Bull. Fac. Fish. Hokkaido Univ.
38(3), 191-202. 1987.

On the Growth Pattern of the Neptune Whelk, *Neptunea arthritica* BERNARDI

Katsuaki FUJINAGA*

Abstract

Growth patterns of the neptune whelk, *Neptunea arthritica*, of Usu Bay, which is located within Volcano Bay, Hokkaido were studied, from August 1977 to April 1981.

(1) No significant growth differences were found between males and females.

(2) The growth rate of *N. arthritica*, which exhibits distinct seasonal changes, is higher from late spring to autumn, and retarded from late autumn to early spring. Growth rates are higher in younger year classes, decrease with increasing age, and are reduced considerably after sexual maturity.

(3) The growth of *N. arthritica* is strongly affected by water temperature and reproduction.

(4) The growth in shell height of *N. arthritica* is summarized as follows: the time of hatching, 9.0 mm; 1-year old, 18.3 mm; 2-years, 34.3 mm; 3-years, 55.1 mm; 4-years, 69.8 mm; 5-years, 82.3 mm.

(5) Recruitment into the adult population of *N. arthritica*, which is marked by sexual maturity occurs at 2 years of age in males, and 3 years in females.

(6) A linear relationship between shell height and shell diameter of *N. arthritica* is maintained throughout life.

(7) The processes in growth of *N. arthritica* apply best to the growth formula of Gompertz, both over the life span and seasonally.

So far, studies on the growth of marine gastropods (Prosobranchia) center mainly on species which inhabit from the intertidal zone to the uppermost of the sublittoral zone. With the exception of abalones, species living in the sublittoral, such as top shell *Turbo cornutus* (Ino, 1953; Amio, 1955; Uno, 1962; Nonaka et al., 1969; Yoshiya et al., 1987), *Babylonia japonica* (Ino, 1950; Kubo & Kondo, 1953; Yoshihara, 1957), *Buccinum undatum* (Hancock, 1963), *B. tsubai* (Kato, 1979) are objects of studies on growth. The amount of research on marine gastropods in the sublittoral, however, is much less than that on species in the intertidal.

Neptunea arthritica, belonging to the family Buccinidae, lives in shallow waters from the upper sublittoral to approximately 10 m in depth along Tohoku, Hokkaido, Sakhalin and other coastlines. It is fished commercially and occupies an important position as one of the main fishing products from these regional shallow waters. Research efforts on fishery biology of *N. arthritica* are restricted to investigations of the reproductive biology (Miyawaki, 1953; Takahashi et al., 1972; Takamaru & Fuji, 1981; Fujinaga, 1985), the estimation of the stock number by trap fishing (Ito & Tachizawa, 1981), and annual growth rate estimates using laboratory-reared specimens and a marking experimental procedure (Ito, 1982). Information on

* *Laboratory of Mariculture, Faculty of Fisheries, Hokkaido University* (Present address: *Liberal Arts, Dohto University, 7 Ochiishi-cho, Monbetu, Hokkaido*)
(北海道大学水産学部鹹水増殖学講座，現：道都大学教養部，北海道紋別市落石町 7)

growth that provides the basis for analysis of population dynamics, together with what is known about reproductive patterns and the survival phenomenon are also basic items for studies of resource control such as the estimation of the optimum catch quantity. However, until now the survey concerning the growth of *N. arthritica* has not been undertaken at all beyond Ito's report (1982) on the amount of annual increases.

In the present paper patterns of *N. arthritica* growth in both shell height and shell diameter during the course of seasons are described first, and secondly growth formulae which quantify the mean rate of individual growth are mentioned.

The author wishes to thank Prof. Akira Fuji of the Faculty of Fisheries, Hokkaido University, for his guidance and encouragement. Thanks also to Associate Prof. Sigeru Nakao of the same University, for his helpful advice. The late Mr. Masao Ishikawa of the Muroran Branch of Hokkaido Hakodate Fisheries Experimental Station also provided valuable assistance in the field, for which the author is grateful.

Materials and Methods

The investigations were carried out in Usu Bay, located in the back of Volcano Bay, Hokkaido (Fig. 1), during periods from August 1977 to September and from September to April 1981. Usu Bay has a length of approximately 120 m in the bay mouth, 400 m in overall bay length, 900 m in bay width, and an area of 23.7×10^4 m^2 at mean tide level. During the first period, neptune whelk samples were collected via SCUBA diving at regular monthly intervals. After individual samples were

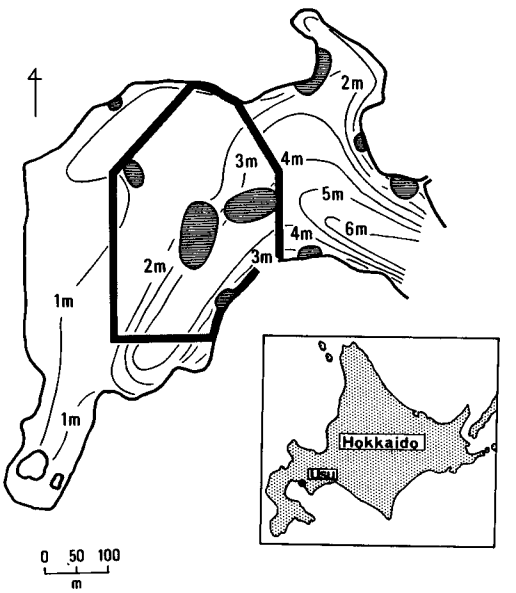

Fig. 1. Map of Usu Bay showing the locatins of investigations and approximate water depths. ▤: areas where whelks were sampled from August 1977 to September 1979, ▭: area where whelks were measured under water from September 1979 to April 1981.

measured in the laboratory for both shell height and shell diameter, they were returned to their original sampling sites as soon as possible. During the latter period, at nearly monthly intervals, excluding winter, shell heigh of individual samples was measured with a slide caliper while SCUBA diving, and immediately following this underwater measurement, they were returned to their original positions. In the case of such places where many individuals cohabit the same position, they were measured on boat. Taking into account differences in growth from place to place, and changes of habitat accompanying growth. Fig. 1 shows the 9 districts marked with the striped lines for the initial period, and the dark zone area for the latter period that were established over the total area of the Bay for collecting neptune whelks.

Results

Growth of shell height and shell diameter: The difference in growth between male and female of *N. arthritica* in Usu Bay was investigated, distinguishing the sex of individuals on the basis of the presence of a penis, for 6 months from April to September 1978. The size frequency distributions in shell height and shell diameter for male and female populations were analysed by Harding (1949) probability paper. The means in shell height and shell diameter of cohorts obtained are shown in Table 1, and there are no significant differences between male and female for the corresponding cohorts in every month ($Pr\{to > |t|\} < 0.001$). This means that investigations on the phenomenon of growth, based on shell diameters, need not be separated into male and female categories.

The size frequency distributions in shell height and shell diameter from August 1977 to September 1978, with male and female individuals, combined are shown in Fig. 2. These frequency distributions represented as polymodal distributions were separated into cohorts by the probability paper (Harding, 1949), with 5 or 6 obtained. The size of juveniles hatched from egg masses in September are 6-12 mm shell height and 5-7 mm shell diameter. Depositions of egg masses are almost completed, as for *N. arthritica* in Usu Bay (Fujinaga, 1985). These facts indicate that the first cohort appearing after September (Fig. 2) is in the 0-year class hatched from egg masses deposited in that year, and that it is valid for each year class increasing by 1 in July. The growth processes of *N. arthritica* using the means in shell height and shell diameter for each year class obtained at monthly regular intervals are shown in Fig. 3. Using those values shown in Fig. 3, monthly growth rates, expressed as values of monthly growth increments in shell height and shell diameter for each year class, divided by the mean of the respective dimention in the beginning of the month, were calculated as shown in Fig. 4. Fluctuations in monthly growth rates for each year class show the same tendency through seasons in both shell height and shell diameter. They exhibit distinctive seasonal changes; growth rates are rapid from late spring to autumn and slower from late autumn to early spring. By comparing growth rates among year classes, it is shown through characteristic growth patterns that the older the year class is, the lower the growth rates are. In the 2-year class, growth rates are reduced considerably, and growth in the 3- and 4-year classes nearly ceases during winter, while in the 0-year class, growth is maintained at low rates.

Table 1. Mean values in shell height (SH) and shell diameter (SD) for each group of both male and female from April to September 1978, analysed using the probability paper.

Shell height

Sex	Month					
	Apr.	May	June	July	Aug.	Sep.
Male	36.1±3.3	35.3±4.0	37.8±5.2			27.5±2.9
	53.5±4.5	54.4±5.7	55.4±5.4	40.0±6.0	42.2±5.4	43.4±5.0
	67.4±5.1	68.7±4.8	69.9±5.0	57.4±5.3	59.7±5.4	61.2±5.6
	84.0±4.6	83.4±2.3	84.2±1.9	69.5±5.3	71.4±4.2	73.5±3.7
				84.2±3.4	84.4±2.8	83.7±4.2
Female	36.6±4.3	35.0±3.7	36.6±5.8			23.7±2.9
	53.9±5.8	53.8±6.0	56.2±4.9	37.3±5.1	39.9±6.0	42.3±5.4
	67.0±4.6	68.8±4.5	69.4±4.5	57.3±5.8	59.2±6.3	62.8±6.6
	81.3±2.5	81.6±2.9	81.2±4.0	70.9±4.7	72.7±4.5	75.1±4.1
				83.8±3.8	84..8±3.9	85.3±3.5

Shell diameter

Sex	Month					
	Apr.	May	June	July	Aug.	Sep.
Male	21.7±2.5	22.1±3.3	22.8±3.5			16.4±1.9
	32.6±3.0	32.8±3.3	33.1±2.7	23.4±3.0	25.0±3.4	25.8±3.2
	40.7±3.4	41.0±3.3	41.3±3.8	33.8±2.9	35.3±2.8	37.1±3.4
	52.8±2.0	50.6±2.5	51.9±2.5	41.7±3.0	42.6±3.2	45.1±1.8
				50.5±1.1	50.5±1.9	50.9±0.7
Female	21.5±2.6	22.0±2.8	22.0±3.5			14.8±1.9
	32.5±3.8	32.8±3.2	33.3±2.9	22.7±3.2	24.5±3.7	25.7±3.6
	41.0±3.3	41.3±3.6	41.7±3.6	33.7±2.9	36.3±3.4	37.9±3.8
	50.5±1.1	49.7±2.0	50.6±1.3	42.2±2.9	43.1±2.8	44.8±2.1
				49.6±1.9	49.9±1.9	51.1±1.9

The growth formulae: As mentioned above, the fact that the monthly growth rates in both shell height and shell diameter show the same seasonal tendency for all year classes suggests that increases in the two dimentions take place synchronously, and that the relationship between the two remains linear throughout a life span. The relative growth of shell diameter (SD) to shell height (SH) was examined, using the means of respective months in shell height and shell diameter for each year class, and obtained the probability paper (Harding, 1949) from the size distribution (Fig. 2), as shown in Fig. 5. The relationship between the two dimentions is expressed as the following linear equation:

$$SD = 0.60\ SH + 0.158$$

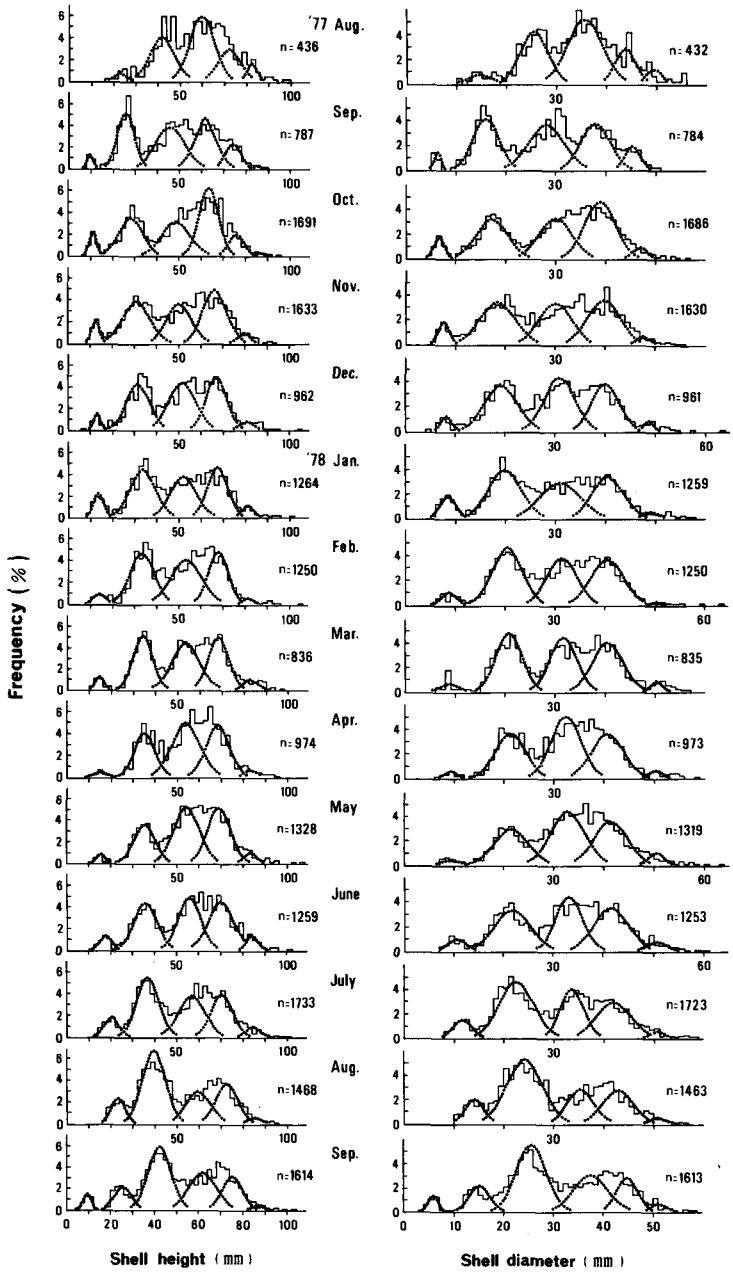

Fig. 2. Size frequency distributions in shell height and shell diameter. Dotted lines represent normal curves, analysed using the probability paper.

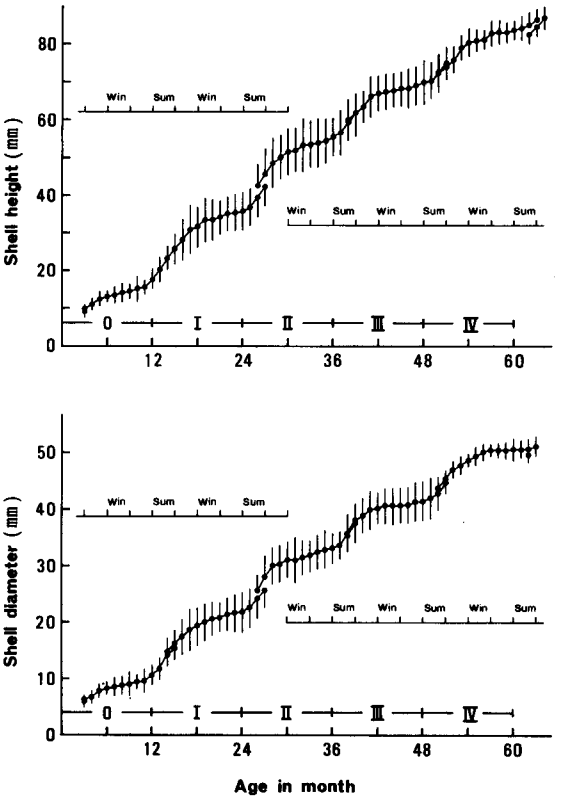

Fig. 3. Growth of *Neptunea arthritica* in shell height and shell diameter. Dots and vertical bars represeent mean and standard deviation, respectively. Roman numerals indicate year classes.

This means, in investigating the growth phenomenon of *N. arthritica*, there is no difference between the representations of shell increases even though variable dimensions were adopted. Therefore, the following further analyses of growth are examined in terms of shell height, which represent increases in the direction of the longer axis.

The size frequency distributions in shell height, investigated from September 1979 to April 1981 at nearly monthly intervals excluding the winter months were similarly separated into year classes by the probability paper (Harding, 1949). The mean shell heigh at age in month is shown in Fig. 6. There are some variations from year to year in shell height, represented as ages in months; the tendency is particularly marked in the younger year classes. However, it is considered that there are no significant differences among years ($Pr\{to> |t|\}<0.001$). Therefore, concerning the growth patterns traced for *N. arthritica* in Usu Bay, the mean values in shell height at age in month for respective year classes over several years during August 1977 to April 1981 were adopted, as shown by the solid circles in Fig. 6. As the intervals between investigations in the latter period are not exactly a month, in obtaining the mean of growth at age in month, the mean shell height on the first day

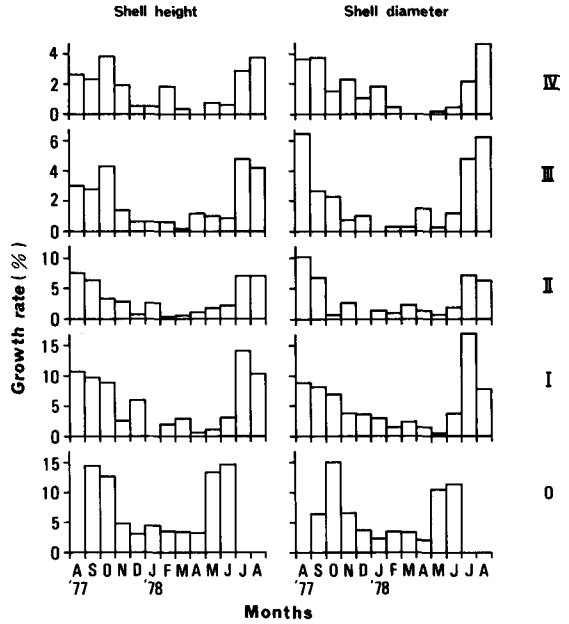

Fig. 4. Monthly growth rates in shell height and shell diameter for each year class. Roman numerals on the right indicate year classes.

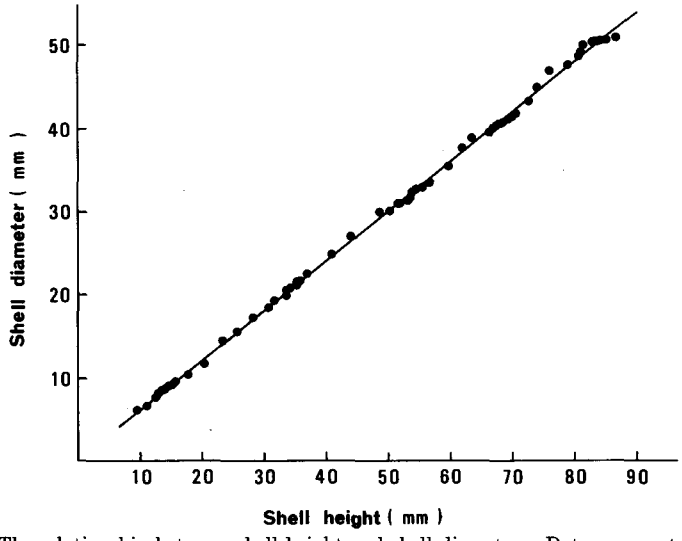

Fig. 5. The relationship between shell height and shell diameter. Dots represent means from the size frequency distributions, analysed using the probability paper. The regression line was determined by the least square method.

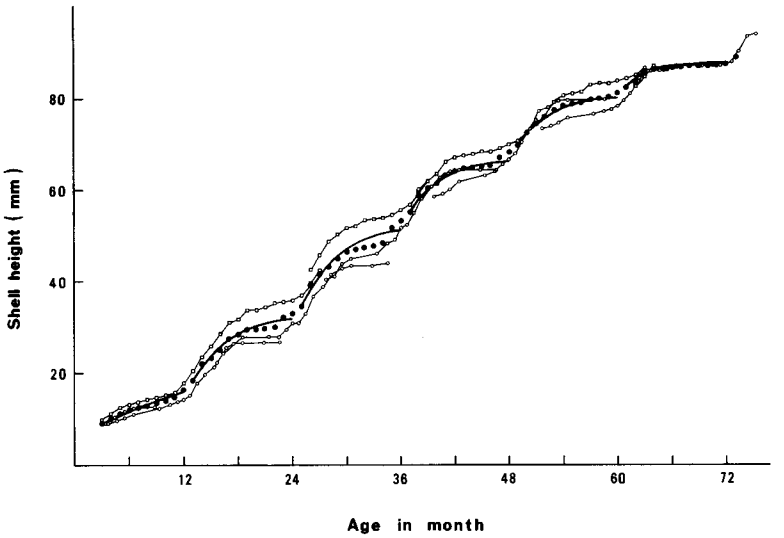

Fig. 6. Growth of *Neptunea arthritica* in shell height and growth curves (solid line) calculated by applying the Gompertz's growth equation. □——□ : period from August 1977 to September 1978, ○——○ : period from September 1979 to April 1981, ● ; mean during the period from August 1977 to April 1981.

of every month for each month for each year class calculated by the simple proportional allotment was adopted.

To appreciate the phenomenon of growth quantitatively is one of the important aspects of resources control ; as the means of separating the population into groups. To investigate the process of growth in *N. arthritica* for satisfactory correspondence to the three growth formulae of Robertson, Bertalanffy and Gompertz, an examination was made with Walford's graph (1946), using the means of shell height (0-year class : 9.0 mm, 1-year class : 23.1 mm, 2-year class : 60.4 mm, 4-year class : 74.6 mm, 5-year class : 85.6 mm) in Septembr (Fig. 7), when juveniles hatched from egg masses recruit into the *N. arthritica* population.

The resulting correspondence to that of Gompertz was the highest obtained for

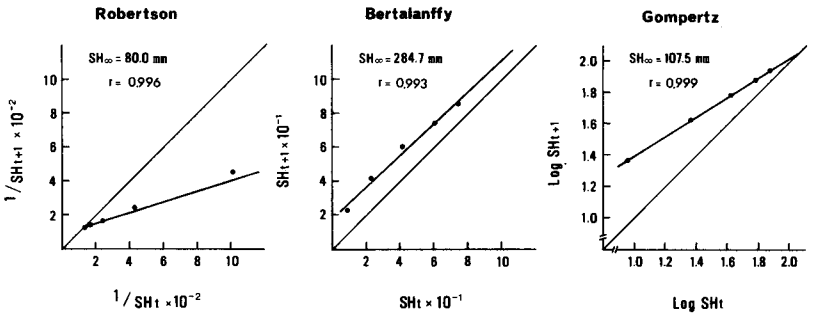

Fig. 7. Walford's graphs indicating satisfactory correspondence to the formulae of Robertson, Bertalanffy and Gompertz, using mean of shell height for each year class in September. Regression lines are determined by the least square method.

Table 2. The growth formulae in shell height at age in month obtained by applying the Gompertz's growth equation: $SH_t = SH_\infty e^{-ae^{-b(t-12m)}}$; where SH_t is the length (mm) at age in month (t), SH_∞ is the ultimate length (mm) and a, b, m are constant. For only 0-year class t is the age in month from the time of hatching (September).

Age in month (t)	SH_∞	a	b	m
1～10	23.55	1.057	0.099	0
13～24	32.51	0.769	0.288	1
25～36	52.12	0.555	0.280	2
37～48	66.99	0.258	0.276	3
49～60	80.72	0.189	0.269	4
61～72	87.90	0.101	0.412	5

N. arthritica. According to Lockwood (1974) who states that the growth formula can be applied to depict seasonal growth, the relationships between age in month (t) and shell height (mm) for each year class, were calculated using the Gompertz growth formula to obtain the increasing pattern of shell height with growth (Table 2). The growth curves are depicted in Fig. 6, traced in solid lines.

Discussion

Hitherto, the differences in growth between male and female in some marine gastropods are indicated (Magalhaes, 1948; Comfort, 1957; Wilbur & Owen, 1964; Hyman, 1967; Pearce & Thorson, 1967; Edwards, 1968; Nagai, 1974; MacIntosh & Paul, 1977), but it is considered that such gender differences are not recognized in *Buccinum undatum* (Hancock, 1963), *Tegula funebralis* (Frank, 1965), *Heminerita japonica* (Nakano & Nagoshi, 1980), *Monodonta lineata* (Wikkiamson & Kendall, 1981), and *M. labio* (Nakano & Nagoshi, 1984). It is concluded that there is statistically no significant difference ($Pr\{to > |t|\} < 0.001$) in growth between male and female as for *Neptunea arthritica* in Usu Bay.

Numerous growth formulae as the growth equations of organisms have been previously proposed, but in marine gastropods that of Bertalanffy is most often employed (e.g. Hancock, 1963; Frank, 1965; Phillips, 1969; Rao, 1976; Kato, 1979,; Bretos, 1980; Hayashi, 1980; Hughes, 1980). However, in the present study on the growth of *N. arthritica* the formula of Gompertz was adopted. Correlation coefficients obtained by the least square method from Walford's graph (1946), 0.999 for the Gompertz and 0.993 for Bertalanffy, indicate a high correspondence both formulae. Comparison of growth curves in these two formulae, denotes decreasing growth with increasing age using Bertalanffy's formula, while in that of Gompertz the increase is evidenced in the central portion of the curve with reductions reduce before and after. The growth of *N. arthritica* in Usu Bay is the largest during the period between 2 and 3 years old, and is lower before and after this period. The ultimate shell height obtained from Walford's graph is 284.7 mm with the formula of Bertalanffy, and with that of Gompertz it is 107.5 mm, which is very approximate to the observed values (Fig. 2). In this perspective, the application of the Gompertz formula to depict the growth of *N. arthritica* is considered to be the

best.

As in many other gastropods, the seasonal growth for all year classes of *N. arthritica*, reflects maximum growth during summer when water temperature is high, and shows slower rates during winter when the temperature is lowest. Comparison of growth rates for individual year classes, however, reveals considerably decreasing growth rates in classes post 2 years. Also, in the younger year classes growth does not cease during winter, while in the older classes during the same period, growth nearly stops. In investigations on the reproductive biology of *N. arthritica* (Fujinaga, 1985), size at sexual maturity was determined to be 50 mm shell height in the male and 60 mm in the female, based on histological observations of seminal vesicles and gonads, respectively. Growth in shell height of *N. arthritica* traces the following patterns: at hatching: 9.0 mm, 1-year old: 18.3 mm, 2-years: 34.3 mm, 3-years: 55.1 mm, 4-years: 69.8 mm, 5-years: 82.3 mm (Fig. 6). Therefore, *N. arthritica* in Usu Bay is considered as belonging to the adult population at 2 years old in the male and at 3 years in the female. In general, the phenomenon of growth is closely connected with reproduction (Orton, 1928; Sakai, 1960, 1962; Williams, 1964a, b; Morton, 1969; Feare, 1970; Creese, 1981). In studies of the *N. arthritica* reproductive cycle (Takamaru & Fuji, 1981; Fujinaga, 1985) it is indicated that winter is the mature period in the adult female and likewise in the male, with maturation of the seminal vesicle. These results suggest that the phenomenon of growth is closely connected with the maturation of gonads in *N. arthritica*. However, it is desirable that these implications should be further investigated according to seasonal changes for each year class in feeding activity and allocation of energy ingested into each component of body such as gonad, soft parts, and shell etc.

References

Amio, M. (1955). On growth and development of spines of the top shell, *Turbo cornutus Solander*. *J. Shimonoseki Coll. Fish.* **4**, 57-68. (In Japanese with English summary).

Bretos, M. (1980). Age determination in the keyhole limpet *Fissurella crassa* LAMARCK (Archaeogastropoda: Fissurellidae), based on shell growth rings. *Biol. Bull.* **159**, 606-612.

Comfort, A. (1957). The duration of life in molluscs. *Proc. malac. Soc. Lond.* **32**, 219-241.

Creese, R.G. (1981). Patterns of growth, longevity and recruitment of intertidal limpet in New South Wales. *J. exp. mar. Biol. Ecol.* **51**, 145-171.

Edwards, D.C. (1968). Reproduction in *Olivella biplicata*. *Veliger* **10**, 297-304.

Feare, C.J. (1970). Aspects of the ecology of an exposed shore population of dogwhelks *Nucella lapillus* (L.). *Oecologia* (Berl.) **5**, 1-18.

Frank, P.W. (1965). Shell growth in a natural population of the turban snail, *Tegula funebralis*. *Growth* **29**, 395-403.

Fujinaga, K. (1985). The reproductive ecology of the neptune whelk (*Neptunea arthritica* BERNARDI) population, with special reference to the reproductive cycles, depositions of egg masses and hatchings of juveniles. *Bull. Fac. Fish. Hokkaido Univ.* **36**, 87-98. (In Japanese with English summary).

Hancock, D.A. (1963). Marking experiments with the commercial whelk (*Buccinum undatum*). *Spec. Publs. Int. Comm. N.W. Atlant. Fish.* **4**, 176-187.

Harding, J.P. (1949). The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K.* **28**, 141-153.

Hayashi, I. (1980). Structure and growth of a shore population of the ormer, *Haliotis tuberculata*. *J. mar. biol. Ass. U.K.* **60**, 431-437.

Hughes, R.N. (1980). Population dynamics, growth and reproductive rates of *Littorina nigrolineata* GRAY from a moderately sheltered locality in North Wales. *J. exp. mar. Biol. Ecol.* **44**, 211-228.

Hyman, L.H. (1967). The *Invertebrates*: *Mollusca* I. 792 p. MaGraw-Hill Book Co., New York.

Ino, T. (1950). Life history of Japanese ivory shell, *Babylonia japonica* (REEVE) and its propagation method. *Stud. Aquat. Anim.* **No. 1**, 11-24. (In Japanese).

Ino, T. (1953). Ecological studies of *Turbo cornutus* SOLANDER-I. Changes of the spines on the shell due to environments. *Bull. Japan. Soc. Sci. Fish.* **19**, 410-414. (In Japanese with English summary).

Ito, H. and Tachizawa, S. (1981). An estimation of the density of the available stock of a sea snail, *Neptunea arthritica*, by trap fishing. *Bull. Hokkaido Reg. Fish. Res. Lab.* **46**, 113-119.

Ito, H. (1982). Distribution of a sea snail, *Neptunea arthritica*, and its surroundings in the Lagoon Furen-Ko. *Reports of the engineering research on all-round constructions of fishing grounds in the region of Nemuro Bay*, 107-114. (In Japanese).

Kato, F. (1979). Study on the management of basket trap fishing of Tsubai-whelk (*Buccinum tsubai*) at the fishing grounds off Niigata, in the Japan Sea. *Bull. Jap. Sea Reg. Fish. Res. Lab.* **30**, 29-40. (In Japanese with English summary).

Kubo, I. and Kondo, K. (1953). Age-determination of the *Babylonia japonica* (REEVE), an edible marine gastropod, basing on the operculum. *J. Tokyo Univ. Fish.* **39**, 199-207.

Lockwood. S.J. (1974). The use of the von Bertalanffy equation to describe the seasonal growth of fish. *J. Cons. int. Explor. Mer.* **35**, 175-179.

MacIntosh, R.A. and Paul, A.J. (1977). The relation of shell length to total weight, edible-meat-weight, and reproductive organ weight of the gastropods *Neptunea heros*, *N. lyrata*, *N. pribiloffensis*, and *N. ventricosa* of the eastern Bering Sea. *Proc. Nat. Shellfish. Ass.* **67**, 103-112.

Magalhaes, H. (1948). An ecological study of the snails of the genus *Busycon* at Beaufort, North Carolina. *Ecol. Monogr.* **18**, 377-409.

Miyawaki, M. (1953). Some observations on spawning of the whelk *Neptunea arthritica* BERNARDI. *Zool. Mag. Tokyo* **62**, 199-201. (In Japanese with English summary).

Morton, B.S. (1969). Studies on the biology of *Dreissena polymorpha* PALL. III. Population dynamics. *Proc. malac. Soc. Lond.* **38**, 471-482.

Nagai, T. (1974). Studies on the marine snail resources in the eastern Bering Sea I. Species composition, sex ratio and shell length composition of snails in the commercial catch by snail-basket-gear in the adjacent waters of Pribiloff Islands, 1973. *Bull. Far. Seas Fish. Res. Lab.* **10**, 141-156. (In Japanese with English summary).

Nakano, D. and Nagoshi, M. (1980). Growth and age structure of *Heminerita japonica* (DUNKER), population of the Shima Peninsula, Japan (Prosobranchia). *Venus* **39**, 101-108. (In Japanese with English summary).

Nakano, D. and Nagoshi, M. (1984). Growth and death in an intertidal population of *Monodonta labio* (LINNAEUS), (Prosobranchia, Trochidae). *Venus* **43**, 60-71. (In Japanese with English summary).

Nonaka, M., Nakagawa, M., Sasaki, T. and Matsuura, K. (1969). Ecological studies on the rocky shore resources off Shizuoka Prefecture — VII. The effect of transplantation of the Japanese top-shell, *Turbo cornutus*, off Izu-Shimoda with special reference to the growth, distribution and recapture. *Bull. Shizuoka Pref. Fish. Exp. Stat.* **2**, 59-66. (In Japanese).

Orton, J.H. (1928). Observations on *Patella vulgata*. Part II. Rate of growth of shell. *J. mar. biol. Ass. U. K.* **15**, 863-874.

Pearce, J. and Thorson, G. (1967). The feeding and reproductive biology of the red whelk, *Neptunea antiqua* (L.). (Gastropoda, Prosobranchia). *Ophelia* **4**, 277-314.

Phillips, B.F. (1969). The population ecology of the whelk *Dicathais aegrota* in western Australia. *Aust. J. mar. Freshwat. Res.* **20**, 225-265.

Rao, M.B. (1976). Studies on the growth of the limpet *Cellana radiata* (BORN) (Gastropoda: Prosobranchia). *J. moll. Stud.* **42**, 136-144.

Sakai, S. (1960). On the formation of the annual ring on the shell of the abalone, *Haliotis discus* var. *hannai* INO. *Tohoku J. Agric. Res.* **11**, 239-244.

Sakai, S. (1962). Ecological studies on the abalone, *Haliotis discus hannai* INO — IV. Studies on the growth. *Bull. Japan. Soc. Sci. Fish.* **28**, 899-904. (In Japanese with English summary).

Takahashi, N., Takano, K. and Murai, S. (1972). Histological studies on the reproductive cycle of the male neptune whelk, *Neptunea arthritica*. *Bull. Fac. Fish. Hokkaido Univ.* **31**, 314-326. (In Japanese with English summary).

Takamaru, N. and Fuji, A. (1981). Reproductive cycle of the neptune whelk, *Neptunea arthritica* (BERNARDI), in southern Hokkaido. *The Aquaculture* **29**, 78-87. (In Japanese with English summary).

Uno, Y. (1962). Studies on the aquaculture of *Turbo cornutus* SOLANDER with special reference to the ecology and periodicity of the growth. *J. Tokyo Univ. Fish.* **6**, 1-76. (In Japanese with English summary).

Walford, L.A. (1946). A new graphic method of describing the growth of animals. *Biol. Bull.* **90**, 141-147.

Wilbur, K.M. and Owen, G. (1964). Growth. (p. 211-242) In Wilbur, K.M. and C.M. Yonge *Physiology of Mollusca* 645 p.**1**, New York and London, Academic Press.

Williams, E.E. (1964a). The growth and distribution of *Littorina littorea* (L.) on a rocky shore in Wales. *J. Anim. Ecol.* **33**, 413-432.

Williams, E.E. (1964b). The growth and distribution of *Gibbula umbilicalis* (da Costa) on a rocky shore in Wales. *J. Anim. Ecol.* **33**, 433-442.

Williamson, P. and Kendall, M.A. (1981). Population age structure and growth of the trochid *Monodonta lineata* determined from shell rings. *J. mar. biol. Ass. U. K.* **61**, 1011-1026.

Yoshihara, T. (1957). Population studies on the Japanese ivory shell, *Babylonia japonica* (REEVE). *J. Tokyo Univ. Fish.* **43**, 207-248.

Yoshiya, M., Kuwahara, A. and Hamanaka, Y. (1987). Study on the growth and survival of the young topshell *Batillus cornutus* in connection with algal vegetation and hydrographic conditions. *Nippon Suisan Gakkaishi* **53**, 239-247. (In Japanese with English summary).