

# 北海道立水産試験場研究報告

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Yoichi, Hokkaido, Japan

October, 2006

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# 北海道立水産試験場研究報告

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（2006年10月）

# SCIENTIFIC REPORTS OF HOKKAIDO FISHERIES EXPERIMENT STATION

No. 71

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(October, 2006)

# 網走湖におけるヤマトシジミの産卵及び初期生活史に関する生態学的研究<sup>\*1</sup>

馬場 勝寿<sup>\*2</sup>

## Ecological study on spawning and early life stage of the brackish water bivalve *Corbicula japonica* in Lake Abashiri<sup>\*1</sup>

Katsuhisa BABA<sup>\*2</sup>

The spawning probability of *Corbicula japonica* is expressed with temperature and salinity by the following equation: (1)  $1/\{1+\exp[-(-16.12+0.57T-12.64S+0.59TS)]\}$ , ( $T$ : Temperature,  $S$ : Salinity). The occurrences of the planktonic larvae can be well predicted by the equation in Lake Abashiri. *C. japonica* failed to spawn when the temperatures and the salinity did not exceed the threshold environments for the spawning; the threshold environments are expressed by the equation(1). The failure of the spawning was not an exceptional phenomenon in Lake Abashiri; the failure probably occurred in 10 out of 21 years for which data were available. The ovaries after the spawning season in the spawning-failure years were histologically characterized by massive atretic oocytes.

The vertical heterogeneities of abundances and size compositions of the planktonic larvae were observed in the water column. The most of larger (shell length: 170 to 200  $\mu$  m) larvae were observed near the surface of the lake. On the other hand, the smaller (shell length: 140 to 170  $\mu$  m) ones were mainly observed near the boundary between the well-oxygenated oligohaline upper stratum and anoxic polyhaline lower stratum. The salinity of the near the boundary was higher than shallower depths. I thought the heterogeneities probably related to the enhancement of the survivorships for the salinity-sensitive larvae. The larvae probably assemble to the higher salinity zone to gain sufficient salinity for the larval development in the early stages. The larvae migrate to the surface where the higher possibilities are expected to be transported to the marginal area of the lake, the habitat of *C. japonica*.

Few settled juvenile were observed on the muddy sediments. The favorable sits for the juveniles were sites where the content of silt-clay plus very fine sand was less than 36.9 %. Other restrictive sediment-environment factors, such as organic carbon, water content and total sulfide were highly correlated with the site-clay plus very fine sand; i. e. one factor can represent the favorable sediment conditions for the juvenile. Understanding the favorable conditions is very important for the management of fisheries grounds and it also facilitates the judgments about which sites are appropriate for the release of seed clams.

The juvenile growth of *C. japonica* in Lake Abashiri was extremely slow; it grew to the shell length of 0.7 mm at age 1 and 2.1 mm at age 2. I elucidated the proximal factor of the extremely slow growth by modeling between the environmental factors and the growth. The proximal factor was the less susceptible growth response to the environmental factors until the second winter. In many species of bivalve, populations from higher latitudes have a slower initial growth rate; but longevity and ultimate size in these populations are frequently greater than at lower latitudes. The extremely slow growth of *C. japonica* juvenile in Lake Abashiri is probably an extreme example of this phenomenon.

Key words: *Corbicula japonica*, spawning, early life stage, ecology

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## GENERAL INTRODUCTION

The native range of brackish and fresh water bivalve *Corbicula* is from Africa to the Far East ranging from the tropical to the cold-temperate zone <sup>1)</sup>. *Corbicula* extended its range to the cold-temperate zone only in the Far East (Fig. 1). Lake Abashiri lies near the northern limit of its range.

In Japan, there are three species of *Corbicula*, i.e. *C. japonica* Prime, *C. leana* Prime, *C. sandai* Müller <sup>2)</sup>. The native range of *C. japonica*, a brackish-water species, is from the southern part of Sakhalin to Kyushu. The native range of *C. leana*, a fresh-water species, is from Honshu to Kyushu. *C. sandai*, a fresh-water species, is endemic to Lake-Biwa water system including Yodo River. Among *Corbicula*, only *C. japonica* successfully extended its range to the cold-temperate zone (Fig. 2).

The phylogenetic relationships among the three species were inferred from observations of their chromosomes <sup>3)</sup> and from isozyme polymorphisms <sup>4, 5)</sup>. These reports suggested that the lacustrine *C. sandai* had first speciated from the brackish *C. japonica* and then the fluvial *C. leana* had derived from *C. sandai*. The each species has a specific reproduction system. *C. japonica* is an oviparous dioecious species and the larva hatches out in the blastula stage. *C. sandai* is an oviparous dioecious species and the larva hatches out after it developed to D-shaped larva in the egg. The prolonged development in the egg is probably to adapt to freshwater environments. *C. leana* is a viviparous hermaphroditic species and it reproduces by the self-fertilization; and the fertilized eggs are incubated in the inner demibranchs through the trochophore and the pediveliger stage. The reproductive properties of *C. leana* probably adapt to lotic environments. The self-fertilization systems of *C. leana*, which is called spontaneous androgenesis, is very characteristic; i. e., the all of maternal genome of zygotes is extruded as two polar bodies and the only chromosomes derived from one male pronucleus constitute the metaphase of the first cleavages of zygotes <sup>6)</sup>. Such spontaneous androgenesis is reported only in *C. leana* in the phylum Mollusca.

In the artificial and established range of *Corbicula*, especially in North America, it has become a major biofouling pest for industrial and domestic water supply systems <sup>7, 8)</sup>. On the other hand, *Corbicula* spp. are popular food sources for human in Asia. The annual catch ranged

from 19,000 to 27,000 t in 1995 to 2000 in Japan <sup>9)</sup>. Among *Corbicula* spp., *C. japonica* is the main species for the fisheries.

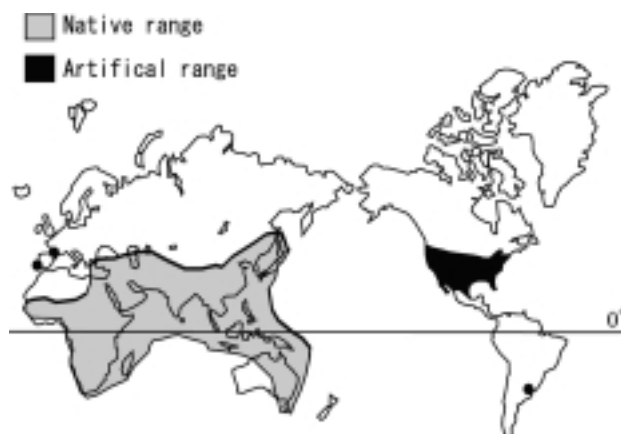


Fig. 1 The distribution of *Corbicula* (Morton 1986).

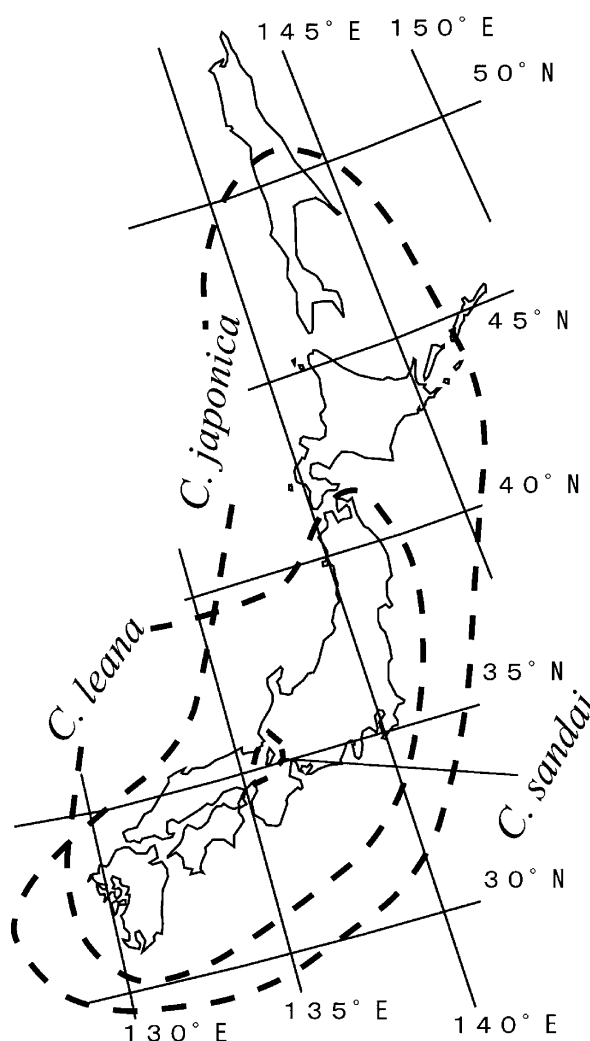


Fig. 2 The distribution of *Corbicula* in Japan and Sakhaline

The habitats of *Corbicula* spp. are near the milieu of human being, therefore, the populations of *Corbicula* have been much influenced by developments such as land reclamations and irrigations. Actually some habitats of *Corbicula* were devastated and fisheries of it were diminished by such developments <sup>10)</sup>. On the other hand, there are some resources, which were once devastated, drastically revived by its high reproductive potential and fast growth in southern habitats when limiting factors were mitigated. For example, the resource in Lake Hachiro, which was devastated by the irrigation developed in 1965, revived by a seawater inflow when a typhoon attacked the area in 1987 <sup>11)</sup>. The limiting factor caused by the irrigation is that the salinity became too low for the reproduction. The production of *C. japonica* decreased to less than 100 t from about 1,000 t by the irrigation, and it was much enhanced to 10,900 t in 1990 by the seawater inflow. For other example, the resource in Lake Jinzai, which was much decreased by inflow of muddy sediment from the land around the lake, revived by an outflow of the muddy sediment when a flood attacked the area in 1973 <sup>12)</sup>. The limiting factor of Lake Jinzai was that the sediment condition was too muddy for the settlement of *C. japonica*. The production was less than 30 t before the flood and it increased to 100-500 t after the flood.

All of these drastic revivals of the resources were reported in southern habitats of *C. japonica*. It is questionable whether such revival would occur in northern habitats because such revival has not been reported and ecological study of *C. japonica* is limited in northern habitats. Asahina <sup>13)</sup> reported the spawning ecology, and gonadal and larval developments in Lake Mokoto, Hokkaido (northern habitat). Maru <sup>14)</sup> studied the reproductive cycle by histological observations in Lake Abashiri, Hokkaido. Utoh <sup>15)</sup> investigated the growth by the observations of annual rings formed at the surface of the shell in Lake Abashiri. These reports are not enough to judge whether drastic revival of the resources would occur in northern habitats because 1) the conditions, temperature and salinity, needed for the spawning are not clear, and 2) the growth of juvenile is still unknown. Asahina <sup>13)</sup> reported the influences of temperature and salinity on the larval developments, but on the spawning. Utoh <sup>15)</sup> also reported the differences between the actual shell lengths of the individuals that were thought as aged one year and the

shell length at the first annual ring; i. e. the actual juvenile growth has not been clarified.

I carried out present studies to clarify these unknown parts of the ecological properties of *C. japonica* and to considered important viewpoints, especially in the northern habitats, for the resources conservation and management.

In my thesis, I elucidate remarkable ecological properties of *C. japonica*, an economically important species, in Lake Abashiri; some of them are specific in the northern habitats. Chapter I shows the favorable environments, temperature and salinity, for the spawning with field observations for six years and laboratory experiments including spawning inductions and histological observations. Chapter II shows vertical heterogeneities of abundance and size of the planktonic larvae in the water column. I inferred the reasons of the heterogeneity from the vertical changes of environmental factors in the water column and incubation experiments of the planktonic larvae in the laboratory. The pre-settlement processes were hypothesized from the viewpoint of larval survivorship. Chapter III shows the favorable sediment environments for the juvenile. The relationship between the sediment conditions and the juveniles are important information for the enhancement of *C. japonica* resources. For example, in Lake Jinzai, Shimane Prefecture, the resources of *C. japonica* were remarkably enhanced by the improvement of the sediment condition <sup>12)</sup>. Chapter IV shows the extremely slow growth of the juvenile in Lake Abashiri. I inferred the proximal factor of the extremely slow growth by modeling the relationships between the juvenile growth and the environmental factors.

## CHAPTER I

### Effects of temperature and salinity on spawning of the brackish water bivalve *Corbicula japonica* in Lake Abashiri

#### Abstract

The abundance of planktonic larvae (veliger) of *Corbicula japonica* in Lake Abashiri, which is near the northern limit of this species' range, was extremely low in 1995 and 1996, compared to other years (1989, 1990, 1994 and 1997). In histological examinations, the female genital tubules were filled with the atretic oocytes after the

spawning season of 1995. Therefore, it was concluded that most *C. japonica* failed to spawn in 1995. The effects of temperature and salinity on the spawning of *C. japonica* were examined in a spawning induction experiment under laboratory conditions. Probability of spawning by *C. japonica* in the experiment was described by the equation:  $1/\{1+\exp[-(-15.57+0.57T-12.64S-0.55Gam+0.69T\cdot S-0.10T\cdot S\cdot Gam)]\}$ , ( $T$ : temperature;  $S$ : salinity;  $Gam$ : dummy variable of 1 or 2, i.e. 1 denotes each group to which the gamete suspension was added and 2 each group to which the gamete suspension was not added). The probability of spawning within the group to which the gamete suspension was added (i.e.  $Gam=1$ ) explained well both annual and seasonal fluctuations of larval occurrence in Lake Abashiri in past years. The spawning of *C. japonica* may have been extremely low in 1995 and 1996 because of low temperature and low salinity. Such unfavorable conditions for spawning are not exceptional and occurred in 10 out of 21 years for which data were available. In *C. japonica*, reproduction succeeds less frequently in northern than in southern populations because the probability of spawning depends markedly on the temperature.

### Introduction

*Corbicula* spp. are harvested commercially in Japan. The annual catch ranged from 19,000 to 27,000 t in 1994 to 2000<sup>9)</sup>, among which *Corbicula japonica* was the main species. *C. japonica* is distributed in brackish water lakes and tidal flats of rivers from the south of Japan (about 35°N) to south of Sakhalin (about 50°N)<sup>16)</sup>. Lake Abashiri, which is near the northern limit of this species' range, is connected to the Sea of Okhotsk by 7.2 km of the Abashiri River. Because sea water flows back into the lake, depending on the tide, the lake has a well-oxygenated oligohaline upper stratum and an anoxic polyhaline lower stratum. The habitat of *C. japonica* is restricted to the upper stratum<sup>17)</sup>.

The maximum water temperature, the salinity of the upper stratum, and the depth of the boundary between water masses in Lake Abashiri differed markedly from year to year<sup>18)</sup>. The depth of the boundary and the salinity of the upper stratum change mainly according to the amount of precipitation and wind strength<sup>17)</sup>. When drought conditions continue for several years, the depth of the boundary becomes shallower. Strong winds, which

sometimes occur in spring or autumn, cause upwelling of the polyhaline water of the lower stratum. The upwelling of the lower water probably occurs more frequently under conditions with a shallower boundary. Upwelling of the polyhaline water causes the salinity of the upper stratum to increase and forces the boundary between the water masses deeper (Abashiri Local Office of Hokkaido Development Bureau unpubl. data).

Maru<sup>14)</sup> reported the spawning season of *Corbicula japonica* to be July to September. However, my recent work revealed that recruitment of *C. japonica* was extremely low in 1995<sup>19)</sup>. To clarify the cause of such low recruitment, I examined the relationships between temperature, salinity and spawning by means of an experiment performed under laboratory conditions, and verified the relationships with field data. This report is very important for resource management because it is the first to elucidate the environmental conditions necessary for the spawning of *C. japonica*.

### Materials and Methods

#### Occurrence of planktonic larvae during spawning season

Samplings of planktonic larvae (veliger) were carried out 3 to 9 times during the spawning seasons of 1989 to 1990 and 1994 to 1997 at 1 to 3 sites. In 1997, there were duplicate samples at each site. Sampling locations and dates are shown in Fig. 1-1 and Table 1-1. Larvae were collected by a plankton net hauled vertically from the depth of the boundary between the upper and the lower strata (depth from 5 to 7 m) to the surface. A 300 mm diameter plankton net of NXX-13 (mesh:  $95 \times 95 \mu\text{m}$ ) was used. The numbers of planktonic larvae were counted after the samples had been fixed with 3 % neutralized formalin.

#### Environmental data

Temperatures and salinities at the water surface during the spawning season (July to September) were obtained for Lake Abashiri from unpublished data of Abashiri Local Office of Hokkaido Development Bureau from 1994 to 1997. The data were collected once or twice a week.

Additional data on monthly water surface temperatures and salinities (1977 to 1993), as well as annual maximum temperatures, were obtained from Results of Water Quality



Analysis in Public Waters' <sup>20)</sup>. Collection locations for environmental data are shown in Fig. 1-1.

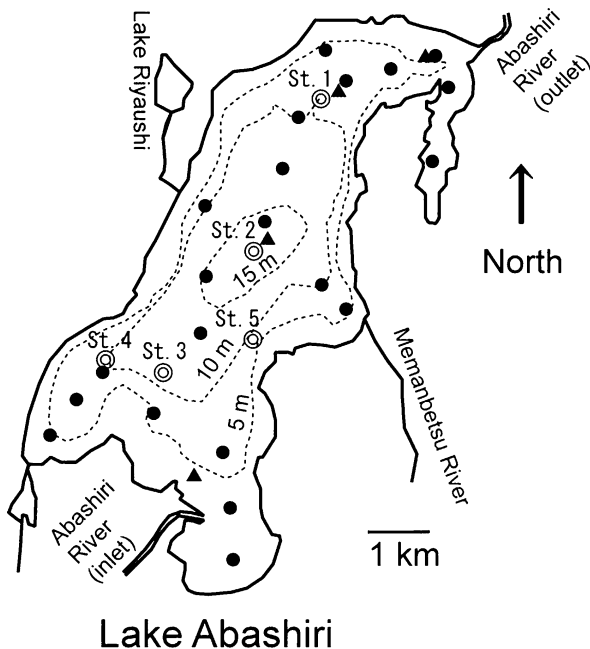


Fig. 1-1 Location of sampling sites in Lake Abashiri. Planktonic larvae of *Corbicula japonica* from different stations (◎) each year as follows: 1989, 1990 (Stn 5), 1994 (Stn 2), 1995 (Stn 2 and 4), 1996 (Stn 2, 4 and 5), 1997 (Stn 1, 2 and 3). Measurements of temperature and salinity were taken at (▲) 4 sites from 1977 to 1993 and (●) 21 sites from 1994 to 1997.

### Histological examination

A histological examination was performed on the gonads of 10 to 20 individuals (20 to 30 mm shell length) sampled monthly in 1995 and 1997. Tissues were fixed in Bouin's solution and dehydrated through a graded alcohol series, embedded in Histprep 568 (Wako Pure Chemical Industries, Ltd.) and cut serially at 7  $\mu$ m thickness. The sections were stained with Mayer's hematoxylin-eosin double stain for examination under a light microscope.

### Spawning induction experiment

The experiment on induction of spawning was carried out from 31 August to 6 September 1996. In 1996, few planktonic larvae were observed in Lake Abashiri. Twenty individuals were incubated in 10 L circular

containers with 6 L of salinity- adjusted water. Salinity was adjusted to 0.0 (tap water only), 1.2, 2.3, 3.4, and 4.5 psu (practical salinity units) with seawater and tap water. Salinity was measured by an inductivity coupled salinometer (Model 601 Mk 1 V, YEO-KAL Environmental Electronics, Sydney). The containers were kept in incubators, with temperatures adjusted to 21.5, 22.5, 23.5, 24.5 and 26.0 °C.

In half the groups, spawning was stimulated by adding 50 mL of gamete suspension from incubation water of groups previously spawned at 4.5 psu and 26 °C. Success or failure of spawning induction was determined after 36 hours of incubation. The success or failure was easily distinguished because the incubation water became turbid with the gametes released by spawning groups. In the dilution procedure, not only salinity but also food, nutrients or other substances might be changed in incubation water. I thought these changes would not affect the results because of the short duration of the experiments.

The results of the experiment were analyzed by logistic regression calculated by the maximum-likelihood method. Logistic regression is useful for analysis of binary data <sup>21)</sup>. The result of spawning induction was used as a binary dependent variable (i.e. a value of 1 was assigned to the each group in which spawning was induced and a value of 0 to a group without spawning). Temperature and salinity were used as continuous independent variables. Addition or exclusion of a gamete suspension was used as a categorical independent variable (i.e. a dummy variable of [1] was assigned to each group to which the gamete suspension was added and [2] was assigned to each group to which the gamete suspension was not added). A dummy variable is usually used in the logistic regression when a categorical variable is treated as an independent variable <sup>22)</sup>.

Two steps were applied to select independent variables for the logistic analysis. In the first, the main effects, i.e. temperature ( $T$ ), salinity ( $S$ ), adding gamete suspension ( $Gam$ ), and their combinations were used as independent variables (7 cases). The best combination of the main effects was selected by the Akaike Information Criterion (AIC). In the second, the interaction terms, i.e.  $T \times S$ ,  $S \times Gam$ ,  $T \times Gam$ ,  $T \times S \times Gam$ , and their combinations were added to the best combination of main effects (15 cases). The best model using both the main effects and the interaction terms was selected by the AIC.

The AIC was calculated as:  $AIC = -2 \times \ln(\text{maximum-likelihood}) + 2N$ , where  $N$  is the number of regression coefficients in the model. The AIC is useful for simultaneously comparing models with consideration for both maximum-likelihood and number of parameters<sup>23)</sup>. In the AIC, a difference of 1 or more is regarded as statistically significant<sup>24)</sup>. The equation of

the logistic regression used in this study was:  $f(T, S, Gam) = 1/(1+\exp(-g(T, S, Gam)))$ ,

where

$$g(T, S, Gam) = a_0 + a_1 T + a_2 S + a_3 Gam + a_4 T \cdot S + a_5 S \cdot Gam + a_6 T \cdot Gam + a_7 S \cdot Gam,$$

and  $a_i$  ( $i = 0$  to  $7$ ) are the regression coefficients, which are not simultaneously zero.

$f(T, S, Gam)$  represents the probability of spawning in *Corbicula japonica*.  $g(T, S, Gam)$  is a linear component of the regression equation representing a log-odds ratio between the probabilities of a positive response and no response to spawning induction.

### Salinity and larval development

Fertilized eggs obtained by the spawning induction experiment were incubated in water of the same salinity (i.e. 1.2, 2.3, 3.4, or 4.5 psu) at room temperature (21 to 23 °C) for 24 hours to determine whether the eggs could develop to the D-shaped veliger at each salinity. Twenty-four hours after spawning, the number of D-shaped veligers among about 300 swimming larvae at each salinity was counted. Results were analyzed by logistic regression with the maximum-likelihood method. The logistic regression is useful for analysis of ratio data<sup>21)</sup>. I did not feed the larvae during the experiment.

### Results

Occurrence of planktonic larvae in each year are shown in Table 1-1. Numbers in 1995 and 1996 were extremely low compared with the other years (1989, 1990, 1994 and 1997).

Histological changes in female and male gonads during the spawning season in 1995 and 1997 are shown in Fig. 1-2. The female genital tubules were filled with

Table 1-1 *Corbicula japonica*. Abundance of planktonic larvae during spawning season in Lake Abashiri.

Year (site)	Larval abundance (n/m <sup>3</sup> ± SD) (Sampling date)								
1989 (Stn 5)	0 (14Jun)	0 (13Jul)	612 (21Jul)	642 (7Aug)	1217 (21 Aug)	698 (31 Aug)	0 (11 Sep)		
1990 (Stn 5)	0 (21Jun)	0 (31Jul)	1390 (21Jul)	0 (9Aug)	1820 (24 Aug)	1656 (6Sep)	0 (23Sep)		
1994 (Stn 2)	91 (1Aug)	5832 (19Aug)	17694 (30Aug)						
1995 (Stn 2, 4)	0 (23Jul)	15 ±15 (3Aug)	2±2 (22Aug)	0 (6Sep)	0 (16Sep)				
1996 (Stn 2, 4, 5)	0 (12Jul)	0 (8Aug)	0 (12Aug)	7 ±2 (20 Aug)	0 (27 Aug)				
1997 <sup>a</sup> (Stn 1, 2, 3)	0 (15Jul)	26 ±21 (25Jul)	479 ±47 (1Aug)	603 ±655 (13 Aug)	3 ±2 (19 Aug)	74 ±46 (29Aug)	141 ±75 (9Sep)	95 ±40 (16Sep)	0 (3 Oct)

<sup>a</sup>Sampling was duplicated at each site

mature oocytes at the beginning of the spawning season in both 1995 and 1997 (Fig. 1-2A, C). After the spawning season in 1995, female genital tubules were filled with atretic oocytes (Fig. 1-2B), but in 1997, it was observed that the genital tubules were either vacant or contained some oocytes degenerated by phagocytosis (Fig. 1-2D, E). Tubules filled with the atretic oocytes were observed in all the females examined in 1995, but none in 1997. The characteristics of the atretic oocytes of *Corbicula japonica* observed in 1995 were that the nucleus lost its basophilic properties, the cytoplasm became clear, the oocytes appeared terminally empty, and finally the cell membranes ruptured.

The male genital tubules were filled with mature sperm at the beginning of the spawning season in both 1995 and 1997 (Fig. 1-2F, H). After the spawning season in 1995, the genital tubules were filled with intensive degenerating sperm cells (Fig. 1-2G), whilst in 1997 small degenerating cells were observed and few sperm remained (Fig. 1-2I, J).

Results of the spawning induction experiment are shown in Table 1-2. Spawning or sperm release was observed in most individuals of the spawned groups. The results of logistic regression are shown in Table 1-3, where only the best models for each set using the same number of independent variables are indicated as representative examples. Model-5, which used the 3 main effects ( $T$ ,  $S$ ,  $Gam$ ) and the 2 interaction terms ( $T \times S$  and  $T \times S \times Gam$ ), was the best in terms of AIC. Model-5 and model-6 were not significantly different in terms of AIC, but I selected model-5 as the best, because it showed the lowest AIC and used a lower number of independent variables. Model-5 was used to calculate the probability surfaces in Fig. 1-3.

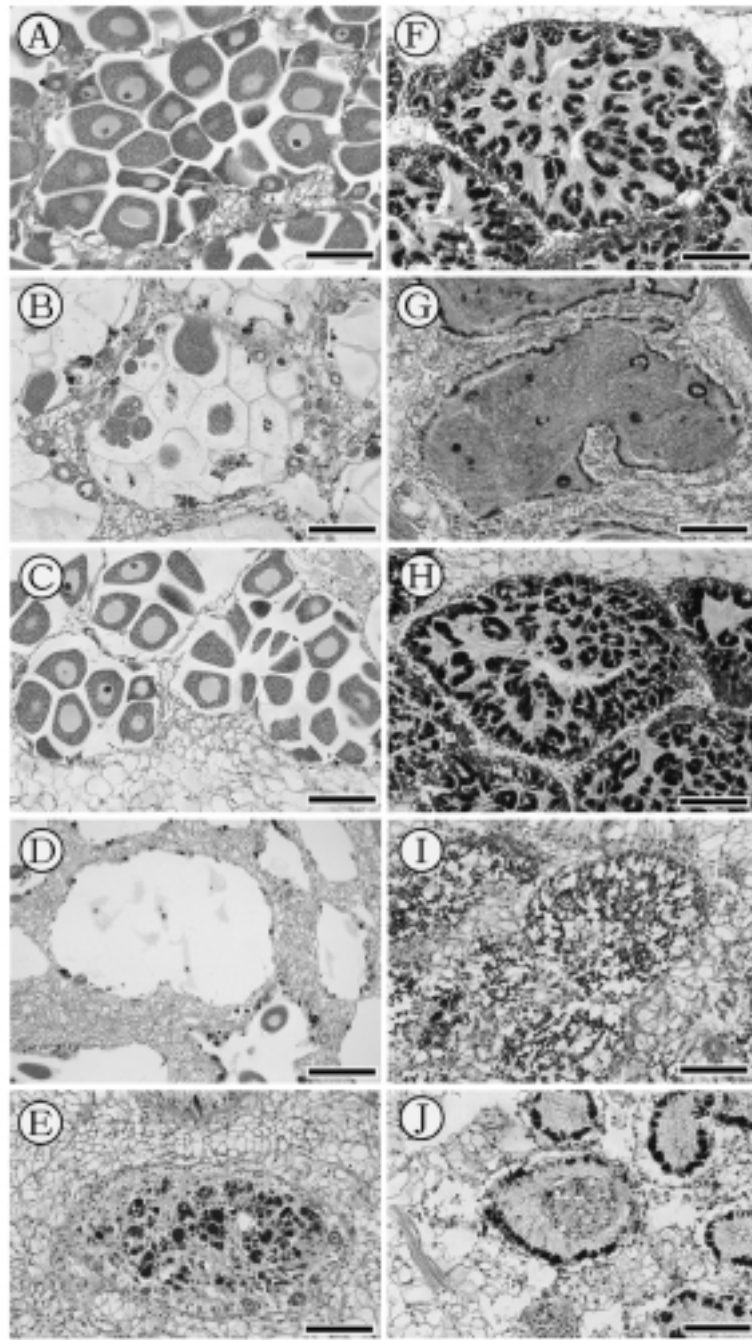


Fig. 1-2 *Corbicula japonica*. Histological changes in gonads of *Corbicula japonica* in 1995 and 1997 (A-E: Female, F-J: Male). (A) Female gonad at the beginning of the spawning season in 1995 (3 August) showing genital tubules filled with mature oocytes. (B) Female gonad after the spawning season in 1995 (13 October) showing genital tubules filled with atretic oocytes. (C) Female gonad at the beginning of the spawning season in 1997 (1 August) showing genital tubules filled with mature oocytes. (D, E) Female gonad after the spawning season in 1997 (24 October) showing empty genital tubules (D), and some oocytes degenerated by phagocytosis (E). (F) Male gonad at the beginning of the spawning season in 1995 (3 August) showing genital tubules filled with mature sperm. (G) Male gonad after the spawning season in 1995 (13 October) showing genital tubules filled with many degenerating sperm. (H) Male gonad at the beginning of the spawning season in 1997 (1 August) showing genital tubules filled with mature sperms. (I, J) Male gonad after the spawning season in 1997 (24 October) showing few sperm remaining in the genital tubules (I), or some degenerated sperm (J). Bars = 100  $\mu$  m

Table 1-2 *Corbicula japonica*. Results of spawning induction experiments. Values are number of spawning-induced groups/ number of experimental groups.

Gamete suspension added						Gamete suspension not added					
Salinity	Temperature (°C)					Salinity	Temperature (°C)				
(psu)	21.5	22.5	23.5	24.5	26.0	(psu)	21.5	22.5	23.5	24.5	26.0
4.5	0/1	1/2	2/2	1/1	2/2	4.5	0/1	0/2	0/2	0/1	0/2
3.4	0/1	1/2	1/2	1/1	2/2	3.4	0/1	0/2	0/2	0/1	2/2
2.3	0/1	0/2	2/2	1/1	2/2	2.3	0/1	0/2	0/2	1/1	2/2
1.2	0/1	0/2	1/2	1/1	2/2	1.2	0/1	0/2	0/2	1/1	0/2
0.0	0/1	0/2	0/2	0/1	0/2	0.0	0/1	0/2	0/2	0/1	0/2

Table 1-3 *Corbicula japonica*. Logistic regression results from spawning induction experiment. Only the best models using the same number of independent variables are shown. *T*: temperature (°C), *S*: salinity (psu), *Gam*: adding gamete suspension (dummy variable 1 or 2)

Model no.	Used independent variables	Regression coefficients								AIC	p
		a <sub>0</sub>	a <sub>1</sub>	a <sub>2</sub>	a <sub>3</sub>	a <sub>4</sub>	a <sub>5</sub>	a <sub>6</sub>	a <sub>7</sub>		
Main effect only											
1	<i>T</i>	-18.7	0.75							85.8	1.2 × 10 <sup>-5</sup>
2	<i>T, Gam</i>	-25.8	0.95		254					71.8	2.4 × 10 <sup>-8</sup>
3	<i>T, S, Gam</i>	-32.5	1.17	0.71	302					63.7	8.4 × 10 <sup>-10</sup>
Main effect plus interaction term											
4	<i>T, S, Gam, S × Gam</i>	-35.1	1.34	2.29	0.62			-1.08		60.8	3.4 × 10 <sup>-10</sup>
5	<i>T, S, Gam, T × S, T × S × Gam</i>	-15.6	0.57	-12.6	-0.55	0.69			-0.10	56.3	6.1 × 10 <sup>-11</sup>
6	<i>T, S, Gam, T × S, S × Gam, T × S × Gam</i>	-18.0	0.66	-25.3	-0.53	1.22		9.33	-0.48	57.1	1.2 × 10 <sup>-10</sup>
7	<i>T, S, Gam, T × S, T × Gam, S × Gam, T × S × Gam</i>	-14.7	1.03	-23.8	-6.76	1.16	-0.25	8.12	-0.43	59.0	3.9 × 10 <sup>-10</sup>

Occurrence of planktonic larvae, temperature and salinity during the spawning seasons, and the spawning probability calculated by model-5 with the dummy variable *Gam*=1 in 1994, 1995, 1996 and 1997 are shown in Fig. 1-4. The occurrences of the planktonic larvae are well corresponded with the spawning probabilities calculated by the model-5. I did not have such intensive environmental data for 1989 and 1990 so I excluded these years.

Some delay was observed from a peak in the spawning probability to a peak of larval occurrence in 1995, 1996 and 1997. Very high density of planktonic larvae was observed at the end of August in 1994. This high density corresponds to increased salinity from about 2.2 to 2.5 psu. The spawning halted in mid August 1997 due to decreased temperature and resumed at the end of August when temperature increased. The densities of planktonic larvae were very low in 1995 and 1996 during the spawning season.

The isopleths of the spawning probability (0.1, 0.25, 0.5, 0.75, 0.9) calculated by model-5 with the dummy variable *Gam*=1, the larval occurrences in Lake Abashiri, and the temperature and salinity (mean ± SD) of the surface of the upper stratum at the maximum temperature in the lake in past years are compared in Fig. 1-5. The maximum water temperature and the salinity in the upper stratum of the lake differ markedly from year to year. Maximum water temperatures ranged from 19 to 22 °C in cold summer years and from 26 to 28 °C in warm summer years. Salinity at the maximum temperature ranged from 6.5 to 0 psu.

The isopleths can be regarded as an environmental border range for the spawning of *Corbicula japonica*, because they explained the larval occurrences of past years. Unfavorable conditions for spawning are not exceptional and occurred in 10 out of 21 years for which data were available.

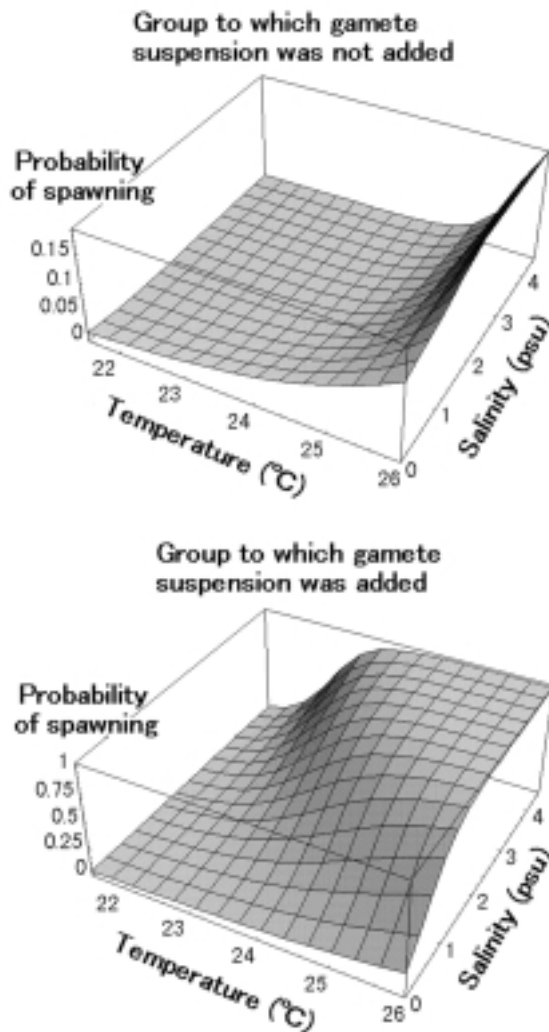


Fig. 1-3 Relationship between spawning probability, temperature and salinity in *Corbicula japonica* predicted by model-5 in Table 3. Upper panel shows the relationship between spawning probability, temperature and salinity of the groups to which the gamete suspension was not added (i.e. the dummy variable Gam =2 in model-5). Lower panel shows the relationship from groups to which the gamete suspension was added (i.e. the dummy variable Gam =1 in model-5).

Twenty-four hours after spawning, the mean percentages  $\pm 95\%$  confidence intervals of the D-shaped veliger at each salinity are shown with the probability estimated from the logistic regression in Fig. 1-6. The equation for the logistic regression was  $f(x) = 1/\{1+\exp[-(-6.42+2.37x)]\}$ , where  $x$  is salinity ( $p < 0.01$ ). The salinity at probability 0.5 of the logistic regression

was 2.7 psu. At 2.3 psu, 72.2 % of the swimming larvae did not reach the D-shaped veliger stage within 24 hours, and some were abnormal (swollen). Not only might their development have been delayed, but also some damage may have occurred at 2.3 psu. At 1.2 psu, most fertilized eggs developed to the morula stage 12 hours after spawning and many abnormal (swollen) blastulae were observed after 24 hours. No D-shaped veliger stage was observed at 1.2 psu.

## Discussion

Temperature and salinity appear to regulate spawning in *Corbicula japonica* (Table 1-3, Fig. 1-3). More spawning occurs when environmental conditions exceed the border range (isopleths of spawning probability from 0.1 to 0.9), especially when favorable conditions persist (Figs. 1-4 and 5). Much less spawning occurs when conditions do not exceed the border range (Figs. 1-4 and 5).

There is the potential that some of the interannual variation might be attributed to differences in sampling sites from year to year. In 1994, large numbers of planktonic larvae were observed in the central portion of Lake Abashiri, even though the habitat of *Corbicula japonica* is restricted to the margins. In 1995, 1996 and 1997, sampling was more intensive than in 1994. However, I found few planktonic larvae in 1995 and 1996. In 1997, there were fewer planktonic larvae than in 1994. Consequently, I believe my observations actually reflected the magnitude of population spawning in each year. Furthermore, Larval abundance seemed to be associated more with changes in the temperature and the salinity than the sampling location.

In years unfavorable for spawning, intensive oocyte atresia occurs in mature gonads of individuals after the spawning season. This is the first report of such intensive oocyte atresia in *Corbicula japonica*. Oocyte atresia is also regulated by environmental conditions in other marine bivalves such as *Pecten maximus*, in which the borderline water temperature is 15.5 to 16.0°C<sup>25, 26)</sup>. I observed oocytes degenerated by phagocytosis after the spawning season in 1997. Degeneration of oocytes by phagocytosis was also reported by Maru<sup>14)</sup>.

As shown in Fig. 1-4, there was some delay between a peak in the predicted spawning probability and a peak in larval abundance in 1995, 1996 and 1997. It takes about 1

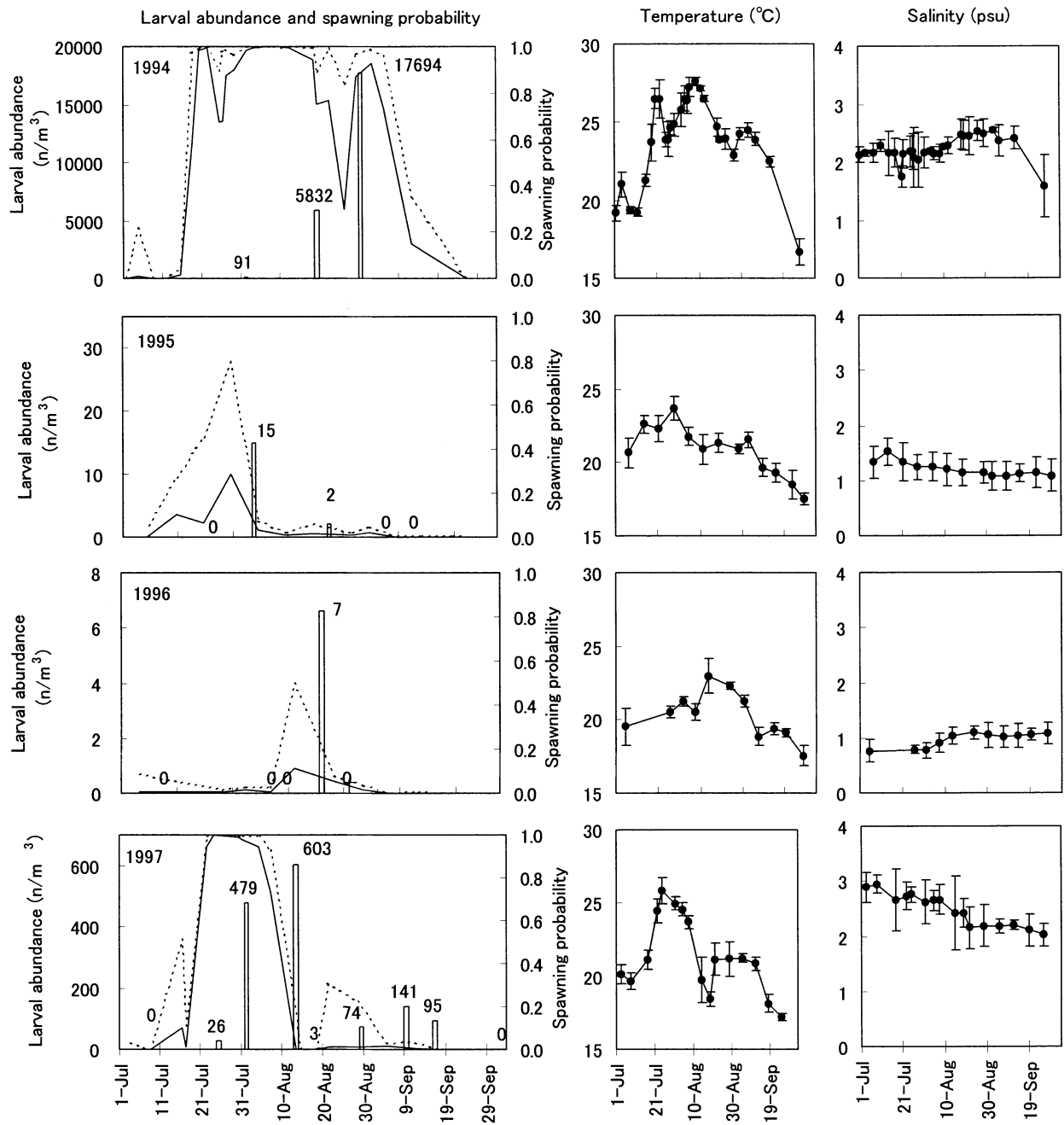


Fig. 1-4 Temperature and salinity changes (mean $\pm$ SD), larval abundance (bars), and spawning probabilities (solid and dashed lines) calculated from model-5 with dummy variable Gam=1, during spawning season from 1994 to 1997. Solid line is the spawning probability calculated from average temperature and salinity. Dashed line shows the maximum probability on each day.

days to reach the veliger stage after fertilization, and the planktonic phase is about 6 to 10 days in *Corbicula japonica*<sup>27)</sup>. The time required to pass through these phases may cause the observed delay.

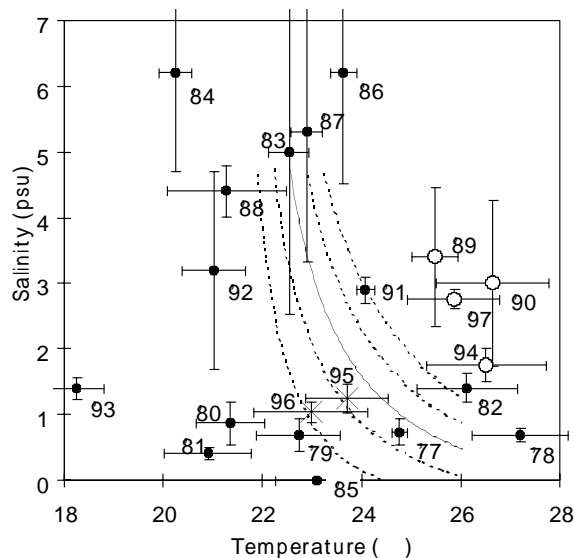


Fig. 1-5 Isopleths of spawning probability calculated from model-5 with the dummy variable  $Gam = 1$ , larval occurrence (○ abundant, × few, ● no data), and maximum surface temperature and salinity (mean  $\pm$  SD) of Lake Abashiri in past years. Solid line shows the probability 0.5, dashed lines show probabilities 0.9, 0.75, 0.25, 0.1 from upper right to lower left respectively. The number indicates each year.

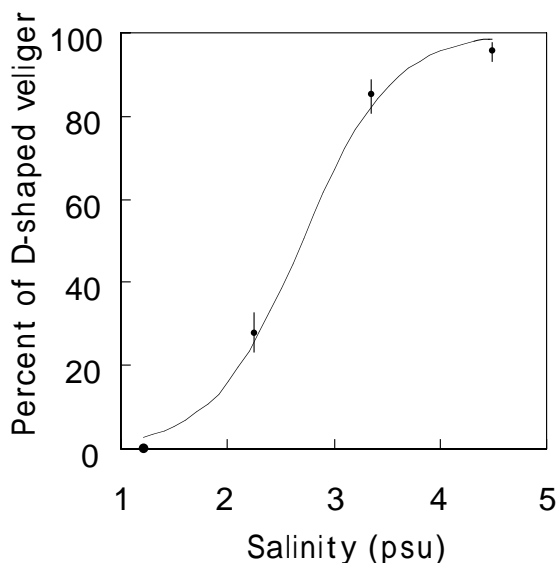


Fig. 1-6 Mean percentages  $\pm$  95 % confidence intervals of D-shaped veliger of *Corbicula japonica* 24h after spawning at each salinity and probability of the logistic regression.

In 1997, spawning seemed to cease in mid August when temperature declined, but then resumed when temperature increased. The magnitude of the second spawning event was greater than one might have expected from the spawning probability estimate (Fig. 1-4). Model-5 with the dummy variable  $Gam=1$  explained the timing of larval occurrences during the spawning season, but not the precise magnitude of the events. Perhaps time series models that include cumulative effects of environmental variables would be more useful in predicting the abundance of larvae.

In *Corbicula fluminea*, a fresh-water ovoviviparous hermaphroditic species, release of juveniles begins when temperature rises above 18 to 19 °C, but declines when temperatures rise above 26 °C<sup>7)</sup>. In *C. japonica*, a brackish-water oviparous dioecious species, spawning began at temperatures above 22 °C, and inhibition of spawning by high temperature was not observed (Figs. 1-3 and 4). This suggests *C. japonica* may be more adapted to high temperatures than *C. fluminea*.

In the spawning induction experiment, some groups spawned at salinities of 1.2 or 2.3 psu (Table 1-2, Fig. 1-3), but these salinities were insufficient for larval development (Fig. 1-6). Asahina<sup>13)</sup> reported that the development of the embryo could proceed at salinities from 3 to 28 psu in *Corbicula japonica*, and Sasaki<sup>28)</sup> reported that the range was from 0.6 to 6.1 psu. Neither study determined whether the embryo could reach the veliger stage. In my experiment, the salinity that guaranteed embryonic and larval development to the D-shaped veliger stage was 3.1 psu, and the value at which half of the swimming larvae reached the veliger stage was 2.7 psu (Fig. 1-6). Under natural conditions, many planktonic larvae were observed in 1994 in the low-salinity upper stratum of Lake Abashiri (Figs. 1-4 and 5). A large portion of the planktonic larvae were found near the boundary between the oligohaline upper stratum and the polyhaline lower stratum in 1997 (unpubl. data). These observations suggest that larvae of *C. japonica* may be capable of salinity-related movement. A salinity-related response at the larval stage has also been reported in the marine bivalve *Mercenaria mercenaria*<sup>29)</sup>.

A substantial increase in abundance of planktonic larvae occurred between 1 August and 19 August 1994 and corresponded to an increase in salinity from 2.2 to 2.5 psu. Although this salinity change may seem small, it

occurred within a range at which there was a steep slope in the relationship between salinity and percentage of D-shaped veliger 24 hours after spawning (Fig. 1-6), suggesting that small changes within this salinity range could have important effects on larval survival and development.

Unfavorable environmental conditions for spawning are not exceptional, and in fact were observed in about half the years studied (Fig. 1-5). Reproduction appears to succeed less frequently in northern than in southern populations of *Corbicula japonica*, because the necessary environmental conditions for spawning depend heavily on temperature.

## CHAPTER II

### Pre-settlement processes in planktonic larva of the brackish water bivalve *Corbicula japonica* in Lake Abashiri

#### Abstract

I found the vertical heterogeneities of the planktonic larva (D-shaped veliger) densities and shell length compositions of *Corbicula japonica* in water column. A large portion of smaller size planktonic larvae (shell length 140 to 170  $\mu$ m) were observed near the boundary between a well-oxygenated oligohaline upper stratum and an anoxic polyhaline lower stratum (depth about 6 m). On the other hand, most of larger planktonic larvae (shell length 170 to 200  $\mu$ m) were observed near the surface of the lake (depth 0.2 m). To confirm the size of competent settling stage and the postponement of planktonic phase, I carried out an incubation experiment of the planktonic larvae under laboratory conditions. As the results, the planktonic larva reached the competent settling stage at the shell length of around 160  $\mu$ m. The planktonic larva postponed their planktonic phase from 3.6 days to 4.4 days or from 6.3 days to 8.8 days when the bottom was changed from sand to seawater. From these results and my previous reports (Chapter I in this thesis), I hypothesized the pre-settlement processes in the planktonic larva of *C. japonica*. First, the early-stage planktonic larvae assemble to the higher salinity zone, which formed near the boundary to gain the sufficient salinity for the larval developments. Second, the well-developed larvae migrate to near the surface, where

higher possibility of being transported to the favorable habitat for the larval settlement is expected. These pre-settlement processes probably enhance the survival of the salinity-sensitive planktonic larvae in the specific environment of brackish-water lakes.

#### Introduction

*Corbicula* spp. are harvested commercially in Japan. The annual catch ranged from 24,000 to 27,000 ton in 1994-1996<sup>9)</sup>, among which *Corbicula japonica*, a brackish-water oviparous dioecious species, was the main species. *C. japonica* is distributed in brackish water lakes and tidal flats of rivers from the south of Japan to the south of Sakhalin<sup>16)</sup>.

Lake Abashiri has a well-oxygenated oligohaline upper stratum and an anoxic polyhaline lower stratum because seawater flows back into the lake through 7.2 km of the Abashiri River depending to the tide. The salinity of the surface and the boundary depth between the two strata change from year to year, and they range from 0.0 to 7.0 psu (psu, practical salinity unit) and from 5 to 7 m respectively in recent years<sup>17, 30)</sup>. Therefore, the habitat of *C. japonica* is restricted to the marginal area of the lake, shallow than about 5 m.

Baba et al.<sup>30)</sup> reported spawning probability of *C. japonica* was expressed by the equation:

$$1 / \{ 1 + \exp[-(-15.6 + 0.57T - 12.6S - 0.55Gam + 0.69T \cdot S - 0.10T \cdot S \cdot Gam)] \},$$

(*T*: temperature; *S*: salinity; *Gam*: dummy variable of 1 or 2, i. e. 1 designated each group to which the gamete suspension was added and 2 each group to which the gamete suspension was not added), and this equation with *Gam*=1 can explain occurrences of the planktonic larvae in Lake Abashiri.

They also reported the probability to be D-shaped veliger 24h after spawning in *C. japonica* was expressed by the equation:

$$1 / \{ 1 + \exp[-(-6.42 + 2.37S)] \}$$

where *S* is Salinity. Figure 2-1 shows these two equations, the first equation with *Gam*=1 and the second equation. In the Fig. 2-1, the salinity was classified to three ranges for the larval development, i. e. lethal, limiting and non-limiting, according to Yamamuro et al.<sup>31)</sup> in which these three ranges were proposed for a function expressing a limiting effect of an environmental factor to a macrobenthos. I used probability 0.05 and 0.95 as border points for the classification. As shown in Fig. 2-1, the spawning probability reaches maximum within the



limiting salinity range for the larval development.

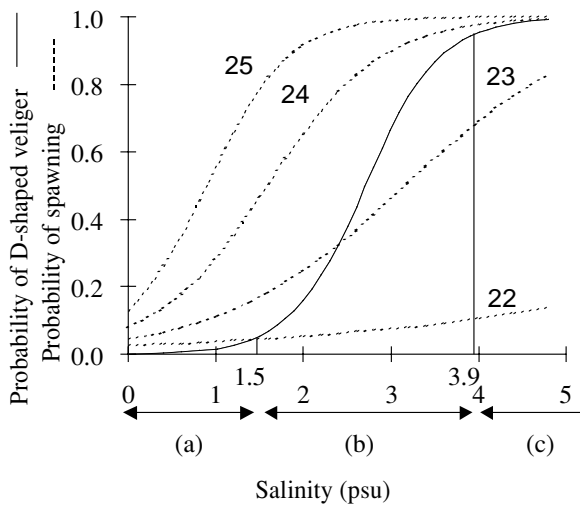


Fig. 2-1 Relationships between salinity and the probability of the D-shaped veliger 24h after spawning (solid line) and relationships among salinity, temperature and the spawning probability (dashed line) in *Corbicula japonica* (Baba et al. 1999). Vertical lines show the salinity at the probability 0.05 (right) and 0.95 (left) of the D-shaped veliger. (a), (b), (c), ranges for the larval development; (a), lethal; (b), limiting; (c), non-limiting.

The anoxic polyhaline lower stratum covers about 78 % of the lakebed in Lake Abashiri. On the other hand, the planktonic larvae of *C. japonica* were observed in most the well-oxygenated oligohaline upper stratum<sup>32)</sup>.

Two questions were arisen from these previous reports. First, when *C. japonica* spawns in the limiting salinity range for the larval development, whether high mortality occurs on the planktonic larvae or the planktonic larvae have some mechanisms to alleviate the bad effects of the low salinity? Second, whether most the planktonic larvae locate above the anoxic polyhaline lower stratum die or the planktonic larvae have some behavior to enhance survivability? To answer these questions, I investigated the vertical change of the planktonic larvae distribution and environments at the midst of spawning season in 1997 and I confirmed postponement of planktonic phase and shell lengths in which *C. japonica* become the competent settling stage in a laboratory experiment.

## Materials and Methods

### Vertical distribution of planktonic larvae

Samplings of planktonic larvae were carried out at the central part of the lake in the daytime on August 7, 1997 (Fig. 2-2). Two hundreds litter ( $0.2 \text{ m}^3$ ) of waters were pumped up from each depth of 0.2, 2, 4, 5, 6 and 6.8 m. The waters were filtrated with a plankton net NXX-13 (mesh:  $95 \times 95 \mu\text{m}$ ). The sampling was duplicated at the each depth. The samples had been fixed with 3 % neutralized formalin. The planktonic larvae were sorted and counted under a binocular microscope. The shell lengths of the planktonic larvae were measured under a profile projector (V-12, Nikon Ltd.) with 100 magnitude using a digital caliper (Digimatic caliper, Mitutoyo Ltd.).

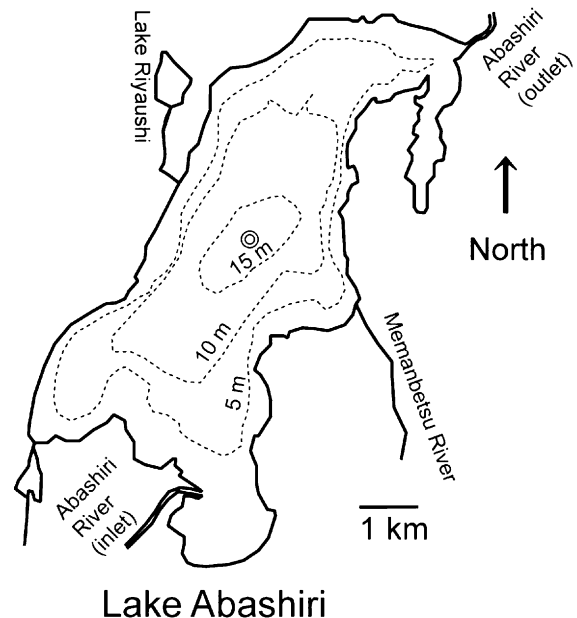


Fig. 2-2 Location of sampling site (○) in Lake Abashiri.

### Environmental data

Salinities (psu, practical salinity unit), water fluorescence (equivalent to uranin density,  $\mu\text{g/L}$ ), turbidity (ppm, equivalent to kaoline density) and temperatures ( $^{\circ}\text{C}$ ) with interval of 0.1 m depth were obtained from unpublished data of Abashiri Local Office of Hokkaido Development Bureau. The environmental factors were measured by Memory Chlorotec (ACL-1180-OK, Alec Electronics Ltd.). The environmental factors were measured at the same site and the same day as the larval sampling.

### Incubation experiment of planktonic larvae

Spawning was induced at 25 °C and 4 psu with 30 individuals, which have shell lengths from 20 to 30 mm, in 10 L circular containers. Twenty-four hours after spawning, 1 L of incubation waters, which contain veliger stage of *C. japonica*, were transferred to six aquariums (L × W × H, 585 × 280 × 340 mm) with 35 L of 4 psu incubation waters. The salinity of the incubation waters was adjusted by tap water and seawater. One day after start of incubation, the average density of the veliger was 4.1 ind./ mL. Before transfer the veliger, sand were laid on the bottom of the two aquariums (sand bottom group). Median diameter, skewness and kurtosis of the sand are 0.87 mm, 1.28 and 2.26 respectively. After transferred the veliger, 10 L of seawaters were calmly poured under the incubation water of the four aquariums with a rubber hose (seawater bottom group). Forty mL of a solution which contain about 107 cells / mL of *Pavlova lutheri* was added to the each aquarium everyday as foods for the larvae. Very little aeration had been performed at the surface of incubation water during the experiment. The incubation experiments were carried out under the room temperature (from 24 to 26 °C).

Sixty-five mL of incubation water was sampled from each aquarium everyday. The samplings were conducted with a 10 mm diameter glass tube with following methods. The tube was vertically inserted into the incubation water from the surface to the bottom of the aquarium, the top of the tube was sealed with a silicon rubber, and then water inside of the tube was harvested. These procedures were replicated four times at different sites of the each aquarium to minimize sampling error. The samples had been fixed with 3 % neutralized formalin. The planktonic larvae were sorted and counted under a binocular microscope. The shell lengths of the planktonic larvae were measured under a profile projector (V-12, Nikon Ltd.) with 100 magnitude using a digital caliper (Deigimatic caliper, Mitutoyo Ltd.).

Density (ind./65 mL) changes of the planktonic larvae were analyzed by logistic regression calculated by maximum-likelihood method. The logistic regression is useful for analysis of proportion <sup>21)</sup>. Two types of equations were fitted to the density changes of the each group. The equations were as follows:

$$f(t)=1/\{1+\exp[-(a_1+a_2t)]\} \text{ (model-1) and}$$

$$f(t)=a_0/\{1+\exp[-(a_1+a_2t)]\}+(1-a_0)/\{1+\exp[-(a_3+a_4t)]\}$$

(model-2)

where  $f(t)$  = (planktonic larvae densities  $t$  days after spawning)/(initial planktonic larvae density),

$t$  = days after spawning

$a_0, a_1, a_2, a_3, a_4$  = coefficients of the equation ( $0 \leq a_0 \leq 1$ ).

The log-likelihood function for the both equations is as follow:

$$\log L = \sum_{t=ini}^{end} D_t \times \log ( f ( t ) )$$

$$+ \sum_{t=ini}^{end} ( D_{ini} - D_t ) \times \log ( 1 - f ( t ) ),$$

where  $ini$  = initial day of larval density calculation,  $end$  = end day of larval density calculation,  $D_t$  = larval density  $t$  days after spawning.

The coefficients ( $a_0, a_1, a_2, a_3, a_4$ ) were estimated as values that maximize the log likelihood. A day in which the maximum larval density was recorded was set as the initial day of the density calculation ( $ini$ ). The initial day was two in the sand-bottom group and three in the seawater-bottom group respectively. A day in which the zero larval density was recorded was set as the end day of the larval density calculation ( $end$ ). The end day was 8 in the sand-bottom group and 12 in the seawater-bottom group.

## Results

Vertical changes of the planktonic larvae abundances and the environments are shown in Fig. 2-3. These mean abundances were significantly different for the total data set in SS-STP (SS-STP, sum of squares simultaneous test procedure;  $p < 0.01$ ). Shell length composition of the each depth is shown in Fig. 2-4. These shell lengths were significantly different among the groups in Kruskal-Wallis test ( $p < 0.01$ ). A large portion of smaller size planktonic larvae (shell length 140-170  $\mu$  m), about 65 % of total number of the smaller size larvae in the samples, distributed at a depth of 6 m near the boundary between the well-oxygenated oligohaline upper stratum and the anoxic polyhaline lower stratum. The salinities drastically increased between the depth of 5 m and 6 m. The salinity at the depth 6 m reached the non-limiting range for the larval development. On the other hand, a large portion of the larger size planktonic larvae (shell length 170-200  $\mu$  m), about 77 % of total number of the larger size larvae in

the samples, distributed at a depth of 0.2 m, where salinity was lower than deeper sites.

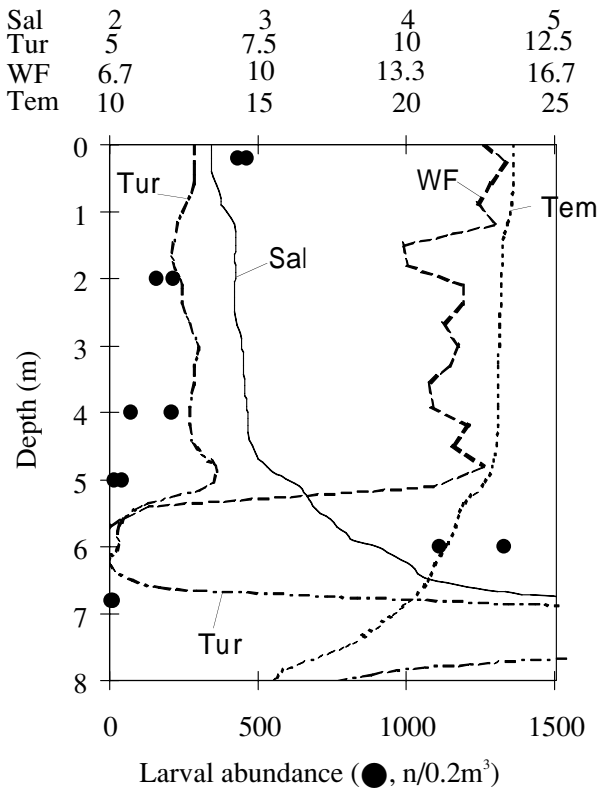


Fig.2-3 Vertical changes of the planktonic larvae abundance of *Corbicula japonica* and environmental factors at the sampling site. The larval abundances were shown by ● (n/0.2m³). Each line showed the change of the environmental factor. Sal, Salinity (psu)(Solid line); Tur, Turbidity (mg/L) (chain line); WF, Water fluorescence (equivalent to uranin  $\mu$ g/L)(long dashed line); Tem, Temperature (°C)(dashed line).

Density changes of the planktonic larvae and probabilities of the logistic regression during the planktonic larvae incubation experiment are shown in upper panel of Fig. 2-5. The results of logistic regressions are shown in Table 2-1. The model-2 was significantly better than the model-1 for the both sand-bottom and seawater-bottom groups with likelihood ratio test (Table 2-1). The slopes of the model-2 of the both groups are shown in lower panel of Fig. 2-5. In the sand bottom group, 78 % of the planktonic larvae settled around 3.6 days after spawning and 28 % of them settled around 6.3 days after spawning. On the other hand, 52 % of the planktonic larvae settled around 4.4 days after spawning and 48 % of them settled around 8.8 days after spawning in the seawater bottom group. The planktonic larvae postponed their planktonic phase from 3.6 to 4.4 and from 6.3 to 8.8 days when the bottom conditions were not suitable for the settlement.

Changes of the shell length composition during the experiment are shown in Fig. 2-6. Two days after spawning, the shell lengths and their variances were not significantly different between the two groups (shell length,  $p > 0.05$  in Kruskal-Wallis test; variance,  $p > 0.05$  in Bartlett's test). Three to seven days after spawning, the shell lengths were significantly different between the two groups ( $p < 0.01$  in Kruskal-Wallis test). *Corbicula japonica* seemed to become the competent settling stage at shell lengths from 155 to 165  $\mu$ m because few individual with shell lengths more than 165  $\mu$ m was observed in the sand bottom group and some individuals with shell lengths 155-160  $\mu$ m were inferred as the planktonic phase postponing individuals in the seawater bottom group (Fig. 2-6).

Table 2-1 Results of modified logistic regression from larval incubation experiment in *Corbicula japonica*.

Model	Regression coefficients					AIC	p	Likelihood ratio
No.	a1	a2	a3	a4	a5			test
Sand bottom group								
1	5.94	-1.41				2623.0	<0.001	
2	18.79	-2.97	11.96	-3.29	0.22	2448.7	<0.001	**
Seawater bottom group								
1	4.23	-0.66				9920.4	<0.001	
2	11.61	-1.32	8.73	-1.98	0.48	9640.3	<0.001	**

\*\*: significantly better model with  $p < 0.001$

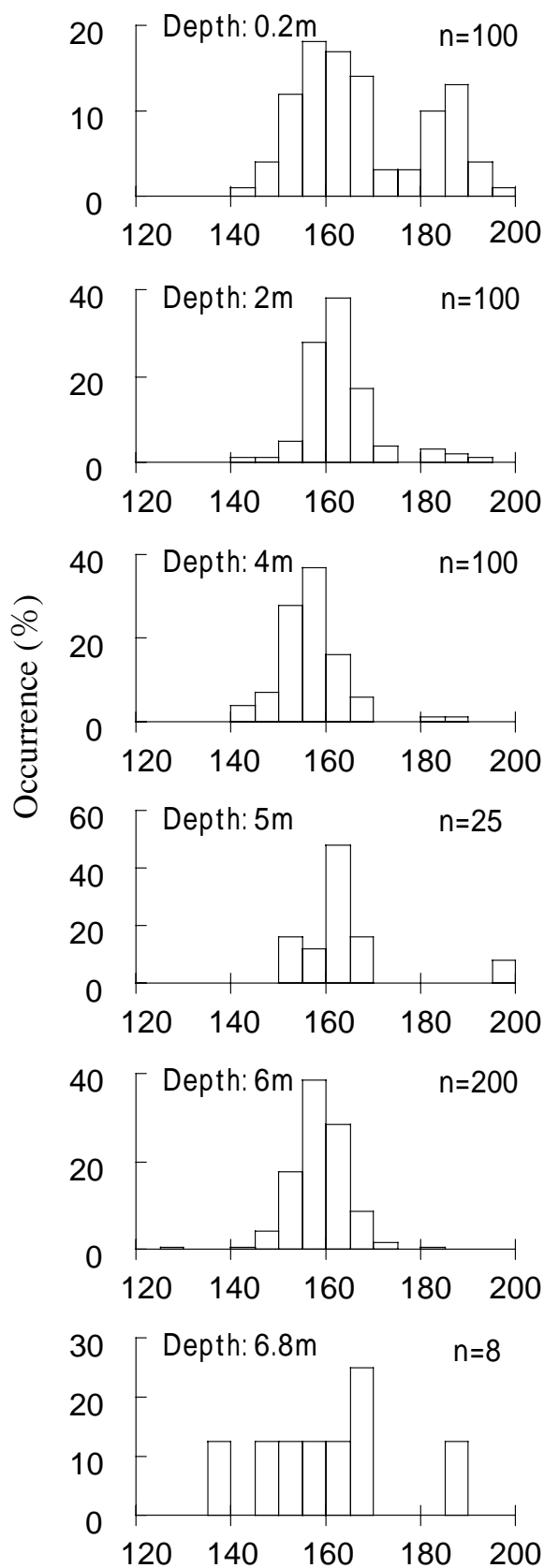


Fig. 2-4 Vertical change of shell length compositions of the planktonic larvae of *Corbicula japonica*. n, number of measured individuals.

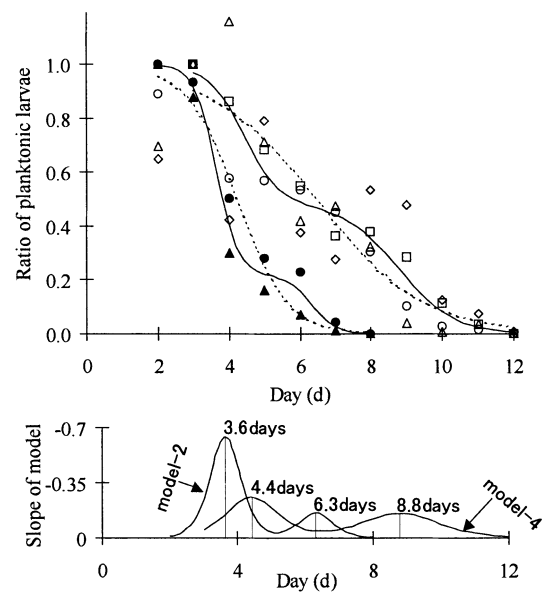


Fig. 2-5 Density changes of the planktonic larvae of *Corbicula japonica* during the planktonic larvae incubation experiment (upper panel). Filled marks (●) represent ratios between planktonic larvae densities at t days after spawning and the planktonic larvae density at the initial day of the density calculation (2 days after spawning) in the sand bottom group. Blank marks (○) represent ratios between planktonic larvae densities at t days after spawning and the planktonic larvae density at initial day of the density calculation (3 days after spawning) in the seawater bottom group. Vertical lines represent standard deviations. Solid lines show the model-2 in the Table 2-1. Lower panel shows the slopes of the model-2.

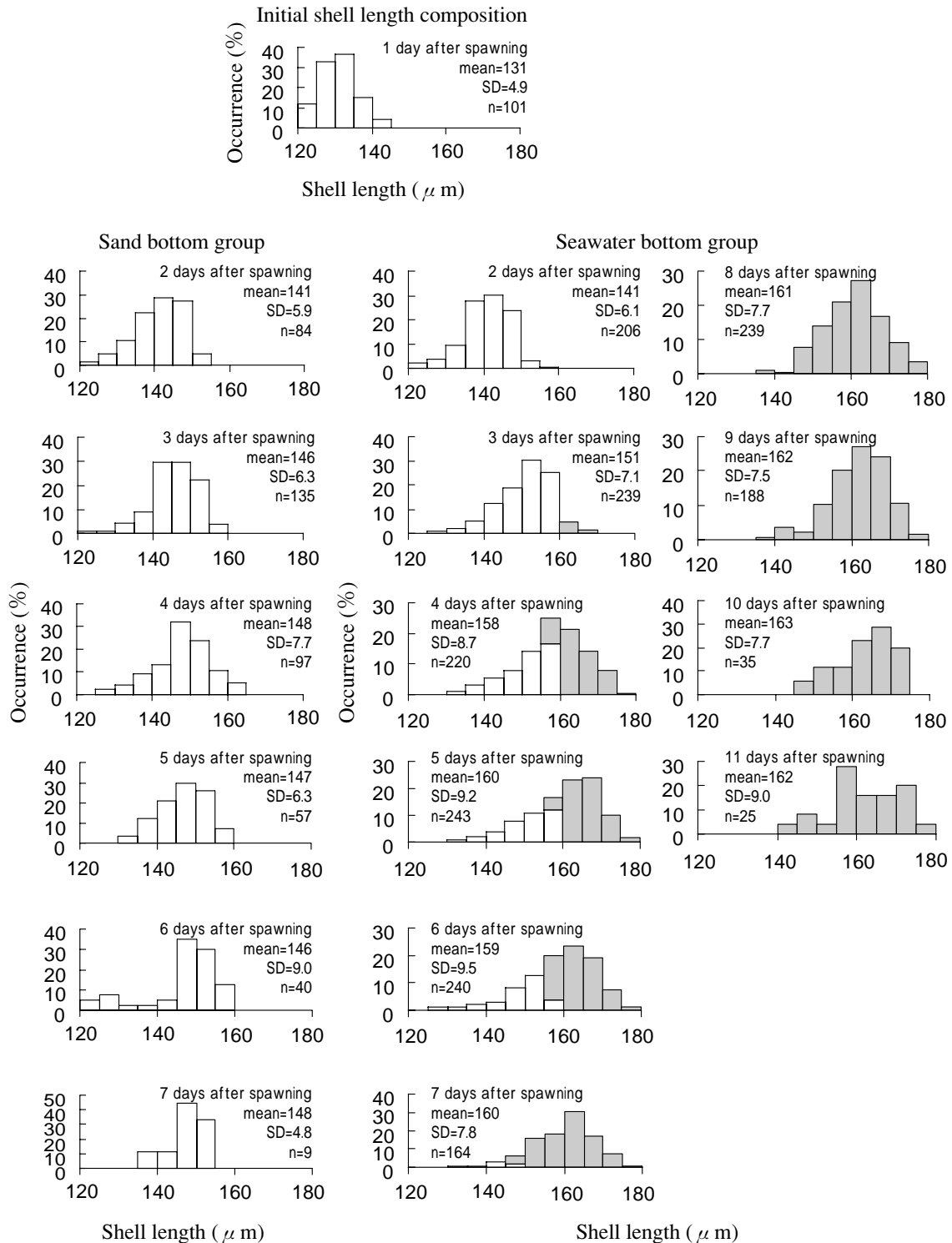


Fig. 2-6 Changes of shell length compositions of *Corbicula japonica* during the planktonic larvae incubation experiment. The top panel shows the initial shell length composition, the shell length composition at one day after spawning. The filled bars show the planktonic phase postponing individuals inferred by the differences of the shell length compositions between the two groups. n, number of measured individuals.

## Discussion

I schematized my hypothesis on the pre-settlement processes of *Corbicula japonica* in Fig. 2-7. I thought the early stage planktonic larvae assembled to near the boundary to gain sufficient ambient salinity for the larval development, i. e. the planktonic larvae have a mechanism to alleviate bad effects of the low salinity when *C. japonica* spawned in the limiting salinity range for the larval development. This behavior is important as one of the pre-settlement processes because Baba et al.<sup>30)</sup> reported the spawning probability reaches maximum within the limiting salinity range for the larval development to D-shaped veliger (Fig. 2-1). As shown in Fig. 2-3, water fluorescence and turbidity drastically declined at around the depth of 6 m than the shallower depths. Therefore, the food availability was not factor for the assemblage of the smaller planktonic larva. I thought the salinity was probably the most important factor that induces the assemblage of the early stage planktonic larvae.

Most the larger size planktonic larvae were observed near the surface of the lake, where the salinities were lower than the deeper sites (Fig. 2-3, Fig. 2-4). In Lake Abashiri, about 78 % of the lakebed is covered by the anoxic polyhaline lower stratum, whereas planktonic larvae of *C. japonica* are observed in most the well-oxygenated oligohaline upper stratum<sup>32)</sup>. In the lake, the migration toward the surface probably enhances the survival of the planktonic larvae. Larger disturbance is expected at the surface than deeper sites because the surface is more influential area of winds than deeper sites. The larger disturbance increases the chance to be transported to marginal area of the lake where sediments are not covered by the anoxic polyhaline lower stratum. The upward migration probably prolongs postponement of the planktonic phase more than it observed in the larvae incubation experiment because many planktonic larvae with shell lengths from 180 to 200  $\mu\text{m}$  were observed near the surface of the lake whereas the maximum shell length in the planktonic phase postponing individuals of the experiment were less than 180  $\mu\text{m}$  (Fig. 2-4 and Fig. 2-6). The postponement of the planktonic phase also increases the chance to be transported to the marginal area of the lake.

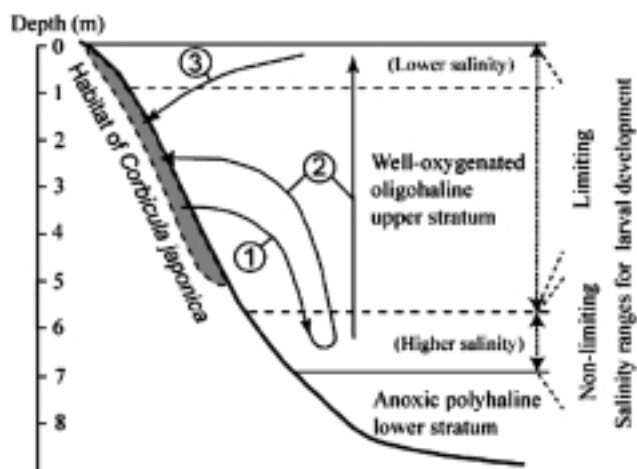


Fig. 2-7 Schematization of my hypothesis on the pre-settlement processes of *Corbicula japonica* when *C. japonica* spawned in the limiting salinity range for the larval development. First, the early stage planktonic larvae assemble the higher salinity zone, the nursery zone, to gain sufficient salinity for the larval development because the spawning probability reached maximum within the limiting salinity range for the larval development (Fig. 2-1, Fig. 2-3, Fig. 2-4). Second, the later stage planktonic larvae migrate upward may due to change of salinity preferences after they acquired tolerance to the low salinity. When the larvae encountered the favorable sediments for the settlement during the upward migration, the larvae would settle. When the larvae did not encounter the favorable sediments, the planktonic phase would be postponed and the larvae grow up to 200  $\mu\text{m}$  at the surface of the lake. Third, the location of the larger size planktonic larvae (shell length 170-200  $\mu\text{m}$ ) at the surface may increase their chance to be transported to the habitat of *C. japonica*, the marginal area of the lake, because larger diffusion is expected at the surface than deeper sites due to influences of winds. When the larger size planktonic larvae were transported to the marginal area, the larvae would settle.

I thought the most possible factor that induces the upward migration of the larger size planktonic larvae is salinity, i. e. *C. japonica* changes its responses from salinity-positive in the early stage planktonic larvae to salinity-negative in the later stage after they acquire tolerance to the low salinity. The salinity difference

between the depth of 0.2 (2.7 psu) and 2 m (2.9 psu) may seem small. However, I thought *C. japonica* is sensitive to the range because it occurred within a range at which there was a steep slope in the relationship between salinity and the probability of D-shaped veliger (Fig. 2-1). The planktonic larvae of *C. japonica* do not have pallial eye, therefore, photo stimuli is probably not a factor for the upward migration. Salinity-related responses at larval stages have also reported in some marine bivalves<sup>29,33</sup>.

These distribution changes between the early stage and the later stage planktonic larvae of *C. japonica* were quite different from previous reports in marine bivalves. The early stage planktonic larvae of some marine bivalves swim upward as photopositive and/or geonegative and then the later stage larvae swim downward as photonegative and/or geopositive response<sup>29,33</sup>. If I attributed the distribution changes in the planktonic larvae of *C. japonica* to the change of the salinity preference, the differences between *C. japonica* and the marine bivalves can be explained. Few planktonic larvae were observed at the depth of 6.8 m (Fig. 2-3). The anoxic conditions might become crucial at the depth.

The shell lengths just after spawning were 120-145  $\mu$  m (Fig. 2-6). On the other hand, few planktonic larvae with shell lengths less than 140  $\mu$  m was found at the central part of the lake (Fig. 2-4). I thought it took more than 3 days to be diffused from *C. japonica* habitat to the central part because the planktonic larvae reached shell lengths from 140 to 160  $\mu$  m at three days after spawning in the planktonic larvae incubation experiment (Fig. 2-6).

In the planktonic larvae incubation experiment, 78 % of the planktonic larvae settled around 3.6 days after spawning and 28 % of them settled around 6.3 days after spawning in the sand bottom group (Fig. 2-5). On the other hand, 52 % of the planktonic larvae settled around 4.4 after spawning and 48 % of them settled around 8.8 days after spawning in the seawater bottom group (Fig. 2-5). I could not find the factor, among experiment conditions, which caused the two phases of the settlements.

There are three species of *Corbicula*; *C. japonica*, *C. sandai* and *C. leana*, in Japan. *C. japonica* is a brackish-water oviparous dioecious species inhabiting in brackish water lakes and tidal flats of rivers from Hokkaido to Kyushu. *C. sandai* is a fresh-water oviparous dioecious species endemic to Lake Biwa and its water system. *C. leana* is a fresh-water viviparous hermaphroditic

species inhabiting rivers and ponds from Honshu to Kyushu. It was reported that *C. japonica* diverged from the ancestral species first and *C. sandai* and *C. leana* subsequently differentiated from each other<sup>3,4,5</sup>. *C. japonica* hatches out at blastula stage<sup>13</sup> and needs substantial salinity for the development to be the D-shaped veliger (Fig. 2-1). On the other hand, other *Corbicula* species have different systems of larval developments. *C. sandai* hatches out at stage of D-shaped larvae<sup>34</sup>. *C. leana* hatches out and is incubated until pediveliger in the inner demibranchs<sup>35,36,37</sup>. *C. sandai* and *C. leana* probably acquired their reproductive system to adapt fresh water environment, i. e. low salinity, during the phylogenic processes.

The anoxic polyhaline lower stratum has been dealt as an abominable existence in brackish water lakes. Because sometimes upwelling of the anoxic polyhaline water are caused by strong winds, and the temporal anoxic conditions caused by the upwelling kill fishes and shrimps inhabiting in the well-oxygenated oligohaline upper stratum<sup>17,18</sup>. On the contrary, I thought the polyhaline lower stratum has two important roles for the recruitment of *C. japonica*. First, it forms a nursery zone, i. e. a higher salinity zone, for the early stage planktonic larvae near the boundary between the oligohaline upper stratum and the polyhaline lower stratum. Second, the polyhaline stratum is one of the main sources for providing salinity to upper stratum via the upwelling caused by strong winds<sup>18</sup>. The substantial salinity is needed for the spawning and the larval development in *C. japonica*.

## CHAPTER III

### Favorable sediment environments for juveniles of the brackish water bivalve *Corbicula japonica* in Lake Abashiri

#### Abstract

To determine the favorable sediment environments for juveniles of the brackish-water bivalve *Corbicula japonica*, the relationship between the presence of juveniles and limiting factors of the sediment environment that are negatively correlated with juvenile density was investigated in Lake Abashiri, one of the northernmost areas of this bivalve's distribution in Japan. Correlations between

juvenile density and sediment factors were estimated by Spearman's rank correlation coefficient. Logit models were made between the presence or absence of juveniles, as the dependent variable, and limiting sediment factors, as independent variables. The models were compared by the Akaike Information Criterion (AIC). The values at probability 50 % of the logit models (V50s) and the standard errors of the univariate logit models were calculated for each sediment factor. I defined favorable sites as those where any of these values are less than the V50s, which seem to provide good criteria to distinguish between favorable and unfavorable sediment conditions for juveniles. The V50s for limiting factors were: organic carbon 1.10 %, organic nitrogen 0.15 %, organic carbon/nitrogen ratio 7.43, ignition loss 4.45 %, water content 40.97 %, and silt-clay (particle diameter < 0.063 mm) plus very fine sand (0.063 - 0.125 mm) 36.88 %. A significant logit model could not be made for total sulfide. These criteria may provide important information for the management of *C. japonica* resources.

### Introduction

The brackish-water bivalve *Corbicula japonica* is distributed in brackish lakes and tidal flats of rivers in Japan and Sakhalin<sup>16)</sup>. Lake Abashiri is one of the northernmost areas of its distribution in Japan. *Corbicula* spp. are commercially harvested in Japan. The annual catches ranged from 24,000 to 37,000 tons during 1990-1994<sup>9)</sup>, among which *C. japonica* was the dominant species.

The influence of environmental factors on the physiology of *C. japonica* has been studied, including temperature tolerance<sup>38)</sup>, salinity tolerance in adults<sup>27, 38)</sup>, salinity tolerance in juveniles<sup>39)</sup>, sulfide tolerance<sup>40)</sup>, tolerance to anoxic conditions<sup>41)</sup>, metabolic changes due to lack of oxygen<sup>42)</sup>, salinity effect on larval development<sup>13)</sup>, and free amino acid uptake<sup>43)</sup>. However most of these were based on laboratory experiments.

In the fisheries management of brackish-water clams, it would be convenient to be able to assess whether the environmental conditions of a given site are suitable for the clams. In my preliminary analysis, I could not gain sufficient results with commonly used, and ordinary statistical methods such as multiple-regression analysis, principal component analysis, and their combinations, because they showed only non-significant differences and

sometimes did not fulfill the assumptions inherent in a regression analysis, e. g. unbiasedness or homoscedasticity. Transformations were not sufficient to ensure such preconditions were met.

Yamamuro et al.<sup>31)</sup> reported the lethal factors of *C. japonica* in Lake Shinji, western Japan, based on field data. They suggested that the function expressing the limiting effect of each environmental factor ought to be S-shaped, take a positive value between 0 and 1, and be characterized by three ranges: lethal, limiting, and non-limiting. However, in fisheries management I would rather know simply whether the sediment environment is favorable or unfavorable for the clam, because fishermen could then avoid the areas with lethal environments. Therefore, I adopted logit models in the present study; they are similar to the function proposed by Yamamuro et al.<sup>31)</sup>, but can be treated more easily.

In this study, I employed logit models to analyze the relationships between juvenile presence and sediment variables and to clarify which sediment conditions are favorable for *C. japonica*. Understanding the favorable conditions is very important for the management of fisheries grounds and it also facilitates judgements about which sites are appropriate for the release of seed clams. My report is probably the first one demonstrating criteria for judging whether sediment conditions are favorable for juvenile *C. japonica*.

### Materials and Methods

The field investigation was carried out on October 13, 1995, in Lake Abashiri, Japan. The lake is connected to the Sea of Okhotsk by the 7.2 km long Abashiri River. Since sea water flows back into the lake depending on the tide, the lake has a well-oxygenated, oligohaline upper layer and an anoxic, polyhaline lower layer, with a boundary at a depth of around 5 m<sup>18)</sup>; *C. japonica* is restricted to the area above this boundary.

Sediment samples were collected from 32 sites laid out along seven lines (L1 to L7) at depths of 1, 2, 3, 4, and 5 m, except L5 which was sampled only at depths of 1, 2, and 3 m (Fig. 3-1). No sample was collected at a depth of 1 m along L 3 because the sediment was rocky.

A Smith-McIntyre grab was used to collect 0.05 m<sup>3</sup> sediment samples twice at each site. The sediment in the first grab was washed on a 1 mm sieve, and *C. japonica* was sorted from the residue. The sediment in the second



grab was weighed, and about 1/10 of it was washed on a series of four sieves from 0.125 to 1 mm to sort the juveniles. Sorting was completed with a binocular microscope.

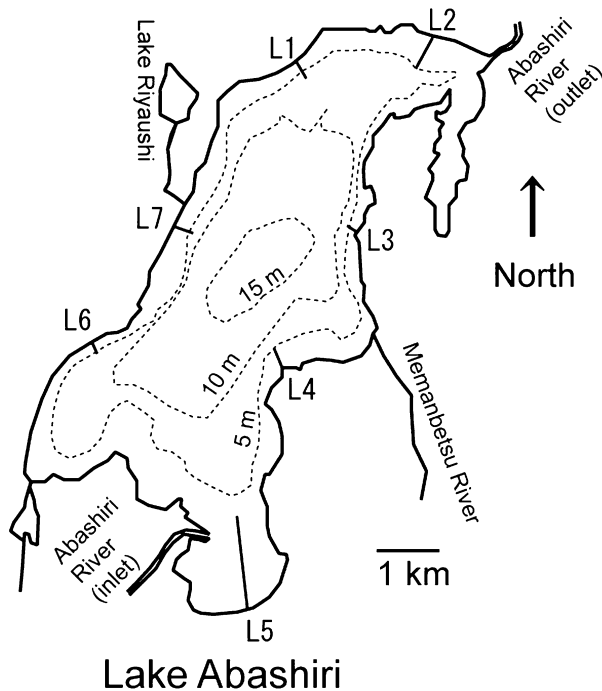


Fig. 3-1 Locations of sampling sites in Lake Abashiri.

Here I define juveniles as individuals that passed through the 1 mm sieve. Juvenile density was calculated according to the ratio of sorted sediment weight to total weight of the sediment sample obtained in the second grab. The minimum shell length of the juveniles was 0.48 mm. The juveniles were at least at age 1<sup>+</sup> because *C. japonica* did not spawn that summer due to the low salinity and low temperature of Lake Abashiri<sup>19)</sup>. The spawning season is normally from July to September in Lake Abashiri<sup>14)</sup>. The size of 1<sup>+</sup> individuals was much smaller than that previously reported by<sup>15)</sup>. Some problems remain concerning the initial growth of *C. japonica* in Lake Abashiri (not discussed in this paper).

The other 90 % of the sediment from the second grab was used for laboratory analysis of the sediment factors described below. Sediment particle size composition was analyzed by a series of sieves: 2.00, 1.00, 0.50, 0.25, 0.125, and 0.063 mm mesh. Organic carbon and organic nitrogen were measured with a C-N analyzer

(Yanagimoto, C-N coder, MT-600) after treatment with 1N HCl for 24h to remove the CaCO<sub>3</sub>. Water content and ignition loss were calculated by weight loss at 80 °C for 24h from wet sediment and at 600°C for 1h from dry sediment, respectively. Total sulfide was measured with a detector tube (Gastec No 102L and No 102H, Kitazawa Sangyo Inc.).

Spearman's rank correlation coefficient was used to estimate correlations between the densities of *C. japonica* and sediment factors, and among sediment factors. Pearson's correlation coefficient can describe only the linear component of the relations<sup>21)</sup>, however, no such relation was observed in some of my data sets. With Kendall's coefficient of rank correlation, it is difficult to calculate probability if the data contain tied ranks<sup>21)</sup>, and since my data sets contained some tied ranks, I used Spearman's rank correlation coefficient.

Empirical logit models were made by the maximum-likelihood method using juvenile presence or absence as the dependent variable and each sediment factor and depth or their combinations as independent variables. Sites where juveniles were present were assigned a value of 1 as a dependent variable and sites where they were absent were assigned a value of 0.

The depth is further raised to the *r*-th power (*r*: real number; see results for the reason). I treated the *r*-th power as a parameter *a*<sub>3</sub> (not as a transformation). The parameter *a*<sub>3</sub> was also optimized by the maximum-likelihood method.

The proportion of silt-clay (particle diameter less than 0.063 mm) plus very fine sand (0.063 - 0.125 mm) fraction in the sediments was used as an independent variable, because a significantly better model, in terms of AIC, was obtained by this variable than either silt-clay or very fine sand alone in my preliminary analysis.

An empirical logit model is useful for analyzing binary data when the sample size is small<sup>21)</sup>. The equations of the logit models used here are as follows:

$$f_1(x_1)=1/\{1+\exp[-(a_0+a_1x_1)]\},$$

$$f_2(x_1, x_2)=1/\{1+\exp[-(a_0+a_1x_1+a_2x_2)]\} \text{ and }$$

$$f_3(x_1, x_2)=1/\{1+\exp[-(a_0+a_1x_1+a_2x_2^{a_3})]\}$$

where *x<sub>i</sub>* (*i* = 1, 2) are independent variables (*x*<sub>1</sub>: each sediment variable, *x*<sub>2</sub>: depth), and *a<sub>i</sub>* (*i* = 0, 1, 2, and 3) are regression coefficients.

The Akaike Information Criterion (AIC) was

calculated to compare the models. This criterion is useful to compare models that use the same dependent variables. In the AIC, one or more difference is regarded as a statistically significant difference <sup>24)</sup>.

The values at probability 50 % (V50s) and their standard errors in the univariate logit models were calculated for each sediment factor. In the case of the dose-response relationship of a poison, this value indicates the dose at which half of the examined animals probably die (lethal dose 50). In fact, the value can also be used for any condition which separates the results, i. e., death or survival <sup>44)</sup>. In my study, I thought this value could be used as an indicator segregating sediment conditions into favorable or unfavorable ones. An advantage of this model is that it does not depend on the density. The density is not determined by the sediment conditions only, because larval supply, which varies depending on both biotic and abiotic environment factors, is also important <sup>45-49)</sup>.

## Results

### *Corbicula japonica* densities and sediment factors

As shown in Table 3-1, the average density of juveniles was much higher than the density of non-juveniles; however, there were more sites where juveniles were absent than sites where non-juveniles were absent. The absent sites were located along only three lines (L2, L4, and L5).

As shown in Table 3-2, seven limiting sediment factors were significantly negatively correlated with juvenile density. Juvenile density and non-juvenile density had similar correlations with the sediment factors; however, there were some exceptions. Juvenile density was significantly negatively correlated with total sulfide but non-juvenile density was not. Depth was not significantly correlated with either juvenile density or non-juvenile density. Juvenile density was not significantly correlated with non-juvenile density. All of the sediment factors were correlated with each other.

### Logit models

The values at probability 50 % (V50s) and their standard errors are shown in Table 3-3. The significant logit models of limiting factors, the V50s, and the densities of juveniles are shown in Fig. 3-2. These figures show that sites with juveniles present predominated on the left side of the V50s. A significant logit model could not

be made with total sulfide. The V50s for the limiting factors were: organic carbon 1.10 %, organic nitrogen 0.15 %, organic carbon/nitrogen ratio 7.43, ignition loss 4.45 %, water content 40.97 %, and silt-clay plus very fine sand 36.88 %.

In a bivariate logit model, all combinations of sediment factors were tested as independent variables, but none of them was significantly better than the univariate logit models in terms of AIC except the combination with depth.

The logit models were significantly improved, in terms of AIC, when depth was added as the independent variable. But upon seeing the plots of Fig. 3-3, I thought a curved surface would be more appropriate than a plane surface for the bivariate logit model. In the logit model analysis, an interaction term (e. g., silt-clay  $\times$  depth) is usually added to the independent variables to describe the curved surface. However, in my preliminary analysis, the bivariate logit models were not improved in terms of AIC by adding such an interaction term. Therefore, I instead raised the depth to the  $a_3$ -th power, which significantly improved the logit model in terms of AIC. The juvenile density scores and V50 isopleths of four of these bivariate logit models are shown in Fig. 3-3.

## Discussion

I could not construct a significant logit model for total sulfide. In Lake Abashiri the sulfide probably has two origins, one related to sediment particle size and organic matter, and the other to water of the anoxic polyhaline lower layer, in which a lot of sulfide is accumulated. The latter is caused by temporary climate conditions, i. e., a strong wind in the *C. japonica* habitat (shallower than 5 m) in Lake Abashiri. This kind of temporary exposure to sulfide should not affect the survival of *C. japonica* because both juveniles and adults of *C. japonica* have a high tolerance for hydrogen sulfide. Half of the examined *C. japonica* survived for 23 days under a condition of 50 mg / L hydrogen sulfide at 18°C <sup>40)</sup>. Therefore, the total sulfide may not be an important factor in determining the most favorable sediment conditions for *C. japonica* in Lake Abashiri.

In this paper, I treated the density data as binary, i. e., present or absent. One may question whether the sites of purported absence are really so. To completely prove absence is very difficult because there remains the

Table 3-1 *Corbicula japonica* densities and sediment factors in Lake Abashiri.

No of line	Depth (m)	Juvenile (n/0.05m <sup>2</sup> )	Non-juvenile (n/0.05m <sup>2</sup> )	C (%)	N (%)	C/N	IL (%)	WC (%)	TS (%)	Silt-clay Silt(%)	VFS (%)
1	1	70	123	0.22	0.04	6.31	1.31	20.87	0.53	1.64	2.14
	2	842	70	0.06	0.01	4.50	1.36	23.73	0.00	1.32	1.02
	3	2065	57	0.05	0.01	4.90	1.22	22.53	0.00	0.78	0.54
	4	846	54	0.47	0.08	5.74	4.48	38.88	0.15	2.98	1.72
	5	1312	116	0.79	0.16	4.97	3.94	34.68	1.28	24.04	8.02
2	1	0	36	0.11	0.02	5.28	1.96	34.10	0.06	2.07	12.05
	2	0	45	1.55	0.19	8.15	4.64	50.14	0.30	29.87	17.69
	3	0	24	1.79	0.22	8.16	5.59	49.63	0.36	28.78	33.59
	4	0	11	2.76	0.31	8.89	8.00	60.80	0.32	53.28	30.41
	5	0	1	2.74	0.30	9.05	8.38	63.86	1.08	61.64	19.49
3	2	260	127	0.08	0.01	5.98	0.91	22.13	0.00	1.96	1.88
	3	395	107	0.17	0.03	5.69	1.47	25.95	0.03	2.50	0.99
	4	954	63	0.31	0.06	5.31	3.27	28.38	0.14	11.36	3.67
	5	2105	88	0.88	0.18	4.75	3.68	41.94	0.00	9.25	8.02
4	1	0	335	0.08	0.02	5.09	1.04	22.58	0.02	1.69	0.77
	2	0	158	0.12	0.02	5.69	1.17	23.97	0.02	2.95	0.83
	3	0	351	1.26	0.18	7.11	4.72	44.20	0.56	21.73	4.31
	4	0	73	1.16	0.15	7.82	4.25	40.81	2.40	24.88	14.13
	5	41	32	1.89	0.22	8.54	6.13	54.27	1.61	61.46	12.95
5	1	8	39	0.13	0.02	8.12	1.56	25.95	0.01	2.82	4.16
	2	0	0	2.52	0.23	10.99	9.66	62.64	0.07	96.71	2.38
	3	0	7	2.94	0.28	10.45	8.72	59.13	0.50	97.90	1.61
6	1	1267	110	0.16	0.02	6.56	1.04	21.42	0.03	1.85	3.52
	2	143	403	0.11	0.02	5.88	0.92	23.11	0.01	1.81	2.37
	3	2321	89	0.10	0.02	5.59	1.20	23.30	0.00	2.16	3.94
	4	195	87	0.09	0.02	5.61	0.94	25.71	0.00	2.38	4.20
	5		48	0.10	0.02	5.83	1.21	26.11	0.01	1.50	6.01
7	1	243	126	0.09	0.01	6.19	0.77	22.35	0.02	1.21	2.75
	2	80	54	0.32	0.05	6.57	2.18	26.64	0.01	2.70	4.87
	3	261	18	0.11	0.02	5.82	1.81	25.23	0.01	1.60	7.42
	4	2679	108	0.22	0.04	6.01	3.12	31.67	0.00	1.97	2.91
	5	906	798	0.10	0.02	4.90	1.60	14.25	0.00	0.81	0.58
Average		565	117	0.73	0.09	6.58	3.19	34.09	0.30	17.49	6.91
Standard deviation		785	158	0.94	0.10	1.68	2.61	14.30	0.55	27.39	8.26

C: Organic carbon, N: Organic nitrogen, C/N: Organic carbon/nitrogen ratio, IL: Ignition loss, WC: Water content, TS: Total sulfide

VFS: Very fine sand, Silt:  $\phi \geq 4$ , Very fine sand:  $4 > \phi \geq 3$ Table 3-2 Spearman's rank correlation coefficients between densities of *Corbicula japonica* and sediment factors and among sediment factors in Lake Abashiri.

	Juvenile <i>C. japonica</i>	C.	Non-juvenile <i>C. japonica</i>	Depth	Organic carbon	Organic nitrogen	Organic carbon/nitrogen ratio	Ignition loss	Water content	Total sulfide
Non-juvenile <i>C. japonica</i>	0.31									
Depth	0.31		-0.18							
Organic carbon	-0.45 **		-0.51 **	0.32						
Organic nitrogen	-0.39 *		-0.47 **	0.41 *	0.98 **					
Organic carbon/nitrogen ratio	-0.61 **		-0.50 **	-0.09	0.69 **	0.59 **				
Ignition loss	-0.38 *		-0.65 **	0.44 *	0.90 **	0.90 **	0.53 **			
Water content	-0.45 *		-0.69 **	0.43 *	0.85 **	0.84 **	0.55 **	0.90 **		
Toatal sulfide	-0.56 **		-0.29	0.11	0.76 **	0.73 **	0.57 **	0.62 **	0.60 **	
Silt-clay+very fine sand	-0.45 *		-0.68 **	0.33	0.84 **	0.81 **	0.66 **	0.80 **	0.88 **	0.62 **

\*: Significant at  $P < 0.05$ \*\*: Significant at  $P < 0.01$

Table 3-3 Empirical logit models and their equations. Sites where juveniles were present were assigned a value of 1 as a dependent variable and sites where they were not present were assigned a value of 0.

Independent variable ( $x_1, x_2$ )	Regression coefficient				Log-likelihood	AIC <sup>*1</sup>	P <sup>*2</sup>	Value at provability 50% (V0.5) and SE <sup>*3</sup> or equations for isopleth of provability 50%	
	$a_0$	$a_1$	$a_2$	$a_3$				V50	SE <sup>*3</sup>
Organic carbon	2.10	-1.91			-13.5	29.1	0.00020 **	1.10	0.30
Organic nitrogen	2.16	-14.70			-14.7	31.3	0.00060 **	0.15	0.04
Organic carbon/nitrogen ratio	6.70	-0.90			-15.0	32.0	0.00080 **	7.43	0.57
Ignition loss	2.67	-0.60			-14.7	31.4	0.00060 **	4.45	0.88
Water content	4.91	-0.12			-13.6	29.1	0.00020 **	40.97	4.46
Silt + very fine sand	1.99	-0.05			-14.1	30.2	0.00030 **	36.88	10.73
Organic carbon, depth	-0.58	-3.74	1.440		-9.7	23.4	0.00002 **	$-0.581-3.738x_1+1.44x_2=0$	
Organic nitrogen, depth	-0.65	-35.36	1.730		-9.6	23.3	0.00002 **	$-0.652-35.361x_1+1.73x_2=0$	
Ignition loss, depth	0.52	-1.54	1.816		-9.7	23.3	0.00002 **	$0.521-1.544x_1+1.816x_2=0$	
Water content, depth	4.78	-0.26	1.717		-8.8	21.6	0.00001 **	$4.780-0.255x_1+1.717x_2=0$	
Silt + very fine sand, depth	-0.34	-0.09	1.184		-10.9	25.8	0.00006 **	$-0.341-0.093x_1+1.184x_2=0$	
Organic carbon, (depth) <sup>a3</sup>	1.96	-7.42	0.012	4.42	-8.0	22.1	0.00001 **	$1.964-7.423x_1+0.012x_2^{4.42}=0$	
Organic nitrogen, (depth) <sup>a3</sup>	2.24	-62.81	0.033	3.76	-8.1	22.1	0.00002 **	$2.237-62.81x_1+0.033x_2^{3.76}=0$	
Water content, (depth) <sup>a3</sup>	13.33	-0.52	0.048	3.64	-7.0	19.9	0.00001 **	$13.331-0.517x_1+0.048x_2^{3.64}=0$	
Silt + very fine sand, (depth) <sup>a3</sup>	2.91	-0.36	0.013	4.69	-7.2	22.4	0.00001 **	$2.911-0.358x_1+0.013x_2^{4.69}=0$	

\*1: Akaike Information Criterion

\*2: Calculated by likelihood ratio test in which the log-likelihood of only intercept was -20.592 and degree of freedom was number of regression coefficient minus 1.

\*3: Standard error

\*\* : Significant at  $P < 0.01$

possibility of finding some individuals if the sample size is expanded greatly. But I consider my judgments of absence to have been adequate, because there is at least assuredly a much lower density (undetectable) than at the present sites.

Tsutsumi & Sekiguchi<sup>47)</sup> proposed three possible processes leading to the absence of benthic bivalves, i. e., avoidance of settling until the larvae encounter preferable sediment, high mortality at the unfavorable sites, and subsequent transportation after settlement. In my analysis, I could not elucidate which processes have led to the absence of *C. japonica* juveniles at some sites in Lake Abashiri. Juveniles of *C. fluminea* have been reported to prefer fine and coarse sand but not mud for settlement<sup>7, 50)</sup>. Thus, it is likely that the first process, avoidance of settlement, also applies to *C. japonica* in Lake Abashiri.

As shown in Fig. 3-3, the V50s increased with depth. The reason for this is unknown, but there might be some survival-promoting or dispersion-restricting (i. e., retention-promoting) factors such as higher salinity in the deeper sites. *Corbicula japonica* requires a salinity of at least 3.1 psu (psu: practical salinity unit) for the development of its planktonic larva<sup>13)</sup>. The favorable

salinity for juveniles (shell length about 0.2 mm) is more than 1.7 psu<sup>39)</sup>. On the other hand, the salinity of the oligohaline upper layer in Lake Abashiri varies from 1 to 1.5 psu during June to November in 1995<sup>19)</sup>. Salinity does not vary within the oligohaline upper layer (variation was between 0.1 and 0.5 psu), but it increases to around 15 psu near its lower boundary<sup>51)</sup>. On windy days the polyhaline lower layer rises to shallower depths than its usual upper boundary in Lake Abashiri<sup>13)</sup>. The anoxic conditions and hydrogen sulfide, which temporarily coincidentally increase along with a rise in salinity, may not affect the survival of *C. japonica*, because *C. japonica* has a high tolerance for them<sup>40-42)</sup>.

Yamamuro et al.<sup>31)</sup> found that high mud content is the most limiting factor for the distribution of *C. japonica* among several environmental factors: dissolved oxygen saturation, chlorinity, pH of bottom water, ignition loss and mud content of sediment. They found the lethal mud level was 91.5 %. In this study, the highest silt-clay content at sites where non-juveniles were found was 97.9 %, whereas the highest silt-clay content at sites where the juveniles were present was 61.5 %, and the V50 of

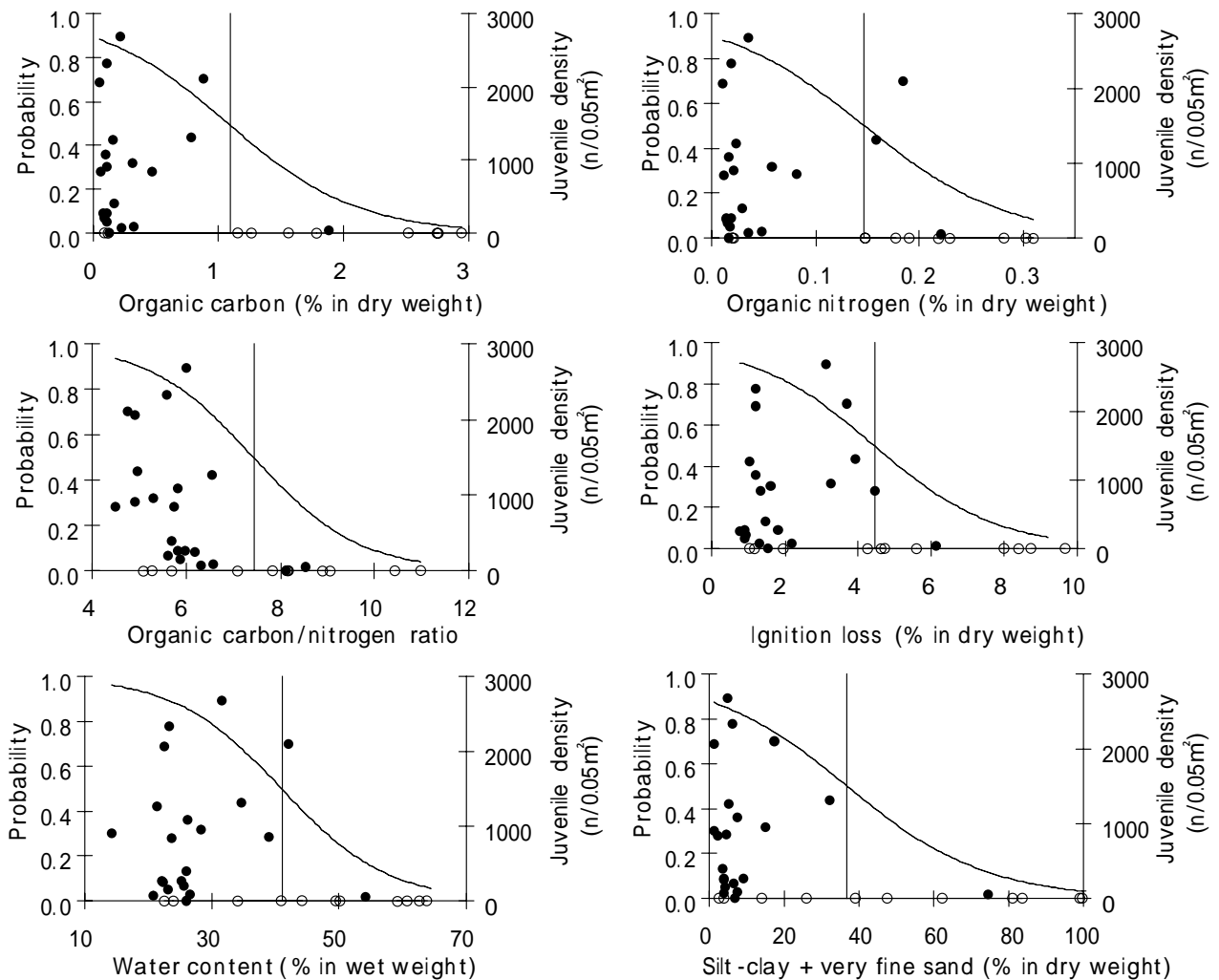


Fig. 3-2 Logit models made with limiting sediment factors for the presence of juveniles and densities of *Corbicula japonica* juveniles. Closed circles indicate sites where juveniles were present. Open circles indicate sites where juveniles were absent. The S-shaped curve represents the logit model. The vertical line indicates the V50 (the value at probability 50 %) of the logit model.

silt-clay plus very fine sand was 36.9 % (if silt-clay or very fine sand was separately used as the independent variable of the logit model, the V50 was 27.2 % and 10.7 % respectively). These findings suggest that large individuals have a higher tolerance for different sediment conditions.

As shown in Fig. 3-2, the V50s seem to be good criteria for judging whether a site is favorable for juveniles because the juvenile presence sites were predominately on the left side of the V50 among the limiting factors. Failure of *C. japonica* recruitment, maybe due to poor sediment conditions, has been reported in several places in Hokkaido, Japan (Rumoi Hokubu Fisheries Technology

District Training Center, unpublished data; Nemuro Hokubu Fisheries Technology District Training Center, unpublished data); therefore, these criteria should be useful in plans to enhance *C. japonica* resources.

Here, I have clarified the favorable sediment conditions for juveniles of *C. japonica*. On the other hand, there remain some unresolved problems concerning the distribution of *C. japonica*, i. e., the relationship to the larval supply or mortality not related to sediments. I need further investigations to clarify these problems.

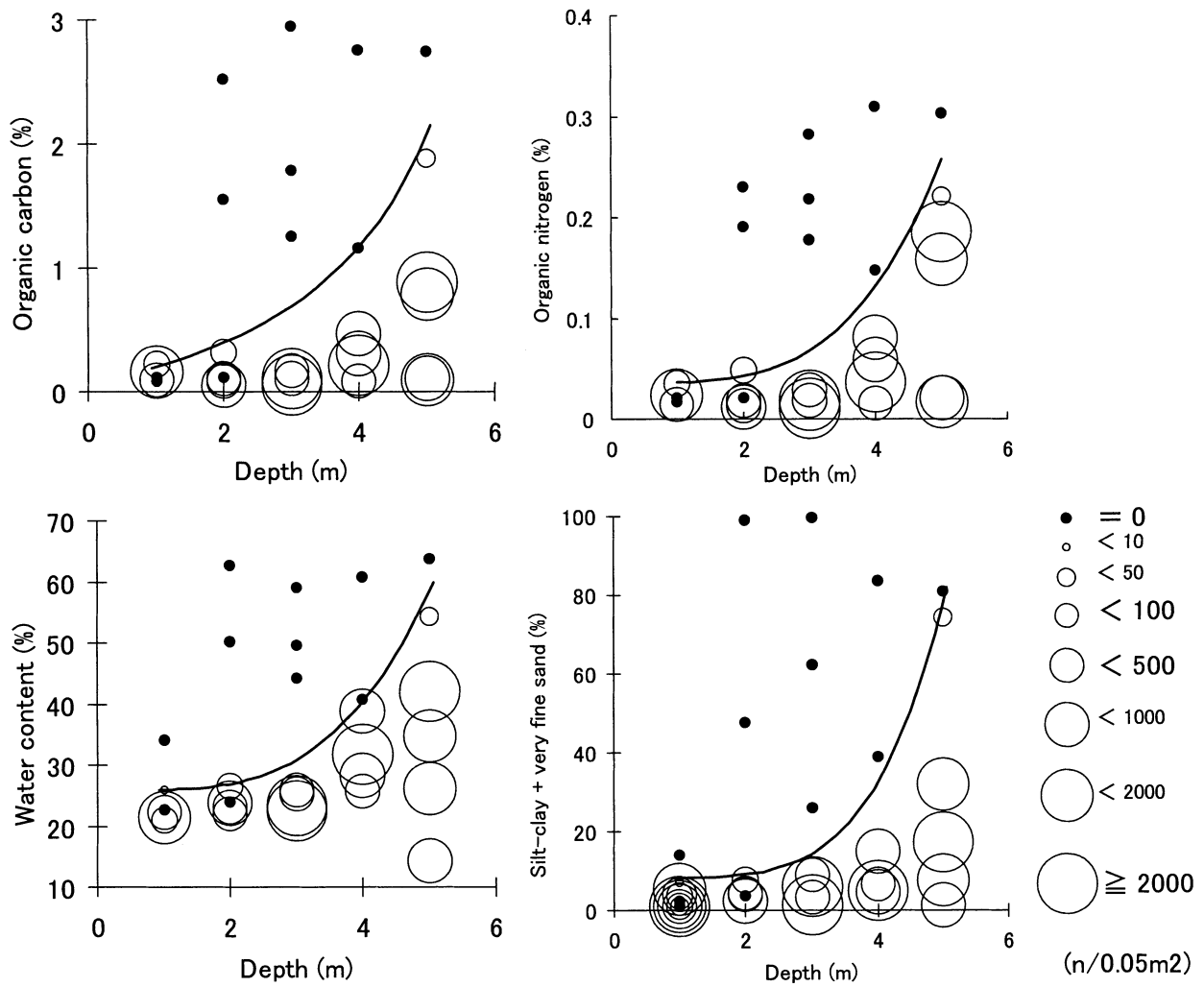


Fig. 3-3 Plots of *Corbicula japonica* juvenile density scores and an isopleth of V50 of the logit model made with depth and the other sediment factors. Open circles indicate sites where juveniles were present, and their size indicates the density of the juveniles. Closed circles indicate sites where juveniles were absent.

## CHAPTER IV

### Growth of *Corbicula japonica* juveniles in Lake Abashiri: application of an environmentally based growth model that uses finite difference calculus with maximum likelihood method

#### Abstract

I present a growth analysis model that combines large amounts of environmental data with limited amounts of biological data. The model uses the maximum-likelihood method with the Akaike Information Criterion (AIC), which provides an objective criterion for model selection. An adequate distribution for describing a single cohort is selected from available probability density functions, which are expressed by location and scale parameters. Daily relative increase rates of the location parameter (dRIRL) are expressed by a generalized multivariate logistic function using environmental factors for each day and categorical variables indicating animal ages as independent variables. Daily relative increase rates of the scale parameter are expressed by an equation describing the relationship with the dRIRL. *Corbicula japonica* grows to a modal shell length of 0.7 mm during the first year in Lake Abashiri. Compared with the attainable maximum size of about 30 mm, the growth of juveniles is extremely slow; this is due to less susceptible growth response to environmental factors until the second winter. The extremely slow growth in Lake Abashiri could be a geographical genetic variation within *C. japonica*.

#### Introduction

The extreme fluctuations, both short-term and seasonal, in food availability (e.g., phytoplankton density) make it difficult to derive relationships between the growth of filter-feeding bivalves and environmental factors<sup>52)</sup>. On the other hand, it is becoming easier to acquire large amounts of environmental data through the use of data loggers, submersible fluorometers, or remote-sensing satellites. The development of these devices could solve difficulties in data collection, because the devices enable environmental monitoring at daily or shorter intervals. However, analytical methods of combining large amounts of environmental data with limited amounts of biological data (e.g., shell length) are

not yet well developed. I present an environment-growth model that combines such unbalanced numbers of data sets. This model is useful in elucidating relationships between environmental factors and growth of filter feeders from field data.

Complex box models, ecophysiological models, can derive the relationships between environmental factors and the growth of filter-feeding bivalves<sup>53-55)</sup>. These models are useful to estimate impacts of cultivated species on an ecosystem and/or carrying capacity<sup>56-58)</sup>. However, they are suitable for animals that have been widely studied, such as *Mytilus edulis*, because they were derived by integrating a huge amount of ecophysiological knowledge acquired mainly from laboratory experiments. Furthermore, extrapolation of such knowledge to natural conditions is still controversial<sup>52,59)</sup>. On the other hand, my model treats complicated ecophysiological processes as a black box; I constructed it directly from fluctuations in environmental factors and growth rates. My approach is reasonable for animals for which ecophysiological knowledge is limited, especially when the main purpose of investigation is to derive the relationships between environment and growth.

I applied the model to a single cohort of *Corbicula japonica* juveniles spawned in August 1997. I did not need to consider bias caused by adjacent cohorts because *C. japonica* failed to spawn in 1995, 1996, and 1998 in Lake Abashiri due to low water temperatures during the spawning season<sup>30)</sup>. Such investigations provide important basic information, such as the shape of the distribution of a single cohort, and the relationship between growth rate and expansion rate of size variation in a single cohort.

*Corbicula fluminea* is an invasive pest and a fast-growing short-lived species in North America, growing to a shell length of 16-30 mm in the first year and living 1.5-3 years<sup>7)</sup>. On the other hand, other *Corbicula* species are harvested commercially in Japan. The annual catch of *C. japonica* ranged from 770 - 800 metric tons during the years 1991 to 2000 in Lake Abashiri<sup>9)</sup>. The species is distributed in brackish lakes and tidal flats of rivers from the south of Japan to the south of Sakhalin<sup>16)</sup>. Lake Abashiri lies near the northern limit of its range. Its life span is quite long, at least ten years in Lake Abashiri<sup>15)</sup>. I found extremely slow growth of juveniles compared with the maximum attainable size of about 30 mm, and interpreted this factor by my model.

## Materials and Methods

### Model formulation

#### Selection of adequate function to describe a single cohort

An adequate function to describe a single cohort of each animal should be selected to avoid biases caused by any inadequacies of the function. Probability density functions of many distributions are applicable for the purpose. Characteristics of many distributions are well described by Evans et al.<sup>60)</sup>. I used three distributions: normal distribution, largest extreme value distribution, and smallest extreme value distribution. The normal distribution is symmetric. The largest extreme value distribution is asymmetric with a longer tail toward the larger side. The smallest extreme value distribution is asymmetric with a longer tail toward the smaller side. All are expressed by a location parameter and a scale parameter.

To use all the information inherent in data, parameters of the distribution functions are estimated from raw data (e.g., lengths), not from summarized data such as length frequency. This estimation method is described by Sakamoto et al.<sup>24)</sup>. The most adequate distribution is selected by the Akaike Information Criterion (AIC)<sup>23)</sup>. Log-likelihood functions of the distributions take the following forms:

normal distribution;

$$\log_e L_{normal}(a, b) = \sum_{i=1}^n \log_e \left\{ \frac{1}{\sqrt{2\pi b^2}} \exp\left[-(l_i - a)^2 / 2b^2\right] \right\} \quad (1),$$

largest extreme value distribution;

$$\log_e L_{largest}(a, b) = \sum_{i=1}^n \log_e \left\{ (1/b) \exp\left[-(l_i - a)/b\right] \right\} \times \exp\left\{-\exp\left[-(l_i - a)/b\right]\right\} \quad (2),$$

smallest extreme value distribution;

$$\log_e L_{smallest}(a, b) = \sum_{i=1}^n \log_e \left\{ (1/b) \exp\left[(l_i - a)/b\right] \right\} \times \exp\left\{-\exp\left[-(l_i - a)/b\right]\right\} \quad (3),$$

where  $n$  = number of data;

$l_i$  = length of  $i$ th individual;

$a$  = location parameter; and

$b$  = scale parameter.

The location parameter is a mean in the normal distribution. The location parameter is a mode in the largest and the smallest extreme distributions. The scale parameter is a standard deviation in the normal distribution.

The AIC is calculated by

$$AIC = -2 \log_e (\text{maximum likelihood}) + 2m \quad (4),$$

where  $m$  = number of parameters to be estimated. The AIC is an information-theoretic criterion extended from Fisher's likelihood theory and is useful for simultaneous comparison of models<sup>23, 61)</sup>. The model with the minimum AIC is the best model. A difference of more than 1 or 2 is regarded as significant in terms of AIC<sup>24)</sup>.

#### Introduction of finite difference calculus into growth model

Values of the location and scale parameters usually increase with the growth of an animal. The relative increase rate in a certain time step is defined as

$$r_i = (P_i - P_{i-1}) / P_{i-1} \quad (5),$$

where  $r_i$  = relative increase rate of a parameter in the  $i$ th time step; and  $P_i$  = parameter value after the  $i$ th time step.

Relationships between the parameter value and the relative increase rate of the parameter can be expressed by

$$\begin{aligned} P_1 &= P_0(1 + r_1) \\ P_2 &= P_1(1 + r_2) = P_0(1 + r_1)(1 + r_2) \\ P_3 &= P_2(1 + r_3) = P_0(1 + r_1)(1 + r_2)(1 + r_3) \quad , \quad (6) \\ &\vdots \\ P_n &= P_0 \prod_{i=1}^n (1 + r_i) \end{aligned}$$

where  $P_0$  = parameter value at the first sampling;

$P_i$  = parameter value after the  $i$ th time step; and

$r_i$  = relative increase rate of the parameter in the  $i$ th time step.

I used one day as the time step in this study. In my environment-growth model, I assumed that the daily relative increase rate of location parameter (dRIRL) depends on the age of the animal and on environmental factors for each day. Sigmoid functions that take values



between 0 and a certain maximum are empirically appropriate for expressing the relationships between the dRIRL and independent variables, especially for measures such as shell length that do not show negative growth. Therefore, using categorical variables indicating animal ages and environmental factors for each day as independent variables, I express the dRIRL by the generalized multivariate logistic function,

$$s_i = s_{\max} / \left\{ 1 + \exp \left[ - \left( \sum_{j=1}^{n_A} \alpha_j A_j + \sum_{k=1}^{n_E} \beta_k E_{ki} \right) \right] \right\} \quad (7)$$

where

$s_i$  = dRIRL on the  $i$ th day from the first sampling;

$s_{\max}$  = potential maximum dRIRL of the animal;

$\alpha_j, \beta_k$  = coefficients of each independent variable;

$A_j$  = categorical variable (a dummy variable indicating animal ages) that takes the value 1 or 0;

$E_{ki}$  = the  $k$ th environmental factor on the  $i$ th day from the first sampling;

$n_A$  = number of age categories; and

$n_E$  = number of environmental factors.

The categorical variable takes the value of 1 when the animal comprises the category, otherwise it takes 0. A method of giving a value to the categorical variable is described by Zar<sup>62)</sup>.

The daily relative increase rate of scale parameter (dRIRS) and dRIRL must be correlated because the dRIRS is larger when the dRIRL is larger. Therefore, I estimated the dRIRS from an equation expressing the relationship to the dRIRL. I tested two functions,

$$t_i = \begin{cases} \gamma_1 + \gamma_2 s_i & (\gamma_1 + \gamma_2 s_i > 0) \\ 0 & (\gamma_1 + \gamma_2 s_i \leq 0) \end{cases} \quad (8),$$

and

$$t_i = \begin{cases} (s_i - \gamma_1)^{\gamma_2} & (s_i - \gamma_1 > 0) \\ 0 & (s_i - \gamma_1 \leq 0) \end{cases} \quad (9)$$

where  $t_i$  = dRIRS on the  $i$ th day from the first sampling;

$\gamma_1, \gamma_2$  = coefficients of the equations; and

$s_i$  = dRIRL on the  $i$ th day from the first sampling.

The location and scale parameters at the first sampling ( $a_0$  and  $b_0$ ), the coefficients of equation (7) ( $s_{\max}$ ,  $\alpha_j$  and  $\beta_k$ ), and the coefficients of equations (8) and (9) ( $\gamma_1$  and  $\gamma_2$ ) are estimated as values that maximize total

log-likelihood. The total log-likelihood is evaluated by the adequate probability density function selected in the first step. The log-likelihood functions take the following forms:

Normal distribution;

$$\log_e L_{normal}(a_0, b_0, s_{\max}, \alpha_j, \beta_k, \gamma_1, \gamma_2) = \sum_{q=1}^N \sum_{i=1}^{n_q} \log_e \left\{ \frac{1}{\sqrt{2\pi b_q^2}} \exp \left[ - (l_{qi} - \hat{a}_q) / 2b_q^2 \right] \right\} \quad (10),$$

Largest extreme value distribution;

$$\log_e L_{largest}(a_0, b_0, s_{\max}, \alpha_j, \beta_k, \gamma_1, \gamma_2) = \sum_{q=1}^N \sum_{i=1}^{n_q} \log_e \left\{ (1/b_q) \exp \left[ - (l_{qi} - \hat{a}_q) / b_q \right] \times \exp \left\{ - \exp \left[ - (l_{qi} - \hat{a}_q) / b_q \right] \right\} \right\} \quad (11),$$

Smallest extreme value distribution ;

$$\log_e L_{smallest}(a_0, b_0, s_{\max}, \alpha_j, \beta_k, \gamma_1, \gamma_2) = \sum_{q=1}^N \sum_{i=1}^{n_q} \log_e \left\{ (1/b_q) \exp \left[ (l_{qi} - \hat{a}_q) / b_q \right] \times \exp \left\{ - \exp \left[ (l_{qi} - \hat{a}_q) / b_q \right] \right\} \right\} \quad (12),$$

where  $a_0, b_0$  = values of the location and scale parameters respectively at the first sampling,

$s_{\max}, \alpha_j, \beta_k$  = coefficients of equation (7),

$\gamma_1, \gamma_2$  = coefficients of equations (8) and (9),

$N$  = number of samplings,

$n_q$  = number of data at the  $q$ th sampling,

$\hat{a}_q$  = location parameter at the  $q$ th sampling estimated by equation (6) ( $r_i = s_i$ ),

$\hat{b}_q$  = scale parameter at the  $q$ th sampling estimated by equation (6) ( $r_i = t_i$ ), and

$l_{qi}$  = length of the  $i$ th individual at the  $q$ th sampling.

AIC is used to select significant environmental factors, the age categorization, and the equation to express the relationship between dRIRL and dRIRS, i.e., equation (8) or (9).

Estimation of confidence interval of coefficient

To evaluate uncertainties of coefficients' values and model selection, I estimate the 95% confidence intervals

of all coefficients—i.e.,  $a_0$ ,  $b_0$ ,  $s_{\max}$ ,  $\alpha_j$ ,  $\beta_k$ ,  $\gamma_1$ , and  $\gamma_2$ —based on profile likelihood. For example, the 95% confidence interval of  $a_0$ — $a_{0,95}$ —is estimated as an interval that suffices in the following equation:

$$2 \left\{ \max \log_e L(\hat{a}_0, \hat{b}_0, \hat{\alpha}_j, \hat{\beta}_k, \hat{\gamma}_1, \hat{\gamma}_2) - \max \log_e L(\hat{a}_0, \hat{b}_0, \hat{\alpha}_j, \hat{\beta}_k, \hat{\gamma}_1, \hat{\gamma}_2 | a_0 = a_{0,95}) \right\} \leq \chi_1^2(0.05) \quad (13)$$

where  $\chi_1^2(0.05)$  = value of a chi-squared distribution at an upper probability of 0.05 with 1 degree of freedom, i.e., 3.84.

The characteristics of the interval are explained by Burnham and Anderson<sup>61)</sup>.

I used Microsoft Excel as the analysis platform, and Solver as the non-linear optimization tool.

### Field study and model selection

#### Sampling of *C. japonica* juveniles

To collect juveniles of *C. japonica* spawned in August 1997, sediments were sampled with a 0.05 m<sup>2</sup> Smith-McIntyre grab once or twice a month during the period from September 1997 to July 1999 at a depth of 3.5 to 4.0 m in Lake Abashiri (Fig. 4-1). The habitat of *C. japonica* is restricted to areas shallower than 6 m depth because the deeper area is covered by anoxic polyhaline water, that is the lower stratum of the lake. The selectivity of the sampling gear on *C. japonica* juvenile is probably negligible because the gear grabs the juveniles with the sediment. Because the magnitude of spawning in 1997 was relatively small<sup>30)</sup>, I selected a sampling site where I found abundant settled juveniles in my preliminary investigations. Samples could not be obtained during winter because of ice cover. Sediments were washed with tap water on 2-mm and 0.125 mm mesh sieves during the period from September 1997 to October 1998, and on 4.75 mm and 0.125 mm mesh sieves during the period from April to July 1999. To separate the juveniles from the retained sediments, I treated the sediments with zinc chloride solution as described by Sellmer<sup>63)</sup>. Then I sorted the juveniles under a binocular microscope. Identification of the cohort spawned in 1997 was quite easy, because *C. japonica* failed to spawn in 1995, 1996, and 1998 due to low water temperatures during the spawning season<sup>30)</sup>. I regarded all the individuals which passed through the larger-mesh sieves and retained on the smaller-mesh sieve

as the cohort spawned in 1997. Shell lengths were measured under a profile projector (V-12, Nikon Ltd.) at  $\times 50$  magnification with a digital caliper (Digimatic caliper, Mitsutoyo Ltd.), which has a 0.02 mm precision.

### Environmental factors

Values for water temperature (°C), water fluorescence (fluorescence equivalent to uranin density,  $\mu\text{g}\cdot\text{L}^{-1}$ ), salinity (psu, practical salinity unit), and turbidity (equivalent to kaolin density, ppm) were obtained for 0.1 m intervals from unpublished data of the Abashiri Local Office of the Hokkaido Development Bureau. The variables were measured by a submersible fluorometer (Memory Chlorotec, ACL-1180-OK, Alec Electronics Ltd.) at four sites in Lake Abashiri at intervals of about one week (Fig. 4-1). The average values of each variable between the depths of 1 m and 6 m were used for later analyses. Values between the measured dates were interpolated linearly for subsequent analysis with the environment-growth model. The water fluorescence reflects the density of phytoplankton.

### Model selection for application to *C. japonica*

I used three procedures of model selection to achieve the best model. First, I constructed an *a priori* set of candidate base models from the point of view of biological reasonability; and then I selected the best base model. Second, I excluded insignificant factors from the best base model. Third, I checked the significance of environmental factors that were not included in the base models. If one was significant, I included it in the best base model. All of these procedures were performed by AIC. The construction of the *a priori* set of candidate models is partially subjective, but it is an important part of the model construction<sup>61)</sup>.

Seasonal growth in bivalves is influenced by water temperature and food supply<sup>64)</sup>. The growth rate of *Corbicula fluminea* changes with age<sup>7)</sup>. Therefore, I constructed base models combining water temperature, water fluorescence, and categorical variables indicating age for the independent variables of equation (7). I tested two types of categorization of age. The first segregates ages based on real age, i.e. two categories: 0<sup>+</sup> or 1<sup>+</sup>. The second segregates ages relative to winter, i.e. three categories: before the first winter, from the first to the second winter, and after the second winter. For the

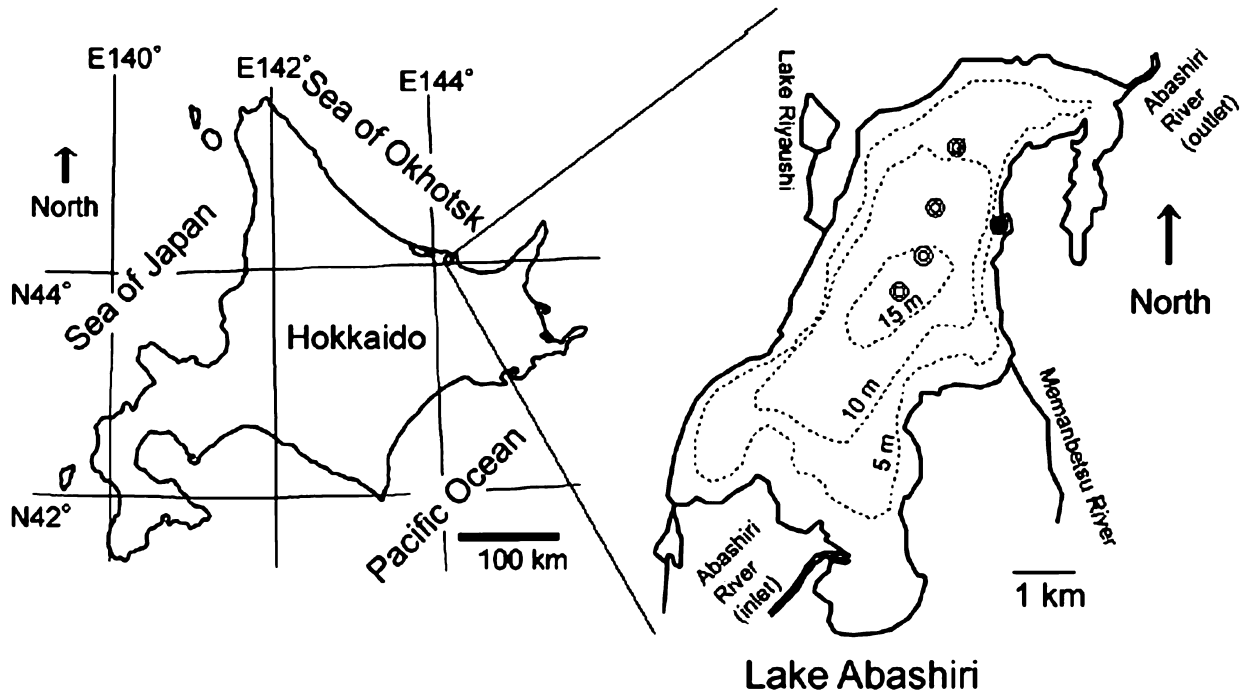


Fig. 4-1 Location of sampling site of *Corbicula japonica* juveniles in Lake Abashiri, Japan ●. Environmental factors—water temperature, water fluorescence, salinity, and turbidity—were measured at four sites, designated by ○.

real-age categorization, age was segregated based on 1 September, because the spawning season was in August 1997. For the winter-base age categorization, I segregated ages based on 1 January. No biases should occur due to the segregation date of the winter-base categorization because the growth of *C. japonica* is negligible during winter. Four base models were constructed combining the two types of age categorization and two types of equations expressing the relationship between the dRIRL and the dRIRS, i.e. equation (8) or (9). I selected the best base model by AIC.

To check the significance of each environmental factor and age categorization, I removed the independent variables one by one from the best base model and re-optimized the model. When the model was significantly improved by the removal in terms of AIC, the effect of the variable was insignificant on the model, so I excluded it.

To check the significance of salinity and turbidity, which were not included in the base models, I included them one at a time into the best base model and re-optimized the model. When the model was improved by the inclusion, the effect of the variable was significant on the model, so I included it.

## Results

### Selection of adequate function to describe a single cohort

The largest extreme value distribution was the best in terms of AIC except for data sampled on 13 May 1998 (results are not shown). The exception is due probably to the small sample size ( $n = 38$ ) on that date. The largest extreme value distribution was therefore used to evaluate likelihood in later analyses: I selected equation (11) from equations (10), (11), and (12). The result of fitting the three distributions to the shell lengths sampled on 22 April 1999 is shown in Fig. 4-2 as a representative example. The largest extreme value distribution is apparently the most suitable for describing the single cohort of *C. japonica* spawned in 1997.

### Model selection and application

Model 4 was the best in terms of AIC among four base models (Table 4-1, Model 1 to 4); ages were categorized based on winter; and the relationship between dRIRL and dRIRS was expressed by equation (9).

Four models were made by removing each independent variable from model 4 (Table 4-1, Model 4-1 to 4-4). The effect of one age categorization—segregation of ages between the first and second winters—was

Table 4-1 Values of location and scale parameters at the first sampling, coefficients, log-likelihood and AIC of constructed models. The best AIC among four base models (Models 1 to 4) is enclosed by a single line. The best AIC of all models is enclosed by a double line. dRIRL = daily relative increase rate of location parameter, dRIRS = daily relative increase rate of scale parameter, Temp = water temperature, WF = water fluorescence, Sal = salinity, Turb = turbidity, C1 = before the 1st winter, C2 = from the 1st to the 2nd winter, C3 = after the 2nd winter.

Model no.	Parameters at 1st sampling		Max. dRIRL $s_{\max}$	Age categorization			Environmental factors				Expressing relationship between dRIRS and dRIRL					
	$a_0$	$b_0$		$A_1$	$A_2$	$A_3$	Temp $\beta_1$	WF $\beta_2$	Sal $\beta_3$	Turb $\beta_4$						
				$\alpha_1$	$\alpha_2$	$\alpha_3$					$\gamma_1$	$\gamma_2$	Eq. No	Log-L	AIC	
				0+	1+											
1	0.299	0.04	0.012	-62.6	-23.7		0.16	2.61			0	1.69	(8)	850.4	-1683	
2	0.297	0.04	0.011	-56.1	-22.1		0.2	2.44			0.0001	0.89	(9)	852.3	-1687	
				C1	C2	C3										
3	0.299	0.042	0.011	-16.8	-16.7	-9.1	0.61	0.41			-0.0076	2.90	(8)	950.4	-1881	
4	0.299	0.042	0.011	-17.5	-17.6	-9.6	0.65	0.42			0.0034	0.76	(9)	952.2	-1884	
4-1	0.299	0.042	0.011	-18.3 <sup>(1)</sup>		-10	0.68	0.44			0.0034	0.76	(9)	952.2	-1886	
4-2	0.297	0.038	0.005	-127.9	-26.8 <sup>(1)</sup>		0.34	4.15			0	0.90	(9)	735	-1452	
4-3	0.295	0.037	0.008	-47.3	-16.3	-8.8		1.47			0.0033	0.77	(9)	848.9	-1680	
4-4	0.299	0.041	0.013	-4.9	-8.9	-4.9	0.4				0.002	0.81	(9)	909.6	-1801	
4-5	0.299	0.042	0.011	-16.7 <sup>(1)</sup>		-9.1	0.62	0.42	-0.25		0.0033	0.76	(9)	952.4	-1885	
4-6	0.299	0.042	0.011	-18.5 <sup>(1)</sup>		-10.2	0.68	0.44		0.007	0.0034	0.76	(9)	952.2	-1884	

(1): One common coefficient for the two categorical variables.

Table 4-2 95% confidence limits of location and scale parameters at the first sampling and coefficients of the best model (Model 4-1 in Table 1) estimated by profile likelihood method. dRIRL = daily relative increase rate of location parameter, dRIRS = daily relative increase rate of scale parameter, Temp = water temperature, WF = water fluorescence, Sal = salinity, Turb = turbidity.

	Parameters at 1st sampling		Max.	Age categorization			Environmental factors				Expressing relationship between dRIRS and	
	$a_0$	$b_0$	$s_{\max}$				Temp	WF	Sal	Turb	$\gamma_1$	$\gamma_2$
				$\alpha_1$	$\alpha_2$	$\alpha_3$						
Lower 95												
%	0.294	0.039	0.01	-26.6 <sup>(1)</sup>		-14.6	0.41	0.27			0.0027	0.734
Upper 95												
%	0.304	0.045	0.013	-11.5 <sup>(1)</sup>		-6.4	1.00	0.64			0.0039	0.793

(1): One common coefficient for the two categorical variables.

insignificant on the model, because the model was significantly improved by its removal in terms of AIC. The effects of the other independent variables were significant on the model, because the model was significantly worsened by their removal in terms of AIC. The effects of salinity and turbidity were insignificant on the model, because adding each variable significantly worsened the model in terms of AIC (Table 4-1, Models 4-5 and 4-6). Consequently, model 4-1 was the best model to describe the relationships among environmental factors, ages, and growth of *C. japonica* juveniles spawned in 1997.

The coefficient value for age categorization of before the 2nd winter (-18.3) is much smaller than that of after the 2nd winter (-10.0) (Table 4-1). This difference suggests that the growth response of *C. japonica* juveniles is much less susceptible to environmental factors before the second winter than after.

Peaks of the dRIRL corresponded with peaks of water fluorescence, when the water temperature was warmer than about 10 °C, especially before the second winter (Fig. 4-3B, C). Therefore, food supply is the most influential factor when the water temperature is above about 10 °C. The slow or no growth during winter is due

to the low water temperatures. The dRIRL reached a plateau after 30 May 1999. This is due to two factors: Water fluorescence was relatively large after 30 May 1999 (Fig. 4-3B); and the growth response of *C. japonica* to the environmental factors was more susceptible after the second winter than before.

The largest extreme value distributions estimated by model 4-1 fitted the shell lengths of *C. japonica* juveniles very well (Fig. 4-4).

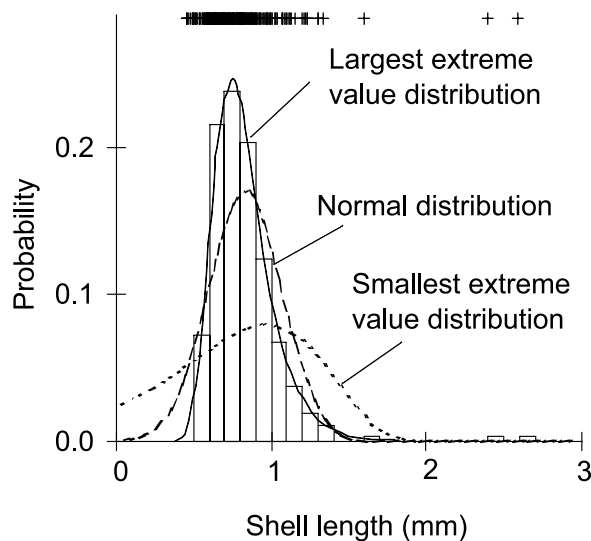


Fig. 4-2 Three distributions fitted by the maximum-likelihood method to the shell lengths of *Corbicula japonica* juveniles spawned in 1997 and sampled on 22 April 1999. Raw data are shown by +. The shell length composition is shown by histogram.

## Discussion

### Model formulation and application

Largest extreme value distribution is apparently better than the other distributions to describe the single cohort of *C. japonica* spawned in 1997. This distribution has a mode and a longer tail toward the larger side. I thought that the shell length distribution of the cohort was already asymmetric just after settlement. Such a distribution might be influenced by fluctuations in larval settlement during the spawning season; and larval settlement would be influenced by fluctuations in larval supply from the water column. During the spawning season of 1997, the average planktonic larval density gradually increased from 26 ind·m<sup>-3</sup> on 25 July to a

maximum of 603 ind·m<sup>-3</sup> on 13 August. Then it sharply decreased to 3 ind·m<sup>-3</sup> on 19 August<sup>30)</sup>. Such a pattern of larval density fluctuation might have caused the asymmetric distribution of shell lengths of the settled juveniles. An other possible factors that influenced the shapes of the shell length distributions and the relationship between dRIRL and dRIRS is size-dependent mortality, e.g. predations and fisheries. Size-dependent mortality has been reported in several marine bivalves<sup>65)</sup>. Potential predators of *C. japonica* are fishes, such as Japanese dace *Leuciscus hakonensis*, far eastern dace *L. brandti*, carp *Cyprinus carpio*, and mullets *Liza haematocheila* (Kawasaki). In my study, the size-dependent mortality is negligible because the range of the shell lengths observed in this study is very narrow.

The shape of the distribution to describe a single cohort should be determined from the data. In contrast, single cohorts are usually separated from multi-cohort data by assuming a normal distribution of lengths in a single cohort<sup>66)</sup>. Therefore, it is possible that multi-cohort analysis done without selection of an adequate distribution to describe a single cohort causes substantial bias in estimations of various stock features of animal populations, such as age composition, growth, mortality, and recruitment.

Relatively large confidence intervals were obtained in the coefficients of the linear component of equation (7), i.e.,  $\alpha_j$  and  $\beta_k$  (Table 4-2). The relatively large confidence intervals may indicate that the number of estimated coefficients is somewhat larger than the number of samplings. Therefore, to estimate these coefficients more precisely, I may need to investigate more cohorts spawned in other years in future investigations.

### Growth of *C. japonica*

I identified extremely slow growth of *C. japonica* juveniles, which grew to a modal shell length of 0.7 mm during the first year in Lake Abashiri, which lies at 43.7°N. Spats of *C. japonica* collected during 1992 to 1997 in Lake Shinji, which lies at 35.5°N, grew to a mean shell length of 6.7 mm in natural conditions by the first winter<sup>67)</sup>. Using environmental factors measured in Lake Shinji during 1990 to 1998 at monthly intervals<sup>68)</sup>, I simulated the growth of *C. japonica* by model 4-1. It grew to a mean shell length of 1.4 mm (standard error, 0.37) by the first winter in the simulations. Therefore, the large difference in

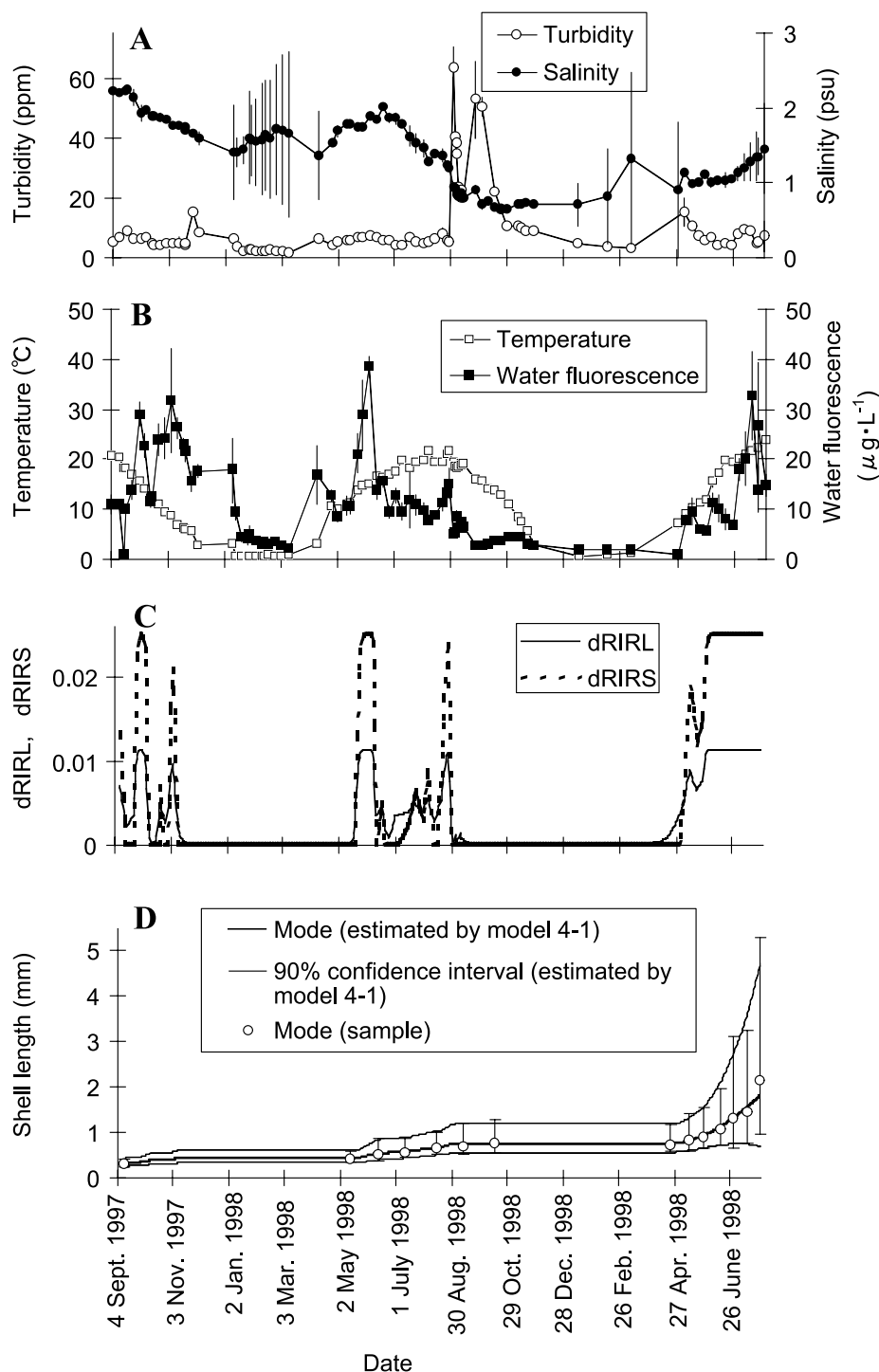


Fig. 4-3 Environmental fluctuations and prediction of the growth of *Corbicula japonica* juveniles spawned in 1997 in Lake Abashiri by the best model (Model 4-1 in Table 4-1). (A) Insignificant environmental factors (excluded factors by model selection), turbidity (equivalent to kaolin density, ppm) and salinity (psu, practical salinity unit). (B) Significant environmental factors (included factors by model selection), temperature (°C) and water fluorescence (equivalent to uranin density,  $\mu\text{g}\cdot\text{L}^{-1}$ ). (C) Daily relative increase rate of location parameter (dRIRL) and daily relative increase rate of scale parameter (dRIRS) estimated by the model. (D) Growth of *Corbicula japonica*; vertical bars represent 90-% confidence interval of the shell length of the samples.

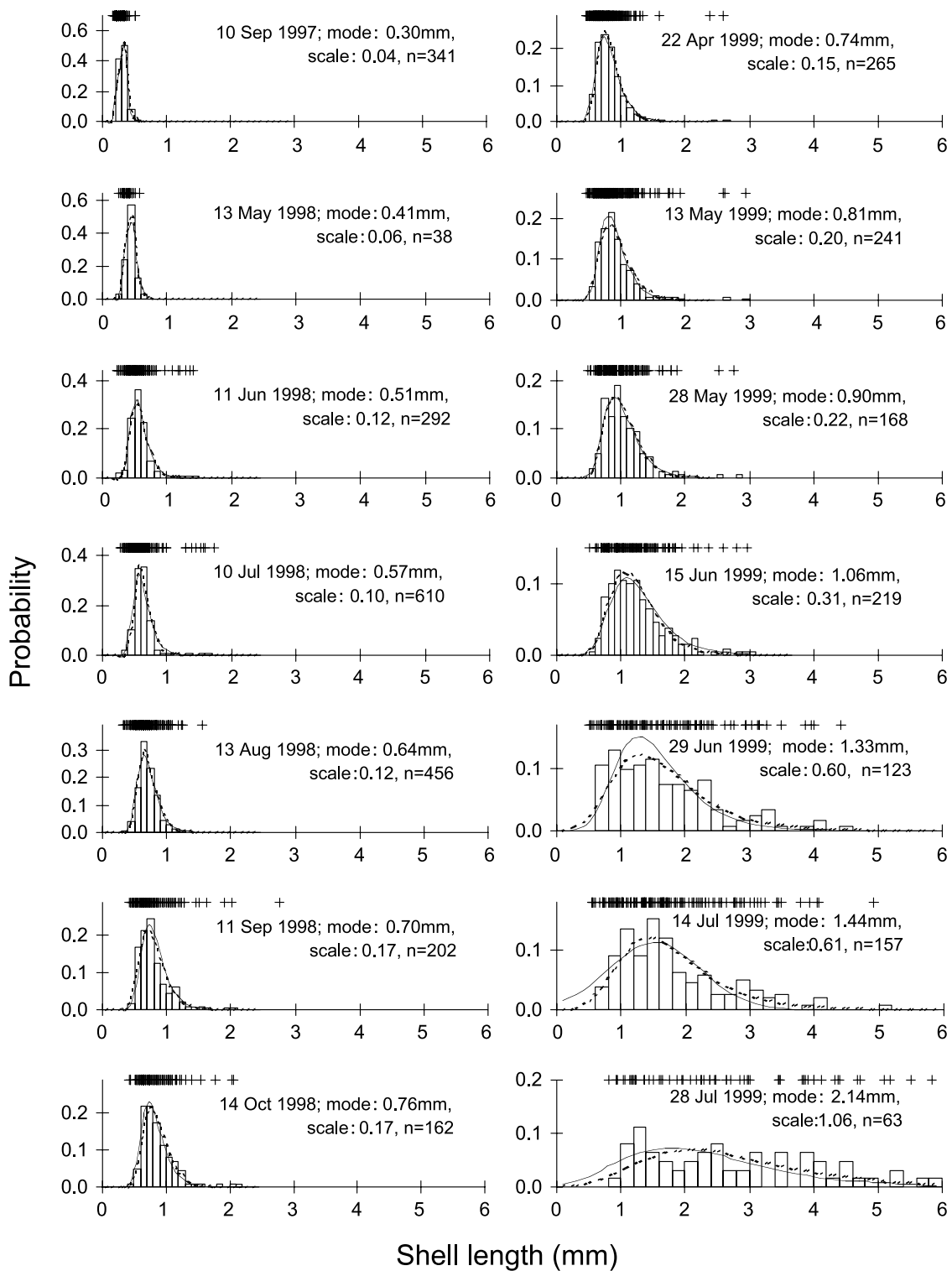


Fig. 4-4 Shell length compositions of a single cohort of *Corbicula japonica* spawned in 1997. The raw data (shell lengths) are shown by '+'. The largest extreme value distribution estimated by the best model (Model 4-1 in Table 4-1) is shown by a solid line. The largest extreme value distribution independently fitted by the maximum likelihood method is shown by a dashed line. The sampling date and values of location parameter (mode) and scale parameter independently fitted by the maximum likelihood method are shown in each panel

juvenile growth between the two habitats cannot be explained by environmental differences, because the results of the simulation were apparently an underestimate. I conclude that the extremely slow growth of the juveniles (prolonged phase of meiobenthic development) in Lake Abashiri is a geographical variation, which is probably genetically determined, within *C. japonica*. Prolonged phases of meiobenthic development have been reported in some marine bivalves<sup>65, 69)</sup>. However, a prolonged phase of meiobenthic development as a geographical variation is rarely reported.

In many species of bivalve, populations from higher latitudes have a slower initial growth rate; but longevity and ultimate size in these populations are frequently greater than at lower latitudes<sup>70, 71)</sup>. The extremely slow growth of *C. japonica* juveniles in Lake Abashiri may be an extreme example of this phenomenon.

The growth response of *C. japonica* juveniles is much less susceptible to environmental factors before the second winter than after. This unsusceptible growth response is the proximate factor for the extremely slow growth rate. *Nuculoma tenuis*, a detritus feeder, develops its palp proboscides, its feeding apparatus, during the prolonged phase of meiobenthic development<sup>69)</sup>. The changes of growth susceptibility to environmental factors in young ages may suggest that some functional morphological changes occur in *C. japonica*, also a filter feeder. In my preliminary analyses, I could not find a better model when I used different values of  $s_{\max}$  in equation (7) between ages instead of categorical variables indicating ages. Therefore, I conclude that the difference in growth rates between ages is not due to a difference in potential maximum growth rate.

Utoh<sup>15)</sup> investigated the growth of *C. japonica* in Lake Abashiri using a resting zone formed on the shell surface that is regarded as an annual ring. He concluded that *C. japonica* grows to a mean shell length of 5.7 mm in the first year. This is apparently an overestimate, owing to difficulties in recognizing the resting zone on small individuals. I inferred the mean shell length of the 5.7 mm reported by Utoh<sup>15)</sup> may be the mean shell length of a cohort aged 3 years because some shell lengths of aged 2 years in my research overlapped with the shell lengths of the first year reported by Utoh<sup>15)</sup>. To understand overall growth of *C. japonica* in Lake Abashiri, I integrated my results of the juvenile growth and the report of Utoh<sup>15)</sup>

and draw a growth curve in Figure 4-5. The growth curve of *C. japonica* in Lake Abashiri is S-shaped, and attainable maximum mean shell length is 31 mm. Maru<sup>14)</sup> reported *C. japonica* matures at shell length of 15 mm in Lake Abashiri. Therefore, it is inferred that *C. japonica* matures at 5 years old in Lake Abashiri.

## GENERAL DISCUSSION

### Spawning

The spawning season of *Corbicula japonica* is summer in general<sup>13, 14, 30, 72, 73)</sup>. Before the report of Baba et al. 1999 (Chapter I), neither the threshold temperature for the spawning nor the phenomena of the spawning failure in the natural conditions had been known. In Lake Abashiri, lies near the northern limit of this species range, *C. japonica* fails to spawn when the summer temperature is lower than the threshold temperature. The failure of the spawning is not exceptional phenomenon; it is estimated that the failure occurred in 10 out of past 21 years. The plans of resources managements are usually worked out based on the magnitudes of the new recruitments. Growth analyses without the information of the spawning conditions causes crucial biases because the failure of the spawning causes lacks of cohorts. Therefore, whether the spawning had occurred or not-occurred is important information for the resources managements and the ecological studies of *C. japonica*.

The spawning failure is histologically characterized by massive atretic oocytes in the female gonads after the spawning season<sup>30)</sup> (Chapter I). The atretic oocyte is apparently different from the degenerating oocyte, which commonly observed after spawning season in many bivalves. The degenerating oocyte is characterized by extensive phagocytosis, whereas the atretic oocyte do not accompany with the extensive phagocytosis in *C. japonica*. In some marine bivalve, mainly in the scallops (Pectinidae), the atretic oocytes are also observed during the phases of oogenesis<sup>26, 74-76)</sup>. The annual fluctuations of recruitments are quite large in these species<sup>77, 78)</sup>. However, the relationships between the recruitment fluctuations and ovarian conditions had not been studied. I thought the ratio of the atretic oocyte would be a good criterion for the evaluation of the ovarian conditions; and it would be one of important physiological clues for the prediction of recruitment magnitudes.



### Pre-settlement processes

The anoxic polyhaline lower stratum in brackish water lakes has been dealt as an abominable existence because the anoxic water sometimes upwelled by strong wind and the temporal anoxic conditions killed fishes and shrimps inhabiting the well-oxygenated oligohaline upper stratum. To vanish the anoxic stratum or make the boundary deeper, some developments have been planned in some brackish lakes. However, I revealed that the boundary zone is probably important for the early stage of the planktonic larvae of *C. japonica*, especially when the salinity of the upper stratum is not enough for the larval development (Chapter II). From viewpoint for the conservation of *C. japonica* resources, not only the salinity of the upper stratum but also the boundary depth should be considered when development of brackish water lakes is planned.

### Sediment environments

Muddy sediment conditions are apparently one of the most restrictive factors for *C. japonica* habitat because few juveniles are observed on the muddy sediments (Chapter III). Such muddy sediments distribute near the mouths of the inlet and the outlet rivers around Lake Abashiri (Baba and Takahashi 199b). Therefore, the conservations of natural environment, such as forestry and reed fields, around the lake are also important to protect the habitats because the silt and clay are provided from the upper streams of the rivers. As a concrete example, juveniles of *C. japonica* have not been observed in Lake Panke (Horonobe, Hokkaido) since 1986 in spite of the abundant planktonic larvae were observed in some years (Sakai 2000). It is probably due to the muddy sediment conditions. The farm land constructions, which started from 1974, are suspected as the factor that make the sediment conditions muddy.

In Lake Abashiri, the muddy sediments occupy about 30 to 40 % of the shallower area than depth 5 m, where the sediment are not covered by the anoxic polyhaline lower stratum. In the southern habitat, the resources enhancements were succeeded by the sediment improvements. For example, the abundances of *C. japonica* changed from 400 ind. / m<sup>2</sup> to 1,580 ind. / m<sup>2</sup> in two years after the muddy sediments were covered by 30 cm-thick sand layer in Lake Jinzai, Shimane, Japan

(Nakamura 2000b). However, the effects of the sediment improvements on the resources enhancements are probably limited in the northern habitat because the spawning dose not occur in some years (Chapter I) and the juvenile growth is extremely slow (Chapter IV) in the northern habitat. Therefore, the conservation of the natural environments around the habitat is much more important in the northern habitat than the artificial resources enhancement efforts.

### Juvenile growth

The juvenile growth of *C. japonica* in Lake Abashiri is extremely slow; it grows to the shell length of 0.7 mm at age 1 and 2.1 mm at age 2. The extreme slow growth is due to the less susceptible growth responses to environmental factors until the second winter (Chapter IV). The population growths of *C. japonica* are very rapid in the southern habitat. For example in Lake Hachiro, the fisheries' harvest of *C. japonica* devastated after land reclamation; and it decreased to less than 100 t in 1980. In August 1987, seawater flowed back into Lake Hachiro when a typhoon attacked there. After the typhoon, the population rapidly enhanced from less than 5 ind. / m<sup>2</sup> (before the typhoon) to 3,000 ind. / m<sup>2</sup> (shell lengths from 3 to 5 mm) in July 1988; and the fisheries harvest drastically increased to 10,900 t in 1990 and it quickly decreased to 281 t in 1994 and 58 t in 1995 (Satoh 2000). Therefore, the southern populations are characterized by strong reproductive ability, rapid individual growth in the early life stage. On the contrary, the northern populations are characterized by unstable reproduction (they do not spawn in the low temperature summer year) (Chapter I), extremely slow juvenile growth (Chapter II), and quite long life span. For example, the fisheries harvest had been kept in the range of 100 to 150 t during 1992 to 1996 in spite of that few juvenile have observed since 1986 in Lake Panke, Horonobe, Hokkaido. Only in recent years, the fisheries harvest decreased to 63 t in 1999 in Lake Panke; i. e. it took more than 10 years until the fisheries harvest decrease from the reproduction systems were destroyed. In the northern habitat, the fisheries harvest is stable due to the long life span; however, different from the southern populations, the rapid population growth can not be expected if the populations were once devastated. Therefore, environment conservations are much more important in the northern habitat than the southern ones.

There are two important points for the conservations. 1) The salinity of the upper stratum should be monitored whether the range is within the appropriate for the spawning. 2) The environments around lakes and inlet rivers, especially woods and reed field, should be conserved not to increase the influx of muddy sediment.

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# 北海道北部に分布するマガレイ資源の特徴とコホート解析

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Features and cohort analysis of brown sole *Pleuronectes herzensteini* population  
in northern Hokkaido, Japan

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To reconsider the area of stock assessment of brown sole *Pleuronectes herzensteini* stock from the Sea of Okhotsk to Ishikari Bay, components of commercial landings, abundance index of juvenile fish and relationships of catch between districts were examined. Positive correlation was observed in the annual catch fluctuation between the present stock assessment area and the Tomamae district. Age structures and occurrence pattern of abundant year class of commercial landings show a geocline from the Sea of Okhotsk to Ishikari Bay. Positive correlation was observed between the abundance index of age one fish in the Ishikari Bay and that of the Sea of Okhotsk. Based on these results and previous mark-recapture studies, we concluded that the brown sole stock from the Sea of Okhotsk to Ishikari Bay is composed of one population. Results of cohort analysis indicate that population size of brown sole stock from the Sea of Okhotsk to Ishikari Bay are influenced by recruitment of dominant year class.

キーワード：マガレイ，漁獲物組成，資源評価，コホート解析

## まえがき

北海道の日本海中部からオホーツク海にかけての水深150m以浅の海域にはマガレイ *Pleuronectes herzensteini* が分布し，沿岸漁業および沖合底曳き網漁業の重要な漁獲対象となっている<sup>1)</sup>。このマガレイ資源に関する調査研究は1920年代に始まり，標識放流による個体の移動追跡<sup>2-9)</sup>，漁獲物の生物測定や年齢・成長解析<sup>2,4,10-18)</sup>，寄生虫を指標とした群判別<sup>19)</sup> および小型桁網を用いた幼魚の分布調査<sup>17, 20-25)</sup>が実施された。こうした調査研究の結果，本資源は産卵場所や生育場所の異なる3群から構成される

と考えられるようになった<sup>1)</sup>。このうち最も広い海域に分布するのが日本海とオホーツク海を行き来する群で，この群は日本海で生まれ卵から仔魚期にオホーツク海に移送され，未成魚期までの2～3年間でそこで生活することから<sup>2, 3, 10, 11, 13)</sup>，オホーツク海育ち群と呼ばれている<sup>1, 13)</sup>。一方，一生を日本海で生活する群もあり<sup>15)</sup>，これらは日本海育ち群と呼ばれている<sup>1, 13)</sup>。日本海育ち群はオホーツク海育ち群と比べ成長が遅いという特徴を持ち，石狩湾を中心に分布すると考えられている<sup>1, 9, 15)</sup>。これら2群とは別に，紋別から知床半島沿岸で産卵する群もあり<sup>17, 18)</sup>，

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Nagasawa and Maruyama<sup>19)</sup>は橈脚類の一種 (*Haemobaphes diceraus*) の寄生率の違いから、この群はオホーツク海育ち群とは異なる群であると位置付けている。これら3群は生活史や成長様式および産卵場の違いが認められるものの、こうした違いが遺伝的な差異を伴うものか、あるいは卵や幼稚魚期における偶発的な移動の結果3群に分かれるのかについては明らかにされていない。

北海道では本マガレイ資源を含む23魚種47海域について資源調査を実施し、資源状態を評価して漁業者や関係団体に公開している<sup>26)</sup>。本資源では評価対象海域が日本海北部（初山別以北）～オホーツク海海域と設定され、日本海における分布域のうちおよそ半分の海域が評価対象とされていない。しかしながら、標識放流試験によると、オホーツク海で放流された個体が初山別以南の海域で漁獲された例や<sup>2,3)</sup>、礼文島沖で放流された個体が小平沖や小樽沖で漁獲された例が確認されている<sup>4)</sup>。逆に、石狩湾や留萌沿岸で標識放流した個体の中には、初山別以北で再捕獲された事例も見られる<sup>6-9)</sup>。さらに、漁獲物の年齢・体長組成からは、日本海育ち群とオホーツク海育ち群は初山別以南の海域で混生している可能性が指摘されている<sup>10,12,13,27)</sup>。したがって、本資源は石狩湾～オホーツク海の海域で連続した1つの資源単位とみなせる可能性がある。

初山別以北日本海～オホーツク海におけるマガレイの資源調査は1970年代から継続的に行われてきた。また、石狩湾～初山別以南の日本海においても1990年代から継続して資源調査が行われ、これまでに14年分の調査結果が蓄積された。本研究ではこれらの資料をもとに海域間における漁獲物組成や漁獲動向の類似性を明らかにし、従来の知見と併せて、本資源の構造とその成因を考察し、資源評価の対象海域を再検討した。さらに、コホート解析で石狩湾～オホーツク海における資源動向を推定した。

## 材料及び方法

### 1. 漁獲量の動向

本マガレイ資源の産卵期は4月～6月のため<sup>1)</sup>、資源評価上の誕生日を7月1日と定義している。これに従って漁獲量は7月から翌年6月までを各年度の集計期間とし、1985年度から2003年度までを収集した。沿岸漁業による漁獲量は北海道水産現勢の統計数値を集計し、集計の範囲は知床半島西岸のウトロ地区から稚内地区を経て石狩湾西部の積丹地区までとした。沿岸漁業の海域区分はオホーツク海南部（ウトロ地区～雄武地区）、オホーツク海北部（枝幸地区～宗谷地区）、初山別以北日本海（稚内地区～初山別地区）、苫前海域（羽幌地区～苫前地区）、小平海域（小平地区～増毛地区）および石狩湾（浜益地区～

積丹地区）とした（図1）。なお、Nagasawa and Maruyama<sup>19)</sup>がオホーツク海他海域とは異なる群が分布するとした網走湾（ウトロ地区～網走地区）は、オホーツク海全体の漁獲量に占める割合が低いことから（1985～2003年の平均で3.6%）、オホーツク海南部に含めた。沖合底曳き網漁業（以下、沖底漁業）による漁獲量は北海道沖合底曳き網漁場別漁獲統計年報の200海里専管水域内の中海区「道西」および「オホーツク」の統計数値を集計した。このうち中海区「道西」については現行の評価海域内の海域（稚内ノース場、利札周辺、武蔵堆および島周辺）と、これ以外の海域（雄冬沖、積丹沖および余市沖）に分けて集計し、前者を日本海北部、後者を日本海中部と定義した（図1）。

海域間における1985～2003年度の漁獲量の相関関係を共分散構造分析で調べた。この分析では、各海域の漁獲量データについて総当たりの相関を設定したモデルを作り、海域間の相関係数およびその有意確率について統計ソフト（SPSS, Amos 5.0）を用いて算出した。

### 2. 漁獲物組成および年齢別漁獲尾数

上記の海域区分毎に漁獲量の多い地区を選定し、銘柄別に5～12kgのマガレイ標本を採集して各個体の体長、体重を測定し、西内<sup>16)</sup>に従って耳石の輪紋数から年齢を査定した。これを銘柄別に集計して1991年から2004年ま

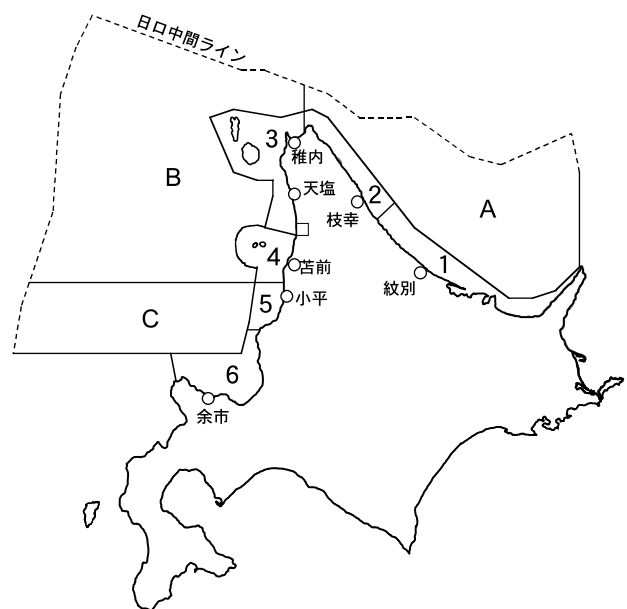


図1 サンプルングを実施した漁協の位置（○）および海域の区分  
1：オホーツク海南部，2：オホーツク海北部，3：初山別以北日本海，4：苫前海域，5：小平海域，6：石狩湾，以上沿岸漁業，A：オホーツク海，B：日本海北部，C：日本海中部，以上沖合底曳き網漁業，□は初山別地区を示す。

での標本組成を求めた。あわせて、各銘柄の漁獲重量を集計し、これを用いて銘柄別の標本組成を重み付けして漁獲物全体の組成に換算した。沿岸漁業の標本採集地区は、オホーツク海南部は紋別地区（一部の標本は湧別地区）、オホーツク海北部は枝幸地区、初山別以北日本海は稚内地区（秋季～冬季）および天塩地区（春季）、苫前海域は苫前地区、小平海域は小平地区および石狩湾は余市地区とした。また、沖底漁業の標本は、オホーツク海は枝幸機船漁業協同組合（1999年に枝幸漁協と合併したため、これ以降は枝幸漁協所属の沖合底曳き網漁船）の漁獲物を採集し、日本海北部は稚内機船漁業協同組合で標本採集を行った。標本を採集した地区の漁獲物組成がその地区を含む海域全体の組成を代表していると仮定して、各海域区分の総漁獲重量で標本採集地区の年齢別漁獲尾数を引き延ばした。これを全海域分集計して石狩湾～オホーツク海海域における年齢別漁獲尾数とした。ただし、日本海中部の沖底漁業は標本採集を実施しなかったため、年齢別漁獲尾数にはこの海域の漁獲量分を含めなかった。なお、標本の採集、測定および解析は、紋別地区は網走水試、余市地区は中央水試、その他の地区は稚内水試が担当した。

各標本採集地区の年齢および体長組成の1991～2004年における平均値を求め、地区間における組成の類似性を類似度指数（木元の  $C\pi$ <sup>28)</sup>）により評価した。この指数は0～1の間をとり、2群間の組成が類似している場合に1に近い値を示す<sup>28)</sup>。木元の  $C\pi$  の算出には小椋<sup>29)</sup> の付属ソフトを用いた。

### 3. 年級群豊度

漁獲物の地区間における年級群豊度の類似性を比較するために、各年級群の1～5歳時における漁獲尾数の合計を年級群豊度と定義した。なお、後述の通り本資源では、漁獲物の70%以上が5歳以下である。ただし、1999年級群および2000年級群は、5歳までの漁獲が終了していないことから、それぞれ1～4歳魚および1～3歳魚の漁獲尾数の合計を年級群豊度とした。

### 4. コホート解析

本研究ではPope<sup>30)</sup> の近似式を用いて各年齢の資源尾数および漁獲係数（F）を算出した。加入年齢は1歳とし、8～10歳をプラスグループとした。自然死亡係数は田中<sup>31)</sup> の方法で西内<sup>20)</sup> が求めた値（雌：0.208、雄：0.250）を用いた。最近年の資源尾数のうち3歳以上は最近年のFを過去3年の平均値と仮定して資源尾数を求めた。1歳の資源尾数は幼魚期の密度指数<sup>20, 24)</sup> とコホート解析による1歳資源尾数との直線回帰式から算出し、2歳の資源尾数は前年度の1歳資源尾数から自然死亡と漁獲尾数を差し引く前進計算により求めた。この最近年資源尾数の

算出方法は、現行の資源評価海域（初山別以北日本海～オホーツク海）向けに考案されたものだが<sup>32)</sup>、本研究では石狩湾～オホーツク海の資源に対しても適用可能と仮定した。雌の8+のFは同年度の7歳魚と等しいと仮定した。雄は6歳以上の個体が多く、多くの年度においてサンプルに出現しなかったことから、6歳～8+のFは同年度の5歳のFと等しいと仮定した。本資源の雄は、4歳以降成長が鈍化するため<sup>9, 16)</sup> 漁獲圧が大きく変化するとは考えにくいことから、この仮定は妥当と推定される。幼魚の密度指数としては現行の資源評価で用いているオホーツク海の雄武町沿岸における1歳魚密度指数に加え、日本海の小平町沿岸における0歳魚密度指数<sup>33)</sup> および石狩湾における1歳魚密度指数<sup>34)</sup> を用いた。これらの指数はそれぞれ資源尾数と漁獲量と関連することが示されている<sup>33, 34)</sup>。幼魚密度指数は海域によって調査に使用した船舶や漁具が異なることから、下式により1993～2000年級群の平均値を100とした相対値にそれぞれ標準化した。

$$I_s = 100 \cdot I_o / I_a$$

ただし  $I_s$  は標準化した密度指数、 $I_o$  は各年級群の密度指数および  $I_a$  は1993～2000年級群における密度指数の平均値である。

各海域における標準化した幼魚密度指数と、コホート解析で求めた石狩湾～オホーツク海海域における1歳資源尾数との相関関係に基づき、最適な資源量指数を探索した。なお、1993年級群を除き10歳までの漁獲が終了していないが、現行の評価海域の資源尾数では、3年間の漁獲データをもとに推定した資源尾数は、漁獲終了年度までの漁獲データから算出した資源尾数との誤差が-8～+11%であることから<sup>32)</sup>、本研究においても1994～2000年級群の1歳資源尾数は誤差が小さいものと仮定し、幼魚密度指数との相関分析に用いた。

## 結 果

### 1. 漁獲量の動向

各年度の漁獲量を図2に示した。現在資源評価対象としていない海域における漁獲量は、総漁獲量の28～50%を占めていた。漁獲量の変動幅は現行の評価海域で大きかった。特に総漁獲量が多い年において現行の資源評価海域の漁獲量が多く、総漁獲量に占める割合が高かった（1985、1995、1997および2003年度に特徴的）。小区分した海域間で漁獲量の相関関係を調べた（表1）。苫前海域は初山別以北日本海と、初山別以北日本海はオホーツク海南部の沿岸漁業と正の相関を示した。オホーツク海の南部の沿岸漁業は、日本海北部および中部の沖底漁業と正の相関を示した。

月別の漁獲量の動向を1985～2003年度の平均値として



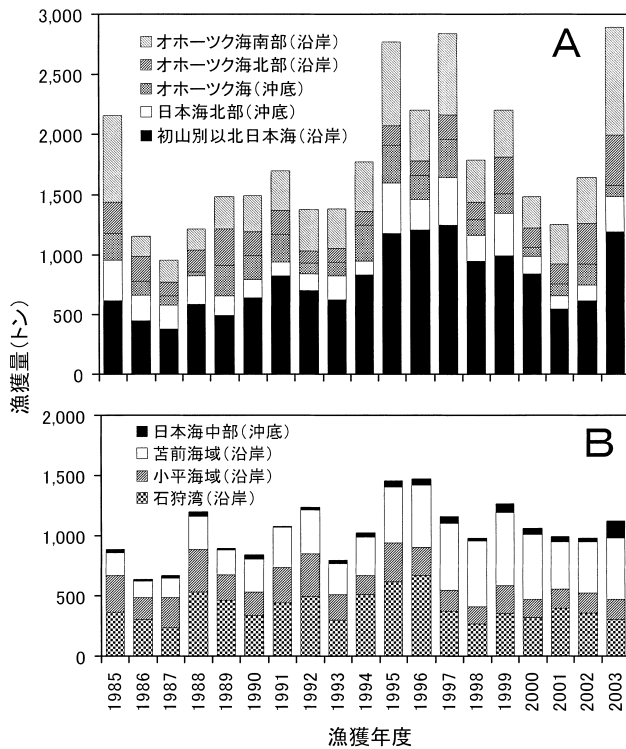


図2 石狩湾～オホーツク海におけるマガレイの漁獲量の推移  
A：現行の資源評価対象海域，B：資源評価対象以外の海域。

表1 マガレイ漁獲量の地区間における相関係数

	オホーツク海南部(沿岸)	オホーツク海北部(沿岸)	オホーツク海(沖底)	日本海北部(沖底)	初山別以北日本海(沿岸)	苫前海域(沿岸)	小平海域(沿岸)	石狩湾(沿岸)
オホーツク海北部(沿岸)	0.452							
オホーツク海(沖底)	0.437	0.061						
日本海北部(沖底)	0.643*	0.233	0.338					
初山別以北日本海(沿岸)	0.689*	0.121	0.418	0.576*				
苫前海域(沿岸)	0.415	0.143	0.108	0.321	0.825**			
小平海域(沿岸)	0.003	0.175	0.016	0.247	0.092	0.279		
石狩湾(沿岸)	0.118	0.249	0.407	0.125	0.348	0.129	0.494	
日本海中部(沖底)	0.676*	0.528*	0.090	0.442	0.631*	0.584*	0.248	0.065

漁獲量データは1985～2003年度を使用( $n=19$ )

星印は有意な相関を示す(\*:  $p<0.05$ , \*\*:  $p<0.01$ )

図3に示した。沿岸漁業のうちオホーツク海の南部では11月に、北部では7月と10月に漁獲量のピークがあった。初山別以北日本海では4月と11月の2回漁獲量のピークがあった。苫前海域、小平海域および石狩湾では、3～6月に集中して漁獲があり、漁獲量のピークは4月または5月であった。沖底漁業は、オホーツク海では9～10

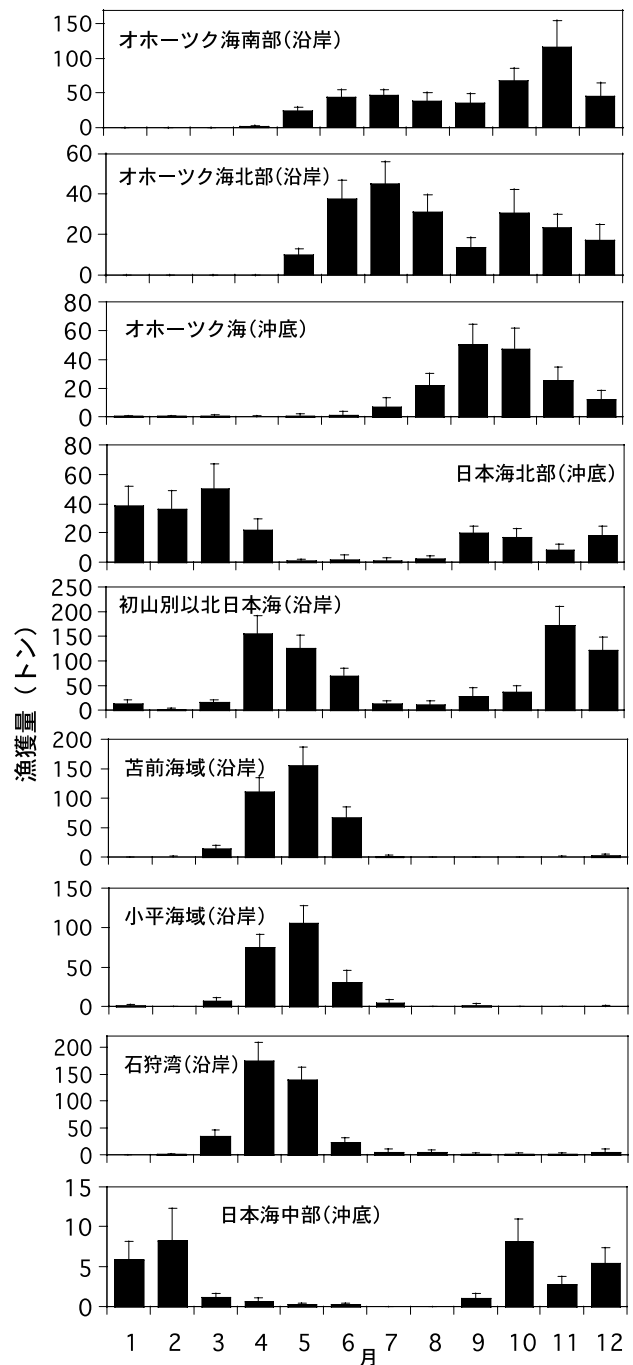


図3 マガレイの地区別・月別漁獲量  
1985～2004年の平均値とその標準誤差で示す。

月の漁獲量が多く、日本海では北部、中部ともに9～3月の漁獲量が多かった。

## 2. 漁獲物組成

地区毎の漁獲物の年齢組成を図4に、地区間における類似度指数を表2に示した。沿岸漁業のうちオホーツク海から宗谷海峡に位置する地区(紋別地区、枝幸地区お

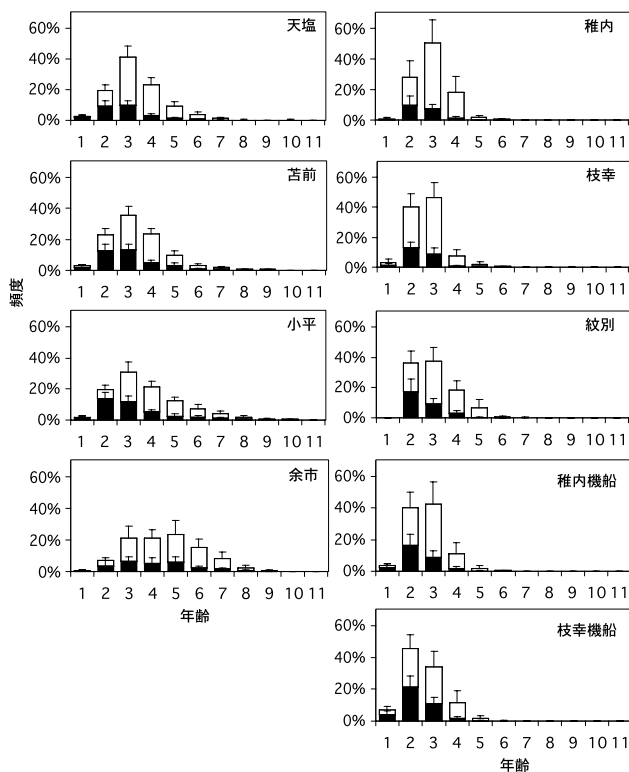


図4 石狩湾～オホーツク海におけるマガレイ漁獲物の年齢組成  
1991～2004年の平均値およびその標準誤差。  
□:雌, ■:雄。

表2 石狩湾～オホーツク海で漁獲されたマガレイの地区間における年齢組成の類似度指数(木元の $C_{\pi}$ )

	紋別	枝幸	枝幸機船	稚内機船	稚内	天塩	苫前	小平
枝幸	0.93							
枝幸機船	0.96	0.92						
稚内機船	0.97	0.99	0.96					
稚内	0.93	0.95	0.86	0.95				
天塩	0.95	0.86	0.84	0.89	0.94			
苫前	0.94	0.80	0.87	0.85	0.85	0.96		
小平	0.89	0.71	0.80	0.78	0.77	0.91	0.98	
余市	0.67	0.50	0.51	0.54	0.58	0.77	0.80	0.87

よび稚内地区)の漁獲物は主に2～3歳魚で構成される点で類似し、これらの地区間における類似度指数は全ての組み合わせで0.93以上と高かった。また、沖底漁業の漁獲物の年齢組成もこれらの地区との類似性が高かった(0.86～0.99)。一方、天塩地区～余市地区にかけての漁獲物は枝幸地区や紋別地区のものとは比べ、4歳以上の比率が高かった。この傾向は南ほど顕著であり、最南に位置する余市地区の漁獲物は3、4および5歳魚がほぼ同率でそれぞれ約20%を占め、6歳魚の比率も15%あった。類似度指数によると、余市地区の漁獲物の年齢組成は隣接する小平地区やその北に位置する苫前地区や天塩地区とは0.87～0.77と高いものの、稚内地区、枝幸地区および紋別地区とはこれらと比べ低い値(0.67～0.50)を示

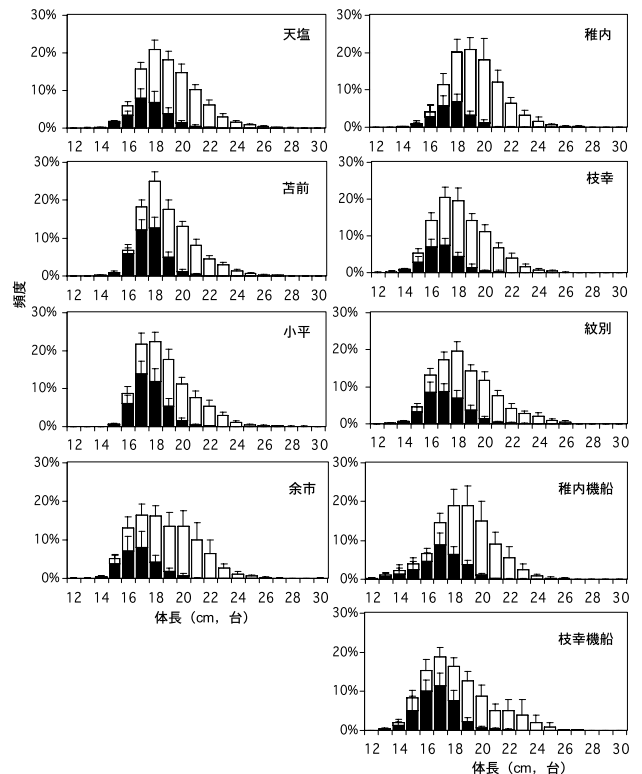


図5 石狩湾～オホーツク海におけるマガレイ漁獲物の体長組成  
1991～2004年の平均値およびその標準誤差。  
□:雌, ■:雄。

表3 石狩湾～オホーツク海で漁獲されたマガレイの地区間における体長組成の類似度指数(木元の $C_{\pi}$ )

	紋別	枝幸	枝幸機船	稚内機船	稚内	天塩	苫前	小平
枝幸	0.96							
枝幸機船	0.97	0.91						
稚内機船	0.95	0.93	0.90					
稚内	0.90	0.88	0.81	0.98				
天塩	0.96	0.94	0.89	0.99	0.98			
苫前	0.95	0.89	0.92	0.96	0.92	0.96		
小平	0.95	0.89	0.94	0.94	0.88	0.94	0.99	
余市	0.97	0.97	0.93	0.97	0.93	0.97	0.92	0.91

した。天塩地区および苫前地区は隣接する稚内地区や小平地区との類似度指数が特に高かった(0.94～0.98)。

漁獲物の体長組成は全ての地区で単峰型を示した(図5)。余市地区の体長組成は他の地区と比べピークが不明瞭な分布型を示し、16～20cmの各サイズクラスはほぼ一定の頻度(15%前後)を占めた。(図5)。組成のピークを示す体長は、枝幸地区、枝幸機船および余市地区では体長17cm、稚内地区では19cm、これ以外の地区では体長18cmであった。ただし、類似度指数は全ての組み合わせで0.81～0.99と高く(表3)、地区間の差は小さかった。

### 3. 年級群豊度

1990～2000年級群の年級群豊度を沿岸漁業の海域毎に図6に示した。年級群豊度の動向は苫前海域および初山

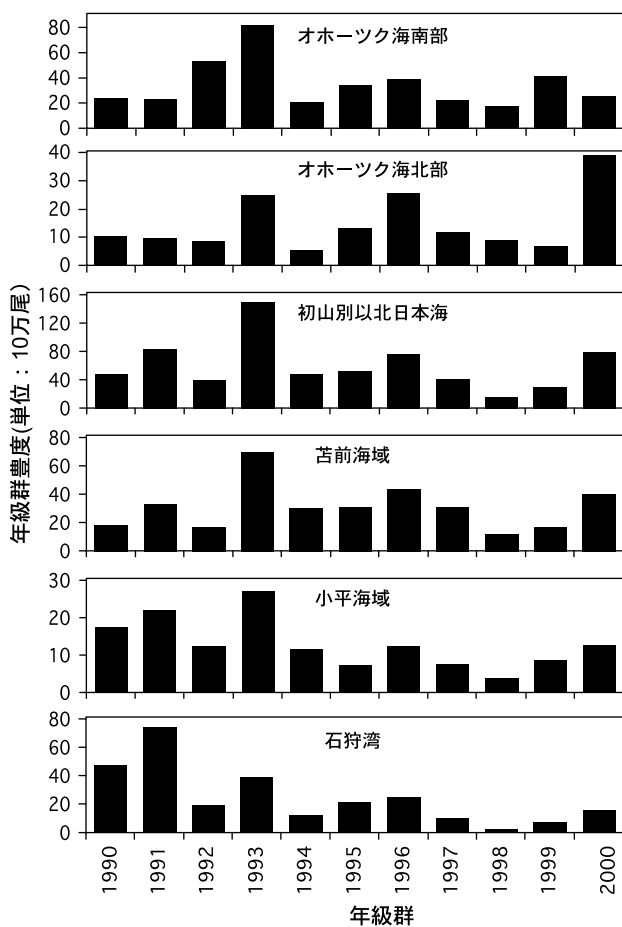


図6 オホーツク海～石狩湾の沿岸漁業におけるマガレイの年級群豊度  
年級群豊度は1～5歳魚の漁獲尾数の合計。ただし、1999および2000年級群はそれぞれ1～4歳魚および1～3歳魚の漁獲尾数の合計。

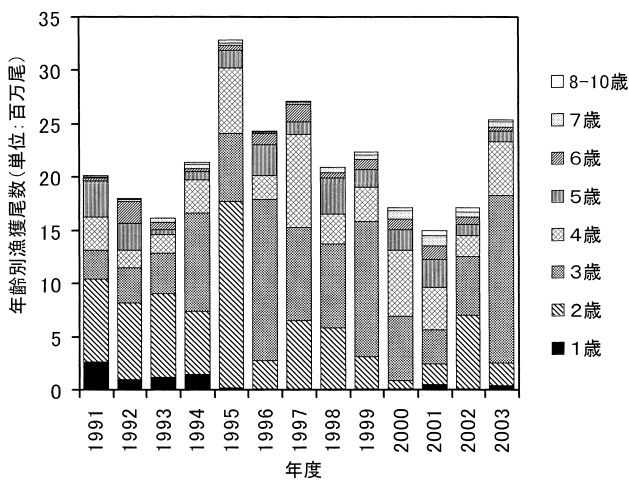


図7 石狩湾～オホーツク海におけるマガレイの年齢別漁獲尾数

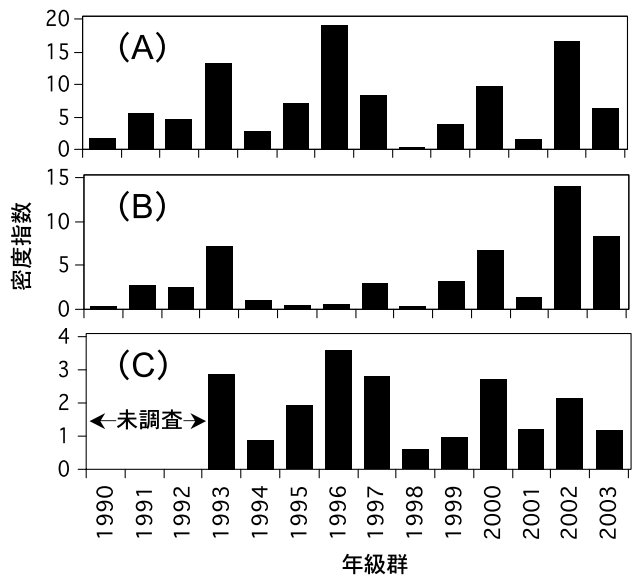


図8 各海域におけるマガレイ幼魚の密度指数  
A：雄武沖1歳魚，B：小平沖0歳魚，C：石狩湾1歳魚。

別以北日本海の間で非常に良く一致し、両海域とも1993、1996および2000年級群の豊度が高いという特徴があった。一方、石狩湾における年級群豊度は1990および1991年級群で顕著に高く、この点で苫前海域、初山別以北日本海およびオホーツク海と異なっていた。両者の中間に位置する小平海域は双方の特徴を示し、1990、1991年級群の豊度が高いと同時に、1993、1996および2000年級群の豊度も高かった。オホーツク海における年級群豊度は苫前海域および初山別以北日本海とほぼ同様の動向を示したが、オホーツク海南部において1992年級群の豊度が高い点では他海域と異なっていた。

#### 4. 年齢別漁獲尾数

石狩湾～オホーツク海における年齢別漁獲尾数(図7)は1995年度に増加し、3,287万尾に達した。これはこの年の2歳魚、すなわち1993年級群の漁獲尾数が多かったためで、総漁獲尾数の半数以上を占めた。1993年級群は1996および1997年度も漁獲物の中心となり、この時期の豊漁を支えた。1999年度になると1993年級群は約103万尾が漁獲されただけとなり、これに代わって1996年級群が漁獲尾数の半数以上を占めるようになった。その後1996年級群の減少に伴い総漁獲尾数は2001年に1,493万尾にまで減少した。2003年度は2000年級群が3歳魚として1,583万尾漁獲され、総漁獲尾数は2,542万尾に増加した。

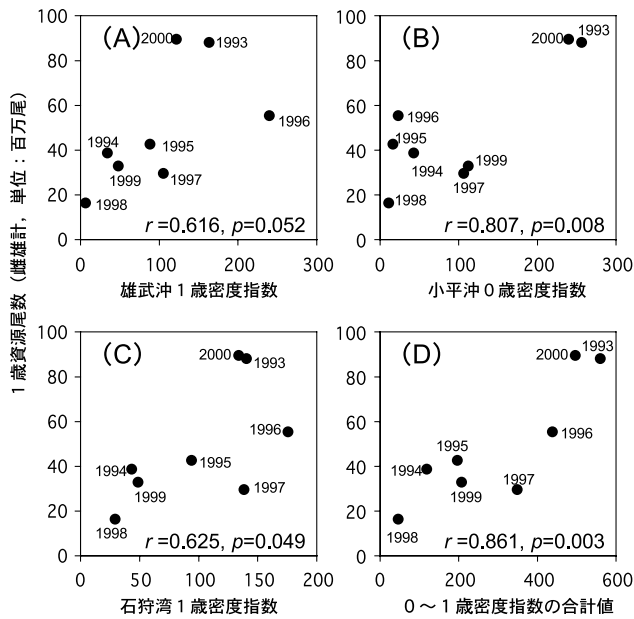


図9 コホート解析で算出したマガレイ1歳魚の資源尾数と標準化した幼魚密度指数との相関関係。マーカー横の数値は年級群を示す。幼魚密度指数は雄武沖1歳魚(A)，小平沖0歳魚(B)および石狩湾1歳魚(C)の値。(D)はすべての幼魚密度指数を合計した場合を示す。

##### 5. 幼魚の密度指数と1歳資源尾数との関係

各海域における0歳または1歳幼魚の密度指数を図8に示した。雄武沖1歳魚の密度指数は、1993、1996、2000および2002年級群で高かった。小平沖0歳魚密度指数は、1993、2000および2002年級群が高い点では雄武沖1歳魚と共通していたが、1996年級群が低い点では異なっていた。1996年級群を除くと両者の動向は良く一致し、高い正の相関が認められた( $r=0.852$ ,  $p<0.001$ )。石狩湾の1歳魚密度指数は、雄武沖の1歳魚密度指数と同様に1993、1996、2000および2002年級群で高く、両者の間には高い正の相関が認められた(1996年級群を含めた場合： $r=0.856$ ,  $p=0.001$ ，1996年級群を含めない場合： $r=0.785$ ,  $p=0.007$ )。なお、石狩湾1歳魚密度指数と小平沖0歳魚密度指数との間には、相関は認められなかった(1996年級群を含めた場合： $r=0.190$ ,  $p=0.575$ ，1996年級群を含めない場合： $r=0.428$ ,  $p=0.162$ )。

コホート解析を用いて前述の年齢別漁獲尾数から石狩湾～オホーツク海における1993～2000年級群の年齢別資源尾数を算出し、このうち各年級群の1歳資源尾数を抽出して、標準化した幼魚密度指数との相関関係を調べた(図9)。雄武沖1歳魚密度指数は1歳資源尾数と有意な相関は得られず(図9-A,  $r=0.616$ ,  $p=0.052$ )、また

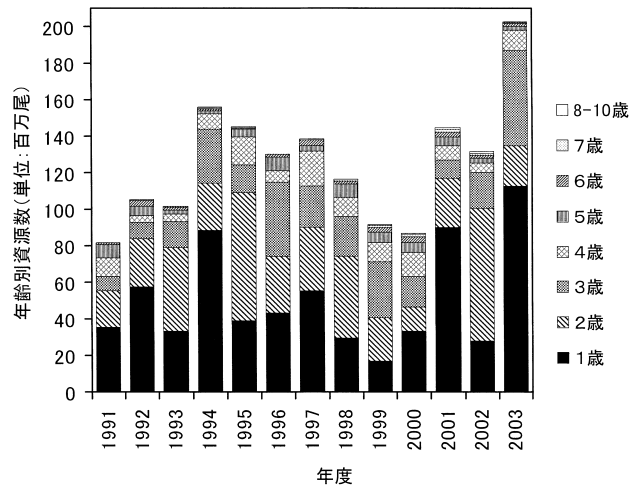


図10 石狩湾～オホーツク海におけるマガレイの資源尾数

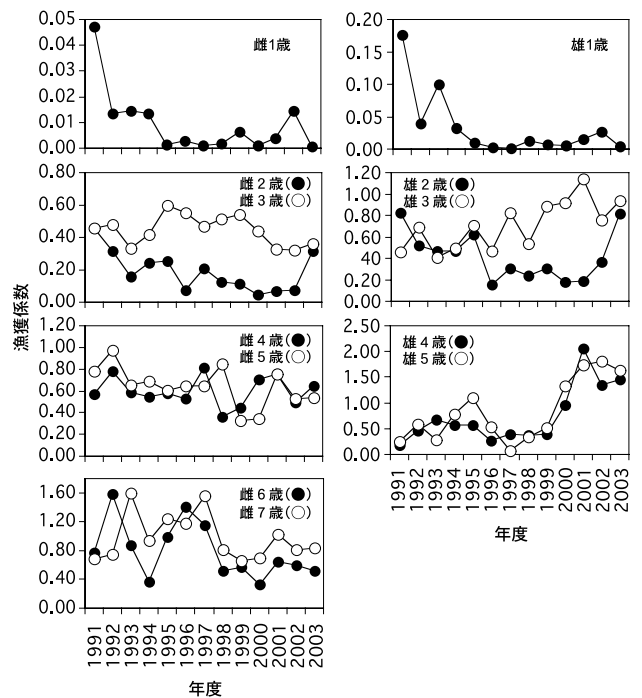


図11 石狩湾～オホーツク海におけるマガレイの漁獲係数

石狩湾1歳資源尾数はかろうじて正の相関が検出された(図9-C,  $r=0.625$ ,  $p=0.049$ )。小平沖0歳幼魚密度指数は1歳資源尾数と高い正の相関が得られたが( $r=0.807$ ,  $p=0.008$ )、散布図(図9-B)は1993および2000年級群の影響が大きいことを示している。これら3海域の幼魚密度指数は、単独では1歳資源尾数の予測に有効とはいい難かった。そこで、これら3海域の標準化した密度指数の和を求め1歳資源尾数と相関分析を試みたところ、両

者の間には高い正の相関が認められ( $r=0.861, p=0.003$ ), また, プロットの偏りは見られなかった(図9-D)。したがって, 本資源の1歳の最近年の資源尾数を推定するには, 3海域の幼魚密度指数を併用した推定手法が適していると予想される。ここでは便宜的に3海域の幼魚密度指数の和を用い, 図9に示した1歳資源尾数を雌雄に分離して, それぞれの資源尾数を目的変数( $y$ , 単位: 百万尾), 3海域の標準化した幼魚密度指数の和を説明変数( $x$ )とした回帰分析を行い, 下記の直線回帰式を得た。雌,  $y=0.0993x+7.5308$ ,  $R^2=0.705$ ,  $p=0.009\cdots$  (1) 雄,  $y=0.0249x+4.6387$ ,  $R^2=0.554$ ,  $p=0.035\cdots$  (2)

## 6. 資源尾数および漁獲係数の動向

2001および2002年級群について式(1)および式(2)に3海域における標準化した幼魚密度指数の和(2001年級群: 128, 2002年級群: 805)を代入し, 各年級群の1歳資源尾数を求めた。さらに, 2001年級群については1歳資源尾数から1歳時の漁獲尾数および自然死亡を差し引いて, 2003年度における2歳資源尾数を求めた。この他の年級群の資源尾数はコホート解析の後退法で算出し, 1991~2003年度の資源尾数を求めた(図10)。1991年度に8,183万尾であった総資源尾数は, 1994年度に豊度の高い1993年級群が加入したことで1億5,573万尾に増加した。1997年度に加入した1996年級群の豊度も高く, 両年級群が1994~1998年度の資源の中心となった。両年級群が漁獲と自然死亡により減少した1999~2000年には総資源尾数は1億尾以下となったが, 2001年に豊度の高い2000年級群が加入したことで資源尾数は1億4,456万尾となった。2003年度にはさらに高豊度の2002年級群の加入により, 総資源尾数は2億尾に達したものと推定された。ただし, 近年, 主に2歳魚以上を漁獲対象としていることから, 2003年度の漁獲量は資源尾数の伸びほどには増加していない(図7)。

1991~2003年度における漁獲係数の経年変化を図11に示した。1~2歳魚の漁獲係数は1991年度以降低下する傾向にあったが, 2003年度の2歳魚および2002年度の1歳魚(ともに2001年級群)は過去7年間と比べ高い値を示した。逆に, 2003年度における1歳魚(2002年級群)の漁獲係数は雌雄ともこれまでで最も低い値(雌: 0.0006, 雄: 0.0037)を示した。雌の3~7歳魚の漁獲係数は際だった経年変化は認められず, 3歳魚は0.4前後, 4~5歳魚は0.6前後, 6~7歳魚は0.8前後を推移した。雄の3~5歳魚の漁獲係数は1990年代後半から上昇した。この傾向は特に4~5歳魚に顕著で, 2000年度以降1.5程度の高い値を示している。

## 考 察

本研究の結果によると, 漁獲物の年齢組成はオホーツク海では2~3歳の若齢魚が多いのに対し, 日本海では3~4歳魚が主体で南部ほど高齢魚の比率が高かった。オホーツク海に若齢魚が多いことは, 福田<sup>2)</sup> および山本ら<sup>3)</sup> が1960年代はじめに実施した枝幸地区および網走地区の調査結果で明らかにしている。また, 菅間<sup>10, 12)</sup> は1965~1969年に天塩地区~増毛地区で実施した漁獲物調査に基づいて増毛地区に高齢魚が多いことを見出し, さらに, 加賀・菅間<sup>15)</sup> は1960年代中盤の調査結果から石狩湾の漁獲物には5歳以上の割合が高いことを報告している。近年では星野<sup>27)</sup> が2002年の稚内地区~小平地区の産卵期の漁獲物を調べ, 小平地区で高齢魚が多いことを確認している。本研究の結果はこれらの知見から類推されてきた年齢組成の地理的傾斜, すなわちオホーツク海では若齢, 日本海では南ほど高齢といった傾向が, 本資源の一般的特性であることを明らかにした。

年齢組成が海域間で変化する原因について, 菅間<sup>10)</sup>, 高<sup>13)</sup> および加賀・菅間<sup>15)</sup> は日本海南部では成長の遅い日本海育ち群が多く, 逆に日本海北部には成長の速いオホーツク海育ち群が多いためであると考察している。星野<sup>27)</sup> も小平地区で高齢魚が漁獲されるのは, オホーツク育ち群の高齢魚が多いこと, および日本海育ち群の比率が高いためと推定している。菅間<sup>10)</sup> は増毛沿岸で漁獲されるマガレイには高成長の若齢魚と低成長の高齢魚の2群が認められ, 前者がオホーツク海育ち群, 後者が日本海育ち群に相当すると述べている。本研究の資源豊度の動向では, 増毛沿岸を含む小平海域は, 苫前以北日本海~オホーツク海と石狩湾の双方の特徴を併せ持っていた。また, 苫前海域の漁獲量はその北方に位置する初山別以北日本海と正の相関を示した。これらの知見は, 苫前海域~小平海域においてオホーツク海育ち群と日本海育ち群が混生していることを示唆する。

オホーツク海育ち群は未成魚期の2~3年間でそこで過ごした後, 繁殖期が近づく日本海へと移動し, 4~6月に日本海の沿岸一帯で繁殖を行う<sup>1)</sup>。このことは, 古くは1928~1930年に行われた標識放流で予見され<sup>2)</sup>, その後, 1960年代に実施された標識放流<sup>3,4)</sup> や, 生物測定調査<sup>2,11,13)</sup> によって確認された。宗谷海峡を通過する時期について福田<sup>2)</sup> は1920年代に実施された標識放流調査の際の復命書を引用して11~12月と推定している。福田<sup>4)</sup> および福田<sup>11)</sup> もまた, 1965~1966年に実施した天塩海域および礼文水道海域における漁獲物調査に基づき, オホーツク海から回遊してきた群は11月上旬に礼文水道海域に達すると推定している。本研究の月別・地区別の漁獲動向でも, 初山別以北日本海では11~12月に漁獲量が増

加した。これは初回産卵に向けてオホーツク海から日本海へと移動する魚群が、この時期に宗谷海峡付近を通過した際に漁獲されることを示している。

以上のように本研究は、本資源の構造やその成因について限られた海域・年代の調査結果をもとに考えられてきた仮説を、最近14年間における広域的かつ継続的な調査結果から支持した。すなわち、本資源は主にオホーツク海育ち群と日本海育ち群から構成され、前者は産卵期直前の秋から冬にかけて宗谷海峡を通過し日本海へと移動する。一方、石狩湾から小平・苫前にかけての海域には日本海育ち群が分布し、産卵期の日本海において両育ち群が混合する。それぞれが漁獲物に占める割合には地理的傾斜があり、小平・苫前海域で両者が拮抗すると考えられる。こうした資源構造、および1歳幼魚の密度指数が石狩湾とオホーツク海との間で正の相関を示すことや、これまで行われた標識放流において、初山別海域の南北での個体の移動が確認されている<sup>24,6-9)</sup>ことも考え合わせると、本資源は石狩湾以北日本海～オホーツク海において連続性があり、何らかの分布境界が初山別海域に存在するとは考え難い。したがって、石狩湾以北日本海～オホーツク海のマガレイ資源を2つの育ち群から構成される1つの個体群とみなし、資源状態を評価することが適当であると結論づけられる。

コホート解析によると、石狩湾～オホーツク海におけるマガレイの資源尾数は、1994年度の1億5,573万尾をピークに減少し、1999および2000年度には1億尾を下回った。2001年度以降、資源尾数は再び増加し、2003年度には2億尾に達した。こうした資源尾数の増減には高豊度年級群の有無が大きく影響し、近年の資源回復は2000および2002年級群によってもたらされている。ただし漁獲係数から見ると、2002年級群の1歳時の漁獲係数は、非常に低い値を示していることから、1歳資源尾数が過大推定となっている可能性がある。逆に、2001年級群の1歳資源尾数は2,806万尾と少なく見積もられているが、2003年における2歳時の漁獲係数は過去1～2番目に相当する高い値を示し、資源尾数が過小推定となっている可能性が考えられる。本資源では資源量指数の調査年数が少ないため、そこから導かれる最近年の1～2歳資源尾数の推定精度が高くない可能性があり、資源評価に際しては漁獲係数に基づいて資源尾数の妥当性を検討することも必要である。

漁獲係数の推移は、1990年代後半から1歳魚に対する漁獲圧が低下する一方で、2000年以降4～5歳の雄に対する漁獲圧が上昇したことを示している。1歳魚に対する漁獲圧が低下した原因としては、近年魚価が低迷し特に最小銘柄の魚価が安いこと<sup>35)</sup>、1歳魚が水揚げ対象

とされなくなったことが考えられる。また、1996年に締結された体長15cm未満の未成魚の漁獲を制限する資源管理協定が、一定の効果を上げていることも考えられる。4～5歳の雄のほとんどは成魚で、その多くが春の繁殖期に日本海で漁獲される。日本海における漁獲物の性比には月変化が認められ、繁殖期前半の4月には雄が多く漁獲されるのに対し、繁殖期後半の5月には雌の比率が高まることが知られている<sup>27)</sup>。近年特に留萌支庁管内では盛漁期が4月に移行しつつあり<sup>35)</sup>、このことが雄成魚に対する漁獲圧の上昇と関係している可能性がある。

本研究では、石狩湾以北日本海～オホーツク海のマガレイ資源を1つの資源単位とみなして資源解析を行うことで、その動向や資源加入の状況が明らかになった。その一方で、本研究の結果や既往の知見は、漁獲対象となる年齢組成や生活史ステージ、育ち群が海域によって変化することも示している。したがって、海域毎の資源状態を明らかにし、漁業現場に還元することも重要である。現行の資源評価海域においては、オホーツク海と日本海に分けて資源状態を推定し、漁況予測として公表している<sup>36)</sup>。今後は漁獲対象の特性に基づいて4海域、すなわち、オホーツク海（オホーツク海育ち群の未成魚が漁獲対象の海域）、稚内地区～利尻島・礼文島海域（産卵のため日本海へ向かうオホーツク海育ち群が漁獲対象の海域）、天塩地区～小平地区（主にオホーツク海育ち群成魚が漁獲対象の海域）および石狩湾（主に日本海育ち群の成魚が漁獲対象の海域）に分けて漁況予測を行う必要がある。

本研究では1歳の最近年資源尾数を算出する際に、3海域で調査した0～1歳の密度指数を標準化し、その単純な和を用いた。しかし、この方法はそれぞれの密度指数によって代表される海域の広さや資源尾数、さらには密度指数の年齢差を考慮していないという問題がある。今後、調査結果の蓄積を待って、最適な重み付け方法を開発する必要がある。

## 要 約

石狩湾以北日本海～オホーツク海に分布するマガレイ資源の特徴を、漁獲物組成や幼魚の密度指数および漁獲動向から調べ、従来の知見と併せて資源評価海域を再検討した。現在資源評価対象としていない海域における漁獲量は、総漁獲量の28～50%を占めていた。日本海における現行の評価海域（初山別以北日本海）での漁獲量は、その南側に位置する苫前海域と高い正の相関を示した。漁獲物の年齢組成はオホーツク海では若齢、日本海では南方ほど高齢魚の比率が高くなった。年級群豊度は、石狩湾においては1990および1991年級群で高く、苫前以北日本海～オホーツク海では1993、1996および2000年級群

で高く、両者の間に位置する小平海域は双方の特徴を併せ持っていた。1歳幼魚の密度指数は石狩湾とオホーツク海との間で正の相関が認められた。以上の結果、およびこれまで行われてきた標識放流の結果に基づくと、石狩湾以北日本海～オホーツク海のマガレイ資源は連続性があるものと考えられ、この海域の資源を1つの個体群とみなし、資源状態を評価することが適当であると結論づけた。コホート解析によると、石狩湾以北日本海～オホーツク海のマガレイ資源の動向には、数年に1度の高豊度加入群の影響が大きいと考えられた。

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付表1 年齢・体長組成の推定に用いたサンプルの水揚げ地区, 漁獲年・月・日および使用したサンプルの尾数

紋別	枝幸 (沿岸漁業)	枝幸 (沖底漁業)	稚内	稚内機船	天塩	苫前	小平	余市
1991. 6. 26 ( 84) *	1991. 6. 28 (197)	1991. 10. 8 (276)	1991. 12. 3 (263)	1991. 3. 19 (189)	1991. 5. 15 (114)	1991. 5. 15 (125)	1991. 5. 16 (226)	1992. 5. 15 (152)
1991. 10. 7 (247) *	1991. 10. 8 (195)	1992. 10. 6 (232)	1994. 11. 16 (270)	1992. 3. 26 (281)	1992. 4. 21 (122)	1992. 4. 21 (122)	1992. 4. 21 (206)	1993. 4. 22 (219)
1992. 7. 1 (135) *	1992. 6. 15 (192)	1993. 10. 28 (337)	1995. 12. 12 (123)	1994. 3. 15 (284)	1992. 5. 18 (118)	1992. 5. 18 (114)	1992. 5. 18 (222)	1994. 4. 26 (169)
1992. 10. 14 ( 78) *	1992. 11. 9 (206)	1994. 10. 18 (308)	1996. 11. 12 (138)	1995. 3. 28 (170)	1993. 4. 21 ( 97)	1993. 4. 20 (100)	1993. 5. 17 (166)	1995. 4. 26 (204)
1993. 6. 17 (156) *	1993. 6. 28 (152)	1995. 10. 3 (240)	1997. 11. 10 (189)	1996. 3. 14 (316)	1993. 5. 27 (112)	1993. 5. 18 (110)	1994. 5. 10 (189)	1996. 4. 30 (334)
1993. 10. 20 (169) *	1993. 10. 20 (140)	1996. 10. 28 (220)	1998. 11. 30 (176)	1997. 3. 17 (220)	1994. 4. 27 (127)	1994. 5. 11 (114)	1995. 5. 8 (226)	1997. 5. 1 (308)
1994. 6. 29 (137) *	1994. 7. 4 (184)	1997. 11. 17 (200)	1999. 11. 16 (185)	1998. 2. 23 (300)	1994. 5. 24 (104)	1995. 5. 9 (176)	1996. 4. 16 (230)	1998. 4. 24 (238)
1994. 11. 17 (252) *	1994. 10. 4 (246)	1998. 11. 30 (199)	2000. 12. 20 ( 86)	1999. 2. 21 (193)	1995. 4. 17 (113)	1996. 5. 13 (200)	1996. 5. 13 (212)	1999. 4. 13 (159)
1995. 6. 20 (209) *	1995. 10. 23 (296)	1999. 10. 20 (173)	2001. 12. 13 ( 82)	2000. 2. 25 (244)	1995. 5. 24 (122)	1997. 5. 12 (186)	1997. 4. 22 (234)	2000. 4. 19 (216)
1995. 11. 13 ( 89)	1996. 7. 2 (282)	2000. 10. 26 (189)	2002. 12. 2 ( 82)	2001. 3. 26 (161)	1996. 4. 22 (127)	1998. 5. 18 (199)	1997. 5. 12 (228)	2001. 4. 18 (287)
1996. 6. 15 (126)	1996. 10. 14 (366)	2001. 11. 11 (192)	2003. 11. 12 (161)	2002. 4. 4 (287)	1996. 5. 20 (120)	1999. 5. 18 (129)	1998. 5. 18 (199)	2002. 4. 24 (247)
1996. 11. 12 (112)	1997. 6. 27 (166)	2003. 10. 6 (170)	2004. 12. 4 (136)	2004. 1. 13 (199)	1997. 4. 14 (126)	2000. 4. 17 (202)	1999. 4. 12 (185)	2003. 4. 15 (185)
1997. 6. 25 (146)	1997. 10. 13 (205)	2004. 10. 15 (157)			1997. 5. 7 (135)	2000. 5. 15 (121)	1999. 5. 17 (202)	2004. 4. 7 (247)
1997. 11. 14 (149)	1998. 7. 7 (211)				1998. 4. 23 (137)	2001. 4. 23 (192)	2000. 4. 17 (188)	
1998. 6. 18 (101)	1998. 10. 1 (305)				1998. 5. 29 (129)	2001. 5. 17 (183)	2000. 5. 13 (193)	
1998. 11. 27 (100)	1999. 6. 30 (269)				1999. 4. 15 (135)	2002. 4. 12 (213)	2001. 4. 23 (137)	
1999. 6. 15 (120) *	1999. 10. 20 (136)				1999. 5. 26 (124)	2002. 5. 9 (199)	2001. 5. 17 (182)	
2000. 6. 15 (157)	2000. 8. 3 (209)				2000. 4. 20 (138)	2003. 4. 14 (389)	2002. 4. 12 (257)	
2000. 11. 28 (124)	2000. 12. 8 (236)				2000. 5. 16 (122)	2003. 5. 15 (267)	2002. 5. 9 (272)	
2001. 6. 8 (122)	2001. 6. 26 (303)				2001. 4. 25 (134)	2004. 4. 12 (221)	2003. 4. 15 (217)	
2001. 10. 23 (138)	2001. 12. 4 (326)				2001. 5. 21 (252)	2004. 5. 10 (179)	2004. 4. 16 (128)	
2002. 7. 26 (153)	2002. 6. 27 (326)				2002. 4. 15 (255)			
2002. 10. 6 (187)	2003. 6. 25 (230)				2002. 5. 10 (248)			
2003. 6. 6 (230)	2003. 10. 6 (200)				2003. 4. 24 (284)			
2003. 11. 14 (203)	2004. 6. 21 (196)				2003. 5. 20 (248)			
2004. 7. 21 ( 96)	2004. 10. 15 (200)				2004. 4. 26 (184)			
2004. 11. 19 (204)					2004. 5. 14 (199)			

( ) 内は使用したサンプルの尾数を示す。

\* : 湧別地区でサンプリングを実施。

# 北海道北部産マガレイの耳石輪紋径に基づく「育ち群」判別 第1報 漁獲物の1～3歳における「育ち群」

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Distinction of growth group based on otolith diameter length of brown sole  
*Pleuronectes herzensteini* in northern Hokkaido, Japan

I. Growth group of commercially captured fish at age one to three

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Growth group of brown sole *Pleuronectes herzensteini* population in northern Hokkaido Japan, were distinguished based on otolith diameter length. The Okhotsk Sea growth group was regarded as 91.1% of the commercial landings at the Esashi fish market on the Sea of Okhotsk in autumn of fish age one to the winter of fish age three. All individuals of commercial landings at the Wakkanai fish market in the Soya Strait in the winter of age two were the Okhotsk Sea growth group. Over 86% of the commercial landings at Teshio to the Yoichi fish market in the Sea of Japan in the spring of age two were regarded as the Okhotsk Sea growth group. These results suggested that some of Okhotsk Sea growth group migrate to the Sea of Japan at age two in the winter and arrive in the Ishikari Bay at spawning season at age two. The body size of age two and three fish of the Japan Sea growth group captured by the survey in the Ishikari Bay and the coast of Obira, were smaller than that of commercial landings. We estimated that most of the Japan Sea growth group will be commercial landings after age three in the spring.

キーワード：オホーツク海育ち群，資源構造，耳石，日本海育ち群，マガレイ，輪紋径

## まえがき

北海道沿岸の日本海中部からオホーツク海にかけての海域にはマガレイ *Pleuronectes herzensteini* が広く分布し、沿岸漁業や沖合底曳き網漁業の重要な漁獲対象となっている<sup>1)</sup>。このマガレイは主に石狩湾から利尻島沿岸にかけての日本海で産卵し、卵や仔魚期に宗谷暖流によって

オホーツク海へと移送される群と、そのまま日本海に留まる群とに分かれると考えられている<sup>1)</sup>。前者はオホーツク海育ち群と呼ばれ、未成魚期の2～3年間オホーツク海で生活した後、成熟期が近づくと日本海へと回帰する<sup>1-5)</sup>。一方、日本海に留まった群は日本海育ち群と呼ばれ、一生を日本海で生活すると考えられている<sup>1, 3, 4)</sup>。

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日本海の資源は両群の成魚と日本海育ち群の未成魚から構成され、海域によってそれぞれの構成比が変化すると推測されている<sup>3-5)</sup>。日本海育ち群はオホーツク海育ち群と比べて成長が遅いという特徴を持ち<sup>3-5)</sup>、この成長差を利用して体長組成から両群を判別することが試みられてきた。たとえば菅間<sup>3)</sup>は増毛沿岸で漁獲されたマガレイの体長組成が大型群と小型群から成る双峰型であることを示し、前者がオホーツク海育ち群、後者が日本海育ち群に相当すると推定している。また、小平町～天塩町沿岸の漁獲物についても、体長組成から育ち群の分離が行われている<sup>6)</sup>。しかし、この方法は簡便ではあるものの、体長組成が明瞭に分離できる場合にしか適用できないという欠点を持つ。また、統計学的手法に基づいて群を分離するため、分離基準の生物学的根拠が明確ではない。

魚類では鱗や耳石などの硬組織に刻まれた輪紋から過去の成長過程を推定することが広く行われている<sup>7)</sup>。マガレイの耳石（扁平石）には不透明帯と透明帯が交互にみられ、それぞれ1年に1本ずつ形成されることから、年齢形質として有効とされている<sup>8)</sup>。また、耳石径と体長との相関関係を利用して、各年齢で形成された輪紋径から成長過程を推定することも行われている<sup>8-10)</sup>。本マガレイ資源でも0～1歳時に形成される輪紋径の育ち群差を利用することで、漁獲物の育ち群判別が可能であると報告されている<sup>11)</sup>。しかし、この報告ではオホーツク海で漁獲された個体の44%が日本海育ち群と判別され、従来の知見と大きく矛盾する結果となっている<sup>11)</sup>。この原因として、単一年級群の0～1歳時輪紋径を基準に複数年齢群の育ち群を判別したために、オホーツク海育ち群のなかの成長の悪い年齢群を日本海育ち群と誤判別した可能性が指摘されている<sup>11)</sup>。

本研究では、1歳時の体長が育ち群間で顕著な差を示す年齢群を選定し、漁獲物標本からその年齢群を抽出して、1歳時の耳石の輪紋径を基準に育ち群を判別した。本報告では特に1～3歳時にオホーツク海と日本海で漁獲された個体の育ち群を明らかにする。

## 材料及び方法

### 1. 育ち群判別の基準標本

オホーツク海育ち群は最短で2歳の秋から冬に日本海へと移動するため<sup>12)</sup>、この頃にオホーツク海育ち群と日本海育ち群の混合が始まると推測される。したがって両群を判別する基準となる標本は、2歳の秋以前にオホーツク海と日本海のそれぞれで採集する必要がある。本研究では、オホーツク海の雄武町沿岸と日本海の小平町沿岸で毎年8月に実施しているカレイ類幼魚調査<sup>13-16)</sup>で得られた1歳魚（約1歳2ヶ月）を各育ち群の基準標本と

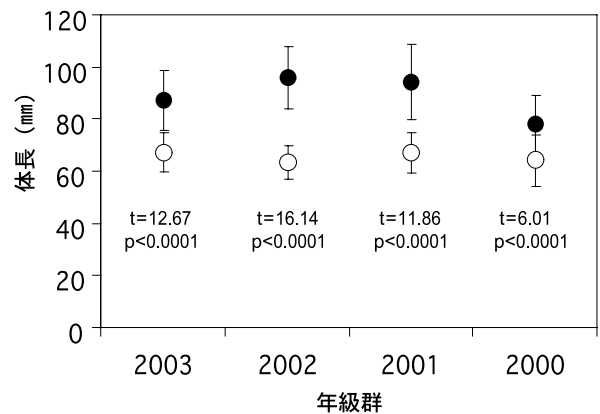


図1 幼魚調査で採集された1歳魚の平均体長±標準偏差 (●:雄武沖, ○小平沖) および海域間における平均体長のt検定の結果

した。すなわち、本研究では雄武町沿岸と小平町沿岸で採集された1歳魚が、それぞれオホーツク海育ち群と日本海育ち群を代表していると仮定した。育ち群間の体長差が顕著なほど、耳石径の差が大きくなり、群識別が容易になると予想されることから、近年で最も大きな体長差を示した2002年級群を本研究の調査対象とした(図1)。なお、幼魚調査によると2002年級群の1歳密度指数は、調査を開始した1975年級群以降3番目に高く<sup>14)</sup>、漁獲物中に出現する可能性が高い。

### 2. 基準標本の耳石の測定

マガレイの耳石は左右で形態が異なり、無眼側の耳石は同心円状の楕円形であるのに対し、有眼側は中心が尾部方向に偏った形態をしている<sup>8)</sup>。予備的な観察によると1歳時に形成される輪紋は無眼側の耳石で鮮明であったことから、本研究では無眼側の耳石の長径および第1不透明帯の内径を、実体顕微鏡に接続した計測装置（ニコン、DSカメラコントロールユニットDSL-1、DSカメラヘッドDS-5M）を用いて1/100mm単位で測定した(図2)。

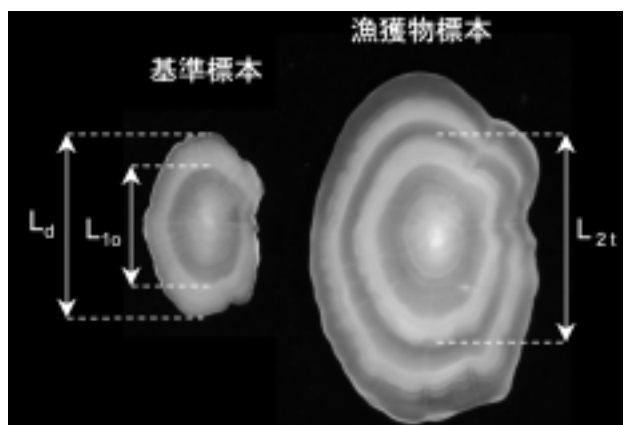


図2 基準標本および漁獲物標本の耳石（無眼側扁平石）の測定部位  
 $L_d$ : 耳石径,  $L_{1o}$ : 第1不透明帯内径,  $L_{2t}$ : 第2透明帯内径。

基準標本の採集日はオホーツク海では2003年8月19～21日、日本海では2003年8月20～21日であった。日本海では5～8月に不透明帯が形成されることから<sup>17)</sup>、標本採集日は不透明帯から透明帯への移行期にあたり、1歳魚の耳石径は第2透明帯の内径に相当する。一方、オホーツク海では、9月に不透明帯から透明帯へ移行するため<sup>10)</sup>、オホーツク海の基準標本については下式を用いて耳石径( $L_d$ )を第2透明帯内径( $L_{2t}$ )に換算した。

$$L_{2t} = L_d + 41 \cdot (L_d - L_{10}) / 112$$

ただし、 $L_{10}$ は第1不透明帯の内径である。この式では、不透明帯が6月1日～9月30日の153日間に形成されること、およびこの間耳石は直線的に成長すると仮定している。これらの仮定に基づく、標本採集日は不透明帯の形成開始から112日目に相当する。

### 3. 漁獲物および幼魚調査で得られた標本の輪紋径の測定

沿岸漁業で漁獲されたマガレイを、枝幸漁業協同組合(オホーツク海)、稚内漁業協同組合、北るもい漁業協同組合天塩支所および苫前支所、新星マリン漁業協同組合鬼鹿支所および余市郡漁業協同組合(以上、日本海)で銘柄別に5～12kgずつ採集し、体長および体重の測定と耳石(扁平石)の摘出を行った。耳石の輪紋数から年齢を査定し<sup>10)</sup>、2002年級群について耳石の第2透明帯内径を測定した(図2)。銘柄毎の第2透明帯内径の組成を求め、これを銘柄別の漁獲重量で重み付けし漁獲物全体の組成を推定した。

雄武町沿岸および小平町沿岸におけるカレイ類幼魚調査、および石狩湾におけるカレイ類未成魚分布調査<sup>18)</sup>で、いずれもソリネットで採集した2002年級群の2～3歳魚についても、漁獲物と同様の方法で耳石の第2透明帯内径を測定した。なお、一部の個体は有眼側の耳石標本のみを保存していたため、これらについては下に示した有眼側耳石径( $L_r$ , mm)と無眼側耳石径( $L_l$ , mm)との回帰式で無眼側の値に換算した。

$$L_l = 1.0051 \cdot L_r - 0.0924$$

ただし、 $R^2 = 0.9401$ ,  $p < 0.0001$ ,  $n = 34$

## 結 果

### 1. 基準標本の第2透明帯内径

基準標本の第2透明帯内径は両海域とも性差が認められなかったことから(平均値±標準偏差, 単位: mm, オホーツク海: 雄,  $3.51 \pm 0.317$ ,  $n = 138$ , 雌,  $3.54 \pm 0.301$ ,  $n = 249$ ,  $t$ 検定,  $t = 1.06$ ,  $p = 0.283$ , 日本海: 雄,  $2.37 \pm 0.197$ ,  $n = 19$ , 雌,  $2.35 \pm 0.222$ ,  $n = 16$ ,  $t$ 検定,  $t = 0.21$ ,  $p = 0.837$ ), 両性を合わせた頻度分布を求めた(図3)。頻度分布は両海域とも正規型を示し、その平均値には海域差が認められた(平均値±標準偏差, 単位: mm,

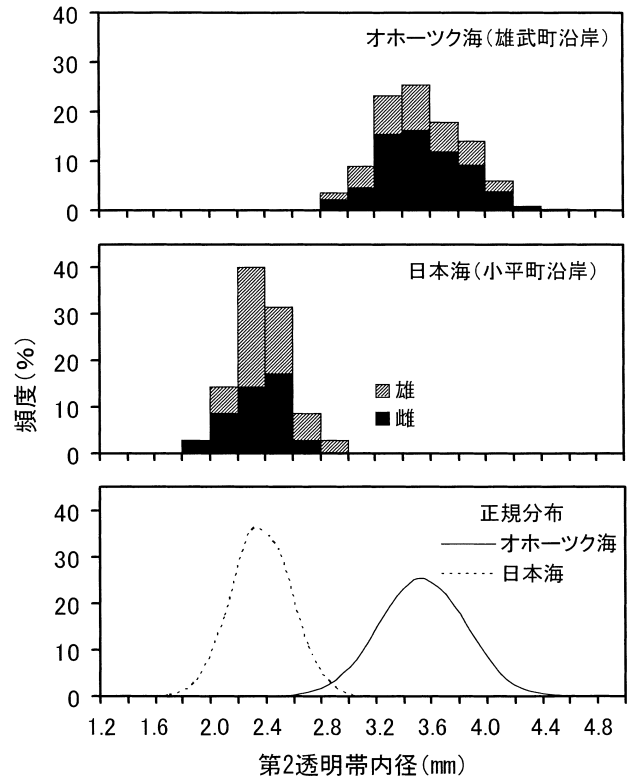


図3 オホーツク海および日本海で採集した2002年級群の基準標本の第2透明帯内径組成および正規分布

オホーツク海:  $3.53 \pm 0.317$ ,  $n = 387$ , 日本海:  $2.37 \pm 0.206$ ,  $n = 35$ ,  $t$ 検定,  $t = 22.00$ ,  $p < 0.0001$ )。それぞれに近似させた正規分布は2.6～3.0mmの範囲で重複していたが、正規分布のうちこの範囲に含まれる面積は、オホーツク海の基準標本では全体の4.2%, 日本海では11.7%であった。したがって、本研究では第2透明帯内径が3.0mm以上の個体を「オホーツク海育ち群」、2.6mm未満の個体を「日本海育ち群」、2.6mm以上3.0mm未満の個体を「判別不能」と定義した。

### 2. 漁獲物の第2透明帯内径と体長

2002年級群の最初の漁獲個体は、2003年10月にオホーツク海に面する枝幸漁業協同組合で確認された。これらの耳石の第2透明帯内径を測定し、その組成を2003年10～12月における枝幸漁協の漁獲量で引き延ばしたところ、2002年級群の総漁獲尾数は約82,000尾、第2透明帯内径の分布範囲は3.8～4.6mm、モードは4.0～4.2mmであった(図4)。基準標本の正規分布(図3)に照らしてみると、この分布範囲はオホーツク海の基準標本のなかの最も大きなサイズクラスに相当した。枝幸漁協では2004年4～9月に約563,000尾の2002年級群が漁獲された。これらの第2透明帯内径は前年に漁獲された個体よりも小さく、3.6～3.8mmにモードがあった(図4)。2004年10～12月および2005年4～9月に漁獲された個体は第2透明帯内

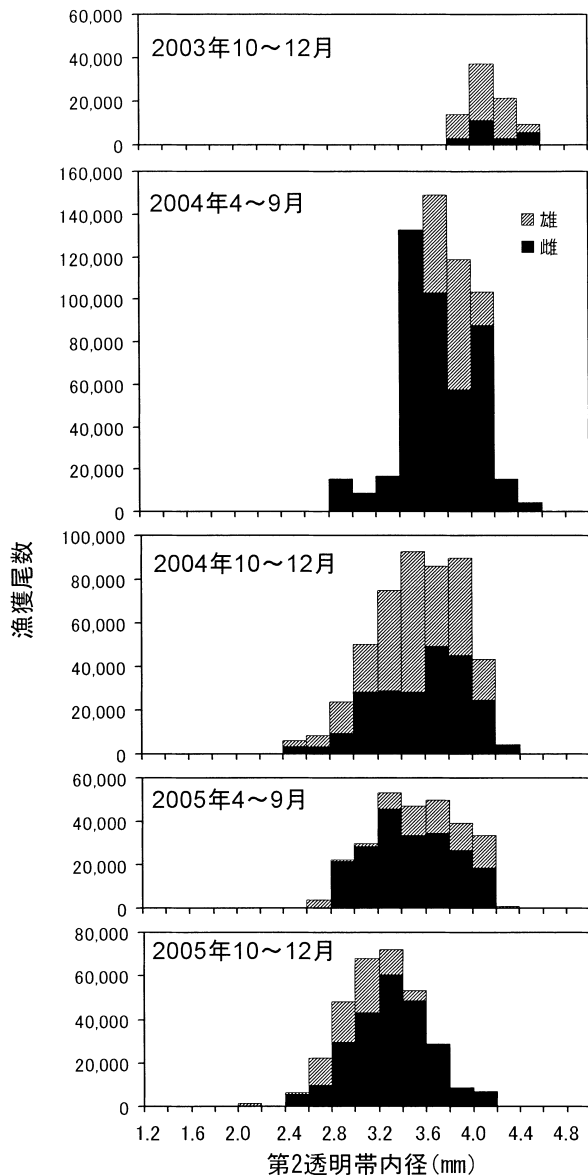


図4 枝幸漁業協同組合で水揚げされた2002年級群の第2透明帯内径組成の推移

径がさらに小さく、2005年10～12月にはモードは3.2～3.4mmにまで小型化した（図4）。これらの漁獲尾数をサイズクラス毎に累計し百分率に換算して基準標本の正規分布と比較したところ、オホーツク海の基準標本とモードが一致した（図5）。ただし、枝幸漁協の漁獲物はモードよりも小さな個体の頻度が基準標本の正規分布と比べ低かった（図5）。2005年12月までに枝幸漁協に水揚げされた2002年級群の漁獲物は、91.1%がオホーツク海育ち群、0.8%が日本海育ち群、8.1%が判別不能であった。枝幸漁協に水揚げされた2002年級群の体長の分布範囲は14～24cm、モードは15cm台～21cm台で、高齢で漁獲された個体ほどモードが大きかった（図6）。ただし、2005年10～12月には雄のピーク（18cm台）と雌のピーク

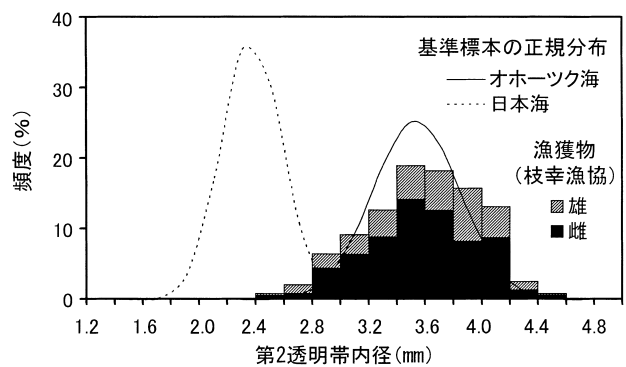


図5 枝幸漁業協同組合で2003年10月から2005年12月に水揚げされた2002年級群の第2透明帯内径組成

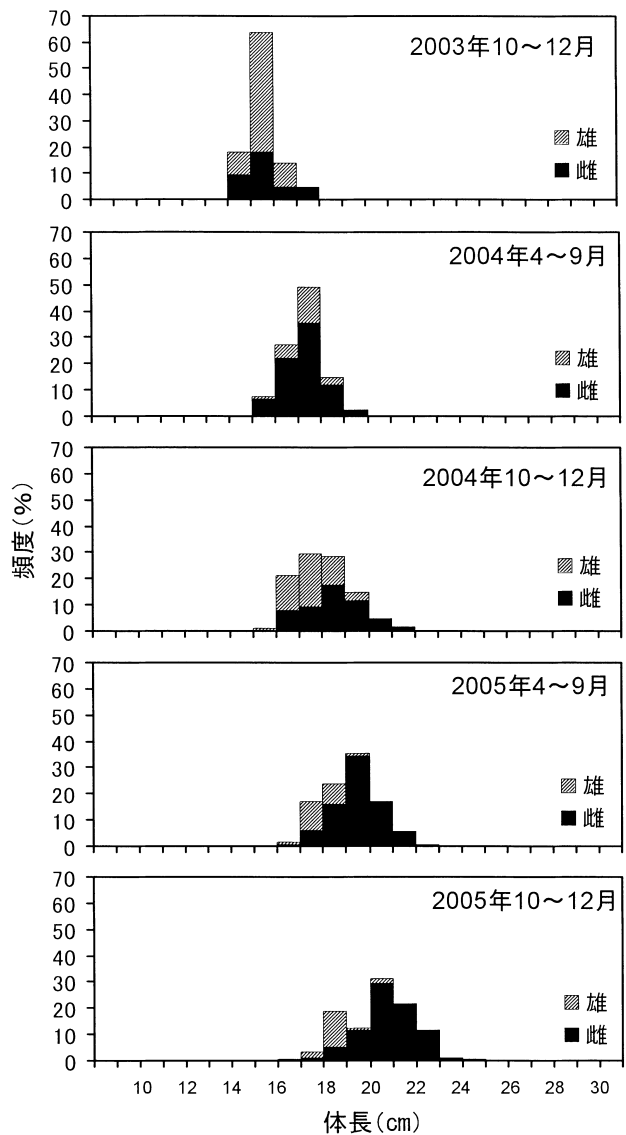


図6 枝幸漁業協同組合で水揚げされた2002年級群の体長組成の推移

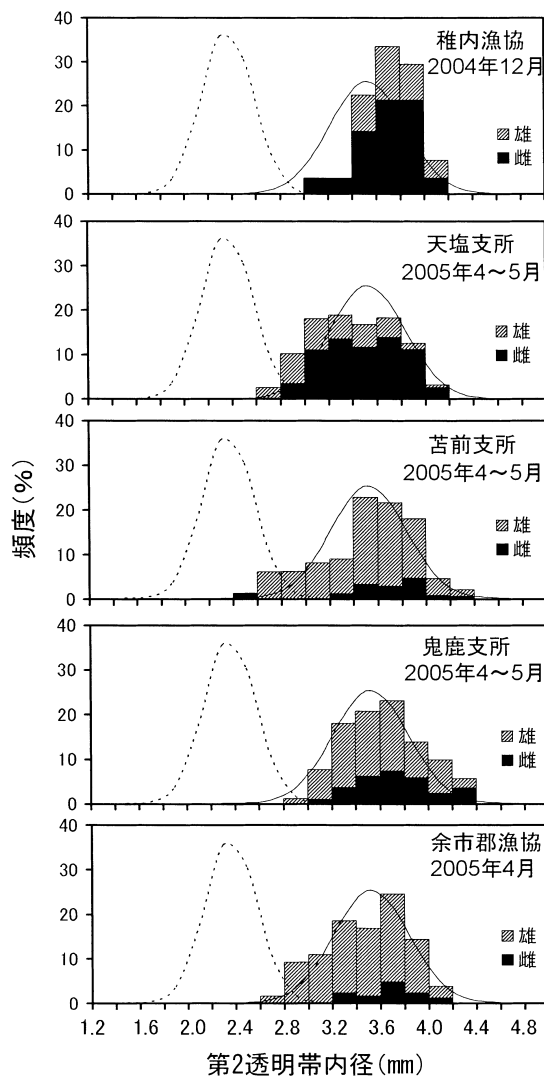


図7 日本海側の漁業協同組合で水揚げされた2002年級群の第2透明帯内径組成  
実線はオホーツク海の、破線は日本海の基準標本の正規分布を示す。

(20cm台) から成る双峰型の頻度分布を示した(図6)。

2004年12月から2005年5月にかけて日本海で水揚げされた漁獲物は、第2透明帯内径が2.8mm以上の個体から主に構成され、そのモードは3.6~3.8mmであった(図7)。オホーツク海育ち群と判定された漁獲尾数の比率は、稚内漁協で100%、天塩支所で87.3%、苫前支所で86.3%、鬼鹿支所で98.8%、余市郡漁協で89.1%であった。日本海育ち群の比率は苫前支所の漁獲物の1.4%のみで、判別不能の比率は稚内漁協で0%、天塩支所で12.7%、苫前支所で12.3%、鬼鹿支所で1.2%、余市郡漁協で10.9%であった。これらの漁協に水揚げされた2002年級群の体長の分布範囲は16~23cmで、モードは17~19cmであった(図8)。

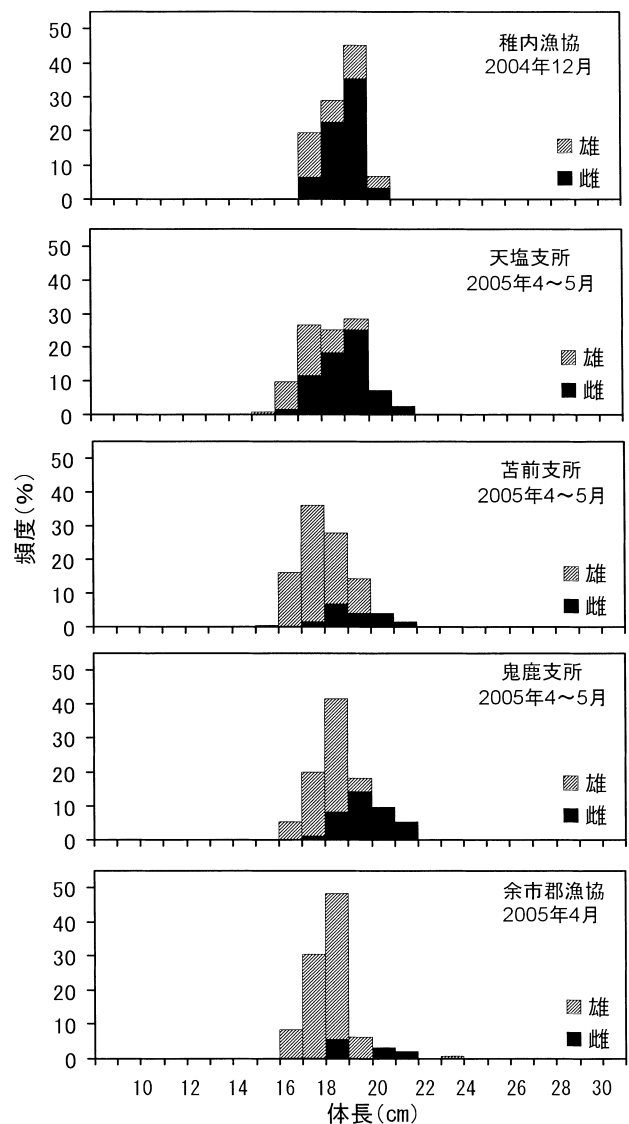


図8 日本海側の漁業協同組合で水揚げされた2002年級群の体長組成

### 3. 幼魚調査で得られた標本の第2透明帯内径と体長

2004年8月に雄武町沿岸で実施した幼魚調査で得られた2歳魚の標本は、第2透明帯内径が2.6~3.0mmの個体が46.4%を占め(図9)、これらの育ち群は判別できなかった。同調査ではオホーツク海育ち群に相当する個体が全体の25.0%、日本海育ち群と判別される個体が28.6%を占めた。このうち日本海育ち群に相当する個体は基準標本を採集した2003年8月には全く確認されていないが(図3)、近隣の枝幸漁協の漁獲物中には2004年10月以降1.3~6.4%含まれていた(図4)。小平町沿岸の幼魚調査で2004~2005年に得られた2~3歳魚の第2透明帯内径は、日本海育ち群に相当する個体が多く(図9)、その比率は2004年で64.0%、2005年で47.1%であった。

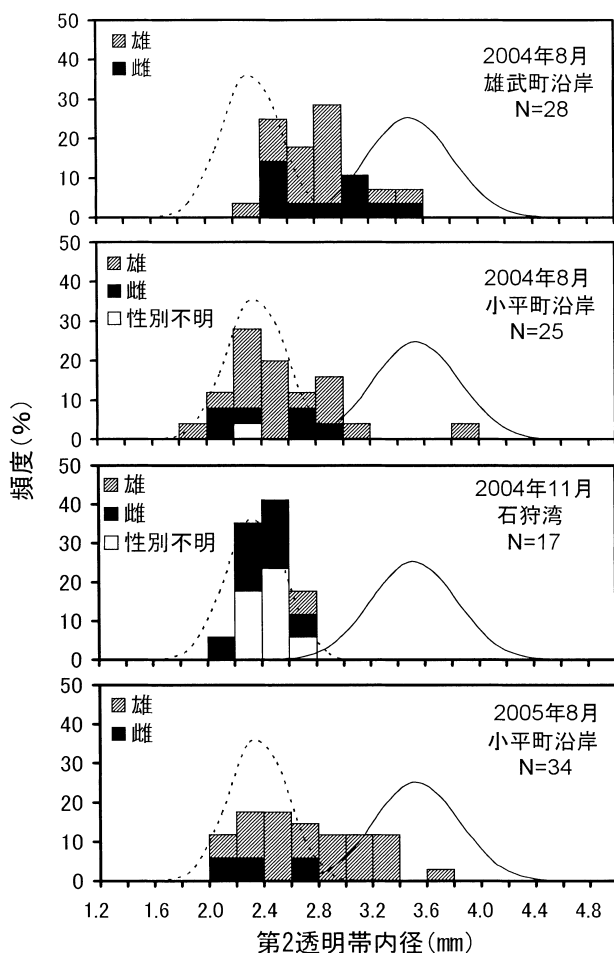


図9 幼魚調査で採集された2002年級群の第2透明帯内径組成  
実線はオホーツク海の、破線は日本海の基準標本の正規分布を示す。

一方、オホーツク海育ち群に相当する個体の比率は2004年で8.0%, 2005年で26.5%であった。2004年11月に石狩湾で採集した2歳魚の標本は、全ての個体の第2透明帯内径が2.8 mm以下で、これらは日本海育ち群に相当する個体が82.4%, 判別不能の個体が17.6%であった(図9)。これらの幼魚調査で採集された個体は、漁獲物中(図8)には出現しない体長8~16cmの小型個体が半数以上を占めた(図10)。日本海育ち群と判別された個体はこれらの小型個体であった。

## 考 察

1歳の10月から3歳の12月にかけて漁獲された2002年級群のマガレイは、86%以上がオホーツク海育ち群と判定され、日本海育ち群の比率は1.4%未満であった。この傾向はオホーツク海の漁獲物だけでなく、日本海の漁獲物にも共通する特徴であった。稚内周辺の日本海では秋季から冬季にかけて宗谷海峡を通過する魚群を対象に

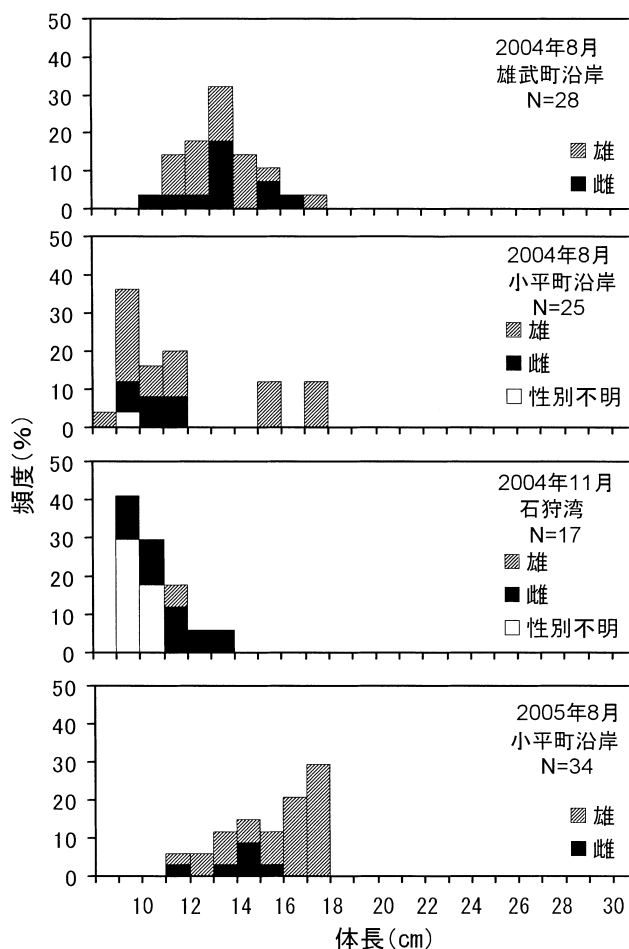


図10 幼魚調査で採集された2002年級群の体長組成

マガレイ漁業が行われ、また、天塩海域から石狩湾にかけての日本海では4~5月に産卵群を漁獲する<sup>2, 16, 19)</sup>。今回の結果は、2歳の秋季から冬季にかけて宗谷海峡を通過したオホーツク海育ち群の中には、2歳春の産卵期に石狩湾まで南下して繁殖を行う個体がいることを示している。これまでは漁獲物の年齢・体長組成に基づいて、オホーツク海育ち群が増毛町沿岸から石狩湾にまで南下すると推測されてきたが<sup>3, 4)</sup>、本研究の結果はこの仮説に生態学的根拠を付加するものである。

一方、石狩湾と小平町沖の幼魚調査で2~3歳時に採集された個体のうち47.1~82.4%が日本海育ち群と判定された。これらの体長は同海域における漁獲物よりも小型の個体であったことから、日本海育ち群の多くは2歳の産卵期までに漁獲サイズに達していないと考えられる。3歳の産卵期以降、日本海育ち群は成長の良い個体から順に漁獲物に出現するようになると予想され、その頻度は加齢に伴って高くなる可能性がある。石狩湾以北の日

本海で漁獲されるマガレイは南方ほど高齢魚の比率が高くなる傾向が認められ、これは低成長のため高齢で漁獲される日本海育ち群の比率が南方ほど高いことによると考えられている<sup>3-5,20)</sup>。本研究では両育ち群の混合比が加齢に伴って各海域でどのように変化するか明らかにできることから、年齢組成の地理的傾斜の成因を育ち群の移動や成長および成熟の面から検証できると期待される。

和田<sup>8)</sup>および加藤<sup>9)</sup>は新潟県産マガレイについて耳石の輪紋から成長解析を行い、高齢で漁獲された個体ほど若齢期の成長が良くない傾向があることを見出し、西内<sup>10)</sup>もまたオホーツク海産のマガレイで同様の傾向を確認している。これらの報告では、こうした現象が起こる原因として、高齢魚における若齢期の輪紋の過小読み取り誤差や漁具の選択性および回遊に伴う漁獲対象の変化が関係すると指摘している。本研究においては、オホーツク海の枝幸漁協に水揚げされた漁獲物で、若齢で漁獲された個体ほど第2透明帯内径が大きい傾向が認められた。このことは第2透明帯形成期、すなわち1歳夏季までの成長が良かった個体から順に漁獲対象となったことを示している。今回用いた標本が刺し網の漁獲物であったことを考えあわせると、本資源の漁獲物標本は漁具の選択性<sup>21)</sup>の影響を強く受けている可能性が高いと考えられる。また、西内<sup>10)</sup>が指摘したように、成長の良い個体ほど成熟年齢が低く若齢でオホーツク海から日本海へと産卵回遊するため、オホーツク海に残った個体は加齢に伴って初期成長の遅い個体の割合が高くなるとことも関係していると考えられる。

2004年8月の雄武町沿岸における幼魚調査で得られた2歳魚の標本には、日本海育ち群と判別される個体が28.6%含まれていた。こうした個体は基準標本を採集した2003年8月には全く確認されていないが、近隣の枝幸漁協の漁獲物中からは2004年10月以降1.3~6.4%確認された。この結果は、次の2通りに解釈することができる。1つめの解釈としては、本研究では雄武町沿岸で採集された1歳魚が、オホーツク海育ち群を代表すると仮定したが、この仮定が必ずしも成立していないことが考えられる。すなわち、オホーツク海の雄武以外の海域に日本海育ち群と同程度に成長の遅い群が分布し、これらが雄武海域に移動してきた可能性が考えられる。2つめの解釈としては、1歳の夏季以降に日本海からオホーツク海へと移動した個体がいた可能性が考えられる。従来、オホーツク海育ち群と日本海育ち群の分岐は卵~仔魚期の浮遊生活期間に起きると考えられてきた<sup>1)</sup>。しかし、小平沖における0歳幼魚の分布密度が翌年の雄武沖における1歳幼魚の分布密度と正の相関を示すことから、着底から1歳夏季までの間に日本海からオホーツク海へと移

動する個体もいると推測されている<sup>6)</sup>。さらに標識放流では、成魚期における日本海からオホーツク海への移動がこれまでに1例確認されている<sup>2)</sup>。本研究の結果も考えあわせると、日本海からオホーツク海への移動は、着底期以後にも起きている可能性があり、海域間移動の生活史ステージとその要因および量的評価について今後精査する必要がある。

## 要 約

石狩湾以北日本海~オホーツク海にかけて分布するマガレイの育ち群を、耳石の輪紋径(第2透明帯内径)をもとに判別した。1歳秋から3歳冬にかけてオホーツク海の枝幸漁協に水揚げされた漁獲物は、91.1%がオホーツク海育ち群、0.8%が日本海育ち群と判定された。稚内漁協で2歳冬に漁獲されたマガレイはすべてオホーツク海育ち群と判定され、続く2歳春の産卵期に日本海の大塩支所~余市郡漁協に水揚げされた漁獲物は、86%以上がオホーツク海育ち群であった。これらの結果は、オホーツク海育ち群の中には2歳冬に日本海へと移動し、産卵期までに石狩湾に達する個体がいることを示している。2004~2005年に日本海の小平沖と石狩湾で実施した幼魚調査において、日本海育ち群に相当する個体が採集された。これらの体長は漁獲サイズに達していなかったことから、日本海育ち群の多くは3歳春以降に漁獲対象になるものと推測された。

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# 北海道南西部日本海沿岸における海藻植生とキタムラサキウニの生殖巣発達の関係

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Gonad production of the sea urchin *Strongylocentrotus nudus* in relation to algal vegetation in shallow waters along the Sea of Japan, southwestern Hokkaido, Japan

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Gonad production of the sea urchin *Strongylocentrotus nudus* in relation to the algal vegetation was clarified through gut content analysis in three sites (Yaoi, Rokujo and Biya) in Suttu Bay along the Sea of Japan coast in southwestern Hokkaido from May to August 2001. The main food algae leading to gonad production were Sargassaceae and *Desmarestia viridis* (Yaoi), *D. viridis* and *Colpomenia sinuosa* (Rokujo) and Laminariales and *D. viridis* (Biya), coinciding with the algae with abundant standing crop that grew at each site, respectively. The gonad index (gonad wet weight  $\times 100$  / body wet weight) was the highest in the *Laminaria religiosa*-dominated site with high algal standing crop. It is considered that gonad production is affected by the nutritive value of the food algae and ease of grazing and by drifts of detrital algae that originate in shallow waters.

Key words : gonad production, *Strongylocentrotus nudus*, algal vegetation, gut contents, Laminariales, Sargassaceae

## Introduction

Growth and gonad production of sea urchin have been shown to be dependent on algal food species and the standing crop<sup>1-9</sup>. Rapid growth and high gonad production of *Strongylocentrotus* spp. are found in Laminariales-dominated beds, whereas growth and gonad production are poor in crustose coralline area<sup>7,9,10</sup>.

The growth of Laminariales and Fucales brown algae is restricted to the area between the lower littoral to the shallow sublittoral, below the shallow sublittoral crustose corallines are widely distributed in the Sea of Japan coast

in southwestern Hokkaido<sup>11-13</sup>. The sea urchin *Strongylocentrotus nudus* densely distribute in crustose coralline area as the settlement and metamorphosis of *S. nudus* larvae are strongly induced by dibromomethane, which is constantly produced by crustose coralline algae<sup>14</sup>. However, as little foliose food algae are available for the sea urchins in crustose coralline area, the dense distributions of *S. nudus* in the crustose coralline area<sup>7,12,15</sup> and hatchery-raised juveniles of *S. intermedius* have been transplanted to the Laminariales- or Fucales-dominated beds to promote the growth and gonad production of the sea urchins due to increase in the

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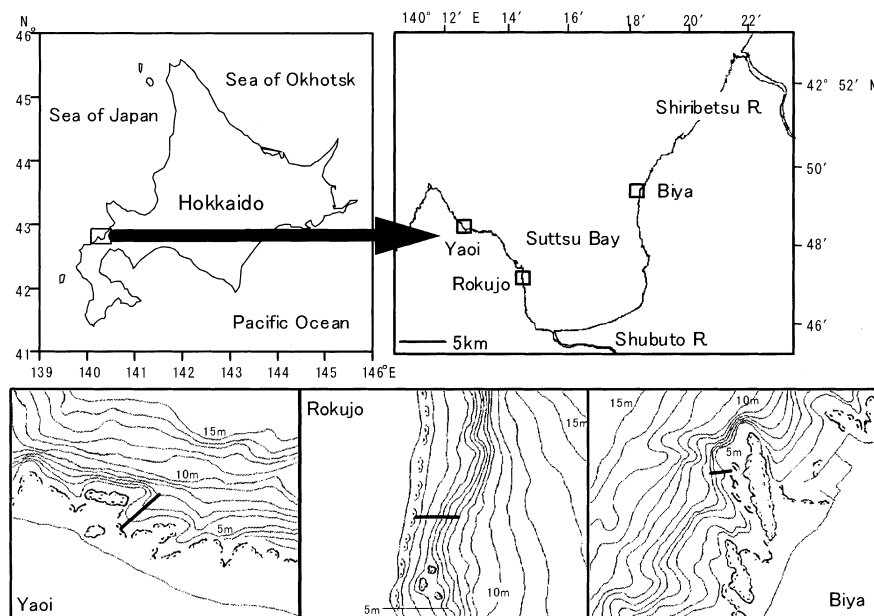


Fig.1. Location of study sites.

fishery production.

The gonads of *S. nudus* shift from the growing stage in spring to the maturing stage in summer under active grazing activity and increase in size in marine forest areas consisting of large brown algae, where available foods are ensured<sup>16)</sup>. However, the effect of the species composition in algal communities attributing to the increase in gonad production has not been examined in the field. The effect of the species composition in algal communities on gonad production should be clarified to make the criteria for suitable sites for transplanting the sea urchin.

In the present study, we studied the gonad production and gut contents of *S. nudus* in relation to algal standing crop along shallow bathymetric gradient areas in southwestern Hokkaido.

## Material and Methods

This study was carried out in the three sites, Yaoi and Rokujo along the western coast, and Biya along the eastern coast in Suttsu Bay along the Sea of Japan coast in southwestern Hokkaido (Fig. 1). At depths of 1, 3 and 7 m in a transect line perpendicular to the coastline in each study site, the sea urchin *S. nudus* and foliose algae were monthly collected by SCUBA diving from May to August 2001. At each depth in three sites, three adult *S. nudus* with > 50 mm test diameter<sup>17)</sup> were collected. In the dominant vegetation at each depth in each site, a 50 ×

50 cm quadrat was placed and foliose algae in the quadrat were collected. No sea urchin and algae was collected at a depth of 1 m at Rokujo in August due to strong wave action. From each sea urchin, gut with its contents was put on a petri dish and the gut wall was removed. The gut contents were preserved in 5% neutralized formaldehyde solution in a 50 ml calibrated bottle. When gut contents were less than 5 ml, all the contents were examined, while it would be subsampled into 1/4 or 1/8, if it were 5-10 ml or > 10 ml, respectively. The algae in the gut contents were sorted to the taxon: species, genus and family under a stereoscopic microscope. Algal fragments were identified by the characteristics of color, morphology, cell shape and tissue structure according to Yoshida<sup>18)</sup>. The material other than algae, such as shell and animal fragments, sea grass, terrestrial plants and sand, summed up as others. The dry weight of each taxon was measured using the electronic balance (to the nearest 0.1 mg) after 12 hrs at 80°C in a convection oven. The foliose algae collected at each depth in each site were identified according to Yoshida<sup>18)</sup>, and the wet weight by species was measured using an electronic balance (to the nearest 0.1 g).

In addition, 10-44 adult *S. nudus* with > 50 mm test diameter were collected at each depth in each site in late June or early July 2001, corresponding to the period of increase in the gonad size<sup>16)</sup>. The body and gonad wet weight were measured and the gonad index (gonad wet weight × 100 / body wet weight) was calculated.

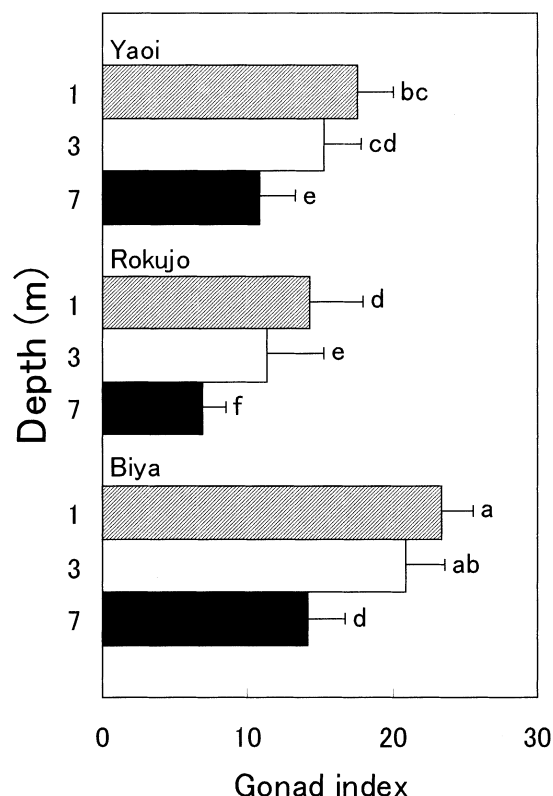


Fig.2. Gonad indices of *Strongylocentrotus nudus* collected in Yaoi, Rokujo and Biya along the southwestern coast of Hokkaido from late June to early July 2001. Bars indicate the standard deviation. Different letters indicate significant difference by Tukey's HSD test.

Significant difference in gonad indices among three depths in the each site and three sites at the each depth was tested by Tukey's HSD.

## Results

The gonad indices of *S. nudus* collected in Yaoi, Rokujo and Biya are shown in Fig. 2. The gonad indices at a depth of 7 m were significantly lower than those at 1 m and 3 m in Yaoi and Biya ( $p < 0.01$ ). The gonad indices significantly decreased with the increase in depth in Rokujo ( $p < 0.05$ ). The gonad indices at each depth in Biya, Yaoi and Rokujo significantly decreased in those order ( $p < 0.01$ ).

The standing crops of foliose algae at depths of 1, 3 and 7 m in Yaoi, Rokujo and Biya from May to August 2001 are shown in Fig. 3. At 1 m in Yaoi, *Sargassum confusum* grew during the study period, this alga dominated there in May, July and August. At 3 m, *Dictyopteris divaricata* dominated in May, June and August. At 7 m, *Desmarestia viridis* dominated there in

May and June, the foliose algae did not grow and the sea bottom was covered with crustose coralline red algae in July and August. From the algal zonation in Yaoi, the standing crops of foliose algae tended most abundant at 1 m.

At a depth of 1 m in Rokujo, *D. viridis*, *Laminaria religiosa* and *Symphyclocladia latiuscula* dominated in May, June and July, respectively. At 3 m, *Colpomenia sinuosa* dominated there in June and July. At 7 m, *D. viridis* dominated there in May, *C. sinuosa* dominated there in June and July. At 3 m and 7 m, the foliose algae did not grow and the sea bottom was covered with crustose coralline red algae in August. The standing crops at each depth were lower than those in Yaoi and Biya.

In Biya, *L. religiosa* consistently grew at the depth of 1 m and 3 m. At 7 m, *D. viridis* grew from May and June, the foliose algae did not grow and the sea bottom was covered with crustose coralline red algae in July and August. The standing crops tended to highest because of the persistence of *L. religiosa*-dominated beds.

Compositions of the main components in the gut contents of *S. nudus* at each depth in Yaoi, Rokujo and Biya from May to August 2001 are shown in Fig. 4. In Yaoi, at a depth of 1 m where *S. confusum* dominated, a high percentage of *D. viridis* was found in the gut contents and the percentage of Sargassaceae, likely to be *S. confusum* was low in May and June, whereas the percentage of Sargassaceae increased in July and August. At 3 m where *D. divaricata* grew, high percentage of *D. viridis* was found in the gut contents from May and June, and the percentage of crustose coralline was high in July and August. At 7 m, the percentage of *D. viridis* in the gut contents was high from May to July, and that of crustose coralline was high in August. In July and August, Sargassaceae in the gut contents abundantly appeared at 3 m and 7 m.

In Rokujo, high percentages of *D. viridis* in May and *Laminariales* in June were found in the gut contents at a depth of 1 m, reflecting the growth at this depth of *D. viridis* and *L. religiosa*, respectively. In addition, high percentage of *C. sinuosa* in May was found. In July, the percentage of crustose coralline was high regardless that *S. latiuscula* grew at this depth. At 3 m and 7 m, high percentages of *D. viridis* in May and June were found, and high percentages of *C. sinuosa* in July were found, reflecting the growth of *C. sinuosa*. The percentages of crustose coralline tended to increase at each depth from

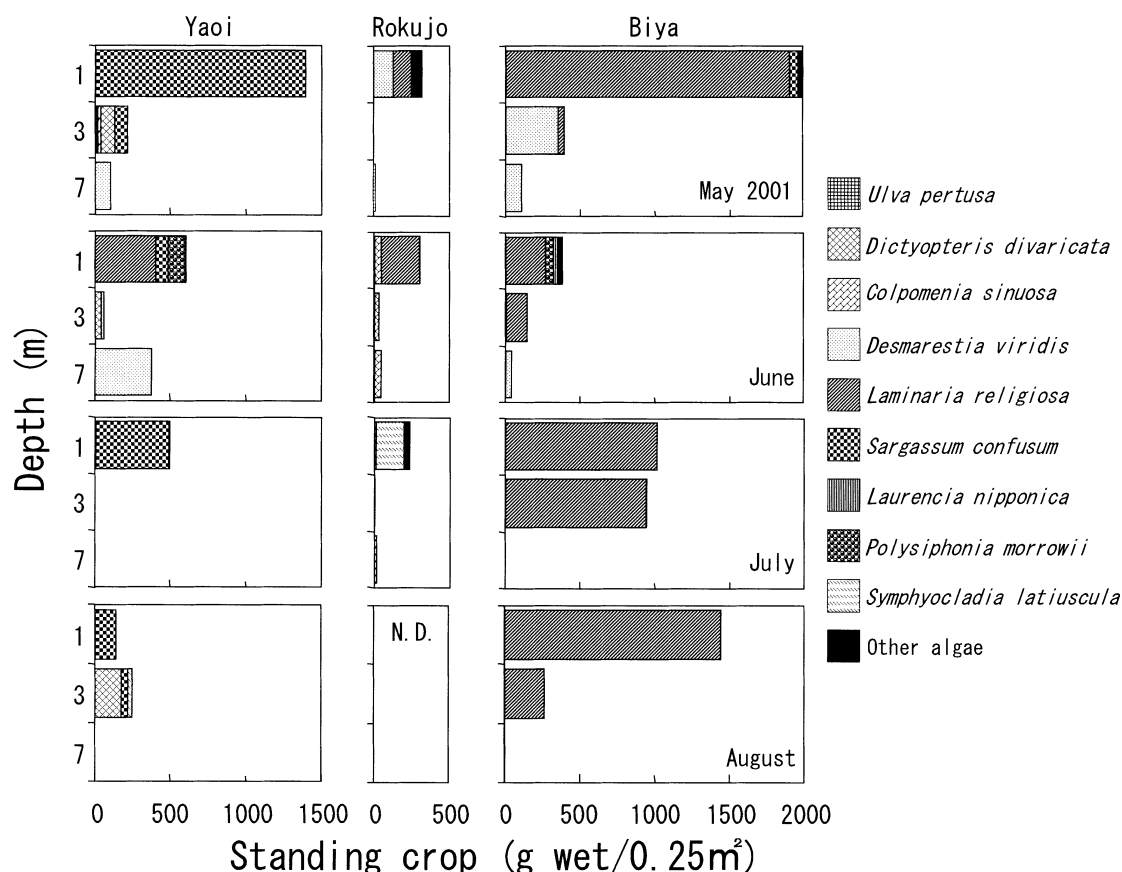


Fig.3. Monthly changes in foliose algal standing crop at different depths in Yaoi, Rokujo and Biya from May to August 2001.

May to August.

In Biya, Laminariales abundantly appeared in the gut contents at the depth of 1 m and 3 m where *L. religiosa* consistently dominated. At 7 m, the percentage of *D. viridis* besides Laminariales was high from May to July. In August, the percentage of *Ulva pertusa* besides Laminariales was high at 7 m. At each depth, the percentage of crustose coralline tended to increase from May to August.

### Discussion

Growth and gonad production are greatly affected by algal species as foods and the standing crops<sup>1-9)</sup>. Hence, this suggests that the growth and gonad production in the field are dependent on the algal assemblages in the sea urchin's habitat.

In the present study, gonad indices of *S. nudus* at each depth in Biya, where *L. religiosa* dominated with the most abundant standing crops, were higher than those in Yaoi and Rokujo. Those in Yaoi where *S. confusum* grew

were high. The lowest gonad indices were found in Rokujo where the annual algae such as *D. viridis* and *C. sinuosa* seasonally grew with extreme low standing crops. In each site, the gonad indices were high in shallow waters where the foliose algae grew and low in deep waters where crustose corallines dominated. These results agree with the reports that gonad sizes of *Strongylocentrotus* spp. in Laminariales-dominated beds were significantly higher than those in crustose corallines area<sup>7,9,10)</sup> and gonad production of *S. nudus* fed *L. angustata* was more clearly promoted than individuals fed *S. confusum* or *D. viridis*<sup>8)</sup>.

Comparison between growing algae and food algae in the gut contents of *S. nudus* showed that *L. religiosa*, *D. viridis* and *C. sinuosa*, which grew in the sea urchin habitat are taken as foods. Contrary to this, *S. confusum* which also grew in the sea urchin habitat were not taken in May and June. However, as *S. confusum* growing in shallower waters appeared abundantly in the gut contents of *S. nudus* at each depth and increased in July and August during the senescence period of this alga<sup>19)</sup>, it is likely that the seceded thalli are grazed. It is considered that living *S. confusum*

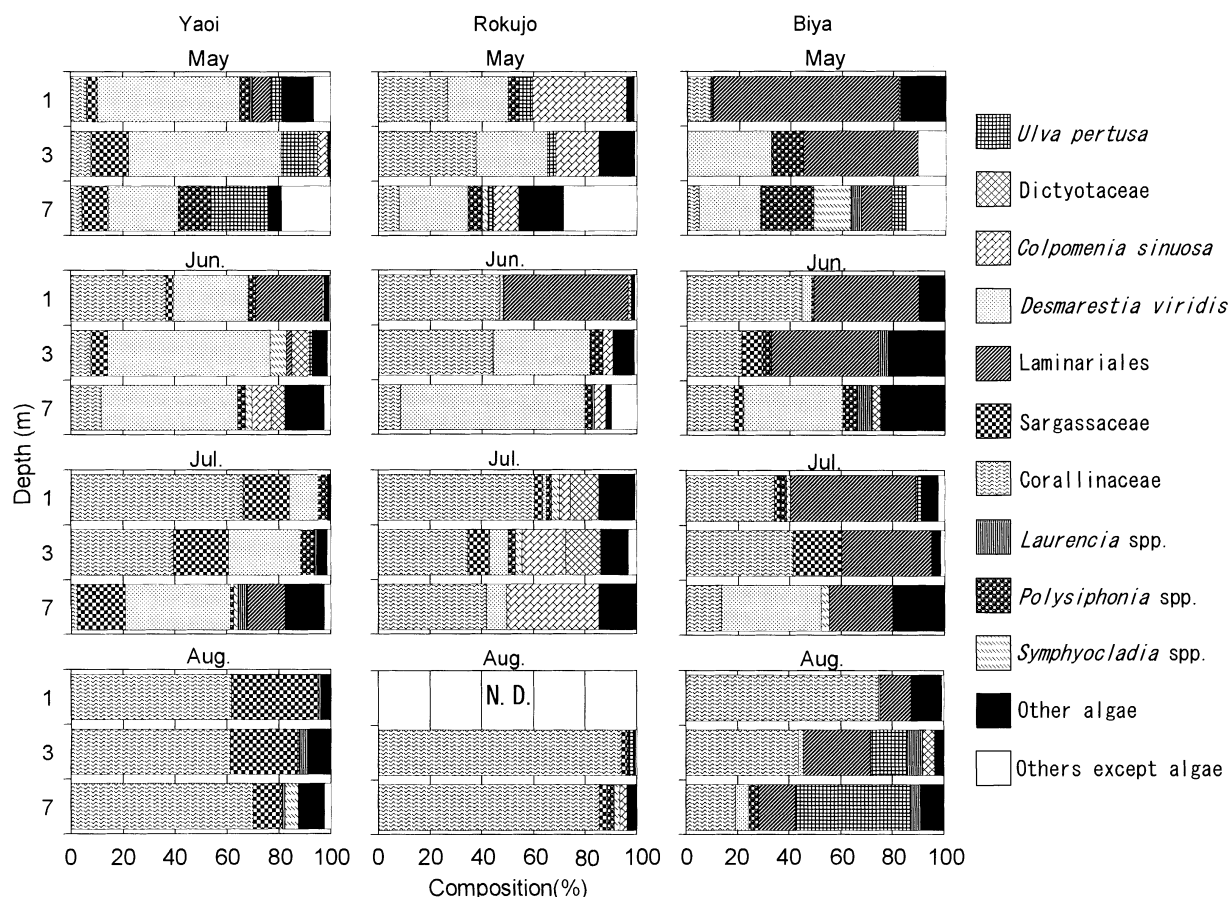


Fig.4. Monthly changes in compositions of the main components in the gut contents of *Strongylocentrotus nudus* in Yaoi, Rokujo and Biya.

is hard to be grazed by sea urchin as it remains erect due to the buoyancy of vesicle<sup>8</sup>. In addition, Fucales brown algae may defend their thalli from grazing of sea urchin by producing polyphenol as a feeding deterrents<sup>20</sup>.

Also, low amounts of *D. divaricata* and *S. latiuscula* were found in the gut contents regardless of their evident co-occurrence with *S. nudus*. It is considered that low amounts of *D. divaricata* which grew at a depth of 3 m in Yaoi was found in the gut contents, as it is clarified that this alga defends their thalli from grazing of sea urchin by producing sesquiterpene as a feeding deterrents<sup>21</sup>. It is possible that *S. latiuscula* which grew at a depth of 1 m in Rokujo also minimizes grazing by producing chemicals deterrents.

The gonad indices of *S. nudus* at a depth of 7 m where crustose corallines dominated were highest in Biya where *L. religiosa* grew in the shallow waters, subsequently in Yaoi where *S. confusum* grew also in shallow water. The indices were lowest in Rokujo. Appearance of the two brown large algae in the gut contents at a depth of 7 m

show that drifts of detrital algae that originate in shallow waters contribute to promote gonad production.

In the present study, it was clarified the gonad index of *S. nudus* was highest in Biya where the main food algae were Laminariales and *D. viridis*, subsequently, those in Yaoi where the main food algae were Sargassaceae and *D. viridis* were high and the gonad index in Rokujo where sea urchins mainly grazed *D. viridis* and *C. sinuosa* was lowest. It is suggested that those differences in gonad indices are also affected by nutritive value and ease of consumption of those main food algae.

### Acknowledgements

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# ホタテガイ貝柱フレークの品質特性に関する研究

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Studies on the quality characteristic of the scallop adductor muscle flakes

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A popular name “scallop flakes” is new food that manufactured from muscular fiber of heat-treated scallop adductor muscles. As for this, a manufacturing method is easy and mass production is possible. There are forms, such as fresh, boiled and frozen, in the adductor muscle of the scallop used as materials. The texture and colors of scallop flakes are greatly different by raw materials. We firstly established an objective method that evaluated the texture and colors of scallop flakes. Scallop flakes manufactured from raw and boiled adductor muscles had good texture and color tone. On the other hand, scallop flakes manufactured from frozen adductor muscles didn't have sufficient texture. The texture was improved by defrosting frozen adductor muscles at low-temperature, but during defrosting a large quantity of sugar phosphates were generated in adductor muscle and the browning degree of scallop flakes was promoted. Therefore, we have thought preventive measures from another viewpoint are required.

キーワード：ホタテガイ，貝柱フレーク，新規食品素材，物性，褐変，凍結，解凍，解糖系

## まえがき

近年、北海道におけるホタテガイは、種苗生産技術や増養殖技術などの進歩により安定した生産量を確保できるようになり、その年間生産量は40万トンを超えている。しかし、価格の面では、生産増大に伴う需給バランスの崩れにより、不安定になりつつある。

これらホタテガイ消費の主体は、生鮮、冷凍貝柱、ボイル製品、乾はたて貝柱の4種類であり、生産量の増大するホタテガイの更なる消費拡大のためには、これら既存の主力製品群に加わる新たな製品素材の開発が望まれている。

これまで水産試験場では、ホタテガイに関する製品の開発や品質向上試験に取り組んできた<sup>1-5)</sup>。その中でも、加熱したホタテガイ貝柱を繊維状にほぐした、通称「貝柱フレーク」は製造方法が簡単で、かつ大量処理が可能なことから、今後の需要増加が期待できる製品である。水産試験場では、すでに貝柱フレークの基本的な製造方法を確立し<sup>6)</sup>、また、製法改良も行ってきている<sup>7)</sup>。

そこで本試験では、各種貝柱（生貝柱、冷凍貝柱、ボイル貝柱、冷凍ボイル貝柱）から製造した貝柱フレークの品質について、レオロジーおよび生化学的な角度から比較検討した。

## 材料及び方法

### 1. 貝柱フレークの物性

#### 1.1 各種貝柱から製造した貝柱フレークの繊維強度と成分

2004年8月に紋別で水揚げされたホタテガイから調製した各種貝柱（生貝柱、冷凍貝柱、ボイル貝柱、冷凍ボイル貝柱）を原料として貝柱フレークを製造し、フレークの繊維強度及び成分を測定した。生貝柱及び冷凍貝柱については、ホタテガイから貝柱を採取して調製した。また、ボイル及び冷凍ボイル貝柱については、ホタテガイを5倍量の沸騰水で7分間煮熟した後、流水中にて10分間冷却後貝柱を採取し、調製した。生貝柱及びボイル貝柱はそのまま、また、冷凍貝柱及び冷凍ボイル貝柱は10℃で4時間解凍後、25分間蒸煮し、サイレントカッター（花木製作所製）で軽く1分間ほぐして貝柱フレー

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クを調製し、試験試料とした。

## 1. 2 冷凍貝柱の解凍条件と貝柱フレークの繊維強度

市販の冷凍貝柱（紋別産，Sサイズ）を未解凍及び雰囲気温度別に10～40℃で解凍したものを25分間煮沸後，20℃のインキュベータ中で放冷し，貝柱中心部分の筋繊維を取り出し，その繊維強度を測定した。なお，解凍は貝柱中心部が0℃以上になるまで行った。

## 2. 貝柱の凍結・解凍が貝柱フレークの褐変に及ぼす影響

2004年9月に紋別で水揚げされたホタテガイを原料とした。冷凍貝柱はホタテガイから貝柱を採取し，3%塩水で洗浄後，アルミパンに並べて-25℃で48時間凍結して調製した。冷凍貝柱フレークについては，冷凍貝柱を10℃のインキュベータ中で，4時間解凍した解凍区，同様に，24時間解凍貯蔵した解凍貯蔵区，また解凍せず凍結状態の未解凍区のもの，それぞれ25分間煮沸した後，1. 1と同様に貝柱フレークを調製し，試験試料とした。

なお，対照としてホタテガイを5倍量の沸騰水で7分間煮熟した後，流水中にて10分間冷却し，貝柱を採取したボイル区についても上記と同様に行った。

### 一般成分の分析

水分：105℃常圧乾燥法にて測定した。

タンパク質量：ミクロケルダール法にて測定した。

### グリコーゲンの定量

各粉碎試料に30%水酸化カリウムを加え可溶化後，エタノールにて精製し，適宜希釈した試料液をアンスロン・硫酸法によりグリコーゲンの加水分解と発色を同時に行った。グリコーゲン量は，この発色液の620nmにおける吸光値を求め，検量線からグルコース量を算出し，これに0.9を乗じて求めた。

### 遊離アミノ酸の定量

各粉碎試料5gにエタノール20mlを加え，ホモジナイズ後，遠心分離（3,000rpm，15分間）し，上澄液を分液ロートに移し，沈殿に80%エタノール20mlを加え同様の操作を行い，上澄液を得た。集めた上澄液にクロロホルムを加えて脱脂操作を行い，濃縮乾固し，0.01N塩酸にて定容した。この試料液をHPLC日立アミノ酸分析システム（L-7500）により分析した。

### 繊維強度の測定

繊維強度測定用試料は，貝柱中心部の閉殻横紋筋を筋繊維に沿って繊維状になるように剥離し，長さ12mm，重さ0.05gとなるよう調製した。また，フレーク試料についても同様の繊維状に調製した。これら試料を不動工業（株）のレオメーター（RT-2002D）による引張り試験（テーブルスピード5cm/分，試料間隔50mm）に供し，このとき得られる繊維の破断応力（g）と伸びた長さ（mm）を測定した。

糖代謝物（グルコース6リン酸，グルコース1リン酸，フラクトース6リン酸；以下G6P，G1P，F6Pと略す。）の定量

貝柱試料については各横紋筋から1個体当たり0.4gをメスで採取し，5個分2gを1区分として，またフレーク試料については，2gを1区分として，以下の処理を行った。すなわち，貝柱片に冷却した6%過塩素酸溶液を30ml加えてホモジナイズした後，遠心分離（10,000g，15分間）を行い，冷却しながら上澄液を水酸化カリウムで中和し，生成した沈殿物を遠心分離により除去後，上澄液を50mlに定容した。この分析試料液を中村ら<sup>8)</sup>の酵素法により分析した。

### L-アルギニンおよびオクトピンの定量

L-アルギニンおよびオクトピンは，糖代謝物分析に使用した分析試料液をSato<sup>9)</sup>らの方法に従って，HPLC（日立L-6200）により定量した。

分析条件は次のとおりである。

カラム：Kaseisorb LC ODS-300-5，4.6×250mm

（東京化成工業），

カラム温度：20℃，

移動相：A液（80% 0.25M トリス塩酸（pH9.5）

+20%アセトニトリル），B液（80%アセトニトリル+20%蒸留水）による2液グラジュエント，

流速：0.8ml/min，

検出波長：励起波長325nm，蛍光波長425nm

### 褐変度の測定

貝柱フレークを110℃の恒温器中で1時間加熱して褐変を進行させ，各試料の褐変の程度を，柞木田ら<sup>10)</sup>の方法に準じて評価した。なお，褐変度は，試料1g当たりの450nmの吸光度をもって次式により算出した。

褐変度＝吸光度（450nm）×100/試料重量（g）

### 有意差検定

試験区内および試験区間の有意差検定はダンカンの多重比較検定により行った。

## 結 果

### 1. 貝柱フレークの物性

#### 1.1 各種貝柱から製造した貝柱フレークの繊維強度と成分

各種貝柱から製造した貝柱フレークの繊維強度をFig. 1に示した。繊維強度は，全区分に有意差がみられた（ $p < 0.05$ ）。貝柱フレークの繊維強度（破断応力，伸びた長さ）は，強い順に冷凍ボイル貝柱（ $108.1 \pm 29.3$  g， $22.9 \pm 3.7$  mm），ボイル貝柱（ $69.3 \pm 20.9$  g， $18.7 \pm 5.2$  g），生貝柱（ $56.3 \pm 22.5$  g， $14.4 \pm 6.1$  mm），冷凍貝柱（ $25.2 \pm 17.9$  g， $8.0 \pm 6.0$  mm）であった。

冷凍ボイル貝柱から調製したフレークの繊維強度は，伸びた長さの個体差が小さかった。一方，ボイル貝柱，

生貝柱及び冷凍貝柱からのフレークでは、伸びた長さにバラツキがみられ、特に冷凍貝柱を原料としたフレークでは繊維強度が著しく弱かった。

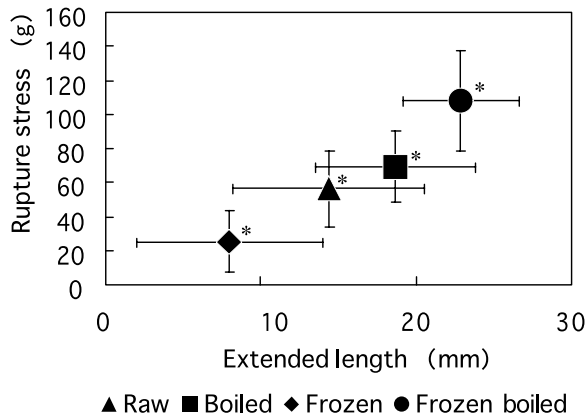


Fig. 1 Texture of the scallop flakes manufactured from each scallop adductor muscle materials. (n=5×10: Ten samples were prepared from one individual.) Bars indicate standard deviation (SD). \*Significantly different from other scallop flakes, p<0.05.

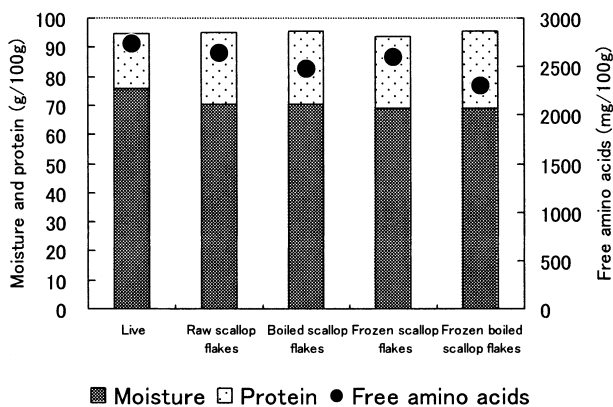


Fig. 2 Contents of protein, moisture and free amino acids in scallop flakes and scallop adductor muscle.

生貝柱及び各種貝柱から製造した貝柱フレークの水分、遊離アミノ酸、粗タンパク質量を Fig. 2 に示した。貝柱フレークの水分は68.9～70.4g/100g、粗タンパク質は、24.7～26.3g/100gであり、原料区分により大きな違いは認められなかった。ボイル貝柱、冷凍ボイル貝柱から製造した貝柱フレークの遊離アミノ酸は2,479、2,295mg/100gと他の貝柱フレーク（生2,641、冷凍2,593mg/100g）と比較して少し低い値を示した。

#### 1. 2 冷凍貝柱の解凍条件と貝柱フレークの繊維強度

凍結状態で蒸煮加熱した冷凍貝柱については、閉殻筋の筋繊維組織が弱く、貝柱フレーク製造工程中に筋繊維が凝集し塊状になった。(Fig. 3)。雰囲気温度別に解凍後、蒸煮加熱した冷凍貝柱の繊維強度を Fig. 4 に示した。繊維

強度は、全区分に有意差がみられ (p < 0.05)、破断応力、伸びた長さともに雰囲気温度が高くなるほど低下した。

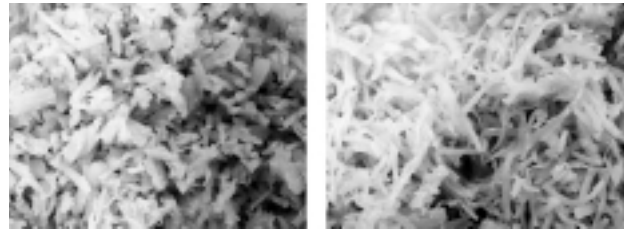


Fig. 3 Forms of scallop flakes.

Left: Scallop flakes manufactured from non-thawed scallop adductor muscles.

Right: Scallop flakes manufactured from boiled scallop adductor muscles.

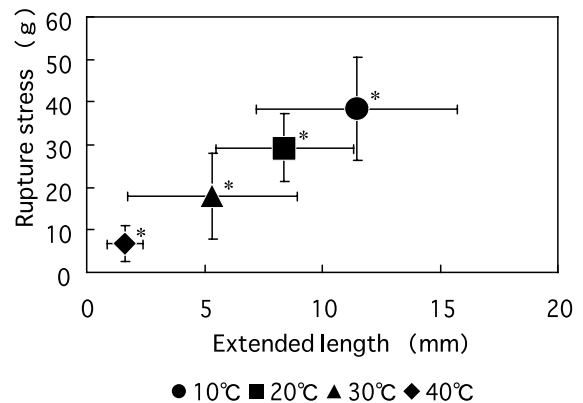


Fig. 4 Texture of scallop flakes manufactured from frozen scallop adductor muscle thawed by different temperature conditions. (n=6×5: Six samples were prepared from one individual.) Bars indicate standard deviation (SD).

\*Significantly different from other scallop flakes, p<0.05.

#### 2. 貝柱の凍結・解凍が貝柱フレークの褐変に及ぼす影響

未解凍区、解凍区及び解凍貯蔵区の貝柱とそれらから製造した貝柱フレークのグリコーゲン量（無水物換算値）を Fig. 5 に示した。貝柱のグリコーゲン量は、未解凍区との比較で、解凍区での変化はみられなかったが、解凍貯蔵区で少し低下した。貝柱フレークのグリコーゲン量は、いずれの試験区とも貝柱よりも低く、その低下率は未解凍区で1.9%、解凍区、解凍貯蔵区で、それぞれ22.9、37.6%であり、解凍貯蔵区での低下が大きかった。

ボイル区、未解凍区、解凍区及び解凍貯蔵区の貝柱の糖代謝物量を Fig. 6 に、各種貝柱より製造した貝柱フレークの糖代謝物量と褐変度を Fig. 7 に示した。貝柱については、G6P量は、ボイル区と未解凍区では少なく、それぞれ4.65、1.23 μmol/gであった。その一方、解凍区、解凍貯蔵区では、17.25 μmol/g、10.61 μmol/gと高い値を示した。G1P量は、全区分で0.06～1.02 μmol/gと少な

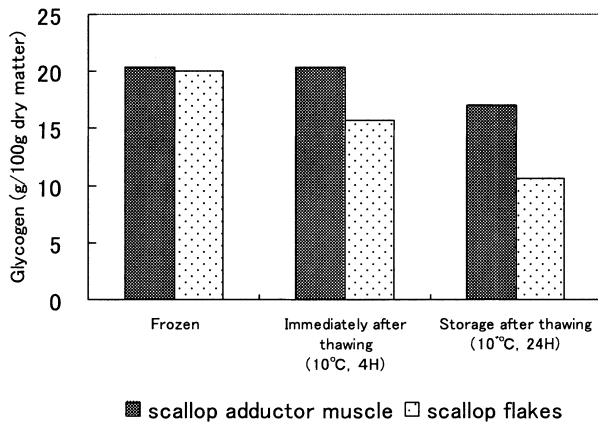


Fig. 5 Contents of glycogen of scallop adductor muscle and scallop flakes.

かった。F6P量は、0~3.35  $\mu\text{mol/g}$ であり、解凍貯蔵区で3.35  $\mu\text{mol/g}$ と少し高い値を示した。貝柱フレークでは、G6P量は1.66~9.07  $\mu\text{mol/g}$ であり、貝柱と同様に解凍区と解凍貯蔵区で、それぞれ、9.07, 6.44  $\mu\text{mol/g}$ と高い値を示した。貝柱との比較では、未解凍区を除く全区分で低下した。G1P量は、0.57~2.46  $\mu\text{mol/g}$ であった。F6P量は、0.46~3.10  $\mu\text{mol/g}$ であった。貝柱との比較では、未解凍区での若干の増加、解凍貯蔵区での減少がみられ

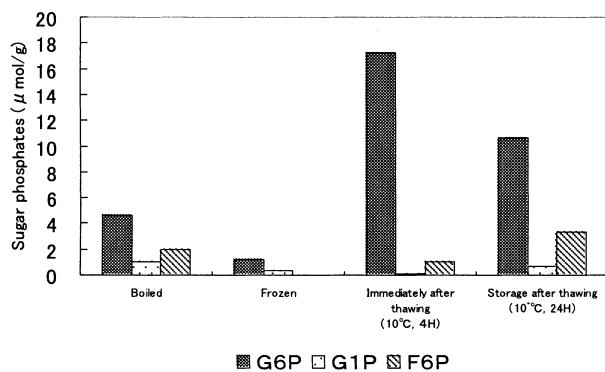


Fig. 6 Contents of sugar phosphates in scallop adductor muscle.

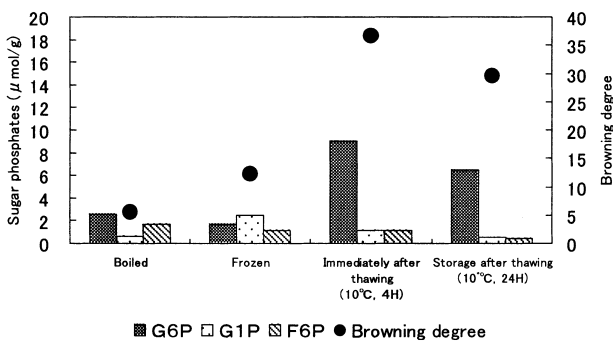


Fig. 7 Contents of sugar phosphates and browning degree in scallop flakes.

た。貝柱フレークの褐変度は、ボイル貝柱が5.5と最も低く、解凍区、解凍貯蔵区でそれぞれ、36.6, 29.6と高くなった。未解凍区の貝柱フレークの褐変度は12.2であり、解凍した冷凍貝柱と比較して褐変が抑制されていた。

ボイル区、未解凍区、解凍区および解凍貯蔵区の貝柱のオクトピン、L-アルギニン量を Fig. 8 に、各種貝柱より製造した貝柱フレークのオクトピン、L-アルギニン量を Fig. 9 に示した。

貝柱については、オクトピン量が、ボイル区、未解凍区でそれぞれ0.99, 1.30  $\mu\text{mol/g}$ と少なく、解凍区、解凍貯蔵区でそれぞれ7.66, 12.75  $\mu\text{mol/g}$ と多かった。L-アルギニン量は、ボイル区、未解凍区でそれぞれ16.04, 12.89と多く、解凍区、解凍貯蔵区でそれぞれ、6.67, 1.01  $\mu\text{mol/g}$ と少なかった。貝柱フレークについては、オクトピン量とL-アルギニン量の傾向は貝柱と類似していた。それらの含有量を貝柱と比較すると、オクトピン量は、ボイル区で1.15  $\mu\text{mol/g}$ とほとんど変化しなかったが未解凍区、解凍区、解凍貯蔵区でそれぞれ、2.45, 9.83, 14.92  $\mu\text{mol/g}$ と少し増加した。L-アルギニン量は、ボイル区、未解凍区、解凍区でそれぞれ、18.30, 15.44, 7.76  $\mu\text{mol/g}$ と少し増加したが解凍貯蔵区で1.00  $\mu\text{mol/g}$ と変化しなかった。

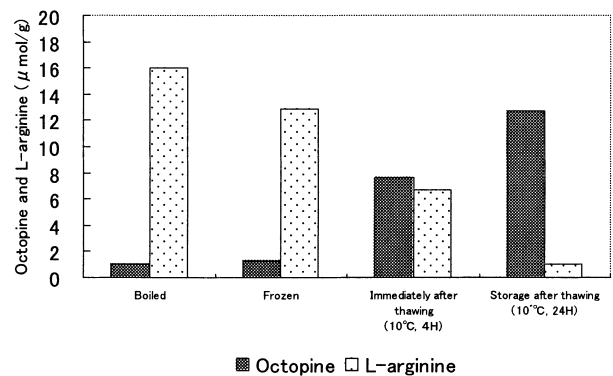


Fig. 8 Contents of octopine and L-arginine in scallop adductor muscle.

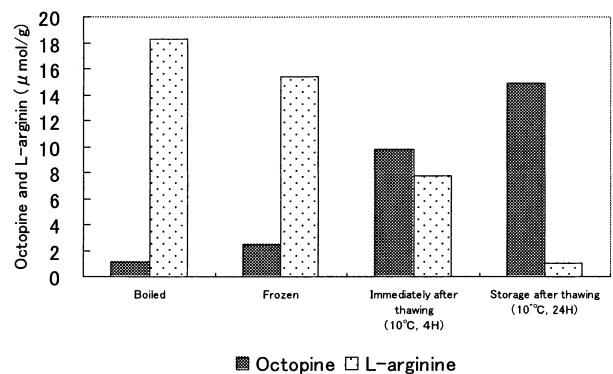


Fig. 9 Contents of octopine and L-arginine in scallop flakes.

## 考 察

本研究において、各種貝柱から製造した貝柱フレークの繊維強度は、冷凍貝柱からのフレークが最も弱かった。これに関しては凍結解凍中における物性の変化が大きく関与すると考えられる。凍結による肉質の変化は、組織構造的変化と膠質構造的変化が知られており、前者は機械的損傷説、細胞破壊説、気体分離膨張説、後者は脱水損傷説、塩基説、pH変化説、タンパク質変性、タンパク質分散密度の変化などである<sup>11)</sup>。これらの説は、一つだけで単独に説明されるものではなく、相互関係を有する場合が多く、複雑である。ホタテガイでも凍結解凍処理中に貝柱の筋原繊維の微細構造が著しく崩壊することが報告されており<sup>12)</sup>、このことは、日常的にも生鮮貝柱と解凍した冷凍貝柱の刺身を食した場合、前者の方が、歯ごたえが強く、コリコリ感があると言われていることから理解できる。

生及びボイル貝柱から製造した貝柱フレークの繊維強度は、比較的良好な食感を示したが、ボイル貝柱フレークの方が、破断応力、伸びた長さともに優れており、繊維強度も安定していた。脱殻時に、ボイル工程を加える方がより効果的であると考えられる。このボイル貝柱の繊維強度が、一般的な貝柱フレークの物性と考えられる。

冷凍ボイル貝柱から製造した貝柱フレークの繊維強度は、最も強かった。他のフレークと比べ破断応力がかなり大きく、品質的に物性が硬くなる傾向を示した。これは、繊維の伸びた長さの個体差が小さくなることから、凍結中に貝柱繊維間での水分の移動、平衡化が進んだことが原因の一つとして考えられる。

以上のように、貝柱フレーク製造に使用する貝柱原料によって、製品の物性に大きな違いがみられた。特に冷凍貝柱から製造する場合には、物性の低下が著しく、その製造条件について検討する必要があると考えられた。

解凍した冷凍貝柱の蒸煮加熱後の物性は、解凍中の雰囲気温度により大きく異なり、雰囲気温度が高いものほど加熱後の貝柱の繊維強度は低下した。市販の冷凍貝柱の多くは、冷蔵庫内の自然解凍、すなわち緩慢解凍による方法での食べ方が推奨されている。本研究でも冷凍貝柱を低温解凍することにより、加熱後の物性に与える影響が少ないことが明らかとなった。これら物性低下の原因は、解凍中の自己消化により筋肉組織が軟化した可能性もあり、今後検討の必要がある。

また、凍結状態の貝柱に対する蒸煮加熱は、物性を著しく低下させた。この原因としては、筋繊維組織内に氷結晶を含む状態で加熱したことから氷結晶の融解とタンパクの加熱凝固が同時に起こり、筋繊維間の隙間が大き

くなって脆くなった可能性や貝柱内外での温度差が大きく、かつ加熱に時間がかかったためプロテアーゼが作用した可能性など考えられるが、明確な要因は断定できない。

以上の結果より、冷凍貝柱から製造される貝柱フレークの繊維強度は弱い、解凍温度条件によりある程度改善できることが明らかとなった。

冷凍貝柱を解凍した場合、解糖系により糖代謝物が多量に生成され<sup>13)</sup>、それらがメイラード反応による褐変に関与することが報告されている<sup>14)</sup>。メイラード反応による褐変は、水産加工品でもよく見られ、カツオ缶詰のオレンジミートや乾はたて貝柱の褐変などが知られている。乾はたて貝柱では、製造工程での一番煮工程が強く関わっており、糖代謝物と色調の関係が調べられ、褐変原因の解明とその防止法が報告されている<sup>15)</sup>。過度の褐変を生じた加工製品は、外観の色調が悪くなり、商取引上かなりの不利益を被る。

本研究でも、褐変要因の解明と防止法の検討のために冷凍貝柱の解凍条件と糖代謝物量及びそれらから製造した貝柱フレークの糖代謝物量と色調との関係を調べた。解凍により貝柱のグリコーゲン量は、解凍貯蔵区で大きく減少した。解凍後のホタテガイ閉殻筋は、未凍結の閉殻筋と比較して、貯蔵中のグリコーゲンの減少速度が著しく速いことが報告されている<sup>12)</sup>。また、解凍区の貝柱では、グリコーゲン量の減少がほとんどみられないことから、解凍後の貯蔵中にグリコーゲンの分解が起こっていると推察された。また、解凍区、解凍貯蔵区の貝柱から製造した貝柱フレークのグリコーゲンの減少は、未解凍区から製造したものと比較して大きかった。これについては、凍結解凍処理での組織の損傷により、解糖系酵素が自由度を増し、加熱されることによりグリコーゲンの分解を引き起こしたものと推測される。これらから調製した貝柱フレークは、著しく褐変した。この褐変を引き起こす要因としては、貝柱中に生成された糖代謝物、特にG6Pが関連していると考えられた。また、貝柱フレーク中のG6P量は貝柱中よりも減少しており、メイラード反応に利用されたものと推測された。

解凍区と解凍貯蔵区の貝柱では、G6P量が著しく増加していた。凍結点付近の温度帯で解糖系も特異的に反応が増大することが知られている。カツオでは、グリセリルアルデヒド-3-リン酸以降の解糖系の反応が停止することにより、G6P、F6Pの増加を引き起こし、オレンジミートを誘発することが報告されている<sup>16)</sup>が、今回はオクトピンの増加、アルギニンの減少がみられるので、解糖系そのものの停止はないと判断された。解凍中にATPが消失するため、ホスホフルクトキナーゼ活性が律速と

して働き、一時的にG6Pの蓄積がみられたのだろう。そのため解凍直後のG6P量が最大になり、貯蔵後は解糖反応より少し減少していた。これらは、川嶋の研究<sup>12)</sup>からも同様の結果が導かれ、同様の結論を提示している。

その一方、ボイル貝柱は、一番煮工程における加熱で解糖系酵素が失活するため解糖系は停止している。また、ボイル貝柱中には極めて糖代謝物が少なく、貝柱フレーク製造中にも糖代謝物が生成しないことから、貝柱フレークの褐変はほとんどみられなかった。

未解凍区の貝柱で製造した貝柱フレークは、製造工程中に解糖系が僅かに進行するもの貝柱中の糖代謝物量が少ないため褐変は小さかった。

得られた結果から、生及びボイル貝柱から貝柱フレーク製造する場合、繊維強度、褐変度ともに良好な品質を有する製品を製造できる。一方、冷凍貝柱から貝柱フレークを製造する場合、その繊維強度の弱さが問題となる。その改善策としては、冷凍貝柱を適切な温度域で解凍することであり、そうすれば、製造工程においてフレークの形状を維持するために必要な物性が保たれた。

しかし、製品の色調という観点からは、冷凍貝柱を解凍することは、褐変の原因物質となる糖代謝物、特にG6Pを大量に生成するため不向きであった。

そのため、冷凍貝柱から製造した貝柱フレークは、製造方法での褐変防止では無く、別の角度からの防止策を講じなければならない。また、製品の殺菌条件、保管温度及び包装形態などを検討する必要がある。

## 要 約

各種貝柱（生貝柱、冷凍貝柱、ボイル貝柱、冷凍ボイル貝柱）から製造した貝柱フレークの成分及び繊維強度を評価し、その品質向上について検討した。

1. 生及びボイル貝柱から製造した貝柱フレークは良好な物性、色調を有していたが、冷凍貝柱を原料とした場合は、繊維強度が不足していた。
2. 冷凍貝柱から貝柱フレーク製造条件について検討し、10℃での低温解凍が物性改善に効果のあることを明らかにした。
3. 冷凍貝柱の解凍により、グリコーゲンの分解物であるG6Pが大量に蓄積し、それから製造した貝柱フレークは強く褐変した。
4. 冷凍貝柱を原料とした場合は、製品の殺菌条件、保管温度及び包装形態などを検討する必要がある。

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# 網走湖におけるヤマトシジミの産卵及び初期生活史に関する生態学的研究（英文）

馬場勝寿

網走湖では、過去の約半数の年は、夏の産卵期における低水温のため産卵・放精が行われなかったと推察される。大型浮遊幼生は表層に、小型のものは塩分躍層付近に分布しており、浮遊幼生時の塩分の必要性に応じた垂直分布をしている。着底直後の稚貝は泥含量の少ない底質地点にのみ分布しており、着底と初期生残には砂礫の底質が必要である。網走湖での初期成長は、南方生息地での報告よりも著しく遅く、満1年で殻長約0.6 mm、満2年で約2.1 mmまでしか成長しない。冷夏の年は産卵されず初期成長も遅いことから、新規加入が不安定で漁獲対象年齢が高いため、北方生息地における本種の資源管理は南方よりも厳格に実施される必要がある。

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## 北海道北部産マガレイの耳石輪紋径に基づく「育ち群」判別第1報 漁獲物の1～3歳における「育ち群」

下田和孝，板谷和彦，室岡瑞恵

石狩湾～オホーツク海にかけて分布するマガレイの育ち群を、耳石の輪紋径をもとに判別した。1歳秋から3歳冬にかけてオホーツク海の枝幸漁協で水揚げされた漁獲物は、91.1%がオホーツク海育ち群、0.8%が日本海育ち群であった。稚内漁協で2歳冬に漁獲されたマガレイはすべてオホーツク海育ち群と判定され、続く2歳春の産卵期に日本海の日塩支所～余市郡漁協に水揚げされた漁獲物は、86%以上がオホーツク海育ち群であった。日本海の小平沖と石狩湾で実施した幼魚調査において、日本海育ち群に相当する個体が採集されたが、これらの体長は漁獲サイズに達していなかったことから、日本海育ち群の多くは3歳春以降に漁獲対象になるものと推測された。

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# 北海道北部に分布するマガレイ資源の特徴とコホート解析

下田和孝，板谷和彦，室岡瑞恵，星野 昇

石狩湾～オホーツク海に分布するマガレイ資源の漁獲動向、漁獲物組成および幼魚の密度指数の海域間における類似性を調べた。日本海における現行の資源評価海域（初山別地区～稚内地区）の漁獲量は、その南側に位置する苫前地区と高い正の相関を示した。漁獲物の年齢組成および年級群豊度は、オホーツク海から石狩湾にかけて連続的に変化した。1歳幼魚密度指数は石狩湾とオホーツク海との間で正の相関が認められた。以上の結果、および過去の標識放流の結果から、石狩湾～オホーツク海のマガレイ資源を1つの個体群とみなし、資源状態を評価することが適当であると結論づけた。コホート解析によると、この資源の動向は、数年に1度の高豊度加入群の影響が大きかった。

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## 北海道南西部日本海沿岸における海藻植生とキタムラサキウニの生殖巣発達の関係（英文）

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海藻植生とキタムラサキウニの生殖巣発達を消化管内容物との対応関係で明らかにするため、2001年5月から8月にかけて、北海道南西部に位置する寿都湾の3地区（矢追，六条，美谷）で調査を実施した。キタムラサキウニは、各地区においてそれぞれ現存量が高いホンダワラ科褐藻とケウルシグサ（矢追），ケウルシグサとフクロノリ（六条），コンブ目褐藻とケウルシグサ（美谷）を主に摂食して生殖巣を発達させた。生殖巣指数は、ホソメコンブが生育し現存量が高い場所で最も高かった。生殖巣の発達には海藻の栄養価，食べられやすさ並びに浅所から供給される流れ藻が影響していると考えられた。

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## ホタテガイ貝柱フレークの品質特性に関する研究

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通称「貝柱フレーク」は，加熱処理したホタテガイ貝柱の筋繊維をほぐして製造する新規食品素材である。これは製造方法が簡単で，かつ大量生産が可能なものである。その原料である貝柱には，生鮮，ボイル，冷凍などの形体がある。貝柱フレークの物性や色調は，原料により大きく異なる。本研究で最初に貝柱フレークの物性や色調の客観的な評価手法を確立した。そして次に，それを指標として，どの原料からでも良好な繊維感を有する貝柱フレークを調製する技術開発を行った。

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