Growth and Population Dynamics of the Tropical Intertidal Gastropod, *Mancinella hippocastanum* (Family Muricidae) in Sesoko Island, Okinawa

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Abstract Growth and population dynamics of the tropical muricacean gastropod *Mancinella hippocastanum* were investigated by mark-recapture method at Sesoko Island, Okinawa. The animal had episodic growth with intermittent extension of the whorl. Growth rates during the warm season were higher than during the cold season with considerable individual variations. Annual growth rates tended to diminish as initial size increased, but these varied individually. The von Bertalanffy equation predicted that animals would attain shell heights of 25 to 35 mm, the most frequent size in the field, at an age of approximately 3 to 5 years. Occurrence of individuals larger than 40 mm in shell height implied that the life span of *M. hippocastanum* may be 10 years or longer. Mortality rates estimated from recapture records of the tagged individuals were about 70% per year. The population of *M. hippocastanum* in the study site decreased throughout the year after April 1989. It seems that the recruitment of young animals in that period was insufficient to offset the high mortality rate.

Key words Growth, Mancinella hippocastanum, Muricidae, Thaidinae, Population dynamics

Introduction

Muricacean gastropods commonly occur at many locations in the world, and some of them are recognized as important components of benthic communities on intertidal rocky shores (e.g. Paine 1966, 1974; Dayton 1971; Lubchenco & Menge 1978; Menge & Lubchenco 1981). The ecology and life history of muricacean gastropods has been extensively studied for many members living in temperate regions (e.g. Phillips 1969; Fotheringham 1971; Spight *et al.* 1974; Palmer 1983; Moran *et al.* 1984), but hardly at all for most of the tropical species. *Mancinella hippocastanum* Linnaeus 1758, characterized by its shell with many thick spines, is commonly found on intertidal rocky shores in tropical and subtropical Indo-West Pacific (Fujioka 1986).

The objective of this study was to investigate the growth, the life span and the population dynamics of M. hippocastanum on Sesoko Island, Okinawa.

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Materials and Methods

Mark and recapture census was conducted at the rocky shore adjacent to Sesoko Marine Science Center, Sesoko Island, Okinawa (Fig. 1). Many individuals of *M. hippocastanum* lived on the eroded limestone platform in the mid-intertidal zone. The study area was about 200 m along the shoreline, and the habitat of the animal was interrupted by sandy bottoms surrounding two piers.

The census was started in October 1988. All individuals that were found were captured during the daytime low tide. Since the animals often hid in crevices, search and collection activities were repeated for three days for four hours to ensure that no specimens had been overlooked.

In the laboratory, shell height (distance from the tip of the spire to the end of the anterior canal) of each individual was measured to the nearest 0.1 mm with vernier calipers, and the condition of its outer shell lip was recorded to study the process of shell growth. Then, in individuals larger than about 25 mm in shell height a 0.8 mm diameter hole was made in the shoulder of the outer shell lip, and a small piece of colored plastic tape (Dymo Tape) with a number on it was attached to the shell with some nylon thread. Because this tagging procedure was unsuitable for small individuals with fragile shells, a different tagging procedure was devised for them. The spire of the dry shell was partially filed with a hand-held electric rotary tool, and a small piece of waterproof paper numbered with black rapidograph ink was attached to the shell and coated with cyanoacrylate glue. Tagged individuals were released into crevices in the study area immediately before tidal immersion.

The recapture of tagged individuals was conducted almost every three months until April 1990. The search for individuals was repeated on three days in each census. Unmarked individuals were brought to the laboratory for tagging and measurement, while recaptured individuals were measured in the field and returned at once. In addition to the regular census, the condition of the outer shell lip of the tagged individuals was examined in August and in September 1989.

Annual growth data were pooled and fitted to the von Bertalanffy curve from a Walford plot (Walford 1946). The formula for the growth curve is:

$$L_{t+1} = L_{\infty} (1 - e^{-k}) + e^{-k} \cdot L_{t}$$

where $L_i = \text{length}$ at age t; $L_{i+1} = \text{length}$ after one year; $L_{\omega} = \text{maximum}$ length; k = instantaneous growth rate. Among these parameters, L_{ω} and k can be extracted from the regression line of the Walford plot. L_{ω} is the length of intersection between the regression line and the line of y = x, and k = -log (slope of the regression line).

Survival rates were estimated from recapture records of tagged individuals. Because the number of individuals tagged in each census was less than 50 after April 1989, the survival rates were calculated only for the individuals tagged in October 1988 and January 1989.



Fig. 1. Map of Sesoko Island, Okinawa, showing the location of the study site.

Results

Process of shell growth

The shell of *M. hippocastanum* grew by intermittently repeating the following process. At first, the animal extended the thin shell whorl about 1/9 to 1/8 of the volution. As the whorl extended, the edge of the outer shell lip bent partially outward, and 3 or 4 halfconelike projections were formed. Subsequently, the extension of the whorl ceased, and the newly extended shell whorl gradually thickened. Then, the sides of the projections would close, completing the formation of the conical spines. The increase in shell height occurred mainly during the extension stage of the thin shell whorl. The duration of each phase varied seasonally and individually. The animals required anywhere from less than 1 month to almost 6 months to extend the whorl, and it was about 1 month to 11 months from the start of one extension to the beginning of the next. In each census, the individuals did not show synchronicity in phase of shell growth.

Growth rate

The growth of the shell of *M. hippocastanum* varied seasonally (Fig. 2). The increase in shell height during the warm season was greater than it was during the cold season. From April to October, almost all animals increased their shell heights. Threemonth growth rates were greater than 1 mm; they declined as the initial size increased. From October to April, increments in shell heights per 3 months were usually less than 1 mm, and many animals showed negative growth due to erosion of the apex and/or breakage of the edge of the outer shell lip.

Almost all individuals increased their shell heights in a year. Annual growth rates decreased with increased initial sizes. Increase in the shell height usually varied considerably among individuals and did not exceed 8 mm (Fig. 3).

The regression line of the Walford plot (Fig. 4) was Y = 0.778 X + 10.906, and the values of L_{∞} and k of the von Bertalanffy curve were 49.6 and 0.251, respectively. Since the size at hatching or settlement could not be established, it was assumed that $L_0 \approx 0$ and $L_1 = 10.906$ (intercept of Y-axis) respectively. From these parameters, the growth curve was calculated (Fig. 5). The growth curve indicated that the animals required 3 to 5 years to attain 25 to 30 mm, the most frequent size class (Fig. 6), and that the largest individual (43.1 mm) was 8 to 9 years old if it had grown at the standard rate.

Population dynamics

The number of individuals of *M. hippocastanum* captured in the study site had declined slightly from October 1988 to January 1989. Allowing for the fact that finding of the animals might become more difficult in winter because of their low activity and hiding in deep crevices, no decline in the population was observed. In contrast, the population decreased markedly from April 1989 to April 1990. Throughout this period, unmarked individuals were seldom encountered (Fig. 6), which suggested that recruitment of young animals was marginal at the study site.

The number of survivors among the tagged individuals declined gradually. Seasonal change in mortality rate was not apparent in survivorship curves (Fig. 7). The survival rate estimated for the individuals tagged in October 1988 and January 1989 was 29.6% and 30.6%, respectively. Thus, the annual mortality rate was estimated at about 70%. Actual mortality rate, however, may be lower because of incomplete accounting of all the tagged animals and the possibility of missing tags.



Fig. 2. Scatter diagram of three monthly growth rates and initial shell height of tagged individuals of *M*. *hippocastanum*.



Fig. 3. Scatter diagram of annual growth rates and initial shell heights of tagged animals.



Fig. 4. Ford-Walford plot of M. hippocastanum. The broken line indicates no growth.



Fig. 5. The bon Bertalanffy growth curve of M. hippocastanum.



Fig. 6. Size-frequency distribution of the population of *M. jippocastanum* found at study site at each time of census. Open histogram indicate unmarked individuals, and solid histogram indicate marked individuals.



Fig. 7. Survivorship curve for tagged individuals of M. hippocastanum.

Discussion

Growth

According to Linsley & Javidpour (1980), many muricacean gastropods grow episodically by rapid extension of the whorl and subsequent thickening of the shell. In a typical growth episode the whorl extends from 1/6 to 1/2 volution within several days or weeks. Because of rapid extension, fragile shells are produced. Linsley & Javidpour (1980) suggested the necessity for behavioral adaptation to avoid breakage of the shell during the extension of the whorl. The growth mechanism of *M. hippocastanum* is similar to that of the episodic growers, however, the extension of the whorl is slow since a short distance is involved in a single growth episode. Such manner of growth reflects adaptation to the local environment with its heavy wave action and scarcity of shelter.

Growth rates of the animals varied individually. Although no evidence was obtained in this study, availability and quality of food may be a possible cause of this variation. The growth rate of many gastropods has been known to change with food availability (e.g. Spight *et al.* 1974; Spight 1981). Quality of food also has been recognized as an important factor influencing the growth rate of snails. Moran *et al.* (1984) demonstrated that the growth rate and the attainable size of the intertidal muricacean gastropod, *Morula marginalba*, varied and depended on the different prey species. West (1988) reported that prey diversity varied among the muricacean gastropod *Thais melones* individuals living at the same locality, and that this variation caused individual variation in growth rates.

Almost all individuals of *M. hippocastanum* examined in the present study were found on a continuous mid-intertidal platform, however, food availability and prey species may vary from individual to individual since they appear to use different prey scattered throughout the habitat.

Population dynamics

The mortality rate of the population of M. hippocastanum on the study site was high, whereas the individuals grew slowly and seemed to have a potentially long life span. Phillips (1969) reported on the growth and the population dynamics of the muricacean gastropod, *Dicathais aegrota* in Western Australia. An individual of this species required about 4 years to attain 38 mm of shell height, and had a maximum longevity of over 17 years. The populations of D. *aegrota* on the intertidal limestone reef platforms showed a high mortality rate that exceeded 70% per year. These traits were similar to M. hippocastanum in the present study.

The decline in the population of *M. hippocastanum* after April 1989 seems to have occurred in response to marginal recruitment. It is assumed that to maintain a stable population, *M. hippocastanum* requires considerable recruitment to compensate for the high mortality rate. The habitat of *M. hippocastanum* is restricted to the mid-intertidal zone. Living in such narrow habitat may induce annual fluctuation in recruitment.

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