

Survival, Growth, and Fecundity of the West Indian Topshell, *Cittarium pica* (Linnaeus), in Various Rocky Intertidal Habitats of the Exuma Cays, Bahamas

by

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Abstract. The West Indian topshell, *Cittarium pica*, is the most intensively fished intertidal marine snail of the West Indies. However, its population dynamics are poorly known. Different habitat types, varying in degree of wave exposure, were chosen to study survival, growth, and fecundity of unexploited Bahamian *Cittarium* populations.

Several aspects of *Cittarium* life history differed between habitats. Snails inhabiting wave-exposed habitat had lower rates of survival and growth and a smaller average shell size than snails of sheltered habitat. Wave-exposed habitat had higher *Cittarium* densities and higher predatory gastropod densities than more sheltered habitats. Dead shells recovered from wave-exposed habitat showed a higher proportion of lethal damage due to shell-drilling and crushing. Size of maturation was smaller and fecundity was lower for snails residing in wave-exposed habitat.

Differences in population structure between habitats were attributed to differences in survival and growth and not to temporal differences in recruitment. Low *Cittarium* abundance in sheltered habitat, despite high survival rate, suggested a lower level of recruitment to such habitat.

INTRODUCTION

The West Indian topshell, *Cittarium pica* (Linnaeus, 1758) (= *Livona pica*) has been harvested since pre-Columbian times (GOULD, 1971) and is the largest shallow-water trochacean gastropod of the western Atlantic, often reaching a shell diameter of 10 cm. This herbivorous snail is sedentary and is found in a variety of rocky intertidal habitats throughout the West Indies. The snail has rarely been found in southern Florida (ABBOTT, 1976) and suffered recent extinction in Bermuda (CLENCH & ABBOTT, 1943).

Information on the biology of *Cittarium* is limited. The snail's anatomy (CLENCH & ABBOTT, 1943; GRAHAM, 1965), shell ultrastructure (WISE & HAY, 1968a, b), and flight response (HOFFMAN & WELDON, 1977) have been

described. Only one study has dealt with *Cittarium* population dynamics (RANDALL, 1964).

The objectives of the present study were to quantify the degree to which survival, growth, and fecundity are habitat dependent and to determine whether low population densities in wave-sheltered habitats are due to low recruitment or low post-recruit survival.

MATERIALS AND METHODS

Field work was conducted between August 1984 and January 1985 in the Exuma Cays Land and Sea Park, between Soldier Cay and Waderick Wells Cay, Bahamas (Figure 1). The park spans a total of 35 km of the Exuma island chain and is 13 km wide. Much of the intertidal zone is rocky and offers potential habitat for *Cittarium*. With winds predominantly from the southeast, the eastern shores of the islands are exposed to ocean swell from the Exuma Sound, while the western shores remain sheltered.

Four categories of rocky habitat were distinguished along

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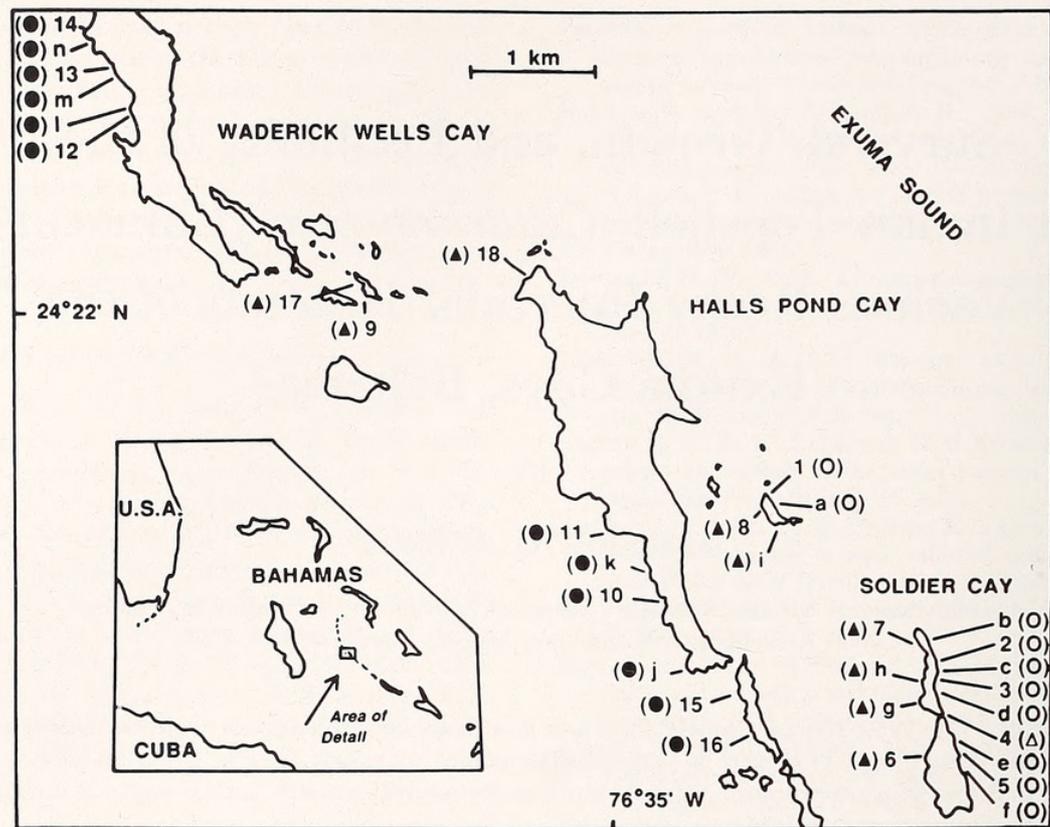


Figure 1

Map of the study area in the Exuma Cays Land and Sea Park, Bahamas, showing the size-frequency collection sites (a-n) and the tag-recapture sites (1-14). Estimates of population density were obtained at all numbered sites except 4 and 13. Habitat types are EXP (○), EXSS (△), INT (▲), and SH (●).

this gradient of wave exposure. Exposed (EXP) habitat generally showed a 30° slope through the splash zone and a nearly vertical drop of 1-1.5 m from the edge of the low tide bench (Figure 2). One-meter-high waves were common. The substrate in this habitat was highly rugose and pitted. The sea urchin *Echinometra lucunter* and the alga *Padina* (*Padina* sp.) were abundant on the low tide bench. In the upper splash zone, the limpet *Acmaea leucopleura* was abundant. EXP habitat was predominant on eastern shores.

Exposed shallow-sloping (EXSS) habitat contrasted with EXP habitat in having a shallow-sloping seabed below the low tide level. EXSS habitat was rare and was the only other habitat type distinguished on wave-exposed shores. Within the study area, EXSS habitat was found on Soldier Cay and Halls Pond Cay.

Intermediate (INT) habitat was found in channels between the islands where the effects of ocean swell were still present and wave heights of up to 0.5 m were common. The habitat had no distinguishing topography, with intertidal slopes varying widely. *Echinometra lucunter* was less abundant than in EXP habitat.

Sheltered (SH) habitat was found on the shallow leeward side of the islands where waves were usually less

than 0.2 m. Typical were the presence of an undercut in the intertidal zone (Figure 2) and less rugosity than in EXP habitat. The undercut caused the intertidal zone of this habitat type to be shaded for large parts of the day. *Echinometra lucunter* was rare, and the lower-intertidal zone was covered by a spongy, sand-laden algal mat. The isopod *Ligia* sp. descended in great numbers into the intertidal zone at low tide.

Densities per unit area were obtained for *Cittarium* and predatory gastropods of the genera *Thais* and *Purpura* (thais) at four EXP, six INT, and six SH sites. At each site, 10 m² of habitat was sampled over the zone of highest snail density, following HUGHES (1971). ANOVA *F*-tests were utilized to compare snail densities between habitat types (KLEINBAUM & KUPPER, 1978). All statistical tests presented in this report are two-tailed tests. Unless otherwise stated, statistical comparisons of parameters between habitat types were not done by pooling recoveries between sites but by considering each site within a habitat class as a single replicate.

Population size-frequency collections were made during the peak of the reproductive season (DEBROT, 1990) at 14 sites in August 1984. Of these, six were EXP, three were INT, and five were SH sites. Sample sites were chosen to

be at least 150 m apart unless they were separated by a sandy beach that prevented dispersal of postlarval individuals of this snail. Distribution of the snails was confined to a narrow, 1–2 m wide intertidal zone, which greatly facilitated sampling. At each site all snails were collected, by snorkeling and wading, from as many meters of coast as was necessary to fill a standard net bag.

To quantify survival and growth, a transplant experiment involving 14 sites was done. A total of 600 small snails with a mean shell width of 22.8 ± 7.2 mm (95% confidence interval) were collected from the ocean side of Soldier Cay. Shell width was defined as the widest diameter across the base of the shell. Oval 2×5 mm plastic tags were attached to the dry shell surfaces of the snails using marine epoxy cement (Underwater Patching Compound, Pettit Paint Co., Spring Valley, CA). One hundred of the snails were double-tagged to estimate tag shedding by the method of GULLAND (1963). The snails were set out at four EXP, one EXSS, four INT, and five SH sites. Forty snails were released at each site except site 4 (the only EXSS site) where 80 snails were released. In addition, a total of 101 large (80.0 ± 13.8 mm) animals were released at three EXP and three SH sites. After approximately 168–174 days at liberty, all survivors that could be found within a 20-m radius from the point of release at each site were collected.

Handling mortality was estimated by recording the live tagged snails seen at each site three days after release and assuming that all handling mortality takes effect within the first three days. After a period of time, Δt , the fraction of snails recovered from the total number of snails released can be expressed as $RT_i = RS_i H$, where RS_i is the recovery rate after period Δt , assuming no handling mortality, and H is handling survival. If natural mortality during the three-day period is assumed negligible, then handling survival can be calculated as:

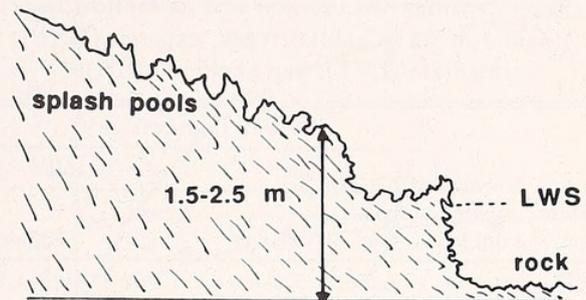
$$H = RT_i / RS_{i-3} \quad (1)$$

where RS_{i-3} is the fraction recovered from snails seen alive three days after release. Estimates were tested for differences with 100% handling survival using a χ^2 goodness-of-fit test (SOKAL & ROHLF, 1981).

Recovery efficiency was defined as the percentage of tagged snails recovered from the site after repetitive sampling. At each site, tagged snails were removed during low tide events until a collection yielded no recoveries. Recovery efficiency was calculated separately for small and large snails using the DeLury method (RICKER, 1975) on data pooled between SH, INT, and EXP sites.

After a period at liberty, expected tagged-snail population densities should be highest near their point of release and should decrease with increasing distance from the release point, assuming random movements. Emigration was, therefore, quantified by fitting a curve to the number of recaptures as a function of distance from the point of release (POOLE, 1974). Of the several curves tried, log-normal curves of the form $Y = a - B \ln(X)$ where Y is

(a) EXP



(b) SH

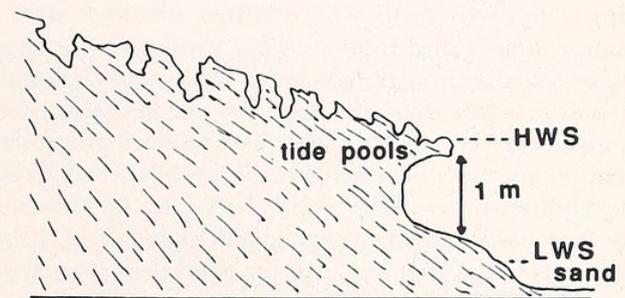


Figure 2

Vertical shore profiles for (a) EXP and (b) SH habitat types. LWS = low tide level, HWS = high tide level (spring tides).

the number of recaptures at distance X (m) each side from the point of release, provided the best fits to the dispersal data. Data for habitats with recoveries at multiple sites were pooled and weighted for equal representation of each site.

Survival for the period Δt for snails of size i was then calculated as:

$$S_{i,t} = R_{i,t} / (N_{i,0} Ta F_i E H) \quad (2)$$

where $R_{i,t}$ is the number of snails of size i that were recaptured at the end of the period Δt , $N_{i,0}$ is the number of snails of size i that were released, Ta is the fraction of tags still attached, F_i is the fraction of snails of size i inside the study site that were also found, E is the fraction of snails still inside the study site, and H is handling survival. Losses due to fishing mortality were considered negligible because of the remoteness of the area and the abundance of other attractive fishing sites in the area. Survival estimates were expressed in terms of annual percent survival (RICKER, 1975). Data were non-normally distributed so that these estimates were compared between habitats using the Kruskal-Wallis test (SOKAL & ROHLF, 1981).

Dead shells (either empty or occupied by a hermit crab) were collected to assess the relative importance of different agents of natural mortality. To avoid double-counting, only relatively fresh shells with shiny nacre and intact spire

Table 1

Population densities of *Cittarium* and its molluscan predators (thaids) in three habitat types: exposed (EXP), intermediate (INT), and sheltered (SH).

Habitat type	Number of sites sampled	Density (numbers/m ²)			
		<i>C. pica</i>		Thaids	
		Average	Range	Average	Range
EXP	4	6.0	3.6-8.5	0.7	0.3-1.1
INT	6	2.3	0.2-5.9	0.0	—
SH	6	0.1	0.0-0.5	0.0	—

tips were used. Shells with extensive breakage were assumed to have died from crushing predation. Shells with either lethal drilling or both lethal drilling and lethal shell breakage were assumed to have died due to drilling. Comparisons of the relative importance of various causes of natural mortality between habitats were done using the χ^2 goodness-of-fit test. The Fisher-Irwin test (χ^2 test-equivalent for cases with low expected cell-frequencies, HODGES & LEHMANN, 1970) was used for equivalent comparisons for specific 10-mm size classes.

Mean shell-width growth increments for the tag-recapture period were expressed as annual shell growth rates and were compared between habitats using an ANOVA *F*-test. Regression analysis was used to estimate the von Bertalanffy growth parameters, L_∞ and K , at sites where both large and small snails were released (RICKER, 1975). The GULLAND & HOLT method (1959) was used to adjust for differences in release time. Confidence intervals were obtained using the routine presented by ABRAHAMSON (1971).

Visceral coils of about 50 snails from each sampling site were preserved in 70% isopropyl alcohol for determination of a gonad index. All snails showing gonadal tissue as determined by visual inspection were considered sexually mature (RANDALL, 1964). A gonad condition index for each specimen was obtained following FEARE (1970). Using a color photo of a cross-section of the visceral coil, the area corresponding to the gonad was expressed as a fraction of the cross-sectional area of the entire visceral coil. Average size at first sexual maturity and size-specific fecundity were compared between habitats using ANOVA *F*-tests.

RESULTS

Cittarium population densities were significantly correlated with exposure ($F_{(2,13)} = 15.85$, $P < 0.001$). Average densities were highest at EXP sites (6.0 snails/m²) and lowest at SH sites (0.1 snails/m²) (Table 1). Predatory thaid gastropod densities were similarly correlated with exposure ($F_{(2,13)} = 19.84$, $P < 0.001$). Thaids were abundant at EXP sites (0.7 thaids/m²) but virtually absent at the

Table 2

Cittarium releases, percent recovery, and percent handling survival (*H*) for small ($\bar{x} = 22.8$ mm) and large ($\bar{x} = 80.0$ mm) snails.

	Total releases		Seen 3 days after release		<i>H</i>
	Number released	Percent recovered	Number seen	Percent recovered*	
Large snails	101	23.8	63	27.0	88.0

* Percent recovered from those snails that were observed to be alive 3 days after release (RS_{-3} in equation 1).

INT and SH sites examined (Table 1). At EXP sites, *Thais deltoidea* constituted 64% of the 96 thaids seen, while *T. rustica* and *Purpura patula* constituted 24% and 12%, respectively. Sixteen of the 18 thaids (89%) recorded over the course of more than two years at INT and SH sites were *T. deltoidea*, while two (11%) were *P. patula*.

Few population modes were evident in the size-frequency data obtained (Figure 3). Population structures at EXP sites were dominated by small snails (*i.e.*, 15-30 mm shell width). Despite large sample sizes ($n = 174-446$), low abundances of large snails precluded meaningful distinction of more than one population mode. Lack of snails in the larger size classes suggested a high rate of extinction of population modes due to low survival or low growth rates at EXP sites. In contrast, population structures at SH sites were dominated by large snails near the maximum size attained by the species. Indistinct modes at SH sites, due to small sample sizes ($n = 56-118$) and combined with the fact that population modes near L_∞ tend to merge (SAINSBURY, 1982), precluded more detailed analysis of the size-frequency data for survival and growth estimation. The size-frequency data, nevertheless, suggested important differences between habitats in growth or survival.

A total of 19 double-tagged shells were recovered with tags still attached. Of these, 9 had one tag and 10 had two tags. Annual tag shedding was estimated at 55% and did not differ significantly from an estimate obtained in a concurrent study (38%; $n = 43$) using the same tags (DEBROT, 1990). Therefore, the combined estimate of 43%/year was used for the purpose of survival estimation.

Handling survival was not significantly less than 100% for either the large ($\chi^2 = 0.22$, d.f. = 1, $P > 0.5$) or small snails ($\chi^2 = 0.18$, d.f. = 1, $P > 0.5$) released (Table 2). Recovery efficiency for small snails did not differ significantly between habitat types ($\chi^2 = 2.40$, d.f. = 3, $P > 0.50$). By the end of recovery, 96% of the small tagged snails present within 20 m from the points of release at INT and SH sites had been recovered (Figure 4). Recovery efficiency for large snails was estimated at 97%. For both

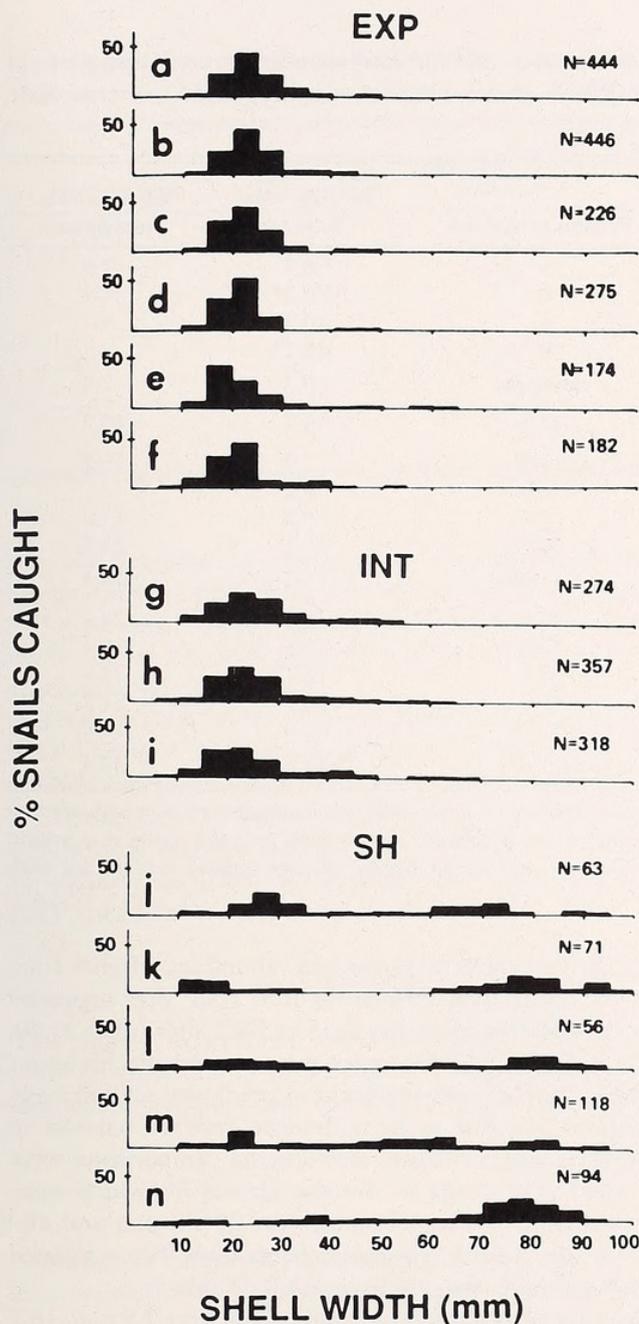


Figure 3

Size-frequency distributions for *Cittarium* collected at the 14 size-frequency collection sites (a-n), grouped by habitat type.

small and large snails, a 100% recovery efficiency was assumed.

Under ideal conditions (*i.e.*, large sample size, no microhabitat selection, and uniform behavior by all members of the population), snail recaptures should decrease with increasing distance from their point of release. In general, recaptures decreased with increasing distance from their point of release (Figure 5). At the EXSS site an estimated 94% of the snails originally released had remained within a 20-m radius from the point of release. At INT sites 67%

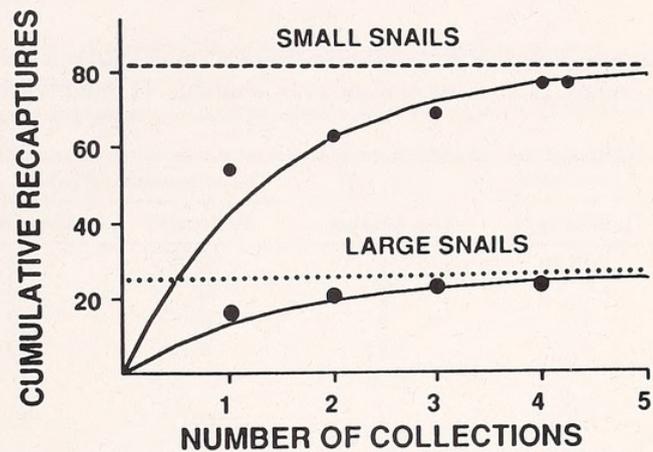


Figure 4

Cumulative number of tagged *Cittarium* recaptured 168-174 days after release versus number of successive collections, for all tag-recapture sites combined. Also shown are the asymptotically estimated numbers of large (.....) and small (---) snails present within 20 m from their points of release.

of the snails had remained within a 20-m radius while at SH sites 85% had. After scaling for differences in total number of recoveries per site, habitat differences in dispersal were significant ($\chi^2 = 15.41$, d.f. = 4, $P < 0.005$).

No dispersal correction factor was calculated for EXP habitat because of few recoveries. However, the two recoveries of small shells made at EXP sites were within 1

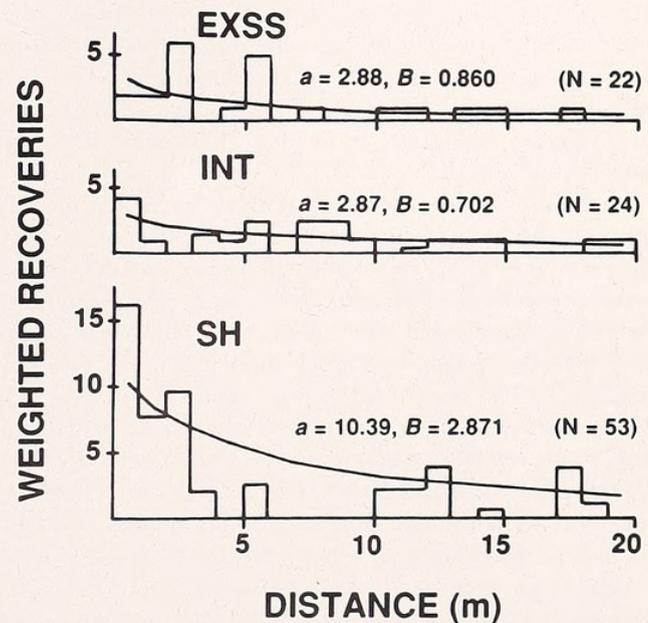


Figure 5

Percentage recoveries of live tagged *Cittarium* as a function of the distance from their points of release, after 168-174 days at large. Fitted curves are of the form $Y = a - B \ln(X)$ where Y is the number of recaptures and X is the distance from the point of release.

Table 3

Tagged-shell releases and recoveries for small *Cittarium* (\bar{x} = 22.8 mm) by site, and the corresponding growth and survival estimates. Dashes indicate data not available. Habitat types: exposed (EXP), exposed shallow sloping (EXSS), intermediate (INT), and sheltered (SH).

Habitat type	Site number	Number of snails		Percent recovered	Survival rate (%/year)	Growth rate (mm/year)
		Released	Recovered			
EXP	1	40	2	5	0.7	7.9
	2	40	0	0	<0.2*	—
	3	40	0	0	<0.2*	—
	5	40	0	0	<0.2*	—
					Average:	0.2
EXSS	4	80	22	27.5	12.7	10.2
INT	6	40	6	15.0	7.2	15.2
	7	40	0	0.0	<0.2*	—
	8	40	2	5.0	0.7	15.2
	9	40	13	32.5	37.5	25.0
					Average:	11.3
SH	10	40	8	20.0	8.0	22.6
	11	40	4	10.0	1.8	19.4
	12	36	10	27.8	16.1	22.4
	13	40	19	47.5	50.7	31.2
	14	40	12	30.0	19.0	16.9
				Average:	19.1	22.4

* Due to the small number of releases and the fact that fractional recoveries are not possible, the estimates of survival are not continuously distributed. For the cases with zero recoveries, mortality estimates are presented as less than (<) the value that would have been obtained with one recovery. In all such cases, a zero survival value was used in calculating average annual survival for each habitat type.

m from the point of release. The low number of recoveries at EXP sites is not believed to be due to unusually high levels of emigration because searches far beyond 20 m from the point of release yielded no additional recoveries. Survival estimates for EXP sites were, therefore, derived using the dispersal correction factor for INT sites, the most conservative choice.

Survival estimates for small snails differed significantly between the habitats for which multiple estimates were obtained ($P = 0.032$, Kruskal-Wallis test). Lowest average survival was at EXP sites (0.172%/year) where only 2 of the 160 snails released were again recovered. Average survival for small snails was much higher at other sites, averaging 12.7%/year, 11.3%/year, and 19.1%/year for EXSS, INT, and SH sites, respectively (Table 3). For the large snails released, average survival estimates were 6.2%/year at EXP sites and 29.8%/year at SH sites (Table 4) but, with a low number of replicates per habitat type, did not differ significantly ($P > 0.10$, Mann-Whitney U test).

Few large dead shells were collected from EXP sites (Figure 6), mirroring their low abundance in the live snail collections. At both EXP and INT sites, most dead shells were classified as lethally crushed (50% and 42%, respectively). At EXP sites, drilled shells constituted the second-largest fraction, while undamaged shells were the least abundant of the three fractions. In contrast, at INT sites, undamaged shells constituted the second-largest fraction

while drilled shells were the least abundant. Higher fractions of drilled and crushed shells at EXP sites suggested higher predation mortality than at INT sites ($\chi^2 = 20.10$, d.f. = 2, $P < 0.005$). However, due to a tendency for larger shells to have a lower incidence of predatory shell damage (Table 5) and due to the difference between habitats in dead-shell size structure, size-specific comparisons were necessary. For snails in the size classes for which comparable samples were obtained (the 30–40 mm and 40–60 mm size classes), P -values of less than 0.06 suggested higher predation mortality in EXP (Table 5).

Average growth rates for small snails were 7.9 mm, 10.2 mm, 18.4 mm, and 22.4 mm/year for EXP, EXSS, INT, and SH sites, respectively (Table 3). Lowest growth rates were in EXP and EXSS habitats, both of which had high snail densities. Small sample sizes precluded statistical comparison of more than two habitats unless estimates from EXP and EXSS habitats were pooled to form a third habitat class. A comparison of growth rates between INT and SH habitats showed no significant differences ($F_{(1,6)} = 1.032$, $P = 0.349$), whereas including a third habitat class (with pooled EXP and EXSS estimates) did result in significant habitat differences ($F_{(2,7)} = 4.918$, $P = 0.046$). For the more limited release of large tagged snails, average growth rates appeared uniformly low among habitat types (Table 4).

Von Bertalanffy growth parameter estimates for EXP

Table 4

Tagged-shell releases and recoveries for large *Cittarium* (\bar{x} = 80.0 mm) by site, and the corresponding growth and survival estimates.

Habitat type	Site number	Number of snails		Percent recovered	Survival rate (%/year)	Growth rate (mm/year)
		Released	Recovered			
EXP	2	17	3	17.6	10.2	4.5
	3	17	2	11.8	4.3	2.6
	5	17	2	11.8	4.3	8.1
				Average:	6.2	5.1
SH	10	17	6	35.3	26.9	3.4
	13	16	8	50.0	56.5	1.9
	14	17	3	17.6	6.1	2.1
				Average:	29.8	2.6

sites also suggested low growth rates compared to SH sites. Using midpoint parameter estimates (Table 6), the age of a 65-mm snail from SH habitat would be about four years, while that of a 65-mm snail from EXP habitat would be about nine years.

Average shell width at first maturity was smallest at EXP sites (\bar{x} = 16.7 mm; range, 14.5–17.8), intermediate at INT sites (\bar{x} = 20.2 mm; range, 18.4–21.4), and largest at SH sites (\bar{x} = 24.2 mm; range, 22.8–27.9), and differed significantly between habitats ($F_{(2,10)} = 23.37$, $P = 0.002$). In addition, fecundity levels were consistently lowest at EXP sites (Table 7).

DISCUSSION

The tagging experiment indicated highest rates of mortality for *Cittarium* in EXP habitat. The higher density of molluscan predators and the higher proportion of lethal

predatory shell damage, as compared to less exposed habitat, may account for these observations. Growth rates, size at first sexual maturity, and fecundity were the least in EXP habitat. Higher *Cittarium* density may reduce *per capita* food availability in EXP habitat. However, other factors, such as differences in wave stress, air and water temperatures, and floral food value, may also be important factors affecting growth rate, size of maturation, and fecundity.

In contrast, EXSS habitat had high densities of large animals. Growth and survival rates were measured at one EXSS site (site 4). Growth, based on 22 recaptures, was similar to that at other high-density EXP sites and was slow compared to growth rates at SH and INT sites. The survival estimate at the EXSS site was much higher than at EXP sites, suggesting that shallow topography may reduce mortality rates. In particular, dislodgement by waves, which is known to subject snails of wave-exposed habitat

Table 5

Number of *Cittarium* shells in each of three shell-damage categories for shells collected from EXP and INT habitats.

Habitat type	Shell damage category	Shell size (mm)						All sizes	Percent of total observations
		0–20	21–30	31–40	41–50	51–60	≥61		
EXP	Drilled	26	61	41	11	3	1	143	37
	Crushed	14	109	43	15	11	1	193	50
	Undamaged	10	24	9	3	2	5	53	13
	Totals	50	194	93	29	16	7	389	100
INT	Drilled	1	2	3	4	3	9	22	25
	Crushed	0	10	7	11	4	5	37	42
	Undamaged	0	1	11	5	5	7	29	33
	Totals	1	13	21	20	12	21	88	100
P^*	—	0.952	0.004	0.059	0.194		<0.005		

* P -values compare size-specific importance of predatory mortality (combined crushed and drilled) and nonpredatory mortality (undamaged) between habitats. Fisher-Irwin tests except the comparison for all shell sizes combined. The latter was done using a χ^2 goodness-of-fit test. Dashes indicate test not made.

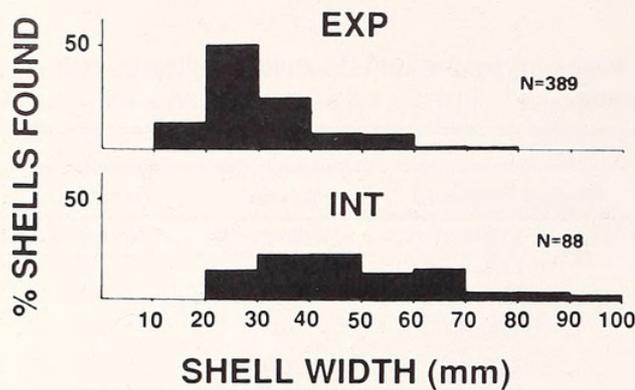


Figure 6

Size frequencies for dead *Cittarium* shells found in EXP and INT habitat types.

to increased predation (UNDERWOOD & DENLEY, 1984; MORAN, 1985), may be less at EXSS sites.

Cittarium size-frequency distributions differed greatly with differences in habitat wave-exposure and topography. A preponderance of small snails was found at EXP sites, where growth rates were low and mortality was high. At SH and INT sites, where growth rates were high and mortality was low, large snails were relatively more abundant.

Large-scale movement of large snails into SH or INT habitat is, in most cases, unlikely because of intervening sandy areas. Because losses due to fishing could also be considered negligible, differences between habitats in terms of survival and growth appear to be the main contributors to the gross differences seen in population structure. Negatively skewed size-frequency distributions, as found in SH habitat, have been described for other reef invertebrates (YAMAGUCHI, 1977). Such distributions may result from size-differential recovery efficiency (APPELDOORN & BALANTINE, 1983; AULT & DEMARTINI, 1987) or temporal variability in recruitment (FRANK, 1969; UNDERWOOD, 1975) but may also be attributed to animals surviving to near their maximum size. Annual growth increments monotonically decrease at sizes approaching L_{∞} , and population modes, consequently, tend to merge (SAINSBURY,

Table 6

Von Bertalanffy growth parameter estimates for *Cittarium* with 95% confidence intervals. Parameter estimates are from snails that were at large August 1984–January 1985. K is expressed as an annual rate.

Habitat type	Site number	n	K	L_{∞} (mm)
EXP	All sites	9	0.056 ± 0.054	167.94 ± 84.13
SH	10	17	0.291 ± 0.036	84.00 ± 5.95
	13	26	0.659 ± 0.034	81.12 ± 2.18
	14	14	0.369 ± 0.022	88.84 ± 2.83

Table 7

Size-specific average gonad indices (G.I.) and sample sizes for *Cittarium* collected in August 1984 in three habitat types.

Size (mm)	Habitat type						P^*
	EXP		INT		SH		
	G.I.	n	G.I.	n	G.I.	n	
11–20	0.10	4	—	—	—	—	—
21–30	0.11	40	0.30	2	0.16	8	0.468
31–40	0.21	36	0.43	3	0.23	14	0.042
41–50	0.08	31	0.42	8	0.26	11	0.000
51–60	0.10	5	0.29	7	0.33	6	0.056
61–70	0.33	3	0.40	7	0.44	17	0.270
71–80	—	—	0.52	1	0.45	11	—
81–90	—	—	—	—	0.40	7	—

* P -values are for statistical comparisons between habitat types. ANOVA F -tests. Dashes indicate data not available or test not made.

1982). The latter may explain the negatively skewed size-frequency distributions in this study for two reasons. The first is that all such distributions were from the habitat where survival and growth rates were highest (SH), and where, therefore, the accumulation of old animals was likeliest. The second is that the implied merging of age-class modes occurred near L_{∞} and not in the intermediate size classes. Large population modes at intermediate size classes would have suggested that other factors, such as temporal variability in recruitment or survival, were also important factors shaping size structure.

RANDALL (1964) noted that *Cittarium* is generally rare on sheltered coasts. Compared to more exposed habitats, lower population densities in SH habitat could either be from lower levels of settlement or lower levels of subsequent survival. In this study it was found that rates of survival and growth for snails greater than 20 mm were comparatively high in SH habitat. Thus, low densities in SH habitat appear to be caused by factors affecting settlement or the early postlarval stages of the snail.

Factors that may affect settlement include the supply of larvae and settlement preferences. Because SH sites had dramatically lower *Cittarium* population densities in spite of their often close proximity to high snail-density EXP and INT habitats, the low population densities in SH habitat were probably not due to reduced supplies of larvae. Reduced survival of juveniles because of desiccation during low tide may contribute to low densities in SH habitat. In contrast to large snails, those smaller than 10 mm did not appear to migrate to lower intertidal zones during low tide but remained in the upper intertidal zones (DEBROT, 1990). In EXP and EXSS habitats such snails would be wet periodically, but in SH habitat they could experience periods of up to 12 hr without immersion.

Although the cause for lower population densities of

young snails in SH habitat remains unknown, the low densities of conspecifics and predators in such habitat seem to translate into higher growth and survival rates for snails of the size range studied.

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