富山湾における浮遊性端脚類Themisto japonica(Bovallius)の出現量,個体群構造及び生活サイクル

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Abundance, Population Structure and Life Cycle of a Hyperiid Amphipod *Themisto japonica* (Bovallius) in Toyama Bay, Southern Japan Sea

**Tsutomu Ikeda**, **Kazumasa Hirakawa** and **Akira Imamura**

Japan Sea National Fisheries Research Institute, 1 Suido-cho, Niigata 951 3), and Toyama Prefectural Fisheries Experimental Station, 364 Takatsuka, Namerikawa, Toyama 936 4)

**Abstract**

A series of vertical hauls (0-500m) with Norpac nets was made at an interval of 2-4 weeks over one full year at an offshore station in Toyama Bay to investigate abundance, population structure and life cycle of the hyperiid amphipod *Themisto japonica*. The results indicated that the biomass of *T. japonica* was low in winter, but it increased in summer together with that of other zooplankton groups. The annual mean of the biomass of *T. japonica* was 11.78 mg wet wt m⁻³, which contributed to 17.9% (annual mean) of the total net zooplankton biomass at the same station. Breeding of *T. japonica* continued throughout the year and peaked in summer season. Additional samples from horizontal tows with MTD nets in June, September and December revealed a diurnal vertical migration of this species, of which magnitude varied depending on the growth stages and seasons. The range of vertical migration was 300-400m in June and December, but reduced to 100-150m in September where the surface water temperature warmed up to 28°C. Most adults and large juveniles (≥3 mm BL) underwent to the diel vertical migration, but small juveniles (<3mm BL) did not and stayed in the upper layer all day. Apparently, the release of the juveniles from the female's marsupium was the event limited to the surface layer. Because of the continuous breeding, life cycle of *T. japonica* was difficult to analyse from only field data of abundance, size composition and maturation. To overcome this problem, the growth model of this species proposed by Ikeda (1990a) was combined with the present data, then estimated least three generations per year. The present results on *T. japonica* are compared with other *Themisto* species from geographically different locations. Further, general trophic significance of *T. japonica* in the ecosystem of the Japan Sea is discussed in light of prey-predator relationships.

**Keywords**: *Themisto japonica*, life cycle, generation, vertical distribution, Japan Sea

As a group of amphipod, those belonging to the suborder Hyperiidea are exclusively marine and planktonic, and a predominated member of zooplankton in cold waters (Shin 1982). A hyperiid *Themisto japonica* is distributed in the

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3) 池田勉，平川和正，日本海区水産研究所
4) 今村明，富山県水産試験場
Okhotsk Sea, Japan Sea, western North Pacific, off the east coasts of northern Japan and southern Kuriles (Bowman 1960). In the Japan Sea, *T. japonica* is the most abundant hyperiid amphipod species and ranks second to fourth in the total net zooplankton biomass (Vinogradov & Sazhin 1978, Hirakawa et al. 1990, Ikeda 1990a). Excepting incidental growth data on the small populations occurred during spring period in Otsuchi Bay, northeastern Honshu, Japan (Sugisaki et al. 1990) and estimated potential growth rates based on laboratory oriented experimental study (Ikeda 1990a), little is known about the life cycle of *T. japonica*.

The present study investigates abundance, population structure and life cycle of *Themisto japonica* using a series of samples taken at a short time interval over one full year at an offshore station in Toyama Bay, southern Japan Sea. Additional samples were taken from various depth horizons at the same station during the selected seasons to evaluate vertical distribution patterns and diel vertical migrations of this species at different growth stages. The present results are compared with those of other *Themisto* amphipods living in different geographical locations. Possible important roles of *T. japonica* in the ecosystem of the Japan Sea are discussed.

**Materials and Methods**

*Abundance, Population Structure, and Life Cycle*

A series of samples was collected every 2–4 weeks (from February 1990 through

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Fig. 1. A. Location of Toyama Bay in the southern Japan Sea. B. The sampling station (circled star) in Toyama Bay, in which depth contours (1000, 500, and 200m) are superimposed.
In January 1991) from aboard R/V "Tateyama-Maru" at an offshore station in Toyama Bay (Figure 1). Each sampling was from 500m depth to the surface using a twin-type Norpac nets (mouth diameter: 45cm, mesh aperture: 0.33 and 0.10mm each, see Motoda 1957). The nets were towed vertically at a speed of 1m s⁻¹. The water volume passed through the net was estimated from a Rigosha flow-meter mounted in the mouth of each net. At sea the samples were preserved immediately in 10% buffered formalin-seawater for detail analysis at land laboratory. CTD casts were made at each sampling to assess the vertical profiles of temperature and salinity at the sampling site. Detail sampling data, together with methods for numerical analysis and biomass (wet weight) determination, have been published elsewhere (Hirakawa et al. 1992).

**Vertical Distribution**
Aboard the R/V "Mizuho Maru" sets of MTD nets (mouth diameter: 56cm, mesh aperture: 0.35mm, Motoda 1971) were used to collect samples from 19 depth horizons between the surface and 600 or 700m depth at the same station mentioned above during June 4–5, September 2 and December 5–6, 1986. The nets were towed at a speed of 1.0–1.5 knot for 0.5–1 h, and the volume of water passed through each net was calculated from the Rigosha flow-meter mounted in the mouth of each net. All samples obtained from MTD nets were immediately preserved in 10% buffered formalin-seawater.

**Body Length, Sex and Maturity**
The maximum distance between the anterior tip of the head and the distal end of the uropods of a straightened body was taken as body length (BL). BL was read under a Wild dissecting microscope to the nearest 0.2mm. Mature males are characterized by the extended second antenna and the excavate organ on the first uropod rami (Kane 1963, Sheader 1981). Mature females have a series of four pairs of enlarged oostigates in which developing eggs and hatched small juveniles are protected (Kane 1963). However, these morphological characters are not sufficient for mature females. Laboratory observations indicated that mature females, once released small juveniles then moulted, have only rudimental oostigates (a character of immature females, see Kane 1963). Therefore, all non-mature male specimens with ≥9mm BL (The minimum size of females carrying eggs or small juveniles in Themisto japonica, Ikeda 1990a) were designated as mature females in this study. Specimens having no mature male characteristics and <9mm BL were classified as juveniles, which were further divided arbitrary into two size groups (<3mm and ≥3mm BL). According to Ikeda's (1990a) growth model for T. japonica, Instars I to VI are included into small juveniles (<3mm BL), and Instars VII to XIV into large juveniles (≥3mm BL).

**Statistical Analysis**
A linear regression model was used to evaluate the correlation between the abundance of animals, and resulted correlation coefficient was tested at p=0.05 level unless otherwise specified. A Kolmogoroff-Smirnov test was used to evaluate the difference distribution pattern of data (Sokal & Rohlø 1969).
Results

Temperature and Salinity
Seasonal changes in the surface temperature ranged from approximately 10°C (February to April) to more than 26°C (August and September) (Figure 2). However, the seasonal variations of the temperature became obscure as the increase of depth and almost diminished below 300m. Vertical stratification of water was most pronounced in August and September, and was weak in February to March.

Salinity changed from <33.0 to 33.6% in the surface water. Salinity higher than 34.2% was observed consistently in 50-200m depth in most seasons (excepting March to May). Salinity maximum (>34.4%) seen August and mid-September is the indication of the intrusion of the Tsushima Current Core water. In terms of salinity, waters below 250m depth was homogeneous throughout the year. Waters characterized by salinity of 34.05-34.10% and temperature <1°C are termed as the “Deep-Water” which widespreads over the entire Japan Sea (see review of Nishimura 1969). This Deep-water occupied below 350m depth in Toyama Bay all seasons of the year.

Abundance and Population Structure
Biomass of *Themisto japonica* was lowest in winter month (December through March, 3-6 mg m\(^{-3}\)) and highest in summer month (July to August, up to 37 mg m\(^{-3}\)) (Figure 3). A moderate biomass peak was seen in early May (ca. 20 mg m\(^{-3}\)). General seasonal pattern seen in the biomass of *T. japonica* is paralleled to that of the total net zooplankton excluded *T. japonica*. Annual mean biomass of *T. japonica* was 11.78 mg m\(^{-3}\) (±8.95(1SD), N=24), and its contribution to the total net zooplankton biomass (annual mean: 62.5 mg m\(^{-3}\), ±32.5(1SD), N=24) was 17.9% (±7.3(1SD), N=24).

Seasonal variations in the numerical abundance of mature males and females, and two size groups of juveniles are showed in Figure 4. Small juveniles (<3 mm BL) were numerically abundant in May to October, during which two prominent peaks were seen in August and September. Similar seasonal pattern, but much reduced, was observed in mature females. Seasonal variation pattern of large juveniles (≥3 mm BL) was different, and its high abundance was in February to March, and early October. Mature males were more abundant in early June and mid-February, but its seasonal pattern was obscure because of a small number of specimens obtained in this study. Mean numerical abundance over the entire study period was 0.815 individual m\(^{-3}\) for small juveniles, 0.190 individual m\(^{-3}\) for large juveniles, 0.179 individual m\(^{-3}\) for mature females, and 0.061 individual m\(^{-3}\) for mature males. Size (=BL) composition of *Themisto japonica* is illustrated in Figure 5. In general, the size composition was broad in most samples with a large proportion of smallest juveniles (1-2 mm) in many samples. A gradual upward shift of the broad size spectrum was recognized for the samples collected from February to June. The first modest peak of the smallest juveniles in May is considered to be derived from those released from overwintered populations from the previous year. Growth of this first generation
Fig. 4. Seasonal variations in the numerical abundance of mature males and females (bottom), large juveniles (middle) and small juveniles (top) of *Themisto japonica* in Toyama Bay. Abundance of a hydromedusa *Aglantha digitale* is superimposed in the top figure (hatched line).

of 1990 was difficult to trace from the size composition data. However, from potential growth data of *T. japonica* by IKEDA (1990a), it can be assumed reasonably that the annual peaks of the smallest juveniles seen in August and September was the second generation of 1990 released from the females of the first generation born in March and April of the same year. Only part of the second generation started in August and September appeared to overwinter, and major overwintering populations were its offsprings (the third generation of 1990).

**Vertical Distribution**

In June, day/night difference in vertical distribution was most marked in mature females and large juveniles (≥3mm BL): a sharp population maximum seen at 20m at night disappeared during daytime and its entire population desended below 200m (Figure 6). Mature males distributed broadly between 10 and 600m with its maximum at 350m at night, but moved below 300m during daylight hours. Vertical distribution pattern of small juveniles (<3mm BL) was quite different; while their abundance maximum was at 75m in the nighttime, two maxima were observed at 50m and 450m in the daytime. The deep maxima
Fig. 5. Seasonal sequence in size (=BL) composition of *Themisto japonica* in Toyama Bay. Populations seen throughout the year were subdivided into I, II, III, II' and III' by hatched lines. Population II' and III' are considered to be originated from populations II and III, respectively, of the previous year. Numerals on the top abscissa indicate the total number of specimens caught. Capital letter with subscript figure on the bottom abscissa denotes the month and date, respectively, of samplings.
Fig. 6. Vertical distribution of numerical abundance during the daytime (open) and at night (shaded) of mature males and females, large juveniles and small juveniles of *Themisto japonica* in Toyama Bay. Water temperature is superimposed by horizontal broken line. Note that the depth scale is not even.
seen only in the daytime was composed largely by Instar I and II juveniles, which were still too early to be released from the female’s marsupium (the release of juveniles from the marsupium is at Instar III, see Ikeda 1990a). This, combined with the coincidence of the depth of numerical abundance of mature females in the same daytime, this deep maxima of small juveniles is considered to be originated from those in the marsupium of the females during the samplings and storage of the specimens. This source of error in analyzing vertical distribution pattern of *Themisto* amphipods has been reported by Shearer (1977), Williams & Robins (1981) and Ikeda (1991). Nevertheless, the present results suggest that the small juveniles do not migrate vertically through day and night and stay in the shallow layers with its population maxima at 50–70m.

In September, water temperature rose significantly in the upper layers (Figure 6). While daytime vertical distributions below 250–300m of mature males and females, and large juveniles were similar to the results obtained in June, nighttime distribution patterns were significantly dissimilar. At night, large juveniles were most numerous at 150–250m, but distributed widely between 20 and 600m. Only part of populations of mature males and females ascended to 150m at night. Despite higher temperature in the upper layers, day/night vertical distribution of small juveniles was similar to that observed in June.

In December, the surface temperature lowered to 17°C. All mature males and females (though its number reduced significantly), and large juveniles exhibited a distinct difference in day/night distribution patterns, as a result of its active diurnal migration (Figure 6). Night population maxima was at the surface for mature males and females, and at 10m for large juveniles. Abundance of small juveniles was low but consistently occurred in shallow depths.

For mature males and females, and large juveniles (≥3mm BL), similarities in the day/night vertical distribution patterns were tested statistically using a Kolmogoroff-Smirnov test. Significant differences were found in 8 out of 9 cases (unexpectedly, those of mature males in December did not show a significant difference, i. e. p > 0.05). Statistical test is not amenable for small juveniles (<3 mm BL) because of its erroneous data. Error involved in the daytime data are possible to remove by omitting the data of the deep maxima. However, this is not the case for nighttime data in which the vertical distribution of small juveniles and that of mature females is well overlapped. Nevertheless, it is clear that the distribution of the small juveniles is limited to the top 100m in June through December.

**Discussion**

**Possible Sampling Biases**

Patchy distributions and net avoidance are two major sources of error in estimating abundance of target zooplankton species by net sampling. While no information is presently available for the patchiness of *Themisto japonica*, Winc (1976) analysed daytime and nighttime catch data of *T. pacifica* and found that this hyperiid was more uniformly distributed at night than during the day. Sugisaki et al. (1990) measured swimming speed of *T. japonica* in the laboratory. According to their data, the swimming speed of *T. japonica* increased with the increase of size of specimens and recorded 4.22 mm s⁻¹ for their largest specimens.
with 14 segments of pleopod rami (=9.4mm BL, see Ikeda, 1990a). Another estimates of the swimming speed of *T. japonica* was 1.3mm s\(^{-1}\) at the maximum for the specimens <19mm BL, based on the field observations (Semenova 1974). Compared with these swimming speeds, both Norpac nets (100cm s\(^{-1}\)) and MTD nets (51-77cm s\(^{-1}\)) used in this study were fast enough to catch this hyperiid amphipod. Wing (1976) discussed possible underestimation of the catches of *T. pacifica* and *T. libellula* with Norpac nets and concluded that there were no evidence of net avoidance by these hyperiids. However, it is evident from the results of vertical distribution range of *T. japonica* (discussed below) that 0-500 m vertical tows of Norpac nets made mostly daylight hours in this study are not satisfactory to catch the entire population of *T. japonica*, then resulting possible underestimation of the abundance of this species.

Immigration and emigration of *Themisto* population out/into Toyama Bay are another source of possible error in analyzing the life cycle of this species. According to the record of moored current meters in Toyama Bay, anticlockwise movement of water has been revealed though its speed varies seasonally (Kitani, personal communication). The extent of any influence of this gyre system on the maintenance of the discrete population of *T. japonica* in Toyama Bay is currently unknown.

**Vertical Migration**

Diurnal vertical migration of *Themisto* amphipods is well documented, i.e. *T. gaudichaudi* in the Southern Ocean (Kane 1966), *T. compressa* (=formerly *T. gaudichaudi*, see Schneppenheim & Weigmann-Haass 1986) in the Northeast Atlantic (Williams & Robins 1981), and *T. pacifica* and *T. libellula* in Alaskan coastal waters (Wing 1976). For *T. japonica*, Semenova (1974) and Hiroki (1988) noted a diel vertical migration behavior in the northwestern Japan Sea and Wakasa Bay (southern Japan Sea), respectively. While Hiroki's (1988) observation was limited to the top 300m, Semenova's (1974) was extended down to 700m thereby comparable to the present study. According to Semenova (1974), both males and females (= mature males and females in this study) and immature males and females (= large juveniles of this study) underwent vertical migration in the range of 400-500m (daytime) to 0-100 depth (at night) every day. Juveniles <5mm BL did not exhibit clear vertical movement and remained in the top 100m all day long. The lack of diel vertical migration of small juveniles (<3 mm BL) of *T. compressa* has also reported in Northeast Atlantic (Williams & Robins 1981).

Semenova's (1976) observation was only in June when the surface water temperature was at 13°C (estimated from Naganuma & Ichihashi 1985). Despite higher surface water temperature the present results of June (17°C) and December (16°C) in Toyama Bay are consistent to the Semenova's results, in terms of the depth of population maxima in the daytime and at night. In Toyama Bay, warming of surface water in September caused no effect on the daytime vertical distribution of *T. japonica*, but upward migration at night was apparently hampered by the increased temperature. As a result, vertical migration range of *T. japonica* estimated from population maxima in September was significantly less (100-150m) than those observed in June and December (300-400m). In other
extensive diurnal vertical migrators such as euphausiids, geographical variations in its vertical distribution range are well known within the same species, and the local changes in the thermal structure of habitats are considered as a main cause for this (cf. review of Mauchline & Fisher 1969).

**Life Cycle**

Multiple broodings (=iteroparity) has been suggested for *Themisto* amphipods from the observation that females with young juveniles in the marsupium generally possess fully developed oocyte in their ovaries (Kane 1963, Sheader 1981). While experimental evaluation of iteroparity is not successful as yet for *Themisto japonica*, Ikeda (1991) estimated a total of 1445 eggs for one female as a result of possible five broods, each separated by moulting, during her life time. Newly hatched specimens of *Themisto japonica* moult twice before leaving from the marsupium of the females (Ikeda 1990a). The present vertical distribution data of small juveniles suggest that this liberation of juveniles from the female's marsupium is the event limited to the top 100m, as was reported on *T. compressa* in Northeast Atlantic (Williams & Robins 1981).

Judging from the continuous occurrence of small juveniles during the year (Figure 4), breedings are not discrete events throughout the year for *Themisto japonica* in Toyama Bay. However, breeding activity was high in May to July and peaked in mid-summer (August and September), with moderate peaks in May to July. Continuous breeding throughout the year with its center in warm season seen in *T. japonica* in Toyama Bay is essentially the same to that reported for *T. compressa* in an offshore station of Northumberland, North Sea (Sheader 1977, 1981) and for *T. pacifica* in Alaskan coastal waters (Wing 1976).

Importance of gelatinous zooplankton as mating sites and, to a lesser extent, as food of *Themisto* amphipods has been postulated (Sheader & Evans 1975). Williams & Robins (1981) reported that a hydromedusa *Aglantha digitale* was most abundant preceding the numerical peak of *T. compressa* (= *T. gaudichaudii*) in Northeast Atlantic. The hydromedusa *A. digitale* was also common and most abundant gelatinous zooplankton in Toyama Bay. To evaluate the relationship between the numerical abundance of *A. digitale* and that of small juvenile *T. japonica* in Toyama Bay, the former in the samples of 0.10mm mesh Norpac nets, was counted and its results were superimposed in Figure 4 (top figure). *A. digitale* was most abundant in April to June, but its correlation to the abundance of small juvenile *T. japonica* was poor (correlation coefficient \( r = -0.007, df = 22, p > 0.1 \)). Re-analysis between the number of the small juvenile *T. japonica* and that of *A. digitale* from preceding sampling resulted again insignificant (\( r = 0.007, df = 21, p > 0.1 \)). This implies that although possible role of *A. digitale* to facilitate reproduction of *T. japonica* cannot be ruled out, the abundance of hydromedusa is not a main factor controlling the reproduction of *T. japonica* in Toyama Bay.

Because of continuous breeding mode, the analysis of the population growth of *Themisto japonica* by tracing the discrete cohorts was difficult, particularly in summer season. From growth model for *T. japonica* proposed by Ikeda (1990a), it is predicted that the small juveniles just released from the marsupium of the females reach the minimum mature adult size in 69–165 days at 5–15°C. Combining size composition data of field populations with the results from Ikeda’s
TABLE 1. SUMMARY OF LIFE HISTORY PARAMETERS AND THE NUMBER OF GENERATIONS PER YEAR OF THEMISTO AMPHIPODS.

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<tr>
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<th>Maximum adult size (mm)</th>
<th>Generations per year</th>
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<td>10(♀♀)</td>
<td>21(♀♂)</td>
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<td>BOGOROV(1940), BOWMAN(1960)</td>
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<td>15(♀♂)</td>
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<td>libellula</td>
<td>Southeastern Alaska</td>
<td>19(♂♂)</td>
<td>22(♂♂)</td>
<td>1</td>
<td>WING (1976)</td>
</tr>
<tr>
<td></td>
<td>Arctic</td>
<td>21(♀♀)</td>
<td>30(♀♀)</td>
<td>0.5-1</td>
<td>BOVALLIUS (1889), DUNBAR (1957)</td>
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<td>30(♂♂)</td>
<td>60(♀♂)</td>
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<td>pacifica</td>
<td>Southeastern Alaska</td>
<td>4.5(♂♂)</td>
<td>8(♂♂)</td>
<td>4-5</td>
<td>WING (1976)</td>
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<td></td>
<td></td>
<td>5.5(♀♀)</td>
<td>10(♀♂)</td>
<td></td>
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<tr>
<td>compressa*</td>
<td>North Sea</td>
<td>3(♀♀)summer</td>
<td>18(♀♂)</td>
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<td>gaudichaudii</td>
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<td>33</td>
<td>1</td>
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<td>KANE (1966)</td>
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<td>japonica</td>
<td>Japan Sea</td>
<td>6(♂♂)</td>
<td>12(♂♂)</td>
<td>&gt;3</td>
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<td>17(♀♂)</td>
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*Formerly gaudichaudii (see SCHNEPPENHEIM & WEIGMANN-HAASS, 1986)

(1990a) growth model hypothetical three generations, at least, were estimated for T. japonica in Toyama Bay (Figure 5). Undoubtedly, each hypothesized generation contains well overlapped cohorts. Both adults originating from Generation I and juveniles from Generation II encounter the annual maximum of their foods (non-Themisto zooplankton) (Figure 3), which facilitate active reproduction and growth of resulted youngs. Positive and significant correlation (r = 0.732, df = 22, p < 0.01) between the biomass of T. japonica and that of total net zooplankton (excluded T. japonica) supports this hypothesis. In other words, population growth of T. japonica in Toyama Bay is depended on its food availability. From this view, direct effect of warming of water in summer may not to be so critical for the population dynamics of T. japonica. This is because this hyperiid is apparently able to control the magnitude of its diurnal vertical migration range, and most importantly the biomass maxima of total net zooplankton is shown to be still well within the vertical migration range of T. japonica in Toyama Bay (HIRAKAWA et al. 1992).

Presently available information about the number of generation per year for Themisto spp. is summarized in Table 1. Among six species listed, T. libellula and T. abyssorum living in Arctic waters requires 2 years to complete its single generations (BOGOROV 1940, DUNBAR 1957). Both species inhabiting lower latitude
waters repeat its generation every year (Hoffer 1972, Wing 1976), indicating warmer temperatures shorten their generation times. One generation per year is also the case for *T. gaudichaudii* distributing in the Southern Ocean (Kane 1966). In contrast with these species with relatively long generation time, 4-5 generations per year has been reported for *T. pacifica* in the southeastern Alaska (estimated from data in Wing 1976), and 6 generations at the maximum for *T. compressa* in the North Sea (Sheader 1981). Thus, the present results of >3 generations per year for *T. japonica* are less than those of *T. pacifica* and *T. compressa*. Because of a large scale diurnal vertical migration and associated temperature changes in the range of <1 to >15°C, representative habitat temperature is difficult to define for *T. japonica* in Toyama Bay. Instead, it is reasonable to assume that species with smaller adult size can mature faster then repeat more generations per year than the species with large adult size. From this view, greater generation number of *T. pacifica* per year is the reflect of smaller adult size of this species. While this was not confirmed for *T. japonica* in this study, summer populations of *T. compressa* have smaller adult size (Table 1), which is considered to be the major mechanism enabling the latter species to repeat as many as <6 generations in a year.

**Trophic Significance**

*Themisto* amphipods are typical carnivores and a wide variety of animal groups, such as copepods, euphausiids, amphipods, chaetognaths, appendicularians, fish

| TABLE 2. STOMACH CONTENT ANALYSIS OF THEMISTO JAPONICA COLLECTED FROM 450 M DEPTH DURING DAYTIME AND 20 M DEPTH AT NIGHT IN TOYAMA BAY DURING JUNE 1986. N = NUMBER OF STOMACHS EXAMINED. (W): WARM WATER SPECIES, (C): COLD WATER SPECIES. |

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<th>Food animals</th>
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<td>Day (N=24)</td>
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<tr>
<td>Copepoda</td>
<td></td>
</tr>
<tr>
<td><em>Calanus sinicus</em> (W)</td>
<td>0.2 (1.3)</td>
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<tr>
<td><em>Mesocalanus tenuicornis</em> (W)</td>
<td></td>
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<tr>
<td><em>Eucalanus bungii bungii</em> (C)</td>
<td>0.05 (0.3)</td>
</tr>
<tr>
<td><em>Clausocalanus arcuicornis</em> (W)</td>
<td></td>
</tr>
<tr>
<td><em>Pseudocalanus minutus</em> (C)</td>
<td>0.2 (1.3)</td>
</tr>
<tr>
<td><em>Scolecithricella minor</em> (C)</td>
<td>0.5 (3.3)</td>
</tr>
<tr>
<td><em>Metridia pacifica</em> (C)</td>
<td>4.3 (28.6)</td>
</tr>
<tr>
<td><em>Pleuromamma</em> sp. (C)</td>
<td>0.3 (2.0)</td>
</tr>
<tr>
<td><em>Acartia omorii</em> (W)</td>
<td></td>
</tr>
<tr>
<td>Unidentified calanoids</td>
<td>1.6 (10.6)</td>
</tr>
<tr>
<td><em>Oithona atlantica</em> (C)</td>
<td>6.8 (48.2)</td>
</tr>
<tr>
<td>Copepod nauplii</td>
<td>0.1 (0.7)</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td></td>
</tr>
<tr>
<td><em>Euphausia pacifica</em> (larvae) (C)</td>
<td>0.7 (4.7)</td>
</tr>
<tr>
<td>Unidentified</td>
<td>0.3 (2.0)</td>
</tr>
<tr>
<td>Total</td>
<td>15.05 (100)</td>
</tr>
</tbody>
</table>
larvae, etc. are commonly found from the stomach of Themisto amphipods (Sheader & Evans 1975, Wing 1976, Yamashita et al. 1985). Stomach contents of part of specimens of Themisto japonica from the present vertical distribution study (see “Vertical migration”) were analysed (Table 2). Copepods and euphausiids were major components for both specimens collected during daytime and at night. Numerically, the most common food copepods were Oithona atlantica for daytime sample and Calanus sinicus for nighttime sample. Among 10 copepod species listed, warm water species contributed 62.9% of the total copepod number in daytime stomach samples, but was only 1.3% in nighttime stomach samples. Hirakawa et al. (1990) noted that the vertical distribution of warm water copepods in Toyama Bay were limited to the top 100–150m, although that of cold water copepods was the entire water column. Thus, the results showed in Table 2 suggest a largely indiscriminate feeding of T. japonica. Siegfried (1965) and Sheader & Evans (1975) have also noted that Themisto spp. are rather indiscriminate feeder, and the preys taken are reflecting the composition of zooplankton in surrounding waters.

In the Japan Sea, Themisto japonica has been reported as an integral prey component of both pelagic and demersal fishes through its characteristic diurnal vertical migration behavior. For pelagic fishes, masu salmon (Oncorhynchus masou) and pink salmon (O. gorbuscha) are reported as major predators on T. japonica (Fukataki 1967, 1969). The common squid (Todarodes pacificus) is another pelagic predator (Okiyama 1965). For demersal fishes feeding on T. japonica, walleye pollack (Theragra chalcogramma) and Atka mackerel (Pleuragrammus azonus) are most important (K. Nashida, S. Kanamaru, personal communication). In addition to these large sized predators, it is highly likely that small juvenile T. japonica which stays in the shallow layers all day long is eaten by fish larvae in the Japan Sea.

In Toyama Bay, Themisto japonica contributed to 17.9% (annual mean) of the total net zooplankton biomass in 0–500m depth. Ikeda (1990b) recorded the biomass of amphipods (mostly T. japonica) as 8.8% (a mean of 9 stations) of the total net zooplankton in April around Yamato Rise, central Japan Sea. While these figures are still insufficient to generalize to the entire Japan Sea, the relative abundance of T. japonica to the total zooplankton in the Japan Sea is presumably high, as compared to 2.4–4.3% being calculated for the Northeast Atlantic congener T. compressa from the data accumulated for a 4 year period (Williams & Robins 1981). All these information about the vital function in food webs and high biomass suggest strongly that T. japonica is a likely key component in the ecosystem of the Japan Sea.

Acknowledgments

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Literature Cited


