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A Short-term Study of Growth and Death in a Population of the Gastropod *Strombus gibberulus* in Guam

by

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Abstract. A month-long study of tagged *Strombus gibberulus gibbosus* Röding, 1798, in Pago Bay, Guam, during the spring of 1981 revealed very high mortality (at least 11%), most of which (93%) was due to shell breakage. No differences in shell size, lip thickness, or age were detectable among snails that died, sustained sublethal injury, and survived unscathed. It is concluded that the thickened adult lip was ineffective in conferring resistance to shell-breaking agents (chiefly xanthid crabs) in this population of *S. gibberulus*.

Juvenile growth rates were very high (mean 0.16 mm/day). Snails cease to grow in length once the lip assumes the flared adult form.

INTRODUCTION

SMALL STROMBID GASTROPODS pose a curious enigma in that they sustain heavy mortality due to breakage despite the strongly thickened and flared outer lip that characterizes the adult shell. Inspection of "dead" shells (including fragments) suggests that breakage accounts for 50 to 100% of the mortality in most populations of *Strombus gibberulus* Linnaeus, 1758, in the tropical western Pacific (VERMEIJ, 1979, 1982). Although the thick lip proved to be an obstacle to the predaceous crab *Calappa hepatica* (L.) in the laboratory, it appeared to be ineffective against other crabs such as *Carpilius maculatus* (Linnaeus) and *Daldorfia horrida* (Linnaeus) (ZIPSER & VERMEIJ, 1978; VERMEIJ, 1982). If such powerful agents of breakage are commonly encountered by *S. gibberulus,* how is the thick lip maintained by selection, and how can populations persist in the face of heavy mortality? These are the questions that prompted the present short-term study.

MATERIALS AND METHODS

We studied a sample of 230 individuals of *Strombus* (*Gibberulus*) *gibberulus gibbosus* Röding, 1798, from the inshore part of the reef flat in a cove near the center of Pago Bay, Guam, Mariana Islands. The study area is covered by at least 3 cm of water at all times and is floored by a thin layer of white sand. There are several intertidal raised limestone ledges with undercut margins. *Strombus gibberulus* is found in and on the sand. The dorsum of the adult shell is always exposed above the sand, and is frequently fouled and pitted by small algae.

All individuals observed during the week of 21–28 May 1981 were collected and marked, and were subsequently censused periodically until final recovery from 21–25 June. We measured shell length (distance from apex to tip of siphonal canal) and lip thickness (at a point midway between the eye-notch and the posterior end of the lip). Each shell was inspected for the presence of repaired injuries (scars) on the body whorl. These scars appear as irregular traces that depart from the normal course of the growth lines. They result from damage to the outer lip, which is repaired by the mantle edge before growth recommences.

In order to mark the snails, two methods were used. First, the anterior dorsal shell surface was filed clean, and a numbered beetag (Fabrik für Bienenzuchtgerate, 7056 Weinstadt-Endersbach, West Germany) was affixed with underwater epoxy. The dorsal and ventral surfaces of the spire were also filed and labeled with a permanent marker. Secondly, a spot of nail polish was painted on the ventral surface of the penultimate whorl, so that individuals that had lost their tags could still be recognized as belonging to the marked sample. If their measurements matched those of a labeled individual that had not hitherto been recovered, the tagless snails were retagged with that number. After the epoxy had dried sufficiently in air, the animals were returned to the field site for release. The 3-h period of exposure to air that was required for labeling apparently had no adverse effect, for snails began to kick actively as soon as they were placed in buckets of seawater for transport back to the field.

The incidence of scars was assessed in two ways. The proportion of repaired individuals was calculated as the

Table 1

Characteristics of the *Strombus gibberulus* population at the time of marking.

Characteristic	Juveniles	Adults
Number tagged	21	209
Proportion of repaired snails	38%	17%
Frequency of repair	0.52	0.18
Lip thickness	0.2–0.8 mm	1.3–2.5 mm

number of snails with scars on the body whorl divided by the total number of snails in the sample. The frequency of repair is the number of scars divided by the number of individuals in the sample. The latter figure is by definition higher than is the former if some members of the scarred population have multiple scars.

If large size and a thick lip conferred resistance to shell-breaking agents in the field, individuals surviving unscathed or in damaged condition would be expected to be larger and to have thicker lips than would individuals that had died as a result of shell breakage. This hypothesis was tested against the null hypothesis of no difference by comparing survivors with individuals recovered as broken shells with respect to the shell length and lip thickness of these individuals at the time of labeling. Because lip thickness in adults was independent of shell length, *t*-tests were used throughout.

RESULTS

Characteristics of the Population

Most of the population of *Strombus gibberulus* is composed of thick-lipped adults (Table 1). Shell repair on the body whorl was much more frequent in juveniles than in adults (Table 1). Two factors may contribute to this difference. In the first place, adult lips are less susceptible to sublethal damage than are thin delicate lips of juveniles. Secondly, the scars on the body whorl of a juvenile come to lie on the penultimate whorl or even in the spire whorls of adults, and would thus not be counted in the adult shell. The overall frequency of repair in the population (0.21) is similar to that in several other Guamanian populations of *S. gibberulus,* but it is higher than are the frequencies of repair in populations of this species from other parts of the tropical western Pacific (VERMEIJ, 1982). Given the high incidence of scars in the Pago Bay population, the potential for selection in favor of breakage-resistant traits is high.

Mortality and Its Causes

We recovered 89 tagged living snails one month after the 230 original animals had been released. Another 7 snails with apical marks but without their numbered tags were also recovered, so that a total of 96 individuals (42% of the original sample) was found again after one month. The percentage of recapture of juveniles (33%) was not significantly lower than that of adults (43%). Two survivors (one juvenile and one adult) sustained sublethal shell injury during the period of observation.

Table 2

Comparison of dead and surviving members of the *Strombus gibberulus* population one month after initial marking. Means are given with standard deviations.

Characteristic	Dead individuals	Survivors
Shell length at time of marking (mm)	36.21 ± 3.41	36.89 ± 3.32
Lip thickness at time of marking (mm)	1.71 ± 0.38	1.85 ± 0.33
Percentage of juveniles	6.3%	7.3%
Frequency of repair	0.24	0.22

Of the 134 individuals not recovered alive after one month, 26 were found dead during our study. The minimum mortality for the period of observation was, therefore, 11%. Most (93%) of the dead, recovered individuals had been crushed. The 17 broken shells that we were able to identify by tag did not differ from individuals that were recovered alive after one month in shell length, lip thickness, proportion of juveniles, or frequency of repair (Table 2). The ratio of juveniles to adults in the sample of broken shells was 1/16 = 0.063, as compared to 7/96 = 0.073 among survivors.

The xanthid crabs *Carpilius maculatus* and *Eriphia sebana* (Shaw & Nodder) live under ledges and large boulders in the study area, and appear to have been largely responsible for the breakage-related deaths of *Strombus gibberulus.* Nearly all broken shells had the ventral or dorsal portion of the body whorl broken away, or had severed spires, and the lip was frequently either missing or cut in half. These types of damage are typical of the prey of large xanthids with molarlike dentition in the crusher claw (ZIPSER & VERMEIJ, 1978). The spiral peeling characteristic of the prey of *Calappa hepatica,* which also occurs in the study area, was observed in only one dead individual. The porcupinefish *Diodon hystrix* (Linnaeus) hunts over the Pago Bay reef flat at night, and we have recovered fragments of *S. gibberulus* from its gut contents. The broken shells that we recovered in the field, however, were too large to have been passed through the digestive system and defecated by the porcupinefish, so that the contribution of that predator to the mortality of *S. gibberulus* could not be established.

Another agent of mortality whose impact we were unable to assess is man. QUOY & GAIMARD (1834:67) already observed that *Strombus gibberulus* was a favorite item of food for the people of Guam. Toward the end of our study, we encountered a girl, about ten years old, clutching six labeled snails and many unlabeled individ-

Table 3

Growth rates of *Strombus gibberulus* juveniles and adults over a period of 30 days. Means are given with standard deviations; numbers of individuals are given in parentheses.

Characteristic	Juveniles	Adults
Growth in shell length (mm)	3.33 ± 1.14 (9)	−0.035 ± 0.3 (81)
Growth in lip thickness (mm)	0.81 ± 0.53 (9)	0.063 ± 0.21 (81)
Daily growth in length (mm)	0.16 ± 0.072 (7)	

uals. We persuaded her to release the marked individuals, but the possibility that many of our labeled snails died in the soup-pot or on the grill cannot be eliminated.

Growth

Measurements of labeled individuals revealed that juvenile growth rates in *Strombus gibberulus* were extremely high, whereas growth ceases once the adult lip has assumed the adult configuration (Table 3). In two juveniles whose lip edge was marked, growth rate in the spiral direction was calculated to be 0.6 and 0.7 mm/day. At these rates, hatchlings could be expected to reach a length of 30 mm (minimum adult length in the Pago Bay population) in about six months. Because small juveniles probably grow even faster than did the rather large juveniles we monitored, all of which exceeded 27 mm in initial length (Table 1), the time required to reach minimum adult size may well be substantially shorter.

DISCUSSION

Although the high incidence of scars in the Pago Bay population of *Strombus gibberulus* suggests a high potential for selection in favor of breakage-resistant traits such as a thick lip, we were unable to detect differences in shell length or lip thickness between snails that survived after one month and those that we recovered as dead broken shells. If selection in favor of resistance to breakage took place, it involved characters we did not examine.

The thick lip may function as a deterrent to predation in other populations of *Strombus gibberulus.* The species is common in grassbeds and on sand flats where boulders under which large shell-crushing crabs find shelter are absent. We suspect that the lip is chiefly effective against calappid crabs, which live in sand, and that the boulder-strewn sand patches of the Pago Bay reef flat are very different in terms of the types of predators encountered by *S. gibberulus* from inshore environments where rocky bottoms are absent. The Pago Bay population may well persist not by virtue of morphological adaptation, but by exceptionally high juvenile growth rates and presumably by high rates of larval settlement, although the latter point requires confirmation.

It is also possible that the thick lip is not adaptive in resisting predators in any population of *Strombus gibberulus,* and that it is instead retained as a legacy of a well-established pattern of determinate growth that was fixed very early in the history of the Strombidae. The combination of determinate growth, modified adult outer lip, and short post-larval life-span is found not only in *S. gibberulus,* but in many other small Indo-west-Pacific strombids and tropical cerithiids as well (HOUBRICK, 1974). Like the larger and longer-lived members of these and other gastropod families, these small species have high growth rates in the juvenile phase. Both adult size and juvenile growth rate may vary by a factor of two to three among individuals from the same site (RANDALL, 1964; FRANK, 1969; SPIGHT *et al.,* 1974; YAMAGUCHI, 1977; VERMEIJ, 1980). If, as seems likely from studies of other gastropods, growth and size are partially determined by genetic factors, these tropical species should display substantial genetic variation on which selection could act.

We realize that the present study concerns only one population during one month in a possibly atypical habitat. It will be interesting to repeat our study in environments in which calappid crabs are the chief predators, and to monitor populations over the course of an entire year or more.

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