Survival After Nonlethal Shell Damage in the Gastropod *Conus sponsalis*[1]

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Abstract—Individuals in a population of *Conus sponsalis* Hwass from Pago Bay, Guam, were marked and released in order to study the short-term consequences of artificially inflicted nonlethal shell damage of a type frequently encountered in the field. Damage to the outer lip had no effect on short-term survival, and the size distribution of injured cones recovered 30 days after release was the same as that at the beginning of the experiment. We conclude that shell damage had no immediate effect on mortality. Repair frequency (number of scars per body whorl) is very low on small individuals and reaches the highest level (0.27) in snails longer than 21 mm. Two size-dependent factors, growth rate and resistance to crushing, probably contribute to the size distribution of repaired shell injuries.

Introduction

Repaired injuries on the shells of gastropods record past nonlethal damage that in many cases was probably induced by would-be predators. Relatively high frequencies of repair have been observed in snails from tropical regions. A collection of *Conus lividus* from Hawaii, for example, contained individuals with as many as 4 scars on the body whorl; the frequency for the whole population was 1.2 scars per body whorl (Currey and Kohn, 1976). This level of damage is not unusual in the genus *Conus* or in many other tropical taxa (Vermeij, 1978, in preparation; Vermeij, Zipser, and Dudley, 1980).

In the present study, we monitored a group of marked *Conus sponsalis* Hwass with and without damaged lips in order to measure growth rates and to discover how sublethal shell damage affects short-term survival. There are several possible reasons why shell damage might affect survival. Resources may be diverted from growth and reproduction in order to repair the shell (see Maiorana, 1977, for an example involving tail loss in salamanders). Moreover, loss of part of the outer lip of the shell alters the shape of the aperture and may destabilize the shell, thus making the animal more liable to dislodgement by water currents or by predators. Damage might enable predators to extract the soft parts without injuring the shell, and may make behavioral escape from predators more difficult.

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Materials and Methods

The work reported here was carried out on the windward reef flat north of the University of Guam Marine Laboratory in Pago Bay, Guam (Mariana Islands). The study area comprised about 100 m^2 of fairly flat intertidal limestone bench with occasional loose coral rubble and a few limestone boulders 3 to 4 m high. Tides fluctuate twice daily, uncovering the bench during low spring tides but always covering the flat during high tides. Many small plants of *Turbinaria ornata* and *Sargassum cristaefolium* occur, and algal turfs consisting of many species are present everywhere.

The density of gastropods on the surface of the bench was assessed on 15 March 1979 midway through the field experiment, by counting and identifying all gastropods in 12 1-m^2 quadrats. *Conus sponsalis* is the commonest species in the area (mean density 1.7 individuals per square meter, range 0 to 7 per square meter). The next most common cone is *C. ebraeus* L. (mean density 0.5 individuals per square meter). Other common gastropods include *C. miliaris* Hwass (0.3 individuals per square meter), *Morula granulata* (Duclos) (0.8 individuals per square meter), *M. triangulata* (Pease) (0.3 individuals per square meter), *Drupa ricinus* (L.) (0.4 per square meter), and *Vasum turbinellus* L. (0.4 individuals per square meter). There are numerous other less common gastropod species. At least two predatory crabs (*Carpilius maculatus* L.) were known to be resident under boulders in the study area; evidence of their feeding was found frequently in the form of broken gastropod shells. The Pago Bay bench fauna and the pattern of relative abundance of *Conus* species are similar to those described for other intertidal benches elsewhere in the Indo-West Pacific (Kohn, 1959, 1968, 1971; Kohn and Leviten, 1976; Taylor, 1976, 1978).

Individuals of *C. sponsalis* were marked and released from 21 January to 3 March, 1979, and were recovered from February to July, 1979. Coralline algae were tapped gently from the shells with a hammer in order to expose the apex for marking. A circular area of about 6 mm in diameter was filed clean on the side of the apex farthest from the aperture; numbers were written with permanent laundry marker or India ink. The number area was coated with a film of Superglue and allowed to dry before snails were returned to the central portion of the study area. The principal difficulty with this system of marking was the overgrowth and partial destruction of the glue by encrusting coralline algae (*Hydrolithon reinboldii*). Shell length was measured to the nearest 0.1 mm from apex to tip of siphonal canal with Vernier calipers.

To simulate nonlethal damage of the type often observed in the field, snails were arranged in pairs of approximately equal size, the odd-numbered snail being damaged. While the soft parts were retracted into the shell, the anterior edge of the lip was broken back with jeweler's pliers so that a fragment about 2 mm wide and 2/3 the length of the lip was removed.

To monitor shell repair in the laboratory, the lips of 20 *C. sponsalis* were broken back and allowed to regrow. Snails were kept in running sea water with a supply of food-containing rubble from the reef flat. Although it is difficult to standardize wet weights of *Conus*, such standardization was attempted by weighing snails after careful drying at room temperature for 30 minutes. The mean weight of shell removed was 0.029 ± 0.013 g; this represents an average of $1.8 \pm 0.6\%$ of the total wet weight of the animal. These values are also representative of the shell removal performed on animals in the field experiments.

Results and Discussion

A total of 273 living *C. sponsalis* was collected from the study area and examined for repaired injuries. The results are expressed as the average number of repairs per body whorl for individuals of a particular size class (Fig. 1). Repair frequencies are lowest on the smallest individuals and highest on the largest cones, reaching a value of 0.27 per whorl for cones 21 mm long.

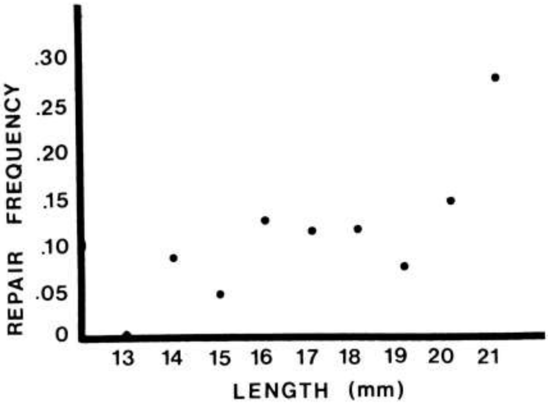

Fig. 1. Repair frequency (number of repair marks per body whorl) in relation to shell length in *Conus sponsalis* from Pago Bay, Guam.

We found no effect of lip damage on the survival of *C. sponsalis* on the reef flat. Of 201 marked snails, 132 (65.8%) were recovered 6 to 10 days after release; 69 of an original 97 control animals (67.0%) were recovered, as compared to 67 of 104 (64.4%) lip-damaged snails. If the populations of damaged and control animals recovered after 30 days are compared, the difference in recovery is even smaller; 41 control animals and 46 experimental ones (42% and 44% of the original populations respectively) were recovered alive.

Survival of lip-damaged snails does not appear to be size-dependent. The average length of snails in the original marked population was 17.3 ± 2.1 mm; the mean length of damaged snails recovered after 30 days (17.2 ± 2.2 mm) is not significantly different from the original size.

Laboratory and field observations suggest that shell repair in *C. sponsalis* is quite rapid. Of the 20 damaged individuals monitored in the laboratory, 4 were completely repaired after 9 days, 10 after 15 days, and 14 at the end of the experiment on the 23rd day. One individual (14.8 mm in length) had barely repaired at all. In the field, 5 of 7 lip-injured cones recovered 12 days after release had repaired completely. The period during which lip injury could directly affect survival is thus quite short.

We have very limited information about the fate of cones not recovered alive. Four shells, one lip-damaged and 3 controls, were recovered as numbered fragments. The mean size of these individuals was 17.0 ± 2.2 mm, which is not significantly different from the mean size of the *C. sponsalis* population at the beginning of the experiment. The absolute minimum loss in individuals to shell-breaking predators is therefore 2% of the population over a 6-month period. Because only the apices of cones were numbered, other fragments found during the experimental period could not be identified, and the 2% breakage figure is almost certainly an underestimate of the loss to predation. Two additional numbered shells were found intact but empty.

Enough cones were measured throughout the experiment to yield a rough estimate of growth rates. If the data are expressed as length increase in millimeters per day (Fig. 2), a relationship between shell length and growth rate may be discerned. Daily growth rates of small animals are quite variable, ranging from 0.0327 mm for a cone initially 13.8 mm long to 0 mm for a 15.4 mm cone. The mean daily growth rate of cones set out at sizes in the lower half of the size range (less than 17.0 mm long) was 0.0077 ± 0.0101 mm; the median growth rate of this population was 0.0075 mm, very close to the mean. In contrast, the average growth rate of cones in the upper half of the size range (17.0 mm or longer) was 0.0014 ± 0.0008 mm, with a range of 0 to 0.0079 mm per day; the median growth rate was 0. The daily growth rates of the two size classes differ significantly at the 0.05 level (Mann-Whitney U-Test).

Although larger cones are more likely than smaller individuals to show no

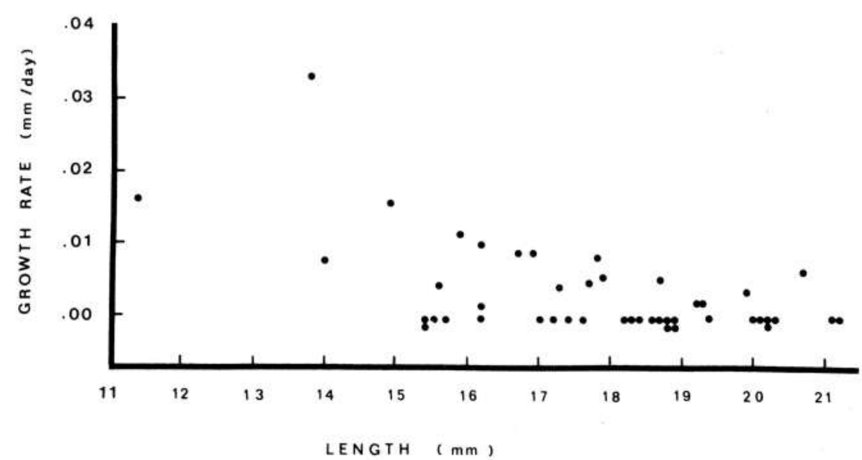

Fig. 2. Growth rate (increase in shell length divided by number of days after marking) in relation to initial size of *Conus sponsalis*. Each dot represents one individual.

discernible increase in shell length over a period of several months, the size at which growth ceases is apparently quite variable. For example, 1 out of 8 cones greater than 20 mm long, and 1 out of 10 individuals in the 18–19 mm size class grew perceptibly during the study. This considerable variation in growth rate and maximum adult size is typical of most gastropods that have been studied (Vermeij, 1980).

Because the data on frequency of repair and growth rate were taken from the same population, we may ask how the susceptibility to nonlethal injury is related to growth. If the attack rate by predators was constant over time and independent of prey size (assumptions for which we have no information), then the decline of growth rate with increasing size will produce a pattern of repair frequencies similar to that depicted in Fig. 1. Attack marks on small quickly growing shells would be concealed rapidly as previously exposed parts of the shell come to lie within the aperture. Individuals of moderate size and growth rate would reach a balance between the acquisition of new scars and the concealment of old ones. The largest cones, which no longer add much shell material to the outer lip, would visibly accumulate the evidence of past injury, and therefore display a large number of scars.

Differential vulnerability of large and small shells to successful crushing probably also contributes to the pattern of scar frequencies. Juvenile snails are often more easily crushed lethally by crabs and other predators than are adults. Very large *C. sponsalis* may be more likely than small ones to survive attacks by the average predator, although they still lie well within the crushing range of large *Carpilius maculatus* (Vermeij, 1976; Zipser and Vermeij, 1978). The damage incurred as a consequence of an unsuccessful attack becomes a repaired scar, whereas the results of successful attacks disappear from the living population. Therefore, the relatively greater immunity of larger individuals to fatal attacks results in a high frequency of repair. Declining growth rate and increasing resistance to crushing are thus two factors that lead to relatively high frequencies of shell repair in large-shelled adults. It is surprising in view of this discussion that no new sublethal shell damage was inflicted on snails in the field during the course of our study.

In summary, shell repair is relatively common in the population of *Conus sponsalis* at Pago Bay. Although repair may have long-term effects on growth and reproduction, we have been unable to show that nonlethal lip damage affects a cone's short-term survival.

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References Cited

Currey, J. D., and A. J. Kohn. 1976. Fracture in the crossed-lamellar structure of *Conus* shells. J. Material Sci. 11: 1615–1623.

Kohn, A. J. 1959. The ecology of *Conus* in Hawaii. Ecol. Monogr. 29: 47–90.

———. 1968. Microhabitats, abundance and food of *Conus* on atoll reefs in the Maldive and Chagos Islands. Ecology 49: 1046–1062.

———. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. Limnol. Oceanogr. 16: 332–348.

Kohn, A. J., and P. J. Leviten. 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. Oecologia (Berlin) 25: 199–210.

Maiorana, V. C. 1977. Tail autotomy, functional conflicts and their resolution by a salamander. Nature 265:533–535.

Taylor, J. D. 1976. Habitats, abundance and diets of muricacean gastropods at Aldabra Atoll. Zool. J. Linn. Soc. 59: 155–193.

———. 1978. Habitats and diet of predatory gastropods at Addu Atoll, Maldives. J. Exp. Mar. Biol. Ecol. 31: 83–103.

Vermeij, G. J. 1976. Interoceanic differences in vulnerability of shelled prey to crab predation. Nature 260: 135–136.

———. 1978. Biogeography and adaptation: patterns of marine life. Harvard University Press, Cambridge. 332 p.

———. 1980. Growth rate, allometry, and adult size; environmental applications. *In* D. C. Rhoads and R. A. Lutz (eds.), Skeletal growth of aquatic organisms; biological records of environmental change. Plenum, New York: in press.

———. in preparation. The occurrence, interpretation, and paleoecological applications of shell repair in gastropods. Paleobiology, submitted.

Vermeij, G. J., E. Zipser, and E. C. Dudley. 1980. Predation in time and space: breakage and drilling in terebrid gastropods. Paleobiology 6(3): 352–364.

Zipser, E., and G. J. Vermeij. 1978. Crushing behavior of tropical and temperate crabs. J. Exp. Mar. Biol. Ecol. 32: 155–172.