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Production of the Limpet *Collisella heroldi* Population in an Intertidal Rocky Shore in Southern Hokkaido

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Abstract

The body weight of 0 year individuals of the limpet *Collisella heroldi* increased throughout the year, while that of the over 1 year adults changed distinctly in accordance with its reproductive cycle. Somatic tissues of the adults showed decrease during the developmental period of the gonads, fast increment after spawning (October-December), and almost no growth during winter. Changes in the energy content of the somatic tissues also showed a reverse relationship with the gonads. Energy allocated to somatic storage declines with age from 90% to 35% for 0-5 year old animals while energy transferred to gonads increases with age from 5% to 64%. The energy transferred to the shell varied from 5% to 1% according to age from 0 to 5 year. Mean annual productions during the study period were 4.74 and 1.12 Cal/m^2 for *Pr* and *Pg*, respectively. The mean *P/B* turn-over rate was 1.67.

Introduction

The small limpet *Collisella heroldi* which distributes widely from Hokkaido to Taiwan, is the numerically dominant species in the intertidal rocky shore community of Usujiri, southern Hokkaido (Fuji and Nomura, 1990). The limpets feed chiefly by scraping the rock surface with their long, toothed radula, rasping off the microscopic film of algae which forms a slimy coating on the rocks (Hawkins and Hartnoll, 1983). Accordingly they contribute to the intertidal carnivorous gastropods via prey-predator interaction (Branch, 1978). Thus, limpets play an important role in the energy flow of the intertidal rocky shore ecosystem (Hawkins and Hartnoll, 1983). Production is an important part in the energy budget of this population. The objective of this study is to provide detailed information on the production of the *C. heroldi* population.

Materials and Methods

Growths of body, somatic tissues and gonad accompanying shell growth

Details of the study site and sampling methods are given in Niu et al. (1992). Every month, from July 1989 to October 1990, about 200-300 individuals were collected and then classified into different age groups (Niu et al., 1992). After the

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shell length was measured, the body was divided immediately into three parts: non-gonad tissues, gonad, and shell. The tissues and shells were dried separately in an oven at about 60°C until constant dry weights were obtained. Then the dry weights were measured with an electrical balance to 0.01 mg. The logarithm of the dry total flesh tissue, soma, gonad and shell weights were related to the logarithm of shell length and also least square regressions were calculated separately. Changes in growth of the different parts of the body accompanying shell growth were then determined by the growth equation (Niu et al., 1992).

Caloric and ash content

After the dry weights were measured, somatic tissue samples of the same age group and all male and female gonad samples of the same month were pooled together and then powdered. Each sample was divided into two parts for measurement of caloric and ash content. Caloric content was measured by the iodate-sulfuric acid wet-oxidation method (Hughes, 1969). Ash content was analyzed by burning the samples inside a furnace at 500°C for at least 8 hours. For a given measurement item each sample was divided into three to five subsamples. In regards to the determination of shell caloric content, it is known that a small amount of energy is transferred into the shell in the form of shell protein (Hughes, 1969). To measure the amount of protein per gram of shell, the mineral contents of a clean dry shell with a known weight was dissolved away using hydrochloric acid (about 0.1 N). The remains were dried in an oven at 60°C for 48 hours and the dry weights were measured. By applying a value of 4.085 cal/mg protein following Parry (1982), the caloric content of the shell was obtained.

Biomass and production

Utilizing the survivorship curves of different year groups of the *C. heroldi* population (Niu et al., 1992), the mean density of the population was obtained. Using the mean density and the total energy of an individual's body by calculated by adding together the energy of all parts of the body obtained from the mean dry weights of the somatic tissue, gonad, shell and the corresponding caloric values, the annual mean biomass (Cal/m^2) of the *C. heroldi* population was calculated. Using the survivorship curves mentioned above and the energy value of somatic tissues of different year groups by month, Allen curves were drawn for the different year groups by plotting the densities of survivors on the ordinate and the energy values of survivors on the abscissa. The area under the curve between any two plots shows the production during that period. Therefore, somatic production (*Pgso*) of different year groups by every month was calculated by the equation as follows.

$$P = N_{t+1} W_{t+1} C_{t+1} + 1/2\ (N_t - N_{t+1})\ (W_{t+1} C_{t+1} - W_t C_t)$$

where P is the production during the period of t to $t+1$; N_t and N_{t+1} are the numbers of survivors at time t and $t+1$, respectively; W_t and W_{t+1} are the mean dry weights of somatic tissues at time t and $t+1$, respectively; C_t and C_{t+1} are the caloric values of the tissues at time t and $t+1$, respectively.

Using the survivorship curve, the mean monthly gonad dry weights and the caloric values of different year groups, and production of gonads (*Pr*) was calculated also by the Allen graphical method (production of male and female gonads were pooled together to get a mean value of gonad production).

Annual production was calculated by adding together *Pgso*, *Pgsh* and *Pr*.

Results

Growth rate of body

Very little difference was found between male and female individuals with regards to shell length-flesh body dry weight relationships (t-test, $P > 0.05$). So the regression lines were computed monthly without separating the sex. Using the growth equation (Niu et al., 1992) and the regression lines, the mean flesh body dry weight of each year group was determined, and the results are as shown in Fig. 1. The 0 year group born in 1989 showed a constant increase, while the 1 year group born in 1988 had a distinct increase starting in May, and reached a peak in July-August, then decreased sharply in September-October. There was little difference among the different years. The groups over 1 year old showed a similar pattern to the 1 year group.

Variation of body parts in year groups coinciding with successive shell growth

A. Gonad

As the gonads became very small during the resting stage, it was extremely difficult to separate them from the other soft tissues especially in small individuals. So, the dry weight of these gonads were considered to be 0 in the present work. Moreover, as the sex also could not be distinguished, and both testis and ovaries consisted mainly of connective tissues and primary gamete cells (Niu and Fuji, 1989), the dry weights of the male and female gonads were thought to be equal during this stage and were measured without separating the sex. It is already known that the sex ratio of *C. heroldi* is 1 : 1, so unsexed samples were divided equally between the two sexes. On this base, the gonadal somatic index (GSI) calculated as the relative amount (%) of gonadal material compared to the total flesh

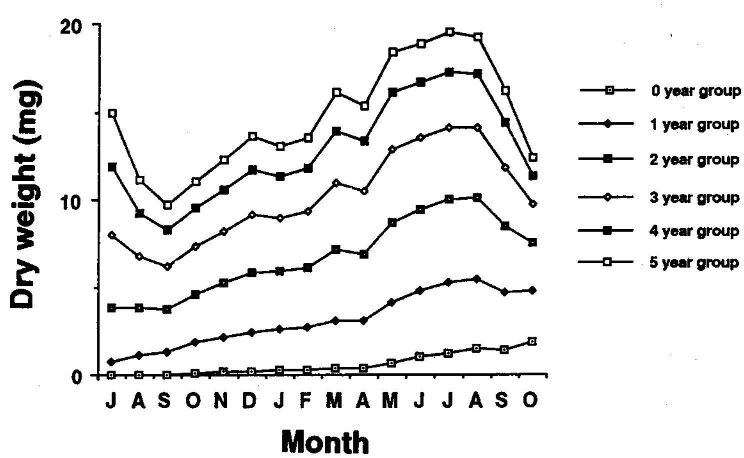

Fig. 1. Growth curves in total body dry weight of each age group of the limpet *C. heroldi* population.

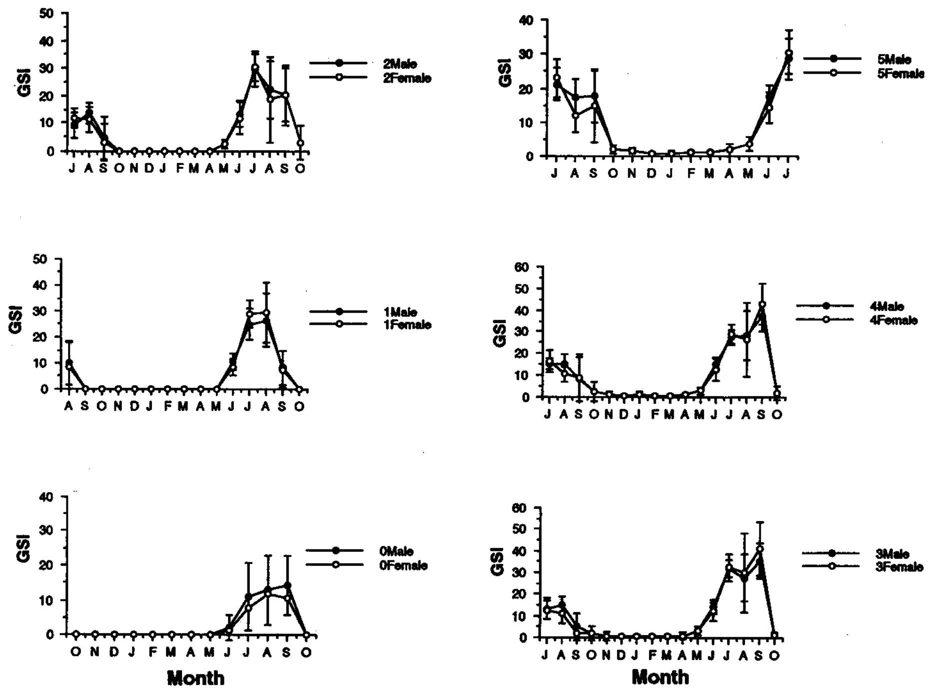

Fig. 2. Seasonal changes in the gonadal somatic index of different age groups of *C. heroldi*.

body dry weight was determined for the adult year groups. The results are as shown in Fig. 2. Age groups under 2 years seemed to spawn a little earlier than the older ones. Using the GSI values shown in Fig. 2 and the total flesh body dry weight of each age group shown in Fig. 1, the monthly male and female gonad dry weights of each age group were calculated and the results are as shown in Table 1. The amount of gametes spawned was thought to be different between dry weights of the most matured gonad in September and the spent gonad in October.

B. Somatic tissues

Somatic tissues were termed as the flesh tissues left after removing the gonad. Their dry weights were calculated by subtracting the gonad dry weight from the total flesh body dry weight.

The results are as shown in Table 2. Fig. 3 shows the seasonal changes in the somatic dry weights of every year group of *C. heroldi*. The 0 year group showed a progressive increment throughout the whole year especially from May to October. But, there was a slight decrease in September, perhaps, because of the use of transformation energy into gamete production as can be seen by consulting with Fig. 2. The 1 year group also showed a fast increment especially in May but a decrease was found in July when the gonads were developing rapidly. In groups older than 2 years, the somatic tissues showed a decrement during the breeding season and increment during the spent period (October-December). The increment of somatic weight ceased in January and February when the sea water temperature dropped to

Table 1. Male and female monthly gonad dry weight (mg) for each age group of *C. heroldi* from July 1989 to October 1990.

Month	Age group 0		I		II		III		IV		V	
	M	F	M	F	M	F	M	F	M	F	M	F
'89 Jul.	—	—	—	—	0.36	0.46	1.06	1.01	1.81	1.97	3.16	3.43
Aug.	—	—	0.12	0.10	0.53	0.44	1.01	0.74	1.38	0.97	1.95	1.33
Sep.	—	—	0.00	0.00	0.17	0.12	0.31	0.12	0.68	0.75	1.73	1.45
Oct.	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.15	0.23	0.23	0.21	0.21
			S : 0.12	0.10	0.53	0.46	0.91	0.86	1.58	1.74	2.95	3.22
Nov.	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.14	0.14	0.22	0.22
Dec.	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03	0.10	0.10	0.11	0.11
'90 Jan.	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.06	0.14	0.14	0.13	0.13
Feb.	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.10	0.10	0.16	0.16
Mar.	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.09	0.12	0.12	0.20	0.20
Apr.	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.09	0.16	0.16	0.29	0.29
May.	0.00	0.00	0.00	0.00	0.21	0.21	0.44	0.44	0.49	0.49	0.68	0.68
Jun.	0.02	0.01	0.52	0.40	1.28	1.12	1.94	1.64	2.54	2.14	3.31	2.72
Jul.	0.14	0.10	1.31	1.53	2.99	3.05	4.51	4.56	4.84	4.98	5.61	5.99
Aug.	0.20	0.18	1.47	1.64	2.25	1.89	3.90	4.25	4.87	4.53	—	—
Sep.	0.20	0.15	0.39	0.35	1.73	1.73	4.20	4.87	5.34	6.19	—	—
Oct.	0.00	0.00	0.00	0.00	0.24	0.24	0.14	0.14	0.22	0.22	—	—
	S : 0.20	0.18	1.47	1.64	2.75	2.81	4.37	4.42	4.62	4.31		

M : Male ; F : Female ; S : Spawn.

the lowest. Overall, the decrease in somatic weight synchronized with the development of the gonads indicating a transfer of energy from the body to the reproductive tissues.

C. Shell

The relationship between the monthly shell dry weight and length was examined. On this basis and using the growth equation, seasonal changes in the shell dry weight of each year group were calculated. The results are as shown in Fig. 4. The dry weight increased distinctly from May to November and growth stopped to increase during winter from December to April.

Caloric and ash contents

A. Gonads

The results of calorific values and ash contents of male and female gonads by month are as shown in Table 3. The sex of the gonads in the resting stage could not be distinguished, so the calorific values of male and female gonads during this stage were assumed to be equal. The calorific values of both testes and ovaries increased with maturity, but the mature ovary had a distinctly higher value than that of the testes. The ash content of fully matured testes varied from 8% to 12%, while that

Table 2. Male and female monthly somatic dry weight (mg) for each age group of *C. heroldi* from July 1989 to October 1990.

Month	Age group 0		I		II		III		IV		V	
	M	F	M	F	M	F	M	F	M	F	M	F
'89 Jul.	—	—	0.78	0.78	3.54	3.44	6.98	7.04	10.09	9.93	11.78	11.51
Aug.	0.01	0.01	1.07	1.08	3.38	3.47	5.83	6.10	7.92	8.33	9.12	9.81
Sep.	0.04	0.04	1.33	1.33	3.61	3.66	5.97	6.16	7.62	7.56	8.07	8.35
Oct.	0.11	0.11	1.86	1.86	4.68	4.68	7.24	7.24	9.30	9.30	10.88	10.88
Nov.	0.18	0.18	2.20	2.20	5.33	5.33	8.22	8.22	10.48	10.48	12.08	12.08
Dec.	0.20	0.20	2.44	2.44	5.89	5.89	9.14	9.14	11.67	11.67	13.56	13.56
'90 Jan.	0.26	0.26	2.61	2.61	5.95	5.95	8.96	8.96	11.25	11.25	12.96	12.96
Feb.	0.28	0.28	2.70	2.70	6.16	6.16	9.31	9.31	11.72	11.72	13.42	13.42
Mar.	0.34	0.34	3.17	3.17	7.24	7.24	10.92	10.92	13.84	13.84	15.87	15.87
Apr.	0.38	0.38	3.11	3.11	6.96	6.96	10.44	10.44	13.16	13.16	15.03	15.03
May	0.65	0.65	4.13	4.13	8.53	8.53	12.45	12.45	15.62	15.62	17.74	17.74
Jun.	1.00	1.00	4.36	4.47	8.25	8.40	11.64	11.94	14.12	14.52	15.53	16.12
Jul.	1.13	1.17	3.98	3.74	7.02	6.96	9.62	9.57	12.45	12.31	13.91	13.53
Aug.	1.33	1.34	4.06	3.90	7.88	8.24	10.20	9.86	12.27	12.61	—	—
Sep.	1.18	1.24	4.32	4.36	6.81	6.82	7.68	7.01	9.09	8.24	—	—
Oct.	1.92	1.92	4.81	4.81	7.34	7.34	9.64	9.64	11.14	11.14	—	—

M : Male ; F : Female.

of the ovary varied from 5% to 8%.

B. Somatic tissues

The results of ash (weight percent) and calories per gram (ash free dry weight) of male and female somatic tissues of different age groups were analyzed using the Kruskal-Wallis test, and no statistically significant differences between male and female were observed ($P > 0.05$). So the results of both sexes were pooled together and are as shown in Table 4. Ash content changed within a range of 10% to 18%, and was generally higher from June to October than in other months. The caloric content varied between 4 and 5 Cal/g ash free dry weight. It reached the peak in May and then kept decreasing until September, corresponding with the breeding season when the gonad developed quickly. An increment was presented in October and November.

C. Shell

The results of the protein content of shell (weight %) is as shown in Fig. 5. No statistically different values were obtained among the different months and the mean content was 1.31%. By applying a value of 4.085 cal/mg protein, the energy content of the shell was obtained ; 0.05335 cal/mg shell.

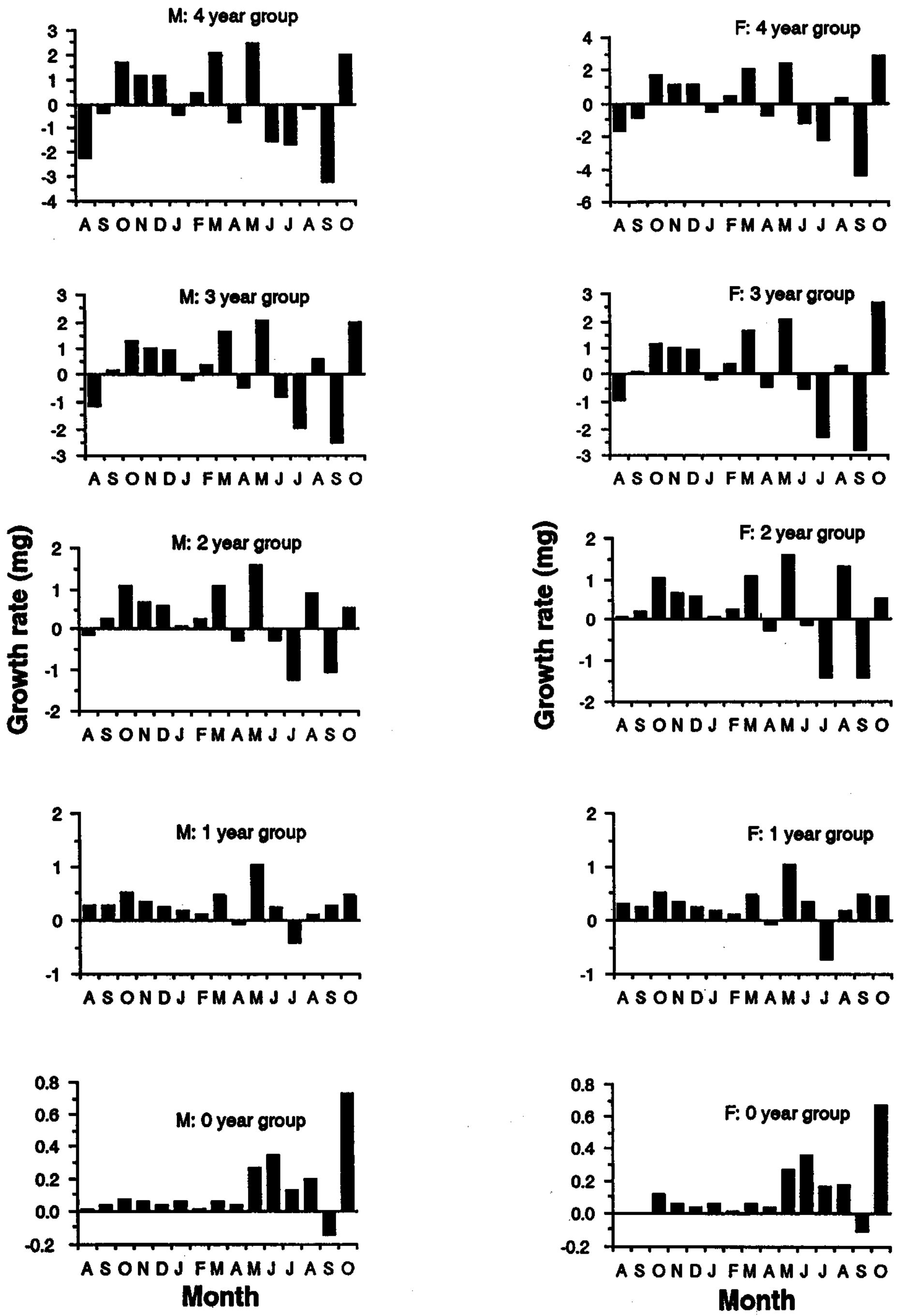

Fig. 3. Monthly absolute growth rates of somatic tissues of different age groups.

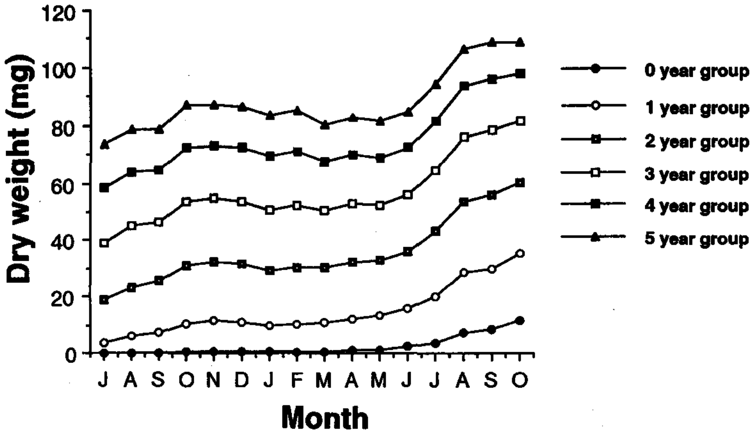

Fig. 4. Seasonal changes in the shell dry weight (mg) of different age groups of *C. heroldi.*

Table 3. Monthly calorific value per ash-free gram and ash content of male and female gonads of *C. heroldi*. Standard error in brackets.

Month	Cal/ash-free g		No. of replicates		Ash (%)	
	Male	Female	Male	Female	Male	Female
Jan.	4.1725 (0.12)	4.1725 (0.12)	2	2	10.18	10.18
Feb.	2.2195 (0.12)	2.2195 (0.12)	2	2	7.35	7.35
Mar.	2.7421 (0.13)	2.7421 (0.13)	2	2	9.24	9.24
Apr.	3.1543 (0.73)	3.1543 (0.13)	2	2	5.14	5.14
May	4.3320 (0.12)	4.3320 (0.13)	2	2	7.58	7.58
Jun.	4.1382 (0.25)	5.3275 (0.22)	5	5	11.63	5.71
Jul.	4.3972 (0.19)	5.7512 (0.14)	5	5	8.26	7.74
Aug.	4.3219 (0.19)	5.0919 (0.48)	8	9	9.12	5.92
Sep.	4.3603 (0.39)	5.3908 (0.40)	7	8	11.57	7.76
Oct.	2.1532 (−)	2.1532 (−)	1	1	7.19	7.19
Nov.	3.8814 (0.07)	3.8814 (0.07)	2	2	7.74	7.74
Dec.	4.0010 (0.03)	4.0010 (0.03)	2	2	6.44	6.44

Production, mean biomass and P/B ratio

The monthly total production was obtained by adding together the production of every year class in the same month. The results of annual production of the gonad is as shown in Table 5. It was calculated according to the reproductive cycle from October when spawning is completely finished to the following Octocer while *Pg* was calculated from August when recruitment started. It is clear from Table 5 that gonad production increases sharply and the minus production from August to October presents the gametes released during the spawning period. In the present study we calculated *Pr* by adding together the gonad production every two months except for in the spawning period. *Pr* in our study is about 20% more than the

Table 4. Monthly calorific value per ash-free gram and ash content in somatic tissues of *C. heroldi*. Standard error in brackets.

Month	Cal/ash-free g	No. of replicates	Ash (%)
Jan.	3.997 (0.60)	26	11.36 (0.84)
Feb.	4.376 (0.34)	28	12.97 (0.34)
Mar.	4.558 (0.52)	28	11.70 (0.85)
Apr.	4.156 (0.58)	16	12.39 (0.46)
May	4.806 (0.26)	23	11.33 (1.07)
Jun.	4.433 (0.43)	46	14.01 (1.27)
Jul.	4.421 (0.46)	49	12.88 (1.12)
Apr.	4.239 (0.35)	28	15.98 (1.92)
Sep.	3.952 (0.53)	40	15.10 (1.42)
Oct.	4.659 (0.39)	19	16.18 (3.11)
Nov.	4.619 (0.49)	25	13.46 (1.56)
Dec.	4.098 (0.69)	28	12.69 (2.02)

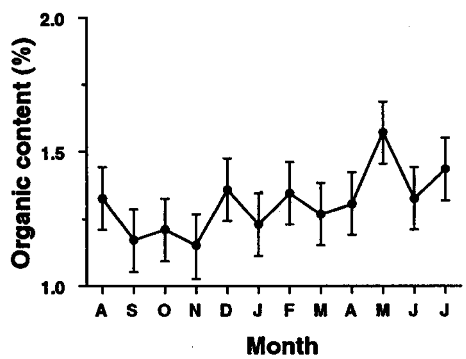

Fig. 5. Seasonal changes in the organic content (%) of the shell. Vertical bar shows the standard deviation.

energy used to release gametes. Mean *Pr* in the study period was 1.12 Cal/m^2.

Using the survivorship curves, the data shown in Table 2 and Table 4, annual production (cal/m^2) of somatic tissues was calculated and the results are as shown in the third column in Table 6. Peak production rate was found from April to June while the lowest was from June to August when the gonads have a distinct development. Annual productions of somatic tissues in the three sampling years were 5.88, 4.22, and 3.25 Cal/m^2, respectively. Mean annual production of somatic tissues during the study periods was 4.45 Cal/m^2.

The results of shell production are as shown in the fourth column in Table 6. Peak production is found from June to August, which is in reverse with the production of somatic tissues. It is clear that the shell increased distinctly at the same time as gonad development took place.

The results of mean biomass, annual production and *P*/*B* ratio of *C. heroldi*

Table 5. Annual production of gonad (cal/m^2) in *C. heroldi* population.

Year	Month	Production	
1986-1987	Oct.-Dec.	−5.21	
	Dec.-Feb.	0.21	
	Feb.-Apr.	1.33	
	Apr.-Jun.	266.98	$Pr=$ 841.60
	Jun.-Aug.	578.28	
	Aug.-Oct.	−703.63	
1987-1988	Oct.-Dec.	−7.06	
	Dec.-Feb.	0.24	
	Feb.-Apr.	1.94	
	Apr.-Jun.	382.25	$Pr=$1145.62
	Jun.-Aug.	768.25	
	Aug.-Oct.	−934.76	
1988-1989	Oct.-Dec.	−9.00	
	Dec.-Feb.	0.67	
	Feb.-Apr.	2.96	
	Apr.-Jun.	454.10	$Pr=$1361.38
	Jun.-Aug.	899.33	
	Aug.-Oct.	−1058.58	

population in the three experimental years are presented in Table 7. The P/B ratio for these three years is relatively stable and the mean P/B ratio during the study period was 1.67.

Discussion

Growth of somatic tissues, gonads and shells are expressions of the storage energy through consumption. Energy allocation among the three parts and many factors that may influence such an allocation as season, age, sex, food, etc. reflect the basic function of growth and reproduction in a species. Branch (1981) reported that a larger number of limpet mature during their first or second year and live for about five years increasing in fecundity each year due to an increase in body size. This is also true with *C. heroldi*. Both the shell length and the body weight of *C. heroldi* grow very fast during the first year (Niu et al., 1992 and Fig. 2). About 90% of the stored energy, is allocated to somatic tissues, only 5% to produce gonads, and 5% for shell growth. Despite the fact that useful data can be gained by calculating separate energy budget for an animal in every size class (Hughes, 1971), few studies have been made where limpets are examined on the energy budgets of different age groups. Thus, no comparisons can be made with our results regarding the energy allocation of individual mature limpets.

C. heroldi of over 1 year old are considered to be adult. Growth efficiency is under 10% and declines with age. While energy used for the development of the gonad increases with age, energy allocated to somatic tissues and shell decrease with

Table 6. Annual productivity (cal/m²) of somatic tissues (*Pgso*), and shell (*Pgsh*) in *C. heroldi* population.

Month	Density (No./m²)	*Pgso*	*Pgsh*	*Pg*
1986 Aug.-Oct.	770	786.52	55.44	841.96
Oct.-Dec.	651	672.49	10.80	683.29
1987 Dec.-Feb.	549	214.54	−7.19	207.35
Feb.-Apr.	463	362.95	17.77	380.72
Apr.-Jun.	390	1146.69	33.67	1180.36
Jun.-Aug.	331	66.87	121.50	188.37
Year 1986-1987		$\Sigma P=3250.06$	$\Sigma P=231.99$	$\Sigma P=3482.05$
1987 Aug.-Oct.	965	1112.57	83.34	1195.91
Oct.-Dec.	803	890.01	14.82	904.83
1988 Dec.-Feb.	667	286.88	−10.39	276.49
Feb.-Apr.	554	471.90	23.38	495.28
Apr.-Jun.	462	1411.70	42.64	1454.34
Jun.-Aug.	383	47.91	151.62	199.53
Year 1987-1988		$\Sigma P=4220.96$	$\Sigma P=305.42$	$\Sigma P=4526.38$
1988 Aug.-Oct.	1746	1516.04	108.49	1624.53
Oct.-Dec.	1388	1194.94	21.32	1216.26
1989 Dec.-Feb.	1105	398.49	−12.72	385.77
Feb.-Apr.	881	630.76	30.72	661.48
Apr.-Jun.	704	1953.93	57.16	2011.09
Jun.-Aug.	559	188.27	196.94	385.21
Year 1988-1989		$\Sigma P=5882.44$	$\Sigma P=401.90$	$\Sigma P=6284.34$

Table 7. Mean biomass (Cal/m²), production (Cal/m²), and *P*/*B* in *C. heroldi* population.

Year	*B*	*P*	*P*/*B*
1986-1987	2.5680	4.3236	1.68
1987-1988	3.5015	5.6720	1.62
1988-1989	4.4300	7.6457	1.72

age as shown in Fig. 6. These trends are similar to that of the common scallop, *Patinopecten yessoensis* (Fuji and Hashizume, 1974). Horn (1986) reported that immature chitons have lower calorific values in their somatic tissues in comparison to mature chitons and this suggests that an energetic advantage is gained by building a growing individual initially out of cheap material until it is capable of

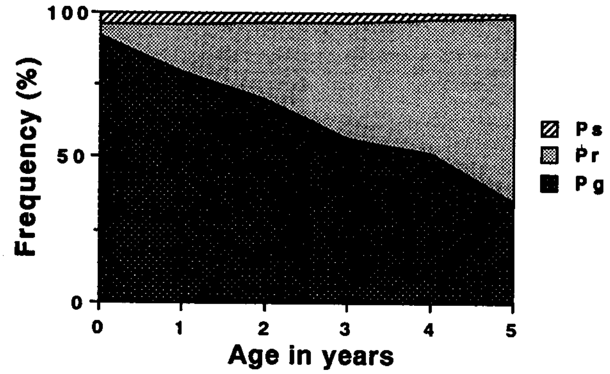

Fig. 6. Diagram showing partition of stored energy among somatic tissue, gonad and shell of *C. heroldi* in relation to its age.

making a genetic contribution to the population. However, no changes in the caloric content of somatic tissues were found among different age groups and between males and females in the present study.

Distinct seasonal changes in the production of somatic tissues, gonads and shells were found in the present study. In autumn from October to December, somatic tissues increased after spawning along with an increase in caloric content (Fig. 3 and Table 4), showing a distinct energy reservation in these tissues. During the same period, gonads maintained a relatively stable low value (Fig. 2), and the caloric content decreased (Table 4), suggesting an absorption of the gametes that remained in the gonad. Shell growth also stopped during this period (Fig. 4). From January to April, there was little production. The decrease in the dry weight of somatic tissues and the relatively low caloric value suggest that reserved energy is utilized for maintenance during this time. Jennifer et al. (1988) in their study of the bay scallop *Argopecten irradians* reported a marked decline in protein reserves to meet requirements of the maintenance energy during winter. In May, the weight and caloric content of somatic tissues showed a sharp increase. The gonads and shell also started to grow quickly. From June to September, somatic tissues declined steadily, while the gonads developed distinctly in both weight and energy content. Shells also increased quikcly synchronizing with gonad development. The reverse relationship between somatic tissues and gonads indicates the energy transfer from the former to the latter. Horn (1986) found a reciprocal relationship between somatic calorific value and gonad index of *Chiton pelliserpentis* and suggested that lipids are stored in the somatic tissue during the gonad resting phase and then transferred to the gonad during gametogenesis. It seems that somatic tissues play an important role as an energy storage site in energy partitioning. The high increment in the shell during the period of gonad build-up in the present study is similar to the pattern in *Collisella limatula*, but is different from that of *Cellana* spp., *Helcion pellucidus*, and *Notoacmea petterdi* (Branch, 1981), which stop shell growth as the gonad becomes mature. MacDonald and Thompson (1986) pointed out that in several bivalve species, there is a shift in the allocation of available energy from somatic and shell growth to gamete production as the organisms increase in age. A similar trend was also found in the present study (Fig. 6).

The turn-over rate of P/B is relatively higher than the same rate in other herbivore populations (Hughes, 1971; Wright and Hartnoll, 1981; Parry, 1982; Horn, 1986; Davies et al., 1990). Distinctly this is because the *C. heroldi* population is mainly composed of young animals 0 to 2 years (Niu et al., 1992).

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