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イガイ科2種の幼生の成長と水温との関係

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Effects of Temperature on Larval Development of Two Mytilid Species and Their Implication

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Abstract: Using larvae obtained by stimulating artificial spawning of *Musculista senhousia* and *Limnoperna fortunei kikuchii* in the laboratory, larval developoment was examined under different temperature conditions (15°C, 25°C, 30°C). At 25°C and 30°C, larvae of *L. fortunei kikuchii* showed faster growth, shorter period from fertilization to settlement, and larger size at settlement than those of *M. senhousia.* At optimum growth temperature (30°C for *L. fortunei kikuchii*, 25°C for *M. senhousia*), size at settlement in larvae of the former species was larger by two times or more than the later species, and the days from fertilization to settlement were shorter by ca. 7 days. On the other hand, larvae of *M. senhousia* grew faster at 15°C than that of *L. fortunei kikuchii.* However, this temperature hampered larval development of the above-mentioned two species, because the larvae did not grow to the pediveliger and did not settle on the bottom until our 25-day experiment ended.

Introduction

Several recent studies indicate that larval recruitment processes (e.g., supply of planktonic larvae, larval settlement, mortality before and after larvae settling on bottom sediment, etc.) are vital for understanding community and population dynamics of marine benthic invertebrates (Underwood & Denley, 1984; Roughgarden *et al.*, 1988; Ólafsson *et al.*, 1994). Ecological studies that focus on the larval recruitment processes have in general been coined by the supply-side ecology. However, except for Kimura (1994) and Sekiguchi *et al.* (1995), dealing with benthic bivalves on tidal flats, studies for the supply-side ecology of marine benthic invertebrates are few (Ólafsson *et al.*, 1994), because of little information on species identification of larvae and because of several difficult problems inherent in sampling design for examining larval transport and/or dispersal in the sea (Underwood & Fairweather, 1989; Sekiguchi, 1991).

* At the 1996 annual meeting of the Malacological Society of Japan, Kimura, T and Y. Shikano read the paper that *Limnoperna fortunei kikuchii* Habe was *Xenostrobus securis* (Lamarck). They are preparing for publishing the paper.

Musculista senhousia was absolutely dominant among fouling animals and among benthos on tidal flats of Lake Hamana before 1975 when *Limnoperna fortunei kikuchii** was first found in the lake, and since then these two species have been predominant together there (Kajihara *et al.*, 1982; Abdel-Razak *et al.*, 1993a; Kimura, 1994). However, deducing from the fact that these two species have similar life forms, these species may compete for preoccupation of available habitats in the lake (Kimura, 1994). Therefore, information on larval recruitment proceses of the two species is vital for making clear interspecific relationships between the two species on the tidal flats of the lake.

In the course of studying the population dynamics of these two species in Lake Hamana with particular reference to larval recruitment processes, we described larval morphologies of the two species, based on artificial spawning and fertilization in the laboratory, and so now have no problem of species identification of the two species larvae found in plankton samples (Kimura, 1994; Kimura & Sekiguchi, 1994). In the present study, based on larvae reared in the laboratory, we tried to examine the effects of temperature on larval development of the two species (i.e. days from fertilization to settlement, size at larval settlement, etc.) that are vital for understanding larval recruitment processes in the two species in the lake.

Materials and Methods

Adult specimens of two mytilid species (*M. senhousia* and *L. fortunei kikuchii*) were collected on tidal flats of Inohana and Shonai Inlets within the blackish Lake Hamana along the Pacific coast of central Japan once a week from August 1991 to August 1993. For stimulating artificial spawning of the specimens in the laboratory, 25 to 100 specimens of each species were individually kept in holes of multi-dish plates with glassfiber-filtered seawater (20‰) and were put under observation in a room without temperature control. However, the specimens which were collected in summer were kept for 2 hours in a box at a temperature of 5°C and then were returned to the room in order to stimulate

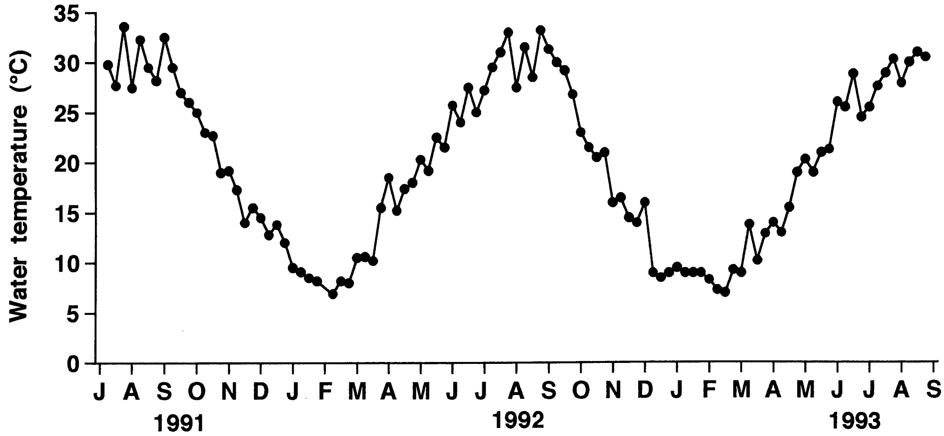

Fig. 1. Surface water temperature in Lake Hamana from July 1991 to August 1993.
1991年7月から1993年8月の浜名湖の表層水温.

spawning. Spawning of *M. senhousia* was observed in specimens collected from August to October while that of *L. fortunei kikuchii* was observed in those collected in August to December.

During one day after artificial fertilization, the eggs and D-shaped larvae of the two species were kept at a temperature of 25°C. Then the D-shaped larvae were divided into 3 groups which were kept at 15°C, 25°C and 30°C, respectively. In shallow water of Inohana Inlet (Fig. 1), surface temperature is below 15°C in winter and spring seasons while that is 25–30°C in summer season. The larvae with a density of 10 inds./ml were kept in 800 ml beakers with glassfiber-filtered seawater. The seawater in the beakers was exchanged once a day when cultured diatoms *Chaetoceros calcitorans* were given as food for the larvae with a density 2.0×10^6 cells/ml per dish.

Observations of larval development of the two species were performed once a day. Four to twenty specimens of larvae were sampled from the beakers every two or three days and their morphologies were examined under a light microscope after fixation with 70% ethyl alcohol. Larvae of *M. senhousia* were kept from September 3 to 28, 1992 while those of *L. fortunei kikuchii* were kept from December 18, 1992 to January 12, 1993.

Results

1. *Musculista senhousia*

Growth characteristics of larvae of the species under different temperature conditions are shown in Fig. 2(a). Growth characteristics of the larvae kept at 25°C and 30°C were as follows: The D-shaped larvae entered the umbo stage 6 days after fertilization, and then the pediveliger stage with eye pigment and foot were found 16 days after fertilization. The larvae began to settle on the bottoms of the beakers 18 days after fertilization, and most of the larvae finished settling on the bottom and entered the spat 21 days after fertilization. The D-shaped larvae had shell lengths of 70–120 μm at 25°C and 70–118 μm at 30°C. The umbo stage larvae, 16 days after fertilization, had average shell lengths of 227 μm at 25°C and 174 μm at 30°C. The pediveliger larvae had shell lengths of 256 μm and more, of which the settling larvae had average shell lenghs of 302 μm at 25°C and 244 μm at 30°C. The spats reached shell lengths of 304 μm at 25°C and 264 μm 30°C when our 25-day experiment ended.

On the other hand, growth characteristics of the larvae which were kept at 15°C were much different from those of the larvae kept at 25°C and 30°C. The D-shaped larvae entered the umbo stage 16 days after fertilization, while these did not enter the pediveliger stage and were still in the umbo stage without settlement until the end of our 25-day experiment. According to preliminary experiments to continue keeping the larvae, they did not settle on the bottoms even 2 months and more after fertilization. The D-shaped larvae had shell lengths of 70–120 μm. The umbo stage larvae had average shell lengths of 143 μm when our 25-day experiment ended.

2. *Limnoperna fortunei kikuchii*

Growth characteristics of larvae of the species kept at different temperature conditions are shown in Fig. 2(b). Growth characteristics of the larvae kept at 25°C were as follows:

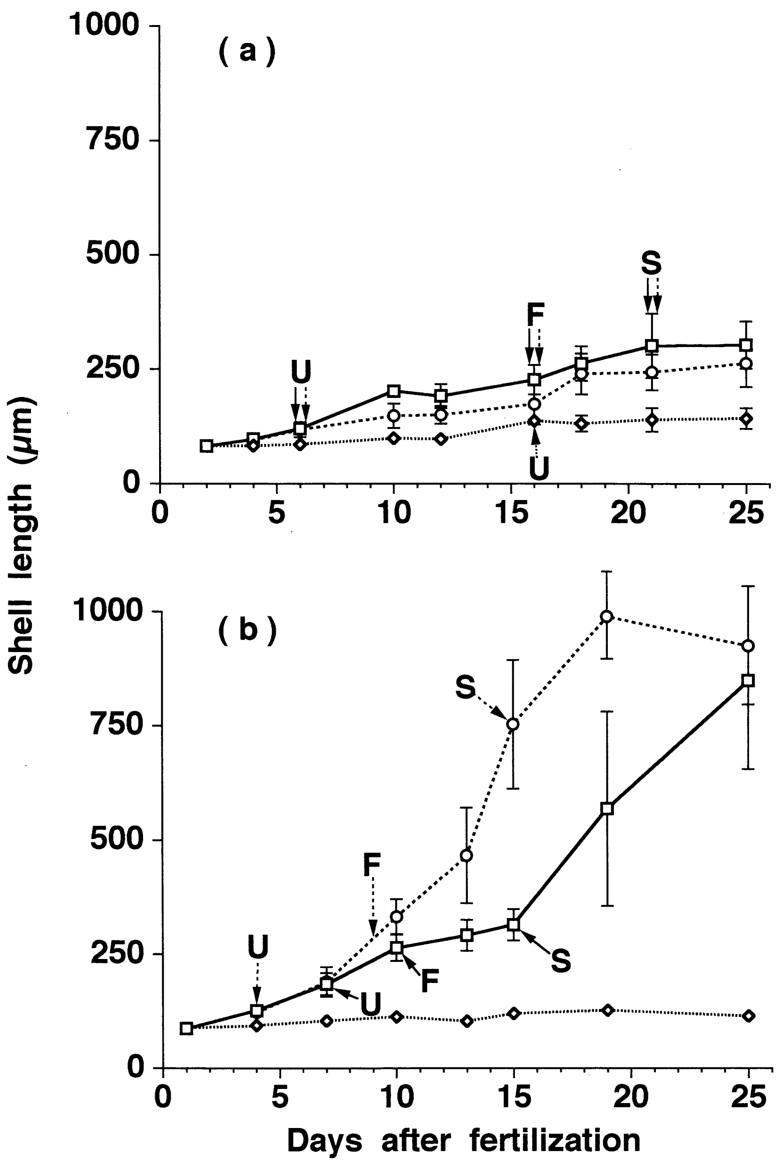

Fig. 2. Growth of *M. senhousia* and *L. fortunei kikuchii* larvae cultured in the laboratory.
(a) *M. senhousia*, (b) *L. fortunei kikuchii*. Dotted line: 15°C, solid line: 25°C, dashed line: 30°C. U: forming of umbo, F: forming of foot, S: most of individuals settled. Vertical bars indicate standard deviation. 人工飼育下におけるホトトギスガイとコウロエンカワヒバリガイの成長特性. (a) ホトトギスガイ. (b) コウロエンカワヒバリガイ. 点線：15℃, 実線：25℃, 破線：30℃. U：殻頂部の形成, F：足の形成, S：大部分の個体が着底. 垂線は標準偏差.

The D-shaped larvae entered the umbo stage 7 days after fertilization, and then the pediveliger stage with eye pigment and foot was found 10 days after fertilization. The larvae began to settle on the bottoms of the beakers 12 days after fertilization, and most of the larvae finished to settle on the bottoms and entered the spat 15 days after fertilization. The D-shaped larvae had shell lengths of 80–127 μm. The umbo stage larvae, 10 days after fertilization, had average shell lengths of 264 μm. The pediveliger larvae had shell lengths of 282 μm and more, of which the settling larvae had average shell lengths of 314 μm. The spats reached shell lengths of 849 μm when our 25-day experiment ended.

Growth characteristics of the larvae kept at 30°C were as follows: The D-shaped larvae entered the umbo stage 4 days after fertilization, and then the pediveliger stage with eye pigment and foot was found 7–9 dyas after fertilization. The larvae began to settle on the bottoms of the beakers 12 days after fertilization, and most of larvae finished to settling on the bottoms and entered the spat 15 days after fertilization. The D-shaped larvae had shell lengths of 80–123 μm. The umbo stage larvae, 7 days after fertilization, had average shell lengths of 190 μm. The pediveliger larvae had shell lengths of 256 μm and more, of which the settling larvae had average shell lengths of 753 μm. The spats reached shell lengths of 925 μm when our 25-day experiment ended. As indicated in Fig. 2(b), shell lengths of the spat when our experiment ended were smaller than those 5 days before. This was caused by selective death of larger spats 5 days before our experiments ended.

On the other hand, growth characteristics of the larvae which were kept at 15°C were much different from those of the larvae kept at 25°C and 30°C. The D-shaped larvae did not enter the umbo stage even when our 25-day experiment ended. The larvae had average shell lengths of 114 μm when our 25-day experiment ended.

Based on the results, the above-mentioned results of our experiments are summarized as follows: At 25°C and 30°C, larvae of *L. fortunei kikuchii* showed faster growth, shorter period from fertilization to settlement, and larger size at settlement than those of *M. senhousia*. At optimum growth temperature (30°C for *L. fortunei kikuchii*, 25°C for *M. senhousia*), sizes at settlement in larvae of the former species were larger by two times or more than the latter species, and the days from fertilization to settlement were shorter by ca. 7 days. On the other hand, larvae of *M. senhousia* grew faster than *L. fortunei kikuchii* at 15°C. However, this temperature hampered larval development of the two species, because the larvae did not enter the pediveliger and did not settle on the bottom until our 25-day experiment ended.

Discussion

According to studies done in Lake Hamana by Kimura (1994), planktonic larvae and larval recruitment to benthic populations of *M. senhousia* and *L. fortunei kikuchii* were observed together in similar seasons: planktonic larvae of the two species were found throughout the year, but the former were mostly abundant in August to December while the later being abundant in August to September. The larval recruitments of the two species were observed in August to October. Then, based on histological studies of gonads of *L. fortunei kikuchii* in the lake, Abdel-Razak *et al.* (1993b) confirmed that mature specimens were collected throughout the year, though larval recruitments occurred mainly in summer.

Chiba (1977) referred that the main spawning season of *M. senhousia* in the lake was in July to August.

Larvae of the two species which were kept 15°C failed to develop to the pediveliger and to settle (Fig. 2). Deducing from the seasonal fluctuation of water temperature in Lake Hamana (Fig. 1), larvae of the two species were found in water with a wide range of water temperature between 10°C to 30°C. Accordingly, the larvae which were found in water having a water temperature less than 15°C in early winter failed to settle on the lake bottoms or tidal flats, with the result that larvae succeeded in recruitments in seasons with water temperature higher than 15°C mainly in summer to autumn.

As mentioned in the result section, larvae of *L. fortunei kikuchii* showed faster growth, shorter period from fertilization to settlement, and larger sizes at settlement at 25°C and 30°C than *M. senhousia*, whose settlement occurs in a wider range of water temperature, particularly in a lower range of temperature. This may indicate that larvae of *L. fortunei kikuchii* has faster growth and larger sizes during settlement in summer, and that they are able to occupy substrata available for settlement earlier than *M. senhousia*, while those of *M. senhousia* occupy substrata available for settlement in autumn to early winter more profitably than *L. fortunei kikuchii*. Recently, *L. fortunei kikuchii* was first introduced

Table 1. Comparison of shell length of mytilid pediveliger.

Species	Shell length of pediveliger (μm)	Days from fertilization to pediveliger	Rearing temperature (°C)	Author
Mytilus edulis	260 ~ 340			Tanaka (1979)
M. edulis	249 ~ 267	43 ~ 2	10 ~ 22	Bayne (1965)
M. edulis	354 ~ 400			Stafford (1912)
M. edulis	300 ~ 360			Nelson (1928)
M. edulis	355			Sullivan (1948)
M. edulis	215 ~ 300			Loosanoff & Davis (1963)
M. corsucus	280 ~ 350			Tanaka (1979)
M. corsucus	280 ~ 320			Yoshida (1936)
Modiolus metcalfi	305			Tanaka (1979)
M. demissus	205			Sullivan (1948)
M. demissus	220 ~ 305			Loosanoff & Davis (1963)
M. nipponicus	310			Tanaka (1979)
M. comptus	270			Tanaka (1979)
Limnoperna fortunei kikuchii	282	10	25	Present study
L. fortunei kikuchii	256	9	30	Present study
Musculus cupreus	338			Tanaka (1979)
M. pusio	225			Tanaka (1979)
Modiolaria marmorata	370 ~ 380			Jφrgensen (1946)
Musculista senhousia	256	16	25,30	Present study
M. senhousia	225			Tanaka (1979)
M. senhousia	210 ~ 250			Yoshida (1937)
M. perfragilis	280			Tanaka (1979)
Vignadula atrata	350			Tanaka (1979)

in Lake Hamana after 1975 and has been one of the dominant intertidal benthos and fouling animals there since 1975 (Abdel-Razak *et al.*, 1993a). However, the two species have a similar life form, e.g., epibenthic life with feeding habits of particle filter-feeding in water. So these two species compete severely for available substrata. *M. senhousia* has been predominant among the intertidal benthos and fouling animals in Lake Hamana before and after introduction of *L. fortunei kikuchii* into the lake. Dominance of the two species in the lake, without exclusion of the species each by other, is related intimately with differences in these larval traits.

Information on growth characteristics of mytilid species is fragmentary. However, data for shell lengths and days from fertilization to the pediveliger are available for a few mytilid species (Table 1): Shell lengths of the pediveligers of *L. fortunei kikuchii* and *M. senhousia* are not so different, though sizes at larval settlement are much different, and are within a range of shell lengths of those of other species. This indicates that sizes at the settlement is more important for understanding interspecific relationships among the benthos with a similar life form. Unfortunately, we have little information on sizes at the settlement.

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要　　約

ホトトギスガイ *Musculista senhousia* とコウロエンカワヒバリガイ *Limnoperna fortunei kikuchii* は，静岡県西部に位置する浜名湖奥部の潮間帯に優占するイガイ類である。筆者らはこれらの人工受精によって得られた幼生を用いて，15 ℃・25 ℃・30 ℃の異なる水温条件下における成長を比較した。飼育水温25 ℃と30 ℃では，いずれの飼育水温においてもコウロエンカワヒバリガイはホトトギスガイよりも浮遊幼生の成長が明らかに速く，着底までの日数も短く，着底時の殻長も著しく大きかった。これら2種の浮遊幼生の好適な飼育水温では（コウロエンカワヒバリガイでは30 ℃，ホトトギスガイでは25 ℃），着底時の殻長は前種は後種の2倍以上大きく，着底までの日数は前種が後種よりも約1週間早かった。一方，飼育水温15 ℃では，逆にホトトギスガイはコウロエンカワヒバリガイよりも成長がよかった。しかし，これら2種の浮遊幼生にとって，この飼育水温は明らかに好適水温ではない。実験終了時までに，ホトトギスガイの浮遊幼生は殻頂期幼生に移行するが着底せず，コウロエンカワヒバリガイの浮遊幼生は殻頂期幼生に移行せず，D型幼生に留まっていた。

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