

**PROCEEDINGS  
OF THE  
EIGHTH SYMPOSIUM  
ON THE  
NATURAL HISTORY OF THE BAHAMAS**

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Gerace Research Center  
San Salvador, Bahamas  
2001

**Cover Illustration:** *Passiflora cupraea* L. Smooth Passion Flower  
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the 2<sup>nd</sup> Edition of **Common Plants of San Salvador** by Lee Kass.

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Printed in USA

ISBN 0-935909-70-2

## **EFFECT OF SALINITY ON THE ECOLOGY OF MOLLUSCS IN THE INLAND SALINE WATERS OF SAN SALVADOR ISLAND: A NATURAL EXPERIMENT IN PROGRESS**

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### **ABSTRACT**

Owing to their geological composition and history, the Bahamas are riddled with a maze of sinkholes, caves, and conduits through which the tides rise and fall within islands, producing tidal ponds, inland blue holes, and lakes of differing salinities. These "islands" of marine habitat are isolated within land islands and, like land islands, have greatly simplified communities. The typical molluscan assemblage consists of just three gastropods and two bivalves. The effect of salinity on the competitive and dominance relations among the molluscs were determined by sampling in matched (i.e., replicate) sites with brackish, fully marine, or hypersaline salinities (i.e., three salinity treatments). In brackish sites, either of two gastropods, each associated with a particular bivalve, can dominate or, if co-occurring in numbers, subdivide their niche space (differing in sizes and depth distributions). The third gastropod was dwarfish in size. In fully marine ponds, the third gastropod was full-sized and dominant; additional molluscs occurred; and the relationships among bivalves varied. With increasing salinities, another factor comes into play: dense communities of microorganisms form a flocculent layer in the water column and produce anaerobic conditions on the bottom. Offshore molluscs must live on or nestle in this living layer of microorganisms. At the hypersaline sites, either one bivalve prevailed or, with a wider salinity range, both occurred; in either case the abundances of the gastropods differed between shorelines and the flocculent layer. These studies on a small, remote island should be extended to larger, less isolated islands of the Bahamas.

### **INTRODUCTION**

Because the islands of Bahamas are entirely composed of carbonate rock that is soluble in rain water, fresh groundwater, and CaCO<sub>3</sub>-saturated groundwater mixing with CaCO<sub>3</sub>-saturated seawater, they afford karst landscapes riddled with, and underlain by, such dissolution features as sinkholes and caves (Myroie and Carew, 1995). With changing sea levels during and since the Pleistocene, conduits to the sea developed at different horizons with shafts connecting them. The result is a maze of passages through which the tides rise and fall within the limestone islands, producing an array of as yet little studied inland saline waters. Tidal brackish blue holes and ponds have marine conduits that intersect with freshwater lenses; tidal fully marine ponds have large and active conduits relative to their size; and non-tidal hypersaline ponds and lakes have modest conduits relative to their large surface areas, so the excess of evaporation over precipitation raises salinities. These diverse anchialine habitats (i.e., fed by saline cave waters; cf. Davis and Johnson, 1989) are "islands" of marine habitat lying isolated within land islands, which may, as in the case of San Salvador, have been remotely set apart by deep (>1,000 m) ocean waters since the Cretaceous.

Owing to the accidents of colonization and extinction, each "island" of saline water affords a natural experiment of some kind, e.g., the effect of the presence or absence of a given species; and all, like land islands, have greatly simplified, and thus easier to study, tropical communities (Edwards, 1996). Gould (1968) treated a fully marine anchialine pond on Bermuda as an experiment in simplification, but found the molluscan assemblage did not differ

between the pond (24 species) and coastal controls. In contrast, the anchialine waters of San Salvador support a core assemblage (typically the total assemblage) of just five ecologically little known molluscs (Edwards *et al.*, 1990): a guild of three herbivore/detritivore Cerithiacean gastropods, *Batillaria minima*, *Cerithidea costata*, and *Cerithium lutosum*, and two suspension-feeding bivalves, *Anomalocardia auferiana* and *Polymesoda maritima*. This core group, as a fossil assemblage, has already been used to distinguish inland saline waters from the transgressions of coastal lagoons during the Sangamon Interglacial (Hagey and Mylroie, 1995). None of the gastropods is likely to have planktonic larvae (Houbrick, 1974; 1984; Yamada and Sankurathri, 1977); whereas, those expected for the bivalves are unlikely to reach and survive in subterranean waters (see Study Sites). Because all five species live in intertidal and shallow mud flats, they may be carried among ponds on the feet of wading birds. Molluscs numerically dominate the island's ponds, and other macrofauna is very poorly represented.

The main aim of this study is to determine the effect of salinity on the competitive and dominance relations among the molluscs by sampling matched (i.e., replicate) sites with brackish, fully marine, or hypersaline salinities (i.e., three salinity treatments). The design of this natural experiment is given in Table 1. Because most of the study sites are new to science and no survey of their molluscs exists, a second aim is exploration.

### STUDY SITES

All of the replicate sites are primarily shallow ( $\leq 3$  m depth) basins whose largely bare, apparently mud substrates are actually beds of molluscan shells in a matrix of soft carbonate mud. Sampling was confined to the basins, so such high-tide marsh species as *Melampus coffeus* were excluded from this study.

The brackish replicates are part of a complex of blue holes at the southwestern corner of San Salvador (Fig. 1). These sites are listed in Table 1 in the order of decreasing size and potential stability of physical factors. Watling's

Blue Hole (WBH) has an area of  $\geq 3,000$  m<sup>2</sup> and a funnel-shaped bottom reaching its conduit at a depth of 6.3 m; the conduit leads to a cave passage at  $\approx 9$  m depth (all depths are relative to mid-tidal levels). Grebe Blue Hole (GBH) and Blue Hole 2 are of moderate ( $\approx 1,100$  m<sup>2</sup>) to small ( $\leq 700$  m<sup>2</sup>) sizes, and only near their centers are they  $\geq 3$  m deep; their conduits extend to  $> 5$  m depths. These circular sites are effectively isolated: Teeter and Quick (unpub. data) dyed GBH and WBH dark red with fluorescent rhodamine B on falling tides, but after nine days using probes sensitive to 50 ppb detected no dye at BH2 or Blue Hole 5 (Fig. 1). Their tidal ranges are similar ( $\approx 80$  % of the ocean's), and their tidal lag times vary from  $\approx 30$  to 40 min.

For comparative purposes, qualitative observations were made at three additional brackish sites. Blue Hole 5 (BH5; Fig. 1) is less saline than the replicate sites, but resembles them in size (BH2 < BH5 < GBH) and other features. Olaf Pond (OP) and North Pigeon Creek Quarry (NPCQ) on the southeast side of the island are small ( $\approx 300$  m<sup>2</sup> and  $\approx 125$  m<sup>2</sup> basins), shallow ( $\leq 1$  m and  $\leq 0.5$  m depths), and potentially less physically stable tidal ponds whose salinities overlap those of the replicate sites.

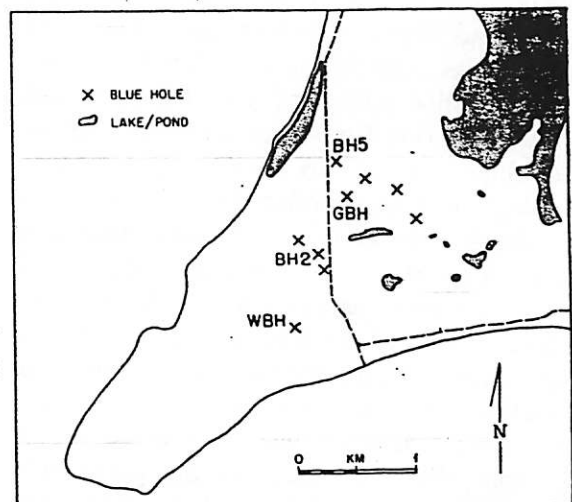


Figure 1. The complex of brackish blue holes at the southwestern corner of San Salvador Island, with study sites designated as in the text. --- = main road.

All of the fully marine sites and the two hypersaline ones studied to date are in northeastern San Salvador, lying south and southeast of the Bahamian Field Station along a system of trails cut to reach them (the BFS Trail). Maps and descriptions of these sites are available in Godfrey *et al.* (1994). The fully marine sites are listed in Table 1 in the order of increasing flocculent layers. Moon Rock Pond (MR) has a bare bottom of fine white mud and no flocculent layer; it is  $\approx 85$  m wide by  $\approx 170$  m long. Pain Pond (PP) is smaller ( $\approx 70$  m X  $\approx 110$  m), has an incomplete flocculent layer (0 to  $\approx 15$  cm thick), and supports a distinctive population of the conduit-dwelling red shrimp, *Barbouria cubensis*. Although PP lies  $< 100$  m northeast of MR and southeast of Crescent Pond, its tidal range is much greater ( $\approx 80$  % vs.  $\leq 40$  % of the ocean's) and its tidal lag time is much less (1.35 hr vs.  $\approx 2.35$  hr) than the other two replicates. Crescent Pond is  $\approx 70$  m wide by  $\approx 525$  m long, and most of its white mud bottom (like MR) is overlain by  $\approx 15$ -30 cm of flocculent layer (whose biota may have been underrepresented in core samples; see Methods). The additional fully marine site, Oyster Pond (Oyster), differed greatly from the replicate sites. It is larger ( $\leq 350$  m diam), has a dense flocculent layer usually 1 m or more above its bare limestone bottom, and is the only brackish or marine site to be ringed by red mangroves; its tidal regime resembles that of Pain Pond  $> 0.5$  km to the northeast. Oyster is the most inland site (1 km from the coast), yet supports by far the most diverse array of marine invertebrates.

Osprey Pond (Osprey) is the only non-tidal, hypersaline site studied in some detail to date. It is large ( $\approx 280$  m X  $\approx 400$  m) and ringed by both red and black mangroves. Its flocculent layer is generally  $< 1$  m thick, lying close to the muddy bottom, and is missing along the downwind (western) shore. Reckley Hill Pond (RHP) is similar to Osprey in size and has a muddy, even goeey, anaerobic mud bottom; it differs in lacking black mangroves, having a distinctive pink flocculent layer that rises to within 1 m of the surface, and being adjacent to extensive, dense red mangrove swamps whose salinities are very brackish. Aside from salinity readings, Little Lake and Great Lake remain unstudied.

## METHODS

The salinity regimes for the brackish replicates from Feb. 1977 through June 1999 were obtained from Hobbs (1978), by J. W. Teeter (1980-1992), by P. J. Godfrey and myself (1987-1995), by myself (since 1996), and occasionally from others. The least accurate salinity readings were made with refractometers whose error ranges ( $\approx 0.1$  ppt) were trivial compared to salinity changes caused by day-to-day weather. When multiple readings were available for a season at a given site and depth ( $\approx 0.5$  m="shallow";  $> 2$ -3 m or conduit mouth="deep"), a mean value was used for that season, site, and depth, so no unusual season with extra readings would bias the results; thus N=seasons for salinity data, with N=65 for winter (Dec-Feb), 8 for spring (Mar-May), and 32 for summer (Jun-Aug).

Salinity data obtained by Drs. Teeter, Godfrey, and myself are less extensive for the fully marine and hypersaline replicates and additional sites, which were inaccessible or even unknown until trails were cut to them. For the fully marine sites (MR, PP, CP, and Oyster), data are available since 1987. For the hypersaline sites, data are available since 1986 for Osprey and 1982 for RHP. In contrast, Olaf Pond was only discovered in 1996. Again, N = seasons, and all values reported here are "shallow."

The basic sampling design for molluscs consisted of taking quantitative cores of 125 cm<sup>2</sup> to 10 cm depth (later to 3 cm depth after no deeper dwelling molluscs had been taken in  $> 80$  of the deep cores) at random intervals along a single transect line (100 m tape measure) bisecting each basin from shore to shore. To explore widely, each site was sampled once in winter (January). At the circular, brackish blue holes, 15 cores were taken along transect lines passing through the deepest areas at the conduits, which, being off-center, meant each transect line was determined by the topography at the site. WBH and BH2 were sampled in 1987, and GBH in 1993. At the fully marine replicate sites, 18, 20, and 20 cores were taken in 1989 at PP, 1990 at MR, and 1994 at CP

along transect lines bisecting ponds along their shorter axes. At Osprey, 15 cores were taken for 50 m along a compass heading out from each of the opposite shorelines and into the flocculent zone in 1995 and 1996. At RHP, 4 cores were taken along a transect extending from the south shore into the flocculent layer in 1990, and one random core was taken near the shore at the southwest (downwind) corner of the pond in 1991. Extra samples were taken at arbitrary points (blind reach or pebble toss) in distinctive places (e.g., muddy ledge or tidal pool on a rocky shore) at WBH (N=3), BH2 (N=2), PP (N=4), and MR (N=4). (All uses of these supplementary data are presented parenthetically in the Results.) A total of 151 cores have been sorted.

With increasingly thick flocculent layers, the coring method took fewer of the molluscs present, so a sampling method using scoops with a circular sieve of 680 cm<sup>2</sup> (=5.44 X the area of cores) was devised. At Oyster 6 scoops were taken at approximate intervals to the center of the pond in 1998. At Osprey in 1999, nine scoops were taken at 25 m intervals along a 200 m transect centered at mid-pond and overlapping the ends of the two 50 m cored transects. In 1996 a further method was used at Oyster, where the boundaries of the pond are effectively a wall of prop roots of red mangroves. At my suggestion, Eric Cole and students from St. Olaf College enclosed three vertical prop roots in large garbage bags and carefully tied them off at 10 cm intervals to examine zonation; I then identified and measured the molluscs.

All cores and scoops were sieved in the field on a 2 mm mesh screen and placed in labeled plastic bags for later sorting. Because small, well-preserved mollusc shells usually comprised most of the sediment, processing a single sample could involve examining tens of thousands of shells and measuring and opening hundreds to count the live animals present. All molluscs were identified and measured ( $\pm 0.1$  mm). Qualitative surveys at the additional brackish sites simply tallied live molluscs encountered in systematic searches until, in the minimal cases, 100 individuals of the commonest species were taken.

## RESULTS

The salinity data indicate both that the replicate sites were as closely matched as is feasible under field conditions (see below) and that the target salinity values for the three treatments (Table 1) were approximated well at all sites sampled to date. Owing to varying patterns of precipitation over several-year spans as well as Hurricane Lili in 1996, salinities at the brackish replicates ranged above and below the target value of 25 ppt; overall, shallow waters averaged  $20.66 \pm 6.96$  SD (N=64 seasonal values), while deep waters averaged  $24.28 \pm 3.69$  SD (N=35). At the fully marine replicates, salinities averaged  $35.13 \pm 1.83$  SD (N=43). Salinities at the hypersaline sites, Osprey and RHP, averaged  $45.45 \pm 11.36$  SD (N=41), but ranged even more widely than those at the brackish sites for similar reasons.

Only the sampling data for the brackish sites has been fully analyzed; for the fully marine and hypersaline sites only numbers and sizes by species are as yet available. Although the composition of the molluscan assemblages varied remarkably within sets of replicates, nonetheless distinctive patterns emerged for each treatment.

### Brackish Sites

Because salinity readings among the replicate sites varied in rough synchrony through a broad range ( $\geq 20$  ppt for shallow depths) with each site at times having the highest value, it was only after 58 "shallow" and 29 "deep" seasonal values (1977-97) were obtained that any significant difference by site was found, i.e., the matching of replicates was good. Using all data to date (N=64 and 35, respectively), however, ANOVA tests show the salinities of the three blue holes differed by depth ( $p < 0.005$ ) and site ( $p < 0.005$ ), but not by season. Specifically, the salinities (ppt) at WBH (shallow= $23.4 \pm 5.5$  SD; deep= $26.2 \pm 2.4$  SD) exceeded those at GBH ( $18.6 \pm 6.9$  SD and  $23.2 \pm 3.2$  SD) and BH2 ( $18.5 \pm 7.8$  SD and  $22.5 \pm 4.4$  SD); whereas the salinities at the latter sites did not differ. The lowest values were recorded after extended periods of heavy rain in

Table 1. The design of a natural experiment on the effect of salinity on the ecology of molluscs. Actual salinities (in ppt) will vary about the target values listed.

REPLICATE	SALINITY TREATMENT		
	BRACKISH ≈25 ppt	FULLY MARINE ≈35 ppt	HYPERSALINE ≈ 45 ppt
1	Watling's Blue Hole	Moon Rock Pond	Osprey Pond
2	Grebe Blue Hole	Pain Pond	(Reckley Hill Pond)
3	Blue Hole 2	Crescent Pond	(Little Lake?)
Additional Sites	BH5, Olaf, NPC Quarry	Oyster Pond	(Great Lake?)

Table 2. Molluscs taken in 50 cores at brackish replicate sites; total N=1,059. Values in parentheses include animals taken in extra samples.

SPECIES	WATLING'S BLUE HOLE	GREBE BLUE HOLE	BLUE HOLE 2
<b>GASTROPODA</b>			
<i>Batillaria minima</i>	485 (600)	62	0 (3)
<i>Cerithidea costata</i>	1 (2)	119	44 (62)
<i>Cerithium lutosum</i>	13 (13)	21	3 (3)
<b>BIVALVIA</b>			
<i>Anomalocardia auberiana</i>	21 (23)	50	4 (4)
<i>Polymesoda maritima</i>	3 (4)	31	14 (62)
<b>TOTAL N</b>	523 (642)	283	65 (134)
<b>TOTAL S</b>	5 (5)	5	4 (5)

Table 3. Molluscs taken in 66 cores at fully marine sites; total N=1,129. Values in parentheses include animals taken in extra samples. p = present.

SPECIES	MOON ROCK POND	PAIN POND	CRESCENT POND
<b>GASTROPODA</b>			
<i>Cerithium lutosum</i>	235 (300)	148 (316)	56
<i>Cerithidea costata</i>	32 (65)	52 (97)	5
<i>Batillaria minima</i>	0 (1)	1 (1)	91
<i>Bulla</i> sp.	1 (2)		
<b>BIVALVIA</b>			
<i>Tellina mera</i>	81 (82)	0 (0)	2
<i>Codakia orbiculata</i>	32 (38)	0 p	26
<i>Brachidontes exustus</i>	37 (37)	0 (0)	0
Unknown <i>Abra</i> ?	0 (0)	5 (5)	0
<i>Anomalocardia auberiana</i>	0 (0)	0 (0)	3
<i>Gemma gemma</i>	0 (2)	0 (0)	0
<b>TOTAL N</b>	418 (527)	206 (419)	183
<b>TOTAL S</b>	6 (8)	4 (5)	6

unusually rainy years. Exceptionally low outlier values (excluded from analyses) were obtained after such rains in Jan. 1997 caused a very rare, impassable flooding in the study area. After 1.5 days I got through by truck to record the following "shallow" and "deep" salinities from the opaque, tannin-stained waters at each site: at WBH, where standing freshwater occurred nearby, 2.0 and 9.0 ppt; at GBH, with no freshwater nearby, 2.2 and 9.5 ppt; and at BH2, into which a moderate waterfall of freshwater was pouring, 2.0 and 2.0 ppt. Thus in the long-term, WBH had a higher salinity; whereas, during rare periods of very low salinities, BH2 was the most vulnerable.

The brackish replicates supported at least a few individuals of all five molluscs of the core assemblage, but no other molluscs (Table 2). The dominance relations in this simple assemblage, however, differed greatly among sites. Among the gastropods, the overwhelming dominance of *B. minima* at WBH was reversed at BH2, where *C. costata* (the rarity at WBH) was dominant and *B. minima* was barely detectable. In contrast, at GBH *C. costata* and *B. minima* co-occurred in substantial numbers. Similarly for the bivalves, the dominance of *A. auberiana* over *P. maritima* at WBH was reversed at BH2 and less evident at GBH; essentially, *A. auberiana* did well where *B. minima* did, and *P. maritima* succeeded where *C. costata* did.

At the sites where the ecologically similar potamidids *B. minima* and *C. costata* were overwhelmingly dominant (and the opposite species rare), there was no difference in their mean sizes ( $p > 0.50$ ; t-test;  $10.17 \text{ mm} \pm 0.06 \text{ SE}$  and  $10.27 \pm 0.37 \text{ SE}$ , respectively), and their size-frequency distributions overlapped broadly. Also at these sites the dominants did not differ in their depths of occurrence ( $p > 0.24$ ; Mann-Whitney U test) and occurred at all depths. Thus at WBH *B. minima*, "a very common intertidal species" (Abbott, 1974), was taken from the high intertidal (extra samples in *Sporobolus virginicus* marsh and on a stone wall) to 6.3 m depths in mud -- an example of the islandic phenomenon of "ecological release" in the absence of competitors and predators. In contrast, at GBH, where both gastropods occurred in numbers, their niche dimensions

differed. Here *B. minima* was markedly larger than *C. costata* ( $p < 0.0001$ ; t-test; Fig. 2) and occurred at shallower depths ( $p < 0.0001$ ; Mann-Whitney U test; Fig. 3). The third gastropod, the cerithiid *Cerithium lutosum*, was never abundant and consistently differed from the dominants in its smaller mean size ( $8.44 \pm 0.28 \text{ SE}$ ) relative to both ( $p < 0.0015$ ; ANOVA), constituting what Houbriek (1974, p. 76) has termed "dwarf" populations.

Mean sizes of the bivalves differed ( $p = 0.001$ ), with *A. auberiana* being smaller ( $12.99 \text{ mm} \pm 0.43 \text{ SE}$ ) than *P. maritima* ( $15.50 \pm 0.63 \text{ SE}$ ). Patterns in the depths of occurrence of the two species were inconsistent.

At the additional brackish sites, one or more species of the core assemblage was missing. The tally of molluscs observed at BH5, the lower salinity site ("shallow" = 10.44 ppt  $\pm 6.8 \text{ SD}$ ;  $N = 7$  seasons), included 190 *C. costata*, 136 *P. maritima*, and 49 *A. auberiana*. The small, shallow sites, OP and NPCQ, differed in that the former site was inundated by a freshwater waterfall in Jan. 1997 ( $\leq 1 \text{ ppt}$ ), and the latter was not (24.25 ppt). At NPCQ (25.50 ppt  $\pm 1.74 \text{ SD}$ ;  $N = 4$ ) in Jan. 1998, *C. costata* outnumbered *C. lutosum* by 100 to 21, with the *C. lutosum* concentrated near mid-pool; and *P. maritima* was the only bivalve taken. In Jan. 1998, OP (19.12 ppt  $\pm 6.30 \text{ SD}$ , excluding the outlier value;  $N = 4$ ) yielded only *C. costata* ( $N = 100$ ) and a modest number of the tiny bivalve *Gemma gemma*.

#### Fully Marine Sites

Salinity readings (ppt) among the replicate sites and Oyster Pond varied through narrow ranges of 5 to 8 (at MR) and did not differ among the replicates ( $p > 0.50$ ) or among the replicates and the additional site ( $p > 0.28$ ). Mean salinities increased insignificantly with the size of the pond: PP ( $34.7 \pm 1.6 \text{ SD}$ ;  $N = 15$  seasons) < MR ( $35.3 \pm 2.4 \text{ SD}$ ;  $N = 14$ ) < CP ( $35.4 \pm 1.5 \text{ SD}$ ;  $N = 14$ ) < Oyster ( $35.9 \pm 1.8 \text{ SD}$ ;  $N = 19$ ).

The fully marine replicates supported at least a few individuals of all three gastropods of the core assemblage, and MR, the site with the most molluscs, yielded an additional one, *Bulla* species (Table 3). In general, *C. lutosum* (which



Table 4. Molluscs taken at Oyster Pond; total N=610.

SPECIES	3 R. mangle prop roots	Open water (floc layer)
<b>GASTROPODA</b>		
<i>Cerithium lutosum</i>	151	51
<i>Cerithidea costata</i>		19
<b>BIVALVIA</b>		
<i>Brachidontes exustus</i>	221	
<i>Isognomon alatus</i>	114	
<i>Pinctada imbricata</i>	7	
Unknown mussel	1	
<i>Anomalocardia auberiana</i>		28
<i>Tellina mera</i>		18
<b>TOTAL N</b>	<b>494</b>	<b>116</b>
<b>TOTAL S</b>	<b>5</b>	<b>4</b>

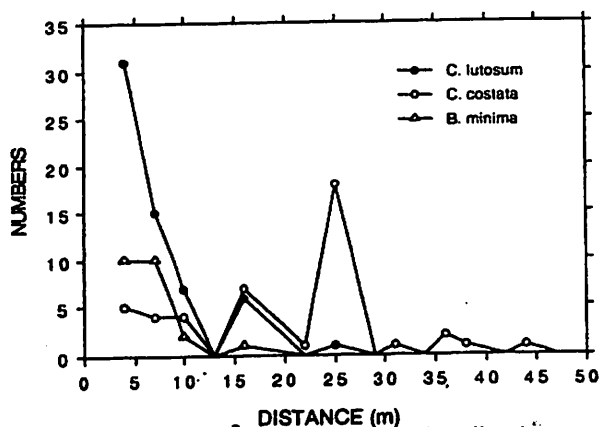


Figure 2. The size-frequency distributions of *Batillaria minima* and *Cerithidea costata* at Grebe Blue Hole.

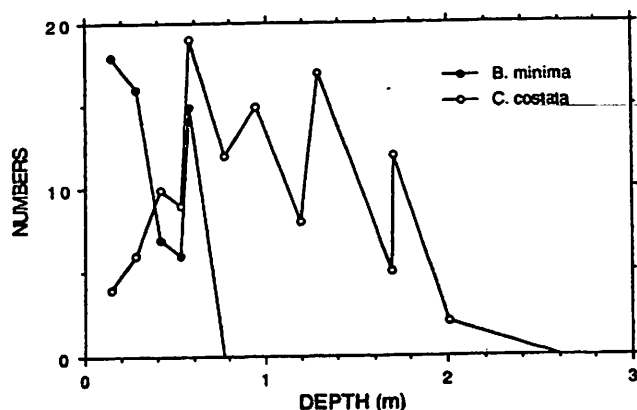


Figure 3. The distributions by depth of *Batillaria minima* and *Cerithidea costata* at Grebe Blue Hole.

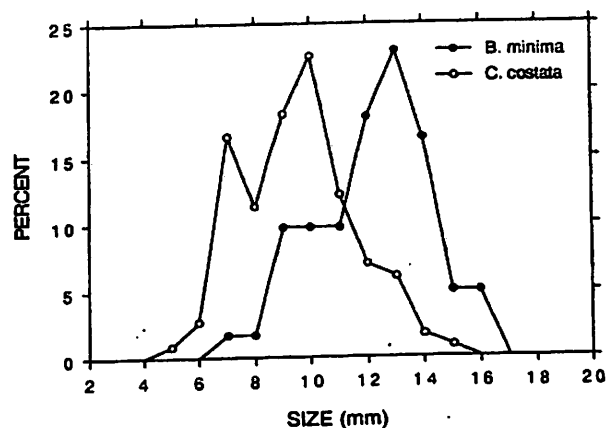


Figure 4. The numbers of gastropods by species taken in 125 cm<sup>2</sup> cores along a transect extending 50 m out from the western shore of Osprey Pond.

was never abundant in brackish sites) was the dominant species within basins, with *B. minima* and *C. costata* being successively relegated to mid-tidal and higher zones. This pattern was least clear at CP, where 91% of the snails were taken in the two cores nearest each shore in dense to thinning (with depth) beds of the seagrass *Ruppia maritima* and where offshore cores (which took only *C. lutosum*) may have underrepresented animals living in the flocculent layer (see below). The mean sizes of *C. lutosum* differed among all three sites, ranging from dwarfish (as at brackish sites) to large as densities decreased: MR (6.75 mm  $\pm$  0.12 SE; N=231) < PP (8.68 $\pm$ 0.19; N=148) < CP (10.68 $\pm$ 0.30; N=56). Although the *B. minima* at MR occur only in a narrow mid-tidal zone, they are very conspicuous because many are deformed giants (apparently forming a terminal shell lip and then recommencing growth; cf. Warmke and Abbott, 1962). This deformity is infrequent at CP and very rare or absent in other populations.

The replicate sites yielded a mixed array of six species of bivalves, including only one of the "core" species (Table 3). (The *A. auberiana* at CP were taken in offshore cores that may have undersampled them; this "infaunal" species nestles in the flocculent layer, a new mode of life for it.) MR was most supportive of bivalves and had a distinctive assemblage of them; it is the only site studied to date where *Tellina mera* was dominant. (CP may have more species, because its unsampled rocky shores and buttonwood trees bear many mangrove oysters, *Isognomon alatus*, and mussels, *Brachidontes exustus*.) *Codakia orbiculata* was the only species detected at all three sites.

The data from the additional fully marine site (Table 4) confirm the dominance of *C. lutosum* among the gastropods, at least on mangrove prop roots, on rocky shorelines (personal observation), and <100 m from shore (numbers of both snails declined with distance from shore). Again (as at CP), this snail achieved large mean sizes: 10.59 mm  $\pm$  0.13 SE on prop roots and 10.09  $\pm$  0.25 SE in the flocculent layer, values that did not differ significantly ( $p < 0.10$ ). Neither did the sizes of

*C. lutosum* and *C. costata* (9.37 mm  $\pm$  0.44 SE) differ in the flocculent layer.

The hard substrate provided by *R. mangle* supported many mussels and oysters. Oyster Pond was named for its consistent conspicuous abundance of the Atlantic Pearl Oyster, *Pinctada imbricata*, whose delicate scaly spines are far longer and more numerous than those illustrated for shells from less quiet coastal waters. The scoop samples took very consistent numbers of *A. auberiana* and *T. mera* dwelling in the microbial floc. The greater numbers of the former accord with its occurrences offshore at CP (see also below). The presence of *T. mera*, an "infaunal deposit feeder," in the flocculent layer here is the first record of a new lifestyle for this species.

#### Hypersaline Sites

Several years of unusually light or heavy rainfall can have an even greater effect on the salinities of hypersaline sites than on brackish ones. Although the mean salinities of Osprey Pond (47.17 ppt  $\pm$  6.94 SD; N=16 seasons) and Reckley Hill Pond (44.35 $\pm$ 13.49 SD; N=25) did not differ ( $p > 0.44$ ; t-test), the range of salinities at Osprey (23 [38.00-61.00 ppt]) was much less than at RHP ( $\approx$ 54 [20.00-73.86 ppt]). Very rainy years both reduce salinities and raise water levels. Osprey Pond rose 27.8 cm from Jan 1993 to Jan 1995, and the initial, well-worn trails at both sites have been under water since then. A major difference between Osprey and RHP is that rising waters at the former site breach the barrier bar between it and the hypersaline Great Lake system of the interior, preventing salinities from dropping below fully marine ones; whereas, no such buffer against low salinities exists at RHP (where rising waters could only merge with the brackish waters of the adjacent mangrove swamps). Owing to small conduits, the waters of both sites can be above or below "sea level" for years at a time (cf. Davis and Johnson, 1989, for RHP).

Only Osprey Pond has been biologically sampled using both cores and scoops; these methods took 611 molluscs, representing all of the core assemblage except *Polymesoda*

*maritima* (plus 1 *Acteocina canaliculata*, a benthic gastropod too small for our methods). Cores along the west shore transect took 60 *C. lutosum* (mean size 6.98 mm  $\pm$  0.21 SE), 44 *C. costata* (7.75 $\pm$ 0.18 SE), and 23 *B. minima* (8.84 $\pm$ 0.24 SE), all of which differed significantly in size, as well as 97 *A. auberiana*; however, only 5 *C. costata* and 4 *A. auberiana* were taken  $\geq$ 29 m offshore where the flocculent layer began (Fig. 4.). On the eastern shore, where mangroves provide shelter from the Trade Winds, the flocculent layer extends nearly to the shoreline; here only 7 *A. auberiana* were taken in 15 cores. On both shores large numbers of gastropods were observed on rock in very shallow water (1-3 cm), where the dominance order was the same as in the nearshore sample in figure 4. The scoop samples from the open water transect show the flocculent layer at Osprey is less inimical to molluscs than the coring data indicated: on average each scoop took  $\approx$ 42 molluscs, which, corrected for area, would amount to  $\approx$ 8 per core (vs.  $\approx$ 1 and  $\approx$  0.5 per core taken in floc on the west and east shores, respectively). The scoops took 125 *C. costata* (mean size 7.79 mm  $\pm$  0.11 SE), 66 *C. lutosum* (9.20 $\pm$ 0.18 SE), 19 *B. minima* (7.87 $\pm$ 0.34 SE), and 169 *A. auberiana*. Thus both the dominance and size relations of the gastropods were reversed between the western shore and open waters. Near shore *C. lutosum* was the most abundant and smallest snail, whereas offshore it was subdominant and significantly larger than the other two species. Offshore *C. costata* became dominant, and its mean size remained unchanged. The flocculent layer was most supportive of *A. auberiana* (as at Oyster Pond) and *C. costata* (unlike Oyster Pond).

The five cores at RHP took 226 molluscs, including all five species of the core assemblage (but no other molluscs), as follows: 92 *C. lutosum*, 25 *B. minima*, 24 *C. costata*, 44 *A. auberiana*, and 41 *P. maritima*. The near-shore gastropods were again (as in Fig. 4) dominated by small *C. lutosum*, with *B. minima* and *C. costata* in lesser roles. The meager numbers taken in the flocculent zone only hint that *A. auberiana* and *C. costata* prevail there. The core at the SW corner of the pond, an area free of floc, detected a nursery area for bivalves;

the size-frequency distributions for both the 34 *P. maritima* and the 29 *A. auberiana* were dominated by a size-class with a mode at 7 mm.

## DISCUSSION

Although the targeted salinity values for the three treatments were well met at all eight replicate sites sampled to date, they did so as averages only. Inevitably in natural experiments each site will differ somewhat and factors other than the intended one may influence results. At the brackish and hypersaline sites, for example, the variation in salinities may be as important as the averages in affecting molluscan abundances. Where salinities vary, one-time sample sets are like snapshots of a potentially changing community; how representative they are of a site depends on the life-histories and response times of the animals. Because 1) salinities at a site can range through extremes in several months time, 2) all of the molluscs live more than one year, and 3) totally different assemblages were recorded (e.g., at WBH and BH2) when salinities were similar (29.5 and 29.0 ppt), the molluscan results appear to reflect the history of a site rather than short-term conditions. How the salinity factor affects the molluscs, whether directly (e.g., through physiological stress), indirectly (e.g., through effects on food supply, etc.), or most likely both, is not known. Another important factor was the presence of a flocculent layer of planktonic microorganisms at some fully marine sites and all hypersaline ones. These essentially new communities (see Edwards, 1996) are dominated by unicellular algae, but contain a diverse array of well over 100 species of microorganisms (Hicks, 1993). Because these flocculent layers produce anaerobic conditions at depth, any molluscs occurring with them must be able to live in or on them, i.e., our "benthic" and "infaunal" species must adopt new, previously unreported modes of life. How the molluscs attain and maintain their positions in the floc is unknown. A careful review of Study Sites and salinity Results reveals how each site is different in some way (e.g., MR and CP have similar salinities, tidal regimes, and white mud, but differ in flocculent layers; etc.). Nonetheless, characteristic patterns

Table 5. A summary of the effect of salinities on the dominant species of molluscs. Gastropods are listed above and bivalves below.

BRACKISH ←Lower, variable salinity		FULLY MARINE	HYPERHALINE Shore→Offshore	
<i>Cerithidea</i> <i>Costata</i>	<i>Batillaria</i> <i>minima</i>	<i>Cerithium</i> <i>lutosum</i>	<i>Cerithium</i> <i>lutosum</i>	<i>Cerithidea</i> <i>costata</i>
<i>Polymesoda</i> <i>maritima</i>	<i>Anomalocardia</i> <i>auberiana</i>	VARIOUS	<i>Anomalocardia auberiana</i>	

in the molluscan assemblages were detected for each salinity treatment.

Although the compositions of the simple molluscan assemblages at the three replicate sites for the "Brackish" treatment differed greatly, they were also distinctively different from those for the other treatments (Table 5). The simplest explanation for the observed differences among the replicates is that the pair, *B. minima* and *A. auberiana*, prevails in more physically stable (and larger?), slightly more saline sites like WBH; whereas, the pair, *C. costata* and *P. maritima*, predominates in less stable (and smaller?), less saline sites like BH2 (Table 5). The results from the additional sites are consistent with this hypothesis: at the lower salinity site, BH5, species abundances closely resembled those at BH2; and at the small, shallow sites (OP and NPCQ), where fewer species occurred, *C. costata* prevailed at both as did *P. maritima* at NPCQ. On South Andros Island, Hutchinson (1998) found only *C. costata* and *P. maritima* in five sites with salinities of 15-25 ppt and took each in further sites down to ≤10 ppt. Evidence from the other treatments also indicates *C. costata* may be the most euryhaline of the gastropods, e.g., at PP and MR it alone occurs in shallow, high-tidal pools subject to severe evaporation and torrential rains.

At GBH, which is less vulnerable to extremely low salinities than BH2 is, all of the potentially dominant species co-occurred in numbers. Here the gastropods subdivided their niche space in two dimensions, their sizes and zonation. Congeners of these species have been characterized as "ecological equivalents" in California salt marshes (Macdonald, 1969), where only large *B. attramentaria* (>10 mm)

eating larger food particles coexist with *C. californica* in their very limited zone of overlap (Whitlatch and Obrebski, 1980). This size differential is very similar to the one shown in Figure 2, and both could reduce interspecific competition. Complementary size distributions and zonation could be maintained locally by selective upside-down floating, adhering to the surface tension of the water; this behavior is fairly common in *B. minima* and *C. costata* (personal observation). Meanwhile, *C. lutosum* was consistently dwarfish at the brackish replicate sites.

The analysis of size and depth data is incomplete for the "Fully Marine" treatment, and the sampling is incomplete for the "Hypersaline" one, yet characteristic patterns are emerging for both (Table 5). At the fully marine sites, *C. lutosum* numerically dominated within basins, with *B. minima* and *C. costata* limited to mid- and upper-intertidal zones, respectively. Houbrick (1974) similarly noted that *C. lutosum* "usually occurs with" *B. minima*, but is lower in the intertidal zone. Further sampling will determine whether the apparent numerical superiority of *B. minima* at CP is real for sites where *Ruppia maritima* is abundant or is simply due to cores underestimating the numbers of *C. lutosum* living in the flocculent layer. (At the brackish replicate sites there was a positive relationship between the numbers of *B. minima* and the presence [none at BH2] and abundance [most at WBH] of *Ruppia*; however, two additional sites, BH5 and OP, had the seagrass, but no *Batillaria*.) The available data shows *C. lutosum* grew to full size (mean ≥10 mm) at CP and Oyster Pond. Overall, fully marine salinities seem to favor *C. lutosum*, variable and low ones *C. costata*, with *B. minima* in an intermediate

position. Consistently complementary zonation patterns (and size distributions?) of the three Cerithiacean gastropods may indicate competition and the sub-dividing of niche space among guild members. Meanwhile, the bivalves of the core assemblage simply lost out to such fully marine species as *Codakia orbiculata* and *Tellina mera*, except where a flocculent layer necessitated the new lifestyles of *A. auberiana* and, even more surprising, the "deposit feeder," *T. mera*.

Because only one site has been fully sampled, generalizations about the "Hypersaline" treatment cannot go much beyond Table 5. The dominance of small *C. lutosum* along shorelines was tallied three times (both shores at Osprey Pond and at RHP), but the offshore dominance of *C. costata* and *A. auberiana* in the flocculent layer was only recorded at Osprey. The occurrence of all five species of the core group at RHP raises questions to be answered in the sampling of January 2000. Can *P. maritima* live in the flocculent layer or even prevail there, or is it limited to wind-stirred shallows and downwind shores where the floc is thin or missing? Could *C. costata* and *P. maritima* simply prove to be the most euryhaline species and dominate at both brackish and hypersaline sites where salinity variations are extreme?

Each new finding raises new questions, some of them larger than the main one being addressed, as the exploration and basic sampling for this natural experiment continues. Meanwhile, similar studies on larger, less isolated islands of the Great Bahama Bank could begin to address not only the present and new issues, but island biogeographic considerations and puzzles as well. The extensive brackish inland waters of South Andros Island, for example, have yielded, paradoxically, fewer molluscan species than this rare habitat (<<1% of inland saline waters) on small and remote San Salvador (Hutchinson, 1998). The inland saline waters in both locations, however, share two islandic features: macrofaunal species diversity is very low, and each site proves somewhat different – a place for new discoveries.

## ACKNOWLEDGMENTS

I am grateful to the directors and staff of the Bahamian Field Station (BFS) for the friendly and helpful way in which they have made this work possible. The amount of cooperation among field scientists at BFS has been such that I am deeply indebted to more people than I can mention. Several friends and colleagues made essential contributions. J. W. Teeter first reached most of the field sites, maintained extensive salinity records, and encouraged my efforts. After I cut the first trail to Crescent and Pain Ponds, P. J. Godfrey contributed more than anyone else to carving out the system of trails that now comprise the "BFS Trail" complex. He has assisted most of my studies logistically and with valuable data, moral support, and ideas. R. L. Davis cut the first trail to RHP, has done much to extend and maintain the trail complex, and offered ideas. My former graduate students, Mark Fregeau and Mark Damon, assisted with sampling and logistics at three sites, and the students of the Five-College Coastal & Marine Sciences Program (C&MS) contributed in many ways to my studies. C&MS at times provided partial travel reimbursement.

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