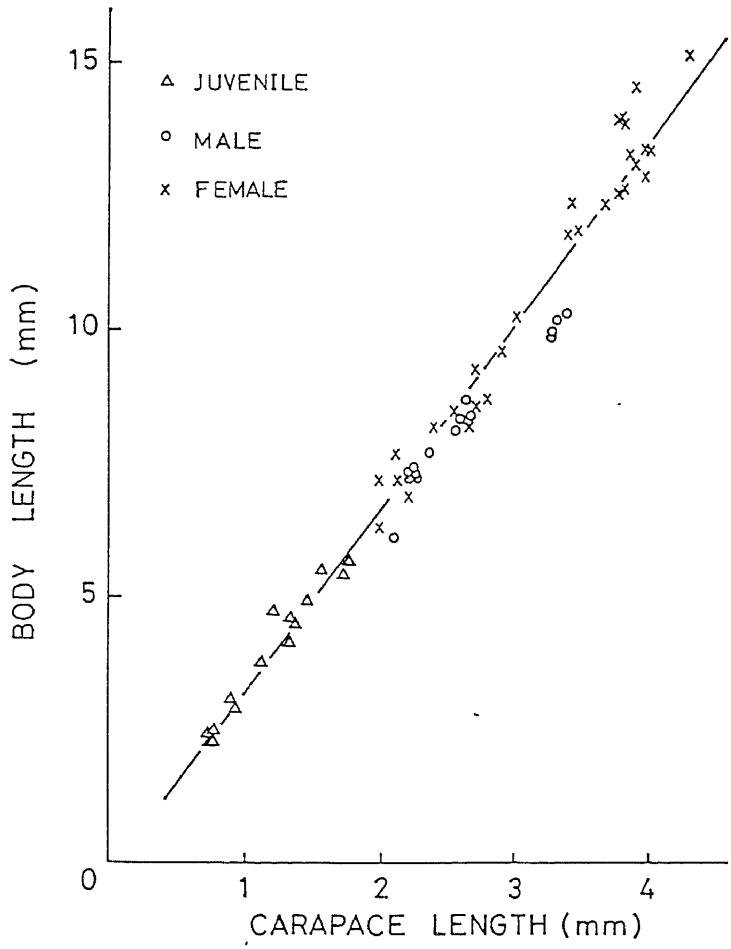

Fig. 15. Relation between body length and carapace length of N. intermedia.

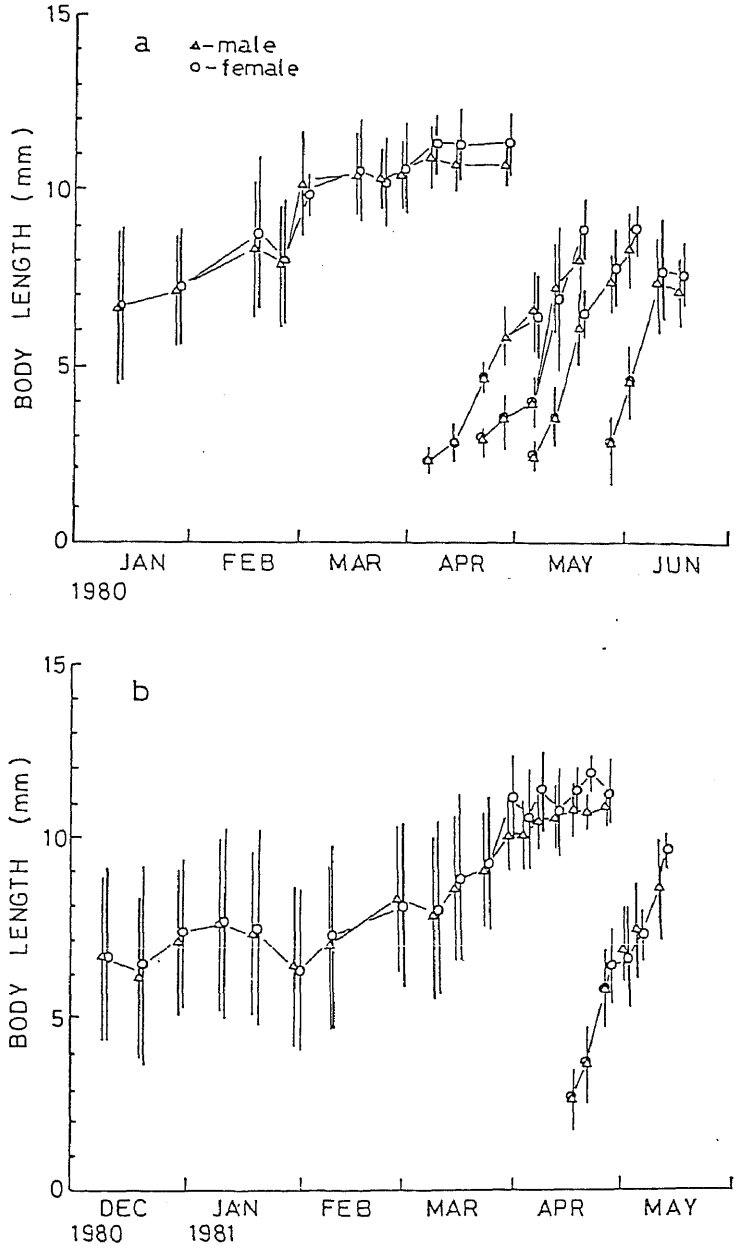

Fig. 16. Changes in body length of individuals in each cohort or population of N. intermedia with time. Vertical bars indicate the standard deviation.

reaching 10 mm in mid-March followed by a further slow increase was observed in 1980, while a steady growth was maintained from early February almost through to early April in 1981. Both sexes did not show any significant difference in the growth rates, although males stopped their growth at a smaller body size than females. Estimated average growth rates in body length of the overwintering population were 0.004 - 0.031 $mm \cdot day^{-1}$ in December and January, and 0.056 - 0.074 $mm \cdot day^{-1}$ between early February and early April.

Individuals in the spring cohort were 2.3 - 2.9 mm in their initial body size and this suggests that they were released from the marsupium just prior to sampling, because the body length of newborn individuals is 2 mm (see next chapter). The average body length of the spring cohort also showed a variation but not as large as that of the overwintering population, and increased almost linearly with time for the first 3 - 4 weeks before maturation. No significant difference was observed in the growth rates between males and females, but the growth tended to stop at a smaller size in males than females. Calculated growth rates were 0.155 - 0.288 $mm \cdot day^{-1}$ for the spring cohorts.

As shown in Fig. 17, a logarithmic relationship was found between the carapace length and the dry body weight over the carapace size range from 0.7 to 4.6 mm, and it was expressed as follows,

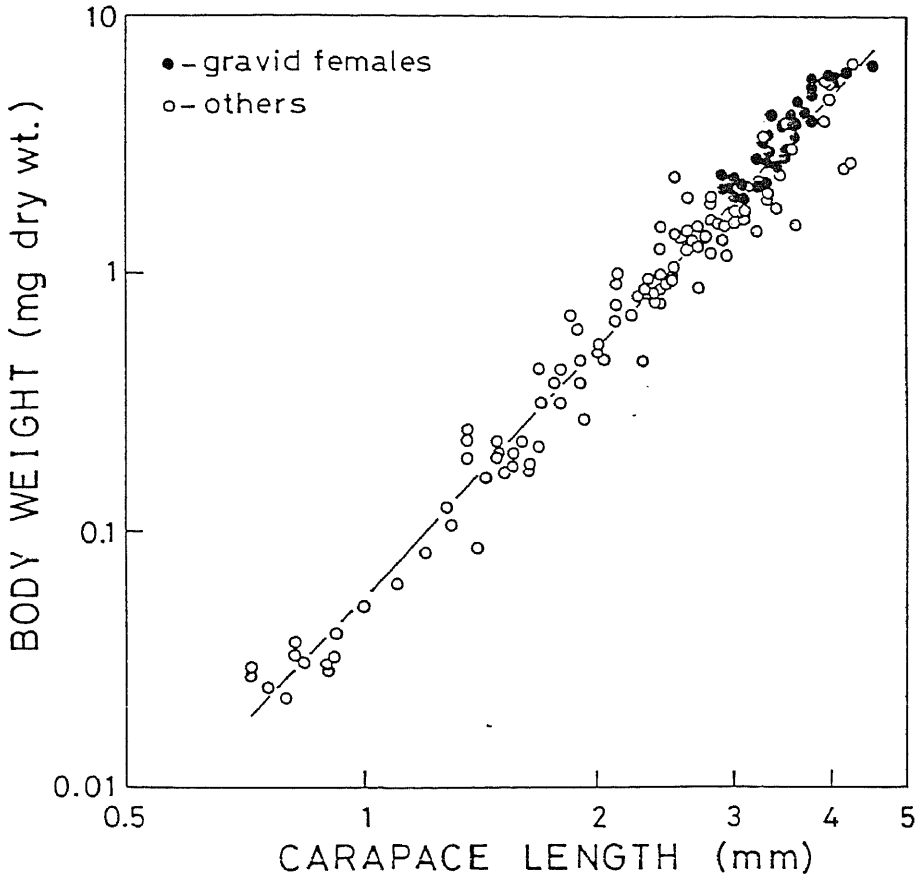

Fig. 17. Relation between body weight and carapace length of N. intermedia.

$$BW = 0.0544 \cdot CL^{3.24} \qquad (n=156,\ r=0.984) \qquad (2)$$

where BW is the dry body weight in mg and CL is carapace length in mm. Using Eq. (2), the growth curves shown in Fig. 16 were expressed in body weight (Fig. 18). It became obvious that the mysids grew almost exponentially with time before maturation. The specific growth rate during the exponential growth period evaluated on the growth curves can then be estimated by a least squares fit of data to the ordinary logarithmic growth formula as follows,

$$SGR = (\ln BW_2 - \ln BW_1) / (t_2 - t_1) \qquad (3)$$

where SGR is the specific growth rate (day^{-1}), and BW_1 and BW_2 are the dry body weight in mg at time t_1 and t_2, respectively. The specific growth rates calculated by Eq. (3) for the overwintering populations were 0.001 - 0.013 (day^{-1}) in December and January and 0.019 - 0.025 (day^{-1}) between early February and early April, and for the spring cohorts 0.12 - 0.16 (day^{-1}). The obtained growth rates were positively related to the in situ water temperature (Fig. 19). The specific growth rate was almost zero at temperature of around 5°C and increased with the increase of temperature showing a maximum of 0.16 (day^{-1}) at around 25°C.

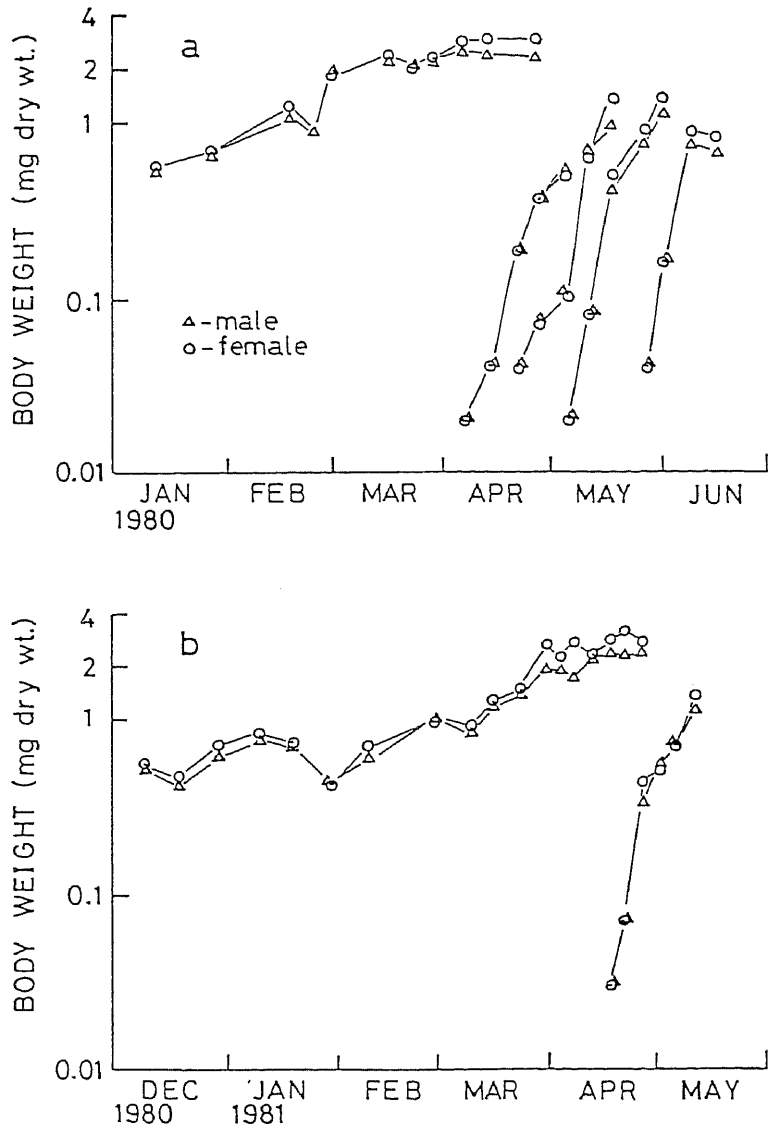

Fig. 18. Changes in body weight of individuals in each cohort or population of N. intermedia with time.

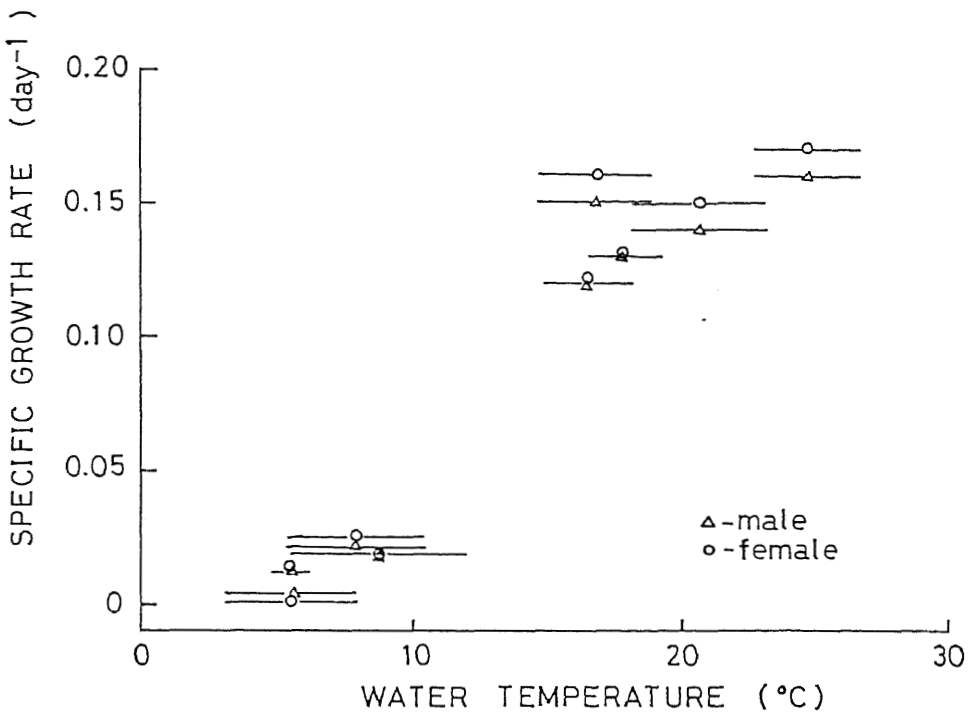

Fig. 19. Relationship between specific growth rate of N. intermedia and water temperature. Horizontal bars indicate the range of water temperature.

Seasonal change in body size of individuals and in brood size of N. intermedia

There was no conspicuous variation in the smallest size class of individuals during the period of continuous release of young between spring and fall; 0.6 - 0.8 mm in carapace length (Figs. 12, 13, and 14). Considering the carapace length of newborn individuals is 0.6 - 0.7 mm in the laboratory (see next chapter), the individuals of smallest size observed in the lake should be released as newborn individuals. No distinct seasonal change in the smallest size occurring in the field suggests that the newborn individuals have consistency in body size.

N. intermedia exhibited a marked seasonal variation in body size of both adult females and males (Fig. 20). The average body size of adult females in the overwintering populations was very large in February (about 13 mm in body length) and progressively became smaller towards spring (Fig. 20 a, b). A sudden decrease in body length occurred in early May when the overwintering individuals disappeared. The body length further declined towards summer, and reached a minimum in June to July. A gradual increase of body length occurred thereafter, though the increase was rather slight in the fall of 1980. Average body size of adult males showed a similar seasonal variation as those of females, but males were always smaller than females (Fig. 20 c). Average body size of adult individuals negatively correlated with

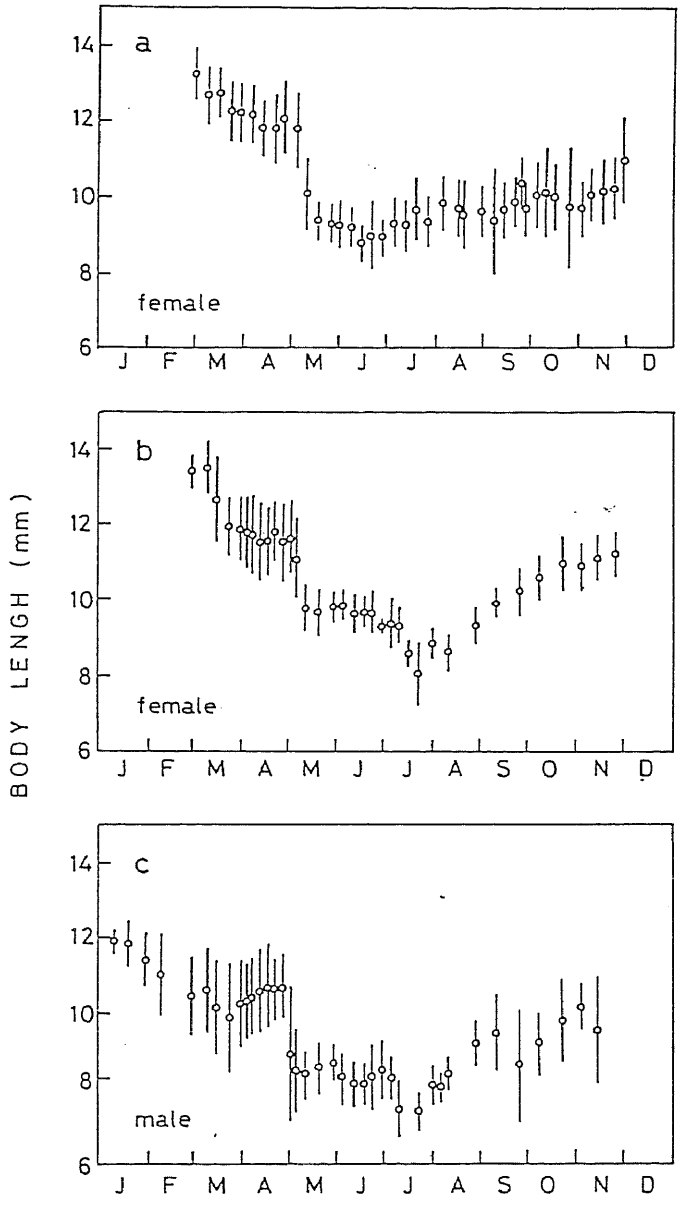

Fig. 20. Seasonal changes in average body length of adult individuals of N. intermedia: (a) adult females in 1980; (b) adult females in 1981; (c) adult males in 1981. Vertical bars indicate the standard deviation.

the mean water temperature during development (Fig. 21), the duration of which was defined as the time from the previous November to sampling time for the overwintering individuals, and as one month before the sampling for the other individuals.

Average brood size also showed a marked seasonal variation in accordance with the change in body size of adult females (Fig. 22). The brood size was as large as 25 - 30 eggs per brood in early spring, decreased to 5 - 10 eggs per brood towards summer, and then increased again slightly (in 1980) or considerably (in 1981) in fall.

III-4. Discussion

During the two year field observations, large bursts of young mysids appeared frequently from spring through fall and some of the bursts were followed until maturation. The winter population tended to show a synchronized growth by the next spring. Based upon the data obtained in the present field observations, the post-embryonic growth of N. intermedia was discussed on the following two aspects; the first was the growth rate and the second was the body size of individuals.

A strong positive relationship was found between the specific growth rate of N. intermedia and the corresponding surrounding water temperature. This emphasizes that the growth rate of the mysid is significantly dependent on the surrounding water

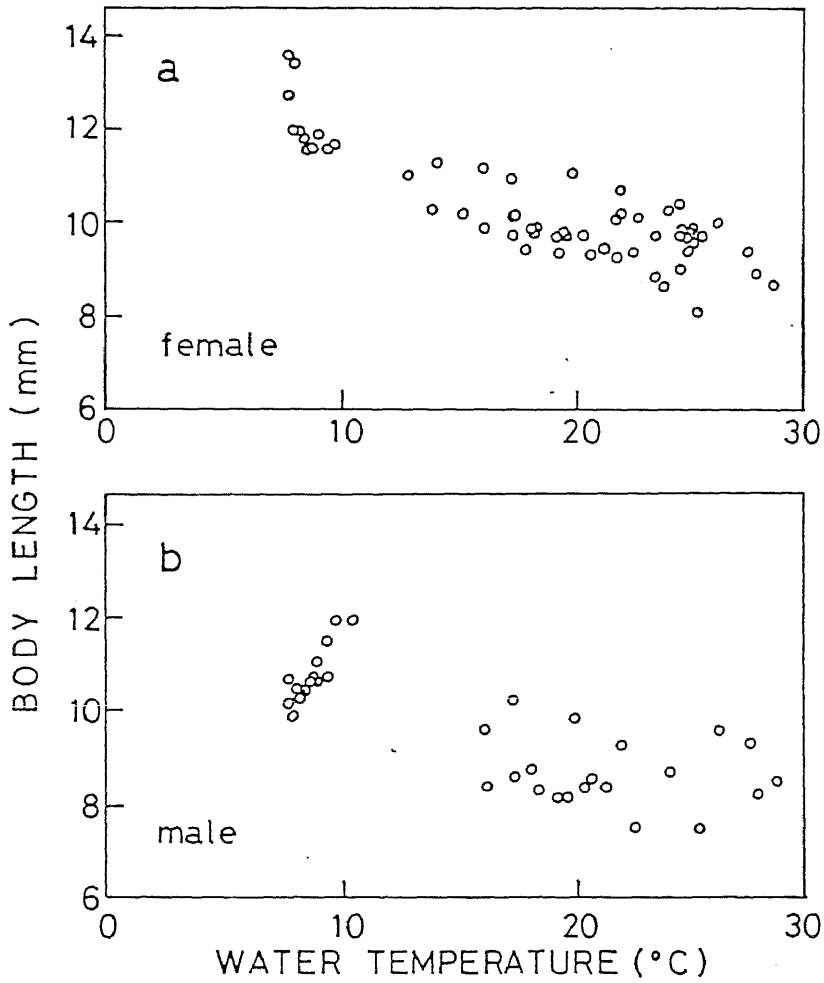

Fig. 21. Relationship between body length of adult individuals and temperature for N. intermedia: (a) adult females in 1980 and 1981; (b) adult males in 1981.

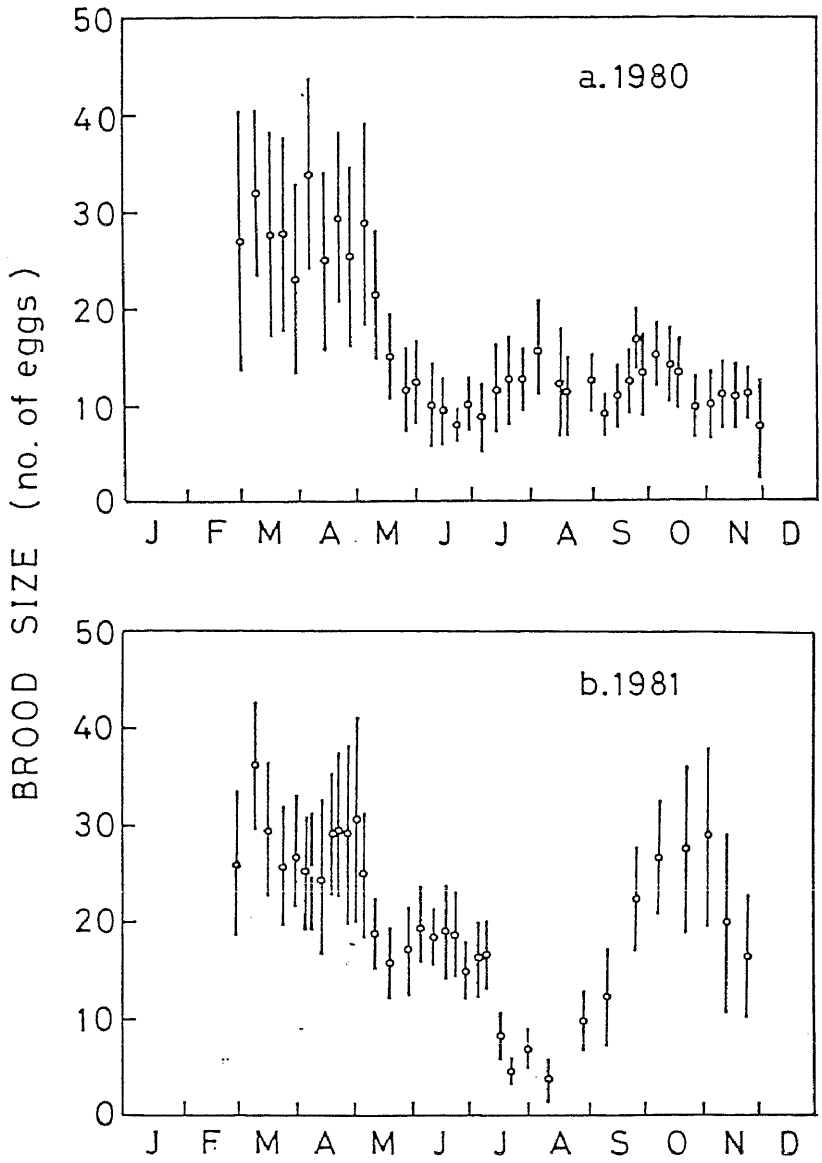

Fig. 22. Seasonal changes in average brood size of N. intermedia: (a) 1980; (b) 1981. Vertical bars indicate the standard deviation.

temperature throughout the year. This was further examined in detail by the Arrhenius plots. The relationship obtained in this way was highly significant for both sexes as follows (Fig. 23),

$$SGR = 6.98 \times 10^{22} \cdot e^{-15967/K} \quad (n=18,\ r=-0.884) \qquad (4)$$

where SGR is specific growth rate (day^{-1}) and K is temperature on the Kelvin scale.

In the studies concerning the growth of Neomysis species, the size of individuals has usually been expressed in terms of unit length, either carapace length or body length, and it has been shown that size increases linearly with time in spring or shows a curve increase in winter (Pezzack and Corey, 1979; Bremer and Vijverberg, 1982). Murano (1964b) showed also a linear size increase at the period from the early post-embryonic stage to the maturation in mysids grown in laboratory culture at 20°, 25°, and 30°C. In the present study, the body length of N. intermedia in the spring cohort increased almost linearly from the early post-embryonic stage to the maturation. In the case of the winter population, the increase in body length almost ceased during the period from December through January, and subsequently an almost linear increase followed until maturation. The growth patterns were further examined based on body weight. The growth of individuals in the spring cohorts was almost exponential until maturation and no significant difference was observed between sexes. The growth of individuals in

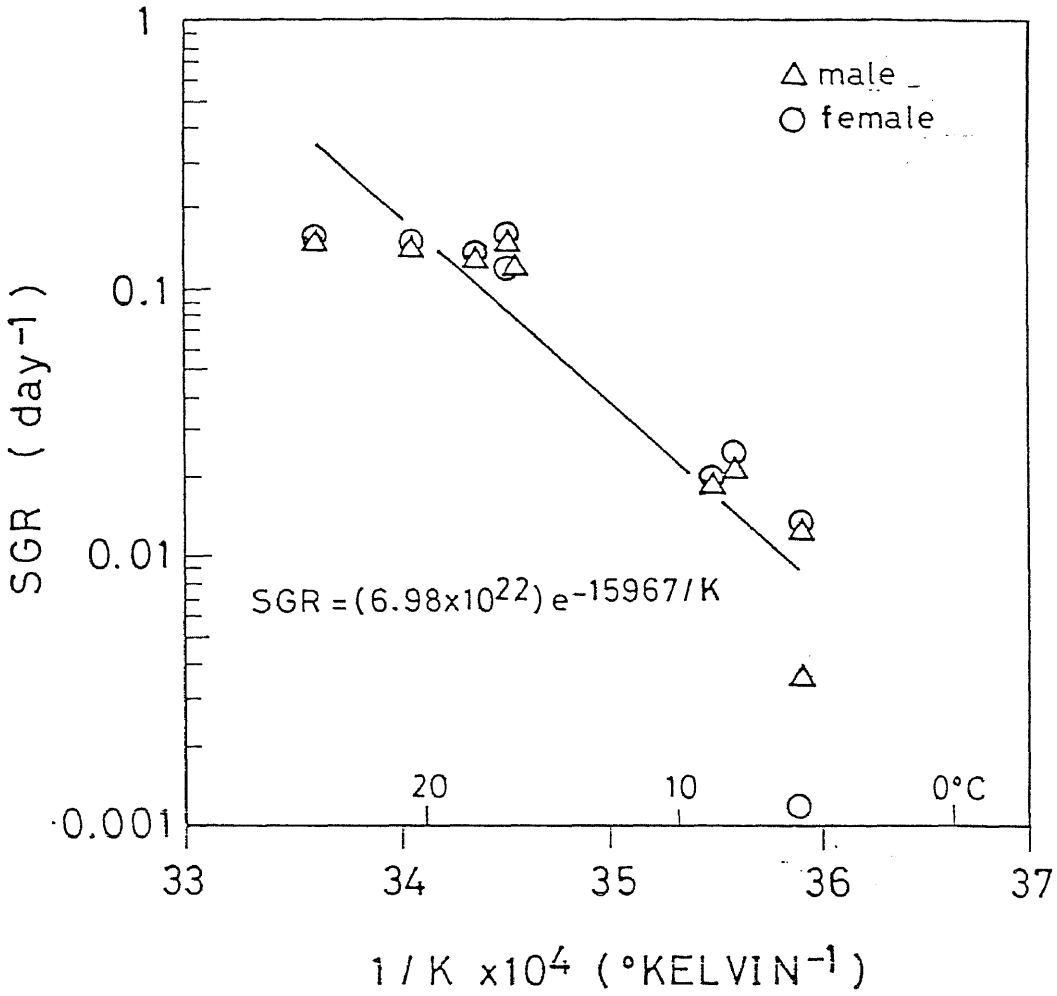

Fig. 23. Relationship between specific growth rate (SGR) and reciprocal of temperature on the Kelvin scale (1/K).

the winter populations was very slow at the early stage and the consistent exponential growth was restricted at the later stage of the development.

As shown in Fig. 23, the growth of N. intermedia depends strongly on temperature, therefore, the possible temperature effects are expected to occur in the growth of each individual. Variation of temperature during the growth period of a given spring cohort, 3 - 4 weeks, was relatively small with a range of 2.8° - $5.2^{\circ}C$. Consequently, the possible effect of temperature on the specific growth rate in the spring cohorts seems to be rather small, and as a result, almost consistent exponential growth will persist until maturation. On the other hand, the temperature difference in the growth period of the winter population was relatively large with a range of 8.3° - $14.6^{\circ}C$ in low temperature seasons, and it is expected to initiate a large difference in the specific growth rate. The growth of individuals in the winter population, therefore, will be extremely slow in mid-winter at a temperature of around $5^{\circ}C$. Once the temperature begins to increase towards spring at the rate of 0.096° - $0.143^{\circ}C \cdot day^{-1}$, the specific growth rate will be accelerated to about 2 - 3%·day^{-1}, and the individual growth rate increases progressively. However, the absolute values of the specific growth rates are still small (0.007 - 0.020 day^{-1}) on the whole, and an almost consistent exponential growth will be observed during the

early spring.

The surrounding water temperature in Lake Kasumigaura varied in a wide range between 10° and 30°C during the period from April to November in which youngs were released continuously. However, the body size of newborn individuals in this period was almost consistent regardless of temperature; an average carapace length was 0.7 mm and an average body length was 2.1 mm. Therefore, it is expected that the body size of individuals at the release from a marsupium is not temperature dependent. On the other hand, the adult body size of individuals was highly temperature dependent, where the body size decreased with the increase of temperature. To make clear the characters of temperature dependencies of the size and of the growth rate, the relations indicated in Fig. 21 were treated with the Arrhenius plots (Fig. 24). The obtained correlations were also highly significant for both sexes. The coefficient for temperature dependency of the body weight was about 4000 ($^{\circ}K^{-1}$) and it was about 1/4 of that for the growth rate. This indicates that temperature dependency of individuals was 4 times stronger in the growth rate than in the size.

The marked seasonal change in adult body size was reflected in brood size. Since brood size directly influences the reproduction rate of zooplankton, temperature may affect the reproduction rate of N. intermedia by changing the adult body size and therefore

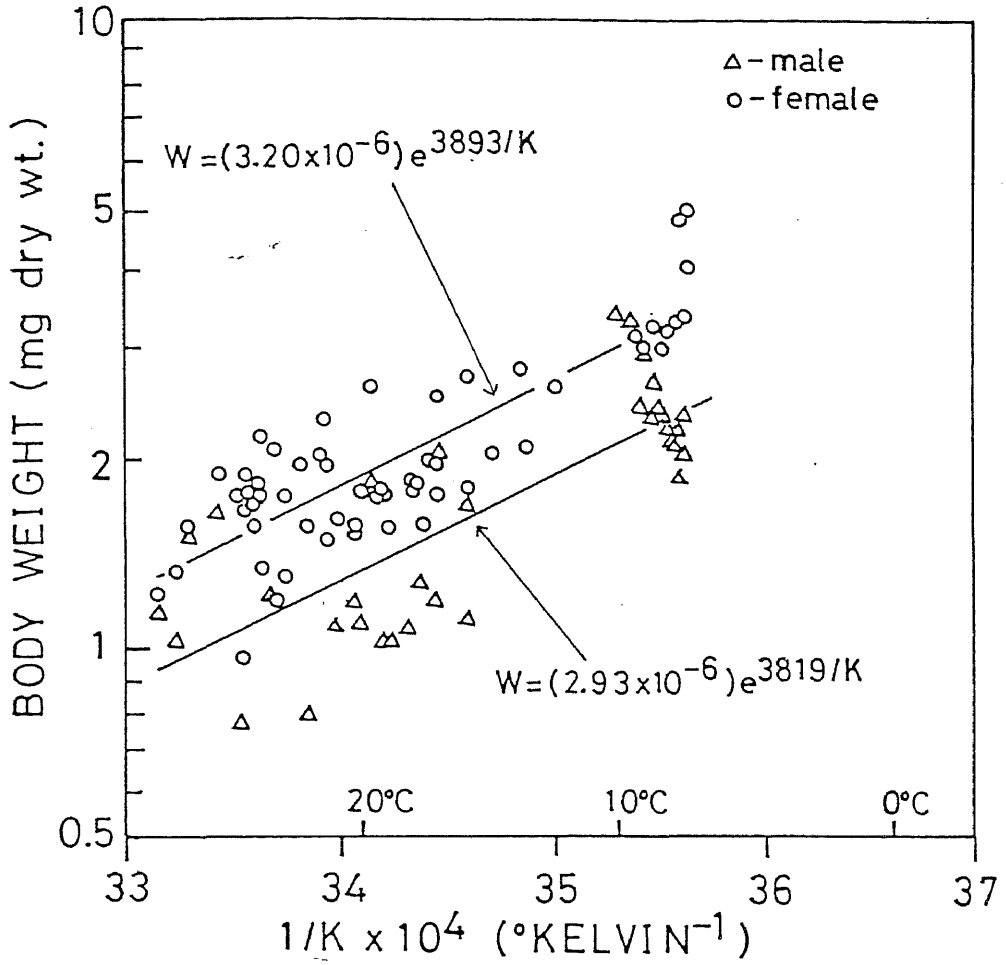

Fig. 24. Relationship between body weight of adult individuals and reciprocal of temperature on the Kelvin scale (1/K).

changing the brood size.

In conclusion, for N. intermedia, the body size of individuals immediately after the release from a marsupium was invariable throughout the breeding season, whereas their growth rate, the adult body size, and the brood size showed a marked seasonal variation in Lake Kasumigaura. It is strongly suggested that both growth rate and adult body size are primarily controlled by the surrounding water temperature in the hypereutrophic lake.

CHAPTER IV

Evaluation of the Environmental Controlling Parameters on the Growth of *Neomysis intermedia* under Laboratory Conditions

IV-1. Introduction

Various environmental parameters which affect the growth of zooplankton, may change temporally and spacially in natural water bodies. Among those parameters, temperature and food have a significant possible effect on the zooplankton growth. In the growth analyses undertaken in the previous chapter, it was found that there was a strong correlation between the post-embryonic growth and temperature for *N. intermedia* in Lake Kasumigaura. This implies that temperature is an important environmental factor affecting the growth of *N. intermedia* in the lake.

However, the correlation analysis is effective for selecting the prominent factors involved, but it does not prove the causal relation. A further experimental analysis is required in order to find out the the possible causal relationship between the growth of *N. intermedia* and temperature.

The purpose of this chapter is to evaluate the controlling effect of temperature on the growth of *N. intermedia* by culture experiments, with respect to body size and growth rate. The possible effect of temperature

on the growth of mysid is extracted by giving an excess amount of food during culture, and an exact relationship between the growth and temperature will be established.

IV-2. Materials and Methods

Experimental conditions and cultivation

N. intermedia were collected with a conical net (0.2 m^2 mouth area, 493 μm mesh size) hauled vertically from the bottom to the surface in the hypereutrophic Lake Kasumigaura. Collected samples were maintained in thermos bottles containing lake water and brought to the laboratory within three hours. Gravid females were sorted from the field samples, placed in glass beakers (volume 1000 ml) filled with 1% seawater, and cultured on *Moina* or *Daphnia* under dim light at room temperature. Newly released animals were placed individually in 150 ml plastic beakers containing 1% seawater. The number of beakers prepared was 10 - 40 for one series culture. All culture experiments were conducted at 7 different temperatures of 3°, 10°, 15°, 18°, 20°, 25°, and 29°C ± 0.5°C with an excess amount of rotifer, *Brachionus*, cultured with *Chlorella* or rotifers collected from a pond. As mysids grew, each animal was transferred into a 500 ml beaker and fed on young *Moina* or *Daphnia* cultured with yeast. During the culture, food was given every day as to be approximately 2000 μg dry weight per liter. Based upon the amount of daily leftover foods of 40 - 80%, the

cultures were decided to be under a condition of no food limitation. All animals were visually checked every morning and an additional checking was made in the evening for the cultures of 25° and 29°C at the early post-embryonic stage. Exuviae were collected carefully and they were placed individually in small vials of 5% formalin for subsequent microscopical examination and measurement. Faecal pellets and residual food were completely removed with a pipet or siphon. Sixty percent of the water was renewed with 1% sea water at 2 - 4 day intervals. Male and female were identified by the presence of a penis or of a marsupium. When the sexual characteristics appeared in animals, a pair was placed together in a 1000 ml beaker and allowed to copulate. Male with the 4th pleopod longer than the base of telson and female bearing embryos or large developed marsupium were recognized as mature.

Treatment of data

Parameters used for the measurement of the size of mysids were carapace length (from the tip of rostrum to the dorsal end of carapace, CL, mm), telson length (from the base to the tip, not including spines, TL, mm), body length (from the tip of rostrum to the tip of telson, BL, mm), and body weight (BW, mg dry weight). Exuviae were used for measurement of the former two parameters under 40x and 100x magnification. As shown in Fig. 25, a clear linear relationship between carapace length and telson length was observed, and it was expressed by a regression

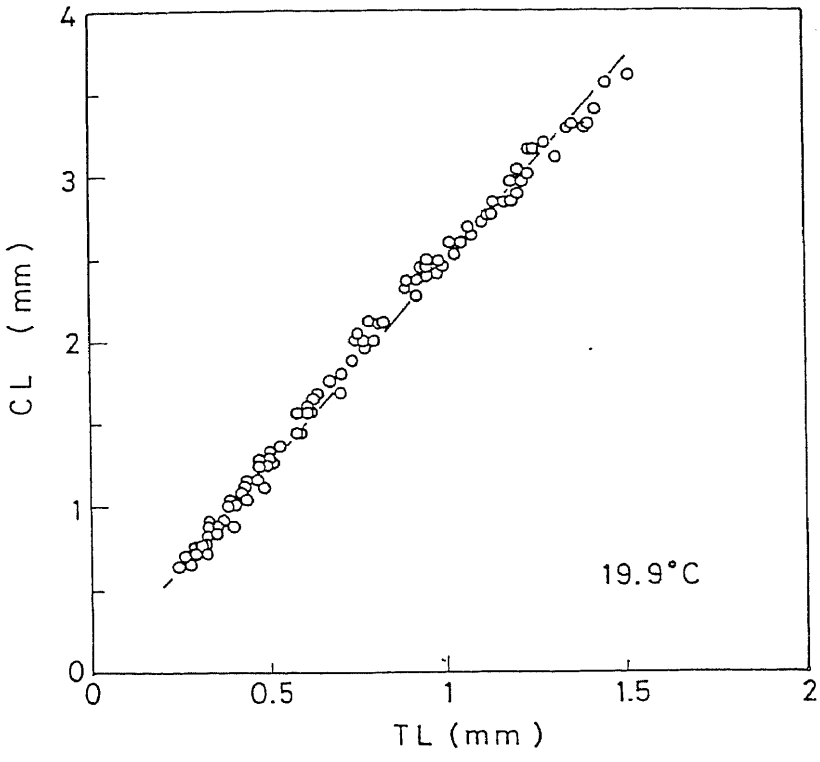

Fig. 25. Relation between carapace length (CL) and telson length (TL) of N. intermedia cultured at 19.9°C. Line was fitted by a linear regression analysis.

equation. However, this linear relation differed significantly according to the culture temperature (ANOVA, $P<0.01$), thereby the regression equation was decided respectively for each culture temperature (Table 1). Since carapace of exuviae was often lost through the eating of them by the mysid cultured, their length was estimated from the telson length using the linear relation obtained.

Carapace length was then converted to body length or body weight using the following equations in the previous chapter,

$$BL = 3.44 \cdot CL - 0.28 \qquad (n=59,\ r=0.988) \qquad (1)$$

$$BW = 0.0544 \cdot CL^{3.24} \qquad (n=156,\ r=0.984) \qquad (2)$$

Where BL and CL are length (mm) of carapace and body respectively, and BW is dry body weight (mg). These equations are based on the field data, and they can be applied directly for the culture samples, because cultured samples show almost the same trend in the relation as shown in Fig. 26.

Brood size of gravid female was estimated from the body length by using the following equation,

$$BR = 3.73 \cdot BL - 18.9 \qquad (n=200,\ r=0.637) \qquad (5)$$

where BR is brood size (number of embryos) and BL is body length (mm). This equation was based on the field data taken from Lake Kasumigaura and those from laboratory were included within the variance of field samples (Fig. 27).

Table 1. Regression equations between telson length (TL, mm) and carapace length (CL, mm) at different temperatures.

Temp.(°C)	Regression equation	n	r
3.Ø	CL = 2.37 TL + Ø.Ø46	28	Ø.993
1Ø.1	CL = 2.25 TL + Ø.Ø77	1Ø4	Ø.998
15.2	CL = 2.41 TL + Ø.Ø42	64	Ø.998
17.9	CL = 2.49 TL + Ø.Ø15	7Ø	Ø.998
19.9	CL = 2.46 TL + Ø.Ø31	158	Ø.997
25.1	CL = 2.83 TL - Ø.11Ø	55	Ø.994
28.9	CL = 2.73 TL - Ø.Ø58	15	Ø.995

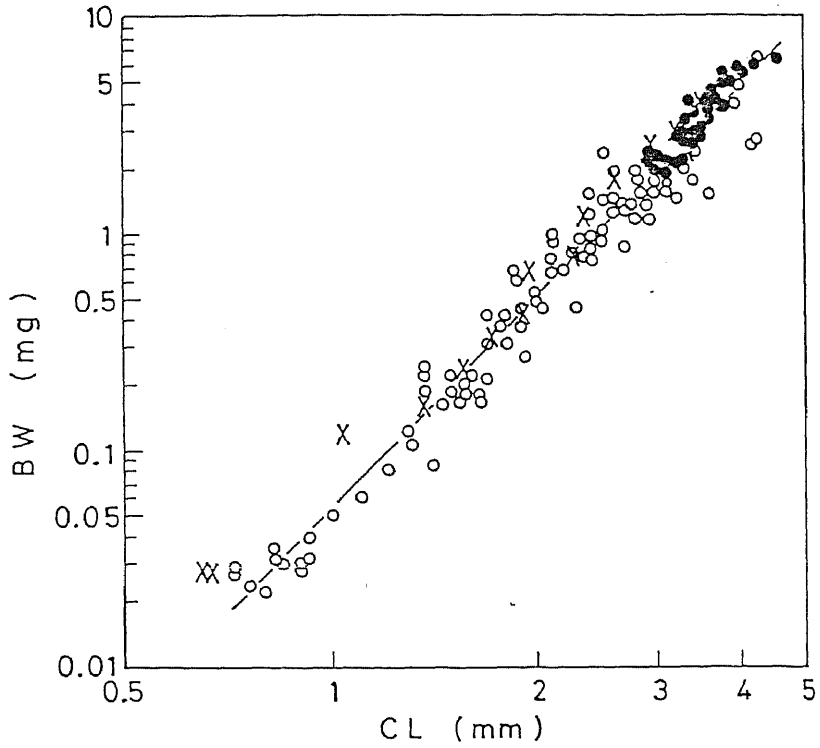

Fig. 26. Relation between body weight (BW) and carapace length (CL) of N. intermedia. Circle, field; cross, laboratory. Closed circle indicates gravid female. Line was fitted by a linear regression analysis for the field samples.

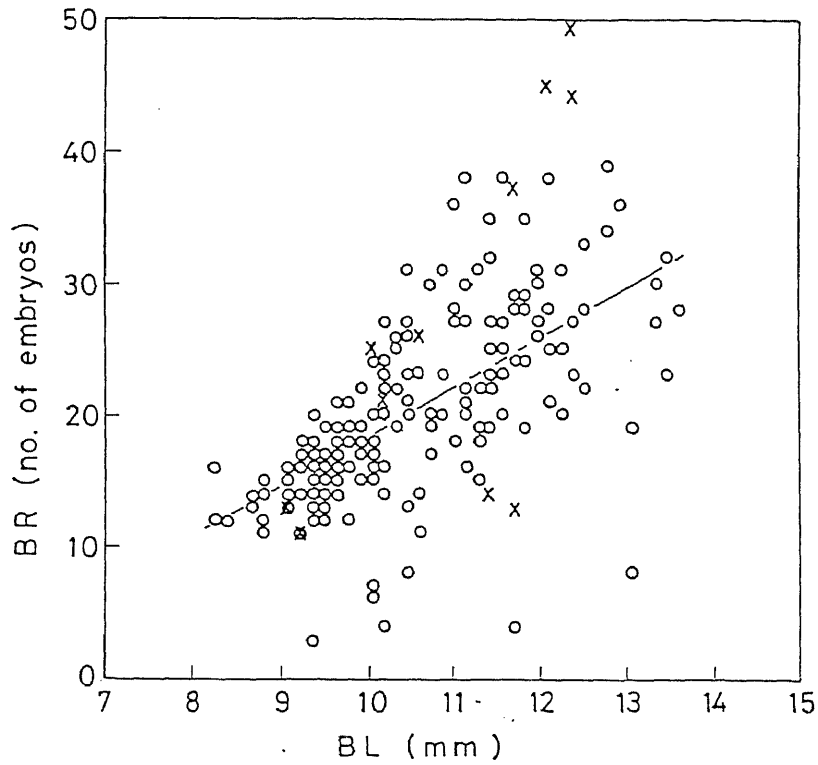

Fig. 27. Relation between brood size (BR) and body length (BL) of N. intermedia. Open circle, data obtained in Lake Kasumigaura on 24 March, 20 May, 6 July, and 9 October in 1981; cross, laboratory. Line was fitted by a linear regression analysis for the field samples.

IV-3. Results

Temperature effects on the size of N. intermedia

Difference in the effect of culture temperature on the size of newly released animals was not obvious and there was no consistent correlation between the size and temperature (Table 2). The body length varied from a maximum of 2.1 mm at 10°C to a minimum of 1.8 mm at 18°C with an average of 2.0 mm in the temperature range of 10° and 25°C. The temperature effect on the body weight was also slightly less than 15% at the maximum. The geometric mean dry weight of the newly released animal was 26.5 µg.

N. intermedia continued to molt and to increase in size throughout their life. There appeared somewhat large individuals between the 3rd and 11th molt for animals cultured at 15°, 18°, and 20°C (Fig. 28). This trend was more conspicuous in the females. Between the 3rd and 11th molt the size of mysids became smaller even at the same molt with deviation of culture temperature from 20°C.

N. intermedia did not always maturate at a particularly decided stage but the maturation occurred at certain period between the 8th and 14th molt (Table 3). The number of molts before maturation decreased fairly with the increase of temperature.

The size of adult mysids correlated inversely to culture temperature (Fig. 29). The average body length of the females at the first breeding was largest, 10.9 mm, at

Table 2. Size of newly released animals of N. intermedia cultured at different temperatures.

Temp. (°C)	Length (mm) (n, SD)	Weight* (µg) (n, SD)
10.1	2.06 (41, 0.09)	24.4 (9, 21.9-27.2)
15.2	1.96 (15, 0.10)	-
17.9	1.84 (15, 0.06)	-
19.9	1.93 (25, 0.12)	28.0 (3, 27.7-28.3)
25.1	1.98 (57, 0.11)	28.2 (9, 24.9-32.0)
average	1.98 (153, 0.12)	26.5 (21, 23.3-30.1)

* derived from log-transformed values

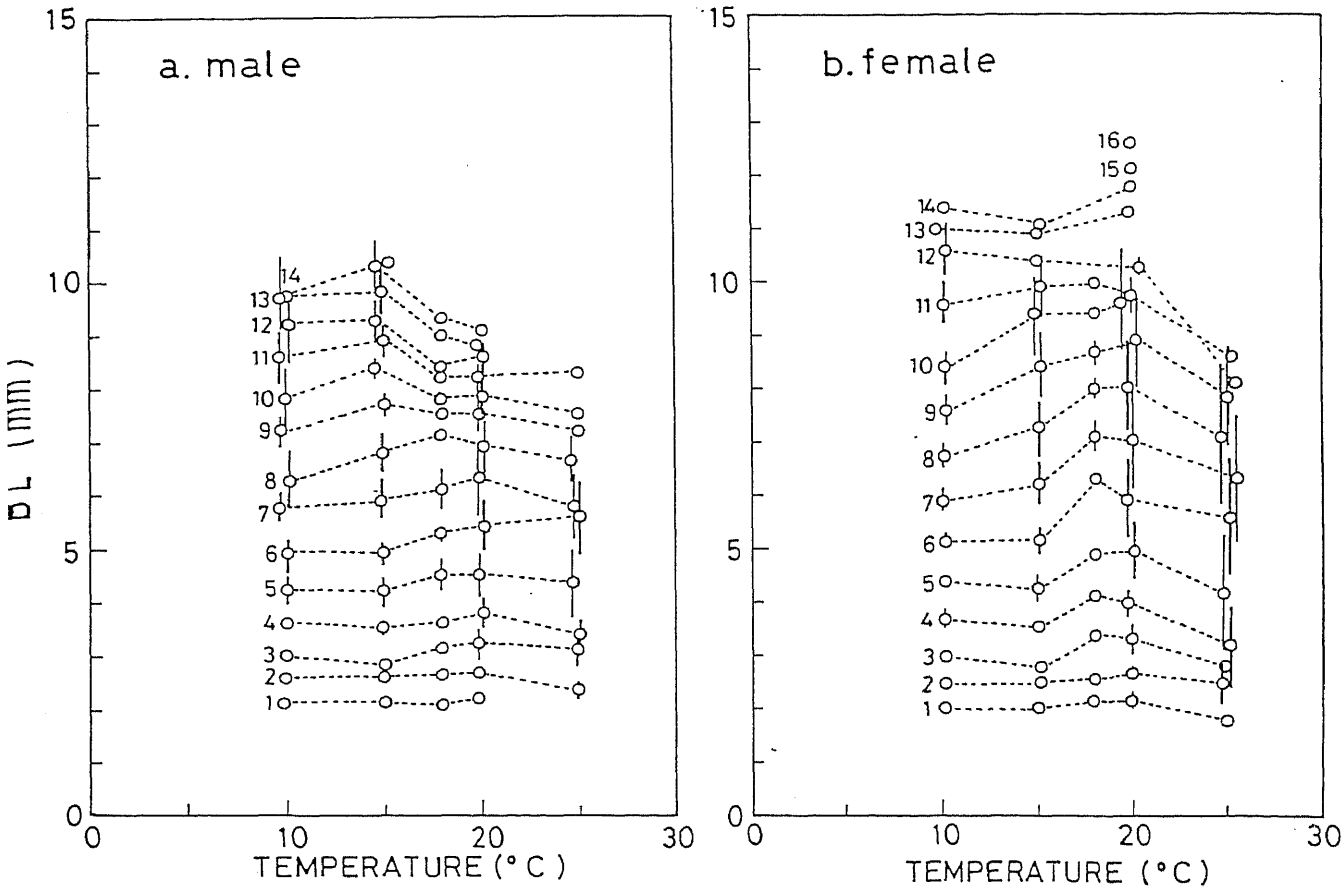

Fig. 28. Body length (BL) of N. intermedia at each molt cultured at different temperatures. Numeral indicates molting number and each vertical bar shows the standard deviation.

Table 3. Number of molts before the first breeding for N. intermedia cultured at different temperatures. Numerals indicate number of breeding females observed.

Temp.	Number of molts					
(°C)	8	9	10	11	12	13
10.1					2	1
15.2		2	1			
17.9	4					
19.9	3	5				
25.1	2	1		1		

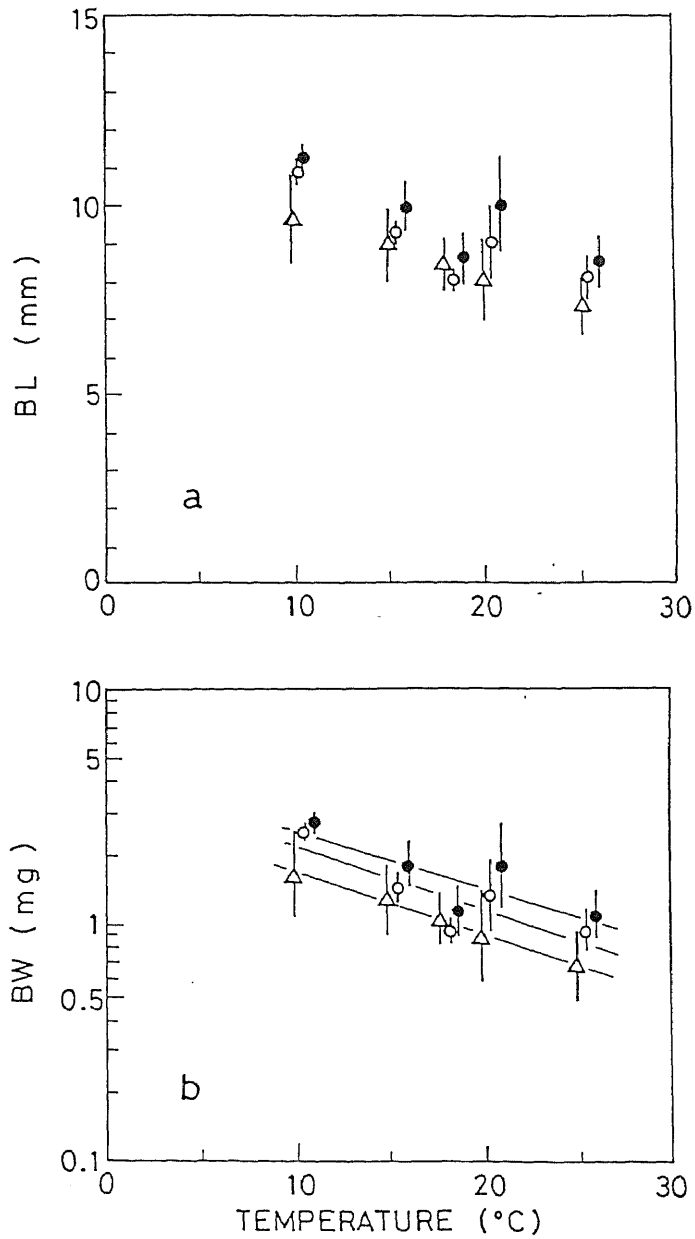

Fig. 29. Body size of adult male (triangle), female at the first breeding (open circle), and gravid female (closed circle) of N. intermedia cultured at different temperatures. Vertical bar indicates the standard deviation. Line was fitted by a linear regression analysis. a, body length (BL); b, body weight (BW).

10°C and decreased almost linearly to the lowest, 8.1 mm, at 25°C (Fig. 29a). In gravid females, the response of body length to temperature was similar to that of the first breeding females but the average size was slightly large, varing between 11.2 mm at 10°C and 8.5 mm at 25°C. The average body length of adult males also decreased with the increase of temperature from 9.6 mm at 10°C to 7.3 mm at 25°C, and it was smaller than that of the adult females.

The relation between body weight of adult mysids and culture temperature is shown in Fig. 29b in a semi-logarithmic scale. The body weight decreased almost exponentially with the increase of temperature. It varied from 2 mg at 10°C to 1 mg at 25°C and the difference between the maximum and the minimum was 2.3 - 2.6 fold. The sexual difference in the body weight of animals was 1.1 - 2.0 fold at each temperature. The values of Q_{10} (temperature dependency of adult mysids) calculated from the reciprocal plots of body weight were 1.7 - 1.8 over the temperature range between 10° and 25°C.

Temperature effects on the growth rate of N. intermedia

N. intermedia showed a rectilinear growth against time at every temperature both in body length and in log-transformed body weight (Figs. 30 and 31). The mysids grew almost linearly in body length and exponentially in body weight at the juvenile stage. However, the growth

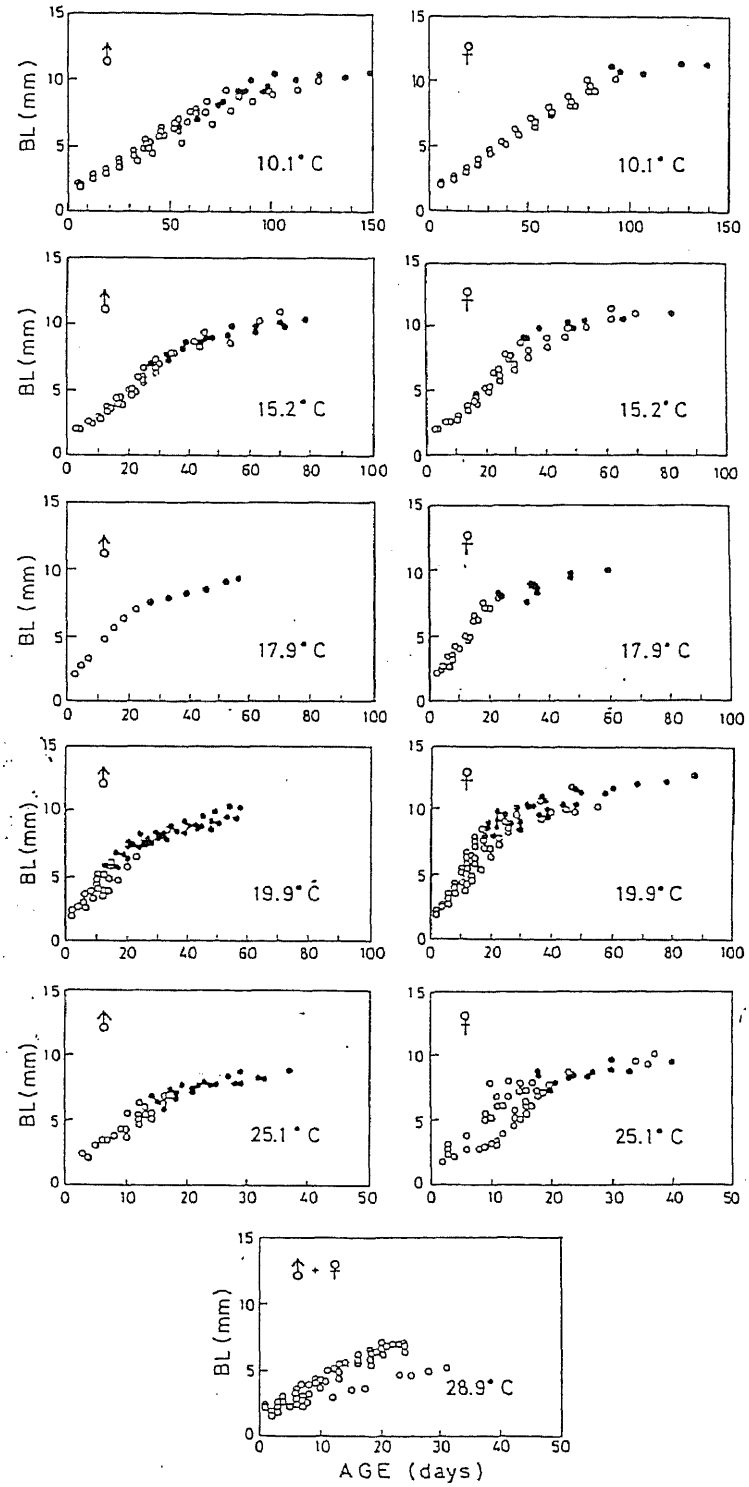

Fig. 30. Individual growth in body length (BL) of N. intermedia cultured at different temperatures. Open circle indicates juvenile, and closed circle adult.

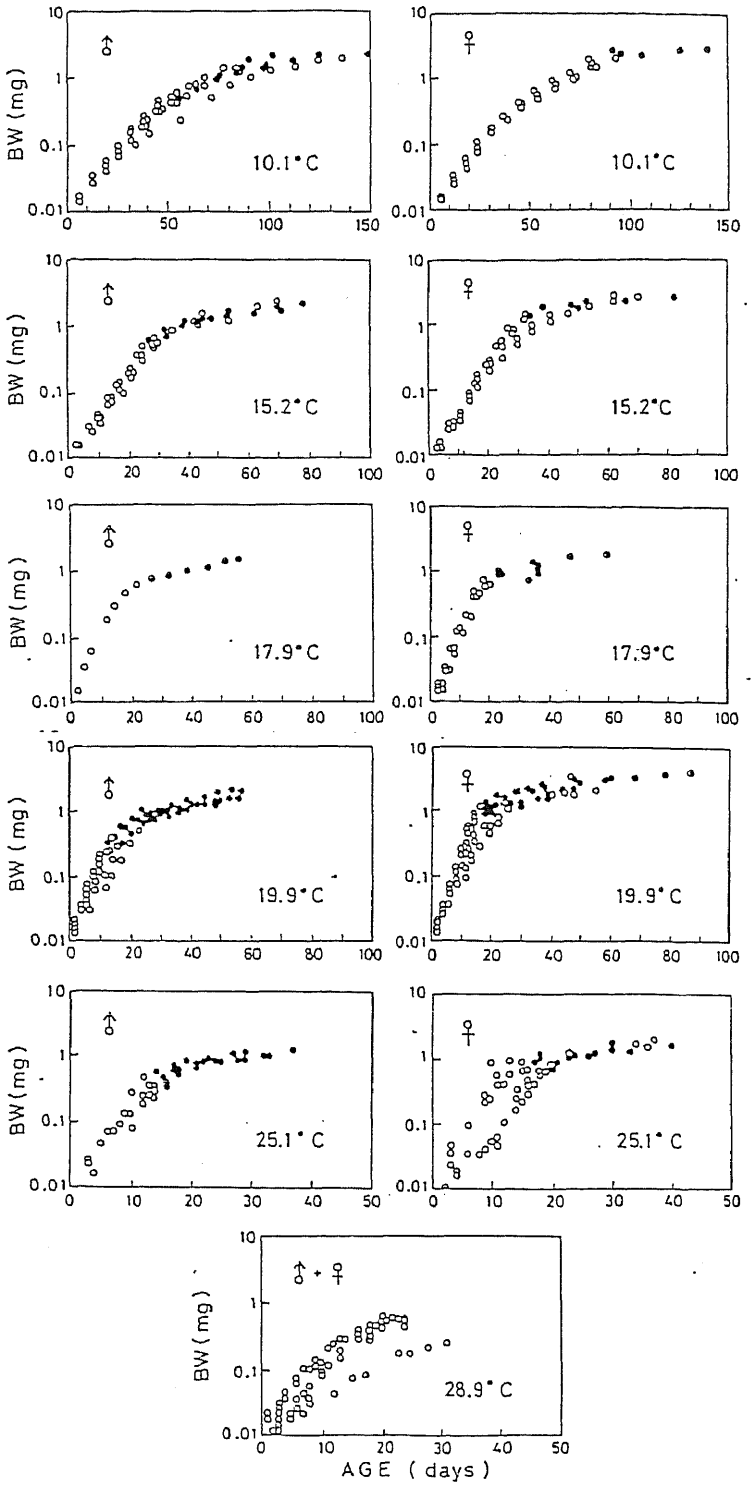

Fig. 31. Individual growth in body weight (BW) of N. intermedia cultured at different temperatures. Open circle indicates juvenile, and closed circle adult. Body weight is expressed in logarithmic scale.

abruptly declined at the adult stage, which is defined as the stage after maturation. Even in the adult stage the body size further increased gradually and this implied a continuous growth of the adult.

The growth rates of individual juveniles and adults were determined by a linear regression analysis. The growth rate of body length (GL, $mm \cdot day^{-1}$) was calculated by the following equation:

$$GL = (BL_2 - BL_1) / (t_2 - t_1) \qquad (6)$$

where BL_1 and BL_2 are body length (mm) at time t_1 and t_2, respectively. The specific growth rate in body weight (SGR, day^{-1}) was calculated by Eq. (3):

$$SGR = (\ln BW_2 - \ln BW_1) / (t_2 - t_1) \qquad (3)$$

where BW_1 and BW_2 are body weight (mg dry weight) at time t_1 and t_2, respectively. In the present study, many animals died before being distinguishable of sex, and no animals reached maturation at 29°C culture. Such being the case, the growth rate at 29°C was determined for all individuals including both sexes. The growth rate at 3°C was determined from various sized individuals collected from field and cultured over 20 - 40 days in the laboratory.

Temperature dependencies of GL and SGR are shown in Figs. 32 and 33. Both GL and SGR of juvenile increased exponentially with the increase of temperature from 0.03 $mm \cdot day^{-1}$ and 0.018 day^{-1} at 3°C to 0.32 $mm \cdot day^{-1}$ and 0.21 day^{-1} at 20°C. The values of Q_{10} were 4.2 for the

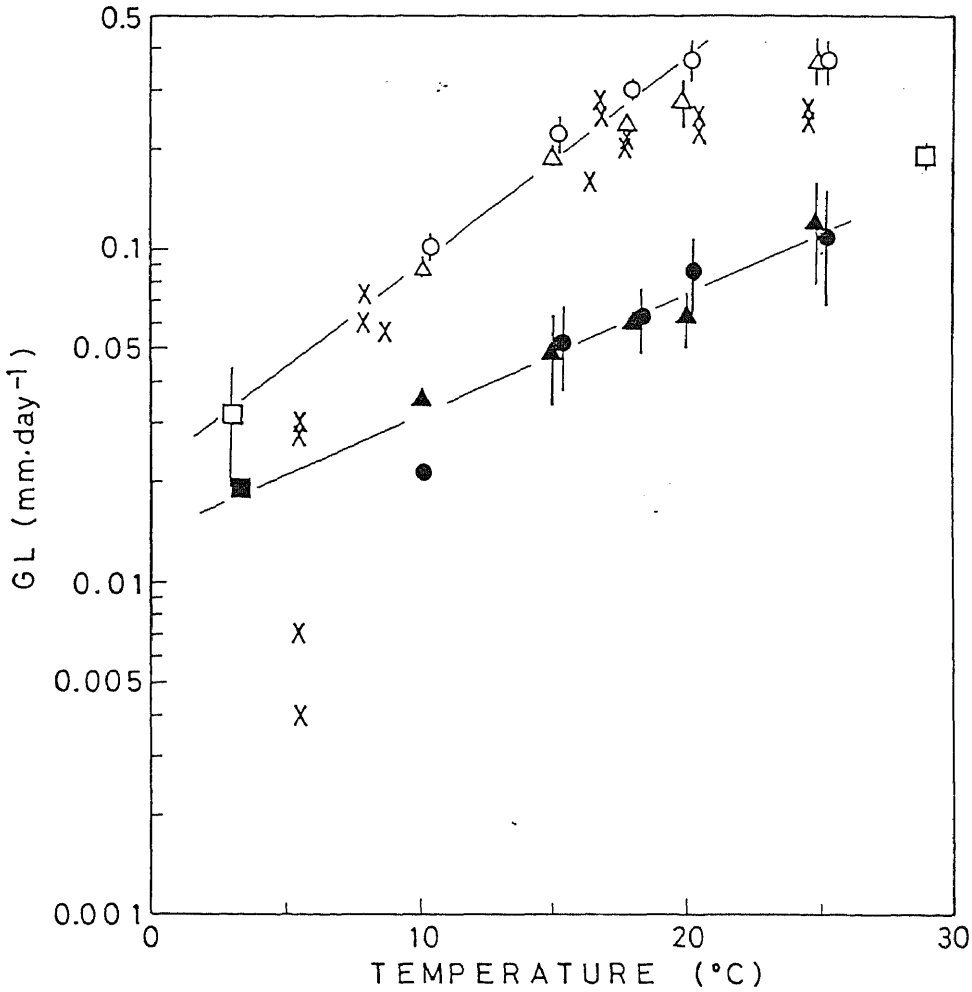

Fig. 32. Growth rate of body length (GL) of N. intermedia cultured at different temperatures. Open symbols indicate juvenile and closed symbols adult. Triangle, male; circle, female; square, both sexes; cross, field. Vertical bar indicates the standard deviation. Line was fitted by a linear regression analysis.

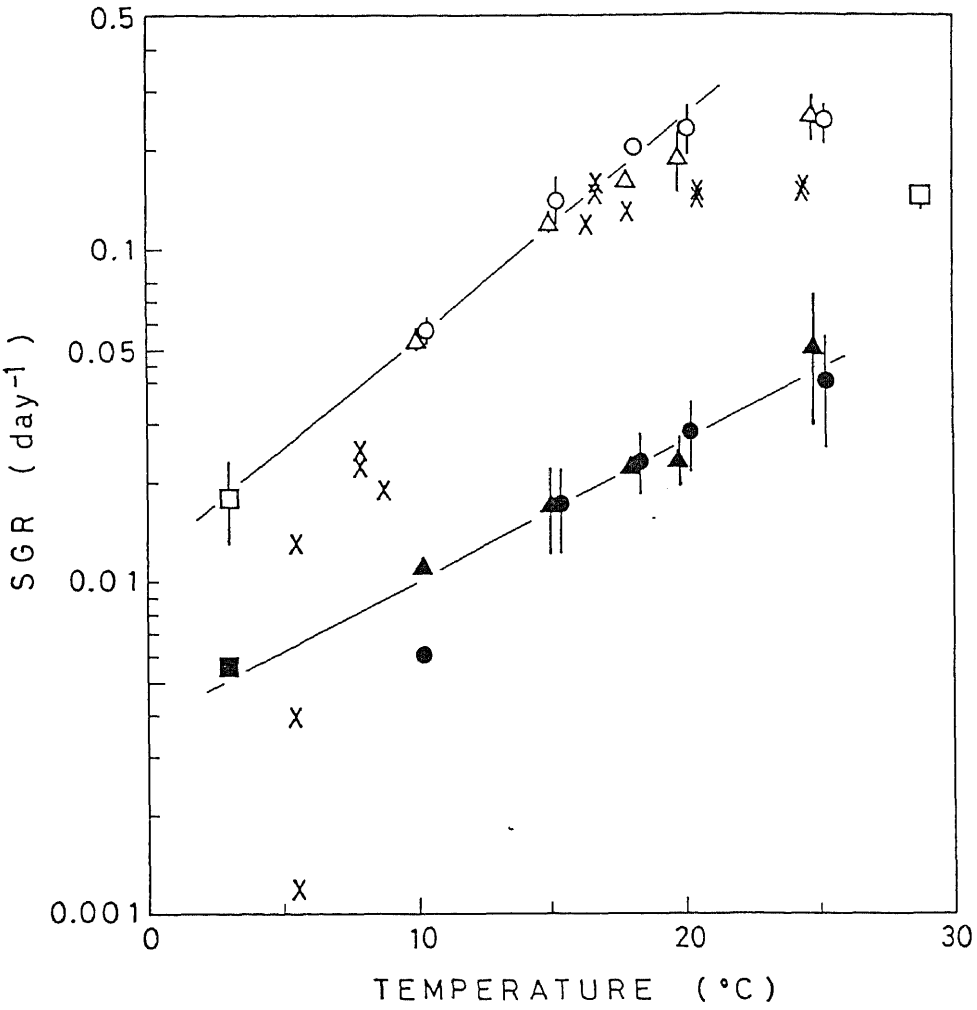

Fig. 33. Specific growth rate (SGR) of N. intermedia cultured at different temperatures. Symbols are the same as in Fig. 32.

former and 4.6 for the latter between 3° and 20°C. Both rates of the juvenile, then, leveled off at 20° - 25°C, and subsequently dropped. Adults also showed an exponential increase in GL and SGR but both parameters were remarkably low compared with those of the juveniles, ranging from 0.02 $mm \cdot day^{-1}$ and 0.006 day^{-1} at 3°C to 0.12 $mm \cdot day^{-1}$ and 0.05 day^{-1} at 25°C. The values of Q_{10} for the growth rate of adults were 2.3 for GL and 2.7 for SGR between 3° and 25°C.

Temperature effects on the reproduction of N. intermedia

Growth parameters such as body length (BL), brood size (BR), brood interval (BI), daily egg production rate in number (EN) and in dry weight (EW), specific reproduction rate (SRR), and specific growth rate (SGR) including reproduction were determined for gravid females at different temperatures and summarized in Table 4.

The size of a brood (BR) was estimated from the body length (BL) by using Eq. (5). The BR decreased with the increase of temperature in a range of 23 eggs at 10°C to 13 eggs at 25°C.

The extrusion of eggs into a marsupium took place at night immediately after the release of the former embryos at higher temperatures, while it occurred on the next night at lower temperatures. Accordingly the brood interval was equivalent to or slightly longer than the embryonic duration. The brood interval (BI) was inversely

Table 4. Body length of gravid female (BL), brood size (BR), brood interval (BI), daily egg production rate in number (EN) or in weight (EW), specific reproduction rate (SRR), and specific growth rate (SGR) including both somatic growth and reproduction of N. intermedia at different temperatures.

Temp. (°C)	BL (mm)	BR (no.)	BI (days)	EN (no. day^{-1})	EW* (µg day^{-1})	SRR (day^{-1})	SGR (day^{-1})
10.1	11.2	22.9	30.3	0.76	23.6	0.009	0.015
15.2	9.9	18.0	15.6	1.15	35.8	0.020	0.037
17.9	8.6	13.2	11.9	1.11	34.5	0.029	0.052
19.9	10.0	18.4	9.5	1.93	60.0	0.033	0.061
25.1	8.5	12.9	6.6	1.95	60.6	0.053	0.093

* calculated by using 31.1 µg dry wt. of each egg.

temperature dependent and decreased greatly with the increase of temperature from 30 days at 10°C to 7 days at 25°C.

The daily egg production rate in terms of egg number (EN, average number of eggs produced per day) was determined by dividing the brood size with the brood interval (BR/BI) at each temperature. The rate showed a clear increase with the increase of temperature within a range between 0.8 eggs·day^{-1} at 10°C and 2 eggs·day^{-1} at 25°C. As the geometric mean dry weight of an egg was 31.1 µg, the daily egg production was converted from the number to dry weight. The daily egg production rate based on dry weight (EW) ranged from 24 µg and 61 µg dry weight·day^{-1} and showed a positive temperature dependence.

The specific reproduction rate (SRR) determined by dividing the daily reproduction rate by body weight increased exponentially with the increase of temperature. The Q_{10} was 3.2 within a temperature range between 10° and 25°C.

The specific growth rate (SGR) of adult female almost doubled when the reproduction rate was included as well as the somatic growth rate. Even in the corrected growth rate, however, the rate was still only 30 - 40% of that for the somatic growth rate attained by juveniles.

IV-4. Discussion

The effect of temperature on the body size of newly released mysids was not obvious, but there was a clear inverse relationship between body size and temperature for adult mysids. A similar inverse relation has also been confirmed by the field observations made in a highly productive lake, Lake Kasumigaura as shown in Fig. 34. Therefore, it can be surmised that there is no significant difference between the culture and field samples for the effect of temperature on the adult body size. This suggests that temperature is a primary factor controlling the body size of adult N. intermedia in the hypereutrophic lake.

Vidal (1980b) proposed a mechanism explaining an inverse relationship between the body size of herbivorous copepods and temperature from laboratory culture experiments. The growth rates of those copepods became temperature independent as they grew, but each molting interval inversely related to temperature throughout the development. The growth rate of copepods at the later stages was then the same irrespective of temperature but the molting interval was prolonged at low temperatures. Consequently, the size increment during each intermolt period became significantly large with decreasing temperature at later growth stages, and therefore the final size was inversely related to temperature.

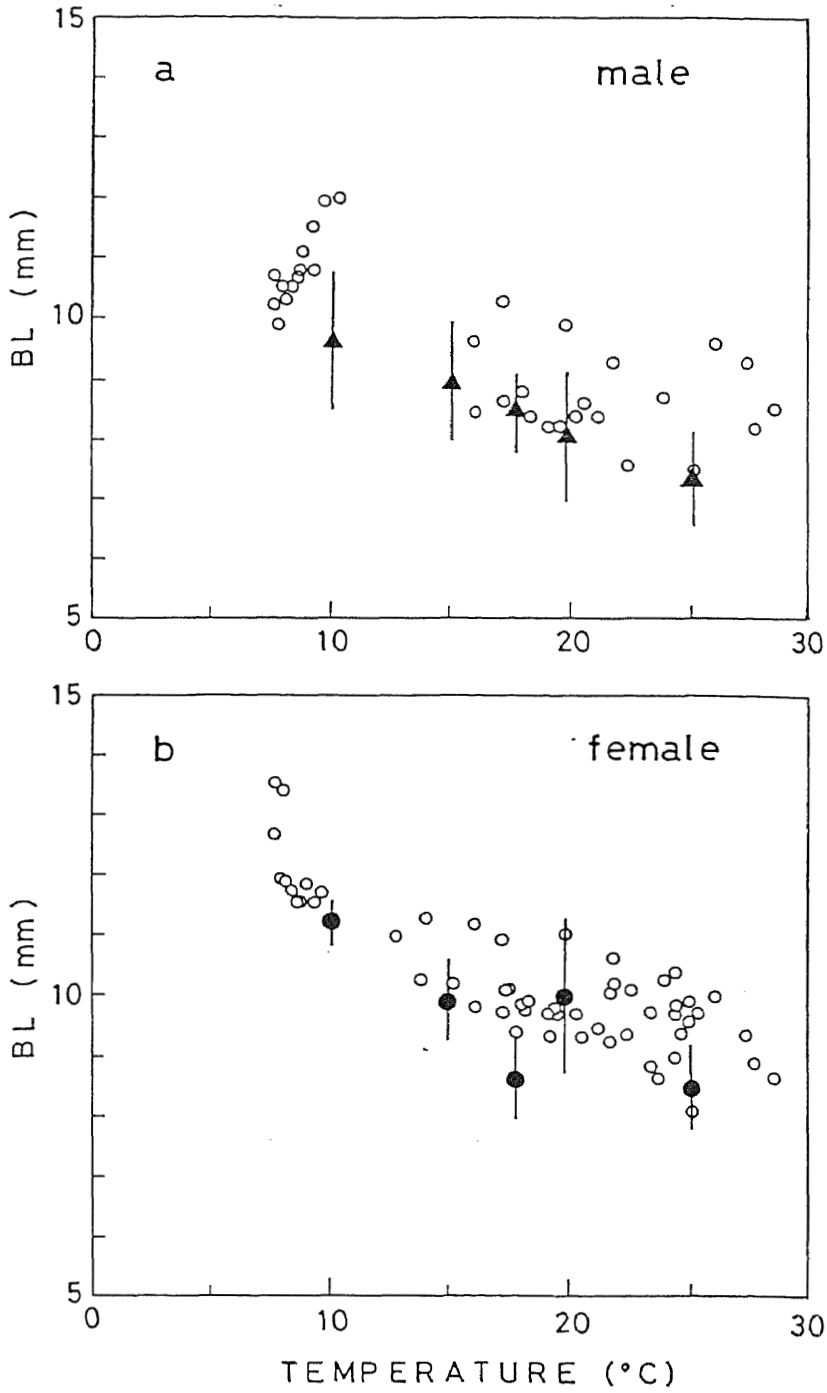

Fig. 34. Relationship between body length (BL) and temperature for adult N. intermedia. Open circle, field; closed symbol, laboratory. Vertical bar indicates the standard deviation.

The size increment during each intermolt period showed the similar trend in the growth process of N. intermedia, but it was only noticed in a temperature range above 20°C. At temperatures lower than 20°C, the increment of size in N. intermedia rather decreased, and the number of molts before maturation increased. This was a striking contrast to copepods. The decrease in size increment during an intermolt period at low temperatures was supplemented with the increase in the number of molts, which resulted in a large size individual at maturation. As the result, an inverse relationship was created between the body size and the temperature in the adult mysid.

It was reported for the mayfly, Baetis rhodani, that the number of instars of small sized mature individuals appearing in summer was fewer than that of large individuals in winter (Elliott, cited in Humpesch, 1981). Variability in the number of molts or instars at larval stage has also been reported in shrimps such as Palaemonetes pugio, P. vulgaris (Broad, 1957), and Palaemon serratus (Reeve, 1969), and euphausiid, Euphausia pacifica (Ross, 1981), although possible temperature effects were not considered. Therefore there are two possible factors causing the inverse relationship between body size and temperature in natural populations of crustaceans: one is the difference in the size increment during each intermolt period as reported by Vidal (1980b),

and the other is the difference in number of instars at the juvenile stage as observed in N. intermedia in the present study.

Under an excess amount of food, the specific growth rate of N. intermedia showed an exponential increase against temperature below 20°C at the juvenile stage and below 25°C at the adult stage. The temperature dependency of the growth rate was extremely large and the value of Q_{10} was 4.6 for juvenile and was 2.7 for adults. Such an exponential relationship between the growth rates of N. intermedia and temperature at the juvenile stage in Lake Kasumigaura was almost identical with that of the cultured sample (Figs. 32 and 33). Some discrepancies in the growth rates at low temperatures are probably due to uncertainty in measurements at extremely low in situ growth rate. Additionally the growth rates of the overwintering populations were determined with the mixed populations consisting of juveniles and adults in the previous chapter, and it is highly possible that the actual in situ growth rate of juveniles will increase with the exclusion of the lowering effects caused by the slow growth rates of adults. Consequently it can be concluded that temperature is a major factor controlling the growth rate of N. intermedia in productive food rich waters such as L. Kasumigaura.

The growth rate of juvenile of N. intermedia above 25°C leveled off, and that at 29°C was rather suppressed.

This indicates that either the limiting process of the growth rate of N. intermedia shifted to the other process with a different temperature dependency mechanism, or the physiological nature of the growth processes was changed by high temperature. Similar depression in growth rate of N. intermedia at a high temperature of 30°C was also observed in the culture experiments by Murano (1964b). The mortality at early post-embryonic growth was extremely high at 29°C and no mysids matured in the laboratory in the present study. Thus, high temperature such as 29°C is harmful for the growth of N. intermedia.

Many Neomysis species living in temperate coastal waters, where seasonal variation in temperature is large, are exposed to a wide variation of temperature and show a great seasonal variation in their generation length (e.g. Mauchline, 1971; Pezzack and Corey, 1979). Among those mysid species, it has been verified from the culture experiments that the growth rate of Neomysis americana at early post-embryonic stage was strongly temperature dependent between 4° and 25°C, and the Q_{10} of 5.6 was calculated from data in Pezzack and Corey (1979). Such strong temperature dependency was comparable with that of N. intermedia observed in the present study. Therefore this strong temperature dependency is probably a unique character for the Neomysis species, and it is very likely that their growth rates and generation lengths are mainly controlled by temperature under natural conditions.

In N. intermedia cultured under no food limitation at high temperatures, the body size of female became small, resulting in small brood size, and the brood interval also decreased. Temperature effects on the brood interval were much greater than brood size. Consequently, the daily specific reproduction rate of N. intermedia, determined by dividing the brood size with the brood interval and body weight, increased with an increase in temperature from 10° to 25°C, and the relation was clearly exponential. The daily specific reproduction rates of the mysid in the field under no food limitation, therefore, are also expected to be controlled by temperature. Similar positive temperature dependency of the daily specific reproduction rates have been known for some marine zooplankton species. Acartia clausi and A. steueri had an exponential increase in the specific reproduction rate with temperature increase and reached a maximum of 60 - 70% of body carbon per day (Uye, 1981). Sac-carrying copepod, Pseudodiaptomus marinus, showed a linear increase in the rate from 3.5% to 26% of body carbon per day with temperature increase (Uye et al., 1982). The daily specific reproduction rate of marine amphipod, Calliopius laeviusculus also became high with temperature increase (Dagg, 1976).

In conclusion, the post-embryonic growth of N. intermedia was controlled by temperature as follows: (1) the size of newly released animals was not affected by

temperature, but the body size became small at high temperatures at maturation; (2) the growth rate at the post-embryonic stage depended exponentially on temperature with the Q_{10} of 4.6 for juveniles and of 2.7 for adults; (3) the size and interval of broods decreased with the increase of temperature, while the daily specific reproduction rate increased exponentially with the Q_{10} of 3.2.

CHAPTER V

Evaluation of the Environmental Control on the Growth Processes of *Neomysis intermedia*

V-1. Introduction

As mentioned in the previous chapters, the post-embryonic growth of mysid shrimp, *Neomysis intermedia*, in the natural habitat, Lake Kasumigaura, is strongly controlled by temperature (Chapter III). This temperature dependency has also been confirmed by the laboratory culture conducted under a condition of no food limitation (Chapter IV). Consequently, it is expected that temperature is one of the most important environmental factors which control the growth of *N. intermedia* under natural condition.

Individual growth of zooplankton is considered as the result of the balance of various metabolic activities and generally expressed by the following growth equation; $G = (I - F) - (M + R + L)$, where G is growth, I is ingestion, F is egestion, M is molt, R is respiration, and L is leakage/excretion. Accordingly, an analytical approach for the evaluation of temperature dependency of the growth of mysid is to reveal the effect of temperature on each parameter in the growth equation. The growth is then reconsidered synthetically referring the information on respective temperature dependency of metabolic activities.

In this way it can be identified which metabolic activity is mostly affected by temperature and consequently actual temperature control on the growth of N. intermedia might be explained on the basis of metabolic activities.

With this prospect in mind, the present study was carried out and the temperature effects on each parameter in the growth equation was examined under laboratory conditions. All parameters were expressed as specific rate and were symbolized by "SR" in this chapter. For example, "SGR" indicates the specific growth rate.

V-2. Materials and Methods

Mysids used in the present study were collected from Lake Kasumigaura. Culture techniques and experimental conditions were almost the same as those described in the Chapter IV.

In order to express all metabolic rates in terms of carbon basis, the carbon contents of the mysids, their molts, and the food (Daphnia) were analyzed with a Yanagimoto CHN Analyzer (MT-II type).

Specific growth rate (SGR, % body C·day^{-1}) determined by the carbon increase per unit time was calculated by SGR = (ln BC_2 - ln BC_1) / (t_2 - t_1) x 100, where BC_1 and BC_2 are body carbon (mg C) at time t_1 and t_2, respectively. Eggs produced during the time period between t_1 and t_2 were included in BC_2. Body carbon was estimated from dry body weight using conversion factors of 0.452 (mg C·mg dry

wt^{-1}) for post-embryonic animals and 0.518 for eggs.

Feeding rate was measured as follows. Mysids used for the experiments were precultured with 1% seawater at 6 different temperatures of 3°, 10°, 15°, 20°, 25°, and 29°C under dim light. A sufficient amount of Daphnia cultured with yeast was supplied as prey. After 2 days, the precultured animals were placed individually in 300 ml or 500 ml beakers and fed on young Daphnia. The mean body length, dry weight, and carbon content of individual Daphnia were 0.74 mm, 3.4 µg, and 6.8% of dry weight, respectively. The concentrations of prey were 300 - 900 individuals per liter, which was equivalent to 1000 - 3000 µg dry weight per liter. Beakers were kept at respective culture temperatures for 6 to 24 h (mostly 24 h) under dim light. After incubation, the number of Daphnia remaining in beakers was counted. Mysids and their exuviae were preserved in a vial with 5% formalin for the measurements of carapace length or telson length.

Ingestion rate was determined from the difference in the number of prey before and after the incubation and converted into dry weight. Since the number of prey in the control bottles (without mysids) varied only within 1% during the incubation, no particular correction was made for the ingestion rates determined.

Specific ingestion rate (SIR, % body C·day^{-1}) was determined by SIR = [(dPC/dt) / BC] x 100, where dPC/dt is ingestion rate on carbon basis and BC is body carbon of

mysid. Dry weight of mysid was estimated indirectly from the carapace length or telson length of exuviae using the regression equations (Eq. (2) and Table 1) presented in the previous chapters and then converted into carbon weight. The amount of ingested carbon (PC) was also determined from dry weight using a conversion factor of Ø.368 (mg C·mg dry wt^{-1}).

The specific loss rate of body carbon by molting (SMR, % body C·day^{-1}) during the intermolt period between t_1 and t_2 was determined by $SMR = [(MC_2/BC_2) / (t_2 - t_1)] \times 1ØØ$, where MC_2 and BC_2 are molt carbon and body carbon at time t_2. The molt carbon was determined indirectly from dry weight by using the following allometric equation (Fig. 35);

$$MW = Ø.ØØ768 \cdot CL^{2.54} \qquad (7)$$

where MW is dry weight of molt (mg) and CL is carapace length (mm). The molt weight was then converted into carbon weight using a factor of Ø.245 (mg C·mg dry wt^{-1}).

Respiration rate was measured as follows. Collected mysids were sorted as uniformly in size as possible and were placed in 5ØØ ml beakers filled with filtered lake water. A sufficient amount of rotifers and cladocerans was added as food, and beakers were kept at different temperatures ranging between 5^{o} and 25^{o}C under dim light for 12 h before the experiments. Lake water filtered twice through a glass fiber filter (Whatman GF/C) was placed in plastic containers of 1Ø l each and kept at

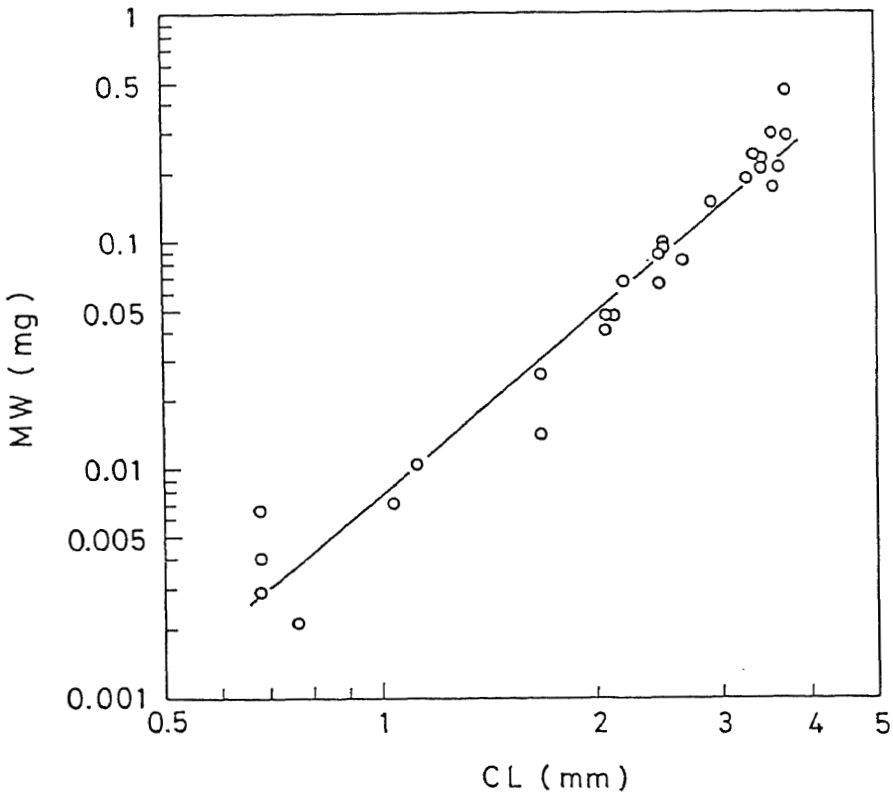

Fig. 35. Relation between molt weight (MW) and carapace length (CL) of N. intermedia. Line was fitted by a linear regression analysis.

respective temperatures. This filtered water was siphoned carefully into 100 ml ground-glass stoppered bottles. Animals of 1 to 10 individuals depending on body size were added to the half of bottles and the other half served as a control. Dissolved oxygen in half of the control bottles was fixed immediately. All the other bottles were stoppered, wrapped with aluminum foil, and kept at each experimental temperature for 4 - 24 h. After incubation, 50 ml of water was carefully siphoned from each bottle and fixed. The oxygen content in both experimental and control bottles was determined by Winkler's titration. The animals in the bottles were placed on aluminum pans, dried at 60°C for 2 days, and weighed with an electrobalance. Exuviae were also checked.

Oxygen consumption was determined from the difference of oxygen contents in control and experimental bottles. The actual oxygen decrease in the experimental bottles was less than 15% of the dissolved oxygen in the water. There was no significant difference in respiration rates measured in the daytime and the nighttime (t-test, $P>0.05$). Thus the respiration rate was usually measured in the daytime. The consumed oxygen was converted into carbon by using the respiration quotient of 0.75, that was proposed for carnivorous zooplankton by Dagg (1976). Namely, the consumed oxygen of 1 mg is equivalent to 0.28 mg C.

V-3. Results

Growth rate and its relation to temperature

As shown in Fig. 36, the specific growth rate (SGR, % body C·day^{-1}) at the juvenile stage increased exponentially with an increase in temperature from 1.8% to 21% body C·day^{-1} in the range of 3° to 20°C but levelled off at 25°C, and subsequently dropped. The SGR of gravid females also showed a similar trend against temperature, but the exponential relationship was continued up to 25°C; 1.6% body C·day^{-1} at 10°C to 10% body C·day^{-1} at 25°C. The SGRs of gravid females were also characterized with lower values such as 1/3 of juveniles'. The temperature coefficient (Q_{10}) of SGR was 4.6 at the juvenile stage in the temperature range of 3° and 20°C, and was 3.4 between 10° and 25°C for gravid females.

Ingestion rate and its relation to temperature

The specific ingestion rates (SIR, % body C·day^{-1}) determined at different temperatures are plotted against dry body weights, both indicated in logarithmic scale (Fig. 37). The SIR varied from the lowest of 2% body C·day^{-1} for large animals at a low temperature to the highest of 140% body C·day^{-1} for small animals at a high temperature. There was no consistent difference in SIR between molting animals and the others. The SIR showed a linear decrease with the increase of body weight at all temperatures in the figure, and the relation was

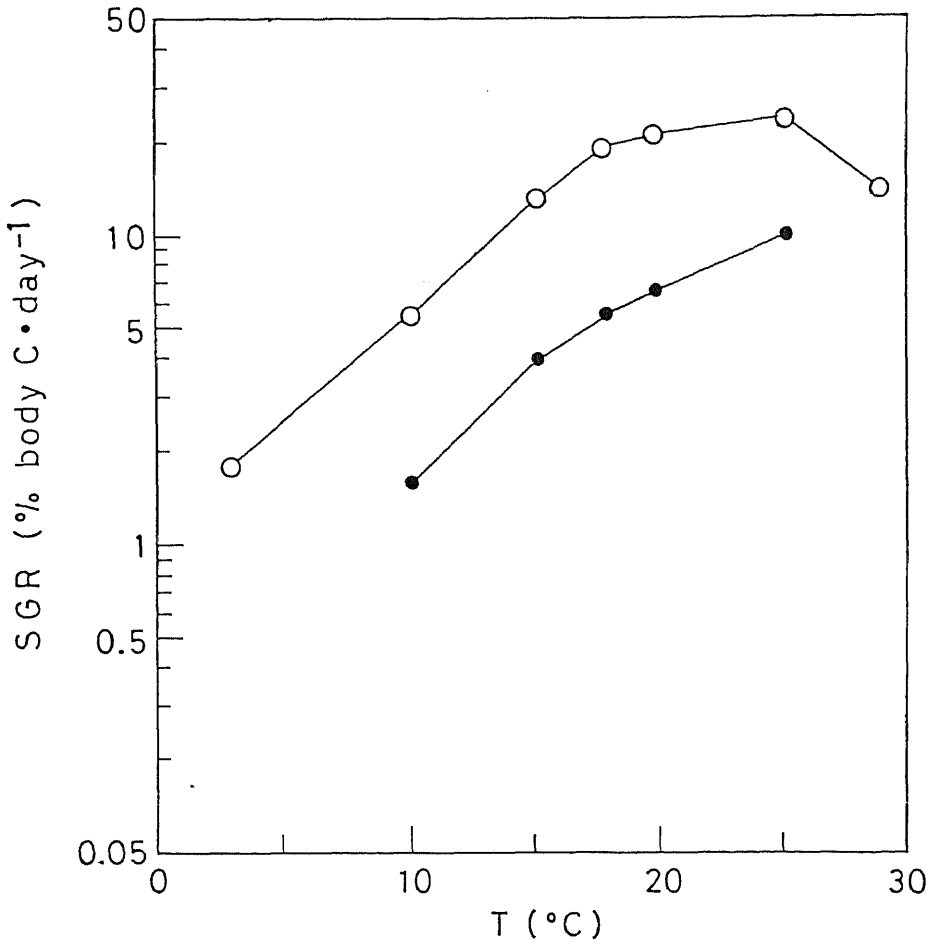

Fig. 36. Relationship between specific growth rate (SGR) and temperature (T) of juveniles (open symbols) and gravid females (closed symbols) for N. intermedia.

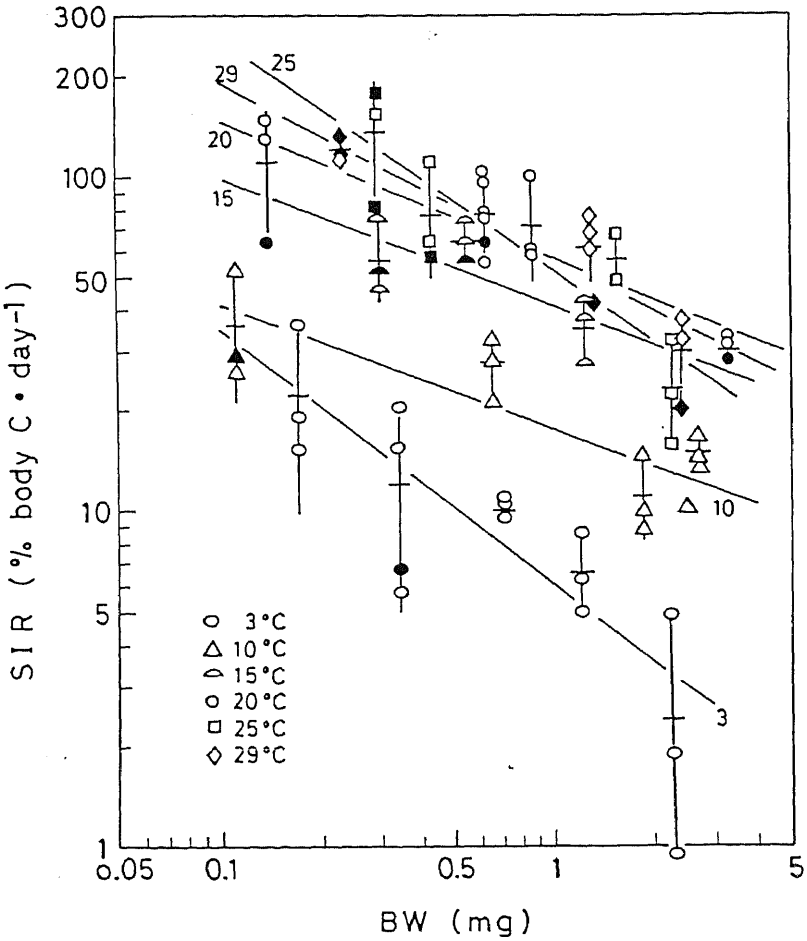

Fig. 37. Relationship between specific ingestion rate (SIR) and body weight (BW) determined at different temperatures for N. intermedia. Closed symbols indicate molting animals and open symbols others. Vertical bars denote the standard deviation, horizontal bars the average. Line was fitted by a linear regression analysis.

approximated by a linear regression analysis at each temperature. The level of SIR increased with the increase of temperature.

Based on the regression lines shown in Fig. 37, the SIRs were estimated at each temperature for juveniles at different body weights and gravid females, and they were plotted against temperature as shown in Fig. 38. The SIR increased almost exponentially with an increase in temperature from 3° to 20°C, reached a maximum at 20° - 25°C, and subsequently levelled off or slightly dropped. The temperature coefficient (Q_{10}) of SIR was 2.6 - 2.7 for small animals at temperatures below 25°C and 3.2 - 3.9 for large animals and gravid females below 20°C.

Molting loss rate and its relation to temperature

The relations between the intermolt period (IMP, days) measured at different temperatures and molting numbers are shown in Fig. 39. There was no significant difference in IMP between males and females. The IMP was short and consistent up to 6 or 7 molting numbers, showed a subsequent gradual increase with the increase of molt number up to 10 or 12, and levelled off thereafter. With the progress of molting the body size of individual animal increased, and so the IMP became longer for large animals than small animals. Although not shown in Fig. 39, at the lowest temperature examined, 3°C, the IMP was 18 days for small animals and 30 days for large animals. Gravid

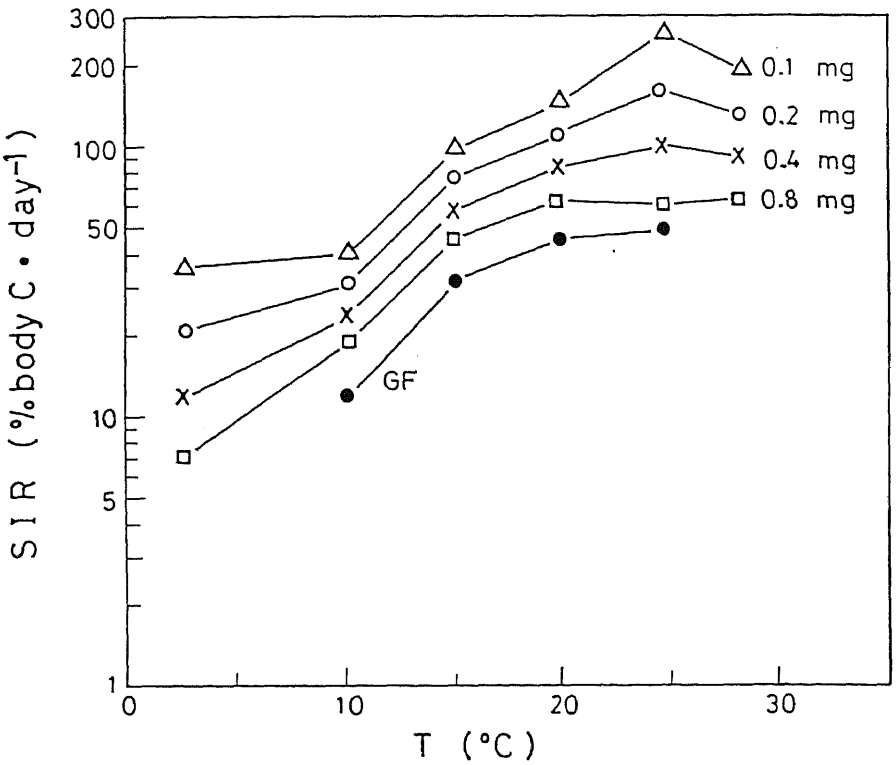

Fig. 38. Relationship between specific ingestion rate (SIR) and temperature (T) of juveniles at different body weights and gravid females (GF) for N. intermedia.

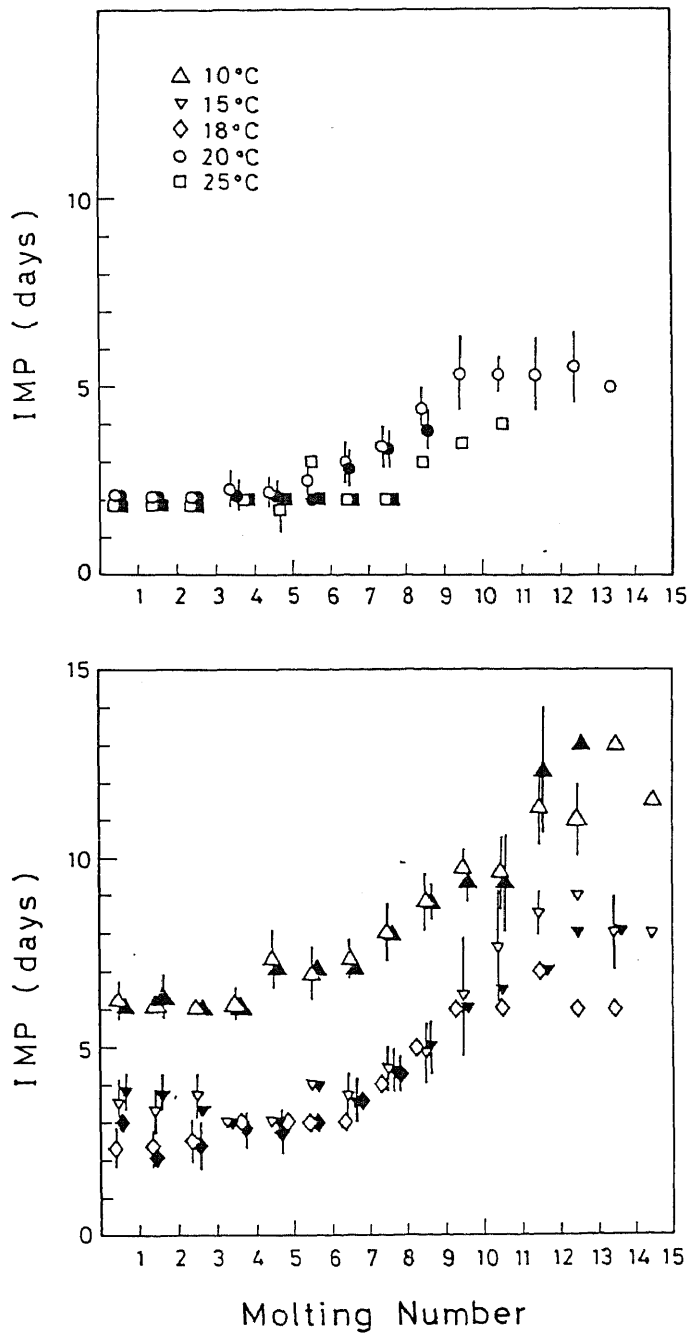

Fig. 39. Relationship between intermolt period (IMP) and molting number observed at different temperatures for N. intermedia. Open symbols indicate males and closed symbols females. Vertical bars denote the standard deviation.

females appeared at molting number of 8 to 13 as shown in the previous chapter (Table 3) and showed a consistent IMP regardless of the molting number at each temperature. Those obtained were on average 30, 16, 12, 10, and 7 days at 10°, 15°, 18°, 20°, and $25^{\circ}C$, respectively. From these results it was obvious that the IMPs of gravid females were extremely prolonged in comparison with those of others. The IMP was shortened at higher temperatures over the entire molting number.

The specific loss rates of body carbon by molt (SMR, % body $C \cdot day^{-1}$) are plotted against the logarithmic body weight which was represented by the geometric mean body weight during the intermolt period (Fig. 40). The lowest SMR was 0.1% body $C \cdot day^{-1}$ for large animals at low temperatures and highest was 5% body $C \cdot day^{-1}$ for small animals at high temperature. No significant difference was observed in SMR between males and females. The considerably low SMR was measured for gravid females because of their prolonged intermolt period. The SMR showed a linear decrease with the increase of body weight at each temperature in the figure, and the data points were treated with a linear regression analysis at each temperature. The level of SMR increased with the increase of temperature.

Calculating from the regression lines in Fig. 40, the SMRs were obtained for juveniles and plotted against the temperature to clarify the effect of temperature on SMR

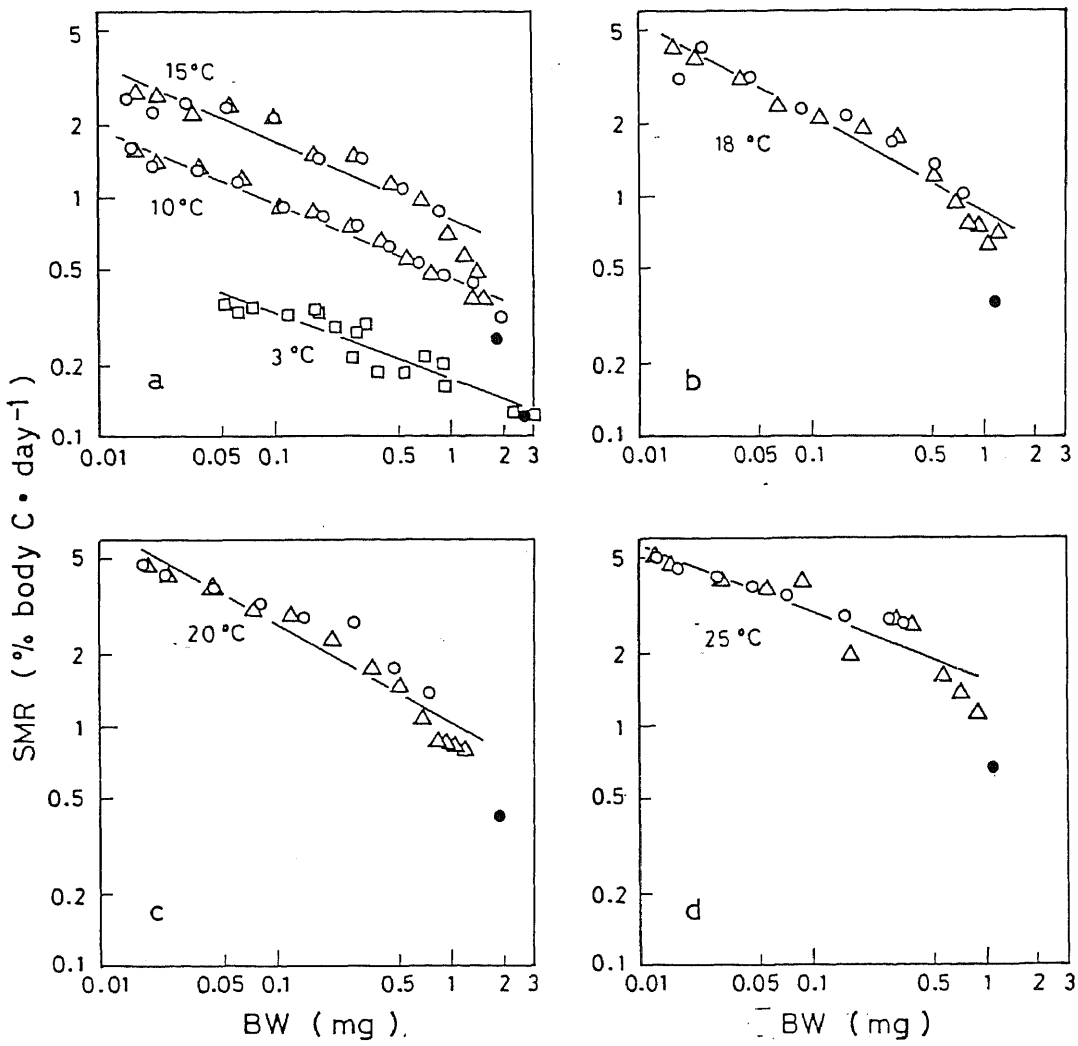

Fig. 40. Relationship between specific molting loss rate (SMR) and body weight (BW) determined at different temperatures for N. intermedia. Triangles indicate males, circles females, and closed circles gravid females. Line was fitted by a linear regression analysis.

(Fig. 41). Those of gravid females were separately calculated from the data mentioned above. The SMR increased exponentially with an increase in temperature from 3° to 2Ø°C and levelled off at 2Ø° - 25°C for juveniles, and the exponential relationship was continued up to 25°C for gravid females. The temperature coefficient ($Q_{1Ø}$) of SMR was 2.9 - 3.6 for juveniles between 3° and 2Ø°C and 3.1 for gravid females between 1Ø° and 25°C.

Respiration rate and its relation to temperature

Specific respiration rates (R_o, μg O_2 · mg dry wt^{-1} $\cdot h^{-1}$) measured at different temperatures are plotted against respective body weights in the logarithmic scale (Fig. 42). There was no apparent difference in R_o between molting animals, gravid females, and others. The R_o decreased with the increase of body weight at every temperature and its relation was generally described by an allometric equation, $R_o = a \cdot BW^{b}$ or $\log R_o = \log a + b \cdot \log BW$, where "a" and "b" are constants and BW is dry body weight (mg). The values of "a" and "b" for samples measured at respective temperatures were calculated and summarized in Table 5. Regression lines obtained using these values are indicated in Fig. 42. It was verified by analysis of covariance that the regression lines were parallel to each other ($P>Ø.Ø5$), so that "b" was consistent, -Ø.222, regardless of temperature. On the

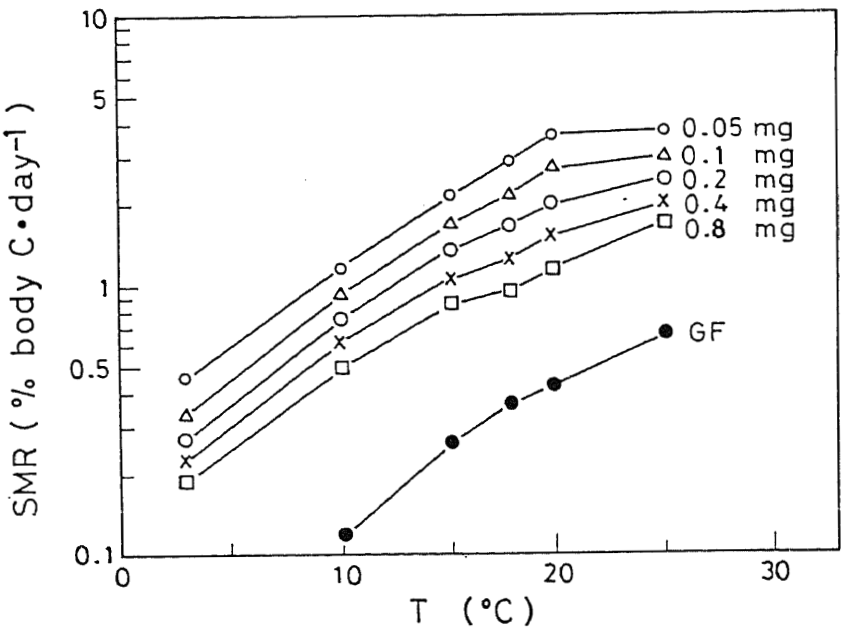

Fig. 41. Relationship between specific molting loss rate (SMR) and temperature (T) of juveniles at different body weights and gravid females (GF) for N. intermedia.

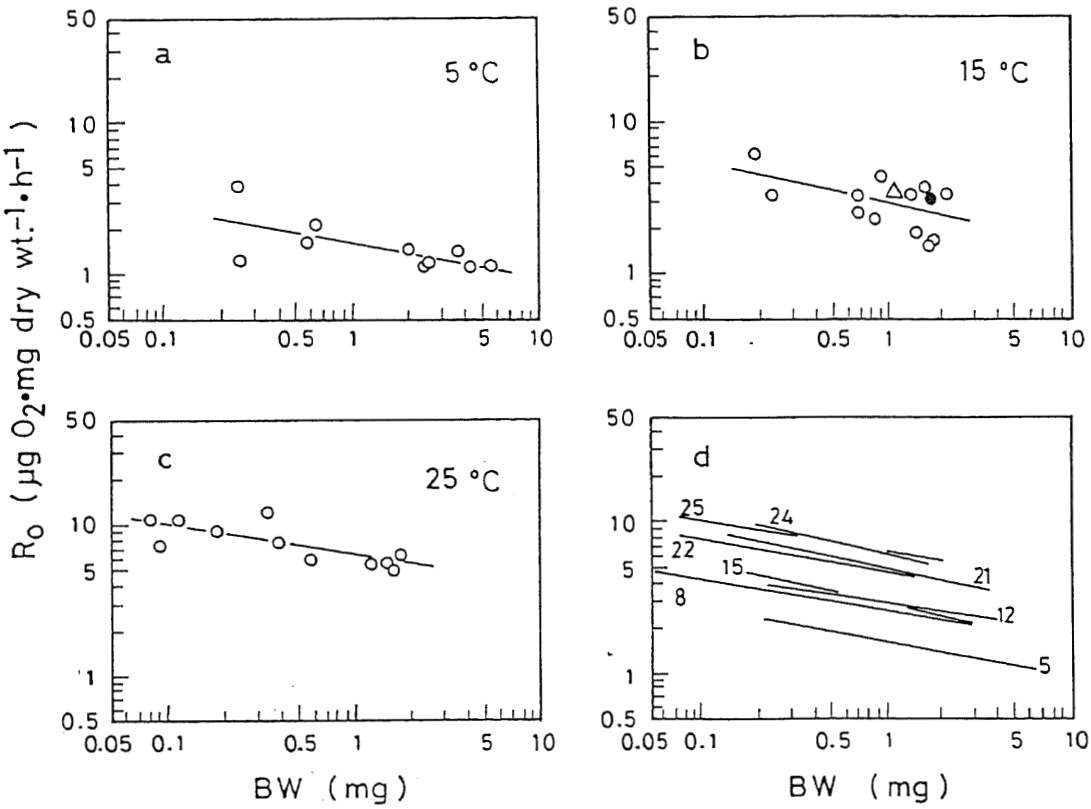

Fig. 42. Relationship between specific respiration rate (R_O) and body weight (BW) measured at different temperatures for N. intermedia. Triangle indicates molting animal, closed circle gravid female, and open circle others. Line was fitted by a linear regression analysis. Numeral on each line in (d) indicates temperature.

Table 5. Constants (a) and (b) of the allometric equation of $R_o = a \cdot BW^b$, where R_o is specific respiration rate ($\mu g\ O_2 \cdot mg\ dry\ weight^{-1} \cdot h^{-1}$) and BW is dry body weight (mg) of N. intermedia.

Exp. temp. (°C)	Field temp. (°C)	replicate number	a	b	r
4.9	5.5	10	1.60	-0.226	-0.667
8.0	9.8	15	2.56	-0.214	-0.939
12.0	14.0	15	2.86	-0.183	-0.524
15.0	15.3	14	2.91	-0.267	-0.526
21.1	22.0	11	4.88	-0.249	-0.812
22.2	23.5	6	4.58	-0.229	-0.834
23.5	23.4	9	5.98	-0.297	-0.636
25.0	24.9	11	6.32	-0.205	-0.778
combined				-0.222	

contrary, the magnitude of "a" increased with an increase in temperature and its relation to temperature was given by $a = 10^{(0.114 + 0.027 \cdot T)}$. Thus R_o ($\mu g\ O_2 \cdot mg\ dry\ wt^{-1} \cdot h^{-1}$) of N. intermedia can be described as a function of body weight and temperature;

$$R_o = 10^{(0.114 + 0.027 \cdot T)} \cdot BW^{-0.222} \quad (8)$$

where T is temperature (°C) and BW is dry body weight (mg). R_o in Eq. (8) was converted into carbon weight basis using the respiration quotient of 0.75 and a carbon content of 45.2% of dry weight for mysids. The specific respiration rate in terms of carbon (SRR, % body $C \cdot day^{-1}$) was then expressed as follows;

$$SRR = 1.49 \times 10^{(0.114 + 0.027 \cdot T)} \cdot BW^{-0.222} \quad (9)$$

The SRRs calculated for juveniles and gravid females by Eq. (9) are shown against temperature to make clear the effect of temperature on the respiration rate (Fig. 43). The SRR ranged from 2% body $C \cdot day^{-1}$ for large animals at low temperatures to 20% body $C \cdot day^{-1}$ for small animals at high temperatures. The temperature coefficient (Q_{10}) of the SRR was 1.9 for juveniles between 5° and 25°C and 2.1 for gravid females between 10° and 25°C.

Leakage/excretion rate and its relation to temperature

Loss rate of body carbon by leakage/excretion was not measured in the present study. Here the value of 30% of the respiration rate, reported for marine carnivorous amphipod Calliopius laeviusculus (Dagg, 1976), was

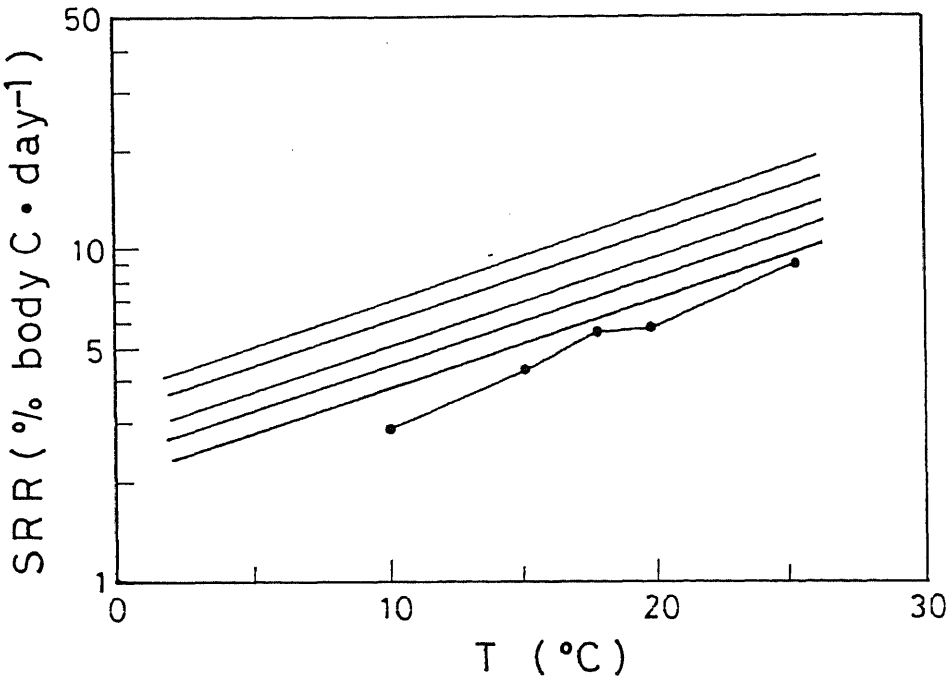

Fig. 43. Relationship between specific respiration rate (SRR) and temperature (T) of juveniles at different body weights (lines represent Ø.Ø5, Ø.1, Ø.2, Ø.4, and Ø.8 mg, from top to bottom lines) and gravid females (lowest line) for N. intermedia.

employed.

Egestion rate and its relation to temperature

Egestion rate was not determined experimentally in the present study, but it can be estimated indirectly from the following equation, F = I - (G + M + R + L), because parameters , I, G, M, R, and L are now available. Dagg (1974) has shown that there was some loss of captured prey into the surrounding water during the feeding and the amount of this loss reached more than 35% of the captured food for marine carnivorous amphipod. The possible effect of this loss also can not be ignored in N. intermedia. A value of 30% was adopted for the correction factor in the present study, and the corrected specific ingestion rate was shown by "SI'R". Values of all parameters determined for the mysid at each given body weight are presented in Table 6 in terms of daily specific rate on carbon basis. The ingestion rate for mysids of 0.05 mg body weight were excluded from the table because of insufficient data, and such small animals may not feed on cladocerans used as prey in the experiment. The molting rates at 29°C were assumed to be similar to those measured at 25°C.

The specific egestion rate (SFR, % body C·day^{-1}) increased almost exponentially with an increase in temperature from 3° - 25°C and slightly dropped at 29°C for smaller animals, whereas it increased exponentially up

Table 6. Specific rates (% body C·day^{-1}) of growth (SGR), ingestion (SIR), egestion (SFR), assimilation (SAR), molting (SMR), respiration (SRR), and leakage/excretion (SLR) of various body weights (BW, mg dry wt.) of juveniles and gravid females (GR) determined at different temperatures (T, ^{o}C).

BW	T	SGR	SIR	SI'R	SFR	SAR	SMR	SRR	SLR
Ø.Ø5	3	1.8	-	-	-	8.1	Ø.4	4.5	1.4
	1Ø	5.4	-	-	-	15.7	1.2	7.Ø	2.1
	15	13.Ø	-	-	-	27.6	2.1	9.6	2.9
	18	19.2	-	-	-	36.9	2.9	11.4	3.4
	2Ø	2Ø.9	-	-	-	41.2	3.5	12.9	3.9
	25	24.2	-	-	-	5Ø.9	3.6	17.8	5.3
	29	14.3	-	-	-	47.2	3.6	22.5	6.8
Ø.1	3	1.8	35.Ø	24.5	17.3	7.2	Ø.3	3.9	1.2
	1Ø	5.4	4Ø.1	28.1	13.9	14.1	Ø.9	6.Ø	1.8
	15	13.Ø	98.2	68.7	43.2	25.5	1.7	8.3	2.5
	18	19.2	124.Ø	86.8	52.7	34.1	2.2	9.8	2.9
	2Ø	2Ø.9	145.6	1Ø1.9	63.9	38.Ø	2.7	11.1	3.3
	25	24.2	261.1	182.8	135.7	47.1	3.Ø	15.3	4.6
	29	14.3	192.4	134.7	92.2	42.5	3.Ø	19.4	5.8
Ø.2	3	1.8	2Ø.6	14.4	8.1	6.4	Ø.3	3.3	1.Ø
	1Ø	5.4	31.5	22.1	9.1	12.9	Ø.8	5.2	1.6
	15	13.Ø	75.7	53.Ø	29.4	23.6	1.4	7.1	2.1
	18	19.2	94.Ø	65.8	34.Ø	31.8	1.6	8.4	2.5
	2Ø	2Ø.9	1Ø9.7	76.8	41.5	35.3	2.Ø	9.5	2.9
	25	24.2	161.2	112.8	69.2	43.7	2.4	13.1	3.9
	29	14.3	132.9	93.Ø	54.7	38.3	2.4	16.6	5.Ø
Ø.4	3	1.8	12.1	8.5	2.8	5.7	Ø.2	2.8	Ø.8
	1Ø	5.4	24.4	17.1	5.4	11.7	Ø.6	4.4	1.3
	15	13.Ø	58.3	4Ø.8	18.8	22.Ø	1.1	6.1	1.8
	18	19.2	72.Ø	5Ø.4	2Ø.6	29.8	1.3	7.2	2.2
	2Ø	2Ø.9	82.7	57.9	24.9	32.9	1.5	8.1	2.4
	25	24.2	99.5	69.7	28.9	4Ø.8	2.Ø	11.2	3.4
	29	14.3	91.8	64.3	29.5	34.8	2.Ø	14.2	4.3
Ø.8	3	1.8	7.1	5.Ø	-Ø.1	5.1	Ø.2	2.4	Ø.7
	1Ø	5.4	18.8	13.2	2.3	1Ø.8	Ø.5	3.8	1.1
	15	13.Ø	45.Ø	31.5	1Ø.9	2Ø.6	Ø.9	5.2	1.6
	18	19.2	56.Ø	39.2	11.Ø	28.2	1.Ø	6.2	1.9
	2Ø	2Ø.9	62.3	43.6	12.5	31.1	1.1	7.Ø	2.1
	25	24.2	61.4	43.Ø	4.6	38.3	1.7	9.6	2.9
	29	-	-	-	-	-	-	-	-
GF	1Ø	1.6	12.Ø	8.4	2.9	5.5	Ø.1	2.9	Ø.9
	15	4.Ø	33.Ø	23.1	13.3	9.9	Ø.3	4.3	1.3
	18	5.6	4Ø.4	28.Ø	14.6	13.4	Ø.4	5.7	1.7
	2Ø	6.6	44.7	31.3	16.7	14.6	Ø.4	5.8	1.7
	25	1Ø.1	48.9	34.2	11.8	22.5	Ø.7	9.Ø	2.7

to 20°C and subsequently levelled off or dropped for larger and gravid animals (Fig. 44). The temperature coefficient (Q_{10}) of SFR was 2.8 - 2.9 for small animals between 3° and 25°C and 4.0 - 5.8 for large and gravid animals between 3° or 10° and 20°C.

Temperature effect on the allocation of the assimilated food materials

In the growth equation mentioned above, (I - F) or (G + M + R + L) indicates the food materials assimilated by the animal which is represented by the specific assimilation rate, SAR (% body C·day^{-1}). The SARs obtained for various body sized animals at different temperatures are shown in Table 6 and Fig. 45. They showed a strong temperature dependency as observed in the specific ingestion rates. The values of Q_{10} of the SAR are 2.7 - 3.0 for juveniles between 3° and 20°C and 2.5 for gravid females between 10° and 25°C.

The assimilated materials are allocated for growth, molting, respiration, and leakage/excretion. Figure 46 shows the temperature effects on the allocation of the assimilated materials for various different sized individuals. The allocation percentage for growth, so called net growth efficiency (K_2), ranged between 25 and 70%, and showed the highest value at around 20°C. At the juvenile stage, the larger individuals had a greater allocation percentage than the smaller individuals. The

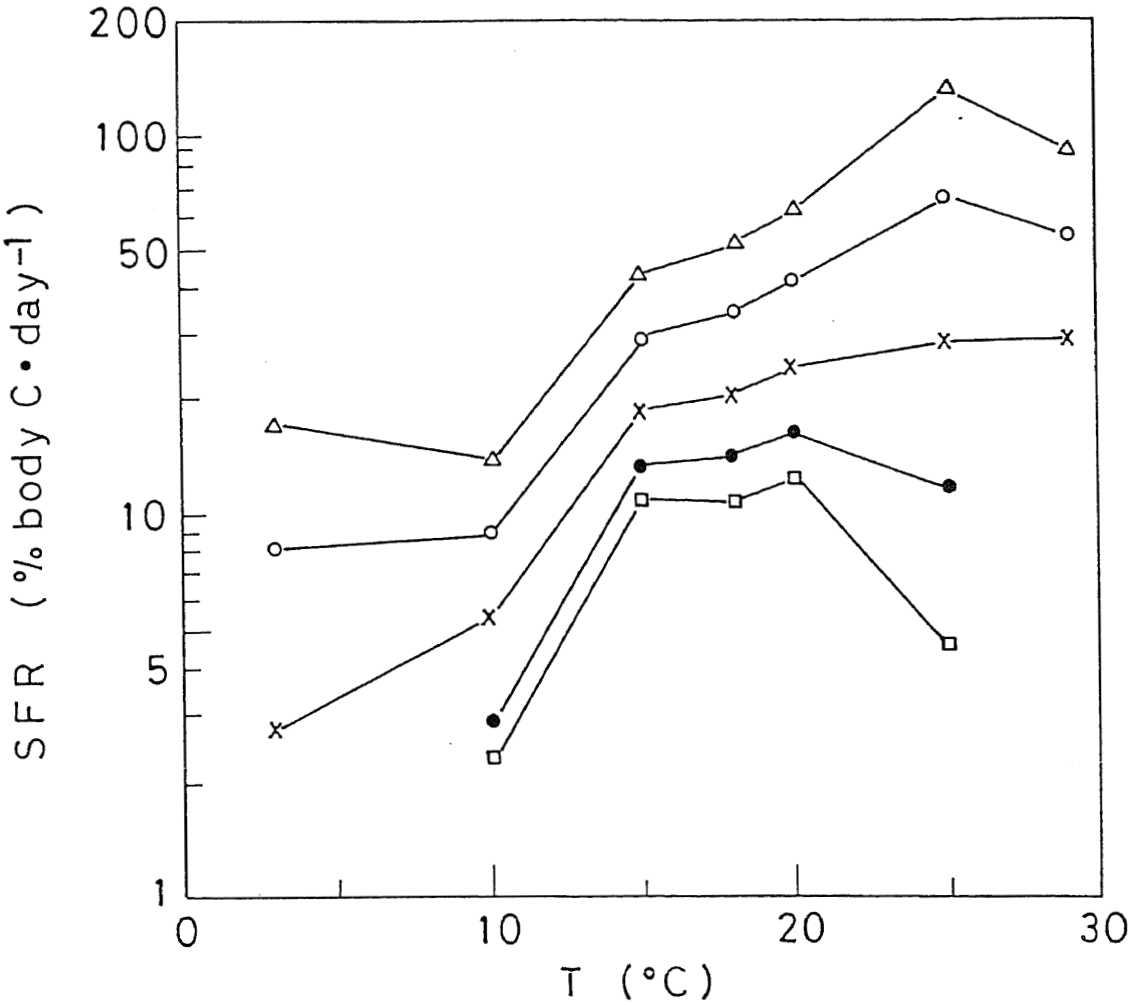

Fig. 44. Relationship between specific egestion rate (SFR) and temperature (T) of juveniles at different body weights and gravid females for N. intermedia. Symbols are the same as in Fig. 41.

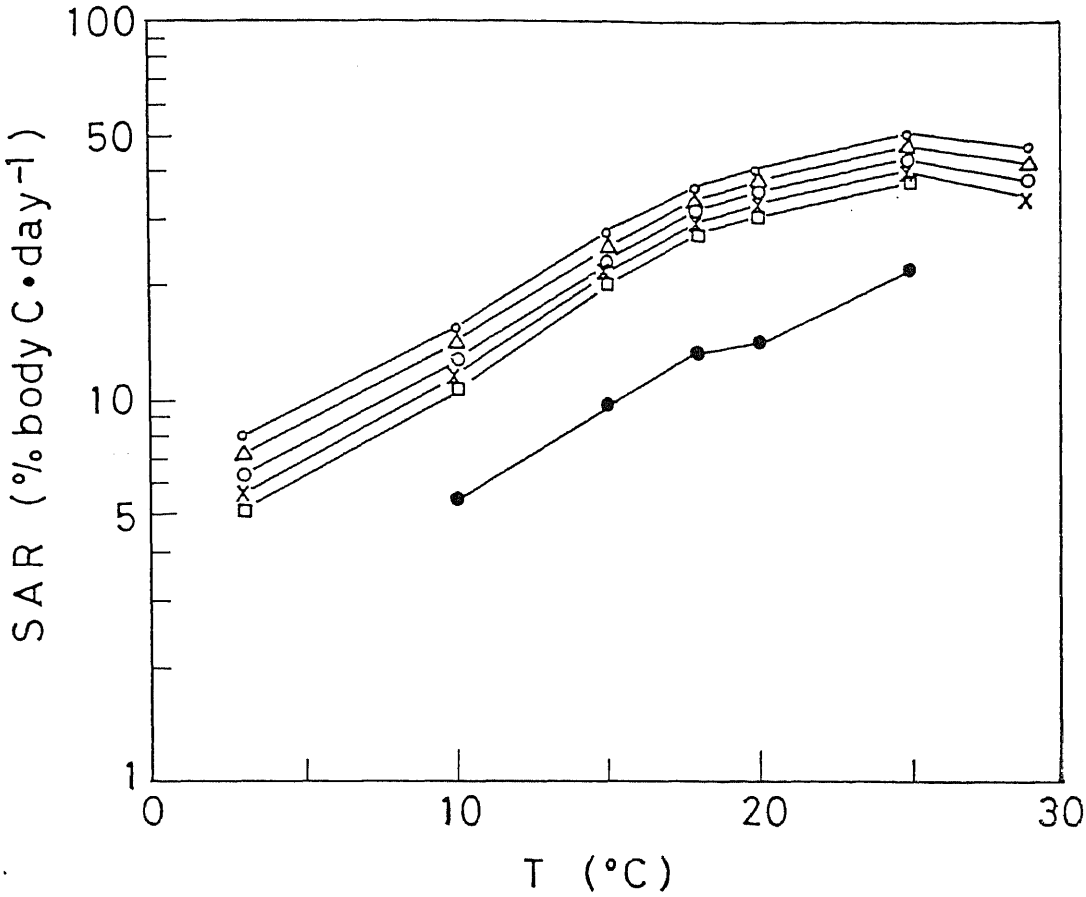

Fig. 45. Relationship between specific assimilation rate (SAR) and temperature (T) of juveniles at different body weights and gravid females for N. intermedia. Symbols are the same as in Fig. 41.

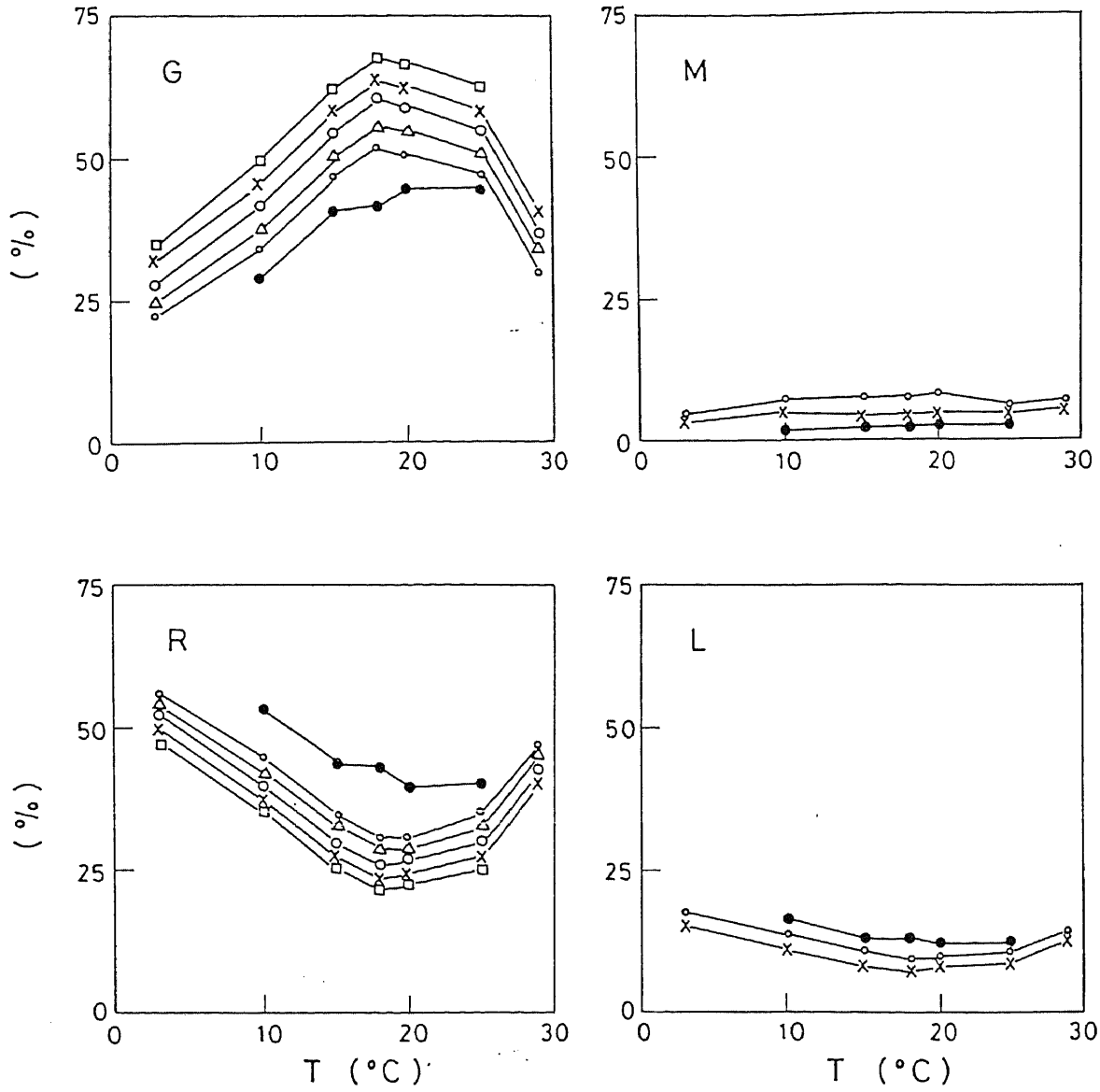

Fig. 46. Allocation percentages of growth (G), molt (M), respiration (R), and leakage/excretion (L) of juveniles of different body weights and gravid females determined at different temperatures for N. intermedia. Symbols are the same as in Fig. 41.

growth allocation percentage for gravid female was the lowest. The allocation percentages for molting and leakage/excretion were both low, and were less than 15%. Respiration reached 20 - 55% in the allocation percentage, and showed a minimum at around 20°C. Gravid females had the highest allocation percentage for respiration and the largest juvenile individuals had the lowest percentages.

V-4. Discussion

Temperature dependency of each parameter in the growth equation differed respectively as summarized in Table 7. The growth rate was greatly affected by temperature, especially for juveniles. Among the parameters in the right part of the growth equation, the ingestion rate, the egestion rate, and the molting loss rate showed a large temperature dependency. The temperature dependency of the catabolic rates, respiration and leakage/excretion, were noticeably small. The original question of this chapter is to discover the mechanism creating the strong temperature dependency of the growth rate. Interpreting this question, allocation of assimilated food materials in the animal was considered as well as the temperature dependency of each growth parameter. As evaluated in the present study, allocation percentages for molting and leakage/excretion were small compared with the other two, growth and respiration. Consequently, the allocation can be simplified as A = G +

Table 7. Temperature coefficient (Q_{10}) of each parameter in the growth equation.

parameter		Juvenile Q_{10}	Juvenile temp. range(°C)	Gravid female Q_{10}	Gravid female temp. range(°C)
SGR		4.6	3 - 20	3.4	10 - 25
SIR	small	2.6 - 2.7	3 - 25	3.9	10 - 20
	large	3.2 - 3.7	3 - 20		
SFR	small	2.8 - 2.9	3 - 25	5.8	10 - 20
	large	4.0 - 5.4	3,10 - 20		
SMR		2.9 - 3.6	3 - 20	3.1	10 - 25
SRR		1.9	5 - 25	2.1	10 - 25
SLR		1.9	5 - 25	2.1	10 - 25
SAR		2.7 - 3.0	3 - 20	2.5	10 - 25

R, and then G = A - R. The strong temperature dependency of the growth rate therefore resulted from the combination of the effects of the assimilation and respiration rates. Temperature dependency of the growth rate, Q_{10}^{g}, can be calculated using the following equation when those for both assimilation, Q_{10}^{a}, and respiration, Q_{10}^{r}, are given;

$$Q_{10}^{g} = Q_{10}^{a} \left[\frac{1 - (Q_{10}^{r}/Q_{10}^{a})^{(T_2-T_1)/10} \cdot (R_1/A_1)}{1 - (R_1/A_1)} \right]^{(T_2 - T_1)/10} \quad (10)$$

where T is temperature, and R_1 and A_1 are respiration and assimilation rates respectively at temperature T_1. Looking at the equation, it is obvious that Q_{10}^{g} is always greater than Q_{10}^{a} if $Q_{10}^{a} > Q_{10}^{r}$. This explains that a greater temperature dependency in assimilation rate than that of respiration rate causes the largest temperature dependency of the growth rate. The greater temperature dependency of the assimilation rate reflected the large dependency of the ingestion rate. This interpretation will be valid in the temperature range below 20°C where a constant Q_{10} was obtained.

Catabolic activity continued to increase steadily with temperature increase at least up to 25°C, whereas the increase in the growth rate levelled off above 20°C and even became negative at higher temperatures. The assimilation rate strongly reflected the growth rate, showing a slight decrease at higher temperatures (Fig.

45). Such a change in the assimilation rate was a reflection of the slowing down of the ingestion rate at higher temperatures (Fig. 38). Therefore it can be concluded that the inhibitory effects of temperature on the ingestion rate but not on the catabolic activity caused the drop in the growth rate at higher temperatures above 20°C. This interpretation seems to be applicable up to 29°C.

The temperature for the maximum growth rate of N. intermedia was found around 20°C, which corresponded to the optimum temperature for the net growth efficiency (K_2). The present study revealed that the strong temperature dependency of the growth of N. intermedia resulted from the large temperature dependency of the ingestion and assimilation rates, and furthermore, from the amplified effects created by the difference in temperature dependency between respective metabolic activities.

CHAPTER VI

General Discussion

As previously mentioned, the post-embryonic growth of zooplankton can be visualized from the three aspects of the growth curve expressed with the weight change against time; those are the body weights at the initial and at the maturation stage, and the growth rate of the body weight.

In the past, almost no observation has been made on the environmental controlling effects on the initial body weight of zooplankton animals. There have been reported several observations for various zooplankton animals, including mysid species, that the maturation body weight varied seasonally (e. g. McLaren, 1963; Mauchline, 1971; Pezzack and Corey, 1979). Using correlation analyses, Deevey (1960) found that the maturation body weight was strongly controlled by the surrounding water temperature under a condition of a large annual temperature variation, and that it was more closely related to food than to temperature under a small temperature variation. Deevey's findings have recently been demonstrated experimentally in laboratory cultures using marine copepods (Vidal, 1980a) and freshwater copepods (Elmore, 1983) collected from the field. From laboratory culture experiments, it has been shown that the growth rate of

zooplankton is mainly controlled by temperature under excess amounts of food (Corkett and McLaren, 1970; Landry, 1975) but by food concentration (Paffenhöfer, 1976; Paffenhöfer and Harris, 1976; Harris and Paffenhöfer, 1976) and food quality (Mullin and Brooks, 1970) at certain temperatures. Vidal (1980a) has shown simultaneous effects of temperature and food concentrations on the growth rate of marine copepods. Under field conditions, the actual zooplankton growth rates are controlled by temperature alone in several neritic waters (McLaren, 1978; McLaren and Corkett, 1981) and by both food concentration and temperature in a small temperate lagoon (Landry, 1978).

In the case of N. intermedia in the present study, it has been shown that temperature was the major environmental controlling parameter for the growth process in Lake Kasumigaura. The temperature controls were evaluated under defined conditions in the laboratory. Obvious temperature effects were detected both on the maturation body weight and on the growth rate. With an increase in temperature, the adult body weight decreased exponentially, whereas the growth rate increased exponentially. However, there was no significant effect observed on the initial body weight. The temperature dependent growth rate of N. intermedia could be interpreted on the basis of metabolic activities. The strong temperature dependency of the growth rate resulted

from the large temperature dependency of the ingestion and assimilation rates, and furthermore, from the amplified effects created by the difference in temperature dependency between respective metabolic activities.

The temperature control on the growth of N. intermedia is schematically shown in Fig. 47. The initial body weight is constant regardless of temperature. At high temperatures, N. intermedia grow rapidly and attain maturation at a smaller body size. On the other hand, at low temperatures, the mysids grow slowly and reach maturation at a larger body size. Figure 48 summarizes the temperature effects on the three aspects of the post-embryonic growth process of N. intermedia determined in the present study; the initial and the maturation body weights, and the growth rate. The constant initial body weight produced a straight line having little slope against temperature, which indicates a temperature dependency of $Q_{10} = 1.1$. The maturation body weight decreased exponentially with an increase in temperature between 10° and $25^{\circ}C$, and the temperature dependency obtained was $Q_{10} = 1.8$. The specific growth rate increased exponentially with an increase in temperature below $20^{\circ}C$, levelled off at around $25^{\circ}C$, and dropped thereafter. The temperature dependency of the specific growth rate below $20^{\circ}C$ was $Q_{10} = 4.6$. The maturation time, which is defined as the time required to reach maturation, was determined by laboratory culture experiments conducted at various

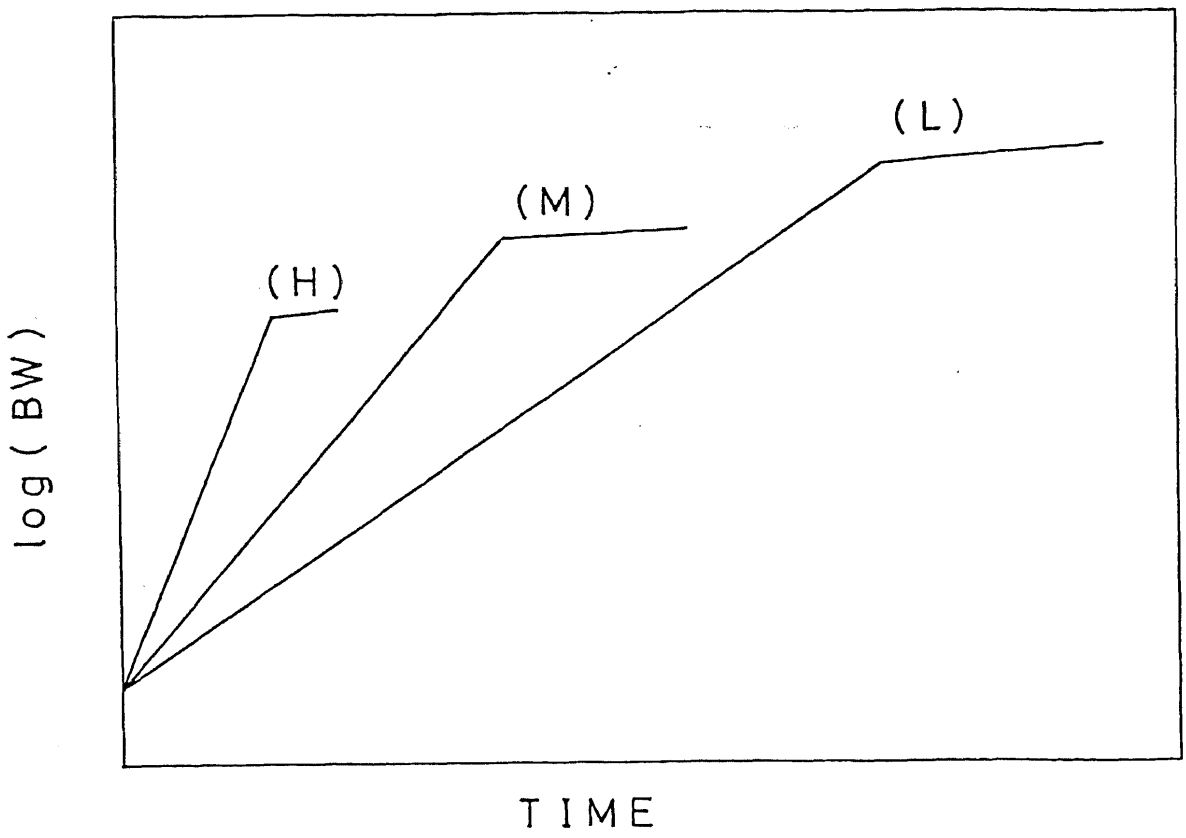

Fig. 47. Schematic individual growth curves of N. intermedia grown at high (H), middle (M), and low (L) temperatures. BW is body weight.

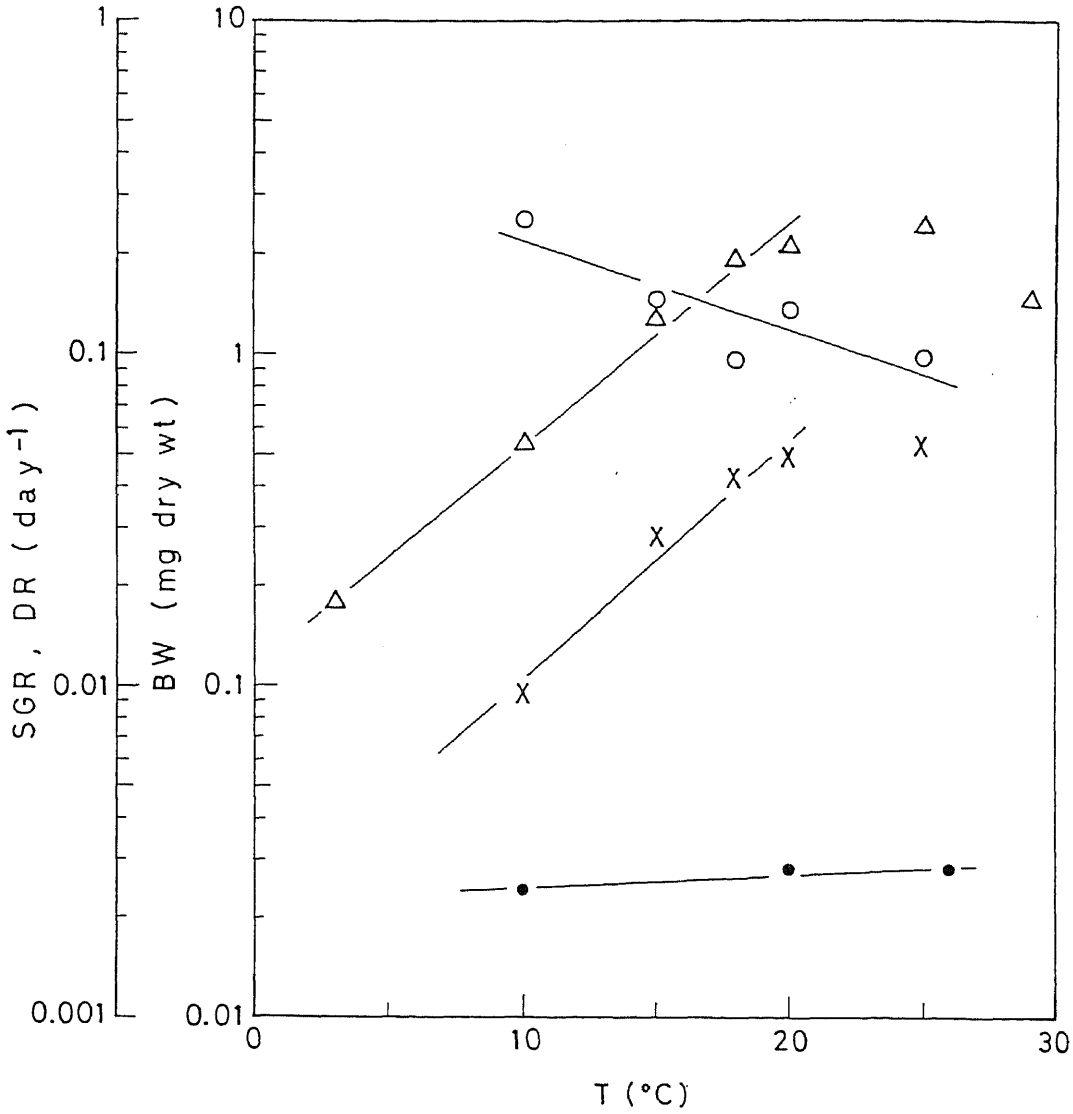

Fig. 48. Temperature dependencies of initial body weight (closed circle), maturation body weight (open circle), juvenile growth rate (SGR, triangle), and reciprocal of maturation time (DR, cross) for female N. intermedia obtained in the culture experiments.

temperatures, and the reciprocal of the maturation time is also plotted in Fig. 48. The reciprocal of the maturation time showed a similar pattern against temperature as that of the specific growth rate, but the temperature dependency of the former was greater than the latter, reaching $Q_{10} = 5.4$ below 20°C. Such a strong temperature dependency of the maturation time was due to the combined effects of the opposite temperature dependencies of the specific growth rate and the maturation body weight.

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