浜名湖庄内湾におけるLimnoperna fortunei kikuchiiの生活史

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Life history of *Limnoperna fortunei kikuchii* in Shonai Inlet,
Lake Hamana

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Abstract

Field observations on the life history of *Limnoperna fortunei kikuchii* were carried out from May
1980 to August 1982 in Shonai inlet, Lake Hamana. Spawning female was observed in higher level
during summer to autumn seasons, whereas male could spawn throughout the observation period.
The first spawning were thought to occur in May or June and larvae were supplied continuously
during summer. Spawned larvae would settle after 37 days when they became 270 \( \mu \text{m} \) in shell
length and grew up to 5 mm at 24—31 days after the settling. Shell length of the first settled
shells in the year were calculated to be 18.9 mm at the end of September and these shells could
spawn the next generations in the first summer. As the mass mortalities were observed in March
and July, generation alternation were supposed to take place in summer.

*Limnoperna fortunei kikuchii* had immigrated into Shonai inlet, Lake Hamana during the period between 1974
to 1979 and excluded *Musculista senhousia*, which had been a dominant fouling bivalve in the inlet\(^1\). In this study, field observations on the life history of *L. fortunei kikuchii* were carried out in Shonai inlet.

Materials and Methods

Gonad development and spawning season

The sample shells of *L. fortunei kikuchii* for the histological observations were collected during May 1980 to
March 1981 from the natural population on the wall of small harbor at St. 7 (Fig. 1). Sample collections were
made 4 times a month from June to September, and once or twice a month in other periods. Number of
specimens collected at each time were 30—158. Samples were fixed with Bouin’s solution for about 24
hours and preserved in 70 % Et-Oh until preparation. Preserved gonads were embedded in paraffin and
serially sectioned to 5—8 \( \mu \text{m} \) in thickness.

Rearing experiments of larvae

The growth during the planktonic stage was observed by rearing the larvae collected from the inlet.
The larvae were collected by towing plankton net (NXX 13) on 27 July 1982 and were divided into four
groups depending on their shell lengths. Initial mean shell lengths of each group were, Group I: 70±11 \( \mu \text{m} \) 
\( (n=175) \), Group II: 91±19 \( \mu \text{m} \) \( (n=150) \), Group III: 151±33 \( \mu \text{m} \) \( (n=105) \) and Group IV: 202±34 \( \mu \text{m} \) \( (n=95) \). Each group was reared in 1 liter beaker contain-

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Key words: *Limnoperna fortunei kikuchii*, Fouling organisms, Lake Hamana, Life history
Fig. 1. Map of Lake Hamana showing the sampling stations in Shonai inlet.

ing 200 ml of sea water. During the rearing period, water temperature was kept at 20 °C and the diatom, Skeletonema costatum was given twice a day to maintain the cell density at 5–6 × 10^5 cells/ml. Shell lengths were measured at 4, 6, 16, 22 and 40 days after starting the experiments.

Growth after settling

Growth rates after settling were estimated by two different methods. One was conducted to estimate the growth rate of smaller shells within one or two months after settling. The test ropes with thread collectors were immersed at St. 2 (Fig. 1) from 22 June in summer and from 7 September in autumn observation. The subsamples of threads were collected serially from the original rope at 14, 35 and 50 days after immersion in summer and at 14, 21, 43 and 50 days after in autumn observation. The shell length compositions were recorded. Another experiment was performed to estimate the growth rate of the shells larger than 7.0 mm. Plastic cages measuring about 25×10×10 cm were used as growth chambers. The mesh size of the cage was 4 mm and the cage was divided into 5 compartments. Shells of L. fortunei kikuchii in various sizes were collected from the natural population in the inlet and divided into four or five size groups. Each size groups was put into the compartment separately. Two cages for each station were immersed at St. 1, St. 3 and St. 6 (Fig. 1). One cage was fixed in intertidal zone and another cage was fixed in infralittoral zone. The cages were washed once a week to remove the fouling organisms during the observation. After 14 to 29 days of immersing period, the survival rate and the mean shell length of each component were recorded. This observation was performed every month from May to September 1981.

Life span

Shell size composition and ratio of dead shells were observed serially on two populations of L. fortunei kikuchii in the inlet. One was done on the population settled on the ropes that were immersed at St. 4 (Fig. 1) from April 1981. One of these ropes was collected every month until August 1982 and the shell length and the survival rate of all attached individuals of L. fortunei kikuchii were recorded. Similar observations were carried out on the natural population attached on the rocks at St. 8 (Fig. 1).

Results

Gonad development and spawning season

Developmental stages of gonads were identified based on the thickness of the mantle and the shape and size of oocytes or spermatocytes under the following features. Undistinguished stage: No ova or sperm can be observed and the genital ducts are usually obliterated by the bulk of connective tissue. Developing stage: The ovarian and testicular follicles can be observed. Small oocytes and sperm mother cell or unripened spermatozoa are observed in female and male gonad, respectively. Spawning stage: Ripe ova with nucleus in the center are observed in female gonad and sperm are observed in male gonad. Inter-follicular connective tissue can not be observed due to the extreme volume of the follicles in both sexes. Spent stage: Nearly all ripe cells are discharged. In female, the small oocytes are observed in the follicles wall. The mantle tissue of both sexes becomes soft, spongy and semitransparent.

Total number of shells examined histologically was 733, which was shared by 299 individuals of female, 312 individuals of male, 26 individuals of bisexual and
91 individuals in undistinguished stage. Among the bisexual specimen, 10 individuals were treated as male in the following gonad maturation analysis, because the testicular region in the gonad was larger than the ovarian region. The others were treated as female.

The shell lengths of the undistinguished individuals ranged from 2 mm to 10 mm. Females were found in the individuals larger than 5 mm, although male individuals were observed even in the size group of 2 mm in shell length. Fig. 2 shows the ratio of undistinguished individuals at each month. The abundance of undistinguished individuals remained in lower level in May to July. It increased in August and reached to the maximum level (34.2%) in September, then gradually decreased to 0% until January, showing some fluctuations.

Changes in the gonad development stage in both sexes are shown in Fig. 3. In the case of female, all individuals were remained in developing stage in May. The ratio of spawning individuals increased to maximum level of 70% in June and fluctuated in higher level during summer to autumn. High percentage of spent stage was observed in August and December. In the case of male, the ratio of developing stage was 0% in May to July and it reached maximum value of 29% in September. The ratio of spawning individuals were in high level throughout the observation period. In May and the period from December to March, no individual in spent stage was observed.

**Growth of larvae**

The results of rearing experiment of the larvae are summarized in Table 1. It was not possible to identify the species of the larvae by morphological observations but most of the larvae were supposed to be those of *L. fortunei kikuchii*. The reasons of this supposition were the dominant species of bivalve in the inlet was *L. fortunei kikuchii* and the spawning season of the cultured oyster, *Crassostrea gigas* starts at late June in Lake Hamana.

D-Shaped larvae of Group I (70 μm in initial mean)

<table>
<thead>
<tr>
<th>Group</th>
<th>Initial mean ± s.d.</th>
<th>Final mean ± s.d.</th>
<th>Time in days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>6</td>
</tr>
<tr>
<td>I</td>
<td>70.5 ± 10.7</td>
<td>89.9 ± 15.0</td>
<td>197.5 ± 16.0</td>
</tr>
<tr>
<td></td>
<td>(n = 175)</td>
<td>(n = 120)</td>
<td>(n = 56)</td>
</tr>
<tr>
<td>II</td>
<td>90.7 ± 19.1</td>
<td>156.3 ± 32.0</td>
<td>236.0 ± 70.2</td>
</tr>
<tr>
<td></td>
<td>(n = 150)</td>
<td>(n = 70)</td>
<td>(n = 50)</td>
</tr>
<tr>
<td>III</td>
<td>151.3 ± 32.6</td>
<td>203.0 ± 30.0</td>
<td>280.0 ± 18.7</td>
</tr>
<tr>
<td></td>
<td>(n = 105)</td>
<td>(n = 70)</td>
<td>(n = 30)</td>
</tr>
<tr>
<td>IV</td>
<td>202.2 ± 34.2</td>
<td>272.0 ± 17.0</td>
<td>297.0 ± 17.1</td>
</tr>
<tr>
<td></td>
<td>(n = 95)</td>
<td>(n = 50)</td>
<td>(n = 50)</td>
</tr>
</tbody>
</table>
Fig. 4. Changes in the size distributions showing the growth of smaller shells that settled on the thread collectors.

grew into D-shaped larvae measured about 90 \( \mu m \) after 4 days. D-Shaped larvae of Group II (91 \( \mu m \) in initial mean) became umbo stage larvae (156 \( \mu m \) in average) after 6 days. The survival rates of Group I and Group II became 0% during the experiment period. The shells settled on the bottom of the beakers were observed 22 days after the start of rearing in Group III (151 \( \mu m \) in initial mean) and 6 days after in Group IV (202 \( \mu m \) in initial mean), when the larvae became about 270 \( \mu m \). Growth rate in the specimen larger than 270 \( \mu m \) became very rapid and the shell length at 40th day was about 500 \( \mu m \) in Group III and 650 \( \mu m \) in Group IV.

Growth after settling

The growth of smaller shells that settled on the thread collectors are shown as the changes in size distributions (Fig. 4). In summer, the maximum shell length was 6 mm at 35 days after immersion and 8 mm after 50 days. The growth in autumn season was retarded when compared to that in summer. More than 95% individuals remained in the range smaller than 1 mm even in 50 days and the maximum shell length after 50 days in autumn observation was 5 mm.

In the growth observation of larger specimens using the growth cages, mortalities higher than 30% were observed in 16 cases. In the other 14 cases, mortalities were lower than 25% and the obtained data could be applied to von Bertalanffy formula* through Wall-}

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* The formula is expressed as:

\[
L_t = L_{\infty} \left(1 - A \cdot e^{-bt}\right)
\]

where \( L_t \): shell length at \( t \)

\( L_{\infty} \): the maximum shell length

\( A, b \): growth constants.

Growth rate at \( L_t \) is calculated as follows:

\[
dL_t/dt = L_{\infty} \cdot A \cdot b \cdot e^{-bt} = (L_{\infty} - L_t) \cdot b.
\]
Table 2. The estimated mortality, growth constant (b), the maximum shell length and growth rate at 12 mm of *L. fortunei kikuchii* during May to September, 1981 (A: intertidal zone, B: infralittoral zone)

<table>
<thead>
<tr>
<th>month</th>
<th>St. 1</th>
<th>St. 3</th>
<th>St. 6</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>A</td>
</tr>
<tr>
<td>May</td>
<td>mortality (%)</td>
<td>61</td>
<td>47</td>
</tr>
<tr>
<td></td>
<td>b (/day)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>L&lt;sub&gt;∞&lt;/sub&gt; (mm)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>growth 12 mm (mm/day)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Jun.</td>
<td>mortality (%)</td>
<td>20</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>b (/day)</td>
<td>3.22×10&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>1.71×10&lt;sup&gt;-2&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>L&lt;sub&gt;∞&lt;/sub&gt; (mm)</td>
<td>18.7</td>
<td>23.9</td>
</tr>
<tr>
<td></td>
<td>growth 12 mm (mm/day)</td>
<td>2.16×10&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>2.03×10&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Jul.</td>
<td>mortality (%)</td>
<td>25</td>
<td>75</td>
</tr>
<tr>
<td></td>
<td>b (/day)</td>
<td>0.45×10&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>L&lt;sub&gt;∞&lt;/sub&gt; (mm)</td>
<td>38.8</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>growth 12 mm (mm/day)</td>
<td>1.11×10&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td>Aug.</td>
<td>mortality (%)</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>b (/day)</td>
<td>1.80×10&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>1.77×10&lt;sup&gt;-2&lt;/sup&gt;</td>
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<td></td>
<td>L&lt;sub&gt;∞&lt;/sub&gt; (mm)</td>
<td>22.7</td>
<td>22.1</td>
</tr>
<tr>
<td></td>
<td>growth 12 mm (mm/day)</td>
<td>1.93×10&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>1.79×10&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
<tr>
<td>Sep.</td>
<td>mortality (%)</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>b (/day)</td>
<td>0.94×10&lt;sup&gt;-2&lt;/sup&gt;</td>
<td>2.70×10&lt;sup&gt;-2&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>L&lt;sub&gt;∞&lt;/sub&gt; (mm)</td>
<td>15.8</td>
<td>14.6</td>
</tr>
<tr>
<td></td>
<td>growth 12 mm (mm/day)</td>
<td>0.36×10&lt;sup&gt;-1&lt;/sup&gt;</td>
<td>0.71×10&lt;sup&gt;-1&lt;/sup&gt;</td>
</tr>
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</table>

The formula used for the estimation is expressed as:

\[ L_t = L_∞ \left(1 - A \cdot e^{-bt}\right) \]

where \( L_t \): shell length at \( t \)
\( L_∞ \): the maximum shell length
\( A \), \( b \): growth constants.

Growth rate at \( L_t \) is calculated as follows;

\[
\frac{dL_t}{dt} = L_∞ \cdot A \cdot b \cdot e^{-bt}
\]

\[
= \left( L_∞ - L_t \right) \cdot b
\]

ford’s graphical method<sup>23</sup>, except the case of intertidal zone at St. 6 in September. Estimated parameters, survival rates and daily growth rates at 12 mm are summarised in Table 2. The mortalities were about 50% in May and decreased in June. Highest mortalities were recorded in July and August, and the mortalities decreased to lowest level in September. The growth rate was highest in June and decreased gradually to the lowest level in September. The growth rates at St. 1 were nearly the same with those at St. 3 and 6 in June, whereas the rates became lower than those at St. 3 in September.

**Life span**

The size distributions of the population on the experimental ropes are shown in Fig. 5. The mode in shell length was observed in the range of 4–6 mm in 22 June and was raise to the range of 12–14 mm in 21 September. During this period, because of the recruitment of newly attached shells, the size distribution became bimodal in several cases. After 21 September, the larger size group exhibited no apparent growth and mode was found in the range of 12–14 mm, whereas the lower mode was observed in the range of 6–10 mm until 18 December. During January to March in the next year, two modes were mixed into one single mode in the range of 12–16 mm and high mortality was observed in March. In April, two modes were observed again. The size range of lower mode was 14–16 mm and that of higher mode was 18–20 mm, although the size distribution became very wide and the bimodal shape was not clear. Second high mortality was observed in July and the size range of the survivor was 18–24 mm. Recruitment of newly attached shells in the second year was observed in August and the size
range of these young shells was 8—10 mm.

In the natural population attached on the rocks (Fig. 6), shell length distributed widely from 10 to 36 mm without prominent peak mode in May and any apparent change in size distribution was not observed until July. High mortality was observed in July and the shell lengths of the survived shells were in the range of 12—30 mm. In August, newly attached group, ranging 0—6 mm in shell length, was observed. In September and October, several size groups were observed in the histograms and there were little changes in peak mode and distribution range until February. The second high mortality was observed in March and the size range of survived shells was 12—34 mm.

**Discussion**

From the rearing experiment, it takes 5 days to become D-shaped larvae from fertilization in this species and it takes 32 days to grow into 270 μm from D-shaped larvae of 70 μm in shell length. If the settlement starts when the shell becomes 270 μm in size, the total duration from the spawning to settlement is calculated to be 37 days.

In the observation on the growth rate of smaller shells (Fig. 4), maximum shell length was 1 mm after 14 days from immersion and 6 mm after 35 days. From
the changes in the maximum shell length of each case, the daily growth rate between 1 mm to 6 mm was calculated to be 0.238 mm/day. Thus the duration needed to grow up to 5 mm from 1 mm was estimated to be 17 days, provided that the daily growth rate remains constant during this period. The shells that belonged to the largest mode were supposed to settle on the collector threads during the first 7 days after immersion and grew up to 1 mm in the next 7 days. As the result, the total period from settlement to 5 mm size was calculated to be 24–31 days.

Consequently, the total duration from spawning to 5 mm in shell length was 61–68 days and the shells of 5 mm observed on 22 June were thought to be spawned at the end of April. However, the results of the histological observation suggested that first spawning of female occurred between May and June. In May, all females were in developing stage and the individuals in spent stage appeared first in June. The contradiction between the two estimations on the first spawning season could be explained by under-estimation of developing speed of larvae or by erroneous estimation of settling stage. In the rearing observation, the larval shells settled on the glassy substratum when they became 270 μm in shell length. In the field observations, it is unusual to find pediveliger smaller than 200 μm on the thread collectors. Thus the error in the estimation on the settling stage was thought to be small. These problems should be discussed again after adequate rearing experiments and detailed field observations in the future.

Among the calculated growth parameters, values in intertidal zone at St. 1 and St. 3 in June, July, August and September are used for the estimation of the growth during this period, because of the lower mortality. The growth of the shell that was 5 mm in shell length on 22 June could be calculated as 7.8 mm, 11.5 mm, 16.3 mm and 18.9 mm at the end of June, July, August and September, respectively. In the size distributions of experimental ropes (Fig. 5), the first attached group, 5 mm in shell length on 22 June, would be the maximum size group in each sampling. The estimated values by the calculation are well explaining the growth of the size ranges.

In the population on the rocks (Fig. 6), the first recruitment of newly attached shells was observed in
August after the high mortality in July. In the population on the experimental ropes (Fig. 5), on the other hand, continuous recruitments were observed and size distributions became very wide during summer season in the first year. However in the second year, first recruitment to the rope population was observed in August, similarly to the rock population. It was supposed that larval shells were not able to recruit into the space where previously attached shells had occupied because of space competition, and that generation alternation took place in summer. In the histological observation, the ratio of female in spent stage increased when their shell length became 10 mm. This means that the individuals first spawned in May or June could spawn again in summer of the same year.

In conclusion, the life history of *L. fortunei kikuchii* in Shonai inlet was estimated as follows. The first spawning of the year occurred at the end of May or the beginning of June and the larvae recruited into the fouling communities if they could find suitable substratum in about a month. The larvae were supplied continuously and recruitments of newly settled shells were repeated during summer season. The settled shells grew up to more than 20 mm in shell length until the end of autumn and could spawn the next generations in the first summer. Some of them died in winter season and the survivors became the first spawner of the next year. Most of the survivor died in July and the next generation recruited into the open space.

References


浜名湖庄内湾における *Limnoperna fortunei kikuchii* の生活史

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浜名湖の一支湾、庄内湾における付着性二枚貝、コウロエンカワヒバリガイ, *Limnoperna fortunei kikuchii* の生活史を、生殖巣の成熟度、幼生の飼育、付着個体の成長などについて調べることで追跡した。雌はほぼ周年成熟していたのに対し、雄の成熟個体は夏～秋に多かった。1年の最初の産卵は5月下旬あるいは6月上旬に行われ、その後は秋まで連続的に幼生が供給されたものと考えられた。幼生は産出後ほぼ37日目に、殻長270 µm 程度になった時点で定着し、定着後24～31日で殻長約5 mm に成長した。1年の最初に定着した個体は秋の終わりまでには殻長20 mm 以上に達し、その年の夏には次世代を産出可能であった。付着個体の大量死滅が3月と7月にみられ、新規加入による世代交代は8月を中心とする夏に起こるものと推察された。