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Ecological Studies on the Life History of the Neptune Whelk *Neptune arthritica*

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Contents

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Introduction

The neptune whelk *Neptunea arthritica*, a large-sized gastropod of the family Buccinidae, lives in shallow waters from the upper sublittoral zone down to a depth of a few 10 meters along Tohoku, Hokkaido, Sakhalin, Primorskij, and other coastlines. In Hokkaido, the neptune whelk was important as one of the main commercial fisheries from the shallow waters until the 1960s, but the whelk population in some embayments decreased due to overfishing in the 1970s (e.g. Ito and Tachizawa, 1981). Furthermore, in the 1980s the whelk fishery in many embayments was subjected to crushing damage by TBT (tributyltin) compounds (Fujinaga et al., 2001). The use of TBT-based antifouling paints on boats of less than 25 m in length and on fish-pen nets was prohibited in 1990. Following this, the relative penis size index (RPSI) of neptune whelks in Usu Cove has drastically declined, which suggests that female neptune whelks in this cove have been recovering from imposex (Fujinaga and Nakao, 1999). Also, in Saroma Lagoon, basing on decreases in RPSI value, frequency of imposex, and sex ratio, the whelks in the lagoon was reported to have recovered from imposex (Fujinaga et al., 2002). However, there exist embayments where the whelk fishery is suspended even now, and even if the whelk fisheries are resumed in some embayments, their landings are far scarce as compared with those before affected by TBT compounds. By the way, with the decrease of *N. arthritica* resources, degree of significance of snails living in deeper waters increased. At present, snails which are important in commercial fisheries in Hokkaido are large-sized gastropods of the family Buccinidae being distributed from 50 m to 200 m in depth. Above all, the genus *Neptunea*, such as *N. polycostata* and *N. intersculpta*, and the genus *Buccinum*, such as *B. isaotakii*, are the focus of the whelk fisheries. In general, those whelks are fished using cages and gill nets. The whelk fishery is inclined to be led into overfishing, because the fishing gear being usually used lacks strong selection in the fishing size (Kubo and Kondo, 1953). Moreover, in Hokkaido, snails except abalones and a turban shell are named tsubu (or tsubugai) generically, and consequently the species being fished and catch among the species lie the condition difficult to comprehend. Thus, the whelk fishery in Hokkaido is thought to include serious problems from the standpoint of resource management.

At present, restoration of the *N. arthritica* populations and resource management of *N. polycostata* and *N. intersculpta* are urgently needed. In designing the restoration of *N. arthritica* resources, ecological knowledge of the species, particularly on life history, plays a very important role. So far, ecological studies of the neptune whelk have centered on reproduction (Miyawaki, 1953 ; Takahashi et al., 1972 ; Takamaru and Fuji, 1981 ; Fujinaga, 1985 ; Kawai et al., 1994 ; Fujinaga and Nakao, 1995, 1998), including growth (Ito, 1982 ; Fujinaga, 1987 ; Suzuki et al., 1996), food organisms and food consumption rates (Fujinaga and Nakao, 1999), migration pattern (Fujinaga and Nakao, 1994), population structure and mortality (Fujinaga and Nakao, 1996 ; Suzuki et al., 2002), and biological production (Fujinaga and Nakao, 1997 ; Fujinaga et al., 2001).

On the other hand, information necessary for the resource management of *N. polycostata* and *N. intersculpta* is very few with the distribution and morphology of an egg capsule (Golikov, 1963), and a report of spawning (Ito, 1957) alone. Also, in accumulating information about the resource management of both species in the future, investigations are presumed not to be easy compared to *N. arthritica* because both species inhabit deeper waters. Therefore, the fisheries oriented resource management for both species would be faced with rather difficulties until their actualization. Accordingly, it is urgently necessary to restore resources of *N. arthritica* living in the shallowest waters of *Neptunea*. The reason is for establishing a model of resource management based on life history in *N. arthritica* and applying the model to resource managements of *N. polycostata* and *N. intersculpta*.

In accumulating information on life history, choice of a study area is very essential. The shallower water and the smaller one facilitate its investigation. Moreover, it is desirable that influence of fishery is less, and that ensuring the number of individuals to some extent is possible. An area with those characteristics is ideal because evolution of the study can be expected. Accordingly, in the present study, the life history of *N. arthritica* was investigated in Usu Cove with characteristics mentioned in the next chapter.

Reproduction, growth and feeding which serve a foundation for the population ecology display their own characteristics by having a close relation to environmental conditions of habitats. The three basic items influence the main subjects of the population ecology, such as distribution, migration, age structure, population dynamics, and biological production, and the relation patterns among them, could be apprehended as the life history of local population in a species. So, in the present study, first the life cycle of the neptune whelk is elucidated based on reproduction, growth and feeding, and secondly distribution, migration, population dynamics and biological production were comprehended on the basis of the life cycle, and in the end, these phenomena were synthesized as the life history.

I. The study area

The investigations were carried out in Usu Cove (42°30′N, 140°47′E), located in the northern part of Funka Bay, Hokkaido (Fig. 1). Usu Cove has a length of approximately 120 m in the cove mouth, 400 m in overall cove length, 900 m in cove width, and an area of 23.7×10^4 m^2 at mean tide level. This bay holds about 6 m in depth in the mouth, somewhat increasing the depth from 2 m to 4 m in the central part. Usu Cove is liable to be affected by weather conditions because of its small size, and monthly mean water temperatures which were measured at a fixed station near the mouth greatly fluctuated from 2.5°C in February to 23.0°C in August (Fig. 2). A hanging culture of oyster rafts (*Crassostrea gigas*) was operated in the central part of the bay, and concrete blocks to anchor the rafts were sunk in several points. In the shallower waters east of the rafts, many iron poles were arranged for laver cultivation. These artificialities were utilized for confirming the investigating positions.

II. Life cycle

To understand main subjects in the population ecology, such as distribution, migration, and population dynamics, it is necessary to elucidate reproduction, growth and feeding which lay a foundation for their comparison. In the present study, reproduction was examined based on reproductive cycles, egg mass deposition, hatching of juveniles, and hatching rate; in growth, growth patterns and growth rates in shell height, shell diameter and soft body were clarified, and then growth equations were obtained ; in feeding, food organisms and food consumption rates were investigated. At the end, results from the three basic phenomena were concisely synthesized as the life cycle of *N. arthritica*.

1. Reproductive biology

(1) Investigated items and methods

Studies on reproduction were carried out from 1977 to 1980. Reproductive cycles were investigated mainly in

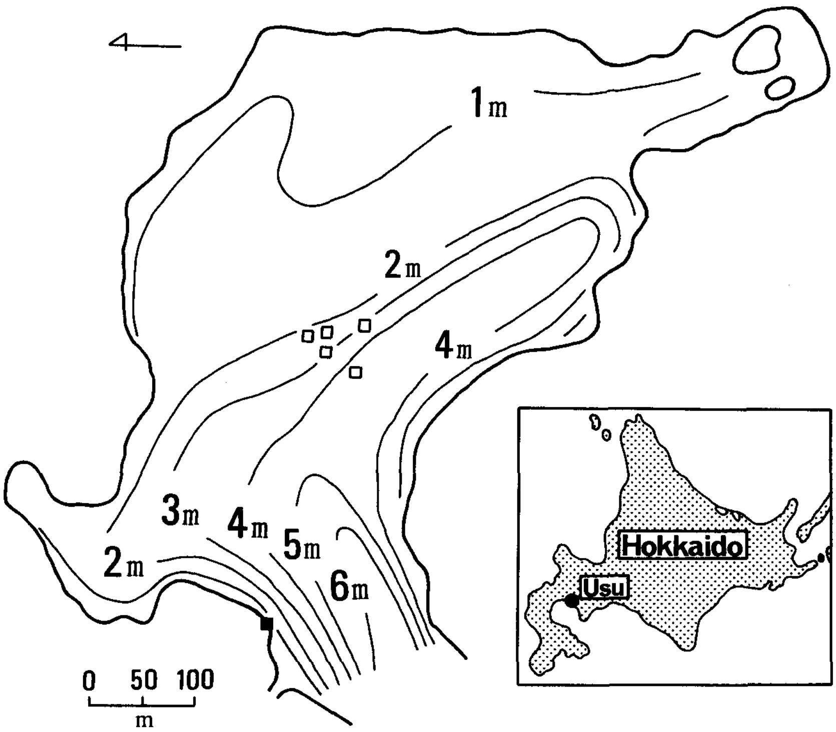


Fig. 1. Map of Usu Cove showing locations of oyster culture rafts (open quadrangles), the station (solid quadrangle) where the water temperature was measured, and the approximate depth in contour lines.

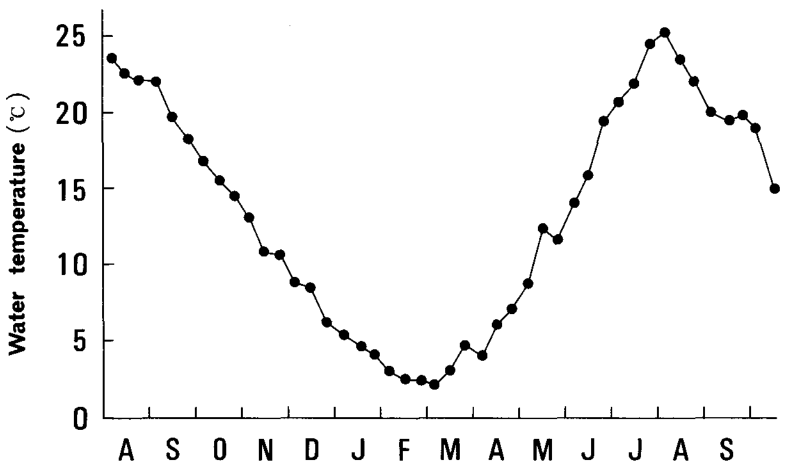


Fig. 2. Seasonal change in water temperatures (1 m below the surface) near the mouth of Usu Cove.

1977 and 1978 ; in addition, embryonic development, an estimate of hatching rate based on hatching process of juvenile population, causes of embryonic mortality, and differences in predation rates among spawning sites were surveyed in 1979 and 1980.

Investigated area

In the present study, egg mass deposition sites of *N. arthritica* in Usu Cove were divided into 20 areas (Fig. 3), and the examined sites differed greatly among investigated objects. Sorts of substratum where egg masses were deposited were surveyed mainly at the sites e, f, k, and r. A hatching rate was investigated at 17 spawning sites (a to q) within the area enclosed by solid lines. Size and abundance of egg-mass substrata, position of egg masses on a substratum, and difference in predation rates on embryos among spawning sites were investigated at 6 spawning sites (e, f, k, q, r, and s), where many

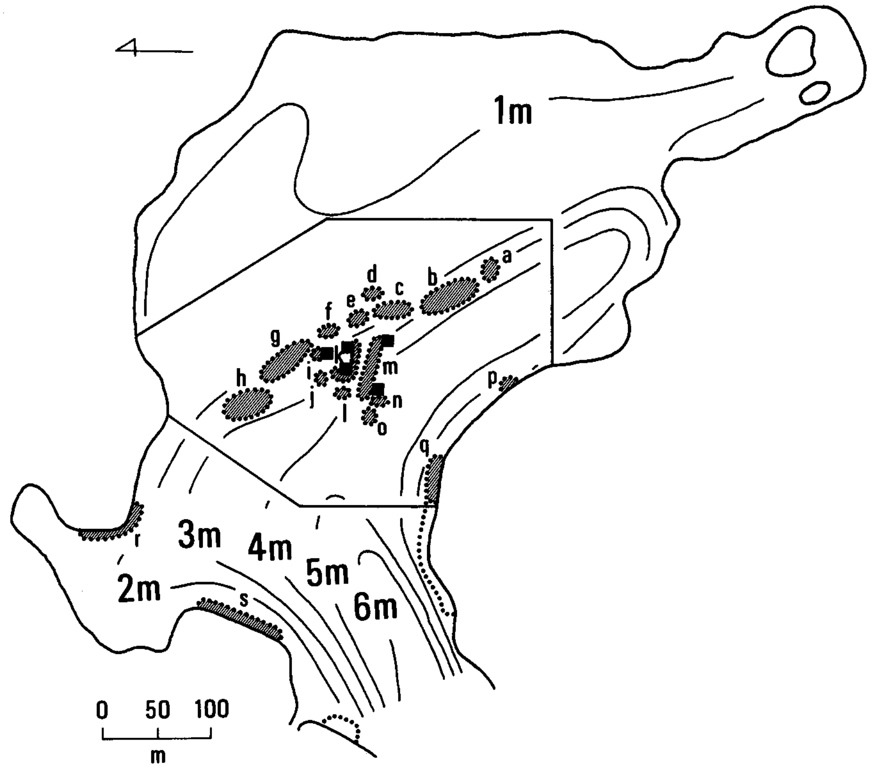


Fig. 3. Map of Usu Cove showing the egg mass deposition sites (⁙) and the sites where investigations on the numbers of egg masses were carried out (▨).

muricid snails such as *Ocenebra japonica*, a predator of *N. arthritica* embryos, were found.

Investigations, such as egg-mass substrata, number of egg masses, and position of egg masses on a substratum, and collection of neptune whelks and egg masses were all done by SCUBA diving.

Reproductive cycle

Neptune whelks were collected mainly in the area with rafts and at spawning site r, monthly from August 1977 to September 1978. After the shell height of the neptune whelks was measured, the soft body was extracted from the shell and weighed (g wet weight). Next, the gonad dorsal of the digestive gland was removed from the soft body and weighed. In males, the coiled portion of the deferent duct which functions as the seminal vesicle was also removed. The extracted body parts were fixed in Bouin solution. The central parts of the fixed tissues were embedded by using the procedure with butanol and paraffin, and then were sectioned with a microtome at a thickness of 8 μm to 12 μm. Staining was done with Delafield's hematoxylin and eosine.

Measurements of shell height of copulating and spawning individuals

Confirmation of copulation in the field was carried out mainly in the area with rafts from August 1977 through September 1978. The shell height of copulating pairs discovered was determined in the laboratory.

Measurements of the shell height of female whelks depositing an egg mass were done mainly at spawning sites e, f, and r in June and July, 1978. The shell height of spawning whelks was determined underwater to the nearest 0.05 mm with a vernier caliper.

Egg-mass substrata and laying position

Investigations related to egg-mass substrata of *N. arthritica* were conducted during 1978 to 1980. In 1978, only sorts of substratum were recorded mainly at spawning sites e, f, k, and r. In 1979, number of egg masses, size and abundance of substrata, and position of egg masses on hard substrata were investigated at six spawning sites (e, f, k, q, r, and s). Furthermore, in 1980, the number of egg masses deposited on each substratum type at spawning site e was inspected. The approximate height (cm; height from the bottom to the highest portion of hard substratum) of hard substratum was estimated visually. In the present study, a hard substratum (including a concrete block) larger than 50 cm in height is referred to as a "rock", and one less than 50 cm in height is considered a "boulder".

Count and collection of egg masses

Number of egg masses at spawning sites a to q were quantified nearly monthly between May and December, 1980. But, the numbers at spawning sites r and s were counted in August 1979. In counting egg masses, in places where an exact position was able to be easily recognized underwater while diving by the artificialities, such as concrete blocks and rafts, determination of number of egg masses at a spawning site was proceeded by counting on each substratum. On the other hand, in places difficult to exactly perceive a underwater position while diving because of no artificialities and sparsely distributed boulders on the muddy sand bottom, counting of egg masses was proceeded by marking the bottom by a finger to avoid an overlap of and an escape from observations.

Egg masses were collected at least once a month from August to December in 1979 and from May to December in 1980. In the laboratory, the number of egg capsules composing an egg mass were counted for each egg mass, and then the state of an egg capsule and the developmental stage of an embryo were investigated for each egg capsule. In an estimation of hatching rate, the proportion of each type of egg capsule was calculated by integrating all egg masses together from each collecting time. But, in an investigation of differences in predation rates on embryos among spawning sites, the proportion of predation was obtained for each egg mass.

Predation rate on embryos

In the estimation of the predation rate on embryos of *N. arthritica*, egg masses collected between mid-August and mid-September, before and after the commencement of hatching of juveniles, were used. The predation rate in an egg mass was calculated by the following equation with the number of egg capsules composing an egg mass (A) and the number of egg capsules with embryos that had been preyed upon (B):

$$\text{Predation rate (\%)} = (B/A) \times 100$$

(2) Results

1) Reproductive cycle

i) Developmental stages in gonads

The neptune whelk is dioecious, and fertilization is internal. The developmental processes in gonads were divided into the following stages, based on Takamaru and Fuji (1981).

Spent stage Many vacant spaces occur in the follicles of gonads owing to discharges of ova or sperms. In the ovarian follicles, relic ova and those in the process of destruction exist here and there (Fig. 4-1). In the testicular follicles, a small amount of relic-sperm mass and relic spermatids exist in the lumen. There are spermatogonia in the epithelium of the follicle, but the number is few (Fig. 4-2).

Recovering stage There are vacant spaces in the lumen of the follicle like spent stage, but germ cells multiply actively in the epithelium. In the epithelia of the ovarian follicles, there exist many oogonia (elliptical or almost round in shape and 8 μm～12 μm × 12 μm ～17 μm in size) with a nucleus containing several nucleoli, and many oocyte (15 μm～30 μm × 20 μm～40 μm in size) with a large nucleus and a clear nucleolus (Fig. 4-3 and 4). Late in this stage, oocytes commencing accumulation of yolk granules appear slightly. In the testicular follicles, there occur many spermatogonia (elliptical or round in shape and 12 μm～15 μm × 18 μm～30 μm in size) with a nucleus containing some nucleoli in the epithelium. But, in a part of the follicles, spermatocytes, spermatids and sperms in the process of destruction exist in the lumen (Fig. 4- 5 and 6). Late in this stage, the first spermatocyte (10 μm～12 μm in size) with dispersed chromosome in a nucleus appears.

Developing stage In the follicles of gonads, growth or maturation of germ cells take place actively. In the ovarian follicles, oocytes accumulate yolk vigorously and striking growth of them proceeds. So, the developing stage was divided into two phases, pre- and post-developing stages, based on the dominant oocyte. In the follicle of the pre-developing stage, the lumen is chiefly filled with oocytes (50 μm～100 μm in major axis and 40 μm～60 μm in minor axis) with small yolk granules (about 1 μm in size) (Fig. 4-7). In the follicle of the post-developing stage, oocytes (180 μm～230 μm in major axis and 100 μm～150 μm in minor axis) which remarkably protrude into the lumen and possess yolk granules increased in size (about 10 μm) become the major components (Fig. 4-8). In the testicular follicles, a lot of the first spermatocytes are formed. Because maturation of germ cells occurs actively, there exist a lot of the secondary spermatocytes (6 μm in size) with dispersed chromosome in a nucleus and spermatids in the lumen (Fig. 4-9). Late in this stage, the spermatid metamorphoses into the sperm actively. The spermatid, which is at first sphere, changes into ellipse, and moreover, into stick (Fig. 4-11). The sperm is composed of a head like a long cord stained by hematoxylin, and a tail stained by eosine. There exist a few sperms, with a head toward the epithelium, gathering in the lumen.

Mature stage The lumen in the ovarian follicle is filled with ova (170 μm～200 μm × 300 μm～400 μm in size) with a nucleus (50 μm～70 μm × 70 μm～80 μm in size) and a nucleolus. The ovum assumes a quadrangle

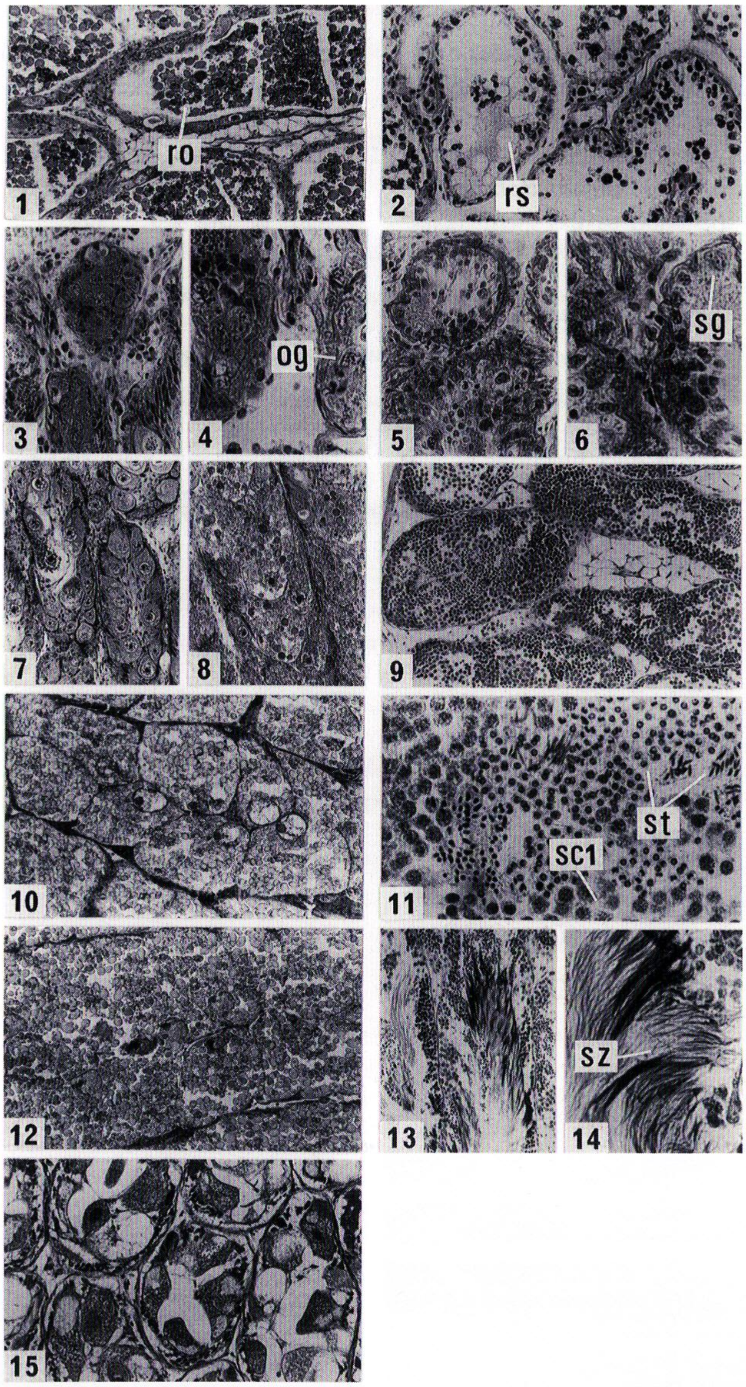


Fig. 4. Photomicrographs of gonad sections in various stages of maturation. Gonads were Bouin-fixed and Delafield's haematoxylin-eosin stained.

1. Ovary ; spent stage. × ca. 200 2. Testis ; spent stage. × ca. 200
3. Ovary ; recovering stage. × ca. 200 4. Oogonium in recovering stage. × ca. 800
5. Testis ; recovering stage. × ca. 400 6. Spermatogonium in recovering stage. × ca. 800
7. Ovary ; pre-developing stage. × ca. 200 8. Ovary ; post-developing stage. × ca. 200
9. Testis ; developing stage. × ca. 200
11. Primary spermatocyte and spermatid in developing stage. × ca. 800
10 and 12. Ovary ; mature stage. × ca. 200 13. Testis ; mature stage. × ca. 200
14. Sperm in mature stage. × ca. 800 15. Ovary ; immature stage. × ca. 400

og : oogonium, ro : relict oocyte, rs : relict sperm, sc1 : primary spermatocyte, sg : spermatogonium, st : spermatid, sz : spermatozoon.

in shape because of compressive contact with adjoining ova (Fig. 4–10). Late in this stage, it becomes very difficult to distinguish individual ova, and the nucleus and the nucleolus reduce their dyed nature and start to disappear (Fig. 4–12). In the lumen of the testicular follicle, many sperms exist and simultaneously the metamorphosis from the spermatid to the sperm takes place actively (Fig. 4–13 and 14).

ii) Accumulation of sperm in seminal vesicle

Sperm duct, which coils intricately through digestive gland into viscera, extends along the right side of the body and reaches to the penis behind the right tentacle. The coiled portion of the sperm duct functions as the seminal vesicle. The process of morphological changes in the seminal vesicle with the development of gonad was divided into the following stages, conforming to Takahashi et al. (1972).

Resting stage Fibrous connective tissues constructing the sperm duct were thick with several layers and displayed a shrunken state. Epithelial cells in the inner layer became cubic and were very thick compared with the other stages. The nucleus, stained deeply by hematoxylin, was a spindle-shape and situated at the base of the cell. Numerous yellow granular bodies occurred in the layer composed of epithelial cells. There yet existed a dash of sperms in the lumen (Fig. 5–16 and 17).

Accumulating stage There accumulated a large quantity of sperms in the lumen of the sperm duct, exhibiting an appearance of convolution. In this stage, epithelial cells were thinned and the nucleus shape changed from a spindle to a circle because of gradual swelling. At the same time the nucleus weakened its dyed nature to hematoxylin. The yellow granular bodies, recognized in the resting stage, disappeared.

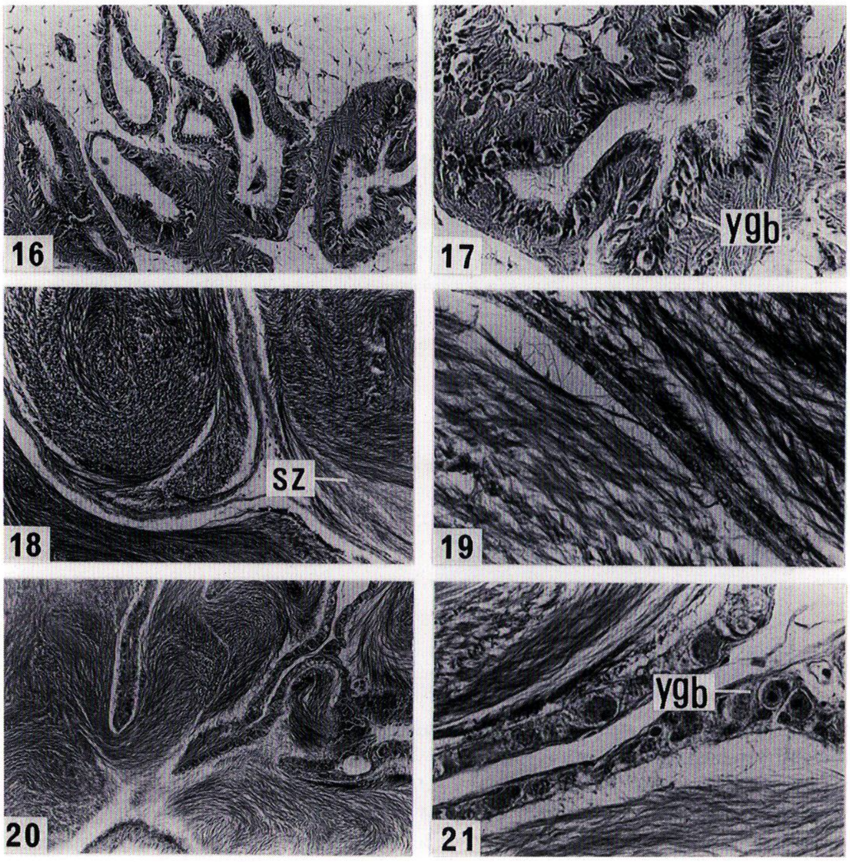


Fig. 5. Photomicrographs of seminal vesicle sections in three stages of maturation. Seminal vesicle was Bouin-fixed and Delafield's haematoxylin-eosin stained.

16. Seminal vesicle ; resting stage. × ca. 200
17. Epithelial cells in resting stage. × ca. 400
18. Seminal vesicle ; accumulating stage. × ca. 200
19. Epithelial cells in accumulating stage. × ca. 400
20. Seminal vesicle ; spent stage. × ca. 200
21. Epithelial cells in spent stage. × ca. 400

sz : spermatozoon, ygb : yellow granular body.

Late in this stage with still more accumulation of sperm, the epithelial cells and nuclei were flattened. Also, fibrous connective tissues surrounding the sperm duct were strikingly thinned (Fig. 5-18 and 19).

Spent stage Abundant sperms yet existed in the lumen of the sperm duct, with less in quantity than in the accumulating stage. The epithelial cells had thickened more and more with decreasing amount of sperms, and the nucleus became round. In this stage, the yellow granular bodies began to appear gradually, and fibrous connective tissues, being the outer layer, increased in thickness (Fig. 5-20 and 21).

iii) *Seasonal maturation*

Seasonal changes in proportions of the gonads and the seminal vesicle in various developmental stages indicate the seasonal maturation in the population, as shown in Fig. 6.

The ovary in spent stage, which appeared from May to August, occupied about 50% of the observed individuals in July. But, then it sharply decreased, disappearing in September. At that time, proportions of the ovary in recovering stage were also high, showing around 20% in July and August. The ovary in pre-developing stage was observed between June and October, exhibiting great occupancy rates (a little over 30%) in August and September. Following this, the ovary in post-developing stage drastically increased after August, occupying most of the female population from September through November. But, then it decreased gradually, and those proportions during February to May were only 10% or so. The ovary in mature stage appeared over a fairly long period from November to July, displaying the maximum (85%~95%) between February and May, with the subsequent sharp decrease. These results suggest that spawning takes place from May to July, reaching the peak in June.

On the other hand, the seasonal maturation in the male population was different from that in the female population. In February and March, the testis in spent stage occupied most of the male population. But, then it decreased gradually and disappeared in August. The testis in recovering stage which was observed over a considerably long period from February to September increased gradually after February and occupied a little over 60% of the male population between June and August. Thereafter, it sharply decreased, disappearing in October. Following this decline, the testis in developing stage increased from July through September, but immediately decreased, with the disappearance in November. Reflecting the decline in developing stage, the testis in mature stage drastically increased after September and occupied the whole of the male population. But, it decreased after December and disappeared in March.

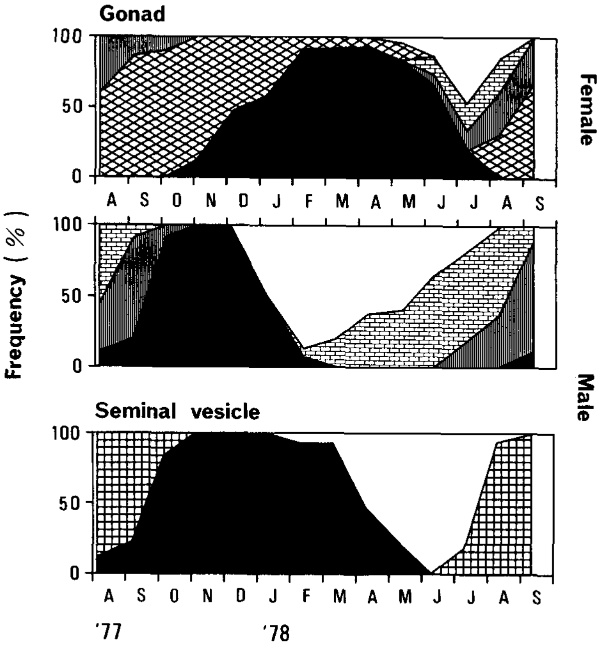


Fig. 6. Seasonal changes in the proportions of gonadal and seminal vesicle stages. □ : spent stage, ▤ : recovering stage, ▦ : resting stage, ▥ : developing stage (male) and pre-developing stage (female), ▩ : post-developing stage, ■ : mature stage (gonad) and accumulating stage (seminal vesicle).

The accumulation process of sperm into the seminal vesicle reflected the seasonal maturation in the testis. The seminal vesicle in accumulating stage emerged over a very long term during September to May. Its proportion sharply increased between September and November, and thereafter it occupied almost all of the male population until March. But, then it sharply decreased, disappearing in June. The seminal vesicle in spent stage also appeared over a fairly long period from February to August. It reached the maximum in May and June, occupying 80% to 100% of the male population. The seminal vesicle in resting stage was observed most in August and September. These results suggest that copulation takes place from March through June.

iv) *Gonad somatic index*

Gonad somatic index (GSI) which quantitatively indicate the seasonal maturation of the gonads was calculated by the following equation.

$$GSI=\{(\text{Gonad weight})/(\text{Soft body weight})\}\times 100$$

where, the weight (g) was wet weight, and the soft body weight included the operculum weight. Seasonal changes in the gonad somatic index are shown in Fig. 7.

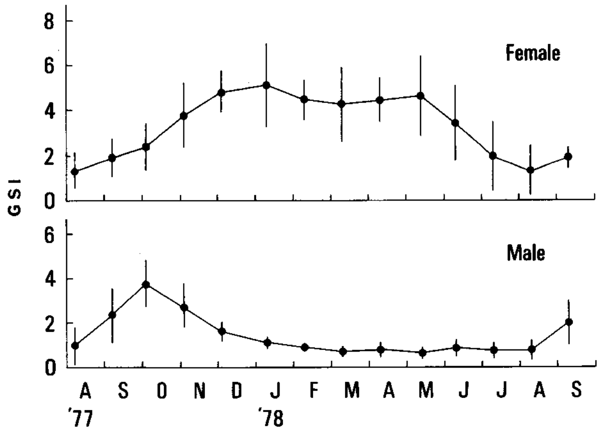


Fig. 7. Seasonal changes in gonad somatic index (GSI). Solid circles and vertical bars indicate the mean and standard deviations, respectively.

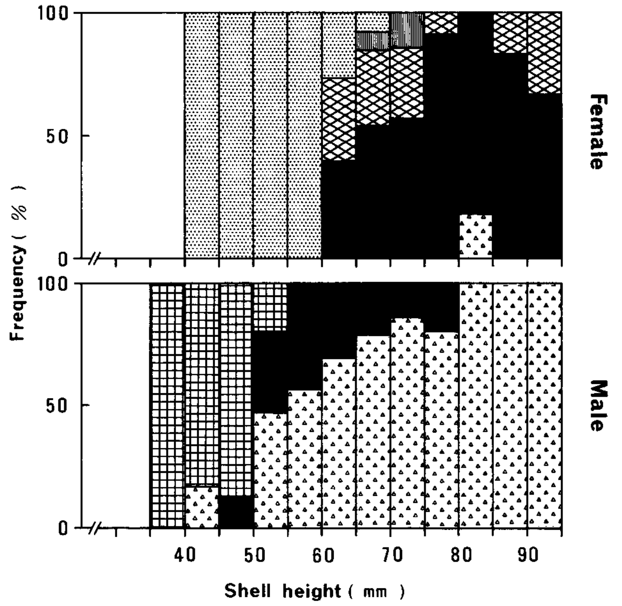


Fig. 8. Changes in the proportions of whelks in various stages of ovary and seminal vesicle with size. ▒ : immature stage, ⁙ : spent stage, ▦ : resting stage, ▥ : pre-developing stage, ▩ : post-developing stage, ■ : mature stage (gonad) and accumulating stage (seminal vesicle).

In the female, GSI rose from August to December and maintained a high value of about 4.5 between January and May. But, then it drastically decreased, showing the minimum in August. Meanwhile, in the male, GSI rose sharply from August through October, reaching the maximum of 3.8 in October, with the subsequent sharp decline until December. It decreased very slowly between December and March, and a low value less than 1.0 continued from April to August. In a time with high GSI values, gonads in the maturation of developing stage or mature stage dominated in both the male and the female populations.

v) Reproductive cycle

On the basis of the seasonal maturations of the gonads and the accumulation process of sperm into the seminal vesicle mentioned in the previous paragraph, the reproductive cycles of the neptune whelk population in Usu Cove are summarized as follows ; in the female population, May and June : spawning period, July : recovering period, August : pre-developing period, September to December: post-developing period, and January to April : mature period, while in the male population, April to June : copulation period, July : recovering period, August and September : developing period, and October to March : mature period.

vi) Sizes at the sexual maturity

In May, being the reproductive time, sizes at the sexual maturity were examined histologically with 227 whelks ranging from 32.2 mm to 95.5 mm in shell height (Fig. 8). At that time, in female the criterion was based on six stages adding immature stage to the five developmental stages in the ovary, while in male it was based on the three stages in the seminal vesicle. Immature stage represents the following gonad ; oocytes before forming yolk and soon after starting accumulation of yolk granules existed in the ovarian follicles, but almost all of them was in the process of collapsing (Fig. 4-15).

In female, individuals with the ovary in mature stage appeared from 60 mm in shell height, and the proportion of individuals in mature stage gradually increased with shell height. In above 85 mm in shell height, almost all individuals possessed ovary with mature stage. On the other hand, in male few individuals ranging from 40 mm to 50 mm in shell height had the seminal vesicle in accumulating stage or spent stage. But, the proportion of individuals not in resting stage substantially increased from 50 mm in shell height. In more than 55 mm in shell height, all individuals possessed the seminal vesicle in either stage. From these facts, neptune whelks in Usu Cove were judged to recruit into the adult population from 50 mm shell height in male and 60 mm shell height in female.

2) *Copulation, spawning, embryonic development, hatching of juveniles, hatching rate, and predation rates on embryos*

i) *Copulation, spawning and embryonic development*

a) *Copulation and spawning*

In the neptune whelk, copulation takes place prior to spawning, and female whelks store sperms in the seminal receptacle until spawning. The copulation behaviour was confirmed in the field, and only 11 copulations were observed (Table 1). The copulation started in November, where most copulations were found at this time. This result was considerably different from the result (Fig. 6) on the histological observation of the coiled portion of the sperm duct functioning as the seminal vesicle. Fig. 9 shows the result comparing the shell height in the copulating pairs, and there was no size preference between male and female.

The neptune whelk deposits a cylindrical egg mass whose egg capsules are piled up spirally. Egg masses of the neptune whelk in Usu Cove were deposited on various substrata, such as rocks (including concrete blocks), boulders, oyster and scallop shells, ropes, and *Laminaria* holdfasts. At spawning site e with four types of substratum, i.e. rocks, boulders, oyster shells and ropes, number of egg masses deposited on each substratum type was enumerated (Table 2). The number on respective substratum type differed between 1979 and 1980, but the ratio between each type showed little change. In both years, almost all egg masses were found on hard substrata, and about 80% were attached to rocks. Only about 10% occurred on boulders and oyster shells.

Egg masses were usually found on the upper part of substrata. On rocks, most egg masses were found in the upper surface, and others on the upper lateral surfaces of the substrata. On boulders, egg masses were restricted to the top of the substrata (Fig. 10). Seaweeds, such as *Chondrus ocellatus*, *Ulva pertusa*, and *Laminaria* spp., were usually abundant on the surface of substrata where egg masses were deposited. Consequently, the egg masses were often not visible from above.

A seasonal change in the number of egg masses within the investigated area (Fig. 3) enclosed by solid lines is shown in Fig. 11. No egg mass was found early in May, but a number of egg masses appeared in late May and June, with the maximum in July. Egg masses in the process of deposition were also observed most in late May and June. Late in May most egg masses were

Table 1. Observations of copulating behaviour in the field.

Date		No. of encounters
1977	2-7 Nov.	6
1978	5-10 Jan.	1
	5-10 Feb.	2
	5-11 Apr.	1
	2-7 May	1

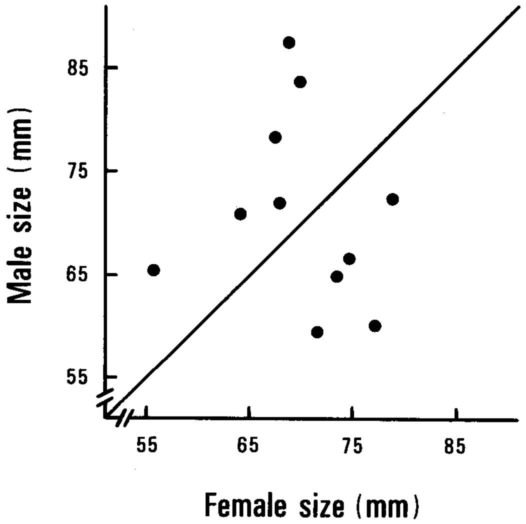


Fig. 9. The shell height of females plotted against males in the copulating pairs.

Table 2. Numbers and proportions (%, in parenthesis) of egg masses deposited on each substratum type at spawning site e.

Substratum type	Number and proportion of egg masses	
	1979	1980
Rocks (including concrete blocks) greater than 50 cm in height	422 (80.5)	284 (80.9)
Boulders less than 50 cm in height	52 (9.9)	29 (8.3)
Oyster shells	21 (4.0)	8 (2.3)
Ropes linking concrete blocks to the oyster culture raft	29 (5.5)	30 (8.5)
Total	524	351

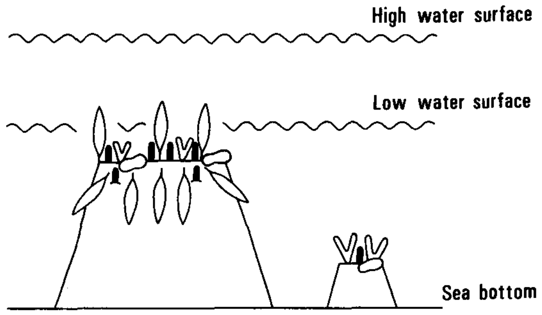


Fig. 10. Sketch showing the positions of *Neptunea arthritica* egg masses deposited on hard substrata. ▮ : egg mass, ⁄ : *Laminaria* spp., V : *Chondrus ocellatus*, ⬭ : *Ulva pertusa*.

under deposition, and such egg masses occupied a half of the egg masses in June. But, egg masses in the process of deposition drastically decreased in July and were not found at all in August. The number of egg masses decreased gradually after July, and reached nearly 0 in December. These facts indicate that egg mass deposition takes place mainly in May and June, and is completed in July.

Size of female whelks depositing an egg mass is shown in Fig. 12. Spawning individuals appeared from 55 mm in shell height, but it was thought that the major spawner in 1978 was composed of individuals from 65 mm to 85 mm in shell height, judging from the shell height frequency distribution. This agrees with the result (Fig. 8) on the histological observation of the sizes at the sexual maturity.

Number of egg capsules composing an egg mass for 3 years during 1978 to 1980 is shown in Fig. 13. In 1978, majority of egg masses was composed of 40 to 65 egg capsules, with the highest mean of 51.1. But, the number of egg capsules diminished during the next two years. In 1980, most egg masses were comprised of 15 to 50 egg capsules, with the lowest mean of 34.9. There were significant differences among the mean number of egg capsules per egg mass during 1978 to 1980 (Analysis of variance, $p<0.01$).

b) Embryonic development

There exist a large number of eggs, together with dense liquid, within an egg capsule. The number of eggs per egg capsule greatly differed among both egg masses and egg capsules within an egg mass. 25 egg capsules from five egg masses in the process of deposition gave the mean of 1,111 (±336) eggs per egg capsule. Of those, the number of juveniles which completed embryogenesis and hatched was nearly an individual (Table 3), and the other eggs served as nurse eggs. A schema of the embryonic development in the neptune whelk is shown in Fig. 14. In the present study, the process was divided into the following four stages, based on the presence of nurse eggs, the color of the embryo, and characteristics of the shell.

Egg-swallowing stage The stages from the com-

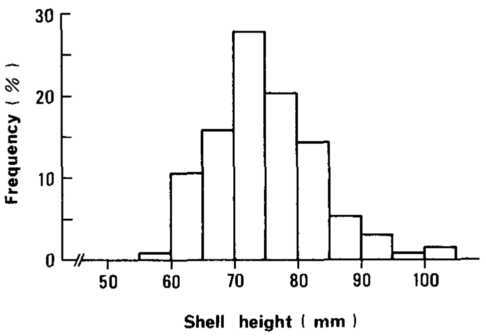


Fig. 12. Sizes of female *Neptunea arthritica* depositing egg masses, June and July 1978.

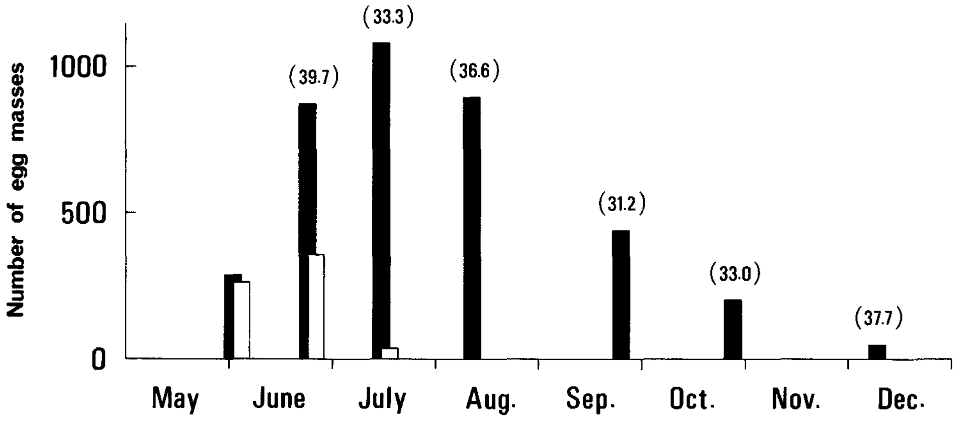


Fig. 11. Number of egg masses observed in the investigated area in 1980. ■ : number of egg masses found (including egg masses being deposited), □ : number of egg masses in the process of deposition. The number in parenthesis represents the mean number of egg capsules per egg mass.

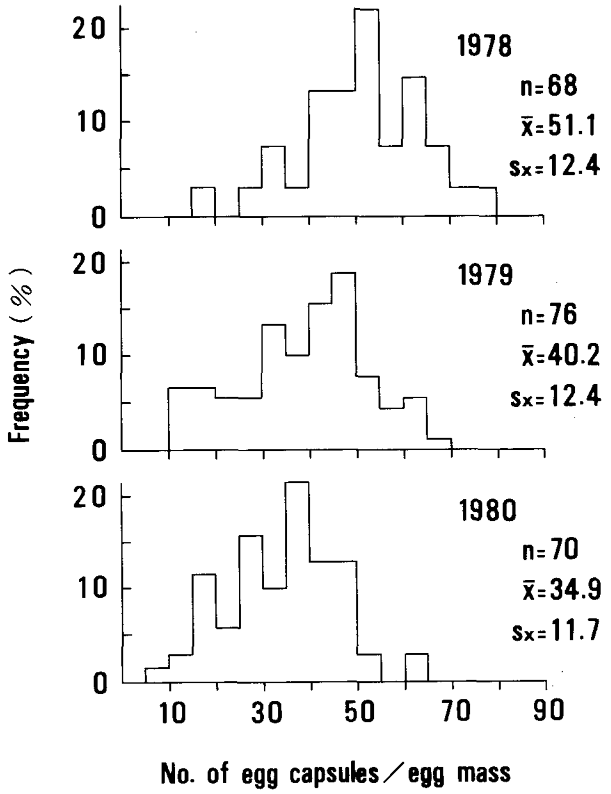


Fig. 13. Number of egg capsules within egg masses during 1978 to 1980. n, $\bar{x}$ and S x refer to the number of egg masses, mean number of egg capsules and standard deviation, respectively.

Table 3. Number of embryos which reached the juvenile within an egg capsule.

Number of embryos	Number of egg capsules
1	2,052
2	14
3	0
4	2
5	0

mencement of embryogenesis to the completion of ingestion of nurse eggs represent the egg-swallowing stage. The embryo in this stage rapidly increased in size, with drastic decrease of nurse eggs surrounding it. The portion, representing the protoconch, was pale yellow. The head changed from rather transparent white to pale ocher with development (Fig. 14A-E).

Protoconch-forming stage This stage included the embryo from the start of torsion to the formation of white shell in the aperture (the outer lip). The portion of the protoconch was pale yellow like the egg-swallowing stage. The semi-transparent white head and the ocher soft body started to become clear, and the transparent shell became recognizable (Fig. 14F-K).

Shell-developing stage The embryos that start to form the outer lip in white and sculpture the spiral sulci in the body whorl were included in this stage. The protoconch and upper body whorl being pale yellowish brown and the lower body whorl being white changed into ashy brown (Fig. 14L-N).

Juvenile stage The juveniles just before hatching, which grew up to 6 mm to 11 mm in shell height and 4 mm to 7 mm in shell diameter, represented the embryos in this stage. The juvenile possessed the hard shell composed of the protoconch (including the penultimate whorl, if any) in ashy brown and the body whorl in pale brown. There existed spiral sulci in the body whorl (Fig. 14O and P).

ii) Hatching of juveniles and hatching rate

a) Hatching of juveniles

Hatching of juveniles in neptune whelk can be distinguished by investigating the developmental stages of embryos within egg capsules. In the present study, the hatching process of juveniles was examined by following seasonal changes in proportions of seven types of egg capsule (Fig. 15), adding the next three types of egg capsule to the four developmental stages mentioned in the previous paragraph: egg capsule with an embryo which suffered predation (there existed one to two round holes by predation in egg capsules), egg capsule with an embryo whose embryogenesis has ceased (including egg capsule with a dead juvenile and egg capsule with few eggs from the start), and egg capsule from which a juvenile has hatched.

In June 1980, all egg capsules possessed embryos in egg-swallowing stage, except for egg capsules with an embryo preyed on and egg capsules with an embryo whose embryogenesis has ceased, which amounted to 11%. The proportion of this type of egg capsule rapidly decreased, with the emergence of egg capsule with an embryo in protoconch-forming stage. In mid-July, proportions of egg capsules with both embryo in egg-swallowing stage and embryo in protoconch-forming stage totalled about 80%. In mid-August in both 1979 and 1980, these two types of egg capsule decreased sharply, and egg capsule with an embryo in shell-developing stage dominated. Thereafter, the proportion of egg capsule with an embryo in this stage diminished gradually, occurring until December. Egg capsule with a juvenile just before hatching, which emerged after mid-August, showed the highest proportions in early and mid-September. Then, this type of egg capsule decreased, disappearing late in October. Egg capsule from which a juvenile has hatched appeared after early September, and reached the maximum early in October.

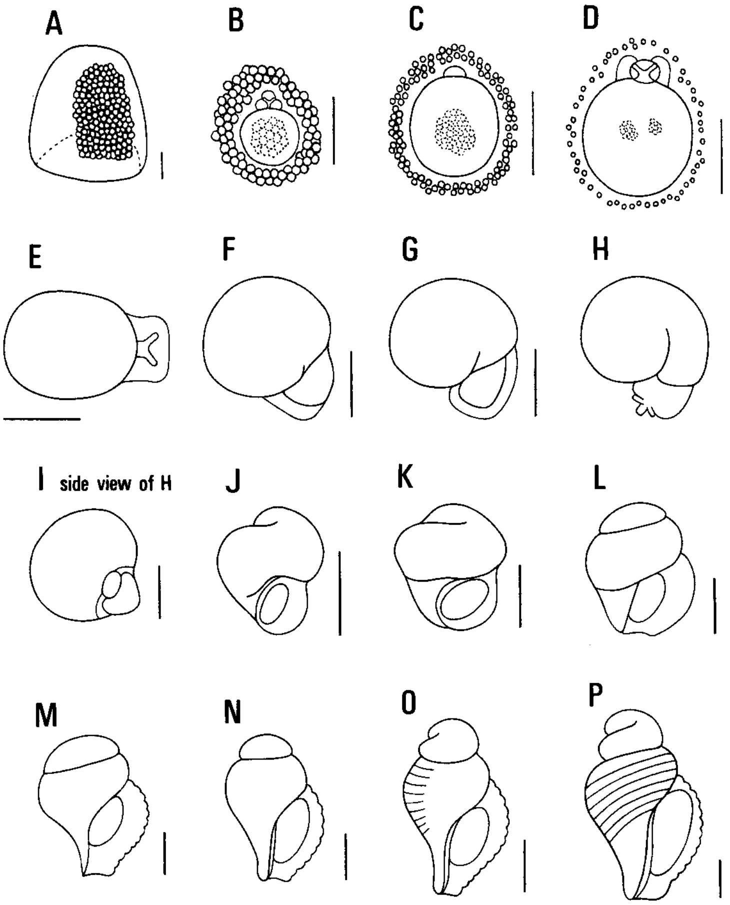


Fig. 14. Sketch showing the developmental process of an embryo in *Neptunea arthritica*. Scale bar = 2 mm. A-E : egg-swallowing stage, F-K : protoconch-formation stage, L-N : shell developing stage, O and P : juvenile stage.

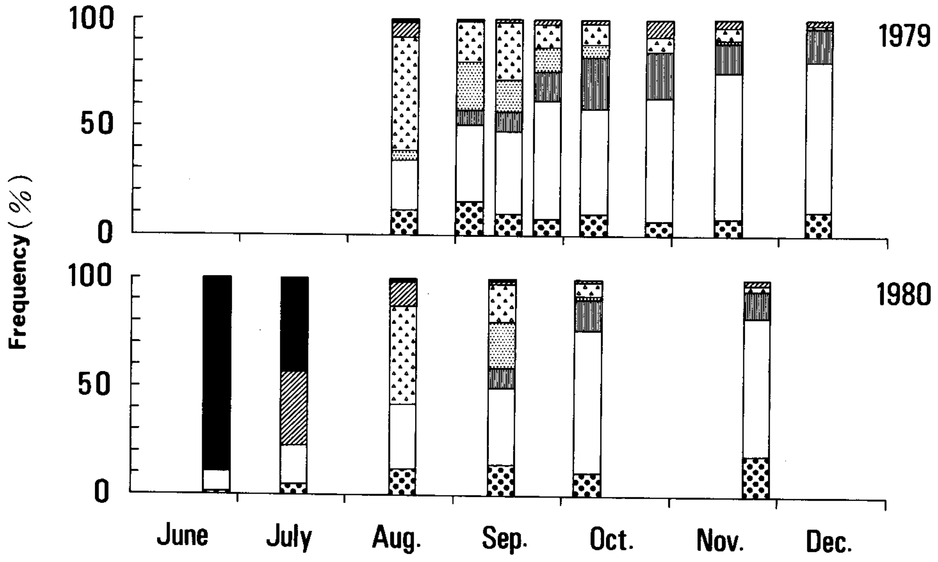


Fig. 15. Seasonal changes in the proportions of seven egg capsule types in 1979 and 1980. ■ : egg capsule with an embryo in egg-swallowing stage, ▨ : egg capsule with an embryo in protoconch-formation stage, ▵ : egg capsule with an embryo in shell-developing stage, ░ : egg capsule with an embryo in juvenile stage, ▥ : egg capsule from which a juvenile has hatched, □ : egg capsule with an embryo which suffered from predation, ⁙ : egg capsule with an embryo whose embryogenesis has ceased.

Both egg capsule with an embryo preyed on and egg capsule with an embryo whose embryogenesis has ceased gradually increased from June through September. Then, the proportion of egg capsule with an embryo preyed on augmented and occupied more than 50% after late September. However, the proportion of egg capsule with an embryo whose embryogenesis has ceased did not show so large fluctuation during that period.

These facts suggest that in Usu Cove most of embryos of the neptune whelk hatched in September, and the hatching finished in October because juveniles just before hatching did not exist after late October.

b) Hatching rate

Seasonal change in number of embryos within the investigated area was followed (Fig. 16), based on the number of egg masses and of egg capsules per egg mass (Fig. 11), and the proportion of embryos in the four developmental stages and the other three types of egg capsule (Fig. 15) in 1980. In June, the number of embryos in egg-swallowing stage was 307.8×10^2 individuals, and the embryos preyed on and embryos with ceased development amounted to about 38×10^2 individuals. In mid-July, the number of embryos in egg-swallowing stage and embryos in protoconch-forming stage totalled to 275.9×10^2 individuals, and the sum of embryos preyed on and embryos with ceased development was 83.7×10^2 individuals. In August, embryos in both egg-swallowing stage and protoconch-forming stage substantially diminished, but embryos in shell-developing stage, embryos preyed on, and embryos with ceased development increased. The number of egg capsules in this month was 326.8×10^2 in total. In September, embryos in juvenile stage and egg capsules from which a juvenile hatched appeared, with decreasing embryos in shell-developing stage. At this time, the number of embryos in shell-developing stage was 25.4×10^2 individuals, embryos in juvenile stage were 28.7×10^2 individuals, and embryos preyed on and embryos with ceased development totalled to 68.5×10^2 individuals. As mentioned above, the total number of egg capsules exhibited the peak in July, and embryos in juvenile stage and egg capsule from which a juvenile hatched emerged after September. Therefore, a hatching rate was calculated on the basis of the following equation.

$$\text{Hatching rate }(\%)=(C/c\cdot d)\times100$$

where, C is the number of juveniles which hatched, c is the number of egg capsules per egg mass in July, and d is the number of egg masses in July. Moreover, C was calculated by using the next equation.

$$C=(1/100)\cdot(e+f+g)\cdot h\cdot i$$

where, e, f, and g are the proportions (%) of embryos in shell-developing stage, embryos in juvenile stage, and egg capsule from which a juvenile hatched, respectively, and furthermore, h and i are the number of egg capsules per egg mass and the number of egg masses in September, respectively. In the calculation of the number of juveniles which hatched, all embryos in shell-developing stage and in juvenile stage in September were assumed to hatch, and, in addition, embryos (1.2% in total) both in egg-swallowing stage and in protoconch-forming stage in the month were excluded because they were thought

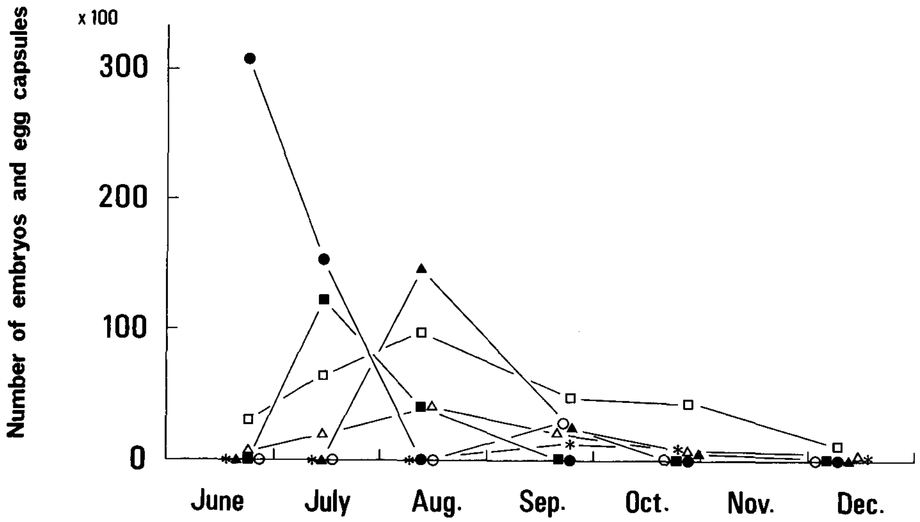


Fig. 16. Seasonal changes in the numbers of embryos and juveniles in the investigated area. ● : egg-swallowing stage, ■ : protoconch-formation stage, ▲ : shell-developing stage, ○ : juvenile stage, * : egg capsule from which a juvenile has hatched, □ : egg capsule with an embryo which suffered from predation, △ : egg capsule with an embryo whose embryogenesis has ceased.

not to hatch as mentioned later. As a result, the hatching rate of the neptune whelk was estimated to be 18.6%.

c) *Causes of mortality*

Causes affecting the hatching rate include decrease in number of egg masses, predation on embryos, cessation of embryonic development and so on. In the present study, causes of embryonic mortality were examined, dividing into egg mass and egg capsule.

Egg mass

Substrata where egg masses of the neptune whelk were deposited were divided into two types: hard substrata, e.g. rocks, boulders, and molluscan shells, and elastic substrata, e.g. holdfasts of *Laminaria* spp. and ropes. There were 942 egg masses on hard substrata and 127 egg masses on elastic substrata found in mid-July 1980. Proportion of the number of egg masses after August to the number of egg masses in July on each type is shown in Fig. 17. On hard substrata, 44% of the egg masses subsisted late in September, when the hatching was nearly completed, while only 16% of those remained on elastic substrata. Egg masses were less in proportion on elastic substrata than on hard substrata. Detachment from the substrata and predation on egg masses were confirmed as causes of the decrease as shown in Table 4, which is the result observed in 1979. In that time distinction between the two types of substratum was not made. The number of egg masses preyed on during the observation period was only six early in August, and the decrease by detachment from substrata was much greater.

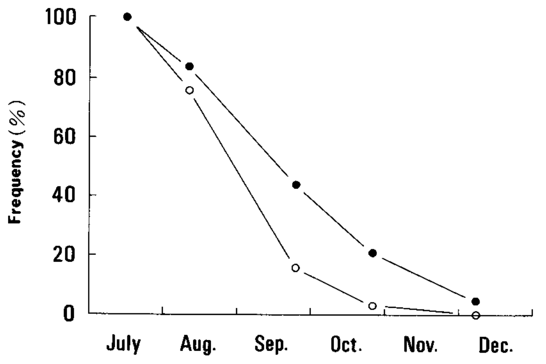


Fig. 17. Difference in the proportion of exfoliation of egg masses between the two types of substratum. ● : hard substratum, ○ : elastic substratum.

Table 4. Numbers of egg masses subjected to predation and exfoliation, observed in 1979.

Duration	Predation	Exfoliation
7 Aug.-14 Aug.	6	13
24 Aug.- 1 Sep.	–	19
15 Sep.-24 Sep.	–	41
10-16 Oct. & 27-31 Oct.	–	53
8 Nov.-19 Nov.	–	43
8-12 Dec. & 18-23 Dec.	–	34

Egg capsule

Predation on embryos and cessation of embryonic development were observed as causes of mortality in embryos (Fig. 11). In this paragraph, egg capsule with an embryo whose embryogenesis has ceased was subdivided into the following three types of egg capsule: egg capsule with few eggs from the start, egg capsule with an embryo whose embryogenesis has ceased at the early stage, and egg capsule with a dead juvenile (including embryos in shell-developing stage). By using the data in August and September, before and during the hatching period, magnitude of the respective causes was compared (Table 5). Except for egg capsule from which a juvenile has hatched, proportion of egg capsules without an embryo was 42.3% in August and 50.1% in September. Of the causes of mortality, predation was the highest with 30% to 35%, followed by the cessation of embryonic development at the early stage occupying 10%. The relationship between proportion of egg capsule with an embryo whose embryogenesis has ceased at the early stage and number of egg capsules per egg mass was examined (Fig. 18). The cessation rate of the

Table 5. Proportions (%) of nine types of egg capsule before and during the period of hatching.

Type of egg capsule	1980	
	15 Aug.	13 Sep.
Egg capsule with an embryo in egg-swallowing stage	0.4	0.2
Egg capsule with an embryo in protoconch-forming stage	12.4	1.0
Egg capsule with an embryo in shell-developing stage	44.9	18.6
Egg capsule with an embryo in juvenile stage	0	21.0
Egg capsule from which a juvenile has hatched	0	9.3
Egg capsule with an embryo which suffered predation	29.9	35.2
Egg capsule with an embryo whose embryogenesis has ceased at the early stage	10.2	10.1
Egg capsule whose few eggs existed from the first	2.2	4.0
Egg capsule with a dead juvenile	0	0.8

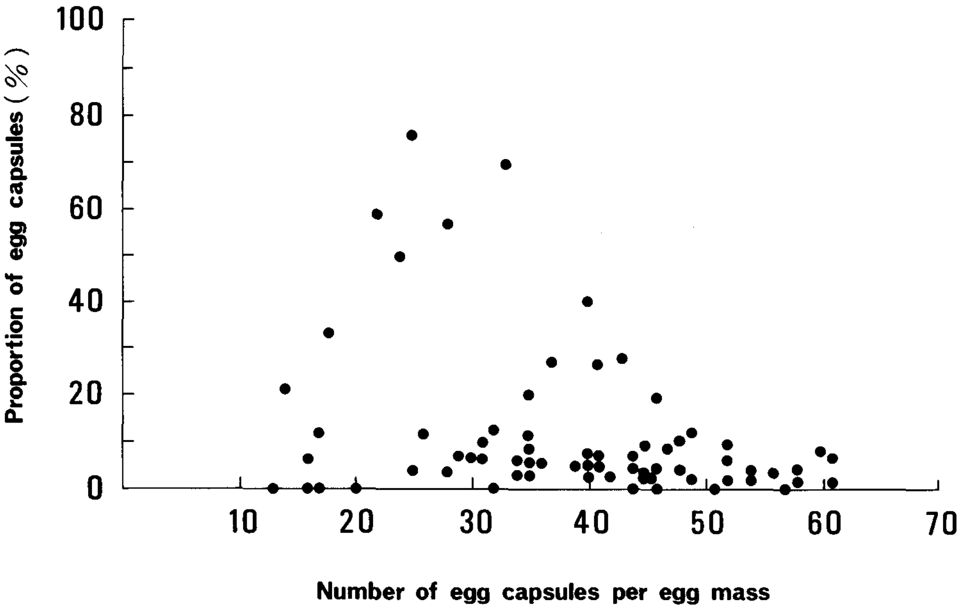


Fig. 18. The relationship between number of egg capsules per egg mass and proportion of egg capsules with an embryo whose embryogenesis has ceased at the early stage.

Table 6. Type and abundance of substrata, and number of egg masses at six spawning sites. Abundance of substrata, − : 0, + : 1-5, ++ : 6-10, +++ : ≧11.

Spawning site	Substratum type				No. of egg masses
	Rocks	Boulders	Oyster shells	Ropes	
e	+++	+++	+++	++	524
f	−	+	−	+	77
k	−	++	+++	−	102
q	−	+++	−	−	72
r	++	+++	−	−	264
s	−	+++	−	−	123

development greatly differed among egg masses, and egg masses with high cessation rates were relatively copious in egg masses with less number of egg capsules. The cessation rate lowered with increase in the number of egg capsules per egg mass, and egg masses showing high cessation rates were not found among egg masses composed of many egg capsules. The proportion of egg capsule with few eggs from the start and egg capsule with a dead juvenile was considerably low (Table 5).

Other causes

Besides the causes mentioned in the previous paragraphs, influences of periphyton making egg masses substrata, in particular coating by sponges, were raised. After October all egg masses with embryos late in the development were covered with sponges, except for 2 out of 33 egg masses.

iii) Predation rates on embryos

a) Size and abundance of substratum, and number of egg masses among spawning sites

Egg masses of the neptune whelk were deposited on various types of substrata, such as rocks, boulders, oyster shells, and ropes. The size and abundance of substrata, and the number of egg masses differed greatly among spawning sites (spawning sites e, f, k, q, r, and s) (Table 6). There were many substrata at each spawning site except spawning site f. But, rocks were confined to spawning sites e and r, and were most abundant at site e. Egg masses were more abundant at spawning sites with more substrata, and the number of egg masses at spawning sites e and r was much more than at spawning sites f, k, q, and s, which had only small substrata. In particular, spawning site e, with the most abundant

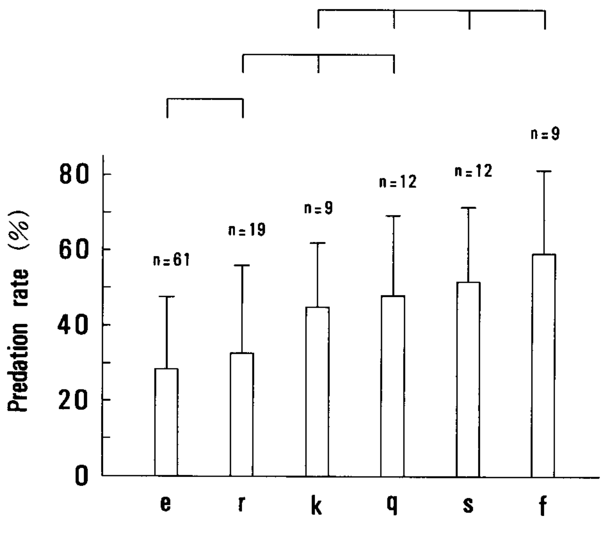


Fig. 19. Predation rates in six spawning sites. The thick and thin bars represent the mean and standard deviation, respectively. n indicates number of egg masses. Means linked by the solid horizontal lines are not significantly different (Analysis of variance, $p>0.05$).

rocks, had more egg masses than any other spawning site.

b) *Differences in predation rates among spawning sites*

Predation rates on embryos of the neptune whelk greatly differed among both egg masses and spawning sites (spawning sites e, f, k, q, r, and s) (Fig. 19). The highest mean predation rate (spawning site f) was 2.1 times higher than the lowest mean predation rate (spawning site e). There was no significant difference between spawning sites e and r, both had large substrata such as rocks (Analysis of variance, $p>0.05$), and the rate at spawning site e was significantly lower than at the other spawning sites (Analysis of variance, $p<0.05$). There was no significant difference among spawning sites f, k, q, and s, where only small substrata occurred (Analysis of variance, $p>0.05$). The mean predation rates for spawning sites e and r was 29.7% and 50.8% for spawning sites f, k, q, and s, with a significant difference between the two (Analysis of variance, $p<0.01$).

(3) Discussion

In the neptune whelk, which has internal fertilization, copulation takes place prior to spawning. In the present study, the copulation time was confirmed on the basis of the histological observation of the coiled portion in sperm duct functioning as seminal vesicle and the observation of copulating behaviour in the field. From the histology of seminal vesicle, it was found that the proportion of male whelks with seminal vesicle in spent stage appearing after February sharply increased in March and April, and that almost all the males were in that stage in May and June. On the other hand, according to the field observation, copulation started in November, and at that time most copulations were discovered. Thus, the two results differed considerably. But, number of encounters in the field during the investigation period was only 11 copulations. Therefore, it was thought that copulation begins from early time of November, but that the peak is from April to June. Also, size preference between male and female in copulating pairs was not recognized, unlike *Kelletia kelletii* (Rosenthal, 1970).

After copulation, the neptune whelk deposits a cylindrical egg mass whose egg capsules are piled up spirally, on various substrata, such as rocks, boulders, molluscan shells, and ropes. Miyawaki (1953) reported that the reproductive period of the neptune whelk in Akkeshi Bay, Hokkaido, is from mid-May to mid-July, and that copulation takes place in the earlier period and spawning in the later period with the peak in mid-July. Also, the spawning period is estimated to be from April to June in Hakodate Bay (Takamaru and Fuji, 1981), and moreover, from May through August in Saroma Lagoon (Kawai et al., 1994). The spawning period of the neptune whelk in Usu Cove is May and June, judging from the histological observation of the gonad, confirmation of spawning behaviour, and seasonal change in the number of egg masses. The spawning period in Usu Cove is almost of the same season with the other three localities mentioned above, though showing the tendency to somewhat late period in higher latitudes.

The period from copulation to spawning differs from species to species. In *Nucella lapillus* (Feare, 1970a), *Thais clavigera* (Amio, 1963) and *T. bronni* (Amio, 1963), copulation occurs just before spawning. Also, *Babylonia japonica* spawns in two to three days after copulation (Ino, 1950), and the neptune whelk does in more than 10 days (Miyawaki, 1953). As mentioned in the previous paragraphs, because the copulation time of the neptune whelk in Usu Cove is from April to June and the spawning period is May and June, the period from copulation through spawning is thought to be roughly the same as the neptune whelk in Akkeshi Bay (Miyawaki, 1953). But, an observation of the seminal receptacle in female whelks is necessary, as the result of the histological examination on copulation time differed from that of the confirmation in the field.

The number of eggs within an egg capsule greatly varies from one species to the other. In the case of the genus *Neptunea*, it amounts to 2,500 in *N. antiqua* (Golikov, 1963), and 5,000 in *N. despecta* (Purchon, 1968). In *N. arthritica*, 1,110 eggs on average existed within an egg capsule. Of a large number of eggs, the number of juveniles which ingest eggs, develop, and hatch is almost all one individual in *N. arthritica*. Up to date, with regards to the embryonic development of the genus *Neptunea*, its characteristics are only briefly described in *N. intersculpta* (Ito, 1957) and *N. antiqua* (Pearce and Thorson, 1967). In the present study, the developmental process was divided into the four stages; egg-swallowing, protoconch-forming, shell-developing, and juvenile stages, based on presence of nurse eggs, torsion, color of an embryos, and characteristics of the shell. The development of *N. arthritica* needs to be examined in more detail.

The period from egg deposit to hatching of marine gastropods is investigated in many species. Amio (1963) compiled papers on 61 species from Japan together states that larvae and juveniles in most of the species hatch in less than a month. But, the period between egg deposit and hatching is two months to three months in *Dicathais aegrota* (Phillips, 1969), three months to four months in *Neptunea bulbacea* (Golikov, 1961), four months in *Purpura lapillus* (Moore, 1938), about six months in *N. antiqua* (Pearce and Thorson, 1967), and furthermore, is about a year in *N. pribiloffensis* (Shimek, 1981). Because spawning of *N. arthritica* in Usu Cove took place in May and June, and hatching in September and October, the period is three months to four months.

The reproductive cycle of the neptune whelk was examined as a series of processes, beginning by gametogenesis in the gonads and accumulation process of sperm in the coiled portion of sperm duct and ending by egg mass deposition and hatching of juveniles. On the basis of the results of the reproductive biology, the reproductive cycle of the neptune whelk population in Usu Cove was summarized as follows (Fig. 20), from the viewpoint mentioned above: in the female population, July: recovering period, August: pre-developing period, September to December: post-developing period, and January to April: mature period, while in the male population, July: recovering period, August and September: developing period, October to March: mature period, continuing the seasonal maturation, April to June: copulating period, May and June: spawning period (birth period), furthermore, July and August: embryogenesis period, and September and October: hatching period.

In the present study, the developmental process of the embryo in the neptune whelk was divided into the four stages of egg-swallowing stage, protoconch-forming stage, shell-developing stage, and juvenile stage. Next, based on this, the hatching process of juveniles was comprehended by seasonal changes in proportions of the following seven types of egg capsule: four types of egg capsules with embryos in the four developmental stages, egg capsule from which a juvenile has hatched, egg capsule with an embryo which suffered predation, and egg capsule with an embryo whose embryogenesis has ceased. On the basis of the hatching process, an estimate of 18.6% as the hatching rate of the neptune whelk in Usu Cove was obtained. This estimation is based on the premise that all embryos (39.6% in total) in shell-developing stage and in juvenile stage in September could hatch. But, both detachment of egg masses from substrata and predation on embryos which would have occurred from September until hatching were not taken into consideration in the estimate. Furthermore, the total number of egg capsules in July did not include lost egg masses through detachment and predation during egg mass deposition to that time. Therefore, the hatching rate seems to be overestimated clearly. Also, egg capsule from which a juvenile hatched could be included in lost egg masses through detachment and predation before September. In this respect, there is a possibility

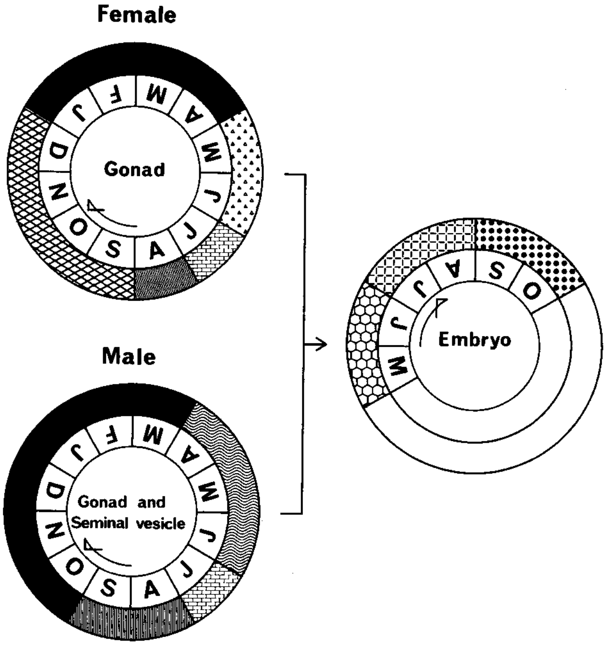


Fig. 20. Diagrams showing the annual cycles of maturation of gonad (including seminal vesicle in male) and development of embryo. ▤ : recovering period, ▥ : developing period (male) and pre-developing period (female), ▩ : post-developing period, ■ : mature period, ▒ : copulating period, ░ : spawning period, ⬡ : birth period, ▦ : embryogenesis period, ▓ : hatching period.

that the hatching rate is underestimated. As one of the methods for correcting the underestimation, it is raised that the values in the respective items at the time of September 1, representative of the commencement time of the hatching period, are utilized. In that case, however, for preventing embryos in shell-developing stage from overestimating, it should be assumed that one-third of them does not hatch. So, the number (C) of hatching juveniles is calculated by the following corrected equation: $C=(1/100)\{(2/3)e+f+g\}\cdot h\cdot i$. By using the values shown in Fig. 11 and Table 5, the values in the respective items on September 1 by interpolation can be attained. The estimation of the hatching rate by the above equation gives a value of 23.0%. Estimates of hatching rate in the neptune whelk based on the hatching process of embryos, predation, and detachment from the substrata in the field are not reported until now, but the hatching rates of 18.6% and 23.0% are fairly low as compared with those in *Thais lamellosa* (57% and 58%) (Spight, 1975, 1977) and *T. emarginata* (57%)(Emlen, 1966), which deposit egg capsules in the intertidal zone. Besides differences among species like hatching size, the difference of the environment in spawning places is thought to affect the rate (Feare, 1970a), because the neptune whelk produces egg masses in the sublittoral, unlike the above two species.

As causes of embryonic mortality in the neptune whelk, predation, detachment of egg masses, cessation of embryonic development at the early stage and so on were confirmed. In Usu Cove, the decreases through predation and detachment occupied the highest proportions, followed by cessation of the development at the early stage. Predation was divided into the two types of predator. One type is the predator that preyed upon the whole egg mass, like *Asterias amurensis*, *Asterina pectinifera*, and *Strongylocentrotus nudus*. The other is the predator that drilled an egg capsule and preyed upon an embryo, like *Ocenebra japonica*. The number of egg masses observed being preyed upon was only 6 during August to December, 1979. But, the proportion of predation on embryos inferred from round holes by boring amounted to about 35% of the egg capsules in the commencement time of the hatching period. It is thought that this high predation rate lowers the hatching rate of the neptune whelk considerably.

Egg masses fairly detached from substrata during from egg mass deposition to hatching, and proportions of detachment differed between the substratum type. Egg masses deposited on elastic substrata, such as ropes and holdfasts of *Laminaria* spp., were more susceptible to detachment than those on solid substrata, such as rocks and boulders. The hatching rate of the neptune whelk usually living on the muddy sand bottom in the sublittoral, different from gastropods in the intertidal of the rocky shore, is greatly dependent on the presence of hard substrata. Prior to spawning, many adult whelks migrate to places with hard substrata (Fujinaga and Nakao, 1994). This migration is possibly associated with detachment of egg masses from substrata.

Cessation of embryonic development at the early stage is related to the number of egg capsules per egg mass. In egg masses composed of a small number of egg capsules, egg mass with high developmental cessation rate was relatively more. The developmental cessation rate lowered with increasing number of egg capsules per egg mass, and the rates were very low in egg masses with many egg capsules. In general, fecundity increases with age and size (Spight and Emlen, 1976; Boag and Pearlstone, 1979; Robertson and Mann, 1982; Perron, 1983). These facts lead to the following suggestion: the possibility that embryonic development ceases at the early stage is higher in egg masses produced by younger and smaller whelks. But, fecundity greatly changes with food consumption (Spight and Emlen, 1976). The relationship between number of egg capsules per egg mass and embryonic developmental cessation rate needs to be examined adding food consumption to age and shell height of spawners.

When egg capsule and egg mass are covered with periphyton, the developmental speed of the embryo is reduced (MacKenzie, 1961; Amio, 1963; Hamada, 1974). Almost all embryos surviving after October had developed in egg capsules within the whole egg mass covered with sponges. As juveniles just before hatching were not found after late October, embryos with retarded development would still have more reduced developmental rate owing to the declined water temperature, and are presumed to die eventually without reaching the juvenile stage. Therefore, the hatching rate was estimated by excluding the embryos in both egg-swallowing stage and shell-developing stage, whose proportion was slight, from the calculation items for the number of hatching juveniles.

Almost all egg masses of the neptune whelk were deposited on hard substrata, such as rocks, boulders, and oyster shells. The egg masses tended to be more numerous at sites with more substrata (Cole, 1942), but there were many more egg masses at spawning sites with large substrata, such as rocks (including concrete blocks) greater than 50 cm in height, than at spawning sites with only small substrata, such as boulders less than 50 cm in height and oyster shells. Moreover, at spawning sites with both rocks and boulders, most egg masses were deposited on the rocks. These observations suggest that neptune whelks prefer large hard substrata for spawning.

Predation rates on embryos in the neptune whelk were closely related to the size of hard substrata. Predation rates at spawning sites with rocks were significantly lower than those at spawning sites with only small hard substrata. However, in the study of predation rates on embryos, spawning sites with relatively more muricid snails like *Ocenebra japonica*, predators on embryos of the neptune whelk, were chosen, out of the spawning sites divided into 20. In the future differences in predation rates on embryos among spawning sites need to be in more detail examined by determining abundance of predators, including farther sites with less predators.

Prior to spawning, most adults of neptune whelks migrate from sites with abundant food organisms to sites with hard substrata and deposit egg masses on the upper part of the substrata (Fujinaga and Nakao, 1994). It seems that this behaviour is to protect the egg masses from predators, since it is more laborious for predators to feed on embryos from egg masses on rocks than on boulders.

Egg masses of the neptune whelk were usually found on the upper part of hard substrata, and concealed by seaweeds, such as *Chondrus ocellatus*, *Ulva pertusa*, and *Laminaria* spp., which were abundant on the hard substrata. Gastropod egg capsules and egg masses are often laid away from the bottom (Federighi, 1931 ; Miyawaki, 1953 ; Hancock, 1959 ; Galtsoff, 1961 ; Amio, 1963). Furthermore, during the period from egg deposition to hatching, embryos of marine gastropods that deposit egg capsules or egg masses would die if covered by mud (Gallardo, 1979 ; Barnett et al., 1980 ; Hughes and Roberts, 1981) and coated by sponges (Fujinaga and Nakao, 1995). Laying egg masses away from the bottom and among seaweeds may protect them from silty mud and sponges. These could contribute to higher hatching rates of the neptune whelk in the upper sublittoral zone. The relations between reducing exposure to silty mud and sponges by egg deposition in higher positions and among seaweeds and hatching rates should be investigated in the future.

To take the hatching rate of embryos, the causes of death of embryos, and the differences in predation rates among spawning sites into consideration leads to the following suggestion. In the propagation of the neptune whelk, it is important to lay large hard substrata in spawning places to enhance hatching rates, in addition to the resource management of adults, such as the regulation of catch size and establishment of a closed season for fishing.

2. *Growth*

(1) Investigated area and methods

Investigations of growth were carried out during periods from August 1977 to September 1978 and from September 1979 to April 1981. The investigation and the collection of neptune whelks were all conducted by SCUBA diving.

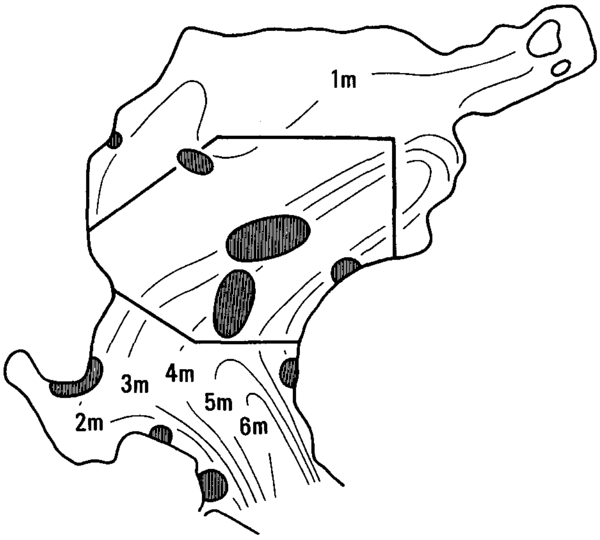


Fig. 21. Map of Usu Cove showing areas where whelks were collected (the striped area) and measured under water (the area enclosed by the thick straight line).

During the first period, neptune whelks were collected at regular monthly intervals in the nine districts, marked with the striped lines in Fig. 21, which were established over the total area of Usu Cove. In the laboratory, individual samples were measured for both shell height and shell diameter, and then sex was distinguished in many whelks on the basis of the presence of a penis. Next, the wet weight of the soft body of about thirty whelks for each sex was determined by choosing three whelks at maximum within each 1 cm-shell height range. But, the distinction between male and female was restricted for six months from April to September in 1978. After the measurements, the neptune whelks were returned to their original sampling sites as soon as possible, except for the whelks being weighed.

During the later period, at nearly monthly intervals, excluding winter, shell height of neptune whelks was measured underwater to the nearest 0.05 mm with a vernier caliper in the area enclosed by the thick straight lines (Fig. 21). But, in the case of such places where many whelks cohabit in the same position, they were measured for shell height on boat and returned to their original sites immediately.

The size frequency distributions in shell height and shell diameter were separated into age-groups by the probability paper (Harding, 1949).

(2) Results

1) Growth

i) Growth in shell height, shell diameter and soft body

The size frequency distributions in shell height and shell diameter for male and female populations from April 1978 to September 1978 were separated into cohorts, and the means of each cohort shown in Table 7 were obtained. Comparison of the means between the corresponding cohorts in shell height and shell diameter showed no significant differences between male and female in every month (*t*-test, $p>0.001$). So, the size frequency distributions in both male and female were combined together to examine growth based on shell height and shell diameter.

The size frequency distributions in shell height and shell diameter from August 1977 to September 1978 are shown in Fig. 22. These frequency distributions represented as polymodal distributions were separated into cohorts, and 5 or 6 cohorts shown with a dotted line in Fig. 22 were obtained. Egg mass depositions of the neptune whelk in Usu Cove were almost completed until July. Furthermore, after three to four months from egg deposition, juveniles that have grown up to 6 mm～11 mm in shell height and 4 mm～7 mm in shell diameter were mostly hatched in September. These facts indicate that it is valid for each age group to increase by 1 in July, and that the first cohort appearing after September is the 0-age group hatched from egg masses deposited in that year. The growth processes of the neptune whelk are displayed as the succession of S-shaped curve shown in Fig. 23, by using the means in shell height and shell diameter for each age group. Moreover, the growth of soft body followed the process shown in Fig. 24, by using regression equations for shell height—soft body weight in Table 8. In preparing the regression equation, the whelk was divided into immature, male, and female, regarding whelks more than 50 mm shell height in male and more than 60 mm shell

Table 7. Mean values (±S.D.) of shell height and shell diameter in each group of both male and female from April to September 1978.

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

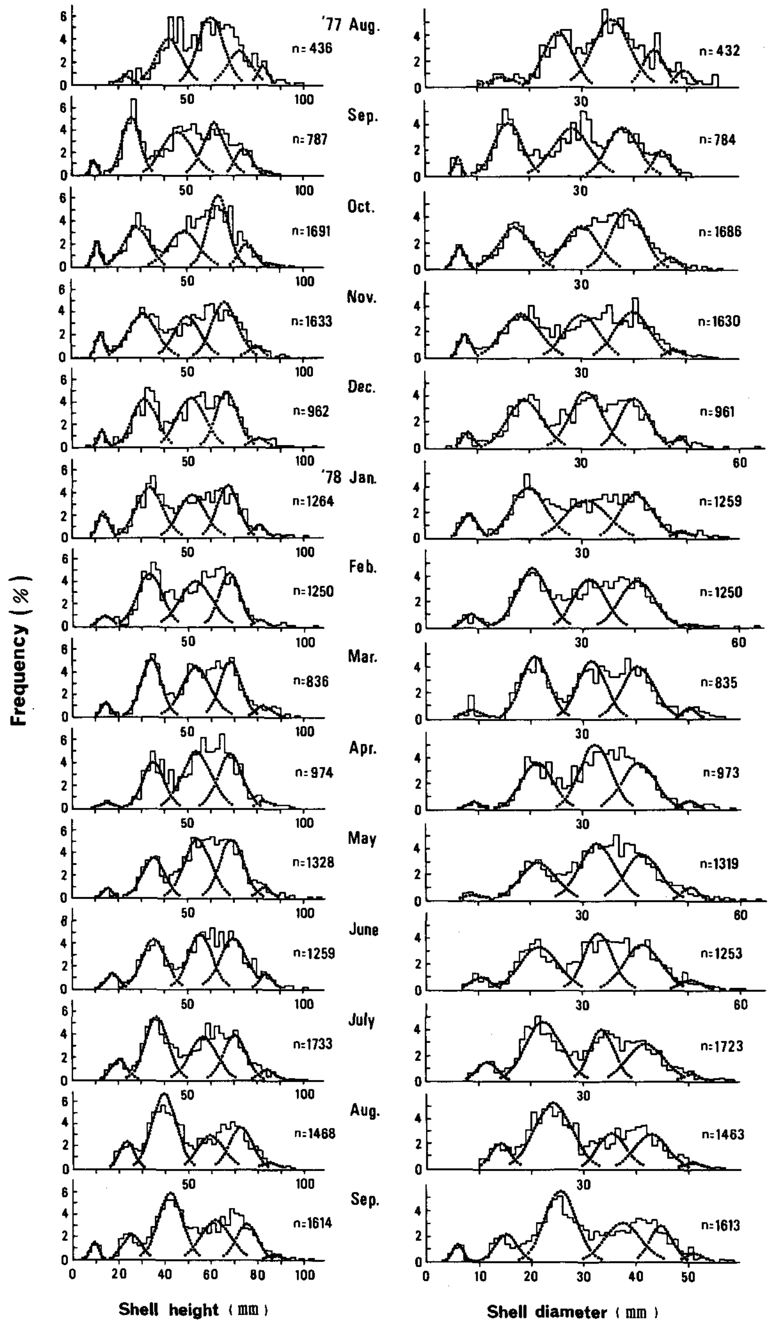


Fig. 22. Size frequency distributions in shell height and shell diameter. Dotted lines represent normal curves, analysed using the probability paper. *n* indicates the number of whelks measured.

height in female as adult on the basis of the sizes at sexual maturity.

ii) Growth rates in shell height, shell diameter and soft body

Using the means of shell height, shell diameter and soft body in each month for each age group in Figs. 23 and 24, monthly growth rates (the percentage of monthly growth increment divided by the mean in the beginning of the month) were calculated (Fig. 25). The monthly growth rates in shell height, shell diameter and soft body were high from early summer to autumn, and low in winter and early spring, when water temperature is low, in all age classes. Also, the growth rates in the three criteria decrease with increasing age. The growth in the three criteria exhibited the same tendency in these two aspects. But, in soft body, the negative growth occurred, the negative growth rate was higher in female than in male, and additionally decrease in the growth rates above II-age class was not so large compared to shell

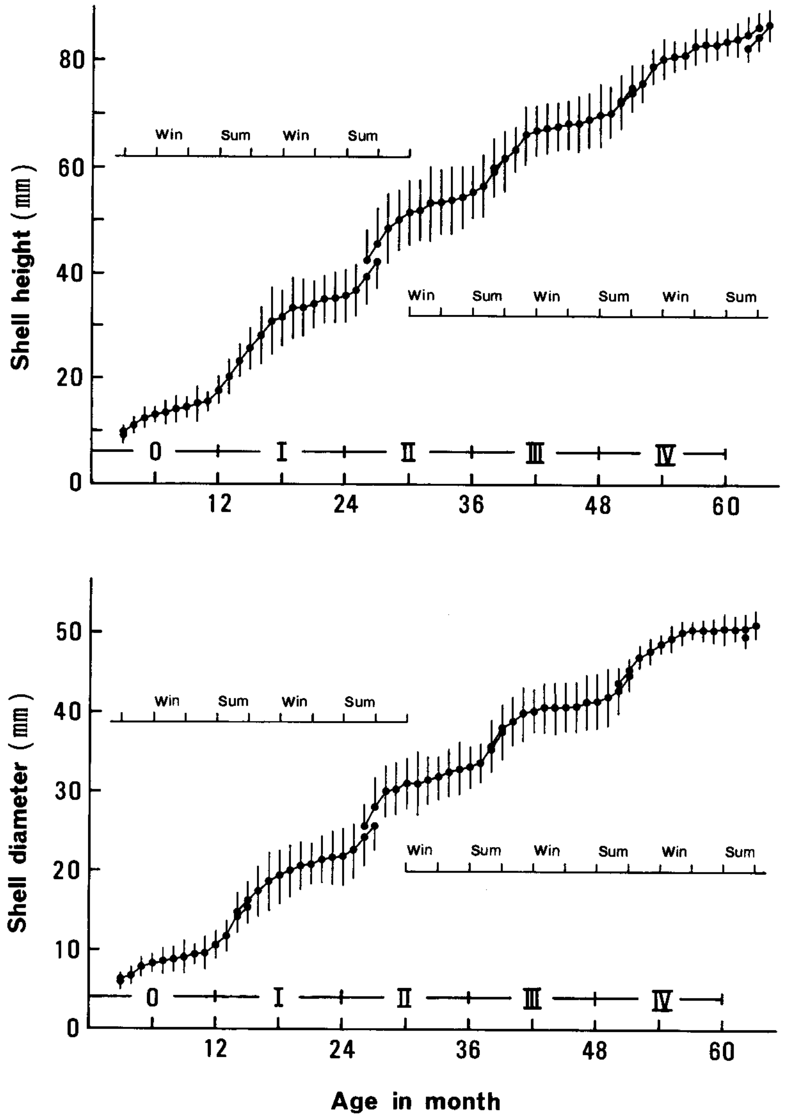


Fig. 23. Growth of *Neptunea arthritica* in shell height and shell diameter. Dots and vertical bars represent mean and standard deviation, respectively. Roman numerals indicate ages.

height and shell diameter, which exhibit the growth pattern peculiar to the soft body.

2) *Growth equation*

i) Relationship between shell height and shell diameter

The seasonal changes in the monthly growth rates in both shell height and shell diameter in each age class showed the same tendency. This suggests that increases in the two criteria take place synchronously, and that the relationship between the two remains linear throughout the life span. The relationship between shell height (X) and shell diameter (Z) was examined by using the means of shell height and shell diameter in each month for each age class in Fig. 23 (Fig. 26). The relationship between the two criteria is expressed as the following linear equation with a very high correlation coefficient:

$$Z = 0.60X + 0.158 \ (r = 0.9996, \ n = 61)$$

This means, in examining the growth of the neptune whelk, there is no difference between the representations of growth based on shell increases even though either of shell height or shell diameter was adopted. Therefore, the following analysis of growth equation was conducted only in terms of shell height, which represents the increase in the longer axis.

ii) Growth equation

Like the earlier period, the size frequency distribution in shell height from September 1979 to April 1981 was separated into age groups, and the mean shell height at age in month shown in Fig. 27 was obtained. There

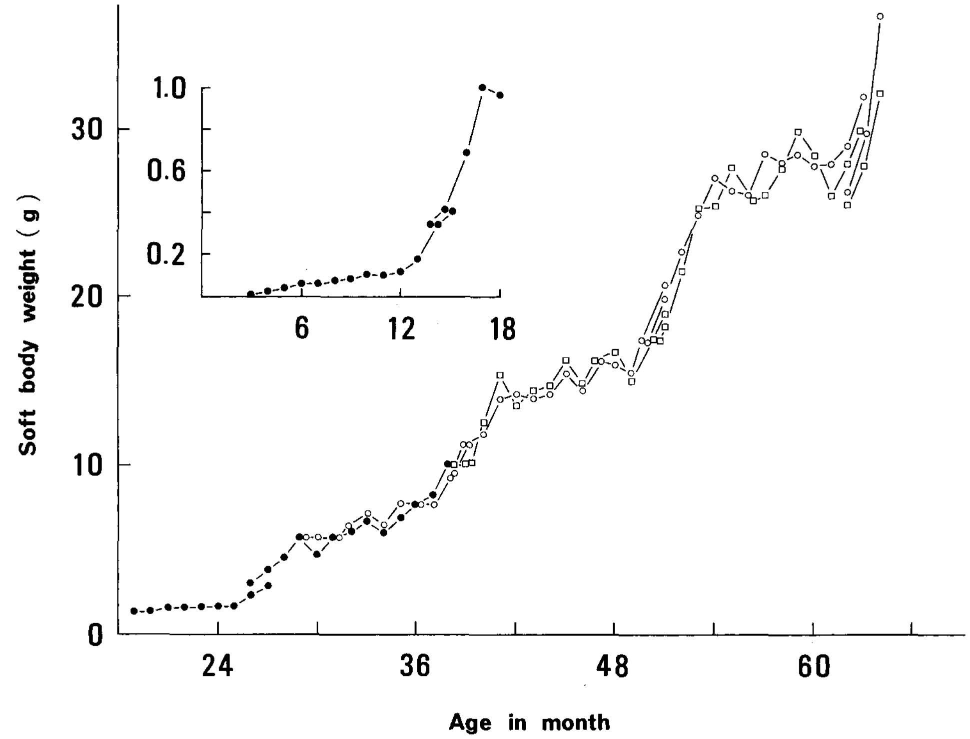


Fig. 24. Somatic growth of *Neptunea arthritica*. ● : immature, ○ : male, □ : female.

Table 8. Shell height (x)-soft body weight (y) regression equations for immature, male, and female *Neptunea arthritica*. Weight is measured in g wet weight, and shell height in mm. Soft body weight includes those of gonad and operculum. $X = \log x$, $Y = \log y$.

Month	Male	Female	Immature
'77, Oct.	$Y=3.589X-5.395$	$Y=2.974X-4.261$	$Y=3.493X-5.234$
Nov.	$Y=3.239X-4.753$	$Y=2.789X-3.891$	$Y=3.572X-5.318$
Dec.	$Y=3.476X-5.194$	$Y=3.399X-5.075$	$Y=3.223X-4.851$
'78, Jan.	$Y=3.468X-5.198$	$Y=3.541X-5.316$	$Y=3.419X-5.110$
Feb.	$Y=3.325X-4.936$	$Y=3.049X-4.415$	$Y=3.311X-4.933$
Mar	$Y=3.159X-4.606$	$Y=2.421X-3.228$	$Y=3.389X-5.027$
Apr.	$Y=3.358X-5.001$	$Y=3.151X-4.609$	$Y=3.187X-4.738$
May	$Y=3.062X-4.425$	$Y=3.277X-4.817$	$Y=3.427X-5.111$
June	$Y=3.054X-4.429$	$Y=2.910X-4.143$	$Y=3.679X-5.518$
July	$Y=3.257X-4.827$	$Y=3.055X-4.468$	$Y=3.766X-5.687$
Aug.	$Y=3.165X-4.646$	$Y=2.911X-4.172$	$Y=3.627X-5.428$
Sep.	$Y=3.087X-4.477$	$Y=3.206X-4.736$	$Y=3.896X-5.883$

were some variations in the growth of the neptune whelk from year to year, and the tendency was marked in the younger age classes. So, in the present study, the growth process was understood with the mean values at age in month during August 1977 to April 1981. The neptune whelk in Usu Cove followed the growth process marked with the solid circles in Fig. 27, and the growth was summarized as follows: at hatching: 9.0 mm, I-year old: 18.3 mm, II-years: 34.3 mm, III-years: 55.1 mm, IV-years: 69.8 mm, V-years: 82.3 mm.

With the aim of quantifying the growth process of the neptune whelk, the satisfactory correspondence to the three growth formulae of Robertson, Bertalanffy, and Gompertz was examined by using Walford's graph (1946) with the mean shell height for the respective age classes (0-age class: 9.0 mm, I-age class: 23.1 mm, II-age class: 41.5 mm, III-age class: 60.4 mm, IV-age class: 74.6 mm, V-age class: 85.6 mm) in September, when

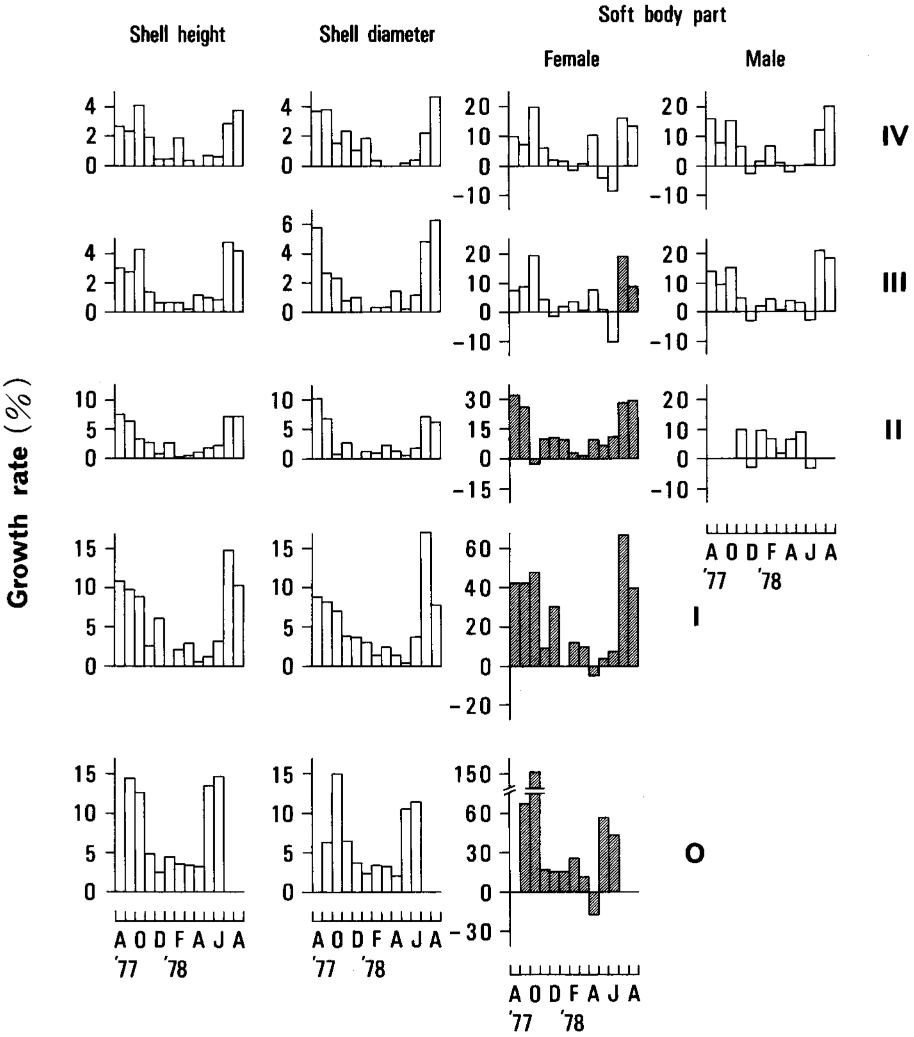


Fig. 25. Monthly growth rates in age classes of *Neptunea arthritica*. Striped bars in soft body of female represent the growth rates of the immature whelks. Roman numerals indicates ages.

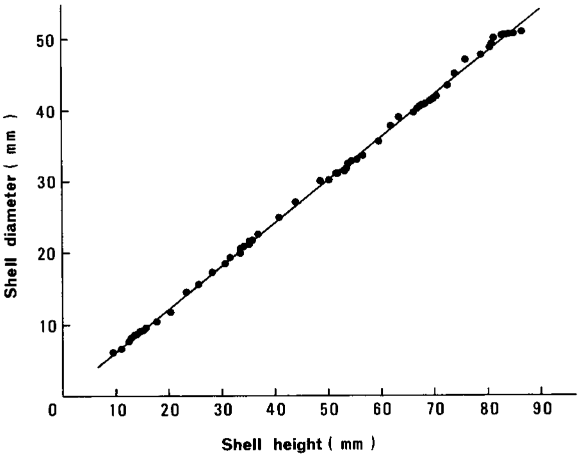


Fig. 26. The relationship between shell height and shell diameter. Dots represent means from the size frequency distributions, analysed using the probability paper. The regression line was determined by the least square method.

juveniles hatch from egg masses (Fig. 28). The growth process in the neptune whelk most fitted to the formula of Gompertz, judging from the correlation coefficient and the ultimate shell height. Furthermore, according to Lockwood (1974), the growth formula can be applied to depiction of a seasonal change in growth. Hence, the growth in each age class was formulated using the Gompertz growth formula. The relationship between age in month and shell height for each age class is shown in Table 9, and the growth formulae trace the processes marked with the solid lines in Fig. 27.

(3) Discussion

Differences in growth between male and female in marine gastropods are examined in many species. The differences between the sex are recognized in a common view (Comfort, 1957; Wilbur and Owen, 1964; Hyman, 1967) and in several species (Magalhaes, 1948;

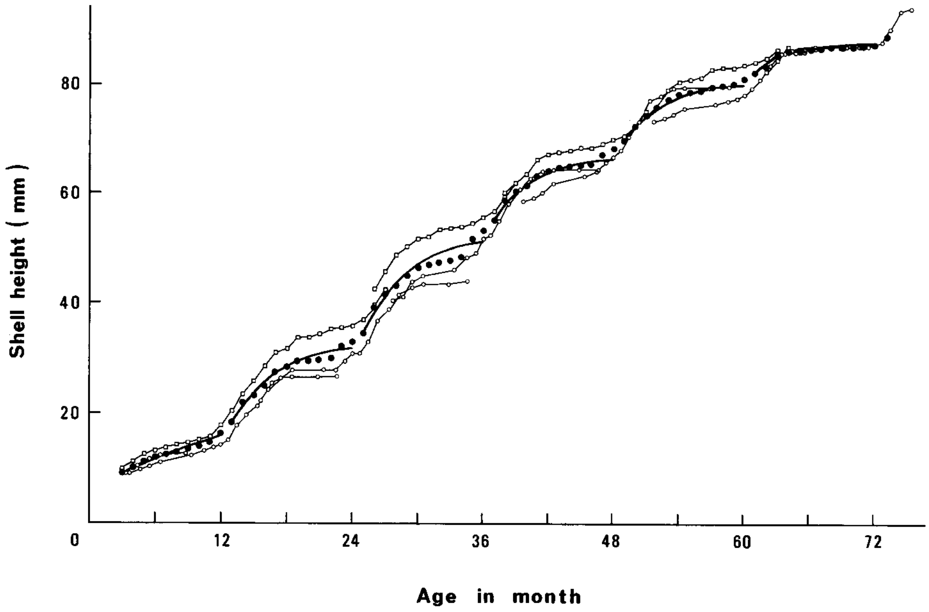


Fig. 27. Growth of *Neptunea arthritica* in shell height and growth curves (solid line) calculated by applying the Gompertz's growth equation. □—□ : period from August 1977 to September 1978, ○—○ : period from September 1979 to April 1981, ● : mean during the period from August 1977 to April 1981.

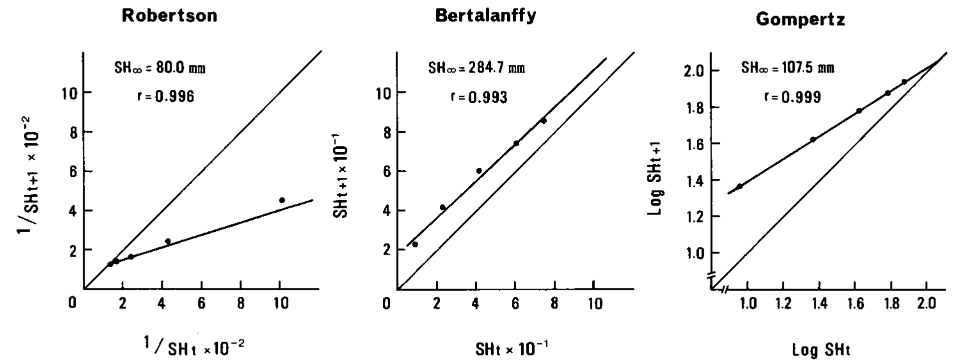


Fig. 28. Walford's graphs indicating satisfactory correspondence to the formulae of Robertson, Bertalanffy and Gompertz, using mean in shell height of each year class in September. Regression lines are determined by the least square method.

Table 9. 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), m is the age in year, and a and b are constants. The age of individuals in years increases in July. For only the 0 age group, t is the age in month from the time of hatching (September).

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

Pearce and Thorson, 1967 ; Edwards, 1968 ; Nagai, 1974 ; MacIntosh and 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 and Nagoshi, 1980), *Monodonta lineata* (Williamson and Kendall, 1981), and *M. labio* (Nakano and Nagoshi, 1984). In the present study, there were statistically no significant differences in growth on the basis of shell height and shell diameter between male and female as for the neptune whelk in Usu Cove (*t*-test, $p>0.001$).

Size at sexual maturity of the neptune whelk in Usu Cove was determined to be 50 mm shell height in male and 60 mm shell height in female, based on the histological observations of the seminal vesicle and the ovary, respectively. On the other hand, the growth in shell height was summarized as follows: at hatching: 9.0 mm, I-year old: 18.3 mm, II-years: 34.3 mm, III-years: 55.1 mm, IV-years: 69.8 mm, V-years: 82.3 mm. From these facts, the neptune whelk in Usu Cove is judged to recruit into the adult population at 2 years old in male and at 3 years in female.

Up to date, many sorts of growth formula for organisms have been proposed, but in marine gastropods the formula 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, the result that the growth of the neptune whelk in Usu Cove is most fitted to the Gompertz growth formula was obtained. The correlation coefficient r obtained by the least square method from Walford's graph (1946), 0.999 for the Gompertz formula and 0.993 for the Bertalanffy formula, indicated a high correspondence to both formulae, with a somewhat higher value in the former. The ultimate shell height SH_∞ was 284.7 mm with the formula of Bertalanffy, and with that of Gompertz it was 107.5 mm, which is very approximate to the observed values (Fig. 22). Furthermore, comparing the two growth formulae in terms of growth in length, the growth decreases with increasing age in the Bertalanffy formula, while in the Gompertz formula the growth is the greatest in the central portion of the curve. The growth of the neptune whelk in Usu Cove was on its peak between 2 and 3 years old, and became smaller before and after these ages. From these three facts, the application of the Gompertz formula in depicting the growth of the whelk in this bay is considered to be the best.

In the present study, the growth in the neptune whelk was examined with three criteria of shell height, shell diameter, and soft body. The growth in the three criteria showed the same tendency in the following respects: the growth rates were high from early summer to autumn, and low in winter and early spring when water temperature is low. But, the soft body exhibited a growth pattern different from shell height and shell diameter in the following points: the negative growth occurred, the negative growth rate was higher in female than in male, and the decrease in the growth rates of more than II-age class was not so large as those in shell height and shell diameter. These facts suggest that the growth is closely related to the gonad maturation. The relationship between growth and reproduction will be discussed in the chapter Biological production, because it seems more adequate to refer to the relationship on the basis of the allocation of assimilated energy.

3. *Food consumption*

(1) Investigated stations and methods

Field observation of food organisms of the neptune whelk was conducted by SCUBA diving monthly from May 1980 to April 1981 (excluding January and March in 1981). Neptune whelk was regarded as feeding if it was observed in close contact with its prey. During the observation, the kind of prey being consumed (including carrion) and number of whelks feeding were recorded. Since the observation was performed simultaneously with an investigation of the population structure mentioned later in the chapter III, the observation area was restricted to 100 stations (including the zone surrounding the area where density was measured) estab-

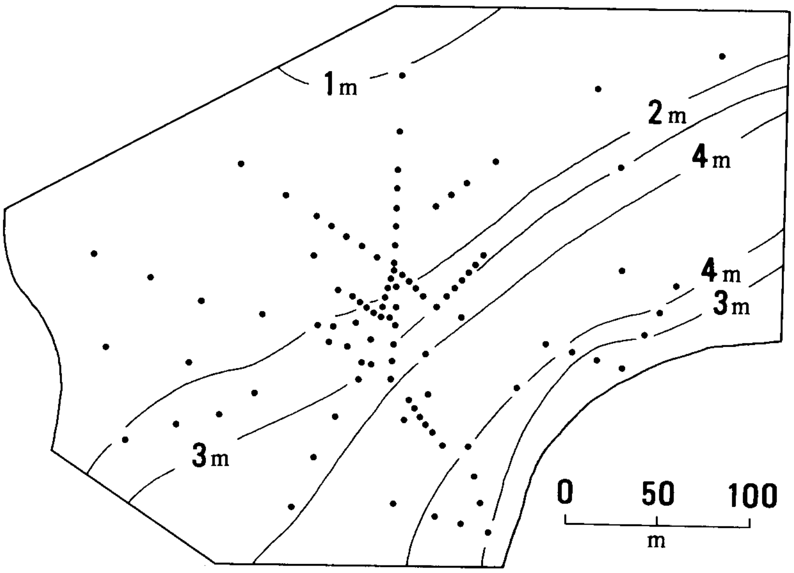


Fig. 29. The stations (solid circles) for observations of food organisms of *Neptunea arthritica*.

lished within the area enclosed by the solid lines in Fig. 21 (Fig. 29).

Laboratory experiments on food consumption rate were carried out using *Mytilus* spp. as food bimonthly from May 1985 through March 1986. The experiment continued for about 30 hours under running water, and was performed twice during four to five days, except in May 1985. Once a neptune whelk ate prey sufficiently, it did not feed nearly at all during the experiment. So, in the present study, food intake during the ca. 30-hour experiment was regarded as the intake in a bout of feeding. Neptune whelks and *Mytilus* spp. were collected from Usu Cove. Water temperatures in the experiments ranged from 2.1°C to 18.0°C. Only natural lighting through windows was used, except during observations of the presence of the prey in the nighttime, when artificial lighting was used. 15 to 33 neptune whelks (37 mm to 93 mm in shell height) that were acclimated and unfed for about 24 hours under running seawater after collection were used for the initial experiment. The specimens were individually placed in 250–650 ml stylo-bottles that had holes drilled at the top and bottom to flow seawater through them. The next experiment started with the passing above 15 hours from the end of the initial one. The food consumption rate was calculated each experiment using the following equation:

$$\text{Food consumption rate } (\%) = (D/E) \times 100$$

where, D is mussel wet weight (g) consumed, and E is soft body wet weight (g) of a neptune whelk. The mussel weight consumed was calculated from the difference between the initial weight before feeding and the final weight after feeding. Mussels were cut into two pieces and offered one at a time. When each mussel piece was completely consumed, it was immediately replaced with a new piece through frequent observation of feeding.

(2) Results

1) Food organisms

Neptune whelks in Usu Cove fed on various animals (including carrion), such as *Mytilus* spp. (live, L), *Patinopecten yessoensis* (L), *Tectonatica* sp. (L), fish (dead, D), *Hemigrapsus* spp. (D), *Pandalus gracilis* (D), and *Strongylocentrotus nudus* (D). Most (75.6%) of the 528 whelks fed on live *Mytilus* spp., followed by dead fish (10.0%) and dead *Hemigrapsus* spp. (8.3%) (Fig. 30). The proportion of neptune whelks feeding on carrion, such as dead fish and dead *Hemigrapsus* spp., was 20.1%, and most whelks consumed live bivalves. In only one case, four whelks seeking or attacking the same prey inserted their proboscises into the muddy sand, so the kind of the prey being eaten was not identified.

Neptune whelks were observed feeding most frequently from July to October, while a few were observed in the winter and early spring (Fig. 30).

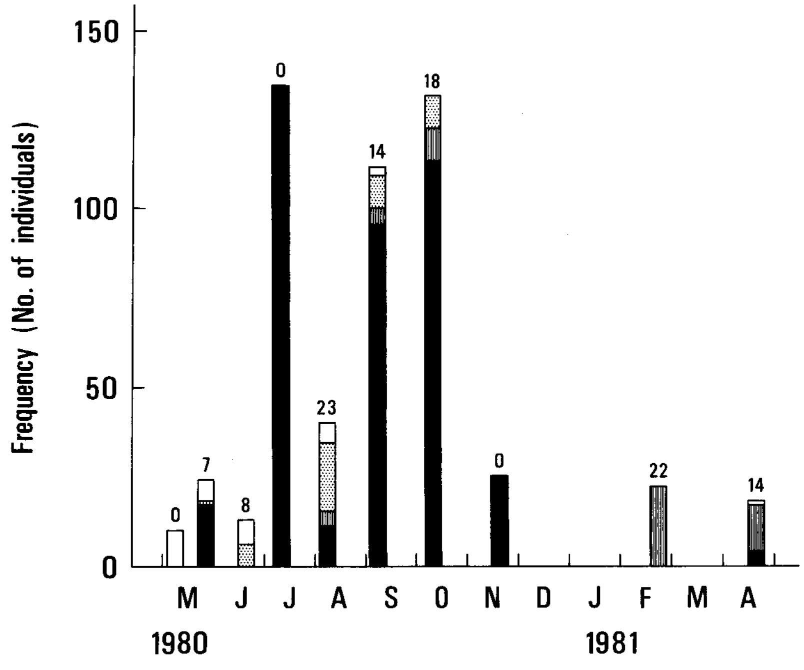


Fig. 30. Food organisms of *Neptunea arthritica*. Numbers above the poles represent the number of individuals observed feeding on carrion. ■ : Live *Mytilus* spp., ▥ : Dead fish, ▒ : Dead *Hemigrapsus* spp., ☐ : Others.

2) ***Food consumption rate***

The frequency of feeding during two experiments differed somewhat individually. Most neptune whelks (63.6% to 95.7%) fed only once (the first feeding) during the experiments, and 26.1% to 48.0% fed twice (the first and second feedings) (Table 10).

The food consumption rate in the neptune whelk was related to body size, and the consumption rate per bout of feeding decreased nearly exponentially with increasing shell height, except in January 1986 (Fig. 31). This indicates that food consumption was greatly correlated with body weight of whelks. There was no significant difference between the slope of the regression of food consumption rate on shell height at the first feeding and the slope of the regression of food consumption rate on shell height at the second feeding in any month (Analysis of covariance, $p>0.01$). But, there was a significant difference in the heights (Analysis of covariance, $p<0.01$), and in whelks which fed twice during the experiments, the food consumption rate at the second feeding was significantly lower than at the first feeding. Also, there were significant differences in both the slopes and heights of the regressions of food consumption rate on shell height at the first feeding in all months (Analysis of covariance, $p<0.01$). These results suggest that water temperature and other factors, in addition to body weight, were closely related to food consumption.

(3) Discussion

Three sources of information can be used to describe food organisms of *Neptunea* : investigation of digestive-tract contents (Blegvad, 1914 ; Taylor, 1978 ; Shimek, 1984), laboratory and field observations (Petersen, 1911 ; Graham, 1953, 1955 ; Fange, 1958), and bait used in the fishery (Petersen, 1911 ; Cole, 1956 ; Nagai, 1975). Investigations of digestive-tract contents are likely to be the most reliable in studies of food organisms. But, Blegvad (1914), Taylor (1978), and Shimek (1984) showed that most organic matter in the tracts is difficult

Table 10. Frequency of feeding during two experiments. Values in parentheses indicate the percentages of individuals.

Month	No. of individuals tested	Frequency of feeding	
		Once	Twice
1985, May	15	12 (80.0)	–
July	20	17 (85.0)	9 (45.0)
Sep.	23	22 (95.7)	6 (26.1)
Nov.	25	22 (88.0)	12 (48.0)
1986, Jan.	31	27 (87.1)	9 (29.0)
Mar.	33	21 (63.6)	9 (27.3)

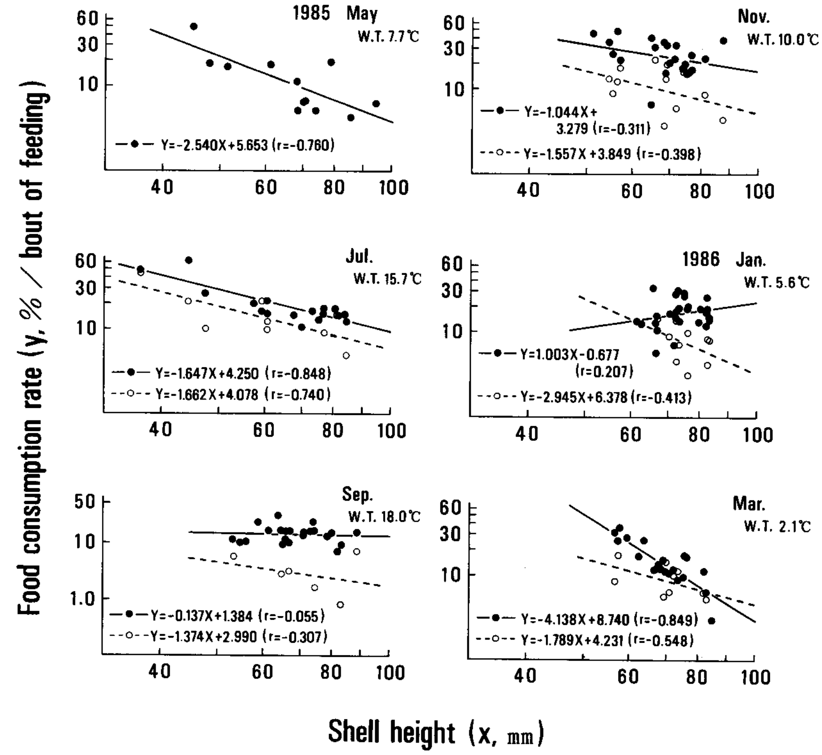


Fig. 31. Food consumption rates (percent per bout of feeding) in *Neptunea arthritica* of different sizes. Solid and open circles show the food consumption rates at the first and second feeding, respectively. $X=\log x$, $Y=\log y$.

to identify. In the present study, food organisms of the neptune whelk was examined during observations while SCUBA diving in the field. It was easy to identify epifaunal and carrion prey by using this method, however, it was difficult to identify infaunal prey. *Neptunea* snails feed on infaunal prey such as polychaetes (Blegvad, 1914; Pearce and Thorson, 1967; Taylor, 1978; Shimek, 1984). The possibility that the prey of four whelks which could not be identified was polychaetes is thought, because of the insertion of their proboscis into the muddy sand. To confirm food organisms of the neptune whelk in more detail, an investigation of digestive-tract contents in addition to observation in the field is needed.

Generally, *Neptunea* is thought to be a scavenger (Nagai, 1981). But, according to my observations, only 20.1% of whelks were observed eating carrion, while most fed chiefly on live bivalves, such as *Mytilus* spp. and *P. yessoensis*. *N. pribiloffensis* and *N. lyrata*, which were once thought to be scavengers, feed on living animals, such as bivalves and polychaetes (Shimek, 1984). Like *Neptunea* in Alaska (Shimek, 1984), the neptune whelk may feed more often as a predator than as a scavenger.

In neptune whelks which ate the prey each experiment, the food consumption rate at the second feeding was significantly lower than the rate at the first feeding. Furthermore, most whelks fed only once during four to five days. These results indicate that the problem of feeding interval will arise when estimating food consumption based on the regression of food consumption rate on shell height. Also, there was a significant difference in the heights of the regressions of food consumption rate on shell height at the first feeding in all months. This signifies that the food consumption rates changed seasonally. To infer the feeding interval in future studies, it will be necessary to confirm the proportions of whelks in the process of feeding at intervals in the field.

The food consumption rate of the neptune whelk was greatly governed by body weight of whelks, like *Hemifusus tuba* (Morton, 1986) and *Babylonia lutosa* (Morton, 1990). Furthermore, on the basis of comparisons of the slopes and heights in the regressions of food consumption rate on shell height by analysis of covariance, it was suggested that water temperature and other factors besides body weight affected the food consumption of the neptune whelk. Reproduction and growth are connected with food consumption. Consumption rates are great in a time of high reproductive activity (Ansell, 1982), and growth is dependent on food availability (Butler, 1954; Spight and Emlen, 1976). For the neptune whelk in Usu Cove, gonad develops conspicuously during September to November, and the whelk grows most rapidly from July through October. In the present study, neptune whelks were observed feeding most often between July and October. These facts intimate the implication of reproduction and growth in food consumption, and the relation between them needs to be clarified by studying seasonal change in feeding activity in the field in detail.

4. *General discussion in the chapter II*

The developmental stage of the neptune whelk that is divided into 3, i.e. the embryo, immature individual, and mature individual, could be subdivided into characteristic life periods, based on reproduction, growth, and food consumption (food consumption is founded on this chapter and seasonal change in assimilated energy in chapter IV). The life cycle of the neptune whelk which is comprehended as the succession of the developmental stages subdivided into some life periods is summarized as follows (Fig. 32).

Embryonic stage

Six months from May, when embryos are produced, to October, when hatching of juveniles completes, represent the embryonic stage. The embryonic stage is subdivided into three periods; birth period, embryogenesis period, and hatching period.

Birth period: May and June This period is the time when egg masses are deposited on hard substrata, such as rocks, boulders, and oyster shells.

Embryogenesis period: July and August This period is the time when embryos grow up to juvenile stage by way of egg-swallowing stage, protoconch-forming stage, and shell-developing stage.

Hatching period: September and October This period is the time when juveniles measuring 6 mm to 11 mm in shell height and 4 mm to 7 mm in shell diameter which completed the embryonic development hatch.

Immature stage

1- and 2-year old individuals which are under 50 mm shell height in male and 60 mm shell height in female represent the immature stage. The annual cycle of life in the immature understood on the basis of growth and food consumption displays a periodic change corresponding to the change in the water temperature. One year in the immature individuals is divided into 2 life periods in terms of growth rate; rapid growing period and slow growing period.

Rapid growing period: June to October Food consumption is much, and both shell and soft body grow rapidly.

Slow growing period: November to May Food

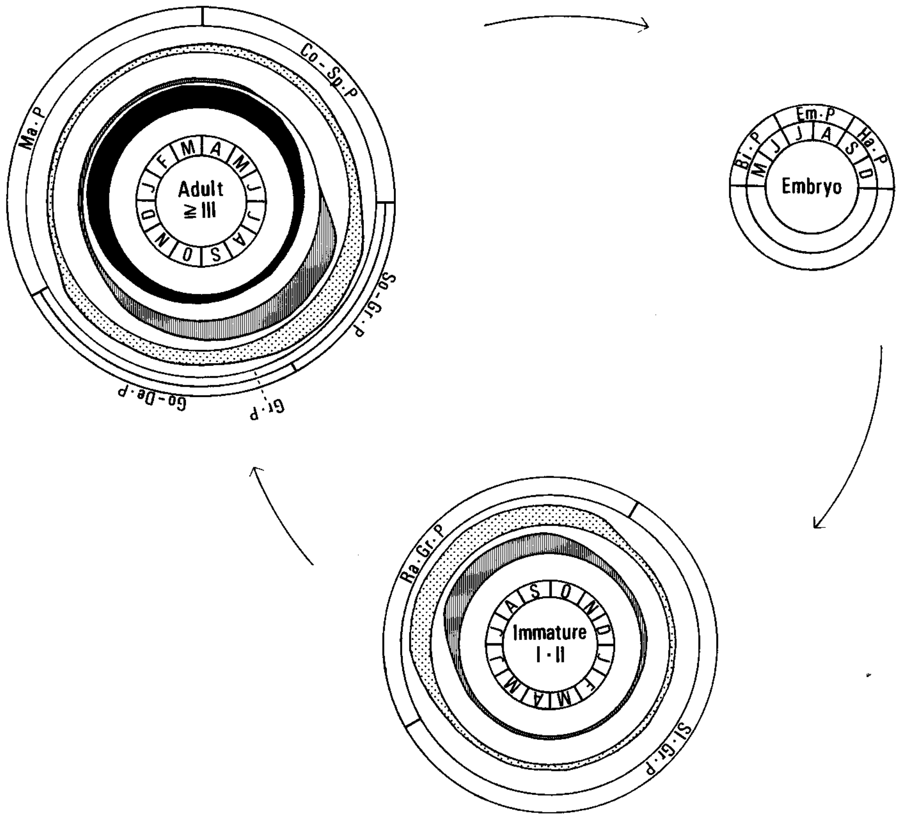


Fig. 32. Life cycle of *Neptunea arthritica*. Roman numerals indicate ages. ■ : Maturation, ▥ : Growth, ▒ : Feeding. Bi•P: Birth period, Co-Sp•P: Copulating and spawning period, Em•P: Embryogenesis period, Go-De•P: Gonad developing period, Gr•P: Growing period, Ha•P: Hatching period, Ma•P: Mature period, Ra•Gr•P: Rapid growing period, So-Gr•P: Soma growing period, Sl•Gr•P: Slow growing period.

consumption decreases, and growth rates in shell and soft body is low.

Mature stage

Individuals more than 3 years old, which are greater than 50 mm shell height in male and 60 mm shell height in female, represent the mature stage. The life of the mature individuals comprehended from reproduction, growth, and food consumption exhibits a periodic change with a cycle in a year. One year in the mature individuals is divided into 3 life periods mainly based on reproduction.

Growing period: July to November Growing period was subdivided into soma growing period and gonad developing period.

Soma growing period: July and August The seasonal maturation in the reproductive cycle is recovering period or developing period in male, and recovering period or pre-developing period in female. The growth of shell and soft body is the most active, and the most food is consumed.

Gonad developing period: September to November The seasonal maturation is developing period or mature period in male, and post-developing period in female. The gonad weight increases strikingly. Growth rates of shell and soft body somewhat decrease, but still maintain high levels. Food consumption diminishes as compared with soma growing period.

Mature period: December to March The seasonal maturation is mature period in both male and female. Shell growth stops nearly. The least food is consumed.

Copulating and spawning period: April to June This period is the time when copulation and spawning take place. Shell growth nearly stops, and the decrease in soft body weight occurs. Food consumtion to some degree increases as compared to mature period.

III. Population dynamics

A study on population dynamics is an item essential for elucidation of life history and model construction for resource management of the neptune whelk. In the present study, distribution and migration pattern being important as the bases of the population dynamics were first clarified, and next, population structure and mortality were examined. All these phenomena were combined with as population dynamics. Also, the distribution, migration pattern, and population dynamics, which are the main subjects of the population ecology, can be closely related to the life cycle of the individual. So, the relationship between those phenomena and the life cycle was examined.

1. Distribution and migration pattern

(1) Investigated area and methods

Investigations of distribution and migration were performed in the area, from 1 m to 4 m in depth, centering on the place with the rafts and concrete blocks (Fig. 33). The investigations were carried out monthly, except during winter, from September 1979 to April 1981. Sixty eight sampling stations were established within the investigated area, taking spawning sites, abundance of egg masses among the sites, and adult whelk density into consideration (Fig. 33). However, the number of the stations in September and October in 1979, when only juveniles after hatching were aimed at, were 32 and 43, respectively. For conducting determination in the same position every time, sampling stations were arranged at 5 m, 10 m, or 20 m intervals by connecting a raft and an iron pole, or two iron poles by a nylon-cord measure. Determination of the density of whelks at each station was done by placing two quadrats (1 × 1 m) in adjacent positions on the substratum. The shell height of all whelks within the quadrats was measured to the nearest 0.05 mm with a vernier caliper while SCUBA diving. In case of many whelks (over about 15 whelks) within the quadrat, they were measured on the boat with subsequent return to the quadrat.

The age of neptune whelks was determined based on the growth formulae (Table 9).

(2) Results

1) Egg mass deposition and feeding activity

In the present study, migration in the neptune whelk was examined in terms of relations to spawning and feeding activities. The seasonal change in the number of egg masses and food organisms were mentioned in life cycle in the chapter II (Figs. 11 and 30). Therefore, in this chapter, feeding activity is referred to, together with the summarization about the appearance of egg mass deposition limited only to the investigated area.

There were 11 spawning sites in the investigated area (Fig. 34). The egg mass deposition from May through August is shown in Table 11. In mid-May egg masses were not yet observed, but from late May to early June many egg masses were deposited. The time was just after the commencement of spawning, and almost all egg masses confirmed were in the midst of being deposited. Late in June the number of females depositing an egg mass was the most, exhibiting the high spawning activity. In mid-July the number of spawning females decreased sharply, and such females were not observed at all in mid-August.

The neptune whelk feeds on various animals, such as live *Mytilus* spp., dead fish, and dead *Hemigrapsus* spp. Out of 497 whelks observed 81.5% was feeding with *Mytilus* spp. in the investigated area. Its distribution in the area was restricted on rocks and boulders being the spawning substrata, and under the rafts and their circumferences. Most of them stayed on the muddy sand bottom under the rafts in masses of the mussels.

Number of whelks feeding in the investigated area are shown in Fig. 35. The duration of investigation was divided into the following three periods : the period

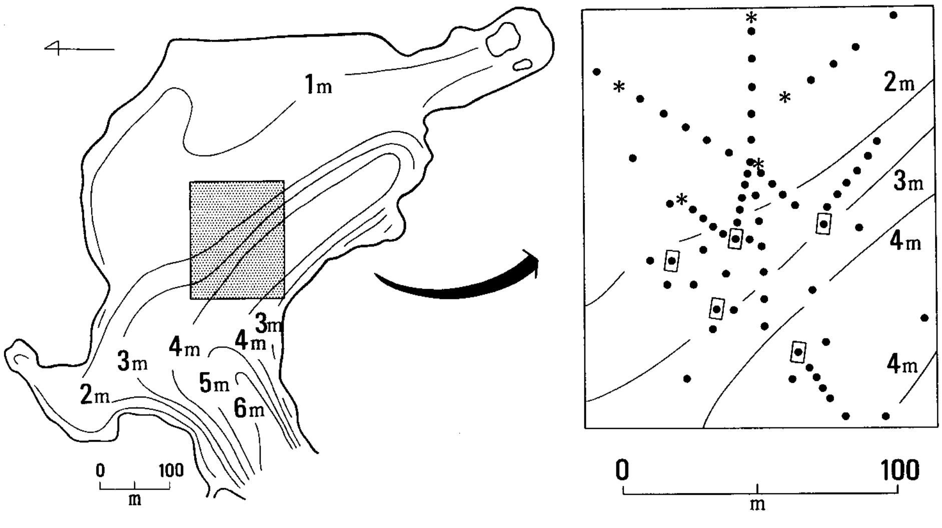


Fig. 33. Map of Usu Cove showing situations of sampling stations (black spots), oyster culture rafts (quadrangles), iron poles (asterisk), and approximate depth contours.

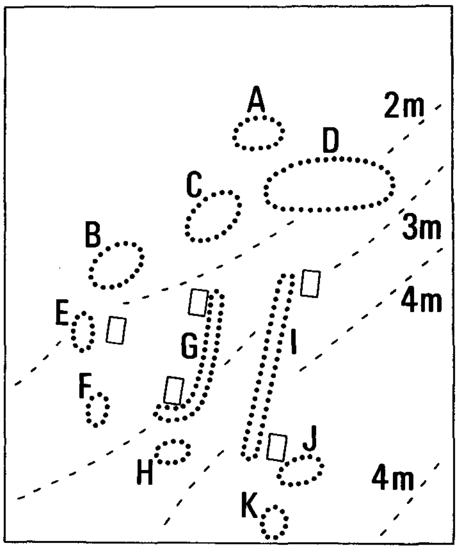


Fig. 34. Egg mass deposition sites in the investigated area.

during July to October, when the growth is active, and the periods before and after July-October. From July to October, 1980, many whelks were observed feeding in and around the rafts enclosed by the solid lines. 95.3 feeding whelks per investigation period on average were confirmed in this period, and 91.3% of them were feeding in and around the rafts. On the other hand, the number of feeding whelks in the other periods drastically decreased to about 10 per investigation period on average, and the proportion of whelks feeding in the areas was approximately 50%.

2) *Migration*

The habitat of the neptune whelk was divided into the following three areas to understand habitat changes with spawning and feeding activities for convenience: spawning site and its circumference (area A: 21 stations), the area in and around the raft with high feeding activity (area B: 12 stations), and the other area (area C: 35 stations) (Fig. 36). The seasonal changes in densities of year classes in the respective areas are shown among age groups in Fig. 37, and are as follows.

0 age-group The density of 0 age-group in area A and area C showed the highest values from October through December, late and just after the hatching period. Thereafter, the density in the areas gradually decreased and 0 age-class was not found nearly after June in 1980 and February in 1981. Conversely, the density in area B slowly increased after October.

I and II age-groups The densities of I and II age-groups in area A and area C were low throughout the year. But, the densities of II age-group in the areas somewhat increased in the spring at the end of 2 years old. On the other hand, the density in area B considerably diminished from winter to spring (in particular, I age-group), but sustained high values as compared with the other areas.

III and ≧IV age-groups The densities of III and ≧IV age-groups in area A and area C showed the minimum in August. But, then they augmented, exhibiting the maximum in May and June. On the other hand, the density in area B showed the seasonal change opposite to the density change in the other two areas, except in July

Table 11. Total number of egg masses at each spawning site as shown in Fig. 31. The numbers in parentheses indicate those of egg masses in the process of deposition.

Spawning site	Date				
	10-12 May	30 May-4 June	21-25 June	13-16 July	10-13 Aug.
c	0	20 (20)	49 (15)	55	59
d	0	9 (7)	17 (4)	31	20
e	0	123 (112)	332 (92)	351 (7)	263
f	0	10 (8)	16 (2)	26 (3)	23
i	0	0	3 (1)	4	4
j	0	11 (10)	35 (21)	48 (2)	51
k	0	8 (8)	35 (22)	109 (11)	88
l	0	8 (8)	27 (17)	42 (2)	25
m	0	9 (8)	50 (34)	51 (2)	46
n	0	20 (18)	102 (65)	123 (4)	105
o	0	7 (7)	42 (23)	41	28
Total	0	225 (206)	708 (296)	881 (31)	712

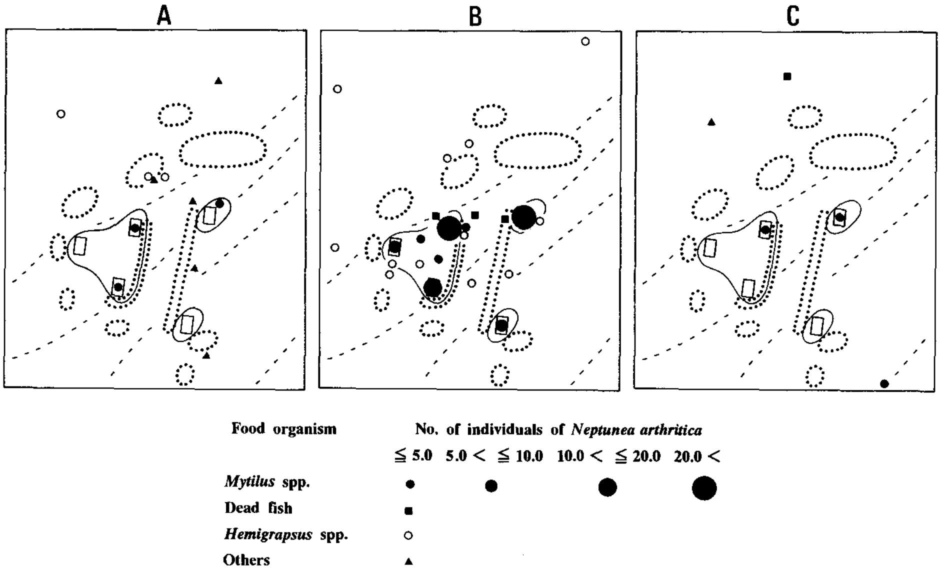


Fig. 35. The feeding sites and numbers of feeding individuals. Sizes of symbols represent number of *Neptunea arthritica* per investigated period between November 1979 and June 1980 (A), July and October 1980 (B), and November 1980 and April 1981 (C). ⁘ : same as in Fig. 31.

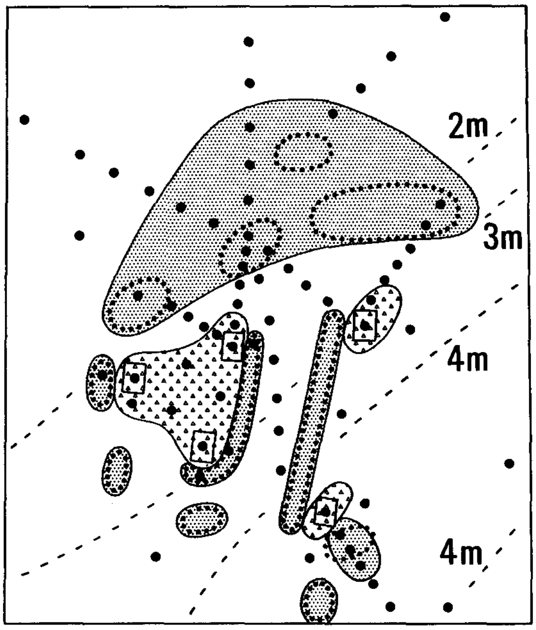


Fig. 36. Areas of three habitat types. ▨ : egg mass deposition site and its neighborhood (Type A), ◌ : raft and its circumference where feeding activity is high (Type B), ○ : area which excludes the above two areas (Type C). ⁘ : sites with hard substrata such as rocks, boulders and mollusc shells, ☐ : oyster culture raft, ● : point where density was determined.

and August when the densities in three areas decreased simultaneously, as the density in area B diminished in the time when the densities in the other two areas increased. Also, the density in area B decreased with age, and conversely the densities in areas A and C increased. In ≧IV age-group whose proportion of whelks participating in spawning increases, whelks were almost evenly distributed over the three areas between April and June.

3) Distribution and migration pattern

The neptune whelk attains its sexual maturity at 2 years old in male and at 3 years old in female. This fact indicates that the migration of the neptune whelk could be understood in terms of the growth stages of hatchling (0 year old), immature whelk (1 and 2 years old), and adult (older than 3 years old). So, when the migration pattern of the neptune whelk is comprehended by associating the relation between spawning and feeding sites and migration with the life cycle, the patterns are summarized as follows.

Hatchling (0 year old) Hatchlings began to migrate from the egg mass deposition site immediately after hatching, and changed the habitat to the area having raft with high feeding activity over several months.

Immature whelk (1 and 2 years old) Immature whelks were distributed centering around the area having raft with high feeding activity throughout the year.

Adult (older than 3 years old) In adult whelks, the change in habitats, such as spawning site and the area with raft, took place in an annual cycle. In August representative of soma growing period, adult whelks were distributed centering around the area having raft with high feeding activity. They began to gradually migrate in gonad developing period, and were dispersed over the whole habitat in April, the beginning of copulating period. In May and June corresponding to

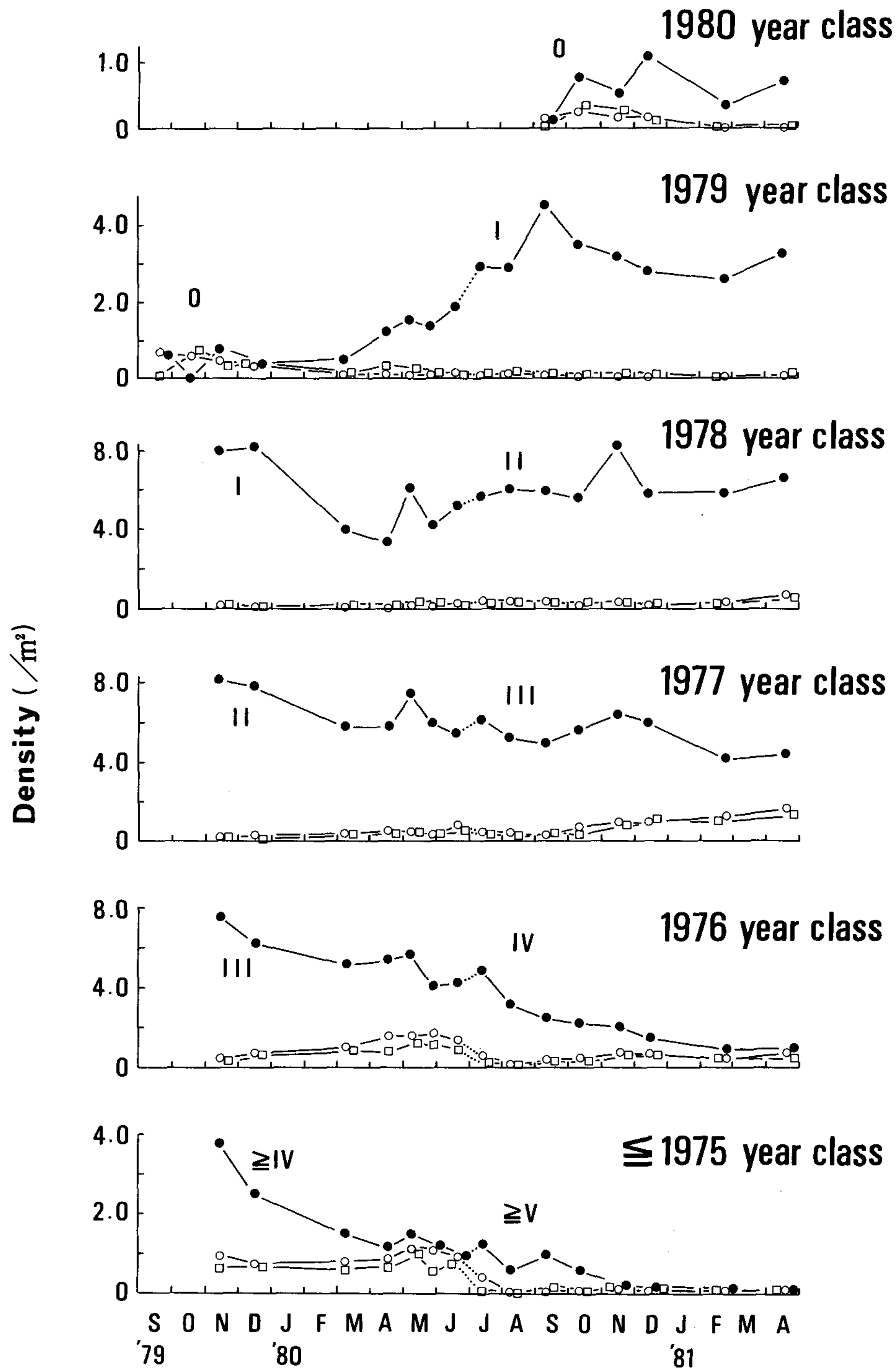


Fig. 37. Seasonal changes of density in three habitat types. White spots show Type A, black, Type B and quadrangles, Type C, respectively. Roman numerals denote age in year classes.

copulating period and spawning period, many adult whelks aggregated in spawning sites. In late June and July just after spawning, adults rapidly migrated to the area having raft with high feeding activity, and during soma growing period their distribution was restricted to the raft and its circumference again.

(3) Discussion

Many papers state that gastropods living in the sublittoral zone migrate from the deeper water to the shallower water with spawning (Chari, 1950; Ino, 1952; Amio, 1955; Carriker, 1955; Cole, 1956; Hancock, 1959; Robertson, 1959; Wolfson, 1968; Weil and Laughlin, 1984; Martel et al., 1986). But, Carriker

(1955), Hancock (1959), and Randall (1964) observed many egg capsules or egg masses in the deeper water as well as in the shallower water. These facts suggest that the direction of the migration with spawning does not necessarily look toward the shallower water. In the case of the investigated area from 1 m to 4 m in depth in the present study, a considerable number of egg masses were deposited not only in the shallower area but also in the deeper water. Almost all egg masses were deposited on hard substrata, such as rocks (including concrete blocks), boulders, and oyster shells, and these substrata scarcely existed in the investigated area, except in spawning places. Therefore, the migration with spawning in the neptune whelk is thought to be greatly dependent on existence of the substratum rather than depth.

Seaweeds, such as *Chondrus ocellatus*, *Ulva pertusa*, and *Laminaria* spp., were usually abundant on hard substrata, such as rocks and boulders, where egg masses of the neptune whelk were deposited. Egg masses were found on the upper part of the substrata, assuming covered by those seaweeds. Between egg deposition and hatching, embryos within egg capsules and egg masses in marine gastropods die due to predation (MacKenzie, 1961; Emlen, 1966; Phillips, 1969; Spight, 1975; Abe, 1983), being detached from substratum (Barnett et al., 1980; Shimek, 1981; Martel et al., 1986), being covered by mud (Gallardo, 1979; Barnett et al., 1980; Hughes and Roberts, 1981), or by physical factors, such as desiccation, high temperature, and low salinity (Carriker, 1955; Feare, 1970a, Spight, 1977; Pechenik, 1978; Hawkins and Hutchinson, 1988). Egg masses of the neptune whelk were detached from the substrata during the period, and proportions of detachment differed between the substratum type. Egg masses deposited on elastic substrata, such as ropes and holdfasts of *Laminaria* spp., were more susceptible to exfoliation than those on solid substrata, such as rocks and boulders. Also, predation rates on embryos at spawning sites with large substrata such as rocks were significantly lower than those at spawning sites with only small substrata, such as boulders and oyster shells (Analysis of variance, $p < 0.01$). From these facts, the reason why neptune whelks migrate to places with hard substrata, such as rocks and boulders, and deposit egg masses on the upper part of the substrata is likely to protect their spawn from detachment, predation, and being covered by mud.

In the present study, the migration in the neptune whelk was understood in terms of growth stages of hatchling (0 year old), immature whelk (1 and 2 years old), and adult (older than 3 years old). Juveniles which hatched through direct development changed their habitat from egg mass deposition site to the area with the raft and its circumference over several months. Immature whelks hardly showed a habitat change and were distributed centering around the area with the raft throughout the year. During July to October representing soma growing period and gonad developing period when adult whelks grow rapidly, they were also distributed centering around the area with the raft. Food organisms, such as *Mytilus* spp., were abundant in and around the area with the raft as compared with the other areas. Between July and October, neptune whelks exhibited the high feeding activity there. Therefore, the residence of immature whelks in the area with the raft all the year round, and the migration from egg mass deposition site to the area with the raft in hatchlings and adult whelks are thought to be closely related to food.

The migration of adults with season which is attributed to reproduction and food occurs in *Nucella lapillus* (Feare, 1970a) and *N. lamellosa* (Emlen, 1966; Spight, 1982) in the intertidal and upper sublittoral zones. Except for the migration for wintering (Lambert and Farley, 1968; Robertson and Mann, 1982; Nakano and Nagoshi, 1984), the migration pattern in adult neptune whelks seems to be fairly similar to that of many gastropods in the intertidal and upper sublittoral zones.

The habitat change in the neptune whelk in Usu Cove was examined in terms of migration related to reproductive and feeding activities. But, the following density changes unable to explain by only migration within the investigated area were recognized: increase of density during June to September, after hatchlings completed the migration, in I-age group in the area with abundant food, decrease of density occurred during winter to spring in immature whelks (I to II-age group) in the area with abundant food, and decrease of density simultaneously took place from July to August in the three areas in adult whelks. As the causes, possibilities of immigration of individuals to the investigated area, emigration from the area, or death are suggested. The density change in the adult could be attributed to mortality of whelks, judging from population structure and mortality mentioned next. However, the density change in immature whelks was not due to migration, but possibly due to lack and inadequate arrangement of sampling stations, because population dynamics over a considerable range of area without immigration and emigration was investigated.

2. *Population structure and mortality*

(1) Investigated area and methods

Investigations on population structure and mortality were carried out monthly in the area shown in Fig. 29, except during winter, from May 1980 to April 1981. One hundred sampling stations were established within the investigated area, taking the distribution and migration patterns of the neptune whelk into account. The investigated area was extended to sites where densities reached 0 or fairly low, to neglect the changes in density due to immigration and emigration of individuals into and out of the study area. Determination of the density of whelks in each station was done by placing two quadrats (1×1 m) in adjacent positions on the substratum. The shell height of all individuals within the quadrats was measured to the nearest 0.05 mm using a vernier caliper while SCUBA diving, except for measurements on a boat with subsequent return to the quadrat in case of many individuals (over about 15 whelks) within the quadrat.

The age of neptune whelks was determined based on the growth formulae (Table 9).

Mortality rates were estimated from changes in the mean density in all sampling stations. A decrease in density over a certain period (several months) without a subsequent large increase and decrease of density was regarded as the change due to death. So, the mortality rate (%) was calculated from the difference between the density in a given month and the density in a subsequent month for a year class.

The age structure of population was estimated based on the mean density in all sampling stations. The occupancy rate (%) of each year class in the population was calculated as the proportion of density of each year class to that of the total population in the investigated area.

(2) Results

1) Seasonal changes in density, and mortality rates

Although densities of neptune whelks in the investigated area showed very large variation, there was a distinct seasonal change in the mean density for each year class (Fig. 38). The seasonal changes of the mean density in Fig. 38 are described for each age group below.

0-age group The density in the 1980 year class increased with hatching of juveniles, reaching the maximum in early October. Then, it decreased gradually until April 1981. The densities in the 1979 year class between May and June, 1980, maintained a constant level, and there was no significant difference in densities between early May and late June (Mann-Whitney U-test, $Z=-1.475$, $p>0.05$). Based on the densities of whelks in October 1980 (0.285 ind.•m^{-2}) and April 1981 (0.110 ind.•m^{-2}), the mortality rate of the 0-age group during this period was estimated to be about 60% (95% confidence limit, 51%–71%).

I-•II-age groups The density in the 1979 year class determined from July 1980 to April 1981 maintained a fairly constant level of about 0.50 ind.•m^{-2}. Although the 1978 year class showed an increase and decrease in density during the investigation period, there was no significant difference in densities between the commencement (May 1980) and the termination (April 1981) of the study period (Mann-Whitney U-test, $Z=-2.852$, $p>0.001$). In the 1977 year class, the density somewhat decreased from May to June in 1980, but a few months

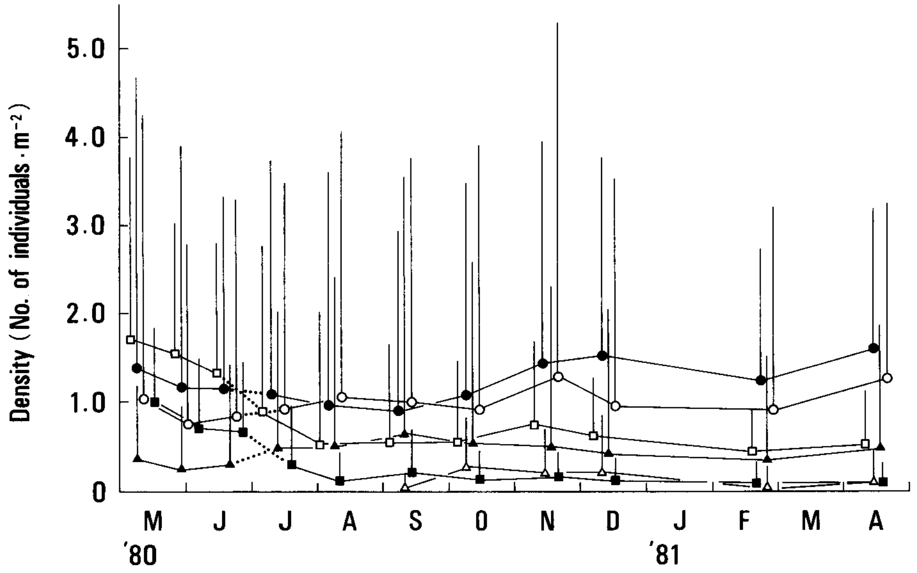


Fig. 38. Seasonal changes in the mean (+S.D.) of density of each year class in the investigated area. Only the positive standard deviation is indicated because of very large variation. Symbols indicate the following year classes (age). △ : 1980(0), ▲ : 1979(0-I), ○ : 1978 (I-II), ● : 1977 (II-III), □ : 1976(III-IV), ■ : ≦1975(≧IV-≧V).

later it increased. From these results, the mortality rates in the I- and II-age groups are thought to be very low.

III-• ≧IV-age groups The seasonal changes in densities of both the III- and ≧IV-age groups showed a similar pattern of fluctuation. The densities decreased drastically from the end (May 1980) of Age III (the 1976 year class) through the beginning (August 1980) of Age IV, and from the end of Age ≧IV (the ≦1975 year class) to the beginning of Age ≧V. During the other period of the investigation, they maintained a considerably stable level, except for the increase and decrease from July 1980 to April 1981 in the 1977 year class, representative of the III-age group. The rate of reduction in the ≧IV- to ≧V-age group was greater than that in the III- to IV-age group. Based on the densities of whelks in the 1976 and ≦1975 year classes, measured in May (the 1976 year class, 1.710 ind.•m^{-2}; the ≦1975 year class, 1.006 ind.•m^{-2}) and August (the 1976 year class, 0.525 ind.•m^{-2}; the ≦1975 year class, 0.120 ind.•m^{-2}), 1980, the mortality rates during these periods were 69.3% (95% confidence limit, 59%-78%) and 88.1% (95% confidence limit, 80%-94%), respectively. Furthermore, combining the 1976 and ≦1975 year classes together, the mortality rate of whelks older than Age III during May to August in 1980 was 76.3% (95% confidence limit, 67%-84%).

2) *Population structure*

The occupancy rates in the neptune whelk population in Usu Cove showed considerable differences among age groups, but the proportions of the respective age groups maintained fairly constant levels seasonally in spite of the recruitment of the 0-age group into the population after September (Fig. 39). As a result, during the period from May 1980 to April 1981 there were little fluctuations in the orders of occupancy rates of age groups in the population. In the investigation period, the III-age group which was the dominant possessed the occupancies of 30% to 40%, followed by the II-age group with the frequencies of 25% to 30%. The next were the I- and IV-age groups. The 0- and ≧V-age groups were the least, showing several percentage. The proportion of the 0-age group in April 1981 represented only about one-fifteenth that of the III-age group.

(3) Discussion

The seasonal change in densities of age groups showed that declines of densities occurred in October 1980 to April 1981 for the 0-age group, and between May and August in 1980 for the III- to IV- and ≧IV- to ≧V-age groups. The densities in the I- and II-age groups, however, did not exhibit distinct seasonal fluctuations. In Usu Cove, neptune whelks older than 3 years old constitute the adult population because females spawn for the first time in May and June at the end of the fourth year. These facts suggest that the mortality of the neptune whelk population in Usu Cove would be understood in terms of the growth stages of hatchlings (0 year old), immature whelks (1 and 2 years old) and adults (older than 3 years old).

The mortality rate of recruits during the period from October 1980 to April 1981, estimated from the differences in densities between October 1980 and April 1981, was about 60%. The causes of mortality are likely

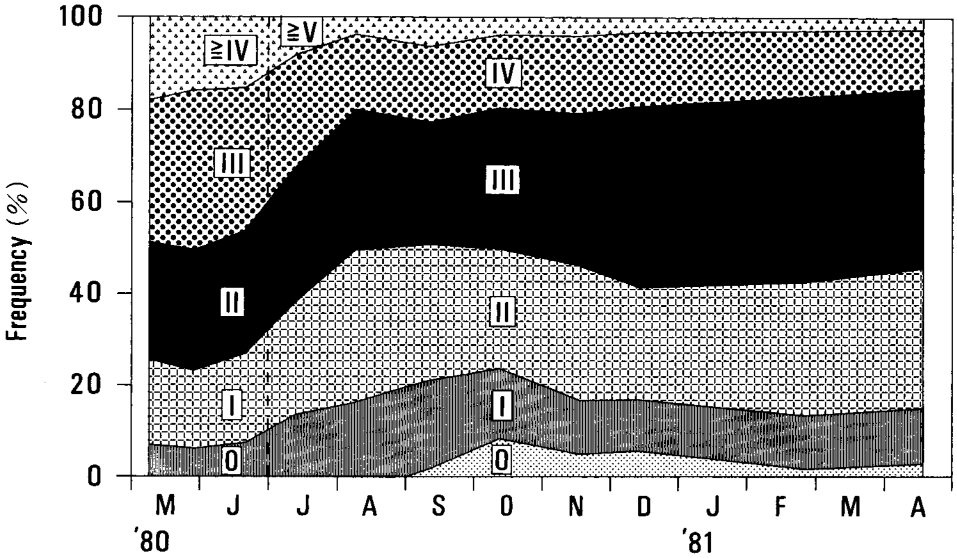


Fig. 39. Seasonal changes in the proportion of year classes in the population. Roman numerals denote ages. Symbols indicate the following year classes. ░ : 1980 (year class), ▥ : 1979, ▦ : 1978, ■ : 1977, ▩ : 1976, ⁙ : ≦1975.

to be due to food shortage soon after hatching (Thorson, 1946), and low water temperatures in winter, as described for gastropods and other animals inhabiting shallow waters (Orton, 1927; Blegvad, 1929; Gibson, 1963; Jones, 1963; Crisp, 1964). The winter in 1981 was considerably colder than usual, and particularly in February surface water of the investigated area was sometimes observed frozen. The causes of mortality in recruits needs to be investigated by examining feeding and physiological tolerances in detail.

The seasonal changes in the densities of immature whelks showed a relatively large increase and decrease over the investigation period, as in the 1978 year class ranging from 0.761 ind.•m^{-2} in the end of May to 1.285 ind.•m^{-2} in November 1980. The reason for these fluctuations may be due to limited migration within the study area. Based on the slight differences in densities between the start (May 1980) and the end (April 1981) of the study period, the mortality rate of immature whelks is likely to be very low.

The mortality of adults from May 1980 to August 1980, the spawning period and soon after the period, decreased the adult population substantially. The mortality rate, estimated from the differences in densities between May and August, 1980, was 76.3%. July is also the time when adults are fished. Therefore, spawning (Russell-Hunter, 1961; Pearce and Thorson, 1967; Fotheringham, 1971; Boerger, 1975) and fishing are thought to be the main causes of mortality in adults.

Based on the hatching rate of the neptune whelk in the same investigated area carried out in 1980, the number of hatchlings (number of egg masses, 1,079; number of egg capsules per egg mass, 33.3; hatching rate, 18.6%) is calculated to be 6,683 individuals. The gross area investigated is about 74,000 m^2, and so the mean density of hatchlings is estimated to be about 0.090 ind.•m^{-2}. Meanwhile, in the investigation on the densities of neptune whelks the 1980 year class exhibited the maximum density of 0.285 ind.•m^{-2} in October, when most juveniles have completed hatching. Although both densities are very low, there is a little difference between the two. In the future, the population dynamics of the neptune whelk needs to be further investigated by increasing the number of sampling stations and designing the arrangement of sampling stations corresponding with the distribution of neptune whelks. This may provide a more accurate estimate of the population.

During the investigation period from May 1980 through April 1981, the neptune whelk population in Usu Cove showed that the III-age group consistently possessed the maximum occupancies. As ages became lesser, the proportions among age groups decreased, and in April 1981 the occupancy rate of the 0-age group represented only about one-fifteenth that of the III-age group. It was still lower than that in May 1980. The sharp declines in the occupancy of the younger age groups are believed to be caused by the excessive decrease in the number of adult whelks. If this reduction is caused by fishing, and such a state continues, then the harvest of neptune whelks in Usu Cove will face a significant crisis in the future (Branch, 1975; Castilla and Durãn, 1985; Moreno et al., 1986).

In general, fecundity increases with age and size (Spight and Emlen, 1976; Boag and Pearlstone, 1979; Robertson and Mann, 1982; Perron, 1983). If large individuals of a resource are reduced excessively, the mean fecundity of the adult will decrease. The decrease of fecundity, evident in the sharp decrease in the mean values of egg capsules per egg mass from 1978 to 1980 (Fig. 13), agrees with the findings that there were substantial yearly reductions in the adult population. These results suggest that the measurements of the number of egg capsules per egg mass over a long term may provide a simple method for the diagnosis of resources, such as gastropods like the genus *Neptunea*, which deposits egg masses.

IV. Biological production

Information about biological production, such as assimilation in age classes and energy budget in a population provides an interpretation of distribution and migration from the viewpoint of energy intake and a weight-based estimate of the optimum catch in terms of energy budget and turnover ratio. Furthermore, the biological production is important because it enables a subject of study to be evolved from a population to a community on the basis of predator-prey relationship. In the present study, the biological production in the neptune whelk was examined in terms of seasonal change in assimilation in age classes and energy budgets in the population.

1. Methods

Energy budget equation

Assimilation A is expressed by the next equation (Branch, 1981; Peck et al., 1987; Kideys and Hartnoll, 1991), summing up growth, reproductive investment, respiration, mucus production, and excreta.

$$A = Pg + Pr + R + M + U$$

where, Pg: growth, Pr: reproductive investment, R: respiration, M: mucus production, and U: excreta. In general, energy directed to shell growth is ignored because of low energy content of the shell. However, in comparing the growth pattern between immature and adult whelks, it is likely that estimation of the energy to the shell elucidates a difference in the pattern between the growth stages more accurately. So, in the present study, growth was divided into somatic growth and shell growth.

The budget equation for a population during a given period in a given area can be represented as follows, partially modified from the equation presented by Kawanabe (1969):

$$\begin{aligned} &Bi+C+Im+Ir \\ &\quad =Pg+Pr+R+M+U+F+ \\ &\quad\quad Lp+Ld+Y+Em+Bf \end{aligned}$$

where, Bi: initial biomass, C: consumption, Im: immigration, Ir: recruitment, F: egesta, Lp: predation loss, Ld: natural mortality, Y: yield, Em: emigration, Bf: final biomass. Then, $(C-F)=A$. In gastropods, U is likely to be insignificant (Branch, 1981; Wright and Hartnoll, 1981; Peck et al., 1987); furthermore, Lp in the neptune whelk is thought to be very low after hatching, as mentioned in population structure and mortality in the chapter of Population dynamics. Taking these matters into account, the above budget equation, expressed in terms of assimilation, can be amended as follows:

$$\begin{aligned} &Bi+A+Im+Ir \\ &\quad =Pg+Pr+R+M+Ld+Y+Em+Bf \end{aligned}$$

Peck et al. (1987) quantified mucus production in the ormer *Haliotis tuberculata*. Because they investigated the energy budget of that species in terms of ingestion, the proportion of mucus production to assimilation was calculated in the present study. As a result, 28% of the assimilated energy in immature whelks, and 36% (the average of 3 different-sized whelks with a value in reproduction) in adult whelks, was regarded herein as being spent on mucus production; moreover, the rate of mucus production was premised herein to show no change throughout a year. The three terms of natural mortality, yield, and emigration were combined together herein as "mortality", because it was impossible to specify the causes of the decrease in density in the present study.

In calculating the energy budget of a population, if the weight and the number of individuals at times t_1 and t_2 are W_1, W_2, and N_1, N_2, respectively, the mean weight and mean number of individuals between the times t_1 and t_2 are $\overline{W}(=(W_1+W_2)/2)$ and $\overline{N}(=(N_1+N_2)/2)$, and the increments in the weight and the number of individuals during the time from t_1 to t_2 are $\varDelta W(=W_2-W_1)$ and $\varDelta N(=N_2-N_1)$, respectively; in addition, $\varDelta W\times\overline{N}$ indicates net production when positive and degrowth or ejection of gonad output when negative, and $\varDelta N\times\overline{W}$ reflects net recruitment or immigration when positive and mortality when negative.

Collection of neptune whelks

Neptune whelks were collected from Usu Cove bimonthly between May 1985 and March 1986. The whelks were submitted to measurements of dry weight and energy content, and experiments on oxygen consumption. In obtaining regression equations, the data of individuals, gonad somatic index and growth in soft body which were previously investigated were added.

Dry weight and energy content

For the neptune whelks collected, the shell height was measured to the nearest 0.05 mm with a vernier caliper, and the shell, soft body, and gonad were separated. They were dried to a constant weight in a oven at about 70°C and weighed. Subsequently, the soft body and the gonad were ground for the analysis of energy content. The energy content was determined by Y.M. Nenken digital type adiabatic bomb calorimeter.

Respiration R

Energy loss through metabolism was estimated by multiplying oxygen consumption by the oxy-calorific equivalent (13.98 J/mg O_2 at *n.t.p.*) (Ivlev, 1934). Experiments on oxygen consumption were carried out bimonthly from May 1985 to March 1986. The experiment was done about 30 hours, taking diurnal rhythm of oxygen consumption rate and influence of oxygen tension into consideration. The oxygen consumption was determined successively at the time intervals not to fall below 50% of the saturation level at the end of the measurement. Water temperature during the experiment ranged from 2.1°C and 18.0°C. Only natural lighting through windows was used, except during preparation and measurement in the nighttime, where artificial lighting was used. Eight to 10 whelks ranging from 30 mm to 95 mm in shell height that were acclimated and unfed for about 24 hours under running seawater after removing extraneous matter from the shell were used for the experiment. The experiment was performed under a closed system and sea water was filtrated with absorbent cotton. One to two specimens were shut in 250-650 ml stylo-bottles without the air bubble and let alone during a time. The dissolved oxygen consumed was calculated as the difference between the initial concentration and the final concentration in a measurement. The oxygen content was titrated by the Winkler method.

Growth Pg

Growth was divided into soft body growth and shell growth. Soft body weight and shell weight of each month in each age-class were estimated by substituting the shell height assessed in the growth formulae (Table 9) in regression equations for shell height-soft body weight and shell height-shell weight. The regression equation of soft body weight on shell height and that of shell weight on shell height was prepared for the immature individuals, male individuals, and female individuals, taking sexual maturity and difference of the reproductive cycle in the former and shell thickening after sexual maturity (Moore, 1938 ; Feare, 1970a) in the latter into consideration. The individuals more than 50 mm shell height in males and more than 60 mm shell height in females were regarded as adult whelk on the basis of the sizes at sexual maturity. The regression equation for shell height-soft body weight was prepared bimonthly, except during the spawning period and the time just after spawning (May to August). But, the same equation was used throughout a year in the relationship between shell height and shell weight.

Reproductive output Pr

The seasonal change of gonad weight in each age-class was estimated by substituting the shell height calculated in the growth formulae (Table 9) in the regression equation of gonad weight on shell height. On the basis of the process of the change in gonad somatic index (GSI) (Fig. 7), the regression equation for shell height-gonad weight was prepared monthly from September to February with decreasing GSI in males, and from May to August representing the spawning period and the time just after the spawning of females. Except during these periods, the regression equation was prepared bimonthly.

2. Results

(1) Assimilation in age-classes

1) Respiration R

Results of the bimonthly experiment on oxygen consumption are exhibited in the form of the mean consumption rate per unit time against body weight under different temperature conditions in Fig. 40. In each water temperature, the oxygen consumption rate of the individual (R : mg $O_2 \cdot ind^{-1} \cdot h^{-1}$) increased exponentially with body weight (W : g dry weight), and the relationship between the two variables is expressed as the equation $R = aW^b$. Where a and b are constant. There was no significant difference among the slopes of the six regression equations at different water temperatures (Analysis of covariance, $p > 0.01$). So, the oxygen consumption rate was estimated by the following multi-

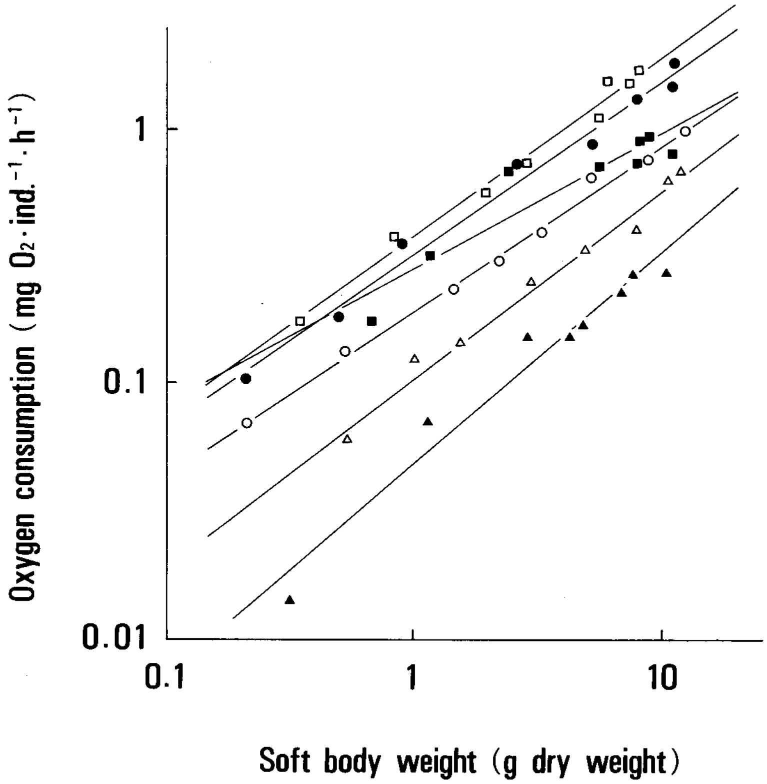


Fig. 40. Relationship between oxygen consumption and soft body weight at different water temperatures. Scale is double-logarithmic plot. ○ : May 1985 (7.7°C), ● : July (15.7°C), □ : September (18.0°C), ■ : November (10.0°C), △ : January 1986 (5.6°C), ▲ : March (2.1°C).

Table 12. Shell height (x : mm)-soft body weight (y : g dry weight) regression equations ($\log y = a\log x - b$) for immatures and matures (male and female). Soft body parts include the operculum, but exclude the gonad in matures.

Month	Mature						Immature		
	Male			Female					
	a	*b*		*a*	*b*		*a*	*b*	
July	3.695	6.258	($r=0.984$, $n=18$)	3.337	5.588	($r=0.946$, $n=17$)	3.772	6.308	($r=0.996$, $n=31$)
Aug	3.578	6.032	($r=0.968$, $n=18$)	3.128	5.165	($r=0.908$, $n=15$)			
Sep-Oct	3.751	6.332	($r=0.983$, $n=32$)	3.305	5.492	($r=0.964$, $n=27$)	3.841	6.418	($r=0.994$, $n=33$)
Nov-Dec	3.815	6.445	($r=0.984$, $n=33$)	3.270	5.408	($r=0.930$, $n=26$)	3.391	5.718	($r=0.990$, $n=35$)
Jan-Feb	3.863	6.554	($r=0.986$, $n=35$)	3.480	5.808	($r=0.939$, $n=30$)	3.413	5.723	($r=0.995$, $n=35$)
Mar-Apr	3.722	6.284	($r=0.970$, $n=34$)	3.008	4.934	($r=0.922$, $n=32$)	3.340	5.590	($r=0.994$, $n=35$)
May	3.602	6.061	($r=0.979$, $n=100$)	3.282	5.421	($r=0.955$, $n=74$)	3.614	6.004	($r=0.996$, $n=30$)
June	3.455	5.791	($r=0.974$, $n=19$)	3.139	5.166	($r=0.952$, $n=17$)			

ple regression equation whose variables were individual dry weight and water temperature.

$$R = 0.060W^{0.690}10^{0.049t} \quad (r=0.953,\ n=48)$$

Where t is water temperature (°C). In the present study, the oxygen consumption per hour was obtained by substituting individual dry weight in each month and the water temperature (Fig. 2) in the multiple regression equation, and respiration loss (the standard metabolism) was estimated by multiplying the oxygen consumption rate by the oxy-calorific equivalent.

2) *Growth Pg*

The dry weights of soft body and shell in each month in each age-class were estimated by substituting the shell height assessed by the growth formulae (Table 9) in regression equations for shell height-soft body weight (Table 12) and shell height-shell weight (Table 13). The monthly growth of soft body and shell, which was the difference in weight between the two successive months, was converted into energy by multiplying by the respective energy content (Table 14).

3) *Reproductive output Pr*

The reproductive material in each month in each age-class was estimated based on the growth formulae (Table 9) and the regression equation of gonad weight on shell height (Table 15). Investment (when positive) and shedding (when negative in copulating and spawning season) of the reproductive material, which were calculated from the difference in weight between the two successive months, were converted into energy by multiplying by the energy content of the respective gonad in male and female (Table 14). In the neptune whelk, the female ejects egg capsule produced in the capsule gland together with the discharge of eggs, and the male stores sperm until the copulation time in the coiled portion of the vas deferens serving as the seminal vesicle. Therefore, production of eggs and sperm and shedding of eggs were merely assessed through the regression of gonad weight on shell height. So, the shedding of egg capsule substance and sperm was estimated based on the decrease of the soft body weight during the copulating and spawning season.

The annual energy allocated for metabolism, growth and reproductive output in each age-class is shown in Table 16.

Table 13. Shell height (x : mm)-shell weight (y : g dry weight) regression equations ($\log y = a\log x - b$) for immatures and matures (male and female).

	Sex	*a*	*b*	
Mature	Male	2.099	2.644	($r=0.939$, $n=100$)
	Female	2.368	3.156	($r=0.905$, $n=59$)
Immature		2.144	2.725	($r=0.957$, $n=29$)

Table 14. Energy content values (±S.D.) for soft body part, gonads and shell.

Body part	Energy contents (KJ • g dry wt^{-1})
Soft body part	21.4±0.3 ($n=18$)
Ovary	28.4±0.7 ($n=7$)
Testis	21.0±0.3 ($n=5$)
Shell	0.2*

*From Vinogradov (1953)

4) *Assimilation and energy allocation*

Assimilation is considered to change closely relating

Table 15. Shell height (x : mm)-gonad weight (y : g dry weight) regression equations ($\log y = a \log x - b$) for male and female.

Month	Male			Female		
	a	b		a	b	
July	5.743	12.228	(r=0.927, n=36)	2.554	5.679	(r=0.297, n=17)
Aug				6.204	12.765	(r=0.663, n=15)
Sep	4.857	10.148	(r=0.808, n=19)	4.862	9.858	(r=0.756, n=27)
Oct	4.612	9.354	(r=0.940, n=14)			
Nov	4.096	8.509	(r=0.914, n=14)	8.961	17.375	(r=0.714, n=26)
Dec	4.675	9.831	(r=0.959, n=19)			
Jan	4.192	9.104	(r=0.928, n=18)	7.241	14.060	(r=0.587, n=30)
Feb	3.717	8.275	(r=0.958, n=17)			
Mar-Apr	4.690	10.185	(r=0.935, n=34)	7.576	14.691	(r=0.827, n=31)
May	4.715	10.229	(r=0.919, n=37)	8.197	15.847	(r=0.574, n=74)
June				3.555	7.207	(r=0.348, n=17)

Table 16. Energy allocation ($\mathrm{KJ \cdot yr^{-1}}$) in each age class in both immature and mature whelks.

Immature

Item	Age		
	0	I	II
Assimilation A	1.7	15.0	65.5
Growth Pg			
Soft body part	0.6	5.9	32.3
Shell	0.2	0.6	1.5
Respiration R	0.9	8.5	31.6

Mature

Item	Age					
	III		IV		V	
	Male	Female	Male	Female	Male	Female
Assimilation A	117.0	123.5	186.9	202.3	219.5	254.1
Growth Pg						
Soft body part	44.1	39.9	63.2	56.7	48.0	41.2
Shell	1.6	1.4	1.6	1.8	1.0	1.2
Respiration R	69.8	76.6	118.1	122.6	163.2	164.6
Reproductive output Pr						
Production	1.6	5.5	4.0	21.2	6.8	47.2
(Ejection)	(0.3)	(2.5)	(2.9)	(19.6)	(6.1)	(46.2)

to life cycle and life history. Particularly in the adult, assimilated energy could be utilized in connection with soft body growth and gonad development, and ingestion of food for sustaining them would occur. The seasonal change in assimilation (excluding U and M) and energy allocated for the respective components was examined for I-age class in the immature individual and for IV-age class in the adult individual (Fig. 41). The assimilation in the immature whelk greatly changed seasonally. In I-age class, the assimilated energy in rapid growing period was $1.88\,\mathrm{KJ \cdot month^{-1}}$. The slow growing period decreased to $0.80\,\mathrm{KJ \cdot month^{-1}}$, which was about 40% of the assimilation in rapid growing period. However, the proportion of energy spent on growth and respiration barely changed seasonally. On the other hand, in case of the assimilation and the energy into

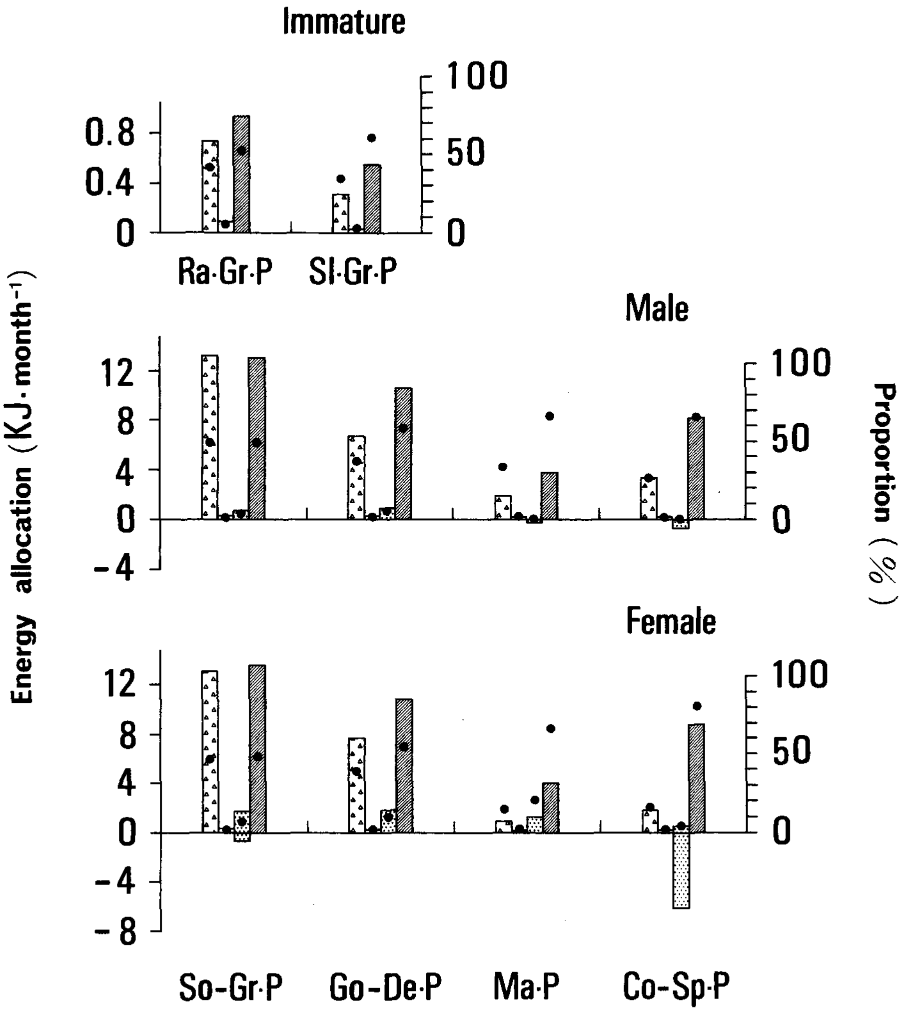


Fig. 41. Energy allocation in 1-year-old and 4-year-old whelks during each life period. Closed and open triangles, and open and closed circles represent the proportion of the assimilated energy directed to soft body part, shell, reproduction, and respiration, respectively. ▦ : soft body part, ☐: shell, ░ : reproduction, ▨ : respiration, Co-Sp•P : Copulating and spawning period (April to June), Go-De•P : Gonad developing period (September to November), Ma•P : Mature period (December to March), Ra•Gr•P : Rapid growing period (June to October), Sl•Gr•P : Slow growing period (November to May), So-Gr•P : Soma growing period (July and August).

each component in the adult whelk, though there was a difference in reproductive output between male and female, both sexes exhibited a similar trend on the whole. In soma growing period, the energy directed to soft body growth was most as compared with the other periods, amounting to about 13.0 KJ•month^{-1} in both male and female. As a result, the assimilation in growing period was considerably more and reached about 6 times greater than in mature period. In gonad developing period, the energy spent on reproduction was 0.83 KJ•month^{-1} in male, and 1.71 KJ•month^{-1} in female, reaching the maximum in this period. In mature period, except for reproductive output in female, all components showed the minimum and the assimilation was 5.86 KJ•month^{-1}. In copulating and spawning period, reproductive material was released, but the discharged energy greatly differed between male and female. In this period, the energy discharged in female amounted to about 9 times greater than in male. Thus, the energy allocation to each component with season corresponded with the life cycle (Fig. 32).

Considering age as an index of growth, changes in energy allocation with growth were examined (Fig. 42). Changes in the proportion of the energy spent on growth greatly differed between soft body and shell. The proportion utilized for shell was reduced by half with aging 1, except for the rate between 3 years old and 4 years old. The proportion of 10.5% in 0-age class decreased to about 0.5% in V-age class. On the other hand, the proportion directed to soft body exhibited the convexity reaching the peak in II-age class. The proportion which was 34.0% in 0-age class showed the

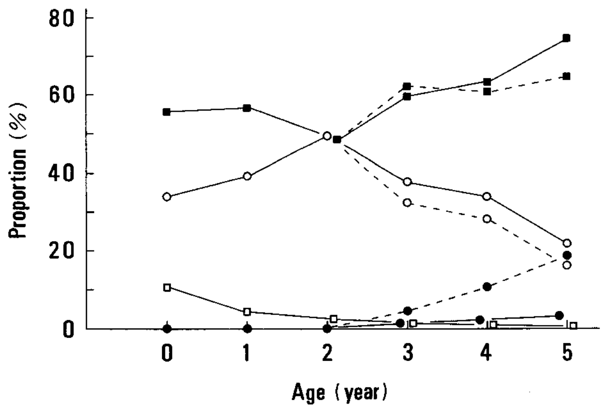


Fig. 42. Changes in energy allocation (%) with age. Each allocation for adults older than 3 years, except shell, is separately indicated for females (dotted line) and males (solid line). ○ : soft body part, □ : shell, ■ : respiration, ● : reproductive output.

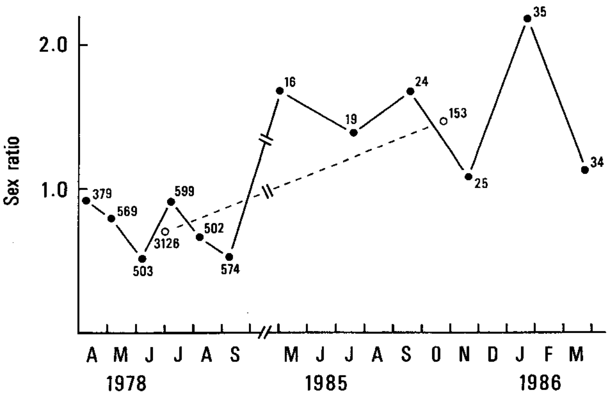


Fig. 43. Seasonal changes in the sex ratio (male/female) of *Neptunea arthritica* more than 60 mm in shell height. Open circles show the ratios during April to September 1978, and during May 1985 to March 1986. The numerals by the right side of circles represent the numbers of whelks distinguished into the sex.

maximum of 49.4% in II-age class, followed by a subsequent decrease. The energy proportion of V-age class was 21.9% in male and 16.2% in female. The proportion of energy loss through respiration was around 60%, except for II-age class and male in V-age class, but it displayed a gradually increasing trend with age. The proportion utilized for reproductive output increased with age in both male and female. However, the energy for reproduction in female reached 3 to 6 times greater than in male (Table 16), reflecting differences of the GSI value (Fig. 7) and the energy content and presence of egg-capsule material.

(2) *Energy budget in year-classes*

1) *Sex ratio*

With specimens collected from April to September in 1978, when the difference in growth between male and female was investigated, and collected from May 1985 to March 1986, sex ratio (male/female) of adult neptune whelks more than 60 mm in shell height was examined (Fig. 43). The sex ratio greatly changed in each investigation. In 1978 the sex ratios ranged from 0.51 to 0.92 during the relatively short period of April to September. In the period between May 1985 and March 1986, the ratios showed a greater fluctuation, from 1.08 in November 1985 to 2.18 in January 1986, because of the paucity of specimens. The sex ratios considerably differed between 1978 and 1985-1986, with much higher in the later period than in the earlier period. Combining all specimens together for each of these two periods, the sex ratio was 0.70 in the earlier period and 1.47 in the later period.

2) *Energy budget*

As mentioned in assimilation in age-classes, the energy allocated for reproduction significantly differed between males and females. This indicates that, in estimating the energy budget of a population, a more precise budget can be obtained by the separation of males and females in modelling the system. In the present study, no distinct pattern of seasonal changes in the sex ratio was found. So, using the combined sex ratios of 0.70 and 1.47 calculated for the populations in 1978 and 1985-1986, respectively, the mean ratio of males to females during the investigation period (the middle point of time being mid-October, 1980) was calculated by interpolation, and the value of 0.95 was obtained. Then, regarding the sex ratio in the adult whelks as 0.95 on average during the investigation period, the energy budget (Figs. 44 and 45) of each year class was calculated based on the seasonal changes in energy assimilation and allocation of each age class, and the seasonal changes in density of each year class (Fig. 38). Because shell growth was included in growth, in the present study, energy allocated for the shell is shown in parentheses in the terms necessary for the calculation of the turnover ratio (P/B).

The energy budget patterns of the year classes were divided into four types on the basis of relations among initial biomass (recruitment), assimilation, growth, mortality, and final biomass.

In the 1980 year class, assimilation was 7.0 times as large as recruitment, but final biomass did not exhibit such a high increase, reaching only 2.3 times greater than at recruitment, owing to mortality claiming one-third of the assimilation. In contrast, in the 1979 and 1978 year

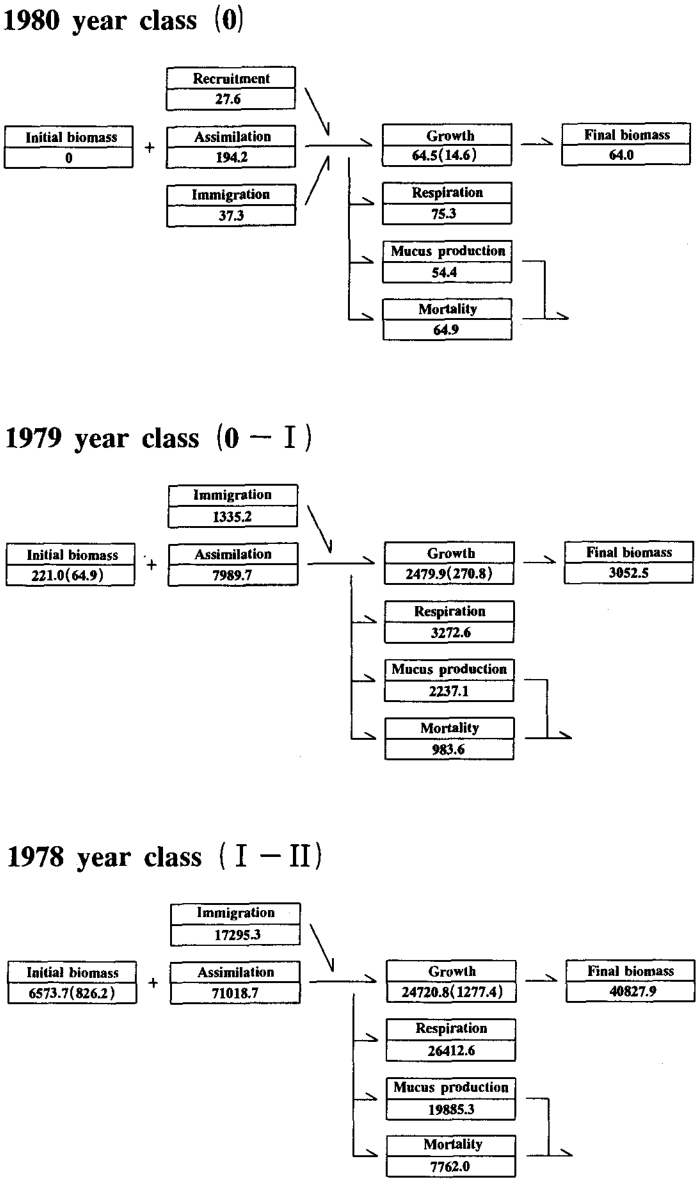


Fig. 44. The annual energy budgets of the 1980, 1979, and 1978 year-classes of *Neptunea arthritica*. Except for biomass, the budgets are expressed in $J \cdot m^{-2} \cdot year^{-1}$, and biomass in $J \cdot m^{-2}$. Roman and Arabic numerals in parentheses indicate ages and energy directed to the shell, respectively.

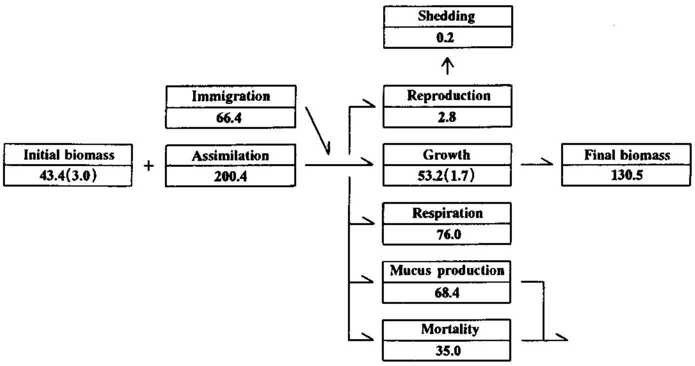
classes, final biomass represented a more considerable increase to 13.8 times and 6.2 times the initial biomass, respectively. These whelks also displayed 36.2-fold and 10.8-fold assimilation and 11.2-fold and 3.8-fold growth as compared to the initial biomass in the respective years, and a low mortality, equivalent to 12.3% and 10.9% of assimilation, respectively. Conversely, in the 1976 and ≦1975 year classes, both assimilation (1.6 times and 0.5 times the initial biomass in the respective years) and growth (34.9% and 6.4%, respectively) were slight, compared with the 1979 and 1978 year classes, but mortality was 0.6 times and 1.9 times as great as assimilation, respectively. As a result, final biomass of these year classes decreased, respectively, to 60.7% and 12.6% of the initial biomass. The 1977 year class as well did not show large assimilation, growth, mortality, or final biomass as compared with the initial biomass. Its energy budget showed an intermediate pattern between those of the 1979-1978 year classes and the 1976-≦1975 year classes.

The turnover ratio in the neptune whelk population during the investigation period was 0.42, reflecting substantial mortality in the ≦1975 year class.

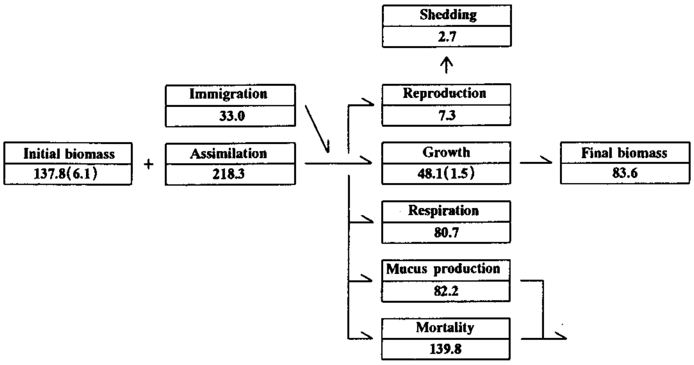
3. Discussion

In studies of biological production, energy spent on shell has not been estimated usually because of its very low energy content. But, Palmer (1981) suggests that

1977 year class (II – III)



1976 year class (III – IV)



≦ 1975 year class (≧IV – ≧V)

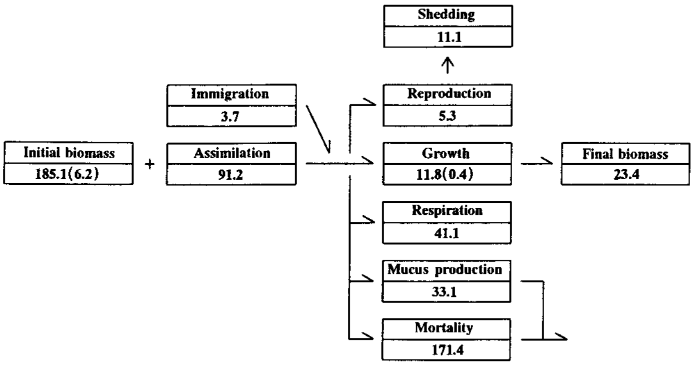


Fig. 45. The annual energy budgets in the 1977, 1976, and ≦1975 year-classes. Except for biomass, the budgets are expressed in $KJ \cdot m^{-2} \cdot year^{-1}$, and biomass in $KJ \cdot m^{-2}$.

shell growth restricts growth rate of soft body. In the present study, the energy utilized for shell was assessed to elucidate the difference in growth pattern between the immature whelk and the adult whelk. Though in the adult the proportion of the energy to assimilation was very low with approximately 1%, 0-age class of the immature whelk exhibited the value of 10.5%. Subsequently, the proportion spent on shell in the immature whelk was reduced by half with age. With decreasing proportion for shell, the proportion of the energy utilized for soft body growth to assimilation increased with age. Thus, in the immature whelk, particularly in the early stage, estimating the energy spent on shell seems to lead to elucidation of more precise growth pattern and acquisition of more accurate information on biological production.

In general, net growth efficiency (proportion of energy utilized for soft body growth to assimilation) in marine gastropods is considered to decline with growth (Hughes, 1986). But, that of the neptune whelk in Usu Cove showed the convexity reaching the peak in II-age class. This fact corresponds with the growth pattern that the growth in terms of shell height is the highest in II-age class and lesser before and after that age. On the other hand, although the proportion of energy loss through respiration followed the gradually increasing trend with age, it showed a relatively limited range of values of approximately 60%, except for II-age class and male in V-age class. Consequently, in the immature whelk the proportion of the energy spent on shell growth exhibited an inverse change to that of the energy for soft body growth, and in the adult whelk the change in the proportion of the energy for reproduction was inverse to that of soft body growth. These results indicate that in the immature whelk energy is allotted maintaining the close connection between soft body growth and shell growth, and that in the adult the proportion of energy allocated for reproduction increases with age and the proportion of energy for growth inversely decreases corresponding with increasing proportion in reproduction. This trend displayed by the adult whelk was conspicuous in female whelk. The production efficiency (proportion of energy utilized for soft body growth and reproduction to assimilation) in the adult ranged from 35% to 40%, except for 25% in V-age class male.

Net growth efficiency or gross growth efficiency (proportion of energy utilized for soft body growth to ingested energy) in marine gastropods are generally presented as a value representing a species (Carefoot, 1967 ; Paine, 1971 ; Hughes, 1971, 1972 ; Wright and Hartnoll, 1981), or as different values with increasing weight (Peck et al., 1987) and with age (Branch, 1981). However, assimilated energy and energy directed to growth and reproduction greatly differed seasonally. In the neptune whelk, the adult whelk showed the maximum assimilation and energy for growth in soma growing period, and accumulated greater energy as reproductive material in gonad developing period. Also, the energy allocated for growth and assimilation was minimum in mature period. On the other hand, assimilation and energy for growth in the immature whelk did not exhibit large seasonal fluctuation as those of the adult whelk. According to the results of the migration pattern, adult whelks of the neptune whelk are distributed in and around the place with abundant food organisms in soma growing period, and immature whelks are distributed in and around the place with abundant food organisms throughout the year. Furthermore, the time when adult whelks begin to migrate gradually from that habitat corresponds with gonad developing period. Thus, seasonal change in assimilation and energy allocated for growth and reproduction is thought to offer important information from the standpoint of energy ingestion, for elucidation of life history such as habitat and migration.

In the present study, the estimation of energy loss by metabolism was based on oxygen consumption. The oxygen consumption was calculated by the multiple regression equation whose variables were individual dry weight and water temperature, which was constructed considering diurnal rhythm of the consumption rate and influence of oxygen tension. However, for more accurate assessment of the loss through respiration, factors aside from mention above, such as activity, feeding, growth and maturation, also need to be taken into consideration (Hughes, 1986). Generally, activity of snails functioning as a scavenger in addition to the role of a predator, like *Buccinum undatum*, is not very high, and a feeding interval is inclined to be fairly long (Himmelman and Hamel, 1993). That of snails like the neptune whelk without the boring organ for feeding and serving more as a scavenger seems to be more inactive with a longer feeding interval. Therefore, energy loss through metabolism assessed by the present method could be underestimated, but in the present study standard metabolism was assumed to be the energy loss. In the future, it would be important to estimate more accurate metabolic energy, taking factors such as growth and maturation into consideration, also.

In most of studies on biological production in marine gastropods, energy directed to reproduction was estimated combining male and female together (Branch, 1981 ; Peck et al., 1987 ; Barkai and Griffiths, 1988). In the present study, the energy for reproduction was assessed separating male and female because of differences in the reproductive cycle, the GSI value and the energy content of the gonads between the sex, and production of egg-capsule substance in female, but the energy content values for testis and ovary were the same throughout the year. Consequently, it was found that the proportion of the energy spent on reproduction to assimilated energy increased with age in both male and female, but that the proportion in female because of the production of the egg-capsule substance ranged from 3 to 6 times the proportion in male. However, the energy content of ovary could greatly differ among season and the maturation (Wright and Hartnoll, 1981). Therefore, the difference between male and female would be larger, in using the energy content of ovary corresponding with the reproductive cycle. The difference in the proportion of the energy for reproduction between the sex observed in the neptune whelk is much greater compared to *Nerita* (Hughes, 1971), *Tegula funebralis* (Paine, 1971), and *Patella vulgata* (Wright and Hartnoll, 1981). Like the neptune whelk, energy spent on reproduction for snails, which produce hard egg capsules, would need to be estimated by separating male and female.

The importance of mucus in marine gastropods was stressed with elucidation of various roles of mucus (Wolcott, 1973 ; Calow, 1979 ; Connor, 1986 ; Connor and Quinn, 1984 ; Garrity and Levings, 1984). Consequently, in the 1980s mucus has been incorporated into the energy budget equation as a single component to measure (Branch, 1981 ; Peck et al., 1987 ; Kideys and Hartnoll, 1991). Also in the neptune whelk, the energy utilized for mucus needed to be included in the investigation of assimilated energy. Furthermore, the energy budgets of the age-classes and the population were not examined in terms of food consumption, but in terms of assimilated energy. In the future, it is necessary to estimate a more precise budget by measuring mucus production seasonally, and moreover, by examining the biological production in terms of food consumption rather than in terms of assimilation.

During the investigation periods from April through September in 1978 and from May 1985 through March 1986, the sex ratio of adult whelks greatly changed with each sample taken, being much higher in the later period than in the earlier period. Taking the migration pattern and occurrence of imposex (Fujinaga and Nakao, 1999) into consideration, causes of the change in the sex ratio could be attributed to a difference in behavioural pattern between male and female (Cole, 1942 ; MacKenzie, 1961) and influence of organotin compounds such as tributyltin (Bryan et al., 1986). However, no pattern in the changes was evident in the present study, and the energy budgets of year classes had to be estimated on the basis of the sex ratio calculated by interpolation (0.95) at the midpoint of the period of population density measurements. In the future, the construction of a more accurate energy budget of the population will require a more detailed investigation of the sex ratio, and further, an examination of the difference in mortality rates between males and females (Moore, 1937 ; Pearce and Thorson, 1967).

The energy budget patterns were different between the 1980 year class, the 1979・1978 year classes, the 1977 year class, and the 1976・≦1975 year classes, based on the relations among initial biomass (recruitment), assimilation, growth, mortality, and final biomass. In Usu Cove, neptune whelks older than 3 years old constitute the adult population; females spawn for the first time in May and June at the end of the fourth year. This means that the 1977 year class, which passed from the II to III age-group during the investigation period, corresponded to the stage of transition from the immature to the adult population. The energy budgets of the neptune whelk population in Usu Cove may thus be nearly understood in terms of the growth stages of hatchlings (the 1980 year class), immature whelks (the 1979 and 1978 year classes), and adults (the 1976 and ≦ 1975 year classes).

Although in hatchlings assimilation was several times as large as recruitment, final biomass did not show a very great increase, because of the rather high mortality. In the immature population, final biomass increased to several times or more the initial biomass, with not less than 10-fold larger assimilation and high growth as compared with the initial biomass, and with mortality equivalent to a little over 10% of assimilation. On the other hand, in the adult population, final biomass substantially decreased due to assimilation roughly equal to or less than initial biomass and little growth, and mortality roughly equal to or exceeding assimilation. These energy budget patterns in the growth stages suggest another necessary consideration, namely the guarantee of food organisms to support a substantial increase of biomass in the immature population, in enhancing hatching rates by setting in place large, hard substrata suitable for egg mass deposition, mentioned in the discussion of reproductive biology. The neptune whelk is said to be a scavenger, but the amount of carrion needed to maintain a scavenging snail population is not thought to occur in natural environments (Kent, 1983 ; Himmelman and Hamel, 1993). Also, the neptune whelk may feed more often as a predator than as a scavenger. Furthermore, immature whelks center their distribution in places with abundant food organisms over the whole year. These facts suggest that merely enhancing hatching rates will not be effective unless a nursery ground to secure food organisms for the immature population is prepared. In particular, the construction of such a nursery ground may be essential for the recovery of the neptune whelk fishery in embayments subjected to destructive damage by the use of TBT compounds, because these compounds have caused deleterious effects on various marine organisms (Evans et al., 1995 ; Smith, 1996), including the food organisms of the neptune whelk. The propagation method of the neptune whelk needs to be quantitatively examined in terms of a community to evolve the energy budget of the population.

The turnover ratio of the neptune whelk population in the density investigation period was low, 0.42, because of the substantial mortality in the older adult population. This value means that the population in Usu Cove is far from the stage at which the population can maintain itself, and that means to drastically decrease the mortality, such as a fishing moratorium ranging over several years, may be needed for recovery of the population. The same conclusion was more cautiously hinted at in the discussion of population structure and mortality. In a study on population structure, it is difficult to accurately estimate the degree of recovery in the population that will follow upon a change in mortality rates, because production and change in standing stock (in weight) cannot be assessed. In the future, it will be desirable to present a forecast of the degree of recovery with changing mortality rates, on the basis of the energy budget.

V. General discussion

In the present study, distribution, migration pattern, population dynamics, and biological production were comprehended on the basis of the life cycle (Fig. 32) of the neptune whelk, that is, the life patterns of the embryo, immature whelk, and adult whelk which were subdivided based on the results of reproduction, growth, and food consumption. Synthesizing all these phenomena, the life history of the whelk is summarized as follows (Fig. 46).

Embryonic stage : May to October

The embryonic stage is subdivided into three periods; birth period, embryogenesis period, and hatching period. This developmental stage is the time when the decrease rate of the number of individuals is the highest.

Birth period: May and June This period is the time when egg masses are deposited on hard substrata, such as rocks, boulders, and oyster shells. Large hard substrata such as rocks (a hard substratum greater than 50 cm in height) play an important role for the spawning. There are more egg masses at spawning sites with large substrata such as rocks than at spawning sites with only small substrata, such as boulders (a hard substratum less than 50 cm in height) and oyster shells. Moreover, at spawning sites with both large substrata and small substrata, most egg masses are deposited on the large substrata.

Embryogenesis period: July and August This period is the time when embryos grow up to juvenile stage by way of egg-swallowing stage, protoconch-forming stage, and shell-developing stage. In embryogenesis period, the number of embryos substantially decreases because of predation on embryos, detachment of egg masses from substrata, cessation of embryonic development at the early stage, and coating by sponges. In 1980, the hatching rate of the neptune whelk in Usu Cove was estimated to be 18.6%. Predation is divided into the two types of predator. One type is the predator that preys upon the whole egg mass, like *Asterias amurensis* and *Asterina pectinifera*. The other is the predator that drills an egg capsule and preys upon an embryo, like *Ocenebra japonica*. Most of predation is attributed to the latter type of predator. Predation rates on embryos are closely related to the size of hard substrata. Predation rates at spawning sites with large substrata such as rocks are considerably lower compared to those at spawning sites with only small substrata, such as boulders and oyster shells. Proportions of detachment of egg masses from substrata differ between the substratum type. Egg masses deposited on elastic substrata, such as ropes and holdfasts of *Laminaria* spp., are more susceptible to detachment than those on solid substrata, such as rocks and boulders. Cessation of embryonic development at the early stage is related to the number of egg capsules per egg mass. Egg masses with high cessation rates are relatively copious in egg masses with less number of egg capsules. The cessation rate lowers with increase in the number of egg capsules per egg mass, and egg masses showing high cessation rates are not found among egg masses composed of many egg capsules. When egg mass is covered with periphyton, particularly sponges, the developmental speed of the embryo is remarkably reduced. Embryos with retarded development because of the cover by sponges are presumed to die without growing up to a juvenile.

Hatching period: September and October This period is the time when juveniles measuring 6 mm to 11 mm in shell height and 4 mm to 7 mm in shell diameter which completed the embryonic development hatch.

Hatchlings begin to migrate from egg mass deposition site immediately after hatching, and change the hibitat to place with abundant food organisms over several months. The death of recruits takes place just after hatching and in winter. The mortality rate of them during the period from October 1980 to April 1981 was estimated to be about 60%. The causes of mortality are possibly attributed to food shortage soon after hatching and low water temperatures in winter.

Immature stage

1- and 2-year old individuals which are under 50 mm shell height in male and 60 mm shell height in female represent the immature stage. Immature whelks are distributed in and around place with abundant food organisms throughout the year. The mortality rate of them is very low. One year in the immature whelks understood on the basis of growth and food consumption is divided into 2 life periods in terms of growth rate; rapid growing period and slow growing period.

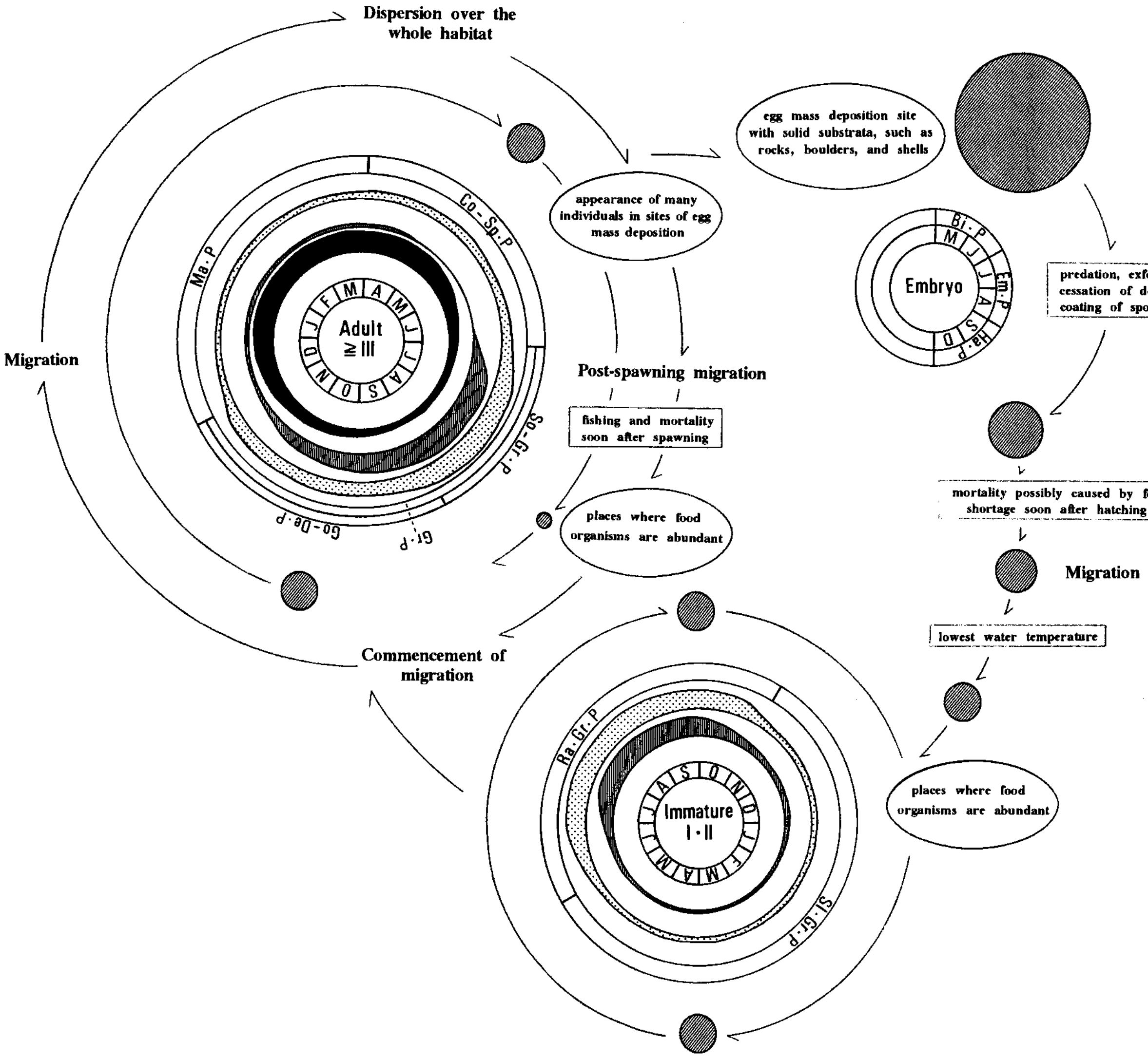


Fig. 46. Life history of *Neptunea arthritica*. Roman numerals indicate ages. Items in ellipses and quadrangles denote habitats and causes of mortality, respectively. Striped circles show diagrammatic changes in number of individuals. ■ : Maturation, ▥ : Growth, ░ : Feeding, Bi•P : Birth period, Co-Sp•P : Copulating and spawning period, Em•P : Embryogenesis period, Go-De•P : Gonad developing period, Gr•P : Growing period, Ha•P : Hatching period, Ma•P : Mature period, Ra•Gr•P : Rapid growing period, Sl•Gr•P : Slow growing period, So-Gr•P : Soma growing period.

Rapid growing period : June to October Food consumption is much, and both shell and soft body grow rapidly.

Slow growing period : November to May Food consumption decreases, and growth rates in shell and soft body is low.

Mature stage

Individuals more than 3 years old, which are greater than 50 mm shell height in male and 60 mm shell height in female, represent the mature stage. The life of the mature whelks comprehended from reproduction, growth, and food consumption exhibits a periodic change with a cycle in a year. One year in the mature whelks is divided into 3 life periods mainly based on reproduction: growing period, mature period, and copulating and spawning period. The production efficiency in the adult is relatively constant. Net growth efficiency decreases with increasing age, but proportion of energy spent on reproduction to assimilation increases with age. Adult whelks change habitats corresponding with the life periods. The death in the adult is due to spawning and fishing.

Growing period : July to November Growing period was subdivided into soma growing period, when the growth rate is high, and gonad developing period, when the gonads develop strikingly.

Soma growing period : July and August The seasonal maturation in the reproductive cycle is recovering period or developing period in male, and recovering period or pre-developing period in female. Adult whelks are distributed in place with abundant food. The growth of shell and soft body is the most active, and the most food is consumed. Many adult whelks die because of spawning and fishing, and the mortality rate become greater in older whelks. In 1980, 76.3% of the adult population was assessed to die in this period.

Gonad developing period : September to November The seasonal maturation is developing period or mature period in male, and post-developing period in female. The gonad weight increases strikingly. Growth rates of shell and soft body somewhat decrease, but still maintain high levels. Food consumption diminishes as compared with soma growing period. In this period adult whelks begin to gradually migrate from place with abundant food.

Mature period : December to March The seasonal maturation is mature period in both male and female. Shell growth stops nearly. The least food is consumed. The distribution area is spread by migration and become dispersed over the whole habitat gradually.

Copulating and spawning period : April to June This period is the time when copulation and spawning take place. Shell growth nearly stops, and the decrease in soft body weight occurs. Food consumtion to some degree increases as compared to mature period. Many adult whelks become found in spawning sites with hard substrata, such as rocks, boulders, and oyster shells.

The study on life history presents bases for methods to implement propagation and culture of organisms. As far as *N. arthritica*, in the past there seems to be no time when information on life history is realized to be so important as at present by the following two reasons. The first is for resuming the whelk fishery from the damage caused by the use of TBT-based antifouling paints. The second is for getting the foundation for the change from monoculture to polyculture in propagation and culture methods.

In the 1980s the whelk fishery in many embayments was subjected to crushing damage by TBT compounds contained in antifouling paints for boat hulls and fish-pen nets (Fujinaga et al., 2002). The use of TBT-based antifouling paints on boats of less than 25 m in length and on the fish-pen nets was prohibited in 1990. Following this, *Babylonia japonica* resources is reported to be resuming (Mizuguchi et al., 1998). On the other hand, as to the neptune whelk in Hokkaido, RPSI of adult whelks in Usu Cove was reported to have drastically declined, which suggests that female whelks in this cove have been recovering from imposex (Fujinaga and Nakao, 1999). Also, in Saroma Lagoon, basing on decreases in RPSI value, frequency of imposex, and sex ratio, the whelks in the lagoon was reported to have recovered from imposex (Fujinaga et al., 2002). However, there exist embayments where the whelk fishery is suspended even now, and even if the whelk fisheries are resumed in some embayments, their landings are far scarce as compared with those before affected by TBT compounds. Consequently, there remains the perception that the whelk still does not recover from imposex. The cause of the difference in restoration speed between the two species could be attributed to the developmental type (*B. japonica* : indirect development, *N. arthritica* : direct development) and the number of juveniles per egg capsule (*B. japonica* : about 40 veligers (Ino, 1950), *N. arthritica* : one juvenile). Mainly the difference in the reproductive capacity between both species is considered to be reflected in the restoration speed of the populations (Gibbs et al., 1988).

The decrease of resources by overfishing and by the use of TBT-based compounds is the decrease of a population and a community, respectively, and the restoration process between the two events differs intrinsically. In the decrease by overfishing, it is expected that resources would resume to some extent after several years unless they are fished. However, in case of the decrease caused by TBT compounds, as recovery would take place one after another from species with a strong reproductive capacity, it seems fairly late for the species with less capacity like the neptune whelk to recover. In the future, restoration of the whelk fisheries necessitates to construct a spawning ground by laying large hard substrata for egg mass deposition and construction of a nursery ground to secure food organisms, together with transplantation of adult whelks and seed production. Thereafter, it would be desirable to set about the resource management of adults, such as regulation of catch size, establishment of a closed season for fishing, and regulation of fishery, when the whelk resources resumed.

In recent years the conversion of a monoculture into a polyculture is recommended, like the polyculture with red sea-bream and sea lettuce (Hirata, 1999) and abalone and laminaria (Sakai, 2000). At present, in some localities along the shore of Hokkaido, the scallop (*Patinopecten yessoensis*) culture by seabed sowing method is conducted at a large scale. These scallops are harvested by using the scallop dredge. When scallops are caught by this fishing gear, it is reported that many scallops are damaged and die (Gruffydd, 1972 ; Caddy, 1973), and that after the trawling, many scavengers, such as seastars, crabs, hermit crabs, and snails, gather to seek food (Kaiser and Spencer, 1996). Ramsay et al. (1998) stated that the aggregating behaviour of those scavengers is a reaction to the trawling. In Japan, many efforts have been devoted to eliminate seastars from the fishing grounds of the scallop. Accordingly, examination of the polyculture (or, combination of propagation and culture) with large-sized gastropods with the same food habit as seastars and the scallop would be proposed. By constructing a spawning ground for large-sized gastropods outside the area where the scallop cultivation by seabed sowing method is conducted, the possibility that the scallop culture ground could play the role as a nursery ground of immature whelks could be created. As the result, food that is supplied to seastars would decrease in some measure, which seems in a way to lower their multiplication speed. In the future, this possibility needs to be examined in detail by accumulating data from investigations and experiments.

In performing the restoration of the whelk fisheries in Hokkaido and the conversion of a monoculture into a polyculture with large-sized gastropods mentioned above, part of information on the life history obtained in the present study has an insufficient elucidation. It is found in food consumption and biological production. In the future, the study must evolve the elucidation of the biological production in a community on the basis of prey- predator relationship.

VI. Summary

The life history of the neptune whelk *Neptunea arthritica* was examined on the basis of reproduction, growth, food consumption, distribution, migration pattern, population dynamics, and biological production, in Usu Cove located in the northern part of Funka Bay, Hokkaido.

(1) On the basis of histological observations of the gonads and the coiled portion of the deferent duct functioning as the seminal vesicle, gonad somatic index, seasonal change in the number of egg masses, developmental process of the embryo, and hatching of juveniles, the reproductive cycle of the whelk population was summarized as follows: in the female population, July: recovering period, August: pre-developing period, September to December: post-developing period, and January to April: mature period, while in the male population, July: recovering period, August and September: developing period, October to March: mature period, continuing the seasonal maturation, April to June: copulating period, May and June: spawning period (birth period), furthermore, July and August: embryogenesis period, and September and October: hatching period.

(2) Size and age at sexual maturity was determined to be 50 mm shell height (2 years old) in male and 60 mm shell height (3 years old) in female.

(3) Size preference between male and female in copulating pairs was not recognized.

(4) The major spawner in 1978 was composed of individuals from 65 mm to 85 mm in shell height.

(5) Egg masses were deposited on hard substrata, such as rocks, boulders and oyster shells, mainly in May and June, and the deposition was completed in July.

(6) The number of egg capsules composing an egg mass decreased year by year. In 1978, majority of egg masses was composed of 40 to 65 egg capsules, with the mean of 51.1. But, in 1980, the number of egg capsules in most egg masses ranged from 15 to 50, with the mean of 34.9.

(7) There existed about 1,100 eggs, together with dense liquid, within an egg capsule. But, the number of embryos which completed embryogenesis within it was nearly an individual, and the other eggs served as nurse eggs.

(8) The developmental process of the whelk embryo was divided into the following four stages, based on the presence of nurse eggs, the torsion, the developmental degree of the shell, and the colour of the embryo and the shell: egg-swallowing stage, protoconch-forming stage, shell-developing stage, and juvenile stage.

(9) The size of juveniles at hatching was 6 mm to 11 mm in shell height and 4 mm to 7 mm in shell diameter.

(10) The period between egg deposition and hatching in the neptune whelk was 3 to 4 months.

(11) Most of juveniles hatched in September, and the hatching finished in October.

(12) On the basis of the number of egg masses, the number of egg capsules per egg mass, and the hatching process of juveniles comprehended by seasonal changes in proportions of seven types of egg capsule, the hatching rate of the neptune whelk was estimated to be 18.6% in 1980.

(13) As causes of embryonic mortality, predation, detachment of egg masses, cessation of embryonic development, coating by periphyton (particularly, sponges) and so on were confirmed. In Usu Cove, the decreases through predation and detachment of egg masses from substrata occupied the highest proportions, followed by cessation of the development at the early stage.

(14) Predation on embryos of the neptune whelk was divided into the two types of predator. One type was the predator that drilled round holes in an egg capsule and preys upon an embryo, like *Ocenebra japonica*. The other was the predator that preyed upon the whole egg mass, like *Asterias amurensis*, *Asterina*

pectinifera, and *Strongylocentrotus nudus*. Most of predations on embryos were attributed to snails with the feeding mechanism through boring.

(15) The proportions of detachment differed between the substratum type. Egg masses deposited on elastic substrata, such as ropes and holdfasts of *Laminaria* spp., were more susceptible to detachment than those on solid substrata, such as rocks and boulders.

(16) Cessation of embryonic development at the early stage was related to the number of egg capsules per egg mass. In egg masses with less number of egg capsules, egg mass whose developmental cessation rate was high was relatively more. The developmental cessation rate lowered with increasing number of egg capsules per egg mass, and the rates were very low in egg masses with many egg capsules.

(17) The presence of large hard substrata played an important role in the spawning of the neptune whelk.

(18) The egg masses tended to be more numerous at sites with more substrata, but there were more egg masses at spawning sites with large substrata, such as rocks greater than 50 cm in height, than at spawning sites with only small substrata, such as boulders less than 50 cm in height and oyster shells. Moreover, at spawning sites with both rocks and boulders, most egg masses were deposited on the rocks.

(19) Egg masses were usually found on the upper part of substrata. Seaweeds, such as *Chondrus ocellatus, Ulva pertusa*, and *Laminaria* spp., were usually abundant on the surface of substrata where egg masses were deposited.

(20) Predation rates on embryos were closely related to the size of hard substrata. The predation rates (the mean predation rate: 29.7%) at spawning sites with rocks were significantly lower than those (the mean predation rate: 50.8%) at spawning sites with only small hard substrata.

(21) There were statistically no significant differences in growth on the basis of shell height and shell diameter between male and female.

(22) The monthly growth rates in shell height, shell diameter and soft body were high from early summer to autumn, and low in winter and early spring, when water temperature was low, in all age classes. Also, the growth rates in the three criteria decrease with increasing age. The growth in the three criteria exhibited the same tendency in these two points. But, in soft body, the negative growth occurred, the negative growth rate was higher in female than in male, and additionally decrease in the growth rates above II-age class was not so large compared to shell height and shell diameter, which exhibit the growth pattern peculiar to the soft body.

(23) The growth of the neptune whelk was closely related to water temperature in the immature whelks, and greatly controlled by the two factors, water temperature and gonad maturation in the adult whelks.

(24) The relationship between shell height and shell diameter remained linear throughout the life span.

(25) The growth in shell height of the neptune whelk was summarized as follows: at hatching: 9.0 mm, I-year old: 18.3 mm, II-years: 34.3 mm, III-years: 55.1 mm, IV-years: 69.8 mm, V-years: 82.3 mm.

(26) The growth process in the neptune whelk was most fitted to the formula of Gompertz.

(27) Neptune whelks in Usu Cove fed on various animals (including carrion), such as *Mytilus* spp. (live, L), *Patinopecten yessoensis* (L), *Tectonatica* sp. (L), fish (dead, D), *Hemigrapsus* spp. (D), *Pandalus gracilis* (D), and *Strongylocentrotus nudus* (D).

(28) Most whelks fed chiefly on live bivalves, such as *Mytilus* spp. and *P. yessoensis*, and the proportion of whelks feeding on carrion was 20.1%. The neptune whelk may feed more often as a predator than as a scavenger.

(29) The food consumption rate in the neptune whelk was related to body size, and the consumption rate per bout of feeding decreased nearly exponentially with increasing shell height.

(30) On the basis of comparisons of the slopes and heights in the regressions of food consumption rate on shell height by analysis of covariance, it was suggested that water temperature and other factors (e.g. growth and reproduction) besides body weight affected the food consumption.

(31) The developmental stage of the neptune whelk that was divided into the embryo, immature individual, and mature individual, was further subdivided into either 2 or 3 characteristic life periods, based on reproduction, growth, and food consumption. The life cycle of the whelk which was comprehended as the succession of the developmental stages is summarized as follows;

Embryonic stage Birth period: May and June, embryogenesis period: July and August, and hatching period: September and October.

Immature stage (1 and 2 years old) Rapid growing period: June to October, and slow growing period: November to May

Mature stage (older than 3 years old) Growing period: July to November (soma growing period: July and August, and gonad developing period: September to November), mature period: December to March, and copulating and spawning period: April to June

(32) Habitat change in the neptune whelk can be understood in terms of the growth stages of hatchling, immature, and adult whelk.

(33) Hatchlings began to migrate from the egg mass deposition site immediately after hatching, and changed the habitat to the place with abundant food organisms over several months.

(34) Immature whelks were distributed in and around the place with abundant food throughout the year.

(35) In adult whelks, the change in habitats, such as spawning site and place with abundant food organisms, took place in an annual cycle. In August representative of soma growing period, adult whelks are distributed in and around the place with abundant food. They begin to gradually migrate in gonad developing period, and are dispersed over the whole habitat in April, the beginning of copulating period. In May and June corresponding to copulating period and spawning period, many adult whelks aggregate in spawning sites. In late June and July just after spawning, adults rapidly migrate to the place with abundant food, and during soma growing period their distribution is restricted to the place with abundant food and its circumference again.

(36) The migration of hatchlings and the distribution of immature whelks were strongly dependent on food, and the distribution and migration of adults were closely related to reproduction and food.

(37) The mortality of individuals after hatching was understood in terms of the growth stages of hatchlings, immature whelks and adult whelks.

(38) The mortality rate of recruits during the period from October 1980 to April 1981 was estimated to be about 60%. The causes of mortality were likely to be the food shortage soon after hatching and low water temperatures in winter.

(39) The mortality rate of immature whelks was likely to be very low.

(40) The mortality of adult whelks occurred almost from May to August, the spawning period and soon after the period. The mortality which could be attributed to spawning and fishing decreased the adult population substantially. In 1980, the adult population was estimated to decrease down to 23.7% at that time.

(41) The occupancy rates in the whelk population showed considerable differences among age groups. During the investigation period from May 1980 through April 1981, the whelk population showed that the III-age group consistently possessed the maximum occupancies. As ages became lesser, the proportions among age groups decreased. In April 1981 the occupancy rate of the 0-age group represented only about one-fifteenth that of the III-age group.

(42) The sharp decrease in the mean values of egg capsules per egg mass agreed with the fact that there were substantial yearly reductions in the adult population. This result suggested that the measurements of the number of egg capsules per egg mass over a long term may provide a simple method for the diagnosis of resources, such as gastropods like the genus *Neptunea*, which deposits egg masses.

(43) Energy loss through metabolism in the neptune whelk was estimated by multiplying oxygen consumption by the oxy-calorific equivalent. The oxygen consumption rate was calculated by the following multiple regression equation whose variables were individual dry weight and water temperature.

$$R=0.060\,W^{0.690}10^{0.049t}$$

Where R is the oxygen consumption rate of the individual (mg $O_2 \cdot ind^{-1} \cdot h^{-1}$), W is individual dry weight (g dry weight) and t is water temperature (°C).

(44) Assimilated energy ($KJ \cdot month^{-1}$) and energy directed to growth and reproduction greatly differed seasonally. The adult whelk showed the maximal assimilation and energy for growth in soma growing period, and accumulated greater energy as reproductive material in gonad developing period. Also, the energy directed to growth and assimilation was minimum in mature period. On the other hand, assimilation and energy for growth in the immature whelk did not exhibit so large seasonal fluctuation as those of the adult whelk.

(45) Changes in the proportion of the energy spent on growth greatly differed between soft body and shell. The proportion utilized for shell was reduced by half with age 1, except for the rate between 3 and 4 years old. On the other hand, the proportion directed to soft body exhibited the convex process reaching the peak in II-age class.

(46) The proportion of energy loss through respiration was around 60%, except for II-age class and male in V-age class, but it displayed the gradually increasing trend with age.

(47) The proportion of energy utilized for reproductive output increased with age in both male and female. However, the energy for reproduction in female reached 3 to 6 times greater than in male, reflecting differences of the GSI value and energy content and the presence of egg-capsule material.

(48) The production efficiency in the adult whelk exhibited the relatively constant value of 35% to 40%, except for V-age class male.

(49) In the immature whelk energy was allotted maintaining the close connection between soft body growth and shell growth. The proportion of the energy spent on shell growth exhibited an inverse change to that of the energy for soft body growth and decreased with increasing age. On the other hand, in the adult whelk

the proportion of energy directed to reproduction increased with age and the proportion of energy for growth inversely decreased corresponding with increasing proportion in reproduction.

(50) The sex ratio (male/female) greatly changed with each investigation.

(51) The energy budget patterns of the year classes could be virtually understood in terms of the growth stages of hatchlings, immature whelks, and adults on the basis of relations among initial biomass (recruitment), assimilation, growth, mortality, and final biomass, reflecting the differences in mortality rate in the growth stages.

(52) The biomass in the hatchlings did not increase very much (2.3 times as large as recruitment) regardless of relatively high assimilation, because of the rather heavy mortality. In contrast, in the immature whelks, the biomass increased considerably (the 1979 year class: 13.8 times, and the 1978 year class: 6.2 times), as the result of high assimilation and growth with little mortality. On the other hand, the biomass in the adult whelks substantially decreased (the decrease to 60.7% in the 1976 year class, and to 12.7% in the ≦1975 year classes) due to little assimilation and growth with high mortality.

(53) The turnover ratio (P/B) of the whelk population during the period from May 1980 to May 1981 showed a very low value of 0.42, reflecting a drastic mortality in the older adult population.

(54) The life history of the neptune whelk comprehended on the basis of its life cycle is summarized as follows.

Embryonic stage: May to October

The embryonic stage is subdivided into three periods; birth period, embryogenesis period, and hatching period. This developmental stage is the time when the decrease rate of the number of individuals is the highest.

Birth period: May and June This period is the time when egg masses are deposited on hard substrata, such as rocks, boulders, and oyster shells. Large hard substrata such as rocks (a hard substratum greater than 50 cm in height) play an important role for the spawning. There are more egg masses at spawning sites with large substrata such as rocks than at spawning sites with only small substrata, such as boulders (a hard substratum less than 50 cm in height) and oyster shells. Moreover, at spawning sites with both large substrata and small substrata, most egg masses are deposited on the large substrata.

Embryogenesis period: July and August This period is the time when embryos grow up to juvenile stage by way of egg-swallowing stage, protoconch-forming stage, and shell-developing stage. In embryogenesis period, the number of embryos substantially decreases because of predation on embryos, detachment of egg masses from substrata, cessation of embryonic development at the early stage, and coating by sponges. In 1980, the hatching rate of the neptune whelk in Usu Cove was estimated to be 18.6%. Predation is divided into the two types of predator. One type is the predator that preys upon the whole egg mass, like *Asterias amurensis* and *Asterina pectinifera*. The other is the predator that drills an egg capsule and preys upon an embryo, like *Ocenebra japonica*. Most of predation is attributed to the latter type of predator. Predation rates on embryos are closely related to the size of hard substrata. Predation rates at spawning sites with large substrata such as rocks are considerably lower compared to those at spawning sites with only small substrata, such as boulders and oyster shells. Proportions of detachment of egg masses from substrata differ between the substratum type. Egg masses deposited on elastic substrata, such as ropes and holdfasts of *Laminaria* spp., are more susceptible to detachment than those on solid substrata, such as rocks and boulders. Cessation of embryonic development at the early stage is related to the number of egg capsules per egg mass. Egg masses with high cessation rates are relatively copious in egg masses with less number of egg capsules. The cessation rate lowers with increase in the number of egg capsules per egg mass, and egg masses showing high cessation rates are not found among egg masses composed of many egg capsules. When egg mass is covered with periphyton, particularly sponges, the developmental speed of the embryo is remarkably reduced. Embryos with retarded development because of the cover by sponges are presumed to die without growing up to a juvenile.

Hatching period: September and October This period is the time when juveniles measuring 6 mm to 11 mm in shell height and 4 mm to 7 mm in shell diameter which completed the embryonic development hatch.

Hatchlings begin to migrate from egg mass deposition site immediately after hatching, and change the hibitat to place with abundant food organisms over several months. The death of recruits takes place just after hatching and in winter. The mortality rate of them during the period from October 1980 to April 1981 was estimated to be about 60%. The causes of mortality are possibly attributed to food shortage soon after hatching and low water temperatures in winter.

Immature stage

1- and 2-year old individuals which are under 50 mm shell height in male and 60 mm shell height in female represent the immature stage. Immature whelks are distributed in and around place with abundant food organisms throughout the year. The mortality rate of them is very low. One year in the immature whelks understood on the basis of growth and food consumption is divided into 2 life periods in terms of growth rate; rapid growing period and slow growing period.

Rapid growing period: June to October Food consumption is much, and both shell and soft body grow rapidly.

Slow growing period: November to May Food consumption decreases, and growth rates in shell and soft body is low.

Mature stage

Individuals more than 3 years old, which are greater than 50 mm shell height in male and 60 mm shell height in female, represent the mature stage. The life of the mature whelks comprehended from reproduction, growth, and food consumption exhibits a periodic change with a cycle in a year. One year in the mature whelks is divided into 3 life periods mainly based on reproduction: growing period, mature period, and copulating and spawning period. The production efficiency in the adult is relatively constant. Net growth efficiency decreases with increasing age, but proportion of energy spent on reproduction to assimilation increases with age. Adult whelks change habitats corresponding with the life periods. The death in the adult is due to spawning and fishing.

Growing period: July to November Growing period was subdivided into soma growing period, when the growth rate is high, and gonad developing period, when the gonads develop strikingly.

Soma growing period: July and August The seasonal maturation in the reproductive cycle is recovering period or developing period in male, and recovering period or pre-developing period in female. Adult whelks are distributed in place with abundant food. The growth of shell and soft body is the most active, and the most food is consumed. Many adult whelks die because of spawning and fishing, and the mortality rate become greater in older whelks. In 1980, 76.3% of the adult population was assessed to die in this period.

Gonad developing period: September to November The seasonal maturation is developing period or mature period in male, and post-developing period in female. The gonad weight increases strikingly. Growth rates of shell and soft body somewhat decrease, but still maintain high levels. Food consumption diminishes as compared with soma growing period. In this period adult whelks begin to gradually migrate from place with abundant food.

Mature period: December to March The seasonal maturation is mature period in both male and female. Shell growth stops nearly. The least food is consumed. The distribution area is spread by migration and become dispersed over the whole habitat gradually.

Copulating and spawning period: April to June This period is the time when copulation and spawning take place. Shell growth nearly stops, and the decrease in soft body weight occurs. Food consumtion to some degree increases as compared to mature period. Many adult whelks become found in spawning sites with hard substrata, such as rocks, boulders, and oyster shells.

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