Growth, Population Age Structure and Mortality of the Limpet *Collisella heroldi* (DUNKER, 1861) (Gastropoda: Acmaeidae) in an Intertidal Rocky Shore, in Southern Hokkaido

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The growth rate, population age structure, and mortality of the limpet *Collisella heroldi* in the intertidal area of Usujiri, Hokkaido were studied. Annual ring method and size distribution were used in determining the growth rate. *C. heroldi* showed a typical seasonal growth pattern: from April to October all individuals grew fast, coinciding with the development of the gonads, while in other months adult limpets showed little growth. A von Bertalanffy growth equation modified by Pauly and Gaschutz gave a good fit to the growth pattern. *C. heroldi* population showed a stable age structure. More than 50% of the population were 0-year juveniles. A stable mortality rate of about 65.5% per year was observed.

Limpets are numerically dominant in the macrobenthos of many intertidal rocky shore communities. As grazers on algae and a food source for carnivorous animals, they play an important role towards the energy transfer in the energy flow of the intertidal rocky shore community¹⁾ and affect community structure by influencing the composition and growth of algal species.²⁾ Therefore, information about the ecology of the limpet is very valuable in any analysis of the structure and dynamics of the intertidal rocky shore community.³⁾ Furthermore, they are a convenient group for examining population dynamics and life history characteristics.⁴⁾ In fact, their life histories, population dynamics and bioeconomics *etc.* have been widely studied (see review by Branch⁵⁾).

Basic knowledge on population dynamics, however, is poor with regard to the small limpet *Collisella heroldi*, which is widely distributed in Japan.⁶⁾ In the present study, the growth, population age structure and mortality of *C. heroldi* were investigated.

The present study was carried out along the intertidal rocky shore in Usujiri, Hokkaido (42°21'N: 140°57'E). The area is about 500 m in length and 80 m in width, and is composed of reefs, boulders, and sand, many benches and slopes. Heights of the three tidal levels (MTL, MLWL and MHWL) are 95 cm, 43 cm and 141 cm, respectively. Further details of the site are given in Fuji and Nomura.⁷⁾ In addition to

C. heroldi, *Septifer virgatus*, *Mytilus edulis*, *Littorina brevicula* and *Chthamalus dalli* are the other dominant species in terms of density in the area.

Materials and Methods

Collisella heroldi was randomly collected using a 25 × 25 cm² quadrat at 44 stations in the littoral area in Usujiri, Hokkaido (Fig. 1). Sampling was done every two months, from August 1986 to June 1989. In each quadrat, all the limpets which could be seen by the naked eye were collected carefully and then fixed in 10% sea water formalin. The shell length of each individual was measured to the nearest 0.1 mm with an electronic digital caliper. Then the total number of the limpets in all quadrats was recorded to obtain the size-frequency distribution of the population.

During the sampling period, it was recognized that the shells obtained in summer usually possessed a light colour and a thin edge (Fig. 2, A), while those in winter possessed a dark colour and a thick edge (Fig. 2, B). It was considered that the dark and thick bands recognized in winter denoted winter growth and the light and thin bands in summer denoted summer growth. Therefore, the band formed from the dark and thick edge to the light and thin edge (Fig. 2, C) was expected to be an age characteristic or growth ring. To ascertain the reliability of the band as

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Fig. 1. Map of the study area with contours based on the datum-plane, showing the sampling stations.

Fig. 2. Photographs showing growth checks on the shell of *Collisella herodi*. A: sample collected in summer showing the light margin (arrow). B: sample collected in winter showing the dark margin (arrow). C: the growth rings (band number).

a growth ring, the time and frequency of the formation of bands were determined by observing the shell edge of 150 individuals collected every two months throughout the sampling period. The age of an individual was determined by counting the number of bands, and then the animals were sorted out into different year classes.

Growth was measured mainly by the growth check method which has been used in the studies of many gastropods.⁸⁻¹⁰⁾ The reliability of this method was examined by comparing the results with size-frequency data.

The number of survivors in each year class was followed and a semilogarithmic plot was drawn to obtain a survivorship curve that would show the mortality rate. Differences in the curves for the different year classes were examined using statistical variance analysis.

Results

Size Distribution

The size of the specimen was determined by its shell length. Fig. 3 shows the size distribution histograms of the limpets collected. The presence of a few modes in most cases suggests that the population may be composed of two or more cohorts. The recruitment of juveniles was first observed either in August or October, as shown by the arrows in this diagram. From October the mean size of juveniles increased continuously in the succeeding months and a marked increase was seen especially from April to August. Most of the juveniles which were under 1.5 mm when they first appeared in the samples grew up to 4–5 mm in shell length after one year. Mean sizes of the other cohorts also showed a distinguishable increment from April to October, but during the winter period, December to April, no growth was observed. Limpets smaller than 8 mm in shell length accounted for over 90% of the whole population.

Age Determination

The occurrence of new bands formed on the shell edge was examined bimonthly. The percentage of individuals with newly formed bands increased suddenly and sharply from February to June. In April it was over 70% and in June it reached 100%. Therefore one band is formed annually on the shell. The annual and quick formation of bands suggests that the bands are year rings.

Fig. 3. Size-frequency distribution for *Collisella heroldi* population from August 1986 to June 1989, in two-month intervals. Arrows show the initial presence of new recruitments.

Table 1. Bimonthly mean sizes (MS) and standard deviations (SD) in each year class as determined by the growth check examination

Month	Year class					
	'88 yr.	'87 yr.	'86 yr.	'85 yr.	'84 yr.	'83 yr.
	MS (mm)±SD	MS (mm)±SD	MS (mm)±SD	MS (mm)±SD	MS (mm)±SD	MS (mm)±SD
'86 Aug.	—	—	—	4.9±1.0	7.0±0.7	9.6±0.7
Oct.	—	—	1.9±0.6	5.6±0.7	7.4±0.8	9.5±0.6
Dec.	—	—	2.2±0.5	5.4±0.6	7.4±0.8	9.2±0.5
'87 Feb.	—	—	2.8±0.8	5.8±0.6	7.5±0.4	9.5±0.5
Apr.	—	—	3.2±0.9	6.0±0.7	7.5±0.4	9.4±0.6
Jun.	—	—	3.4±1.0	6.4±0.7	7.8±0.7	9.8±0.6
Aug.	—	—	4.7±0.8	7.0±0.7	8.8±0.7	10.4±0.9
Oct.	—	1.5±0.4	5.5±0.9	7.2±0.6	8.9±0.9	10.7±0.7
Dec.	—	2.1±0.4	5.5±0.7	7.2±0.5	9.2±0.6	11.0±0.9
'88 Feb.	—	2.6±0.8	5.6±0.7	7.5±0.4	8.8±0.7	11.0±0.5
Apr.	—	3.0±0.9	5.8±0.7	7.4±0.5	8.8±0.5	—
Jun.	—	3.2±1.0	6.0±0.6	7.8±0.4	9.3±0.4	11.0±0.7
Aug.	—	3.9±1.1	6.4±0.7	7.8±0.7	9.4±0.4	12.0±1.7
Oct.	1.2±0.4	4.8±0.9	6.6±0.8	7.8±0.6	9.5±0.4	12.1±1.5
Dec.	1.7±0.5	4.8±0.9	6.6±0.6	7.8±0.5	9.5±0.8	12.1±1.0
'89 Feb.	1.7±0.5	4.9±0.7	6.6±0.6	7.9±0.5	9.5±0.4	11.5±1.1
Apr.	2.1±0.6	5.0±0.9	6.7±0.7	8.2±0.5	9.2±0.6	11.9±1.4
Jun.	2.6±1.0	5.8±0.8	7.2±0.6	8.2±0.6	9.4±0.6	11.6±0.9

Samples were taken from August 1986 to June 1989.

Growth Equation

In this study, only five year classes were distinguished due to the difficulty in confirming growth rings on the shells of limpets older than five years, as well as their limited individual number. Table 1 shows seasonal changes in the mean shell size (MS) and standard deviation (SD) of each year class. Shell sizes of the population increased rapidly during the period from April to October, while a slowing of growth was observed from November to March of the following year, notwithstanding the slight differences among years as well as year classes. The newly settled limpets found in October 1986 at a size of about 2 mm kept growing during the first winter period and reached about 4–5 mm during the summer of the following year. The same trend was found in newly settled limpets collected in October 1987, where shell length reached about 4 mm in August 1988. These results agree well with that of the size distribution histograms (Fig. 3).

As the gonads became ripe in July⁶⁾ and small limpets occurred in August 1986 (Fig. 3), the initial period for determining age was assumed to be August. The mean shell size during the months following birth was obtained from Table 1, and the values were plotted as a function of time (Fig. 4). To show the seasonal growth pattern, the growth equation and curve were determined following the method of Moreau.¹¹⁾ The equation is as follows:

$$L_t = 10.7837 \times (1 - \exp(-0.4476 \times (t/12 + 0.084) + 0.064 \times \sin(6.2822 \times (t/12 - 1.4188))))$$
, where L_t = shell length (mm) at t -month age. This curve shows a close fit to the observed values. The size at first maturation of *C. heroldi* is 5 mm,⁶⁾ thus reading from Fig. 4, the age corresponding

Fig. 4. The growth curve of shell length (mm) versus age (month). Dots indicate the observed means obtained from Table 1.

to first maturation is 12 months. It could be concluded then that most of the limpets first joined the reproductive group in their second year.

Population Age Structure

Using the annual ring method, all samples were sorted into different age groups and the percentage of each group was calculated to show the population age structure (Fig. 5). It is clear that there is a large recruitment into the population every year. The 0 age group juveniles contributed more than 50% and individuals older than three years were few, usually under 10% of the total population. Although recruitment varied a little every year, the population kept a relatively stable age structure during the study period.

Mortality Rate

The initial mortality of juveniles was difficult to determine directly because the changes in their numbers reflected recruitment and death. In each year class the number of juveniles increased during the initial several months until it reached

Fig. 5. Population age structure of the limpet *Collisella heroldi*. Roman letters indicate the age of animals.

Fig. 6. Survivorship curves of different year classes of the *Collisella heroldi* population.

Table 2. Survivorship equations for the different year groups of *C. heroldi* population

Year group	Survivorship equation	R	P
1984	$\text{Log } N = -0.0315 t + 2.7870$	0.8579	<0.001
1985	$\text{Log } N = -0.0287 t + 2.8189$	0.9025	<0.001
1986	$\text{Log } N = -0.0387 t + 3.2164$	0.9719	<0.001
1987	$\text{Log } N = -0.0417 t + 3.2764$	0.9261	<0.001
1988	$\text{Log } N = -0.0518 t + 3.5933$	0.9791	<0.05

a peak whereupon the number of survivors was followed. Fig. 6 shows the relationship between survivorship number and age after birth of each year class. The survivorship equations are presented in Table 2. Analysis of covariance of these semilogarithmic regression lines indicated that there is no statistical difference between their slopes ($P > 0.05$), but their positions were significantly different ($P < 0.001$). It could be deduced that although the recruitment changed from year to year, there was a specified mortality rate, about 65.5% per year, in this population.

Discussion

In the present study, the annual ring method and size-frequency distribution were used in determining growth in the shell length of *C. heroldi*. The disadvantage of both methods is that the older year groups could not be separated satisfactorily due to their slow growth rate and the growth of juveniles could be underestimated because of the successive recruitment of small limpets during their first several months.^{4,9} From the analysis of size distribution, only the first two cohorts appeared clearly in all cases. There was an absolute predominance of smaller limpets under 9 mm in shell length and the larger ones were almost indistinguishable in the histograms.

One problem which should be pointed out in this study is the random sampling method along the shore. In the sea-side stations, the density of the limpets were very high and the animals were seen intermingling with masses of mussels. As a result of the crowded condition, almost all of the samples collected were small and came from the sea-side stations. A few limpets larger than 10 mm in shell length were mainly from the land-side stations, where their density was much lower (unpublished data). Various studies on the different growth patterns of sub-populations of limpets distributed in different zones of a shore have been reported.^{4,12-15} In the present study, the result on the growth pattern of smaller limpets is represented mainly by the sea-side

group because of their absolute predominance in the samples. Most of the individuals here probably survive for only two years, based on the size-distribution method, and reach a mean size of about 7.5 mm in the end. On the other hand, the land-side group probably survive much longer, as is the case in *Collisella scabra*.¹⁶

A typical seasonal change was observed in the growth of *Collisella heroldi*. Therefore, the von Bertalanffy growth equation modified by Pauly and Gaschutz which was introduced in Moreau¹⁷ was used to express the seasonal growth pattern. Unlike some species such as *Notoacmea petterdi* which stopped growth before maturation,⁵ *C. heroldi* grew quickly from April to October with simultaneous active development of the gonad.⁹ This pattern is similar to *C. limatala*,¹⁷ *N. scutum*,¹⁴ and the low shore population of *C. scabra*.¹⁸ As the seasonal growth rate mainly represented that of the sea-side group of *C. heroldi*, the reason for this pattern may be the same as that explained by Sutherland.¹⁸ It is known that growth rate is affected by both physical and biological factors such as desiccation, temperature, availability of food, condition of the gonads, etc.⁴ Further investigations on the effects of various factors on the growth of *C. heroldi* are still needed.

The age structure showed a successive heavy recruitment every year during the sampling period. There was no dominant year class in the population. Although the amount of recruitment varied from year to year (Fig. 6), there was no statistical difference in mortality rate among different year classes ($P > 0.05$). This is clearly different from the well-known limpet *Patella vulgata*, whose recruitment fluctuated sharply in different years and different sites.¹⁹ It was also found that these fluctuations depended largely on the occurrence of frost during the first few weeks after the settlement of spat. *C. heroldi*, however, shows a stable mortality rate after recruitment and this indicates that the size of the population might mainly depend upon the annual recruitment. Thus, physical and biological fac-

tors affecting annual recruitment must be very important for the regulation of the *C. heroldi* population. The study period of the present work was only three years; more observation is needed to find the factors affecting the recruitment of *C. heroldi*.

In this study, *C. heroldi* showed a relatively stable mortality rate. The reason for this phenomenon is, perhaps, because most of the individuals studied lived at the sea side of the intertidal area and intermingled with masses of mussels. The fatal effect of desiccation during summer might be weakened due to the shorter exposure time and to the shading effect of mussels in this area. It was considered that the main sources of mortality and its positive relationship to density were desiccation and a shortage of algal food caused by the desiccation itself.^{16,19)} In subtidal populations of *C. scabra* and *Patelloida alticostata*,¹⁵⁾ there were a relatively stable mortality rate and constant growth during summer. These results are similar to the present study. There have been many studies on the mortality of limpets,^{3,13,15,16,20-22)} In these studies, the mortality rates were found to be positively related to their densities, but negatively correlated with the growth rate for some populations, while in other populations the growth rate has no clear relationship with the mortality rate.¹⁵⁾ More studies should be conducted to find the sources of mortality of *C. heroldi* population.

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